Distribution Agreement

Signature:

________________________________ ________________
Emily Kathryn Brown Date

Cognitive control of memory in nonhuman animals

By

Emily Kathryn Brown
Doctor of Philosophy
Department of Psychology

Robert Hampton, Ph.D.
Advisor

Patricia Bauer, Ph.D.
Committee Member

Michael Beran, Ph.D.
Committee Member

Donna Maney, Ph.D.
Committee Member

Joseph Manns, Ph.D.
Committee Member

David Sherry, Ph.D.
Committee Member

Accepted:

Lisa A. Tedesco, Ph.D.
Dean of the James T. Laney School of Graduate Studies

Date

Cognitive control of memory in nonhuman animals

By

Emily Kathryn Brown
M.A. Emory University, 2015
B.A., Vassar College, 2006

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
2018

Abstract

Cognitive control of memory in nonhuman animals

By Emily Kathryn Brown

Cognitive control is the active, top-down adjustment and selective prioritization of information processing. In humans, cognitive control is a key feature of working memory; the degree to which nonhuman memory systems are accessible to cognitive monitoring and control is less clear. This dissertation collects three manuscripts that describe attempts to better understand cognitive control in three nonhuman species: rhesus monkeys (*Macaca mulatta*), black-capped chickadees (*Poecile atricapillus*), and dark-eyed juncos (*Junco hyemalis*). In paper 1, I describe a metacognition task designed to test how rhesus monkeys monitor memory under conditions that disproportionately encourage use of working memory or familiarity. Memory monitoring is a useful feedback system for cognitive control. Monkeys produced accuracy and latency data consistent with the additive effects of monitoring both working memory and familiarity. In paper 2, I describe a directed forgetting task designed to test how rhesus monkeys selectively engage in cognitively controlled maintenance of memory under conditions that disproportionately encourage use of working memory or familiarity. Monkeys showed evidence of cognitive control similar to rehearsal when remembering items drawn from a small set of repeating images, but not when remembering items from a large set of images that could likely be recognized at test without effortful retention. In paper 3, I describe the effects of concurrent cognitive load on memory and acquisition of novel discriminations in two bird species: the black-capped chickadee, which stores food that is later recovered by memory, and the dark-eyed junco, which does not. I found that chickadees were more adept at managing competing cognitive load than juncos, possibly because chickadees have adapted to flexibly manage memory for food caches. Together, the findings from these studies contribute to a better understanding of the mechanisms of multiple memory systems in nonhumans.

Cognitive control of memory in nonhuman animals

By

Emily Kathryn Brown
M.A. Emory University, 2015
B.A., Vassar College, 2006

Advisor: Robert Hampton, PhD.

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
2018

Acknowledgments

I thank my advisor Rob Hampton for his guidance and encouragement, and for his enthusiasm to pursue the research questions, even when it meant radical changes of approach and species rather late in my degree. I thank David Sherry, for becoming my unofficial second advisor and making me a welcome lab member during my unexpectedly long research visit to Canada. I thank my committee members, Patricia Bauer, Mike Beran, Donna Maney, and Joe Manns for their support. I thank the members of the Hampton and Sherry Labs for providing invaluable feedback, scientific discussion, and advice. Finally, I thank my friends and family, especially Ben, without whose patient, loving support I would never have made it through, and Paul, for being supremely chill in coming along for the ride.

Table of contents

List of Figures

Paper 1: Dissociation of memory signals for metamemory in monkeys

Paper 2: Cognitive control of working memory but not familiarity in rhesus monkeys

Paper 3: Cognitive control in a caching and a non-caching bird species

1. General Introduction

We are constantly bombarded with more information than we can process, learn, and remember. Cognitive control is an active, top-down adjustment that permits the selective prioritization and processing of this information. Cognitive control encompasses a diverse set of related cognitive processes, including set shifting, inhibitory control, selective attention, metacognition, and maintenance of items in working memory (Diamond, 2013). Cognitive control is a key feature of some types of memory.

In humans, different types of memory are characterized by their distinct functional properties and reliance on different neural substrates. A strong argument for dividing memory into systems is to demonstrate functional incompatibility between them: that is, to demonstrate that the very features that make a system good for solving one problem in the environment precludes it from effectively solving another (Sherry & Schacter, 1987).

Studies of nonhuman memory can advance our understanding of the evolution of memory systems. Comparative approaches provide the means to understand the functional properties and neural substrates of memory systems. By comparing memory across taxa, we can better understand the conditions that foster certain cognitive traits. Just as evolution has shaped physical traits, environmental pressures have also shaped cognition and the brain. Comparing one species' memory over the course of seasonal changes can reveal subtle changes in brain and behavior, as can comparisons between multiple species that face varying pressures. Thus, nature manipulates brain and behavior with more subtlety than surgery and without use of invasive techniques.

Determining whether nonhumans also possess multiple memory systems, and whether their memory systems can be reliably mapped onto similar taxonomies, is critical for developing animal models. Rhesus monkeys, in particular, are frequently used as a model of human brain disorders, including traumatic brain injury, neurodegenerative disease, and age-related cognitive decline. Monkeys and other animal models can be used for invasive research that is critical for understanding human disease. Because the cognitive-behavioral signatures of these dysfunctions are marked by deficits in specific memory systems, an appropriate model necessarily relies on established techniques to access analogs of these well-characterized memory systems in nonhumans. Better understanding the functional properties of nonhuman memory allows translational researchers to develop their models as richly as possible.

Working memory is a system that allows the active, relatively short-term maintenance and manipulation of information (Baddeley, 2000, 2003). Familiarity is a passive signal evoked by a stimulus that has been recently seen (Yonelinas, 2002; Yonelinas, Aly, Wang, & Koen, 2010). Both memory systems are useful, but their features create a tradeoff between effort and flexibility. Working memory is subject to cognitive control, is highly flexible, and allows the selective prioritization of information; however, controlled memory is effortful, requires ongoing maintenance, and can be suppressed by distraction. Familiarity is inflexible and does not permit selective prioritization, but does not require effort to encode or maintain; it is automatic and results from mere exposure. In this introduction, I will describe three major paradigms used to understand cognitive control in nonhumans, each of which I have used experimentally in a paper in this dissertation.

1.1 Challenges to testing cognitive control in nonhumans

In humans, cognitive control is so intertwined with language that it is challenging to conceptualize paradigms to test it in nonhumans, yet it is unclear if cognitive control is possible without language. Many memory tests in humans rely on the ability to spontaneously report on remembered items in their absence, but nonhumans lack the language necessary for verbal report (though see Basile & Hampton, 2011; Menzel, 1999). Human cognitive tasks often rely on verbal instructions, whereas nonhumans must learn the “rules of the game” by trial and error. Additionally, a major process for maintaining items in memory under cognitive control is rehearsal, the verbal, subvocal repetition of the to-be-remembered information (Baddeley, 2003). It is unclear what a maintenance process would look like in nonhumans, which do not possess language. Because nonhumans do not have language at any time over the course of their lifespans, investigating their capacity for cognitive control can help to clarify the role of language in memory and which aspects of memory necessarily depend on language. Such questions can be challenging to answer in humans precisely because it is so difficult to block the natural propensity of humans to recode information into language.

A common task for testing memory in nonhumans is delayed match-to-sample. Performance on this task depends on multiple memory systems. The animal studies a sample item that is to be remembered. It then experiences a retention interval, a delay through which the sample item must be remembered. Following the retention interval, the animal sees the original to-be-remembered sample along with distractors not present at study. A correct response involves selecting the previously-seen sample. Match-to-sample is a recognition task. In nonhuman primates, there is good evidence that recognition memory performance is supported by at least two types of memory: working memory and familiarity (Basile & Hampton, 2013; Wittig, Morgan, Masseau, & Richmond, 2016; Wittig & Richmond, 2014). Many tests of cognitive control in nonhumans are created from modified match-to-sample tasks.

Even when researchers develop memory and cognitive control experiments for nonhumans that appear to test human-like cognition, they must remain cautious in overinterpreting behavioral similarity between humans and nonhumans, which could be superficial. In closely related species, it is more reasonable to assume that shared behavior and shared phylogeny imply similar cognition, but even then, caution is warranted. For example, nonhuman primates may balance reliance on automatic and controlled memory differently from humans even when completing highly similar tasks that appear to rely on overlapping mechanisms (Wittig et al., 2016). In humans, reliance on language may make rehearsal a more predominant strategy; for example, humans tend to spontaneously assign verbal names to image memoranda (Hourihan, Ozubko, & MacLeod, 2009).

The study of cognitive control in nonhumans has been traditionally anthropocentric, focusing either on the development of animal models of human cognition, or how “smart” certain species are. Human memory systems are well-characterized and well-studied, so they provide a useful starting point to understand memory in nonhumans. However, it may be that nonhuman memory systems do not map cleanly in all respects to well-characterized human memory systems. The involvement of language likely makes human memory unique in some regards, but other distinctions between memory systems may be universal. For example, the tradeoff between flexibility and effortful maintenance in controlled versus automatic memory systems is likely useful across many species. Three types of tasks that have been used to investigate cognitive control in nonhumans employ metacognitive judgments, directed forgetting, and manipulations of concurrent cognitive load.

1.2 Metacognition paradigms

Metacognition is cognitive monitoring or colloquially, thinking about thinking. Cognitive control is often coupled with cognitive monitoring, because the two processes can provide dynamic feedback for one another (Nelson, 1996). Metacognition paradigms in nonhumans rely on a primary task that requires a cognitive judgment and a secondary metacognitive judgment based on the subject’s perceived likelihood of success on the primary task. In metamemory tasks, the primary judgment is a memory test. The metamemory judgment allows the subject to take adaptive action depending on whether memory is good or poor. For example, monkeys taking a match-to-sample memory test improved accuracy by selectively opting out of difficult trials, indicating that they could monitor when they remembered or did not remember the sample (Hampton, 2001).

Past demonstrations have indicated that old world primates can engage in metamemory, by selectively declining difficult memory tests, re-viewing study information when they have forgotten, seeking information when ignorant, and adaptively wagering rewards on recent test performance (e.g., Basile, Schroeder, Brown, Templer, & Hampton, 2015; Brown, Templer, & Hampton, 2017; Hampton, 2001; Kornell, Son, & Terrace, 2007; Templer & Hampton, 2012; Washburn, Gulledge, Beran, & Smith, 2010). Past research has been devoted to demonstrations of metamemory to determine how widespread it is across taxa, with some evidence that rats and large-billed crows engage in metamemory (e.g., Goto & Watanabe, 2012; Templer, Lee, & Preston, 2017); equivocal evidence from new-world monkeys (e.g., Basile, Hampton, Suomi, & Murray, 2009; Fujita, 2009), and evidence that dogs and pigeons do not generally behave metacognitively in memory tests (e.g., Brauer, Call, & Tomasello, 2004; Sutton & Shettleworth, 2008). Prior work establishes that some species can make metamemory judgments, so a logical step is to investigate what metamemory can tell us about memory in these species.

Metamemory tasks can also be used as a tool to dissociate memory systems. In humans, information that can control metamemory judgments includes whether a memory was successfully retrieved from long-term memory, has been successfully held in working memory, is vivid, was retrieved fluently, and the relative familiarity of test options (Flavell, 1979; Kornell, 2013; Nelson, 1996). A great deal of experimental work has been devoted to understanding the nature of the cues that control metacognitive judgments in nonhumans (Basile & Hampton, 2014; Basile, 2015; Brown et al., 2017; Couchman, Coutinho, Beran, & Smith, 2010; Hampton, 2009a, 2009b; Smith, Couchman, & Beran, 2012; Smith, Redford, Beran, & Washburn, 2010). However, relatively little work has used metacognition paradigms to dissociate specific memory systems.

The timing of the metamemory judgment can be experimentally manipulated to encourage use of different memory systems. Prospective metamemory judgments are presented before the test. Because the test has not yet been seen when the judgment takes place, prospective metamemory tests likely elicit judgments controlled by the contents of working memory. Concurrent metamemory judgments are presented at the same time as the test. Because the sight of the test likely evokes familiarity, concurrent metamemory tests likely elicit judgments based on both working memory and familiarity. In Paper 1, I will describe a metacognition task designed to test which memory signals control metamemory judgments in rhesus monkeys (*Macaca mulatta*).

1.3 Directed Forgetting Paradigms

Directed forgetting paradigms are designed to test for cognitive control of working memory by providing cues after encoding to indicate when it is necessary or unnecessary to remember a studied item. Because maintenance of items in working memory requires effort and monopolizes cognitive resources, subjects may terminate rehearsal when it is unnecessary to remember. This task has proven challenging to interpret for nonhumans, primarily because they cannot be given verbal instructions about whether they need to remember studied items. Instead, subjects must learn “remember” and “forget” cues by trial-and-error, according to whether they typically predict a memory test for the studied item. Monkeys, rats, and pigeons have all been tested on directed forgetting paradigms trained under such contingencies. However, this paradigm has been challenging to implement, as there has been some disagreement on how best to indicate that memory for the sample will not be necessary on “forget” trials.

Originally, directed forgetting paradigms in nonhumans used an “omission procedure,” for which the forget cue predicts the absence of the test. Subjects performed more accurately on memory tests they were cued to remember than on those they were cued to forget (e.g., Roper, Chaponis, & Blaisdell, 2005). These data are consistent with a cognitive control account of performance, but non-mnemonic mechanisms could generate these results. For example, repeated pairings between the “remember”, but not “forget,” cue with tests could come to signal whether there will be an opportunity for food (Kendrick, Rilling, & Stonebraker, 1981). Subjects would therefore develop a positive association with the remember cue and a negative association with the forget cue. Frustration following the putative “forget” cue could create lags in responding or cause subjects to be inattentive to the apparatus, behaviors incompatible with correct response on the memory test (Roper & Zentall, 1993).

The “substitution procedure,” was developed to address problems associated with the omission procedure. In a substitution procedure, the forget cue predicts a different required response unrelated to memory for the sample, such as a different type of discrimination (Washburn & Astur, 1998), or a required response that leads to reward (Grant & Barnet, 1991). If the “forget” cue signals poor or nondifferential reinforcement, a substitution procedure will still evoke indifference or frustration and will not address the confounds of an omission procedure. Ideally, the forget cue in a substitution procedure should precede a test matched to the remember-cued test in difficulty and reinforcement probability. Matched conditions increase the likelihood that the subject will attend to the test and make an effort to respond accurately when they know the answer.

In one such substitution procedure, monkeys were trained to expect a match-to sample memory test following the remember cue and a discrimination following the forget cue (Tu & Hampton, 2014). The rate of reinforcement following the discrimination tests was yoked to memory test performance, such that monkeys could expect similar reinforcement for completion of both tasks. Monkeys were more accurate on memory tests when they were cued to remember than when they were cued to forget. Because matching and discrimination reinforcement was yoked, a likely explanation for this result is that monkeys terminated rehearsal following the cue to forget. This demonstration that directed forgetting paradigms can be used to capture cognitive control in nonhumans indicates an opportunity to use this task as a tool to determine which memory systems are and are not accessible to cognitive control. In Paper 2, I will describe a directed forgetting task designed to test which memory systems are subject to cognitive control in rhesus monkeys (*Macaca mulatta*).

1.4 Competing cognitive load paradigms

Working memory is characterized by active maintenance. In humans, maintenance in working memory is often accomplished by subvocal rehearsal, repeating an item to yourself in your mind (Baddeley, 2003). If cognitive control is prevented or disrupted by a competing task, working memory performance is disrupted (Baddeley, 2003). Although nonhumans cannot engage in verbal rehearsal, they may still engage in the active maintenance of memory; disruption of active maintenance by a competing task would indicate cognitive control of working memory. Tasks for nonhumans either present multiple study items, of which subjects selectively prioritize some items over others, or embed a distracting task within the retention interval of a memory task.

In serial recognition paradigms, subjects are presented with a series of sample items to study. After a retention interval, the subject is given a recognition test. Recognition accuracy varies systematically based on list position. This, and similar effects, have demonstrated in monkeys, pigeons, black-capped chickadees (Basile & Hampton, 2010; Crystal & Shettleworth, 1994; Wright, Santiago, Sands, Kendrick, & Cook, 1985). The first item in the list tends to be well-remembered. One interpretation of this effect is that the first item is well-remembered because it had the most opportunity to be rehearsed, potentially blocking other items from being rehearsed. Evidence that bolsters this interpretation is that when humans are asked to rehearse aloud, they devote the most verbal rehearsal to the earlier list items (Tan & Ward, 2000).

In retro-cue paradigms, subjects must remember several simultaneously presented items. Then, a post-encoding cue predicts which stimulus will be tested on a recognition test. Monkeys benefit from a retro-cue, indicating that they engage in cognitive control to selectively prioritize that item in working memory (Brady & Hampton, 2018).

Dual task paradigms introduce a competing cognitive load during a memory test, though care should be taken that the intervening task has not passively displaced the to-be-remembered item from memory (Washburn & Astur, 1998). When monkeys completed trials of serial reversal learning, a discrimination task that relies on memory for the outcome of a previous trial, a distractor task between trials impaired performance (Hassett & Hampton, 2017). Monkeys made more errors completing reversals following the distractor task than they did in a control task, in which they waited between trials for a delay matched to the duration of the distractor task. That performance was impaired by competing cognitive load, not the mere passage of time, appears to indicate effortful maintenance of the outcome of the previous trial. An intervening task also interfered with monkeys' memory for a sample item in a matching task, in a demand-dependent way (Basile & Hampton, 2013). Taken together, the results of serial recognition, retro-cue, and dual task paradigms indicate that nonhumans can selectively prioritize information to be maintained in working memory. Therefore, these tasks can be used to better understand the relative degree to which different species rely on cognitive control. In Paper 3, I will describe a competing cognitive load task designed to test cognitive control of working memory in black-capped chickadees (*Poecile atricapillus*) and dark-eyed juncos (*Junco hyemalis*)

In this dissertation, I will evaluate the degree to which different types of memory are subject to cognitive control in rhesus monkeys, black-capped chickadees, and dark-eyed juncos. Paper 1 describes a metacognition task designed to test how rhesus monkeys (*Macaca mulatta*) monitor memory under conditions that disproportionately encourage use of working memory or familiarity. Paper 2 describes a directed forgetting task designed to test how rhesus monkeys selectively engage in cognitively controlled maintenance of information under conditions that disproportionately encourage use of working memory or familiarity. Paper 3 describes the effects of concurrent cognitive load on memory and acquisition of novel discriminations in two bird species: the black-capped chickadee (*Poecile atricapillus*), which stores food that is later recovered by memory, and the dark-eyed junco (*Junco hyemalis*), which does not.

2. Paper 1: Provisionally accepted for publication in *Animal Cognition*

Dissociation of memory signals for metamemory in rhesus monkeys (*Macaca mulatta*)

Emily Kathryn Brown[1], Benjamin M. Basile[2], Victoria L. Templer[3], and Robert R. Hampton[1]

[1] Department of Psychology and Yerkes National Primate Research Center, Emory University

[2] Laboratory of Neuropsychology, NIMH, NIH

[3] Department of Psychology, Providence College

Conflict of Interest: All authors declare no conflict of interest.

Acknowledgements: We thank Steven L. Sherrin, Jessica A. Joiner, and Tara A. Dove-VanWormer for assistance with testing animals.

Correspondence concerning this article should be addressed to Emily Brown, Department of Psychology, 36 Eagle Row, Atlanta, GA, 30322. Phone: 404.727.9619. Email: emily.brown@emory.edu

Keywords: metacognition, information-seeking, monitoring, working memory, familiarity

2.1 Abstract

Some nonhuman species demonstrate metamemory, the ability to monitor and control memory. Here, we identify memory signals that control metamemory judgments in rhesus monkeys by directly comparing performance in two metamemory paradigms while holding the availability of one memory signal constant and manipulating another. Monkeys performed a four-choice match-to-sample memory task. In Experiment 1, monkeys could decline memory tests on some trials for a small, guaranteed reward. In Experiment 2, monkeys could re-view the sample on some trials. In both experiments, monkeys improved accuracy by selectively declining tests or re-viewing samples when memory was poor. To assess the degree to which different memory signals made independent contributions to the metamemory judgement, we made the *decline-test* or *review-sample* response available either prospectively, before the test, or concurrently with test stimuli. Prospective metamemory judgements are likely controlled by the current contents of working memory, whereas concurrent metamemory judgements may also be controlled by additional relative familiarity signals evoked by the sight of the test stimuli. In both paradigms, metacognitive responding enhanced accuracy more on concurrent than on prospective tests, suggesting additive contributions of working memory and stimulus-evoked familiarity. Consistent with the hypothesis that working memory and stimulus-evoked familiarity both control metamemory judgments when available, metacognitive choice latencies were longer in the concurrent condition, when both were available. Together, these data demonstrate that multiple memory signals can additively control metacognitive judgements in monkeys and provide a framework for mapping the interaction of explicit memory signals in primate memory.

2.2 Introduction

Performance on memory tasks is supported by a variety of memory systems, each characterized by distinct functional properties and underlying neural substrates (Sherry & Schacter, 1987; Squire & Zola-Morgan, 1991; Yonelinas, 2002). For example, a contestant on a trivia show may answer based on a combination of retrieval of the correct answer and a vague sense of which choice feels most familiar. The memory systems giving rise to these signals differ in flexibility, robustness against interference, and the conditions under which they are available for introspective monitoring. Monitorable memory signals have gained particular attention because they afford subjects the opportunity to control their cognition, such as by seeking additional information or altering response strategy. The way in which subjects monitor and control different memory signals can be assessed using metamemory paradigms.

Metamemory is the ability to monitor and control memory processes. Metamemory is exemplified by the game show “Who wants to be a millionaire?” wherein contestants must answer trivia questions and make judgments about whether they have answered correctly. Contestants are given the opportunity to reconsider their answers after reflection, or to collect additional information by contacting a friend. The metamemory judgments that contestants make can be controlled by whether a memory was successfully retrieved, has been successfully held in working memory, or evokes strong relative familiarity compared to other test options (Flavell, 1979; Kornell, 2013; Nelson, 1996). Just as memory performance often reflects a combination of memory signals, so too do metamemory judgements.

A substantial body of work with nonhuman primate species indicates that they can monitor memory, as indicated by their ability to selectively decline difficult tests, re-view previously studied but forgotten information, seek information when ignorant, or adaptively wager rewards based on recent test choices (Basile et al., 2015; Brown et al., 2017; Hampton, 2001; Kornell et al., 2007; Templer & Hampton, 2012; Washburn et al., 2010). Less experimental work has been directed at determining which specific memory systems are subject to memory monitoring and how different memory signals interact to control metamemory judgments in nonhumans.

Because memory systems provide different types of information, and multiple systems contribute to performance on memory tasks, metamemory is likely controlled by a combination of memory signals. The way that these signals are weighted in metamemory decisions in monkeys is unknown. One possiblity is that in the presence of multiple memory signals, metacognitive choice may be guided by only one, such as the strongest signal. A second possibility is that multiple memory signals contribute additively to metamemory judgments, such that congruent positive signals strengthen the likelihood of a high-confidence metamemory judgment.

To evaluate the degree to which monkey metamemory is controlled by multiple memory signals, we compared metamemory judgments under conditions that always allowed for the use of one memory signal but systematically manipulated the availability of a second memory signal. In nonhuman primates, there is strong evidence that recognition memory performance is supported by at least two types of memory: working memory and relative familiarity (Basile & Hampton, 2013; Wittig et al., 2016; Wittig & Richmond, 2014). Working memory is a limited-capacity system that allows the active, relatively short-term maintenance and manipulation of information (Baddeley, 2000, 2003). Familiarity is a passive signal evoked by the re-presentation of a stimulus that has been seen previously (Yonelinas, 2002; Yonelinas et al., 2010). In matching to sample memory tests, the image seen as a sample on the current trial can potentially be held in working memory during the delay. The sample image is also expected to be relatively more familiar than the distractors presented with it at test, because the sample is the image that has been seen most recently.

The degree to which working memory and familiarity are available for metamemory judgments can be experimentally manipulated. Prospective metamemory judgments are made before the test options have been seen and thus favor monitoring of working memory because information about the relative familiarity of the test options is not yet available. Concurrent metamemory judgments are made in the presence of the memory test. Monkeys can still monitor working memory in concurrent metamemory judgments, and additional information about the relative familiarity of the sample and distractors is also available.

Here, we assessed both prospective and concurrent metamemory judgments. In Experiment 1 we used a decline-test paradigm, in which monkeys chose to avoid some tests for a small, but guaranteed, reward (Fujita, 2009; Hampton, 2001; Suda-King, 2008; Suda-King, Bania, Stromberg, & Subiaul, 2013; Templer & Hampton, 2012; Templer et al., 2017; Washburn et al., 2010). In Experiment 2, we used an information-seeking paradigm, in which monkeys chose to re-view the sample on some trials (Basile et al., 2009; Basile et al., 2015; Beran & Smith, 2011; Call & Carpenter, 2001; Castro & Wasserman, 2013; Iwasaki, Watanabe, & Fujita, 2013; Kirk, McMillan, & Roberts, 2014; Kornell et al., 2007; Marsh, 2014; Marsh & MacDonald, 2012; McMahon, Macpherson, & Roberts, 2010; Vining & Marsh, 2015; Watanabe & Clayton, 2016). Using these two paradigms to assess metacognition, presented both prospectively and concurrently, provides a powerful test of the generalizability of our findings.

To compare the contributions of working memory and familiarity in both decline-test and information-seeking paradigms, we required a common metric. In prior work with the decline-test paradigm, monkeys showed a performance advantage on chosen tests compared to performance on forced tests when there was no option to decline the memory test (Brown et al., 2017; Hampton, 2001; Templer & Hampton, 2012). When monkeys monitored memory to choose when to use the *decline-test* response, they disproportionately chose to take trials when memory was strong and selectively avoided tests on which memory was weak, resulting in higher accuracy on tests they chose to take. Forced trials included both trials on which memory was strong, which would have been chosen had that option been available, and trials on which memory was weak, which may have been declined, had the option been available. This accuracy benefit can be applied equivalently to both decline-test and information-seeking paradigms. On choice trials in the information-seeking paradigm, subjects can either choose to take the test immediately, if memory is strong, or first re-view the sample, if memory is weak. Forced trials, when the option to re-view the sample is omitted, will include some tests that would have been taken immediately and some tests when subjects would have first re-viewed the sample, had the option been available. Thus, adaptive use of the *re-view sample* response in the information-seeking paradigm should result in a performance advantage on chosen trials over forced trials.

If both working memory and familiarity contribute to metamemory performance, then the benefit resulting from use of both the *decline-test* and *review-sample* options will be larger in the concurrent than the prospective condition. This is because both working memory and the familiarity evoked by the test stimuli may jointly guide concurrent metacognitive choices, but only working memory can guide prospective choices.

2.3 EXPERIMENT 1 – DECLINE-TEST PARADIGM

2.3.1 Methods

Subjects

Subjects were 8 pair-housed male rhesus macaque monkeys (*Macaca mulatta*), with a mean age of 7 years at the beginning of these studies. Three subjects had previous experience with a manual metacognition task (Templer &

Hampton, 2012). All subjects had prior training with the concurrent metamemory version of the information-seeking paradigm (Basile et al., 2015). All subjects also had prior training and generalization tests with the decline-test paradigm across a variety of perceptual discriminations, as well as memory tests conducted across a range of retention intervals (Brown et al., 2017).

Apparatus

We tested monkeys in their home cages, using portable touch-screen computer rigs consisting of a laptop computer (Dell, Round Rock, TX) with generic speakers, a 15" color LCD touchscreen (ELO, Menlo Park, CA), and two automated food dispensers (Med Associates Inc., St. Albans, VT) that dispensed into food cups beneath the screen. Food reinforcement consisted of 94 or 97 mg nutritionally complete primate pellets (Bio-Serv, Frenchtown, NJ and Purina TestDiet, Richmond, IN). We presented stimuli and collected responses using programs written in Presentation (Neurobehavioral Systems, Albany, CA).

Procedure

Monkey housing and testing conditions

During testing, paired monkeys were separated by dividers that allowed visual and physical contact through large slots, but prevented access to adjacent testing equipment. Monkeys had *ad libitum* access to their testing rigs up to seven hours per day.

Monkeys completed trials of a four-choice delayed-matching-to-sample (DMTS) task with a metacognitive choice phase (Figure 1). Four clipart images were used across all sessions, such that every image was seen at test on every trial. All responses required two touches (FR2) to prevent recording undirected contacts with the touchscreen as responses. To start a trial, monkeys touched a green ready square at the bottom center of the screen. A sample image then appeared in the center of the screen. Touches to the image resulted in a blank screen for a retention interval ranging from 4 to 28 seconds, depending on the individual monkey.

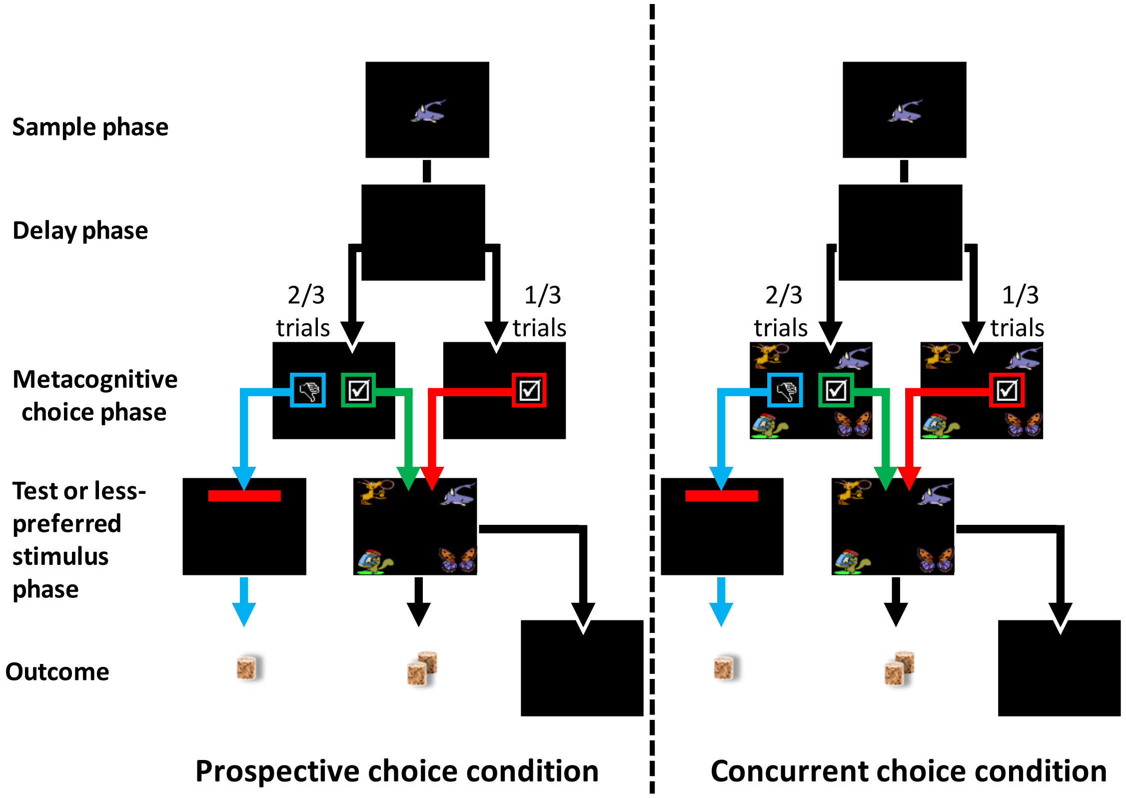


Fig. 1 Trial progression in the decline-test task. Monkeys touched a green ready square to initiate each trial (not shown). A sample clipart image then appeared on screen. Monkeys touched the sample image to advance the trial and initiate the delay interval. At the end of the delay, metacognitive choice images appeared. On *prospective choice* sessions (left), metacognitive choice stimuli appeared before presentation of the test images. On *concurrent choice* sessions (right), metacognitive choice images appeared at the same time as the test stimuli. In concurrent choices, test stimuli were unresponsive to touches until after the metacognitive choice was made. On 2/3 of trials, the *accept-test* and *decline-test* choice stimuli appear together. On 1/3 of trials, the *decline-test* choice did not appear. Selection of the *accept-test* stimulus extinguished choice stimuli and activated test stimuli. Correct choices resulted in food reinforcement

of two pellets; incorrect choices resulted in a black time out screen. Selection of the *decline-test* response caused the *guaranteed small reward* stimulus screen to appear. Touches to this stimulus resulted in guaranteed food reinforcement of one pellet.

Metacognitive choice stimuli appeared after the delay, which allowed monkeys to take the DMTS test for a large reward if correct or avoid the test for a small but guaranteed reward. The metacognitive choice phase consisted of two black and white clipart choice stimuli, which could appear concurrently, at the same time as the test stimuli, or prospectively, before the test stimuli (Figure 1). The *accept-test* stimulus, a check-marked square, was vertically centered on the right side of the screen. Touches to the *accept-test* stimulus extinguished metacognitive choice stimuli and made the test stimuli responsive to touch. Selection of the target image seen at study resulted in a distinctive auditory signal and two food pellets. Selection of a distracter resulted in auditory feedback and black screen for a brief timeout period. The *decline-test* stimulus, a thumbs-down, was vertically centered on the left side of the screen. Selection of the *decline-test* stimulus resulted in the immediate presentation of a red bar at the top center of the screen. Touches to this *guaranteed small reward* stimulus resulted in a distinctive auditory signal and one food pellet.

To ensure that monkeys declined some, but not all trials, we titrated the number of touches required to obtain the guaranteed small reward after each session. The number of touches was increased or decreased by two if the overall decline rate was greater than 70% or less than 30%, respectively, with the minimum possible touches being two. While this titration of the number of responses required for the guaranteed small reward affected the overall rate of use of the *decline-test* response, the titration procedure could not generate different rates of using this response on a trial by trial basis. Thus, titrating this response kept behavior in a range that permitted detection of differences in the use of the *decline-test* response, but could not create such differences.

On 2/3 of trials, monkeys were presented with both metacognitive choice stimuli. On the other 1/3 of trials, only the *accept-test* stimulus was presented, forcing subjects to take the test. Each session consisted of 120 trials, with trial types pseudorandomly intermixed, such that each session contained 80 choice trials and 40 forced trials.

Prospective choice sessions, in which the metacognitive choice stimuli were presented before the test options, were alternated with concurrent choice sessions, in which the metacognitive choice stimuli were presented at the same time as the test options. Prospective and concurrent choice trials were not intermixed within a single session. Monkeys completed 10 sessions of each trial type.

Data analysis

All proportions were arcsine transformed before statistical analysis to better approximate the normality assumption underlying parametric statistics (Keppel & Wickens, 2004, p. 155). Geisser–Greenhouse correction was used, and appropriately adjusted degrees of freedom reported, whenever the sphericity assumption was violated (Keppel & Wickens, 2004, p. 378).

For all experiments, we assessed accuracy by calculating the proportion correct on forced trials and on trials that monkeys chose to take, without declining or re-viewing the sample, when they had the option. We assessed the interaction between trial type (forced, chosen) and timing of the metacognitive judgement (prospective, concurrent) using a repeated measures ANOVA. We used follow-up planned paired t-tests to compare accuracy on forced and chosen trials.

2.3.2 Results and discussion

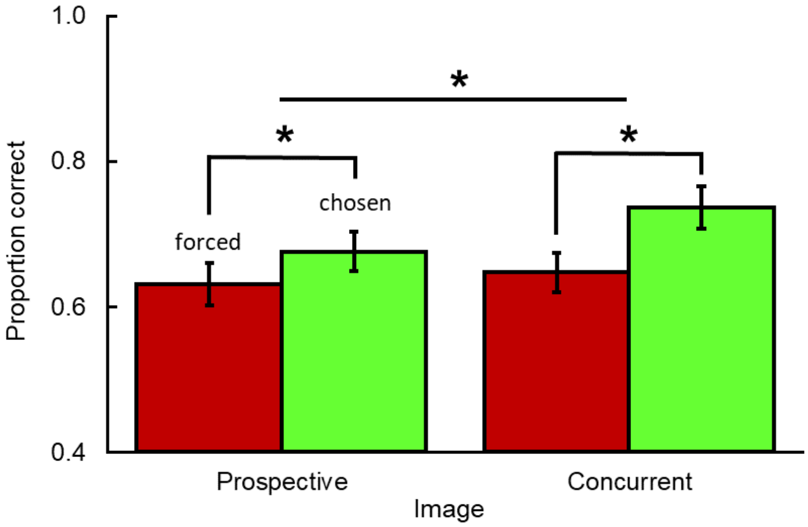


Fig. 2 Monkeys were more accurate on chosen tests than forced tests and this benefit was larger when the metamemory judgment was made concurrently rather than prospectively. Displayed are mean group accuracy (± SEM) as a function of whether the monkeys were forced to take the test (dark red) or chose to take the test (light green) and whether the metamemory judgment was made prospective to the test (left) or concurrently with the test (right). * = $p < .05$ for ANOVA interaction and follow-up t-tests that compared forced and chosen performance in the prospective and concurrent conditions, respectively.

Monkeys improved their accuracy when the *decline-test* option was available and did so to a greater extent in concurrent compared to prospective judgements. Monkeys were more accurate on chosen tests than they were on forced tests (Figure 2; main effect of forced or chosen: $F_{(1,7)} = 39.915$, $P < .001$, partial $\eta^2 = .851$). This benefit was significant on both concurrent and prospective tests when each comparison was analyzed separately (prospective: $t_{(7)}=-4.468$, $P=.003$, d=1.580; concurrent: $t_{(7)}=-6.458$, $P<.001$, d= 2.283). Further, there was a significant interaction between trial type (forced or chosen) and the time of the metacognitive choice (prospective or concurrent), such that the benefit for chosen test accuracy was greater in the concurrent than the prospective condition ($F_{(1,7)} = 17.025$, $P = .004$, partial $\eta^2 = .709$). The difference in forced test accuracy across conditions was not significant ($t_{(7)}=.868$, $P=.414$). The greater benefit of choosing to take the test on concurrent choices than prospective choices is consistent with the hypothesis that additional information controlled metamemory judgments in the concurrent condition, and that this information was provided by the sight of the test items. It is likely that prospective metamemory judgments are controlled by monitoring of working memory, whereas the concurrent metamemory judgements are controlled both by monitoring working memory and familiarity evoked by presentation of the test images.

2.4 EXPERIMENT 2 – INFORMATION-SEEKING PARADIGM

Test accuracy on chosen and forced trials in Experiment 1 provided evidence that more or better information is available for metacognitive judgments made concurrently with memory tests than is available when judgments are made prospectively, before presentation of the tests. This benefit is consistent with the hypothesis that multiple memory signals control metamemory judgments in a manner that is independent and additive. In

Experiment 2, we used a second established metamemory paradigm, information-seeking, to further test whether multiple memory systems control metamemory judgments and to evaluate the generalizability of our finding. In Experiment 2, adaptive metacognitive responding would result in the choice to take tests immediately when memory is relatively strong, and re-view the sample prior to taking the test on trials when memory is relatively weak. We hypothesized that if the *decline-test* and *review-sample* responses are controlled by similar underlying mechanisms, monkeys will show a benefit on trials they choose to take immediately over forced trials. Additionally, if working memory and familiarity signals contribute to performance on these tasks, then we expect that the accuracy benefit of choosing which tests to complete immediately will be larger on concurrent choices, in which familiarity signals resulting from the appearance of test stimuli can additionally guide metacognitive choices, as compared with prospective choices, which are completed before familiarity signals are available.

2.4.1 Methods

Subjects and apparatus

Experiment 2 used all monkeys from Experiment 1 and three additional monkeys (male, full group mean age = 6) that had undergone the training described in Basile et al. (2015). Monkeys were housed in the same conditions, and tested on the same apparatus, as described in Experiment 1.

Procedure

Specifics of the information-seeking paradigm have been published in detail (Basile et al., 2015). Briefly, monkeys studied either a spatial location (Basile et al., 2015, Experiments 1 and 5) or a color photograph (Basile et al., 2015, Experiment 6; see also Figure 3), and had the option to either proceed directly to the memory test or re-view the sample. In the image condition, the same four photographs were used across all sessions, such that every image was seen at test on every trial. In spatial tests, the same four locations were similarly used on all trials. As in Experiment 1, we tested monkeys with a concurrent metacognitive choice, in which the test options were visible while choosing whether to re-view the sample, and with a prospective metacognitive choice, in which the test options were not presented until after the monkey chose whether to re-view the sample (Figure 3).

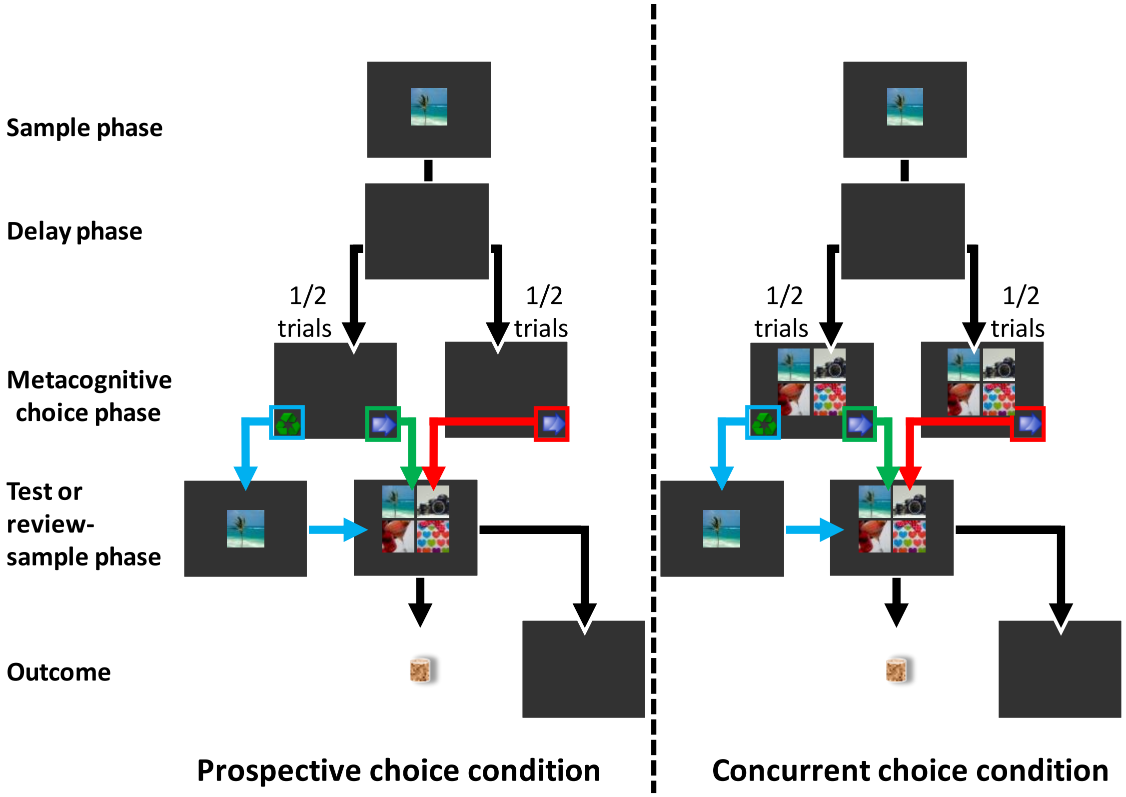


Fig. 3 Progression of trials of the information-seeking task. Monkeys touched the green ready square to initiate trials (not shown). A sample (image condition pictured) then appeared on screen for 200ms and then disappeared. At the end of the programmed delay, metacognitive choice images appeared. On *prospective choice* sessions (left), the metacognitive choice stimuli appeared before the test options. On *concurrent choice* sessions (right), the metacognitive choice images appeared concurrently with test stimuli. On 1/2 of trials, the *accept-test* and *review-sample* choice stimuli appear together. On 1/2 of trials, the *review-sample* response did not appear. Choice of the *accept-test* stimulus caused the metacognitive choice stimuli to disappear and the test stimuli to become responsive to touch. Tests resulted in food reinforcement of one pellet (correct) or a blank time out screen (incorrect). Selection of the *review-sample*

response caused the sample phase to be shown again. After monkeys had the opportunity to review the sample, the test was presented, with the outcome contingencies described above. The location memory version was identical except that all stimuli were identical red dots and the monkeys had to remember the screen location of the sample dot.

To ensure that accuracy and metacognitive bias were stable and at appropriate levels to detect metacognition, we titrated the retention interval and the number of touches required to select each monkeys' preferred metacognitive option. Sessions were 80 trials, half choice trials (Figure 3, left) and half forced test trials (Figure 3, right), intermixed and pseudorandomized such that no trial type appeared more than four times in a row. The retention interval was increased by four seconds or decreased by two seconds at the end of each session if accuracy on forced-test trials was above 67.5% or below 57.5%, respectively. Requiring accuracy to be midway between ceiling and chance ensured that monkeys were performing the task correctly and that we could detect any accuracy benefit of chosen trials relative to forced trials. As done previously (Basile et al., 2015), we also required monkeys to use both the *review-sample* and *accept-test* options regularly, with titration as described previously (Basile et al., 2015). Briefly, the number of touches required to select the preferred metacognitive option was increased or decreased by two following every session in which the monkey chose that option on greater than 75% or fewer than 25%, respectively, of all choice trials. When accuracy and metacognitive bias were within those parameters for two consecutive sessions, we considered those stable data to use for analysis. Monkeys were tested until at least 100 chosen trials were available for analysis from stable performance sessions. Monkeys then progressed through the tasks in the following order: spatial prospective, spatial concurrent, image prospective, and image concurrent.

2.4.2 Results and discussion

Final titrated retention intervals ranged from 2 to 32 seconds. All monkeys preferred the *review-sample* over the *accept-test* metacognitive option. Consequently, the *review-sample* metacognitive option required between 6 and 52 touches to select, depending on the strength of the monkey's preference.

As a result of titrating performance, accuracy did not vary as a function of sample type (Figure 4; spatial or image; $F_{(1,10)} = 3.04$, $P = .11$). Additionally, sample type did not interact with any other factor (all Ps > .098). Monkeys were more accurate on chosen tests than they were on forced tests regardless of sample type ($F_{(1, 10)} = 14.63$, $P = .003$, partial $\eta^2 = .594$). Further, as with the decline-test paradigm, there was a significant interaction between trial type (forced or chosen) and the time of the metacognitive choice (concurrent or prospective), such that the benefit to chosen test accuracy was greater in the concurrent than the prospective condition ($F_{(1,10)} = 7.11$, $P = .024$, partial $\eta^2 = .416$). The difference in monkeys' forced test accuracy across all conditions was not significant ($F_{(3,30)} = 1.83$, $P = .16$). This reproduces the main finding from Experiment 1 using *review-sample* in the place of the *decline-test* response. The larger memory benefit of choosing to take the test on concurrent choices than prospective choices with both paradigms provides converging evidence that information from multiple memory systems act additively to control metamemory choices. Because the most obvious difference between the concurrent and prospective choices is the presence of the test options, the improved accuracy likely results from the additional information available from comparing the relative familiarity of the test stimuli, which is available only on concurrent tests.

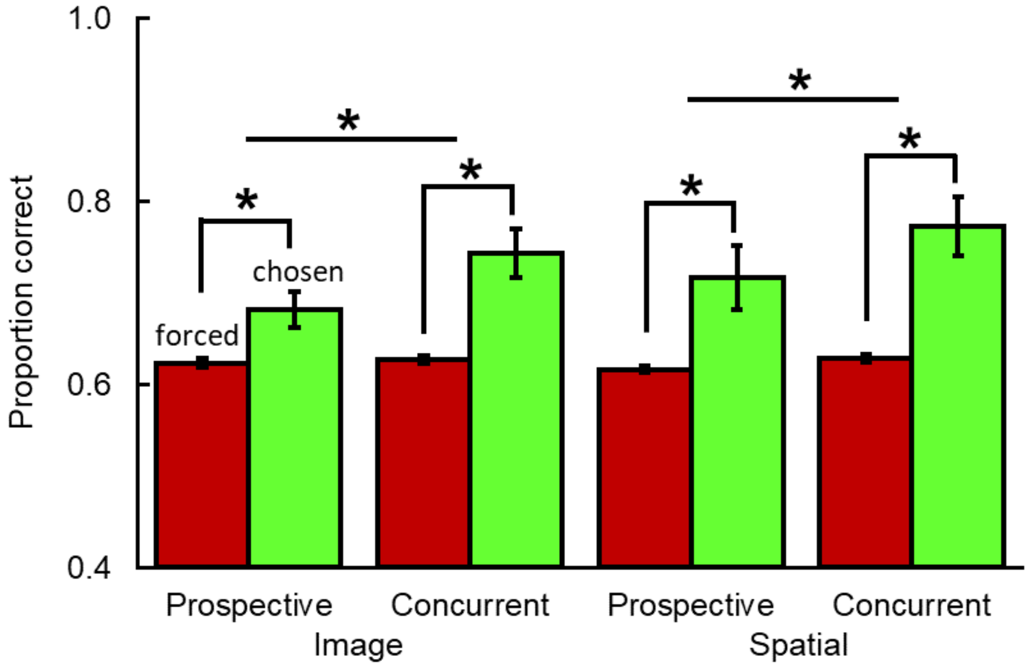


Fig. 4 Monkeys were more accurate on chosen tests than forced tests and this benefit was larger for concurrent than prospective tests. Mean group accuracy (± SEM) as a function of sample type (spatial or image), timing of the metacognitive choice (prospective or concurrent), and whether the monkeys chose to take the test without reviewing the answer or were forced to take the test.

2.5 Analysis of Latency Data

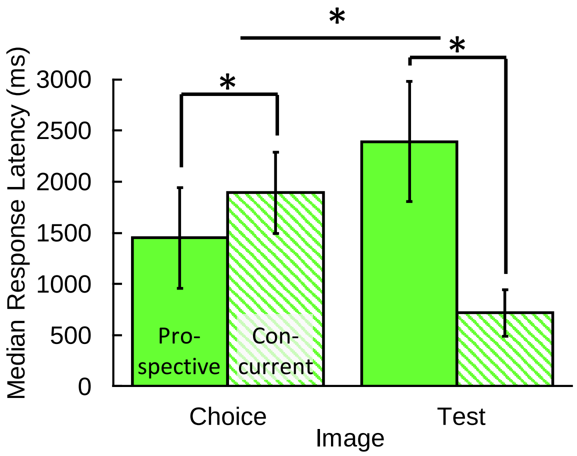
We hypothesized that the results we obtained in Experiments 1 and 2 were due to monitoring working memory in both conditions, supplemented by additional stimulus-evoked familiarity in the concurrent condition. The analyses of accuracy in the decline-test and information-seeking paradigms were consistent with the hypothesis that metacognitive decisions are additively controlled by multiple memory signals. To further evaluate whether an additional familiarity signal contributed to concurrent metacognitive choices, but did not contribute to prospective judgements, we conducted additional analyses of decision latency. If monkeys do indeed evaluate the additional information from the familiarity evoked by the sight of the test items in concurrent tests, then this should be evident as an increased decision time during the metacognitive choice epoch on concurrent judgments as compared to prospective judgments. In contrast, if both prospective and concurrent metamemory judgments are controlled solely by working memory, monkeys should be equally quick during the metacognitive choice epoch in both concurrent and prospective tests because working memory is equally available in both conditions.

Data Analysis

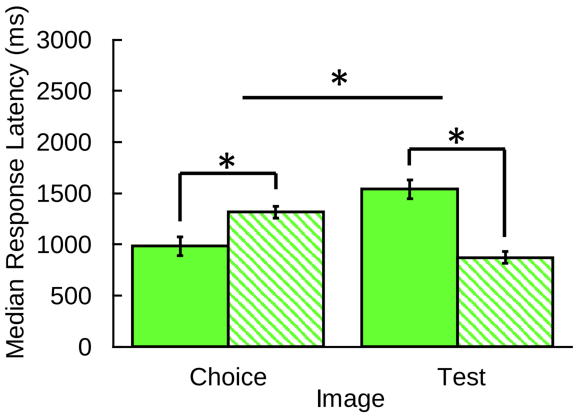
We evaluated the median latency to complete the metacognitive choice and the latency to complete the memory test for all chosen trials, regardless of whether the monkeys selected the correct response at test.

Latency Results and Discussion

A) Decline-test, image



B) Information-seeking, image



C) Information-seeking, spatial

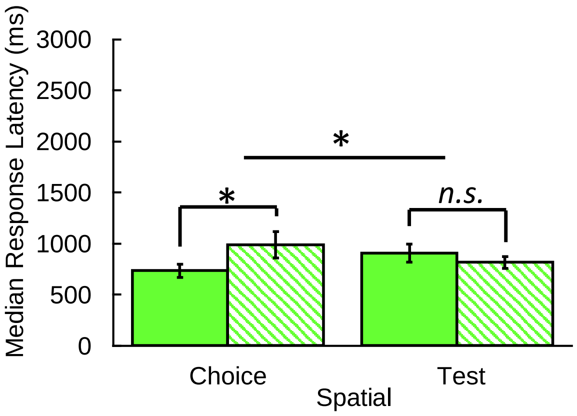


Fig. 5 Monkeys allocated more time to the metacognitive choice in concurrent judgments than in prospective judgments. Panel A depicts decline-test paradigm with image stimuli, panel B depicts information-seeking paradigm with image stimuli, panel C depicts information-seeking paradigm with spatial stimuli. Median response latency in milliseconds (±SEM) as a function of metacognitive choice placement and latency epoch. Metacognitive choice was prospective (solid) or concurrent (striped) with the presentation of the test. Latency epoch was divided into time spent making the metacognitive choice (left) and the test choice (right).

In both paradigms, processing time differed by epoch, as indicated by significant interactions of metacognitive choice placement (prospective or concurrent) with trial epoch (metacognitive choice or memory choice; Figure 5; decline-test paradigm: $F_{(1,7)} = 113.227$, $P < .001$, partial $\eta^2 = .942$; information-seeking, images: $F_{(1,10)} = 99.007$, $P < .001$, partial $\eta^2 = .908$; information-seeking, spatial: $F_{(1,10)} = 5.696$, $P = .038$, partial $\eta^2 = .363$). When making the metacognitive choice to *decline-test* or *review-sample*, monkeys devoted significantly more time to selecting a metacognitive response in the concurrent condition compared with the prospective condition (Figure 5; decline-test paradigm: $t_{(7)} = 10.382$, $P < .001$, d = 3.671; information-seeking, images: $t_{(10)} = 6.899$, $P < .001$, d = 2.080; information-seeking, spatial: $t_{(10)} = 2.425$, $P = .036$, d = .73). When making a memory choice at test, monkeys showed the opposite pattern for both image-memory tests, devoting significantly more time in the prospective condition compared with the concurrent condition (Figure 5; decline-test paradigm: $t_{(7)} = -9.357$, $P < .001$, d = 3.308; information-seeking, images: $t_{(10)} = 7.924$, $P < .001$, d = 2.389), but this difference was not significant for the spatial memory tests of the information-seeking paradigm ($t_{(10)} = 1.793$, $P = .103$, d = .54). Longer time spent on the metacognitive choice epoch is consistent with our hypothesis that information from both working memory and stimulus-evoked familiarity additively control concurrent metacognitive judgments. This is because it should take longer to evaluate two sources of metamemory control than it does to evaluate just a single source of control.

2.6 General Discussion

Across the decline-test and information-seeking metamemory paradigms, monkeys were more accurate on trials they chose to take than those they were forced to take, replicating the basic metamemory findings associated with these paradigms. The accuracy benefit on chosen trials was consistently greater, across paradigms, when monkeys made metacognitive judgments in the concurrent condition than it was in the prospective condition. Monkeys also took longer to make concurrent metamemory judgments, when more information was available, than they were to make prospective metamemory judgments. These findings support the hypothesis that there is more mnemonic information available to cue metacognitive judgments in the concurrent condition than the prospective condition.

The most plausible memory signals controlling monkeys' metacognitive choices in this study are working memory and stimulus-evoked familiarity. In both the concurrent and prospective conditions, working memory for the sample is potentially available through the retention interval, and is a signal likely to control metamemory judgments. It is likely that monkeys actively kept the sample image in working memory because we used task parameters (e.g., small image sets and relatively short retention intervals) that have been shown in previous research to promote active working memory (Basile & Hampton, 2013). In addition, we manipulated the availability of stimulus-evoked familiarity by manipulating the timing of the metacognitive choice. In the prospective condition, the metacognitive choice took place prior to the appearance of the test. Requiring monkeys to make the metacognitive choice prior to the appearance of the test should encourage reliance primarily on working memory because the test stimuli were not present to evoke familiarity. In the concurrent condition, the metacognitive choice appeared simultaneously with the test, such that monkeys could base metacognitive choices on the relative familiarity of the sample and distractors, in addition to monitoring working memory. Familiarity is most often characterized as a signal automatically evoked by the sight of previously-seen stimuli (Jacoby, 1991). Thus, it is reasonable that in the concurrent condition, heightened familiarity for the recently-viewed sample, taken additively with working memory strength, would increase the accuracy of metamemory judgments. We do note that the familiarity of the most recently seen sample image is probably only slightly greater than the familiarity of the distractor images because all of the images have been seen recently in preceding trials. The extent to which familiarity would control test choice, as well as metacognitive choice, would presumably be much greater if memoranda were trial unique images. It is also possible that other memory signals, as well as other non-mnemonic cues contribute to metamemory performance. Identifying these signals and how they interact to support behavior will be an interesting problem for future research.

The longer metacognitive decision times in concurrent tests is consistent with the hypothesis that when multiple memory signals are present, they control metamemory judgements additively. Monkeys spent more time making the metacognitive choices and used that option to greater benefit when the relative familiarity of the test stimuli was available for evaluation compared to when only working memory was available. This increased decision time likely results from additional evaluation of the relative familiarity signals evoked by the sight of the test items. These signals might reinforce or countermand the contents of the monkey's working memory. A slightly different, but not incompatible explanation is that monkeys already have a planned test response in mind, and allocation of response time represents a visual search for that planned test response. This visual search would take place prior to the metacognitive choice in the concurrent test and after the metacognitive choice in the prospective choice.

Although monkeys showed a similar pattern of cognitive processing time in the spatial test, the longer metacognitive choice epoch latency for concurrent trials was greatly attenuated and the longer test epoch latency for prospective trials was absent. One explanation for the difference between image and spatial tests is that monkeys devote less processing time to search for the remembered location in spatial tests compared to tests with images. Although the red dots that mark potential response sites are absent in the prospective test, the remembered screen location is likely encoded relative to landmarks on the screen that are always present because the screen itself is present. This means that monkeys can make a decision about where to respond without scanning the whole screen. In contrast, on tests with images, the location of the correct response must be identified before a selection can be made. The addition of eye-tracking data to this task would provide more evidence to use in identifying the specific search strategy that monkeys employ. For example, monkeys might engage in an exhaustive search prior to metacognitive choice in the concurrent condition with images, but saccade immediately to the intended response in tests of spatial memory.

As in all studies of metacognition, monkeys did not make perfect metamemory judgments (Hampton, 2001; Templer & Hampton 2012; Basile, Schroeder, Brown, Templer, & Hampton 2015; Brown, Templer, & Hampton 2017). Across conditions, monkeys never approached perfect accuracy on trials that they chose to take. Although it is tempting to characterize this as unusually poor performance relative to what we feel we might do as humans, humans have not been tested under these conditions on these paradigms. Even in humans, cognition is not always accurate and metacognition is also subject to errors (Maniscalco & Lau 2012; Nelson 1996). It is likely that the cues controlling metamemory responding are subtle and noisy in both species. Metacognitive sensitivity may represent a continuum across taxa, with some species more attuned to the often-subtle cues that control metacognitive judgments.

The increased benefit to metamemory judgments under the concurrent condition over the prospective condition is likely the result of additive information from multiple memory signals rather than a shift to basing judgments on different systems in the different conditions. Because the same four stimuli were seen on every trial, all stimuli likely evoked high familiarity at tests. Though it appears that the relative familiarity of the sample still provided a useful memory signal for making accurate metamemory judgments, this signal is likely weak and noisy. The addition of information from familiarity to the information from working memory would provide a modest but reliable benefit to accuracy, as obtained here. It has sometimes been suggested that monkeys use the additional information provided in concurrent test conditions to make metamemory judgments (e.g., Hampton, 2009b); however, this is the first study to use a direct comparison between prospective and concurrent judgments to provide strong evidence that this is the case.

In conclusion, monkeys show similar patterns of accuracy and latency across decline-test and information-seeking paradigms, two metamemory tasks commonly used with nonhumans. A similar pattern of performance in both paradigms provides converging evidence that multiple memory signals can additively control metacognitive judgements in monkeys and provides a framework for mapping the interaction of explicit memory signals in primate memory.

Compliance with ethical standards

Ethical approval:

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest:

All authors declare no conflict of interest.

Funding:

This work was supported by the National Science Foundation (grants IOS-1146316; BCS-0745573; BCS-1632477) and the National Institutes of Health (grants RO1MH082819; T32HD071845). This project was supported in part by ORIP/OD P51OD011132.

3. Paper 2

Cognitive control of working memory but not familiarity in rhesus monkeys (*Macaca mulatta*)

Emily Kathryn Brown and Robert R. Hampton

Department of Psychology and Yerkes National Primate Research Center, Emory University

Author's Note:

This work was supported by the National Science Foundation (grants BCS-1632477, IOS-1146316, BCS-0745573) and the National Institutes of Health (grant RO1MH082819; T32HD071845). This project was supported in part by ORIP/OD P51OD011132.

We thank Jessica A. Joiner and Tara A. Dove-VanWormer for assistance with testing animals.

Correspondence concerning this article should be addressed to Emily Brown, PAIS Building, 36 Eagle Row, Atlanta, GA, 30322. Phone: 404.727.9619. Email: emily.brown@emory.edu

Keywords: directed forgetting, cognitive control, working memory

3.1 Abstract

Cognitive control is the active, top-down adjustment of information processing. In humans, active rehearsal of the contents of working memory is one form of cognitive control (Sheard & MacLeod, 2005). Directed forgetting paradigms test for cognitive control by comparing memory accuracy in trials on which subjects are instructed to remember with accuracy in trials on which they are instructed to forget. We used a directed forgetting paradigm to compare the extent to which working memory and familiarity are subject to rehearsal-like cognitive control in rhesus monkeys. Monkeys were presented with a sample image, followed by one of two distinctive cues during the retention interval. The *remember* cue typically predicted a 4-choice match to sample test, for which memory of the sample was critical. The *forget* cue typically predicted one of five perceptual discrimination tests, matched for accuracy to the memory tests, for which memory of the sample was irrelevant. On rare probe trials, the test type other than the type typically predicted by the cue was presented. When cognitive control is in effect, accuracy should be higher on memory tests following the *remember* cue than on those following the *forget* cue. Monkeys showed a benefit of the *remember* cue under conditions that favored working memory but did not do so under conditions that favored matching on the basis of relative familiarity. Working memory, but not familiarity is subject to cognitive control in rhesus monkeys.

3.2 Introduction

In humans, memory is the outcome of multiple processes and these processes differ in accessibility to cognitive control. Imagine that you are going grocery shopping, when you realize that you need eggs. Rather than add to your written shopping list, you try to remember this item. You might accomplish this through rehearsal, mentally repeating "eggs" to yourself. Such rehearsal is a form of cognitive control that maintains information in working memory (Baddeley, 2003). If your partner calls and tells you that they already picked up eggs, you may terminate rehearsal and stop trying to remember the eggs. Terminating rehearsal frees up limited cognitive resources for other mental activities, like remembering to pick up a bag of coffee at the store. Other forms of memory do not require active cognitive control. For example, you can recognize your car in the parking lot without rehearsing to remember what it looks like throughout your shopping trip. The familiarity evoked by seeing a previously studied item is an automatic signal (Yonelinas, 2002; Yonelinas et al., 2010). The familiarity signal that results from seeing your car is not affected by whether you were actively thinking about it and appears not to tax limited cognitive resources. Familiarity is not diminished by termination of cognitively controlled memory maintenance.

As in humans, nonhuman primates recognize items through at least two types of memory: working memory and relative familiarity (Basile & Hampton, 2013; Brady & Hampton, under review; Wittig et al., 2016; Wittig & Richmond, 2014). Working memory in humans is characterized by active maintenance that is often associated with liguistic representations, but cognitive control is not necessarily verbal (Hourihan et al., 2009). There is evidence for cognitive control in nonhumans (e.g., Basile & Hampton, 2013; Brady & Hampton, 2018; Roberts, Mazmanian, & Kraemer, 1984; Roper, Kaiser, & Zentall, 1995; Smith, Coutinho, Church, & Beran, 2013; Tu & Hampton, 2014). A critical feature of cognitive control is that it is effortful and consumes limited cognitive resources. As a result, employing cognitive control necessarily involves tradeoffs. If cognitive effort is directed to remembering to pick up eggs, fewer resources are available for remembering to pick up a bag of coffee, and the probability of forgetting the coffee will increase.

Because working memory depends on cognitive control, working memory performance is disrupted when a competing task diverts cognitive resources from active maintenance (Baddeley, 2003). Using a competing cognitive load paradigm that assessed whether subjects were actively rehearsing memoranda, Basile and Hampton (2013) found that monkeys actively maintained highly familiar images in memory, but they found no evidence of active rehearsal of novel images. There is also evidence that monkeys engage in rehearsal-like cognitive control in a retro-cue paradigm. In retro-cue paradigms, subjects must remember several simultaneously presented items. Then, a post-encoding cue indicates which stimulus will be tested on the upcoming recognition test. Monkeys, like humans, show an accuracy benefit from this post-encoding cue, presumably because it allows limited working memory resources to be allocated to the relevant memorandum (Brady & Hampton, 2018).

Controlled and automatic cognitive processes have also been found in studies with monkeys, pigeons, and rats using "process dissociation" paradigms that distinguished between one-trial memory and habits in a way that closely parallels findings with human subjects (Guitar & Roberts, 2015; Jacoby, 1991; Roberts, Guitar, Marsh, & MacDonald, 2016; Roberts, Macpherson, & Strang, 2016; Roberts, Strang, & Macpherson, 2015; Tu & Hampton, 2012; Tu, Hampton, & Murray, 2011). These studies begin to identify how cognitive control is distributed among memory systems and among species. We used a directed forgetting paradigm to further assess the reliability of previously reported dissociations of working memory and familiarity in monkeys, using converging operations. We tested for the presence of cognitive control while also manipulating the relative usefulness of working memory and familiarity, allowing us to determine the relative importance of cognitive control for working memory and familiarity.

Directed forgetting paradigms demonstrate the existence of cognitive control when humans show better memory for material they have been instructed to remember compared to material they have been instructed to forget. To the extent that remembering a studied item depends on a memory system that is subject to cognitive control, active maintenance should occur when subjects have been cued to remember. Because cognitive control is effortful, and comes at a cost to other cognitive processes, active maintenance should not occur when subjects are cued to forget. When subjects terminate rehearsal, they are free to expend cognitive resources thinking about other potentially distracting or interfering stimuli in their environment. If remembering a studied item depends on an automatic memory process, such as familiarity, the cue to remember or forget cannot affect retention. As you do not need active maintenance to recognize your car in the parking lot, the studied item will evoke familiarity at test to the same extent even if you have made no effort to remember.

Because nonhumans cannot understand verbal cues instructing them to remember or forget, the experimenter instead provides them with cues that predict the type of test that will follow. The remember cue typically predicts a test that relies on memory for the sample. The forget cue typically predicts a test unrelated to memory for the sample. To prevent confounding of active memory with other factors that might affect accuracy, the two types of tests should be of similar difficulty and associated with similar probability of reinforcement (Roper & Zentall, 1993). Additionally, if the forget cue consistently predicts the same response, prospection to this response can passively displace memory for the studied sample (Washburn & Astur, 1998). Therefore, the substituted task should be selected to ensure that active termination of rehearsal, rather than passive displacement, is responsible for the directed forgetting effect, if such an effect is observed. On occasional probe tests, the experimenter tests memory despite having cued the subject to forget. Under these conditions, monkeys demonstrate cognitive control: they are more accurate when cued to expect a memory test than when cued to expect a discrimination matched for probability of reinforcement (Tu & Hampton, 2014). Therefore, the directed forgetting paradigm is well-suited to dissociate memory systems on the basis of whether or not the systems are subject to cognitive control.

If monkeys, like humans, use cognitive control to maintain working memory, test conditions that encourage heavy reliance on working memory should generate stronger directed forgetting effects than do test conditions that favor matching on the basis of relative familiarity. In a typical matching to sample memory tests, a sample image is studied, then must be selected from among distractors following a delay. The sample image can potentially be held in working memory during the delay allowing for matching of the studied sample with the contents of working memory at test. Monkeys might also discriminate the sample from distractors on the basis of relative familiarity. Because the sample is the image that has been seen most recently, it is likely to elicit a stronger familiarity response upon re-presentation at test than distractors do. The size of the pool of images used to generate memory tests has a powerful effect on the utility of relative familiarity as a mnemonic signal for discriminating samples from distractors. When a small set of images is used across trials, proactive interference builds rapidly (Basile & Hampton, 2010; Edhouse & White, 1988; Jitsumori, Wright, & Cook, 1988; Wright, Urcuioli, & Sands, 1986). Because the images are seen frequently, all images are highly familiar. This means that it is difficult to discriminate between the image seen most recently as a sample and the distractors presented with it, because they are all familiar. When relative familiarity is a poor mnemonic signal, working memory is required, and we expect working memory to be maintained by cognitive control (Basile & Hampton, 2013). In contrast, when a large set of images is used, the sample image is highly familiar relative to the distractors that appear with it at test, because the distractors have not been seen for a relatively long time.

Therefore, familiarity may be sufficient to complete tests drawn from a large set, whereas maintenance in working memory may be more critical when taking tests drawn from a small set. A small image set may be necessary to obtain a directed forgetting effect (Roberts et al., 1984). It has also been suggested that directed forgetting effects should be most evident seen at moderately long memory delays, such that memoranda would have faded from working memory if not actively maintained (Maki & Hegvik, 1980). Because memory signals deteriorate over time, both the ability to rehearse and the cost of terminating rehearsal can be affected by delay length.

In the current study, we use a directed forgetting procedure, combined with a manipulation of image set size, to determine the relative accessibility of working memory and familiarity to cognitive control. We manipulated the utility of familiarity as a mnemonic signal, and thus the necessity of working memory for accurate recognition, by using a small set of repeating images in one block of trials, and a large set of images that monkeys saw infrequently in another block. If working memory, but not familiarity, is subject to cognitive control, we should observe a directed forgetting effect for images drawn from small, but not large, image sets. We additionally manipulated the utility of working memory by giving tests after a variety of retention intervals. Because memory is vulnerable to decay after longer retention intervals, the directed forgetting effect could be expected to vary across delays.

3.3 Methods

Subjects

We used 7 pair-housed male rhesus macaque monkeys (*Macaca mulatta*), average age 7 years at the beginning of these studies. Five monkeys had prior experience with a similar directed forgetting paradigm that used different “remember” and “forget” cues and a different discrimination task on “forget trials” (for full description see Tu & Hampton 2014). All monkeys had extensive experience with cognitive testing.

Apparatus

We tested monkeys in their home cages, using portable touch-screen computer rigs consisting of a laptop computer (Dell, Round Rock, TX) with generic speakers, a 15” color LCD touchscreen (ELO, Menlo Park, CA), and two automated food dispensers (Med Associates Inc., St. Albans, VT) that dispensed into food cups beneath the screen. Food reinforcement consisted of 94 or 97 mg nutritionally complete primate pellets (Bio-Serv, Frenchtown, NJ and Purina TestDiet, Richmond, IN). We presented stimuli and collected responses using programs written in Presentation (Neurobehavioral Systems, Albany, CA). Pellets earned during testing were subtracted from monkeys’ daily primate biscuit chow rations, such that monkeys consumed roughly the same number of calories daily, regardless of testing performance. Daily calorie budgets were established by veterinary staff based on weight trajectories and clinical assessments.

General task properties

All tests described here are based on a 4-choice delayed match-to-sample and a 4-choice perceptual discrimination task (Figure 1). All responses required two touches (FR2) to prevent recording undirected contacts to the touchscreen as choices. To start a trial, monkeys touched a green ready square at the bottom center of the screen. A sample image then appeared on the screen. Touches to this image extinguished the sample and caused a memory cue to appear. On 50% of trials, the memory cue was the “remember” cue, a fermata notation. On the other 50% of trials, the memory cue was the “forget” cue, a not-equal symbol. To help ensure that monkeys attended to the memory cue, it was presented in randomly selected locations, and monkeys had to touch it to advance the trial. The cue then dimmed and remained onscreen throughout the delay so that monkeys did not have the increased memory load of remembering the memory cue. Typically, a perceptual discrimination test followed the “forget” cue. The target was presented with three distracters that were identical to one another and different from the target, in the four corners of the screen. Typically, a match-to-sample memory test followed the “remember” cue. During training, the cues were valid and correctly predicted the task that would follow on 100% of trials; during probes, cues were valid on 90% of trials. The sample stimulus seen at study and three distractor items were presented in the four corners of the screen. Correct selection of the sample or the target stimulus resulted in distinctive auditory feedback and food reinforcement of one pellet. Incorrect selection of one of the distractors resulted in distinctive auditory feedback and the screen going blank for a 5-second time out interval.

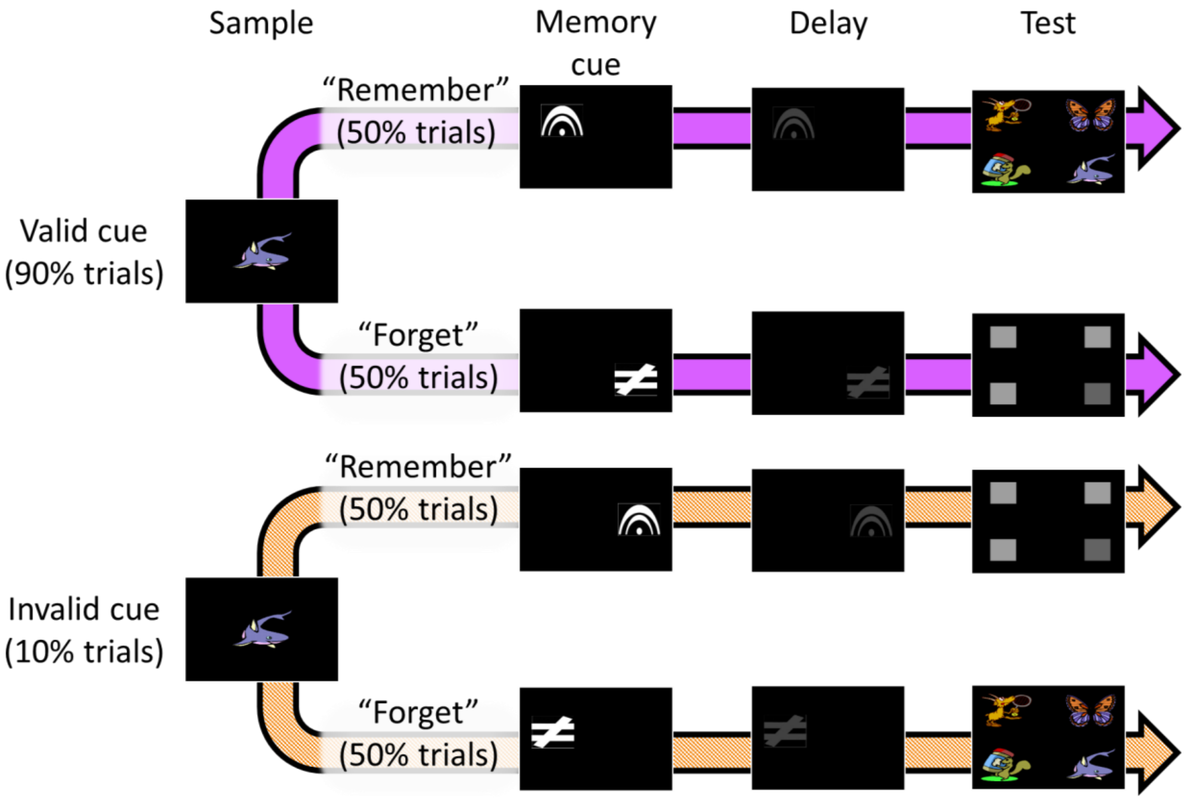


Figure 1. Steps to complete a trial of the directed forgetting task. After monkeys viewed and touched a sample image, a memory cue appeared. During probe sessions, the memory cue correctly predicted the type of test that would follow on 90% of trials (top). On 10% of probe session trials (bottom), the memory cue did not correctly predict the test type. Monkeys were cued to “remember” on half of trials and were cued to “forget” on the other half. The memory cue dimmed and remained onscreen during the delay. Correct selection of the sample on match-to-sample tests or the target item on perceptual discriminations resulted in food reinforcement.

Perceptual discrimination tests

To prevent prospection to the target stimulus, which could passively displace memory for the studied sample, we pseudorandomly selected among five different perceptual discriminations, preventing the monkeys from anticipating any one test (Washburn & Astur, Tu & Hampton 2014). The perceptual tests used were an arc length discrimination, a circle size discrimination, a dot rotation discrimination, a brightness discrimination, and a dot density discrimination (Figure 2). Within each discrimination test, the target stimulus remained the same across trials. Each discrimination consisted of two different distracter values, one lesser (e.g. dimmer) and one greater (e.g. brighter) in magnitude than the target by equal amounts.

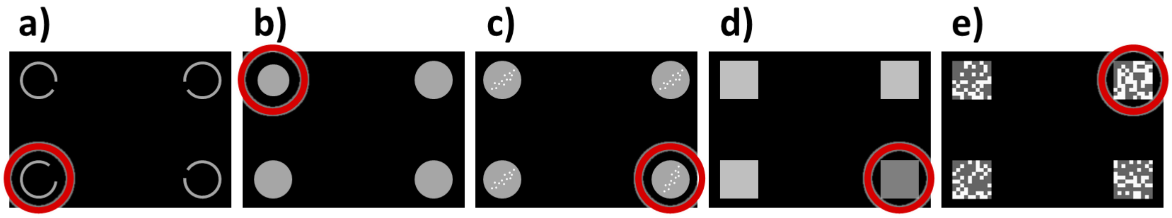
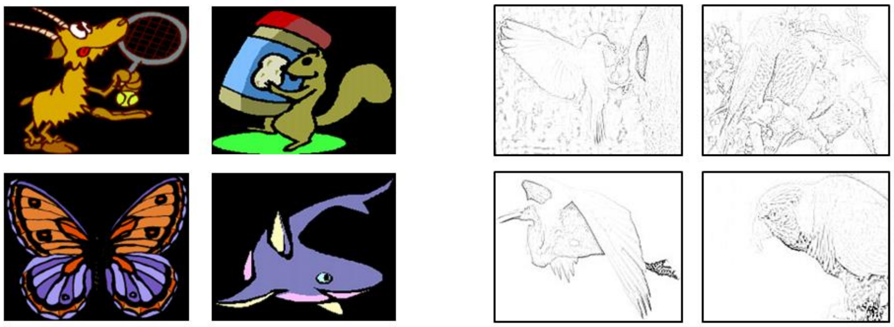


Figure 2. Examples of the five perceptual discrimination tests that could follow valid "forget" cues or invalid "remember" cues. On perceptual discrimination tests, the target could be selected on the basis of a) arc length, b) circle size, c) dot rotation, d) brightness, and e) dot density. The target (circled) was assigned randomly to the four corners of the screen.

Match-to-sample memory tests

First, monkeys completed trials in the small image set condition, wherein the same four clipart images were seen at test on every trial. Second, monkeys completed trials in the large stimulus set condition, wherein images were drawn from a pool of 1600 photos of birds that had been converted into black-and-white line drawings (Figure 3), such that they were seen every 1600 trials on average. We selected perceptually similar stimuli for the large image set condition because otherwise monkeys are accurate in memory tests with prohibitively long delays. Even with the highly perceptually similar large image set described here, some monkeys required delays of over 4 minutes; even longer delays that could be expected with clipart stimuli drawn from a large set are not practical for experiments like these.



Small stimulus set

Large stimulus set

Figure 3. Examples of the memory test stimuli that could follow valid "remember" cues or invalid "forget" cues. In the small image set condition, the same four clipart images were seen on every trial; in the large image set condition, the images were drawn from a pool of 1600 photos of birds that had been converted into black-and-white line drawings.

Training and probe trials

During training, we titrated performance in the memory tests to achieve 50-70% accuracy, where we expected monkeys to be far enough from ceiling and floor performance that a directed forgetting effect would be evident, if present. Monkeys trained on match-to-sample with 100% valid remember cues, until they completed at least 2 sessions in the criterion accuracy range. Monkeys were also trained on the five perceptual discriminations at intermixed difficulty levels until they were highly proficient with the easiest discriminanda. The difficulty level for each discrimination that was closest to the center of the criterion accuracy range of 50-70% was selected for use in directed forgetting probe trials. After probe trials began, discrimination difficulty and delay length were adjusted between sessions to maintain accuracy in the criterion range.

For probes, titrated delays for the small set condition ranged from 3- 120 seconds and titrated delays for the large set condition ranged from 20- 256 seconds. We used the titrated delay to generate a range of delays tailored to each monkey. The "long" delays were double the titrated delay and the "short" delays were half and one quarter of the titrated delay. During probe sessions, the memory cue accurately predicted the test that would follow on 90% of trials, and inaccurately predicted the test that would follow on the remaining 10% of trials. For each set size condition, monkeys completed at least four 3200-trial blocked sessions, of which the last session, which should most closely reflect asymptotic performance, was used for analysis.

Data analysis

All proportions were arcsine transformed before statistical analysis to better approximate the normality assumption underlying parametric statistics (Keppel and Wickens 2004, p. 155).

We used a linear mixed-effect model, with subject as random factor. Linear mixed-effect models are useful in studies with small N because they make separate estimates of slope for each individual that can help to account for random variation, and because they handle changes in variability across repeated observations better than the standard ANOVA (Gueorguieva & Krystal, 2004). The model used to analyze memory accuracy included the image set size (large or small), cue validity (valid or invalid), and retention interval (Delay/4, Delay/2, Titrated Delay, Delay *2). The model used for follow-up tests within each image set size included cue validity and retention interval. The model used to analyze discrimination accuracy included the image set size (large or small), cue validity (valid or invalid), and retention interval (Delay/4, Delay/2, Titrated Delay, Delay *2). Models were fitted using software R Version 3.5.0 (R Core Team, 2014) and R package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2015). Satterthwaite approximations were used for significance levels and degrees of freedom.

For all experiments, we assessed accuracy by calculating the proportion correct for valid cue memory tests (“remember” cue followed by memory test), invalid cue memory tests (“forget” cue followed by memory test), valid cue discrimination tests (“forget” cue followed by discrimination test), and invalid cue discrimination tests ("remember" cue followed by discrimination test, at each of the four retention intervals (Delay/4, Delay/2, Delay, and Delay*2).

3.4 Results

Monkeys were more accurate on memory tests preceded by a valid "remember" cue only when remembering images drawn from the small image set. A linear mixed-effect model showed a significant interaction of image set size and cue validity (Figure 4; $F_{(1,90)} = 11.94$, $P < .001$). We further examined this interaction by conducting follow-up tests within each set size separately. Cue validity significantly affected accuracy for memory tests drawn from the small image set ($F_{(1,42)} = 24.500$, $P < .001$). Cue validity did not affect accuracy for memory tests drawn from the large image set ($F_{(1,42)} = .383$, $P = .540$). We did not find an interaction of cue validity and delay in the small image set, which would have indicated that the importance of rehearsal changed over retention intervals ($F_{(3,42)} = .568$, $P = .639$). Monkeys were significantly more accurate at short delays than long delays, for memory tests drawn from both the small image set ($F_{(3,42)} = 10.220$, $P < .001$) and the large image set ($F_{(3,42)} = 29.638$, $P < .001$).

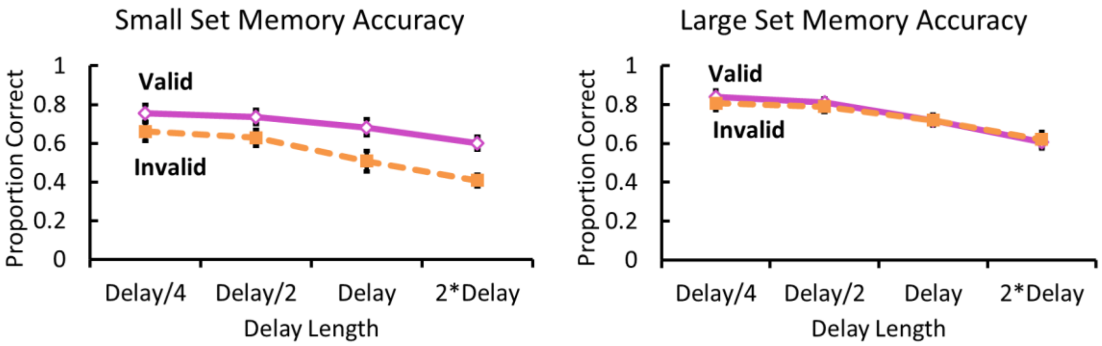


Figure 4. Monkeys were more accurate on memory tests drawn from the small image set when they were preceded by a valid cue to remember (left); cue validity did not affect accuracy on memory tests drawn from the large image set (right). Mean accuracy is shown as the proportion correct ± SEM across each of 4 delays. Tests were preceded by either a valid cue to remember (purple solid) or an invalid cue to forget (orange dashed).

Monkeys were similarly accurate on discrimination tests preceded by valid and invalid "forget cues" cues (Figure 5; $F_{(1,90)} = .51$, $P = .476$). Accuracy on discriminations was significantly different between set size conditions, likely because our blocked training design allowed further opportunity for re-titration of discrimination difficulty ($F_{(1,90)} = 46.35$, $P < .001$). Accuracy on discriminations was also significantly affected by delay length ($F_{(1,90)} = 3.191$, $P = .027$).

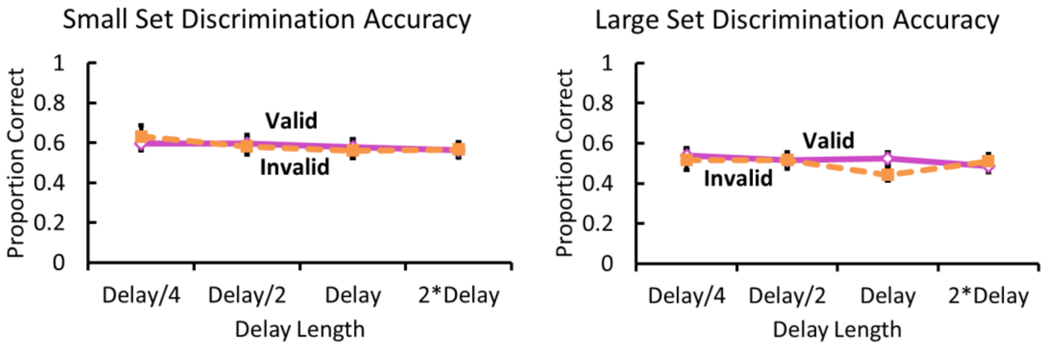


Figure 5. Monkeys were similarly accurate on discrimination tests regardless of the validity of the "forget" cue in both the small set (left) and large set (right) conditions. Mean accuracy is shown as the proportion correct ± SEM across each of 4 delays. Tests were preceded by either a valid cue to remember (purple solid) or an invalid cue to forget (orange dashed).

3.5 Discussion

We found that working memory, but not familiarity, was maintained by cognitive control in rhesus monkeys. When tested with a small set of repeating images, for which relative familiarity is a poor signal for discriminating recently seen samples from distractors, working memory is necessary to discriminate recently seen samples from distractors in memory tests (Basile & Hampton, 2013). Under these conditions we found that monkeys were less accurate on memory tests that followed forget cues than those that followed remember cues, indicating active cognitive control. We did not find this difference when we tested monkeys with a large set of images, for which relative familiarity is a powerful mnemonic signal. Roberts et al. (1984) previously suggested that a small set of images might be a necessary condition for obtaining a directed forgetting effect. These findings show that the contents of working memory, but not familiarity signals, are subject to cognitive control during the delay interval.

Dissociations of cognitive control of working memory and familiarity are based on a model of recognition memory performance that describes performance as the result of contributions from at least two memory systems: working memory and familiarity. Working memory depends on active maintenance of information about the to-be-remembered sample image in mind through a process like rehearsal. In contrast familiarity is a passive and automatic process by which the correct image at test is identified based on relative familiarity (Basile & Hampton, 2013; Wittig et al., 2016; Wittig & Richmond, 2014). By manipulating the size of the set from which images are were drawn, we manipulated the degree to which working memory, and maintenance via cognitive control, was engaged. When test images were drawn from a relatively small set of repeating images, every image had been seen recently and was highly familiar, making familiarity a poor basis on which to identify the most recently seen image. In contrast, when test images were drawn from a large set of infrequently repeating images, the sample was easy to identify on the basis of relative familiarity at test, without active maintenance of information through the delay interval.

It is widely thought that cognitive control and cognitive monitoring work together to optimize cognitive processing (Nelson, 1996). It is likely that cognitive control of working memory is possible during the delay because the memoranda are actively “held in mind,” a process made possible by dynamic feedback from cognitive monitoring. Cognitive monitoring is a process that allows subjects to assess the strength, quality, or presence of a memory. According to this model, monkeys would assess their memory with cognitive monitoring and then bolster it as necessary with cognitive control. In contrast, familiarity can only be elicited once the test images are presented. Because familiarity is a memory signal elicited by the re-presentation of previously seen items, it cannot operate during the retention interval, when no images are present. Thus, monkeys may cognitively monitor familiarity signals if given the opportunity to do so at test, but the current work did not evaluate that.

We observed an effect of the “remember” cue only in the small set condition. But this does not necessitate the conclusion that working memory was not, or could not, be engaged by images from the large set. Because familiarity is not as useful in the small set condition, if monkeys terminate rehearsal during these tests, they are unlikely to choose correctly at test. Thus, active rehearsal is reinforced. In the large set condition terminating rehearsal may have no effect on accuracy because familiarity is such a reliable cue. Rehearsal during the delay in trials with images from the large set may therefore not be reinforced. Alternatively, monkeys may be unable to rehearse images from the large set condition (but see Brady & Hampton, 2018). Rehearsal is likely facilitated by existing representations of specific memoranda, which are already robust in long-term memory. Images drawn from the large set are seen infrequently and it is therefore less likely that they are well-represented to draw upon in rehearsal. If monkeys had existing representations to bolster rehearsal in the small, but not large set condition, they would be able to use the "remember" cue effectively in the small set condition only.

Several facts favor the hypothesis that the images in the large set did not engage working memory. First, monkeys were not performing at ceiling, even in the large set condition, so working memory for the sample image would likely have enhanced accuracy had it been present, and we would have observed an effect of the remember cue. Additional support for this interpretation comes from a previous study in which monkeys were required to remember items drawn from lists (Basile & Hampton, 2010). Monkeys showed robust primacy when remembering list items drawn from small, but not large sets of images, suggesting an advantage for rehearsing familiar items. With the current data set, we cannot differentiate between the hypothesis that monkeys are unable to rehearse less familiar items and the hypothesis that working memory is present with the large set but hidden by the strength of selection by item-familiarity.

We did not find that cognitive control of working memory was significantly greater at long delays, which is inconsistent with the hypothesis put forward by Maki and Hegvik (1980) that longer delays would make successful remembering more dependent on cognitive control. Because memory weakens over time, active maintenance of working memory by cognitive control should be most useful over medium-length delays, when memory for the sample would otherwise be weakened or even lost. An alternative hypothesis is that directed forgetting cues should not be effective at longer delays because cognitive control of working memory can only be maintained for a limited time. Of the monkeys we tested, 5 individuals appeared to show some trend toward a larger directed forgetting effect at longer delays in the small set condition and 2 did not. This could indicate that 5 of the monkeys tended to rely more on working memory compared to the other 2. Memory for unrehearsed items should deteriorate with the passage of time. If monkeys cannot sustain rehearsal at longer durations, their memory for “remember” cued items would therefore be lower at these intervals than for monkeys more effective at rehearsing. One future course of study might be to investigate whether certain monkeys tend to rely on different mnemonic strategies. Titrated delays in the large image set condition tended to be longer than in the small image set condition; however, because the range of tested delays overlapped between the two conditions, it is unlikely that delay length was responsible for the difference in directed forgetting effect between these two conditions.

We used a directed forgetting paradigm to evaluate the extent to which working memory and familiarity are subject to cognitive control in monkeys. We found a directed forgetting effect only for images drawn from small sets, under conditions that we expected to encourage use of working memory. We did not find a directed forgetting effect for images drawn from large sets, under conditions that we expected to encourage use of familiarity. Our results suggest that monkeys, like humans, possess a working memory system that is subject to active cognitive control and a familiarity system that is not, drawing new parallels between human and nonhuman primate memory systems.

4. Paper 3

Cognitive control in a caching and a non-caching bird species

Emily Kathryn Brown[1], David F. Sherry[2], and Robert R. Hampton[1]

[1] Department of Psychology and Yerkes National Primate Research Center,
Emory University

[2] Advanced Facility for Avian Research and Department of Psychology, Western
University

Author's Note:

This work was supported by the National Science Foundation (grants BCS-1632477, IOS-1146316, BCS-0745573) and the National Institutes of Health (grant RO1MH082819; T32HD071845). This project was supported in part by ORIP/OD P51OD011132. This project was supported in part by NSERC Discovery Grant 105542.

Correspondence concerning this article should be addressed to Emily Brown,

PAIS Building, 36 Eagle Row, Atlanta, GA, 30322. Phone: 404.727.9619. Email:

emily.brown@emory.edu

Keywords: black-capped chickadee, cognitive control, working memory

4.1 Abstract

Scatter hoarding black-capped chickadees use memory to relocate hidden food, often after delays of hours or days. The ability of these birds to maintain accurate memories of the location and current status of food caches suggests that their memory may be especially resistant to competing cognitive load. We measured resistance to competing cognitive load during spatial memory tests in black-capped chickadees (*Poecile atricapillus*) and a non-caching species, dark-eyed juncos (*Junco hyemalis*). Birds were presented with 4 intermixed tasks. On *stand-alone* matching trials, birds pecked a sample, which they selected from among 2 distractors at test. On *stand-alone* discrimination trials, birds learned by trial-and-error to select a target from among 2 distractors. On *embedded* matching+discrimination trials, the embedded discrimination was presented in the interval between the sample and test phase of a matching trial. Juncos were significantly more impaired than chickadees in both embedded tasks, especially the embedded matching task, indicating greater vulnerability to competing cognitive load in this species. The need to encode and retain the locations of multiple food caches may have led to the evolution of enhanced cognitive control in black-capped chickadees.

4.2 Introduction

Cognitive control is the active, top-down adjustment of information processing. Cognitive control is likely a cluster of related traits and has been variously described to be involved in inhibitory control, set shifting, and working memory in humans (Diamond, 2013). The extent to which nonhumans engage in cognitive control is less clear. A comparative approach could help to clarify both the selective pressures that have led to cognitive control and the mechanisms that underlie it.

Evolutionary pressures shape cognition, and cognitive control may be useful for many problems faced in the environment. Daily foraging challenges in which cognitive control could potentially be useful for wild animals include learning and remembering good food sources, switching between foraging on food items that are predicted by different cues or require different handling (Bond & Kamil, 1999; Goto, Bond, Burks, & Kamil, 2014; Woodward & Laverty, 1992), and balancing foraging with other demands in the environment, like evading predators (Cresswell, Quinn, Whittingham, & Butler, 2003; Kaby & Lind, 2003). One well-studied example of how evolution has shaped cognition, particularly memory, is in the memory of birds that cache food.

Scatter-hoarding birds store food in uniquely-located caches, which can later be remembered and recovered. These caches are advantageous as a known, predictable food source and as a resource that can be hidden from competitors (Kamil & Gould, 2008). Scatter-hoarding birds use memory to retrieve caches with high spatial fidelity (Balda & Kamil, 1989; Cowie, Krebs, & Sherry, 1981). Because they do not re-use cache sites or cache exclusively in a particular site (Sherry, Krebs, & Cowie, 1981), a given cache site is thereafter empty once its contents have been retrieved. Memory for the locations of cached food must therefore be frequently and flexibly updated.

Black-capped chickadees (*Poecile atricapillus*) and dark-eyed juncos (*Junco hyemalis*) are both small passerine birds that over-winter in southern Ontario, where they face cold temperatures and food scarcity. Both chickadees and juncos face predation risk that must be balanced while foraging (Lima, 1985, 1988). Chickadees and juncos both forage in flocks with a dominance hierarchy (Fretwell, 1969; Smith, 1976). Chickadees and juncos have overlapping diets, with a strong emphasis on seeds in winter. A major difference between these two species is that chickadees cache food and use memory to recover these caches, and juncos do not.

Chickadee memory has been well-characterized through field experiments, observations, and more controlled laboratory tasks. These birds store hundreds of items in unique locations each day which they can then recover with high spatial fidelity (Sherry, 1989). Chickadees are able to remember what, where, and when aspects of previous encounters with food (Feeney, Roberts, & Sherry, 2009, 2011; Sherry, 1984). Some properties of chickadee caching and cache recovery indicate strong resistance to interference from competing cognitive load, which is characteristic to efficient cognitive control of working memory. For example, the rate at which food items are stored—hundreds within a day—suggests that the episode of storing one item is likely still in working memory when a subsequent food item is eaten or stored. Other environmental distractions may occur during the storing episode, for example, birds may be pursued while en route to make a cache (Sherry, 1989). Caching birds sometimes recover and re-store food items after a brief interval (Sherry, 1989). Finally, birds must flag or "delete" sites from memory once they have recovered food or found food unrecoverable due to pilfering or spoilage (Sherry, 1984; Sherry & Vaccarino, 1989; Shettleworth & Krebs, 1982). Flexible updating of information is a signature of cognitive control over memory. But cognitive specialization cannot necessarily be conceptualized as a general improvement in cognitive control. Species-specific cognitive adaptations may influence the duration, capacity, resolution, or modality of memory contents (Smulders, Gould, & Leaver, 2010).

To test whether food caching has biased birds to possess better cognitive control over memory, we tested a caching species, black-capped chickadee (*Poecile atricapillus*) and a non-caching species, dark-eyed junco (*Junco hyemalis*) on two types of spatial memory test, mixed within a session. The two types of memory test differed in their dependence on working memory and therefore varied in the demand they exerted on cognitive control. In the first subset of trials, birds completed discriminations, which had to be learned by trial-and-error. In the second subset of trials, birds completed a match-to-sample task, for which they had to select a remembered sample location from among distractors. In the final subset of trials, the first two tasks were combined: birds were presented a sample, then had to complete a discrimination accurately before proceeding to the match-to-sample test. To assess different aspects of cognitive control, we compared acquisition rates of embedded and standalone discriminations, switch costs at transitions between standalone tasks, and ability to remember the sample through a concurrent cognitive load in the standalone match-to-sample task. If one species is better at maintaining working memory through concurrent cognitive load, then they should have superior accuracy when a habit trial is embedded during the retention interval. If one species is a cognitive control generalist, they will show enhanced ability to shift between tasks; however, if cognitive control is an adaptation specific to memory, there will be no species difference in shifting between tasks.

4.3 Methods

Subjects

Subjects were all single-housed after being caught from the wild in London, Ontario. 5 dark-eyed juncos (*Junco hyemalis*) were caught by mistnet on December 4, 2017 and 5 black-capped chickadees (*Poecile atricapillus*) were caught by potter trap on October 4, 2016 and January 11, 2017. The age and sex of all birds was unknown.

All birds were marked on one leg with two darvic colored legbands. A 12 mm, 125 kHz rfID tag affixed to the pair of bands stored a unique hexadecimal code that allowed birds to be individually identified by computer.

Figure 1. All birds were uniquely identified by darvic legbands with an rfID tag affixed. The darvic bands provided visual identification to observers, and the rfID tag allowed the computer to identify the bird as it completed trials of cognitive testing.

Apparatus

We tested all birds in the aviaries where they lived, using portable touch-screen computer rigs consisting of a laptop computer (Hewlett-Packard, Palo Alto, CA), a 15" color LCD touchscreen (ELO, Menlo Park, CA), 2 rfID readers (GiS mbH, Lenningen, Germany) and antennas, and an automated food hopper that provided access to food through an opening beneath the screen. Food reinforcement consisted of powdered black oil sunflower seed meats. An array of photo beams surrounded the opening of the food hopper to detect pecks and control the duration of access to food. We presented stimuli and collected responses using programs written in Visual Basic (Microsoft Corporation).

The two rfID readers housed in each testing apparatus were connected to the computer that controlled stimulus presentations and collected responses. One antenna was embedded in a porch in front of the apparatus. The other antenna was affixed to the area surrounding the opening where birds accessed the food hopper (Fig. 2).

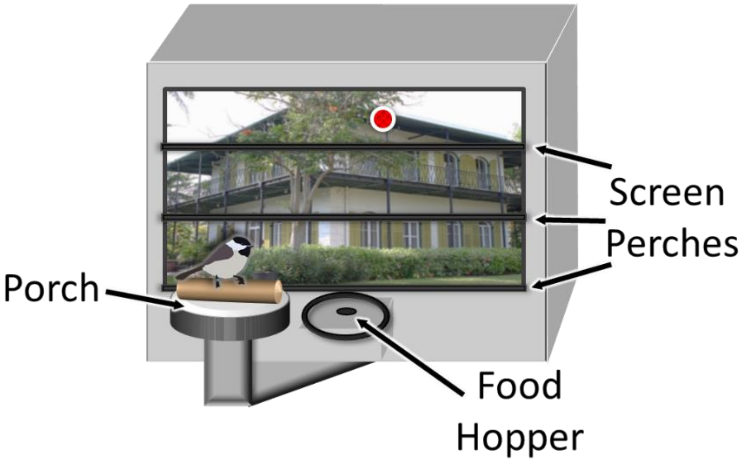


Figure 2. Schematic of bird testing apparatus. Birds landed on the porch, which housed an antenna to register chip reads, to initiate trials and view the sample. They landed on the screen perches to make responses to stimuli onscreen with a peck. Birds returned to the porch to initiate and view memory tests. Following a correct response at test, birds could briefly access reinforcement at the food hopper.

Birds initiated trials by landing on the porch antenna in front of the apparatus. By requiring birds to begin trials at the porch, we ensured that they had an appropriate distance and angle to view stimuli presented anywhere on the screen. At the end of correct trials, birds were again identified at the food hopper. Birds were free to come and go from the testing apparatus at any time. If a bird left the testing apparatus, the experiment resumed when the bird returned.

Procedure

Bird housing and testing conditions

During testing, birds were housed in outdoor aviaries on the roof of the Advanced Facility for Avian Research (AFAR) located at Western University in London, Ontario. Each bird was individually-housed in an outdoor rooftop aviary, with room to fly, branches or shrubs consistent with the local environment where they could perch, and shelter to sleep overnight. Birds had visual and auditory access to conspecifics and wild birds through the mesh fencing walls of the aviary, which permitted limited social contact, but prevented access to adjacent testing equipment. Birds had ad libitum access to their testing equipment. Birds had ad libitum access to water.

Chickadees had ad libitum access to ground, nutritionally-complete Mazuri small bird diet (PMI Nutrition International, Brentwood, MO). They had overnight access to sunflower seed from approximately an hour prior to sunset to approximately 8:30 am on a typical day. This supplemental seed was ground to a powder to prevent birds from storing it in caches that could be recovered during the day. In this way, we attenuated starvation risk in cold temperatures while encouraging birds to work for food access during normal daily foraging times.

Juncos had overnight access to ground, nutritionally-complete small bird diet (Mazuri, Land O'Lakes, Arden Hills, MN) mixed with sunflower seed, from about an hour prior to sunset to 8:30 am on a typical day. Juncos also had access to a budgie seed mix blend from about an hour prior to sunset until after dark each day. Juncos had ad libitum access to grit. Chickadees and juncos had slightly different diets due to different nutritional needs and starvation risk.

Basic training

Initially, the testing apparatus was baited with peanut butter. After birds reliably landed on the surface of the apparatus, they were presented with an autoshaping protocol that reinforced landing in antenna read fields and pecking the screen. Birds learned to initiate trials by landing on the porch antenna, land at the screen to peck onscreen images, and eat food from the hopper below. All responses were trained to require two pecks (FR2) to prevent selection of a stimulus via spurious contact with the screen. All birds had previous computerized cognitive testing experience learning spatial discriminations by trial-and-error and matching to location. The discriminations presented in the embedded task were novel to the birds.

Basic spatial task parameters

The screen was divided into a 12-location grid of 256 x 256-pixel squares, such that each row contained 4 locations and each column contained 3 locations. Locations currently responsive to touch were indicated by 50 x 50-pixel textured red circle with a white border. All tasks relied on spatial memory. On matching trials, birds had to remember a previously viewed spatial location and on discrimination trials, birds had to select a target location from an array of locations on the basis of trial-and-error learning. Arrays of choice locations were configurally-unique, and each array was always presented on the same unique photographic background image.

Sessions consisted of three types of intermixed trials totaling 72 trials. On *stand-alone* matching trials, birds pecked a sample, which they selected from among 2 distractors at test. On *stand-alone* discrimination trials, birds learned by trial-and-error to select a target from among 2 distractors. On *embedded* matching+discrimination trials, the embedded discrimination was presented in the interval between the sample and test phase of a matching trial. One third of trials were stand-alone discriminations. One third of trials were stand-alone matching. One third of trials were embedded matching+discrimination trials. 12 scene-location pairings were used for all matching tests, 12 scene-location pairings were used for stand-alone discriminations, and 12 scene-location parings were used for embedded discriminations.

Following any correct stand-alone trial, the hopper lifted and provided birds access to food for 1 second after their first peck to the hopper was detected. In this way, duration of food access was controlled across subjects, regardless of how quickly the subject initiated access. For embedded trials, the same procedure applied for each portion of the trial completed correctly, such that birds could have two opportunities to access food after correct completion of both the discrimination and matching portions of the test. Following incorrect discriminations, birds received a correction procedure, wherein the same discrimination was repeated until the correct location was selected. Following incorrect matching trials, the trial terminated without food access and without correction procedure. Because discriminations rely on habit memory, ending trials with reinforcement will speed acquisition and help prevent perseverative responding that could hinder task motivation.

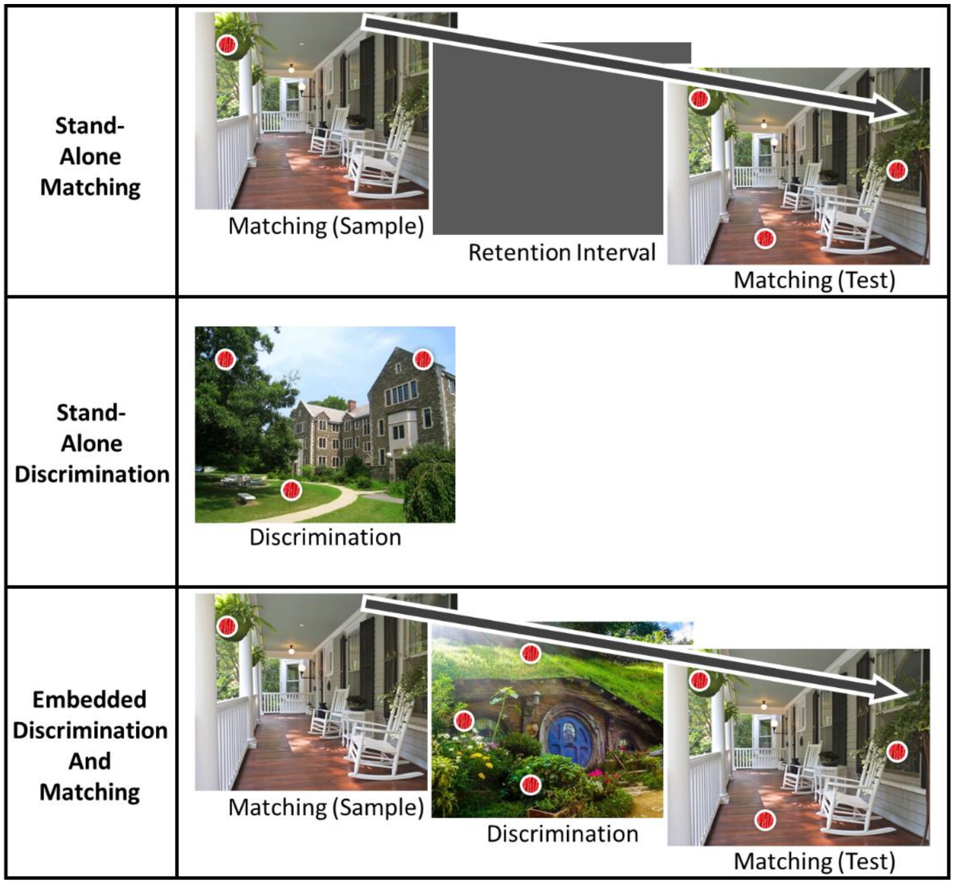


Figure 3. Examples of procedure of trials of the three tasks. On *stand-alone matching* trials (*top*), birds pecked a sample location. Following a retention interval, during which birds had to return to the porch, they saw the sample location together with two marked distractor locations. On *stand-alone discrimination* trials (*middle*), birds selected a target location learned by trial-and-error from among two marked distractor locations. On *embedded discrimination and matching* trials (*bottom)*, birds pecked a sample location. They then completed a discrimination trial before taking the matching test.

Data analysis

All proportions were arcsine transformed before statistical analysis to better approximate the normality assumption underlying parametric statistics (Keppel & Wickens, 2004, p. 155).

We assessed sessions to criterion as the number of sessions it took for subjects to reach 80% correct on a given sub-task: stand-alone matching, embedded matching, stand-alone discrimination, and embedded discrimination. Birds had prior experience with both matching and discrimination tasks, but the discriminations presented here were novel to them. We used Mixed ANOVA to compare the rate at which the two species acquired the tasks (chickadee or junco), the task type (matching or discrimination), and the task condition (presented stand-alone or embedded). We conducted follow-up Repeated Measures ANOVA to examine within species effects of task type and task condition, and planned paired t-tests to examine stand-alone and embedded versions of each task.

We calculated task-switching costs by comparing proportion correct on stand-alone discriminations as a function of congruency. Stand-alone discriminations that followed another stand-alone discrimination were considered “congruent” trials, in that the cognitive set required for the task was the same as for the previous trials; stand-alone discriminations that followed a stand-alone matching trial were considered “incongruent”. To capture any transient effects, we analyzed accuracy across 5-session blocks for each species over the course of acquisition. Task-switching costs are often measured by errors, so we did not expect accuracy decrements to be evident at ceiling performance (Kiesel et al., 2010; Monsell, 2003). Because birds showed high accuracy on stand-alone matching from the start of training, we did not analyze this task for task-switching costs. We used Repeated Measures ANOVA to determine whether trial congruency affected performance over the course of learning.

4.4 Results

Sessions to Criterion

Juncos were more impaired by embedded trials than chickadees were. There was a three-way interaction of species (chickadee or junco) by task type (discrimination or matching) by embedding (embedded or stand-alone) ($F_{(1,8)}$ = 15.046, $P < .01$, partial $\eta^2 = .653$). Within each species, the interaction of task type (discrimination or matching) by embedding (embedded or stand-alone) was maintained (Fig 4. (left), for chickadees, $F_{(1,4)}$ = 17.799, P = .013, partial $\eta^2 = .817$; Fig 4. (right), for juncos, $F_{(1,4)}$ = 33.307, $P < .01$, partial $\eta^2 = .893$). Chickadees took fewer sessions to reach criterion on the stand-alone than embedded matching, but did not show a significant difference in sessions to criterion according to embedding of discriminations (matching: $t_{(4)}$=-4.080, P=.015, d=1.825; discrimination: $t_{(4)}$=-1.000, P=.374, d=.447). Juncos took fewer sessions to reach criterion on the stand-alone than embedded versions of both matching and discriminations (matching: $t_{(4)}$=-5.802, P<.01, d=2.595; discrimination: $t_{(4)}$=-2.806, P=.049, d=1.255).

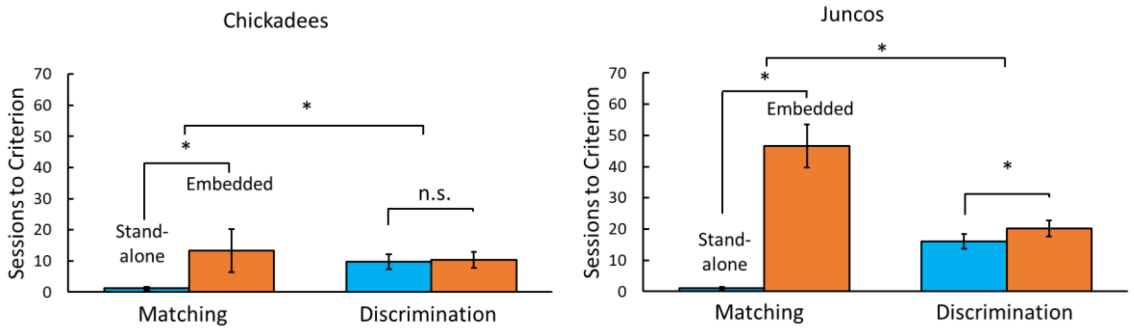


Figure 4. Chickadees reached criterion faster in stand-alone than embedded matching, but showed no such effect on the discrimination task; juncos learned both tasks faster in the stand-alone than the embedded condition. Mean group sessions to criterion (± SD) for chickadees and juncos for the matching (left) or discrimination (right) task, as a function of stand-alone (blue) or embedded (orange) condition. * = $p < .05$ for ANOVA interaction and follow-up t-tests that compared stand-alone and embedded performance in the matching and discrimination tasks, respectively.

Set shifting

Chickadees and juncos both showed a significant main effect of block on proportion correct for stand-alone discriminations (chickadees: $F_{(3,12)} = 56.661$, $P < .001$, partial $\eta^2 = .934$; juncos: $F_{(11,44)} = 27.046$, $P < .001$, partial $\eta^2 = .871$), indicating learning. There was no significant interaction of trial congruency and block for either species (Fig.5; chickadees: $F_{(3,12)} = .985$, $P = .432$, partial $\eta^2 = .198$; juncos: $F_{(11,44)} = 1.057$, $P = .416$, partial $\eta^2 = .209$) or main effect of block for either species (chickadees: $F_{(1,4)} = .447$, $P = .540$, partial $\eta^2 = .101$; juncos: $F_{(1,4)} = 1.294$, $P = .319$, partial $\eta^2 = .244$).

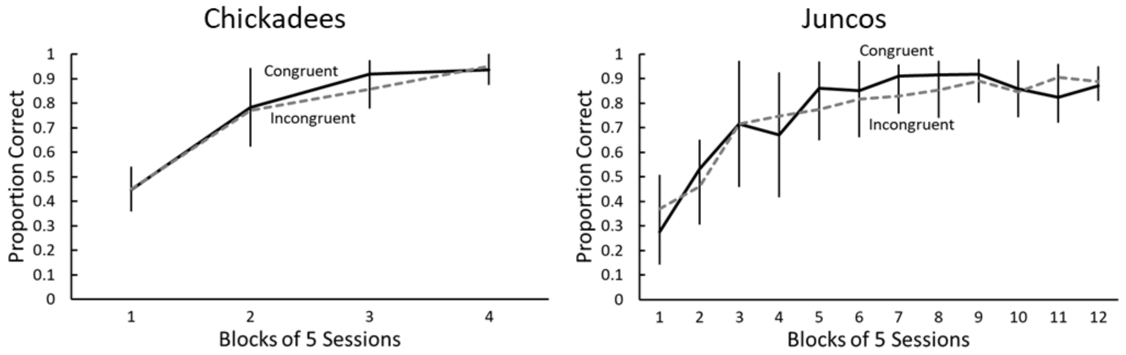


Figure 5. Chickadees and juncos show no benefit for congruent trials, which follow the same type of trial, over incongruent trials, which involve a task switch. Mean proportion correct (± SEM) for chickadees (left) and juncos (right) for congruent (black solid) or incongruent (grey dashed) trials of the stand-alone discrimination task.

4.5 Discussion

Chickadees, a caching species, and juncos, a non-caching species, differed in their management of concurrent cognitive load in the context of a memory test. Juncos were significantly impaired on both embedded tasks compared to the previously-learned stand-alone versions of the tasks. Chickadees were slow to reach criterion on embedded matching compared to the stand-alone version of the task but acquired new discriminations at similar rates. That juncos were so impaired in their acquisition of embedded tasks, particularly matching, may indicate a species difference in the cognitive control of memory in the face of competing cognitive load.

In contrast, neither species showed a task-switching cost on stand-alone discrimination trials that followed a matching trial compared with those that followed a stand-alone discrimination trial. In the wild, both juncos and chickadees face pressure to switch between competing tasks, such as foraging and scanning for predators. That we found a species difference in sessions to criterion but found no effects of task-switching suggests that any cognitive control advantage that chickadees possess is limited to the domain of memory. This is consistent with idea that cognitive specialization should be tailored to the demands of the environment.

Chickadees face significant selective pressure to remember and recover their food caches in the wild. Scatter-hoarding birds are able to retain and update the recovery-status of hundreds of cached food items with high spatial fidelity (Sherry, 1989; Shettleworth, 1990). Because chickadees are rapidly caching food items in multiple locations and retaining those locations, all while also engaging in other distracting activities such as evading predators and potential cache thieves, it is possible that food caching has put significant pressures on the cognitive control required to maintain working memory through concurrent cognitive load.

The demands of caching are a compelling explanation for the superior working memory of chickadees, but this interpretation should be taken with caution. Natural history differences other than caching may drive any between-species effects that we observed. Although black-capped chickadees and dark-eyed juncos share many overlapping features in their natural histories, they do differ according to factors other than caching. Therefore, superior working memory of chickadees may not be due to caching per se. The constraints of testing a wide variety of species on the same task is a limitation of a comparative approach. Ideally, recording data from a more diverse pool of species would help to support the hypothesis that any effects observed were related to caching behavior rather than other other differences between species. We could better evaluate the relationship between caching and working memory with future studies that make use of more exemplar species that do and do not cache, or species of chickadees that are closely enough related to interbreed, but differ in their propensity to cache.

In humans, information is held in working memory during encoding and retrieval for long-term explicit memory. Less is known about the way that information passes between working and long-term memory in passerine birds. Neither the prefrontal cortex, implicated in cognitive control of working memory in mammals, nor a homologous structure exists in birds (Allen & Fortin, 2013). Yet the avian caudolateral nidopallium (NCL) may be functionally similar to the prefrontal cortex, and is likely a product of convergent evolution to address similar selective pressures (Allen & Fortin, 2013; Güntürkün, 2005). Future studies on the maintenance of information through concurrent cognitive load may help elucidate the mechanisms of cognitive control in passerines. Such studies would also clarify the relation between more temporary maintenance of information and longer-term memory often associated with caching.

Here we provide limited evidence that chickadees, a caching species, and juncos, a non-caching species, differ in their cognitive control of memory. Chickadees face significant environmental pressures to encode the locations of multiple food caches in a relatively short period of time that may have improved their cognitive control to manage memory through concurrent cognitive load.

5. General discussion

Cognitive control is the active, top-down adjustment of information processing that helps to selectively prioritize what is remembered. Working memory and familiarity are memory systems that appear to represent a tradeoff between flexible prioritization of information and effortful ongoing maintenance. Cognitive control is a key feature of working memory (Baddeley, 2003), but is not necessary to maintain familiarity (Yonelinas, 2002). Therefore, we can use the presence or absence of cognitive control as an important measure to dissociate memory systems and provide insight into what memory tradeoffs may exist between and across taxa.

In the papers presented above, I evaluated the relation between cognitive control and memory in rhesus monkeys, black-capped chickadees, and dark-eyed juncos. In paper 1, I described a metacognition task designed to test how rhesus monkeys (*Macaca mulatta*) engage in memory monitoring, a useful feedback mechanism for cognitive control, under conditions that disproportionately encourage use of working memory or familiarity. Monkeys produced accuracy and latency data consistent with the additive effects of monitoring both working memory and familiarity. In paper 2, I described a directed forgetting task designed to test how rhesus monkeys selectively engage in cognitively controlled maintenance of information under conditions that disproportionately encourage use of working memory or familiarity. Monkeys showed evidence of cognitive control similar to rehearsal when remembering items drawn from a small set of repeating images, but not when remembering items from a large set of images that could likely be recognized at test without effortful retention. In paper 3, I described the effects of concurrent cognitive load on memory and acquisition of novel discriminations in two bird species: the black-capped chickadee (*Poecile atricapillus*), which stores food that is later recovered by memory, and the dark-eyed junco (*Junco hyemalis*), which does not. All three findings build the foundation of engaging future research questions.

In paper 1, I described a metacognition task designed to test the degree to which rhesus monkeys monitor different memory systems. Cognitive monitoring serves as a feedback system for effective cognitive control (Nelson, 1996). Although familiarity is not subject to control, we found some indication that it is nonetheless available to monitoring. It is also possible that other memory signals, as well as other non-mnemonic cues may contribute to metamemory performance. Identifying these signals and how they interact to support behavior will be an interesting problem for future research. When signals from monitoring familiarity and working memory are congruent, as they should be in these experiments, it seems that monitoring the two signals provides an additive benefit. It is unclear if the signals are combined, or if one countermands another when they are in conflict. According to the logic that underlies another paradigm, the process dissociation procedure, information in controlled one-trial memory is always selected when it is remembered, whereas information from an automatic system is only used when one-trial memory is forgotten (Jacoby, 1991; Tu & Hampton, 2012; Tu et al., 2011). A metamemory experiment that places working memory and familiarity into conflict could further inform our understanding of the relation between cognitive monitoring and control.

In paper 2, monkeys showed evidence of cognitive control similar to rehearsal under conditions that encouraged reliance on working memory, but not under conditions in which item familiarity would be sufficient for recognition at test. In humans, a major mechanism of cognitive control of working memory appears to be subvocal rehearsal, repeating to-be-remembered information in one's mind (Baddeley, 2003). Theoretically, rehearsal aids maintenance because re-coding verbally helps integrate to-be-remembered stimuli with established representations in long-term memory and because naming picture stimuli allows redundant coding in multiple modalities. Future studies should address how nonhumans manage to engage in cognitive control of memory without language. Monkeys may engage in redundant coding or integration with existing representations to "rehearse" without language. Experiments to determine whether similar integration exists in nonhumans could compare the ability to rehearse novel vs. familiar images, the ability to rehearse images that do or do not fit known categories, and examination of working memory for items with known or unknown signs or lexigrams in language-trained apes.

In paper 3, chickadees managed concurrent cognitive load better than juncos, possibly because chickadees have adapted to flexibly manage memory for food caches. Though juncos were especially impaired on embedded matching, they also demonstrated impaired performance on embedded discriminations, unlike chickadees. In discrimination learning and reversals, asymptotic performance relies on an automatic system whereas early learning is marked by working memory for the response and outcome of the previous trial (Hassett & Hampton, 2017). However, discrimination trials in this task were spaced such that multiple discrimination and matching trials were interleaved before the same discrimination trial was seen again. A long duration with substantial intervening cognitive load makes it unlikely that discrimination outcomes were actively maintained in working memory. Juncos may have been impaired on discriminations because effortful maintenance of the sample led to inattentive responding and poor encoding of the response that they made on the embedded discrimination. Past research with chickadees indicates that they have excellent, long-lasting, hippocampal-dependent memory (Sherry & Vaccarino, 1989). Although we used a relatively standard measure of cognitive control to dissociate processes, we do not discount the possibility that additional memory systems could have served to relieve cognitive load. For example, it is possible for humans to use long-term memory over short delays, especially when working memory capacity is exceeded (Jeneson, Mauldin, Hopkins, & Squire, 2011). The current study cannot conclusively determine how chickadees manage concurrent cognitive load. Chickadees may be particularly adept at maintenance in a system similar to working memory, but with different limitations to features such as capacity and duration. Alternatively, chickadees may be especially proficient at offloading and onloading memory between a system that shares features with working memory and a system that shares features with long-term explicit memory. Although chickadee memory does share some characteristics with human memory, we may not share an entire taxonomy of homologous systems.

Birds and modern mammals have undergone very different evolutionary trajectories, the two having diverged approximately 300 million years ago (Hedges, 2002). That we found evidence for cognitive control of memory across such highly divergent taxa seems to indicate that cognitive control of memory is widespread in nonhuman animals. Because human memory systems are well-characterized, they make a natural jumping off point for understanding memory systems in nonhumans. This approach is especially sensible in species that are phylogenetically close to humans, such as rhesus monkeys. Indeed, to the extent that memory systems depend on homologous neural substrates (e.g., Allen & Fortin, 2013; Squire & Zola-Morgan, 1991), animals are an excellent resource for understanding typical and atypical human memory because of the invasive work that they permit. However, an anthropocentric search for human memory systems in more distantly related taxa may have diminishing returns.

Memory systems can be divided according to their functional specialization, that is that features that make a system good for solving one problem in the environment preclude it from effectively solving another (Sherry & Schacter, 1987). Certain key tradeoffs, such as the one between flexible but effortful versus rigid but automatic, seem as though they may represent a critical functional incompatibility that divides memory systems across taxa. Cognitive control therefore appears to be an effective diagnostic tool in designing tasks to dissociate memory systems. Here I considered primarily the contributions of working memory and familiarity, memory systems frequently implicated in recognition performance on the type of paradigms that I used. For instance, memory for items drawn from a small set of images is highly vulnerable to concurrent load, a trait associated with capacity-limited working memory, but not long-term memory. However, other types of memory, such as recollection of material in long-term memory, may have contributed to task performance.

Comparative research uses closely-related species that face different environmental challenges and sympatric but unrelated species. Comparative studies of cognitive control may be useful in understanding other features of memory that differ among species and environmental demands, such as the duration, capacity, resolution, or specific contents of the representations maintained (Smulders, Gould, & Leaver, 2010).

I explored the relation between cognitive control and memory in three species: rhesus monkeys, black-capped chickadees, and dark-eyed juncos. I found that rhesus monkeys monitor multiple memory signals, a feedback mechanism for cognitive control, and engage in effortful cognitive control in tasks that encourage reliance on working memory. I also found evidence that black-capped chickadees and dark-eyed juncos show a species difference in their ability to engage in cognitive control to manage memory through concurrent load, which may have been shaped by the specific demands of their environments. The most comprehensive understanding of any behavior, including cognition, integrates information about both "how" and "why" that behavior functions (Bateson & Laland, 2013). Future work will combine the more mechanistic approach that I used in Papers 1 and 2 with the more comparative approach I used in Paper 3 to improve our understanding of the role of cognitive control in nonhuman memory systems.

6. References

Allen, T. A., & Fortin, N. J. (2013). The Evolution of Episodic Memory. *Proceedings of the National Academy of Sciences, 110*, 10379-10386.

Baddeley, A. (2000). The Episodic Buffer: A New Component of Working Memory? *Trends in Cognitive Sciences, 4*(11), 417-423.

Baddeley, A. (2003). Working Memory: Looking Back and Looking Forward. *Nature Reviews Neuroscience, 4*(10), 829.

Balda, R. P., & Kamil, A. C. (1989). A Comparative-Study of Cache Recovery by 3 Corvid Species. *Animal Behaviour, 38*, 486-495. doi:10.1016/s0003-3472(89)80041-7

Basile, B. M., & Hampton, R. R. (2010). Rhesus Monkeys (Macaca Mulatta) Show Robust Primacy and Recency in Memory for Lists from Small, but Not Large, Image Sets. *Behavioural Processes, 83*(2), 183-190.

Basile, B. M., & Hampton, R. R. (2011). Monkeys Recall and Reproduce Simple Shapes from Memory. *Current Biology, 21*(9), 774-778. doi:10.1016/j.cub.2011.03.044

Basile, B. M., & Hampton, R. R. (2013). Dissociation of Active Working Memory and Passive Recognition in Rhesus Monkeys. *Cognition, 126*(3), 391-396.

Basile, B. M., & Hampton, R. R. (2014). Metacognition as Discrimination: Commentary on Smith et al. (2013). . *Journal of Comparative Psychology*.

Basile, B. M., Hampton, R. R., Suomi, S. J., & Murray, E. A. (2009). An Assessment of Memory Awareness in Tufted Capuchin Monkeys (Cebus Apella). *Animal Cognition, 12*(1), 169-180.

Basile, B. M., Schroeder, G. R., Brown, E. K., Templer, V. L., & Hampton, R. R. (2015). Evaluation of Seven Hypotheses for Metamemory Performance in Rhesus Monkeys. *Journal of Experimental Psychology: General, 144*(1), 85.

Bateson, P., & Laland, K. N. (2013). Tinbergen's Four Questions: An Appreciation and an Update. *Trends in Ecology & Evolution, 28*(12), 712-718.

Beran, M. J., & Smith, J. D. (2011). Information Seeking by Rhesus Monkeys (Macaca Mulatta) and Capuchin Monkeys (Cebus Apella). *Cognition, 120*(1), 90-105. doi:10.1016/j.cognition.2011.02.016

Bond, A. B., & Kamil, A. C. (1999). Searching Image in Blue Jays: Facilitation and Interference in Sequential Priming. *Animal Learning & Behavior, 27*(4), 461-471.

Brady, R. J., & Hampton, R. R. (2018). Post-Encoding Control of Working Memory Enhances Processing of Relevant Information in Rhesus Monkeys (Macaca Mulatta). *Cognition, 175*, 26-35.

Brady, R. J., & Hampton, R. R. (under review). Nonverbal Working Memory for Novel Images in Rhesus Monkeys (*Macaca Mulatta*).

Brauer, J., Call, J., & Tomasello, M. (2004). Visual Perspective Taking in Dogs (Canis Familiaris) in the Presence of Barriers. *Applied Animal Behaviour Science, 88*(3-4), 299-317. doi:10.1016/j.applanim.2004.03.004

Brown, E. K., Templer, V. L., & Hampton, R. R. (2017). An Assessment of Domain-General Metacognitive Responding in Rhesus Monkeys. *Behavioural Processes, 135,* 132-144.

Call, J., & Carpenter, M. (2001). Do Apes and Children Know What They Have Seen? *Animal Cognition, 4,* 207-220.

Castro, L., & Wasserman, E. A. (2013). Information-Seeking Behavior: Exploring Metacognitive Control in Pigeons. *Animal Cognition, 16*(2), 241-254. doi:10.1007/s10071-012-0569-8

Couchman, J. J., Coutinho, M. V., Beran, M. J., & Smith, J. D. (2010). Beyond Stimulus Cues and Reinforcement Signals: A New Approach to Animal Metacognition. *Journal of Comparative Psychology, 124*(4), 356.

Cowie, R. J., Krebs, J. R., & Sherry, D. F. (1981). Food Storing by Marsh Tits. *Animal Behaviour, 29*(4), 1252-1259.

Cresswell, W., Quinn, J., Whittingham, M., & Butler, S. (2003). Good Foragers Can Also Be Good at Detecting Predators. *Proceedings of the Royal Society of London B: Biological Sciences, 270*(1519), 1069-1076.

Crystal, J. D., & Shettleworth, S. J. (1994). Spatial List Learning in Black-Capped Chickadees. *Animal Learning & Behavior, 22*(1), 77-83.

Diamond, A. (2013). Executive Functions. *Annual Review of Psychology, 64,* 135-168.

Edhouse, W. V., & White, K. G. (1988). Cumulative Proactive Interference in Animal Memory. *Animal Learning & Behavior, 16*(4), 461-467.

Feeney, M. C., Roberts, W. A., & Sherry, D. F. (2009). Memory for What, Where, and When in the Black-Capped Chickadee (Poecile Atricapillus). *Animal Cognition, 12*(6), 767.

Feeney, M. C., Roberts, W. A., & Sherry, D. F. (2011). Mechanisms of What-Where-When Memory in Black-Capped Chickadees (Poecile Atricapillus): Do Chickadees Remember "When"? *Journal of Comparative Psychology, 125*(3), 308.

Flavell, J. H. (1979). Meta-Cognition and Cognitive Monitoring - New Area of Cognitive-Developmental Inquiry. *American Psychologist, 34*(10), 906-911. doi:10.1037/0003-066x.34.10.906

Fretwell, S. (1969). Dominance Behavior and Winter Habitat Distribution in Juncos (Junco Hyemalis). *Bird-banding*, 1-25.

Fujita, K. (2009). Metamemory in Tufted Capuchin Monkeys (Cebus Apella). *Animal Cognition, 12*(4), 575.

Goto, K., Bond, A. B., Burks, M., & Kamil, A. C. (2014). Visual Search and Attention in Blue Jays (Cyanocitta Cristata): Associative Cuing and Sequential Priming. *Journal of Experimental Psychology: Animal Learning and Cognition, 40*(2), 185.

Goto, K., & Watanabe, S. (2012). Large-Billed Crows (Corvus Macrorhynchos) Have Retrospective but Not Prospective Metamemory. *Animal Cognition, 15*(1), 27-35.

Grant, D. S., & Barnet, R. C. (1991). Irrelevance of Sample Stimuli and Directed Forgetting in Pigeons. *Journal of the Experimental Analysis of Behavior, 55*(1), 97-108.

Gueorguieva, R., & Krystal, J. H. (2004). Move over Anova: Progress in Analyzing Repeated-Measures Data Andits Reflection in Papers Published in the Archives of General Psychiatry. *Archives of general psychiatry, 61*(3), 310-317.

Guitar, N. A., & Roberts, W. A. (2015). The Interaction between Working and Reference Spatial Memories in Rats on a Radial Maze. *Behavioural Processes, 112*, 100-107.

Güntürkün, O. (2005). The Avian 'Prefrontal Cortex'and Cognition. *Current opinion in neurobiology, 15*(6), 686-693.

Hampton, R. R. (2001). Rhesus Monkeys Know When They Remember. *Proceedings of the National Academy of Sciences of the United States of America, 98*(9), 5359-5362. doi:10.1073/pnas.071600998

Hampton, R. R. (2009a). Focusing the Uncertainty About Nonhuman Metacogntion. *Comparative Cognition & Behavior Reviews, 4*, 56.

Hampton, R. R. (2009b). Multiple Demonstrations of Metacognition in Nonhumans: Converging Evidence or Multiple Mechanisms? *Comparative Cognition & Behavior Reviews, 4*, 17.

Hassett, T. C., & Hampton, R. R. (2017). Change in the Relative Contributions of Habit and Working Memory Facilitates Serial Reversal Learning Expertise in Rhesus Monkeys. *Animal Cognition, 20*(3), 485-497.

Hedges, S. B. (2002). The Origin and Evolution of Model Organisms. *Nature Reviews Genetics, 3*(11), 838.

Hourihan, K. L., Ozubko, J. D., & MacLeod, C. M. (2009). Directed Forgetting of Visual Symbols: Evidence for Nonverbal Selective Rehearsal. *Memory & Cognition, 37*(8), 1059-1068. doi:10.3758/mc.37.8.1059

Iwasaki, S., Watanabe, S., & Fujita, K. (2013). Do Pigeons (*Columba Livia*) Seek Information When They Have Insufficient Knowledge? *Animal Cognition, 16*(2), 211-221.

Jacoby, L. L. (1991). A Process Dissociation Framework - Separating Automatic from Intentional Uses of Memory. *Journal of Memory and Language, 30*(5), 513-541. doi:10.1016/0749-596x(91)90025-f

Jeneson, A., Mauldin, K. N., Hopkins, R. O., & Squire, L. R. (2011). The Role of the Hippocampus in Retaining Relational Information across Short Delays: The Importance of Memory Load. *Learning & Memory, 18*(5), 301-305.

Jitsumori, M., Wright, A. A., & Cook, R. G. (1988). Long-Term Proactive Interference and Novelty Enhancement Effects in Monkey List Memory. *Journal of Experimental Psychology: Animal Behavior Processes, 14*(2), 146.

Kaby, U., & Lind, J. (2003). What Limits Predator Detection in Blue Tits (Parus Caeruleus): Posture, Task or Orientation? *Behavioral Ecology and Sociobiology, 54*(6), 534-538.

Kendrick, D. F., Rilling, M., & Stonebraker, T. B. (1981). Stimulus Control of Delayed Matching in Pigeons: Directed Forgetting. *Journal of the Experimental Analysis of Behavior, 36*(2), 241-251.

Keppel, G., & Wickens, T. D. (2004). *Design and Analysis: A Researcher's Handbook*: Prentice Hall.

Kiesel, A., Steinhauser, M., Wendt, M., Falkenstein, M., Jost, K., Philipp, A. M., & Koch, I. (2010). Control and Interference in Task Switching—a Review. *Psychological Bulletin, 136*(5), 849.

Kirk, C. R., McMillan, N., & Roberts, W. A. (2014). Rats Respond for Information: Metacognition in a Rodent? *Journal of Experimental Psychology: Animal Learning and Cognition, 40*(2), 249.

Kornell, N. (2013). Where Is the "Meta" in Animal Metacognition? *Journal of Comparative Psychology*.

Kornell, N., Son, L. K., & Terrace, H. S. (2007). Transfer of Metacognitive Skills and Hint Seeking in Monkeys. *Psychological Science, 18*(1), 64-71. doi:10.1111/j.1467-9280.2007.01850.x

Lima, S. L. (1985). Maximizing Feeding Efficiency and Minimizing Time Exposed to Predators: A Trade-Off in the Black-Capped Chickadee. *Oecologia, 66*(1), 60-67.

Lima, S. L. (1988). Initiation and Termination of Daily Feeding in Dark-Eyed Juncos: Influences of Predation Risk and Energy Reserves. *Oikos*, 3-11.

Maki, W. S., & Hegvik, D. K. (1980). Directed Forgetting in Pigeons. *Animal Learning & Behavior, 8*(4), 567-574.

Marsh, H. L. (2014). Metacognitive-Like Information Seeking in Lion-Tailed Macaques: A Generalized Search Response after All? *Animal Cognition, 17*(6), 1313-1328.

Marsh, H. L., & MacDonald, S. E. (2012). Information Seeking by Orangutans: A Generalized Search Strategy? *Animal Cognition, 15*(3), 293-304.

McMahon, S., Macpherson, K., & Roberts, W. A. (2010). Dogs Choose a Human Informant: Metacognition in Canines. *Behavioural Processes, 85*(3), 293-298. doi:10.1016/j.beproc.2010.07.014

Menzel, C. R. (1999). Unprompted Recall and Reporting of Hidden Objects by a Chimpanzee (Pan Troglodytes) after Extended Delays. *Journal of Comparative Psychology, 113*(4), 426-434. doi:10.1037//0735-7036.113.4.426

Monsell, S. (2003). Task Switching. *Trends in Cognitive Sciences, 7*(3), 134-140.

Nelson, T. O. (1996). Consciousness and Metacognition. *American Psychologist, 51*(2), 102.

Roberts, W. A., Guitar, N. A., Marsh, H. L., & MacDonald, H. (2016). Memory Systems in the Rat: Effects of Reward Probability, Context, and Congruency between Working and Reference Memory. *Animal Cognition, 19*(3), 593-604.

Roberts, W. A., Macpherson, K., & Strang, C. (2016). Context Controls Access to Working and Reference Memory in the Pigeon (Columba Livia). *Journal of the Experimental Analysis of Behavior, 105*(1), 184-193.

Roberts, W. A., Mazmanian, D. S., & Kraemer, P. J. (1984). Directed Forgetting in Monkeys. *Animal Learning & Behavior, 12*(1), 29-40.

Roberts, W. A., Strang, C., & Macpherson, K. (2015). Memory Systems Interaction in the Pigeon: Working and Reference Memory. *Journal of Experimental Psychology: Animal Learning and Cognition, 41*(2), 152.

Roper, K. L., Chaponis, D. M., & Blaisdell, A. P. (2005). Transfer of Directed-Forgetting Cues across Discrimination Tasks with Pigeons. *Psychonomic Bulletin & Review, 12*(6), 1005-1010.

Roper, K. L., Kaiser, D. H., & Zentall, T. R. (1995). True Directed Forgetting in Pigeons May Occur Only When Alternative Working-Memory Is Required on Forget-Cue Trials. *Animal Learning & Behavior, 23*(3), 280-285. doi:10.3758/bf03198924

Roper, K. L., & Zentall, T. R. (1993). Directed Forgetting in Animals. *Psychological Bulletin, 113*(3), 513-532. doi:10.1037/0033-2909.113.3.513

Sheard, E. D., & MacLeod, C. M. (2005). List Method Directed Forgetting: Return of the Selective Rehearsal Account *Dynamic Cognitive Processes* (pp. 219-248): Springer.

Sherry, D. (1984). Food Storage by Black-Capped Chickadees: Memory for the Location and Contents of Caches. *Animal Behaviour, 32*(2), 451-464.

Sherry, D. F. (1989). Food Storing in the Paridae. *The Wilson Bulletin*, 289-304.

Sherry, D. F., Krebs, J. R., & Cowie, R. J. (1981). Memory for the Location of Stored Food in Marsh Tits. *Animal Behaviour, 29*(4), 1260-1266.

Sherry, D. F., & Schacter, D. L. (1987). The Evolution of Multiple Memory-Systems. *Psychological review, 94*(4), 439-454.

Sherry, D. F., & Vaccarino, A. L. (1989). Hippocampus and Memory for Food Caches in Black-Capped Chickadees. *Behavioral Neuroscience, 103*(2), 308-318.

Shettleworth, S. J. (1990). Spatial Memory in Food-Storing Birds. *Phil. Trans. R. Soc. Lond. B, 329*(1253), 143-151.

Shettleworth, S. J., & Krebs, J. R. (1982). How Marsh Tits Find Their Hoards: The Roles of Site Preference and Spatial Memory. *Journal of Experimental Psychology: Animal Behavior Processes, 8*(4), 354.

Smith, J. D., Couchman, J. J., & Beran, M. J. (2012). The Highs and Lows of Theoretical Interpretation in Animal-Metacognition Research. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1594), 1297-1309.

Smith, J. D., Coutinho, M. V., Church, B. A., & Beran, M. J. (2013). Executive-Attentional Uncertainty Responses by Rhesus Macaques (Macaca Mulatta). *Journal of Experimental Psychology: General, 142*(2), 458.

Smith, J. D., Redford, J. S., Beran, M. J., & Washburn, D. A. (2010). Rhesus Monkeys (Macaca Mulatta) Adaptively Monitor Uncertainty While Multi-Tasking. *Animal Cognition, 13*(1), 93.

Smith, S. M. (1976). Ecological Aspects of Dominance Hierarchies in Black-Capped Chickadees. *The Auk, 93*(1), 95-107.

Smulders, T. V., Gould, K. L., & Leaver, L. A. (2010). Using Ecology to Guide the Study of Cognitive and Neural Mechanisms of Different Aspects of Spatial Memory in Food-Hoarding Animals. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365*(1542), 883-900.

Squire, L. R., & Zola-Morgan, S. (1991). The Medial Temporal-Lobe Memory System. *Science, 253*(5026), 1380-1386.

Suda-King, C. (2008). Do Orangutans (Pongo Pygmaeus) Know When They Do Not Remember? *Animal Cognition, 11*(1), 21-42. doi:10.1007/s10071-007-0082-7

Suda-King, C., Bania, A. E., Stromberg, E. E., & Subiaul, F. (2013). Gorillas' Use of the Escape Response in Object Choice Memory Tests. *Animal Cognition, 16*(1), 65-84. doi:10.1007/s10071-012-0551-5

Sutton, J. E., & Shettleworth, S. J. (2008). Memory without Awareness: Pigeons Do Not Show Metamemory in Delayed Matching to Sample. *Journal of Experimental Psychology-Animal Behavior Processes, 34*(2), 266-282. doi:10.1037/0097-7403.34.2.266

Tan, L., & Ward, G. (2000). A Recency-Based Account of the Primacy Effect in Free Recall. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26*(6), 1589.

Templer, V. L., & Hampton, R. R. (2012). Rhesus Monkeys (Macaca Mulatta) Show Robust Evidence for Memory Awareness across Multiple Generalization Tests. *Animal Cognition, 15*(3), 409-419. doi:10.1007/s10071-011-0468-4

Templer, V. L., Lee, K. A., & Preston, A. J. (2017). Rats Know When They Remember: Transfer of Metacognitive Responding across Odor-Based Delayed Match-to-Sample Tests. *Animal Cognition, 20*(5), 891-906. doi:10.1007/s10071-017-1109-3

Tu, H.-W., & Hampton, R. R. (2012). One-Trial Memory and Habit Contribute Independently to Matching-to-Sample Performance in Rhesus Monkeys (Macaca Mulatta).

Tu, H.-W., & Hampton, R. R. (2014). Control of Working Memory in Rhesus Monkeys (Macaca Mulatta). *Journal of Experimental Psychology: Animal Learning and Cognition, 40*(4), 467.

Tu, H.-W., Hampton, R. R., & Murray, E. A. (2011). Perirhinal Cortex Removal Dissociates Two Memory Systems in Matching-to-Sample Performance in Rhesus Monkeys. *The Journal of Neuroscience, 31*(45), 16336-16343.

Vining, A. Q., & Marsh, H. L. (2015). Information Seeking in Capuchins (Cebus Apella): A Rudimentary Form of Metacognition? *Animal Cognition, 18*(3), 667-681.

Washburn, D. A., & Astur, R. S. (1998). Nonverbal Working Memory of Humans and Monkeys: Rehearsal in the Sketchpad? *Memory & Cognition, 26*(2), 277-286.

Washburn, D. A., Gulledge, J. P., Beran, M. J., & Smith, J. D. (2010). With His Memory Magnetically Erased, a Monkey Knows He Is Uncertain. *Biology Letters, 6*(2), 160-162. doi:10.1098/rsbl.2009.0737

Watanabe, A., & Clayton, N. S. (2016). Hint-Seeking Behaviour of Western Scrub-Jays in a Metacognition Task. *Animal Cognition, 19*(1), 53-64.

Wittig, J. H., Morgan, B., Masseau, E., & Richmond, B. J. (2016). Humans and Monkeys Use Different Strategies to Solve the Same Short-Term Memory Tasks. *Learning & Memory, 23*(11), 644-647.

Wittig, J. H., & Richmond, B. J. (2014). Monkeys Rely on Recency of Stimulus Repetition When Solving Short-Term Memory Tasks. *Learning & Memory, 21*(6), 325-333.

Woodward, G. L., & Laverty, T. M. (1992). Recall of Flower Handling Skills by Bumble Bees: A Test of Darwin's Interference Hypothesis. *Animal Behaviour, 44*(6), 1045-1051.

Wright, A. A., Santiago, H. C., Sands, S. F., Kendrick, D. F., & Cook, R. G. (1985). Memory Processing of Serial Lists by Pigeons, Monkeys, and People. *Science, 229*(4710), 287-289. doi:10.1126/science.9304205

Wright, A. A., Urcuioli, R. J., & Sands, S. F. (1986). Proactive Interference in Animal Memory. In D. F. Kendrick, M. Riling, & R. Denny (Eds.), *Theories of Animal Memory* (pp. 101-125). Hillsdale, NJ: Earlbaum.

Yonelinas, A. P. (2002). The Nature of Recollection and Familiarity: A Review of 30 Years of Research. *Journal of Memory and Language, 46*(3), 441-517.

Yonelinas, A. P., Aly, M., Wang, W. C., & Koen, J. D. (2010). Recollection and Familiarity: Examining Controversial Assumptions and New Directions. *Hippocampus, 20*(11), 1178-1194.