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Recollection and familiarity in rhesus monkeys (*Macaca mulatta*)

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M.A. Emory University, 2009
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An abstract of
a dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
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Abstract

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Think of the last conference you attended. You likely had the common experience of seeing someone that looked very familiar, but were unable to remember their name or where you met them previously. This example illustrates the distinction between recollection, the ability to retrieve detailed information from memory, and familiarity, the vague sense that something you currently experience has been experienced previously. The distinction between recollection and familiarity is fundamental to theories of human memory, but is difficult to test in nonhuman animals. This dissertation collects three papers that describe attempts to characterize recollection and familiarity in a nonhuman primate species, rhesus monkeys (*Macaca mulatta*). Paper 1 provides evidence that monkeys can reproduce simple shapes from memory in a way that parallels the visual recall tests used with humans. Monkeys were more accurate at recognition than at recall, while remembering the same shapes under matched conditions, consistent with the theory that recall performance reflects recollection alone, whereas recognition performance reflects the combined effects of recollection and familiarity. Paper 2 provides evidence that recognition performance reflects two processes: quick familiarity and slow recollection. Recognition errors following quick responses were disproportionally false alarms to familiar but unstudied stimuli, and introducing a response deadline selectively increased false alarms. Paper 3 provides evidence that familiarity-based recognition is passive. A concurrent cognitive demand did not interfere with memory retention of items from a large image set, for which items can be identified as familiar or unfamiliar at test, but did impair retention of items from a small image set, for which familiarity at test was not useful and which likely required active working memory. Together, the findings from these studies represent a small step forward in our understanding of recollection and familiarity in monkeys.

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1. General introduction

> Given the traditional distinctions made between findings based on recall and recognition data, it is intriguing that the question is so inappropriate with animals... Animals, to my knowledge, have not yet been accorded the privilege of having an executive editor rummaging around in a mnemonic file cabinet. They are still denied the power of recollection (Winograd 1971).

When Eugene Winograd wrote these words, he was not denying that nonhuman animals might recollect information. Instead, he questioned whether existing methods could even allow us to ask the question. He concluded that the current situation represented an impasse.

In the subsequent decades, research on memory in nonhumans has flourished (Eichenbaum and Cohen 2001; Matsuzawa 2001; Shettleworth 2010). As a result of clever paradigms and methodological improvements, psychology and neuroscience are currently in the process of overcoming the impasse presented by previous methodological limitations (Fortin et al. 2004; Sauvage et al. 2010; Guderian et al. 2011). In this dissertation, I present a brief overview of recollection and familiarity in humans and nonhumans, followed by three papers describing investigations into recollection and familiarity in rhesus monkeys. It is my hope that these papers represent a small step forward in our understanding of a) what methods are available to test such a distinction, b) the degree to which recollection and familiarity are fundamental processes of memory shared by other species, and c) some of the functional characteristics of recollection and familiarity in monkeys.

1.1 Recollection and familiarity in humans

Recollection refers to the retrieval of detailed information from memory alone, such as when you search your memory for what happened at your last birthday party (Kelley and Jacoby 2000; Yonelinas 2002). It is often self-initiated and under cognitive control. Retrieving information via recollection also often results in the retrieval of associated information, such as when and where your last birthday party was held.

In contrast, familiarity refers to the judgment that something currently experienced has been experienced before, such as when you get the feeling that you have passed a particular landmark previously, or that you are certain that you know a particular party guest from somewhere (Kelley and Jacoby 2000; Yonelinas 2002). It is almost always initiated by the presence of an external stimulus, and it is an automatic response not under cognitive control. Information retrieved via familiarity is vague, in that it does not usually result in the retrieval of associated information. For example, you might find a landmark or party guest familiar without remembering exactly when you first passed that landmark or where you previously met the party guest.

In humans, the contributions of recollection and familiarity to memory retrieval can be assessed using several different behavioral methods. Each method has its own strengths and weaknesses (Yonelinas 2002). The use of multiple methods is necessary to achieve a valid understanding of recollection and familiarity because together they can provide converging evidence that overcomes the weaknesses present in any single methodology. Here, I briefly describe some of these common methods. This is not an exhaustive list, but is meant to illustrate the variety in methods available with humans.

One of the first methods to contrast recollection and familiarity was to compare memory performance on recall and recognition tests (Postman et al. 1948; Craik and Mcdowd 1987; Haist et al. 1992). In a recall test, subjects must reproduce a previously-studied stimulus from memory (Figure 1). For example, subjects respond by speaking the words from a previously-studied list or by drawing a previously-studied shape. Because the subject must reproduce the stimulus without it being re-presented, recall tests are thought to rely primarily on recollection. In a recognition test, subjects must indicate whether a present stimulus was studied earlier (Figure 1). For example, subjects might respond by circling the words on the page that were on the original study list or by pointing to which of four shapes had been previously studied. Recognition tests are thought to rely on both recollection and familiarity. For example, subjects might either recollect the studied item and then search for it among the test items, or search the test items and select ones that seem familiar. Factors that affect recall performance more than recognition performance are thus inferred to affect recollection more than familiarity, and vice versa.

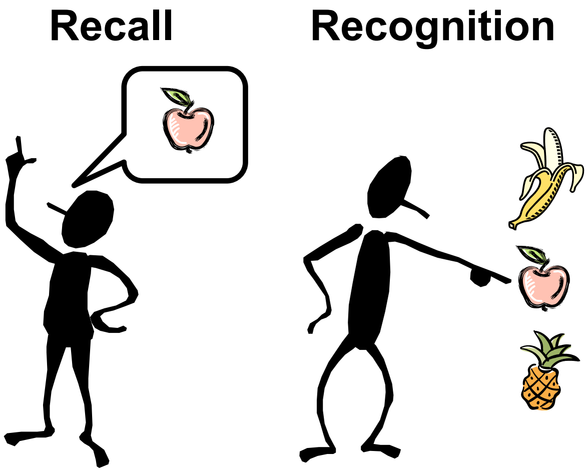

Figure 1. Schematic illustrating the distinction between recall and recognition tests of memory. In recall tests, the remembered stimulus is absent and the subject reproduces it, such as by saying or drawing what they remember. In recognition tests, the subject is presented with a stimulus and must indicate whether it was experienced previously.

Though recall and recognition tests are relatively easy to administer to human subjects, it is not always straightforward to compare the results. For example, data from recall and recognition tests are usually fundamentally un-matched because they have different chance levels, and this leads to the common finding that they produce different levels of performance (Postman et al. 1948; Tulving and Watkins 1973). This produces a scaling problem, in which any particular manipulation may affect the two tests differently simply because performance was not matched during baseline (Yonelinas 2002).

Another common method is to ask subjects whether they recognize a stimulus because they “remember” it or because they just “know” it (Java et al. 1997; Yonelinas et al. 1998; Gardiner et al. 2002). Subjects are instructed to report “remember” if they can retrieve associated details of studying it, such as what they were thinking at the time of study, and to report “know” if they cannot retrieve any associated details. Factors that affect “remember” judgments more than “know” judgments are thus inferred to affect recollection more than familiarity, and vice versa. Though this method provides a good way to distinguish between recollection and familiarity within the same test, it is dependent the how well the subjects understand the remember/know distinction. There is evidence that patients with presumed deficits in recollection due to brain damage may not fully understand what the experimenter means by “remember” (Baddeley et al. 2001), which would naturally interfere with obtaining a valid measure using this test.

A third method is to analyze receiver operating characteristic (ROC) curves. ROC curves plot performance on a yes/no recognition test as a function of different response criteria (i.e., experimenter-provided incentives to be more stringent or lenient with reporting a tested word as studied). Normal human subjects show a curvilinear and asymmetrical ROC curve during normal item recognition tests (Yonelinas et al. 1998) and a linear and asymmetrical pattern (Yonelinas 1997) during tests of paired-associate recognition, which are thought to rely more on recollection than familiarity. In addition, amnesic patients, who show primary deficits in recollecting information, show a curvilinear and

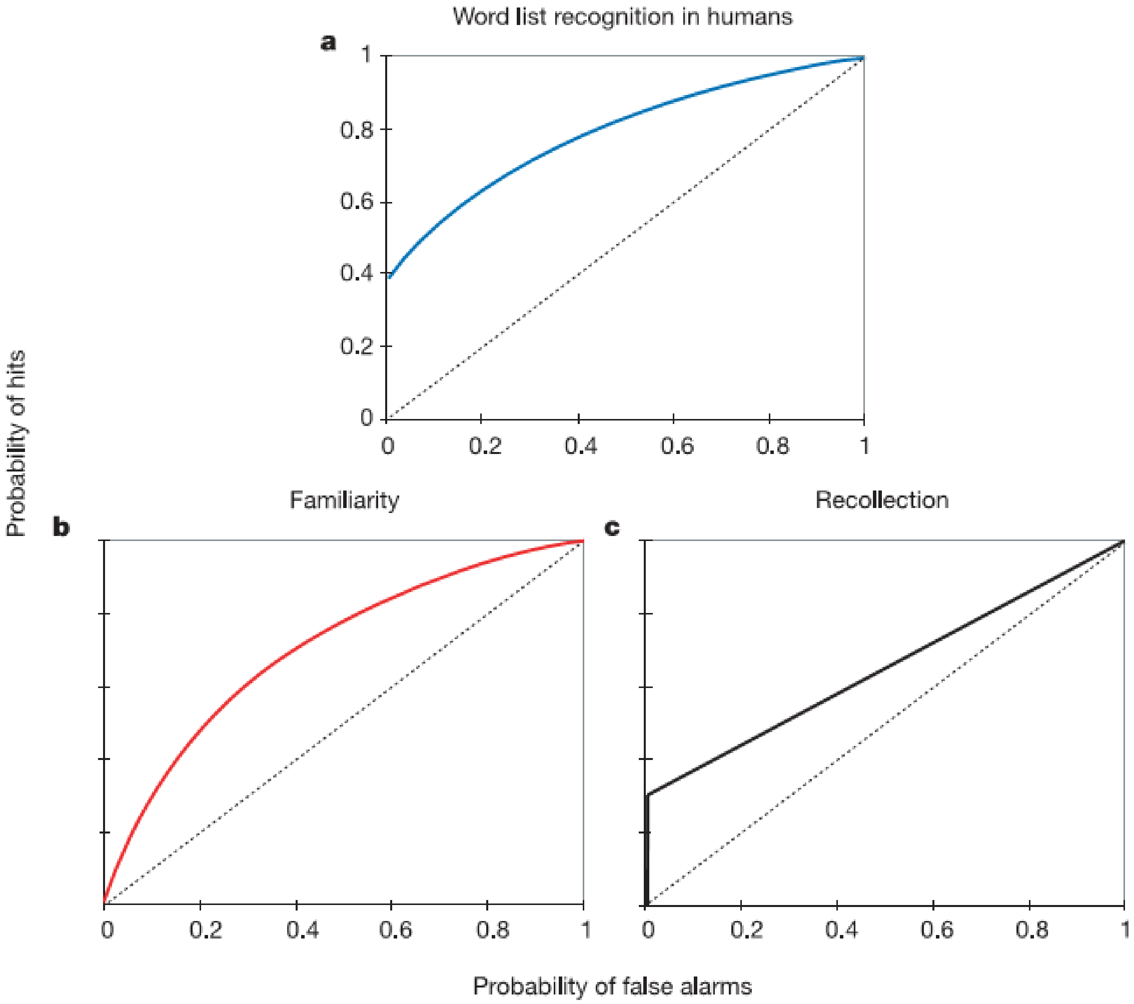

Figure 2. Theoretical ROC curves from human recognition tests. A) The curvilinear and asymmetrical line typical of recognition performance in humans. B) The curvilinear and symmetrical line that represents the proposed familiarity component. C) The straight and asymmetrical line that represents the proposed recollection component. Diagram from Fortin et al. (2004).

symmetrical curve. Thus, the curve of an ROC line is considered diagnostic of familiarity, and the asymmetry of the line is considered diagnostic of recollection (Figure 2). Factors that affect the curve's asymmetry more than its curve are thus inferred to affect recollection more than familiarity, and vice versa. Though ROC curves provide a mathematically nuanced method that does not rely on subjective reports or understanding of task instructions, it does rely on the assumptions that familiarity is a continuous signal, whereas recollection is a threshold signal (e.g., below a certain memory strength, information is no longer recollected). This threshold appears on ROC plots as the line intersecting the y-axis at a point above zero (Figure 2). This second assumption has been challenged by a model that describes both processes as fully continuous, and thus ROC curves can only provide a valid assessment of recollection and familiarity if the underlying assumptions turn out to be true (Wixted 2007; Wixted and Squire 2008; Ingram et al. 2012).

Use of these, and other, methods has yielded substantial informative data about the functional characteristics of recollection and familiarity in humans. Recollection is often under active cognitive control, whereas familiarity is automatic and passive (Jacoby 1991; Anderson et al. 1998). Recollection is relatively slow, whereas familiarity is relatively quick (Yonelinas and Jacoby 1994; Hintzman et al. 1998). Recollection strength declines more gradually over short retention intervals, whereas familiarity strength declines more quickly (Hockley 1992; Yonelinas and Levy 2002). Recollection benefits greatly from elaborative processing, whereas familiarity benefits less (Perfect et al. 1995;

Yonelinas 2001). These and other findings have led to a relatively nuanced understanding of how recollection and familiarity function in human memory, though there are still many questions to be answered.

1.2 Recollection and familiarity in nonhumans

Nonhuman animals do not talk. Thus, the methods used to test recollection and familiarity in humans that require verbal responses cannot be used to assess the same questions in nonhumans. Nonhumans cannot perform verbal recall tests or be given remember/know instructions. Consequently, relatively little progress has been made in our understanding of the extent to which recollection and familiarity are basic memory processes shared by other species, and, if so, whether they function similarly in all species (Shettleworth 2010). Nonetheless, the advancement of behavioral paradigms has given us some insight into the problem (Fortin et al. 2002; Sauvage et al. 2010; Guderian et al. 2011). Here, I discuss several paradigms that researches have used to assess recollection and familiarity in nonhumans. This list is not meant to be exhaustive, as many other methods used to test memory may speak to either recollection or familiarity or both, even if they were originally intended to investigate other memory phenomena.

One of the few methods that have been used in both humans and nonhumans is ROC curve analysis. Like humans, rats and rhesus monkeys show curvilinear and asymmetrical ROC curves during normal item recognition, suggesting the use of both recollection and familiarity (Fortin et al. 2004; Guderian et al. 2011). Further investigations of ROC curves in rats have shown that long retention intervals produced linear and asymmetrical curves, whereas adding a response deadline produced curvilinear and symmetrical curves (Fortin et al. 2004; Sauvage et al. 2010). This suggests that familiarity decays more quickly than recollection, and that familiarity is available sooner than recollection, both of which parallel patterns of data found in humans (Hockley 1992; Yonelinas and Jacoby 1994; Yonelinas and Levy 2002; Koen and Yonelinas 2011). However, if the assumption that recollection represents a threshold process is untrue, as some researchers believe (Wixted and Squire 2008; Ingram et al. 2012), than the results from ROC curves cannot be taken as evidence about the properties of recollection and familiarity.

A second method is to assess memory for the temporal order of stimuli. In these tests, an animal is presented with a series of stimuli at study, then two of those stimuli at test, and is rewarded for selecting the test item that appeared first during study. Because the test stimuli do not provide observable cues about their order during study, memory for the order at test may represent recollection. Rats and monkeys perform well on these order tests, suggesting that they may be recollecting the order of events (Fortin et al. 2002; Kesner et al. 2002; Templer and Hampton 2012). Currently, these order tasks have been used most extensively in rats to assess the brain areas underlying memory for the order of events, but they hold the promise of addressing future questions about the functional characteristics of recollection and familiarity.

Lastly, a series of clever paradigms aimed at testing episodic-like memory in nonhumans have provided good evidence for a recollection process. For example, the ability of scrub jays, a bird species that caches food, to remember how long ago, where, and what food they hid, suggests that they were recollecting that information (Clayton and Dickinson 1998). Similarly, Panzee, a lexigram-trained chimpanzee, will recruit the help of a caretaker in her indoor enclosure to find hidden food items in the outdoor woods, can use lexigrams to report the identity of the hidden food item, and when outdoors, can point to the location of the hidden item, suggesting that she is recollecting the location and identity of the hidden food (Menzel 1999; Menzel 2005) . Although such demonstrations are impressive, and likely do speak to the capacity of the species to recollect information, methods that rely on species-typical foraging behavior or lexigram training do not translate well to other species for comparative work, and it is not clear how one would use these demonstrations to contrast the properties of recollection and familiarity.

To fully characterize recollection and familiarity in nonhumans, we need a wide variety of tests that can provide converging evidence. For example, the conclusion that familiarity has a quicker onset than recollection is supported by several methodologies in humans, including analysis of ROC curves (Koen and Yonelinas 2011), process dissociation paradigms (Yonelinas and Jacoby 1994), analysis of recognition errors (Dosher 1984), and recall/recognition comparisons (Hintzman et al. 1998). In contrast, this same conclusion in nonhumans is supported only by analysis of ROC curves (Sauvage et al. 2010). Similarly, entire paradigms that are common with humans are unavailable with nonhumans, or have been until recently, such as remember/know or recall/recognition comparisons.

The following three papers report recent studies related to the distinction between recollection and familiarity in a nonhuman primate species, the rhesus monkey (*Macaca mulatta*). Paper 1 describes the results of an attempt to design a shape-reproduction test that might be similar to human recall tests, and the comparison of performance in that test with performance in a matched recognition test. Paper 2 describes an analysis of recognition errors, and whether monkeys produce the types of errors that would be predicted from a quick familiarity process and a slower recollective process. Paper 3 describes the effects of a concurrent cognitive demand on memory retention under conditions in which we expect familiarity-based responding, and contrasts it with a condition in which we do not expect familiarity-based responding.

2. Introduction to Paper 1

This paper arose from the question: Is it possible to design a recall test for nonhuman primates? We were unsure that monkeys could ever be trained to reproduce a stimulus from memory. Our approach was to mimic the shape reproduction tasks used with humans (Rey 1941; Vargha-Khadem et al. 1997). This was a difficult problem to tackle because there was little precedent for it in the literature, and future studies may yet discover better methods to achieve the same goal. Nevertheless, we believe it represents a good step towards providing a recall test in monkeys that parallels recall tests in humans.

In the time since this study was published, we have trained six additional monkeys on this task. Subsequent data have replicated the main effects that recognition accuracy is superior to recall accuracy under matched conditions, and that increasing memory delays impair accuracy on both types of tests. However, we no longer detect a statistically significant interaction between test type and delay length. This interaction had been used in the paper to infer different forgetting rates for recollection and familiarity, similar what is seen in humans (Hockley 1992; Yonelinas and Levy 2002). However, failure to see this interaction in subsequent tests means that this interpretation should be treated with caution pending further investigation.

A supplemental video of a monkey doing the shape reproduction task is available here: http://www.psychology.emory.edu/lcpc/BasileRecall.html

This study was published in Current Biology (Basile and Hampton 2011).

3. Paper 1

Monkeys recall and reproduce simple shapes from memory

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3.1 Summary

If you draw from memory a picture of the front of your childhood home, you will have demonstrated recall. You could also recognize this house upon seeing it. Unlike recognition, recall demonstrates memory for things that are not present. Recall is necessary for planning and imagining, and can increase the flexibility of navigation, social behavior, and other cognitive skills. Without recall, memory is more limited to recognition of the immediate environment. Amnesic patients are impaired on recall tests (Vargha-Khadem et al. 1997; Mayes et al. 2002), and recall performance often declines with aging (Craik and Mcdowd 1987). Despite its importance, we know relatively little about nonhuman animals' ability to recall information; we lack suitable recall tests for them and depend instead on recognition tests to measure nonhuman memory. Here, we report that rhesus monkeys can recall simple shapes from memory and reproduce them on a touchscreen. As in humans (Postman et al. 1948; Yonelinas and Levy 2002), monkeys remembered less in recall than recognition tests and recall performance deteriorated more slowly. Transfer tests showed that monkeys used a flexible memory mechanism rather than memorizing specific actions for each shape. Observation of recall in Old World monkeys suggests that it has been adaptive for over 30 million years (Steiper and Young 2006) and does not depend on language.

3.2 Results and Discussion

Humans can “freely recall” information from memory, as when describing a criminal suspect. We can also recognize whether something currently experienced was experienced before, as when choosing a suspect from a line up. *Recall* and *recognition* describe two types of tests or retrieval situations. The critical distinction is whether the material to be remembered is present when you try to remember it. In humans, accurate performance in recall and recognition situations differentially recruits two types of memory: recollection and familiarity (Kelley and Jacoby 2000; Yonelinas 2002). *Recollection* often involves a deliberate retrieval of information, sometimes accompanied by additional details, such as study context. In contrast, *familiarity* produces a relatively vague judgment of novelty or recency, as when you know that you have met someone before, but cannot remember their name or where you met.

Successful *recognition* of something can occur either by recollecting it or by detecting that it is familiar (Yonelinas 1997). In contrast, for successful *recall*, one *must* bring the memory to mind through recollection – the studied material is not present to re-experience as familiar. The ability to recall information is particularly important because it frees memory from exclusive control by immediate time and place. Recognition can only happen when we re-perceive something we have perceived before. Normal tasks, like planning a meeting or giving driving directions would be impossible if the things we needed to remember – meeting attendees or street names – had to be present for us to remember them. Accordingly, loss of recall ability drastically impairs quality of life; poor recall performance is a central deficit in amnesic patients following brain damage (but see Haist et al. 1992; Vargha-Khadem et al. 1997; Mayes et al. 2002) and recall performance often declines during aging (Craik and Mcdowd 1987; Prull et al. 2006). Recall tests are critical to our understanding of the evolution of memory and other cognitive abilities, and to our ability to diagnose and treat memory impairments.

Ask humans what they recall and they can tell you; give them a blank piece of paper and they can draw what they have seen. In contrast, nonhuman animals do not have language and do not naturally draw, making it difficult to create controlled conditions under which we can measure recall. Consequently, virtually all tests of memory used with nonhumans are recognition tests. Nonhumans can be trained to touch, peck, or look at a familiar image when it is re-presented after a delay, thereby reliably measuring memory in a recognition format (e.g., Murray and Mishkin 1998; Sutton and Shettleworth 2008). Some investigators have devised clever tests intended to measure the distinct contributions of recollection and familiarity to memory performance in nonhumans (e.g., Fortin et al. 2004; Sauvage et al. 2008). These tests have led to important insights; however, all of them use recognition paradigms that leave the conclusions controversial (Wixted and Squire 2008). Because the major barrier to testing recall in nonhumans is the lack of language as a “read out” of the contents of memory, it is perhaps not surprising that one of the most convincing demonstrations of recollection in a nonhuman comes from a lexigram-trained chimpanzee (Menzel 1999). After having seen food or a desired object hidden in the forest outside her enclosure, Panzee spontaneously recruited help from human caretakers, pointed outside toward the forest, and touched the lexigram that corresponded to the hidden item. This test situation parallels recall tests because she reported the location and identity of the hidden food while inside - both the forest and the food were out of sight. Panzee's use of lexigrams appears to give researchers a unique tool to access her memory. However, tests of memory using lexigrams can still be reasonably characterized as recognition tests, albeit ones with hundreds of possible choices. "Panzee did not literally draw a lexigram or a map of the forest" (Menzel 2005, p 214), but her performance suggests that she had the necessary information to do so if she could draw. If an animal could draw or reproduce a previously seen image, that would provide a powerful test of recall in nonhumans.

In the current study, we trained five rhesus monkeys on a novel recall test in which they had to reproduce a simple figure on a touchscreen from memory. Our test was modeled after the Rey-Osterrieth Complex Figure Test (Rey 1941), in which humans draw a complicated shape from memory. The Rey-Osterrieth Complex Figure Test is a well-established tool that has been used to diagnose recall impairments in amnesic humans (Vargha-Khadem et al. 1997). At study, monkeys saw a simple shape composed of two or three colored boxes located on a 5x5 grid on a computer touchscreen. At test, one of the boxes appeared in a new location on the grid. Monkeys could reproduce the absent box(es) by touching the appropriate grid locations (Figure 1, top panel; see Supplemental Video 1). When successful, they earned food; errors were followed by a time out and no food.

Critically, monkeys could not solve this memory test using familiarity, because the image to be remembered was not present at test to experience as familiar. We hypothesized that if monkeys have recollection, they would be able to reproduce these simple shapes in this recall format.

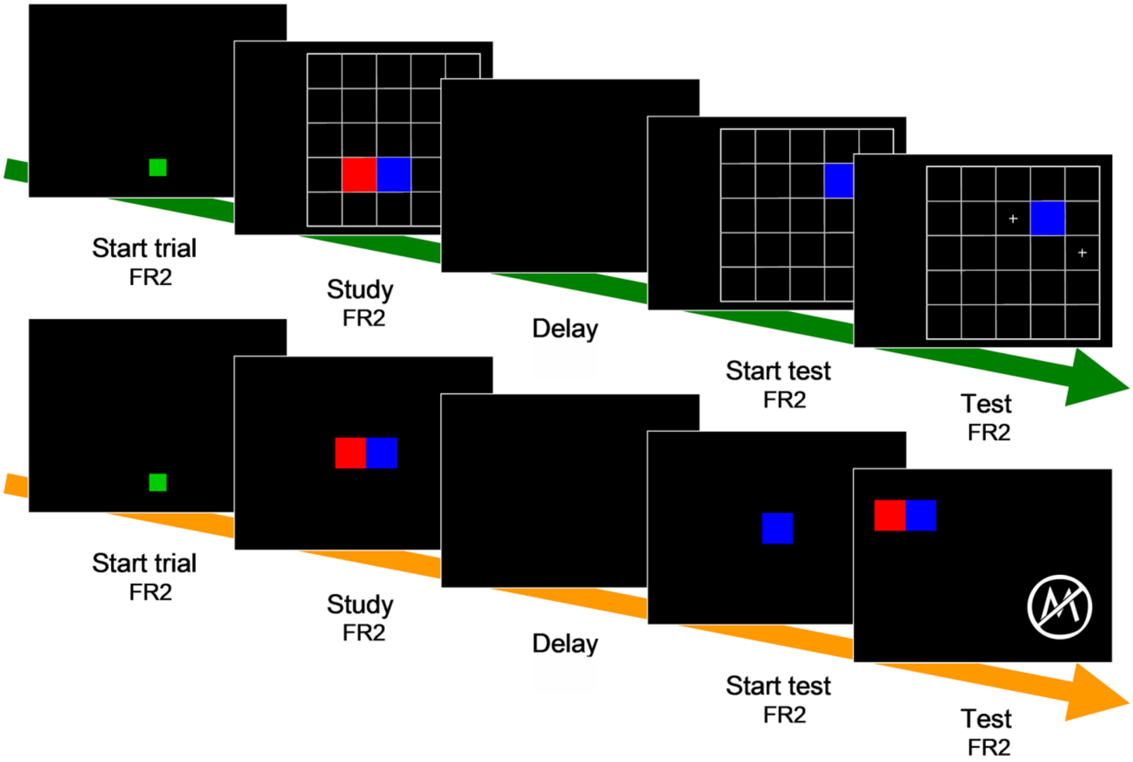

Figure 1. Time course of a recall and recognition trial during comparison. Schematic of the progression of a recall test (top) and matched recognition test (bottom). Monkeys started both tests by touching the green “start box” (FR=2 for all responses). An image then appeared and they had to touch the blue box, ensuring that they had seen the sample image. After a delay, the blue box appeared in a new location and the monkeys touched it to initiate the test phase. *For the recall tests*, monkeys earned food if they

reproduced the studied shape by touching the appropriate grid location for the red box. *For the recognition tests*, monkeys earned food for touching the test stimulus if it was the same as that presented at study (depicted) or the non-match symbol if it was not. The small white crosses shown in the last panel of the recall test indicated to the monkeys which response locations were available. In the first phase of training, the white crosses were present in all the locations abutting the blue box. For the comparison with recognition, we reduced the response locations to two, which allowed us to equate the chance rate in the recall and recognition tests at 50%, permitting us to directly compare performance in the two types of test.

All monkeys learned to reproduce two-box shapes after a brief delay more accurately than expected by chance (chance = 12.5%; mean accuracy = 27.6%; binomial tests; all $p < .002$). This performance parallels the way humans reproduce the Rey-Osterrieth Complex Figure. Unlike recognition tests, in which the target shape would have been present at test, the monkeys had to reproduce the target from memory, making this the first pure recall test for monkeys.

Having established that monkeys can perform in a test methodologically similar to human recall tests, we further assessed the validity of our new paradigm by comparing it to a precisely matched recognition test. We tested for two performance differences diagnostic of recollection and familiarity. First, humans usually recall less information than they recognize (Postman et al. 1948). This is because recall performance is based solely on successful recollection, whereas recognition performance is a combination of both recollection *and* correct familiarity judgments. Second, familiarity makes proportionally more contribution to human recognition performance at short memory delays (Hockley 1992; Yonelinas and Levy 2002). Consequently, higher accuracy on recognition tests should be most evident at short delays. To test for these patterns in our monkeys, we compared performance on our recall test to that on a precisely matched recognition test that had the same chance rate, used the same stimuli, required the same responses, and used the same study-test intervals (Figure 1, bottom panel).

Consistent with the hypothesis that the recall and recognition tests measure different kinds of memory, we found that recognition accuracy was higher than recall accuracy at short delays, but declined more rapidly (Figure 2). The striking similarity of these patterns in monkey recall and recognition performance to performance from comparable human tests (Hockley 1992; Yonelinas and Levy 2002) suggests two things. First, our shape reproduction test measures recollection, similar to human drawing tests. Second, monkey memory is similar to human memory; it likely includes two processes, recollection and familiarity, that contribute differentially to recall and recognition performance.

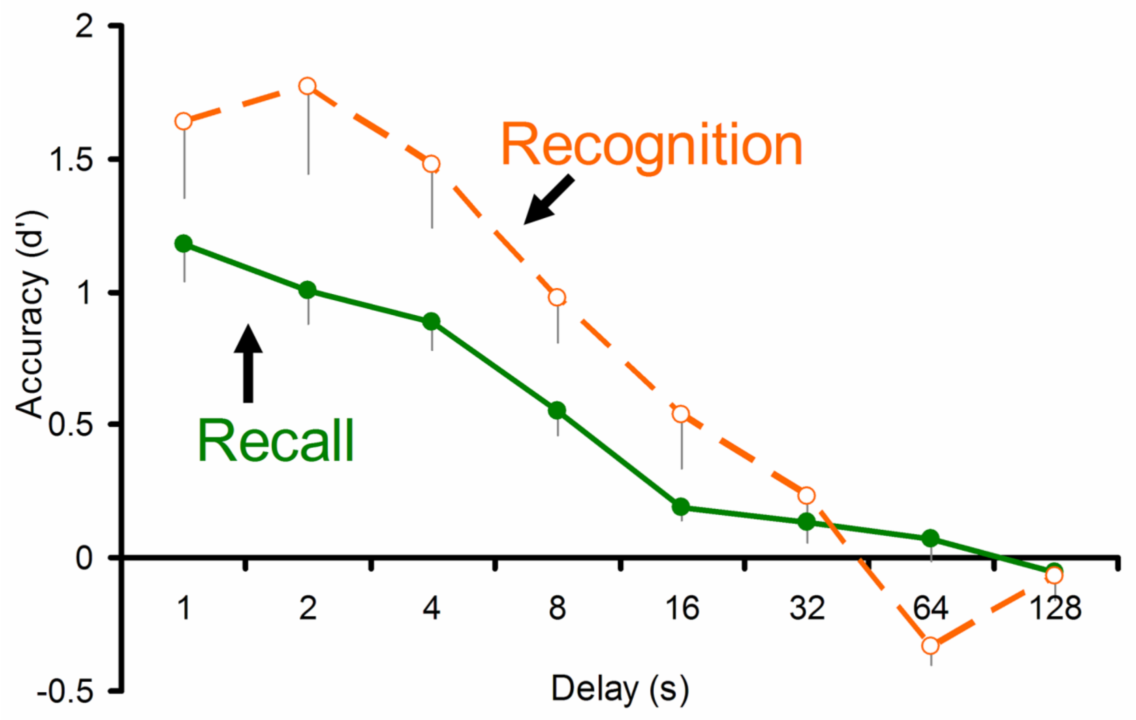

Figure 2. Comparison of recall and recognition accuracy as a function of delay. Under precisely matched testing conditions, monkeys showed greater accuracy and faster forgetting in the recognition test than in the recall test (two-factor within-subject ANOVA (test type X delay): main effect of test type ($F_{(1,4)}$ = 6.66, *p* = .061), main effect of delay ($F_{(7,28)}$ = 38.54, *p* < .001), and interaction ($F_{(7,28)}$ = 3.96, *p* = .004)). Accuracy in both recall and recognition is reported as d' (Macmillan and Creelman 2005), as a function of the delay in seconds between study and test. Error bars represent one standard error of the mean.

One common criticism of studies of nonhumans is that subjects may solve even complex tasks using relatively simple, inflexible stimulus-response rules acquired through extensive training. Monkeys might have learned a fixed response appropriate for each sample image. Such inflexible stimulus-response rules could result in performance that superficially resembled recall, but would not generalize to novel images. To evaluate whether monkeys used flexible recollective memory or rigid response rules, we tested whether performance generalized to novel three-box shapes. We did this both under conditions in which the chance rate remained the same as in earlier tests (reproduce one box of a novel three-box shape), and in which the difficulty was increased (reproduce two boxes of a novel three-box shape). We hypothesized that if monkeys had learned a general reproduction rule rather than inflexible stimulus-response rules, accuracy would be significantly above chance in the first session with each of these novel test conditions.

Monkeys immediately transferred recall performance to novel 3-box shapes (Figure 3). Accuracy was significantly above chance both when monkeys had to produce one box of a novel three-box shape and when they had to reproduce two boxes to complete a three-box shape. Generalization to novel shapes shows that monkeys remembered the images in a flexible way that parallels human recall. The small number of trials received during the generalization tests (144 trials), and the large number of novel shapes (28 three-box shapes), make it unlikely that the monkeys learned a new set of response rules for each new shape.

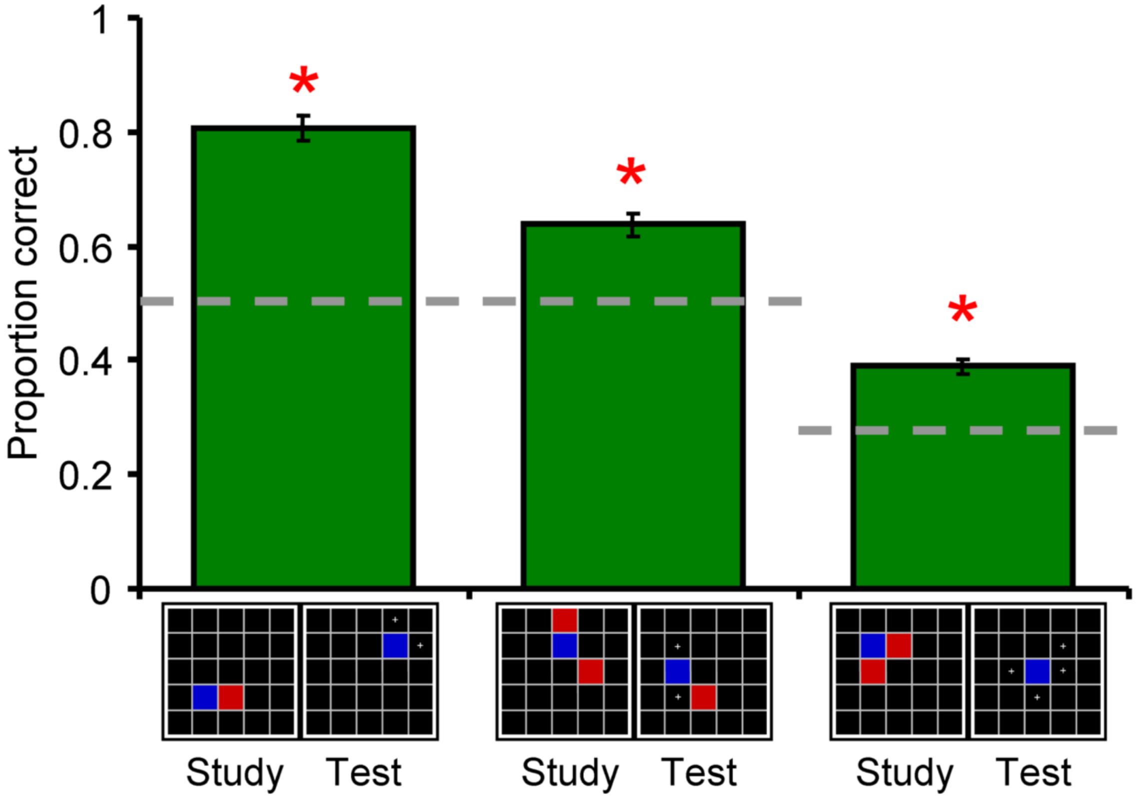

Figure 3. Recall performance on trained shapes and novel shapes during transfer tests. Monkeys successfully generalized to novel shapes. Accuracy was above chance on the first session both when monkeys had to reproduce one box of a three-box shape (middle bar; chance = .5; one-sample t-test: $t_{(4)} = 7.03$, $p = .002$) and when they had to reproduce two boxes of a three-box shape (right bar; chance = .25; one-sample t-test: $t_{(4)} = 10.75$, $p < .001$). Dashed lines represent accuracy expected by chance. Asterisks mark performance that is significantly above chance. Error bars are ± one standard error of the mean.

Comparing recall and recognition is complicated. The two tasks usually require different types of responses and have drastically different chance rates. In the current experiment, we matched the recall and recognition tests on all critical procedural details, allowing us to attribute the observed differences in accuracy and forgetting to the types of memory used in the two tests. The design of our tests also rules out several alternative strategies. Monkeys could not have solved the recall test by constantly touching the location of the studied shape during the delay, because the shape moved between study and test. They could not have solved the task by repeating a motor response made at study, because they were not required to touch all boxes during study. Finally, they could not have solved the task using a set of inflexible stimulus-response rules, because they immediately transferred performance to novel shapes. Monkeys appear to have solved the recall task by recollecting the studied shape when they could not see it.

This new recall test for nonhuman primates advances our understanding of the range of memory types present in monkeys and available for neurobiological study. Comparisons of recall and recognition performance in amnesic patients have stimulated considerable excitement and controversy about the neural substrates of memory (Eichenbaum et al. 2007; Squire et al. 2007). These controversies are difficult to address conclusively in humans because accidental brain damage is rarely selective or complete for a given structure. Studies of nonhumans allow for tighter experimental control over variables of interest, such as prior stimulus exposure and training, and permit methodologies that are difficult or impossible to use in humans. Use of these techniques with this new recall test promises new insights into the organization of human and nonhuman memory.

The presence of recollection in rhesus monkeys suggests that ancestors common to humans and Old World Monkeys evolved under selection pressures favoring the ability to recall as well as recognize. Recollection and familiarity likely evolved because they solved functionally incompatible problems (Sherry and Schacter 1987). For example, familiarity does not support detailed memory for context, but it is quick (Yonelinas and Jacoby 1994) and resistant to distraction (Anderson et al. 1998). Recollection is slower and more vulnerable to distraction, but supports a more detailed and flexible use of memory. Familiarity might better allow rapid responses to foods and predators under distracting conditions, whereas recollection might be necessary to access knowledge of distant food locations or past social interactions for planning future behavior. In this study, we have demonstrated recall performance in monkeys under limited laboratory conditions. Further work will be required to understand how this performance relates to natural behavior.

3.3 Experimental Procedures

3.3.1 Subjects and Apparatus

Five adult male rhesus macaque monkeys (*Macaca mulatta*) were tested six days a week in their home cages, using portable touchscreen computer rigs (see Supplementary Materials). All procedures were approved by the Emory

University Institutional Animal Care and Use Committee and complied with United States law.

3.3.2 Initial Training

Monkeys first learned to touch accurately within the small boxes of the response grid to turn boxes red. Next, they learned to reproduce one box of a stationary two-box shape after a 0-second delay. Finally, they learned to reproduce the box after a 1-second delay when it appeared in different locations in test and in study. The final phase was identical to that in Figure 1 (top) with the exception that white crosses appeared in all eight adjacent grid locations and therefore did not limit the available response locations. See Supplementary Materials for additional training details.

3.3.3 Comparison with Recognition

Monkeys learned a match/non-match recognition test (Figure 1 lower panel) and this new test and the recall test were trained to stability (six sessions with no significant change in accuracy, see Supplementary Materials). Identical shapes were used in the recognition and recall tests. Chance rates in the two tests were equated at 50%, by providing one correct and one incorrect choice at test in both tasks. For the recall test, the blue anchor box was presented with only two possible adjacent choices, indicated by white crosshairs, rather than the eight choices used in initial training. For the recognition test, one shape was presented with a non-match symbol (Figure 1).

One session of each type was given per day with testing order alternated between days, for 11 days. The delay was 1 second on slightly less than half the trials (due to constraints of counterbalancing trial types) and delays of 2, 4, 8, 16, 32, 64, and 128 seconds were mixed pseudorandomly among the other half of the trials. Because the addition of varied delays was novel, we excluded the first session of each test type, leaving 600 trials at the trained delay and 120 trials at each of the other delays from each monkey for analysis.

Because our recognition test was a match/non-match test, we used d' values, which provide a measure of accuracy that is unbiased by any overall tendency to choose match or non-match (Macmillan and Creelman 2005). Using d' scores also allowed us to directly compare accuracy on the match/non-match recognition test with accuracy on the two-choice recall test by transforming the proportion correct scores on the recall test into d' scores (Macmillan and Creelman 2005, Table A5.7).

3.3.4 Transfer of Recall Performance to Novel Shapes

In the first recall transfer test, we assessed whether monkeys would generalize performance to novel three-box shapes under conditions in which they had to reproduce one box at test. At study, monkeys saw a shape composed of one blue box and two red boxes. At test, the blue box appeared in a new location along with one of the red boxes (chosen at random) and two possible response locations indicated by white crosses. Monkeys received a single session consisting of all 504 possible shape/location configurations in a random order. Only the first 144 trials were used to assess transfer, to equate this test with those used in the previous experiments and to limit the opportunity for the monkeys to learn responses specific to each new stimulus.

In the second transfer test, monkeys again saw three-box shapes at study, but only the blue anchor box appeared at test, along with four possible response locations indicated by white crosses (see Supplementary Video). Monkeys had to reproduce both red boxes correctly by touching the two correct grid locations. After one red box was added correctly, one of the two remaining incorrect response locations became unresponsive and the corresponding white cross disappeared. Chance was 50% for each box and 25% for reproducing both boxes correctly. Again, the first 144 trials served as the critical transfer data. Proportions were arcsine transformed prior to analysis to better approximate normality (Aron and Aron 1999).

3.4 Acknowledgments

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4. Introduction to paper 2

This paper began as a post-hoc analysis of the errors monkeys made in the recognition test reported in Paper 1. We reasoned that we might better understand how the monkeys were recognizing the stimuli by looking for patterns in the types of errors they made. Based on studies of processing speed in humans that suggest that familiarity is quicker than recollection (Yonelinas and Jacoby 1994; Hintzman et al. 1998), we analyzed error type as a function of the monkeys' natural response speed.

The results of this paper inform the findings of Paper 1. In Paper 1, monkeys were more accurate at recognizing stimuli than at reproducing them under matched conditions. One interpretation of this accuracy difference is that recognition performance represents the combined contributions of both recollection and familiarity, whereas recall performance represents only the contribution of recollection. In Paper 2, we find a pattern of recognition errors consistent with the presence of two memory processes, suggesting that this is a reasonable interpretation of the accuracy difference from Paper 1.

This paper is currently under re-review at Learning & Memory.

5. Paper 2

Recognition errors suggest fast familiarity and slow recollection in rhesus monkeys

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5.1 Abstract

One influential model of recognition posits two underlying memory processes: recollection, which is detailed but relatively slow, and familiarity, which is quick but lacks detail. Most of the evidence supporting this dual-process model in nonhumans has come from analyses of receiver operating characteristic (ROC) curves in rats, but whether ROC analyses can demonstrate dual processes has been repeatedly challenged. Here, we present independent converging evidence for the dual-process model from analyses of recognition errors made by rhesus monkeys. Recognition choices were made in three different ways depending on processing duration. Short-latency errors were disproportionately false alarms to familiar lures, suggesting control by familiarity. Medium-latency responses were less likely to be false alarms and were more accurate, suggesting onset of a recollective process that could correctly reject familiar lures. Long-latency responses were guesses. A response deadline increased false alarms, suggesting that limiting processing time weakened the contribution of recollection and strengthened the contribution of familiarity. Together, these findings suggest fast familiarity and slow recollection in monkeys, that monkeys use a "recollect to reject" strategy to countermand false familiarity, and that primate recognition performance is well-characterized by a dual-process model consisting of recollection and familiarity.

Keywords: dual-process, recall, false alarms, recall to reject, pattern separation

5.2 Introduction

In 2011, Jeopardy! champion Ken Jennings played an exhibition match against Watson, the artificial intelligence computer program. When asked about his strategy, he said:

> You buzz when you see something that trips some “This looks familiar!” switch in your brain and count on dredging it out in the five seconds after Alex calls on you. Watson can't do this: it only buzzes once it has an answer in mind and a sufficiently high confidence interval. As weird as it sounds, yes, the human brain still has a speed advantage over a 2,880-processor-core computer. (Jennings 2011)

Though he may not have known it, Ken Jennings was describing how human recognition performance is likely supported by at least two major memory processes: a quick familiarity process and slower recollection process (Yonelinas 2002). Familiarity is triggered by current experience of an item and refers to the sense that it has been experienced previously, without memory of the time, place, or context of the initial experience. In contrast, recollection refers to the ability to recall target information from memory, often accompanied by related information such as the time, place, or context of a prior experience. For example, you have probably experienced the phenomenon of seeing an actor and finding them strongly familiar, while being unable to recollect their name or any examples of their work (also see the "butcher on the bus" example in Mandler 1980).

In humans, both familiarity and recollection contribute to normal recognition performance, but the contribution of familiarity occurs more quickly than the contribution of recollection. In one study, subjects were asked to recognize word pairs from a previously-studied list. At test, word pairs were either familiar from the test (e.g., subjects studied OPEN-VEGETABLE), familiar pairs from daily life (e.g., EVIL-SIN should already be a familiar pair), familiar from both experimental study and daily life, or completely unfamiliar. Quick responses were associated with elevated levels of false alarms to familiar word pair lures, but not to unfamiliar word pair lures (Dosher 1984). Similarly, false alarms to lures that are familiar to the target (e.g., if the target were *tree*, the lure might be *trees*) showed a biphasic time course, with an initial rise during quick responses followed by a decrease during slower responses (Hintzman and Curran 1994). This initial difficulty in distinguishing between the familiarity of studied words or word pairs and unstudied but familiar words or word pairs suggests that quick responses were determined by a sense of familiarity that lacked associated detail. The decrease in false alarms at longer response latencies implies the gradually increasing contribution of a recollective process that could distinguish between the familiar targets and familiar lures.

Other studies in humans of memory for items and item source have also concluded that familiarity is quicker than recollection. Subjects were quicker at reporting whether a word had been seen recently, a task that can rely on pure familiarity, than at reporting which of two lists the word had appeared in, a task that may require recollection (Hintzman et al. 1998). Other researchers have used memory for item and item source to calculate numerical estimates of familiarity and recollection (Yonelinas and Jacoby 1994). When those estimates were plotted as a function of response speed, familiarity estimates were highest when responses took between 600 and 800 msec, whereas recollection estimates were highest when responses took between 800 and 1100 msec. Requiring subjects to respond more quickly decreased estimates of recollection, but not estimates of familiarity. Together, these studies provide a compelling case for a quick familiarity process and a slow recollection process in human recognition performance, even though there is still disagreement about other characteristics of recollection and familiarity (Yonelinas 1994; Ingram et al. 2012).

Limited evidence from monkeys suggests that this dual-process model of recognition may characterize not only human memory, but primate memory in general. Most memory tests used with monkeys are recognition tests, in which the studied item is re-presented at test (Mishkin and Delacour 1975; Presty et al. 1987). Because recognition tests can usually be solved on the basis of familiarity, and because familiarity is usually considered an automatic and effortless process (Jacoby 1991), it is often assumed that monkeys use familiarity in recognition tests. It has been more difficult to determine whether recollection also contributes to monkey recognition, but two recent studies suggest that it does. First, monkeys can recall simple shapes from memory and reproduce them on a touchscreen (Basile and Hampton 2011). Unlike standard recognition tests, in which the target stimulus is re-presented at test and can produce familiarity, the recall test required monkeys to reproduce a remembered stimulus from memory, suggesting recollection. Second, receiver operating characteristic (ROC) curves for monkeys performing a recognition test are similar to those seen with humans when familiarity and recollection both contribute to performance (Guderian et al. 2011). ROC curves plot correct recognition of targets and incorrect recognition of lures as a function of the subject's bias to report any stimulus as having been seen before (Yonelinas 1994). ROC curves derived from tests of human recognition are curvilinear, which is diagnostic of familiarity, and asymmetrical, which is diagnostic of recollection (Yonelinas and Parks 2007). ROC curves derived from tests of monkey recognition are also curvilinear and asymmetrical (Guderian et al. 2011), suggesting that both familiarity and recollection contribute to recognition in monkeys. Similar results have also been found for rats (Fortin et al. 2004). However, the proper interpretation of ROC curves has been questioned. Although, there is general consensus that recognition involves the dual processes of recollection and familiarity, there is substantial disagreement about the functional properties of these processes and about whether conclusions based on ROC analyses are valid (Wixted 2007; Wixted and Squire 2008; Ingram et al. 2012). Converging evidence from other methods of analysis are needed to provide strong conclusions about the functional properties of recollection and familiarity in nonhumans.

If this dual-process model of recognition does characterize primate memory, it should also be the case that familiarity and recollection function similarly in humans and monkeys. We tested this proposition by evaluating whether the patterns of errors monkeys made during a standard recognition test were consistent with a quick familiarity process and a slower recollection process, similar to what is seen in human recognition (Dosher 1984; Yonelinas and Jacoby 1994). In Experiments 1a and 1b, we looked for a correlation between response latency and familiarity-based or recollection-based responding in two existing data sets from recognition tests in which rhesus monkeys were required to discriminate previously-studied targets from unstudied lures (Basile and Hampton 2010; Basile and Hampton 2011). In Experiment 2, we evaluated whether this correlation held in a more standard recognition test with an a priori prediction. In Experiment 3, we experimentally tested whether quick responses were disproportionately determined by familiarity by requiring the monkeys to respond more rapidly. Recognition based primarily on familiarity should result in a comparatively high probability of accepting familiar lures in addition to familiar targets, which would be evident in a high level of false alarms and a moderate level of accuracy. Recognition based on a combination of familiarity and recollection should result in a higher probability of rejecting the familiar lures, evident in lower levels of false alarms and the highest level of accuracy. Failure to recognize the image either by familiarity or recollection should result in guessing, evident in chance levels of false alarms and low accuracy. If the contribution of familiarity occurs earlier than the contribution of recollection, then the quickest responses should be characterized by high levels of false alarms and moderate accuracy, and moderately-paced responses should be characterized by a reduction in false alarms and the highest levels of accuracy.

5.3 Experiments 1a & 1b – Post-hoc analysis of recognition errors

Experiments 1a and 1b are post-hoc analyses of recognition errors from two unrelated studies (Basile and Hampton 2010; Basile and Hampton 2011). The methodologies of the two studies differed in many aspects, but both used a computerized match/non-match recognition test presented on touchscreen computers (see Basile and Hampton 2010, Figure 1 ; and Basile and Hampton 2011, Figure 1 bottom panel). On each trial, the monkeys saw a familiar image to remember, experienced a memory delay, and then were tested with either the studied image or an unstudied but familiar image, along with a non-match symbol. If the test image matched the studied image, touching it resulted in a food reward. If the test image did not match the studied image, touching the non-match symbol resulted in a food reward. In either case, touching the other response resulted in a negative audio stimulus and ended the trial. This methodology allowed us to differentiate two types of errors: false alarms, in which unstudied test images were reported as having been studied, and misses, in which studied test images were reported as having not been studied.

5.3.1 Results and Discussion

Initial visual inspection of the error rates revealed two distinct patterns. False alarms plotted as a function of response latency formed a U shape, with relatively high levels occurring at the shortest and longest response latencies (Figure 1, left two panels). In contrast, miss rates were low at the shortest response latencies and higher at the longer latencies (Figure 1, middle two panels). Overall, response times were longer in the data set from Experiment 1b than from Experiment 1a, but the patterns error rates were similar.

For statistical analysis, we grouped trials from each monkey individually into 10 latency bins, each bin containing an equal number of trials. At the quickest response bin, monkeys made significantly more false alarms than misses (Figure 1, right two panels; paired t-test; Experiment 1a: t(4) = 4.10, *p* = .015, *d* = 1.84; Experiment 1b: t(5) = 3.05, *p* = .028, *d* = 1.25), whereas the false alarm and miss rates did not differ for the slowest responses (Figure 1, right two panels; paired t-test; Experiment 1a: t(4) = -0.46, *p* = .672; Experiment 1b: t(5) = -0.63, *p* = .558). This suggests that the quickest responses were governed primarily by judgments of familiarity; the monkeys were highly likely to accept either a familiar target or a familiar lure. In contrast, the slowest responses were not determined by familiarity or any other systematic factor; slow errors were random guesses, equally distributed between false alarms and misses. Equality of false alarms and misses is expected when monkeys are guessing because these experiments contained an equal proportion of match and non-match trials to reduce response bias.

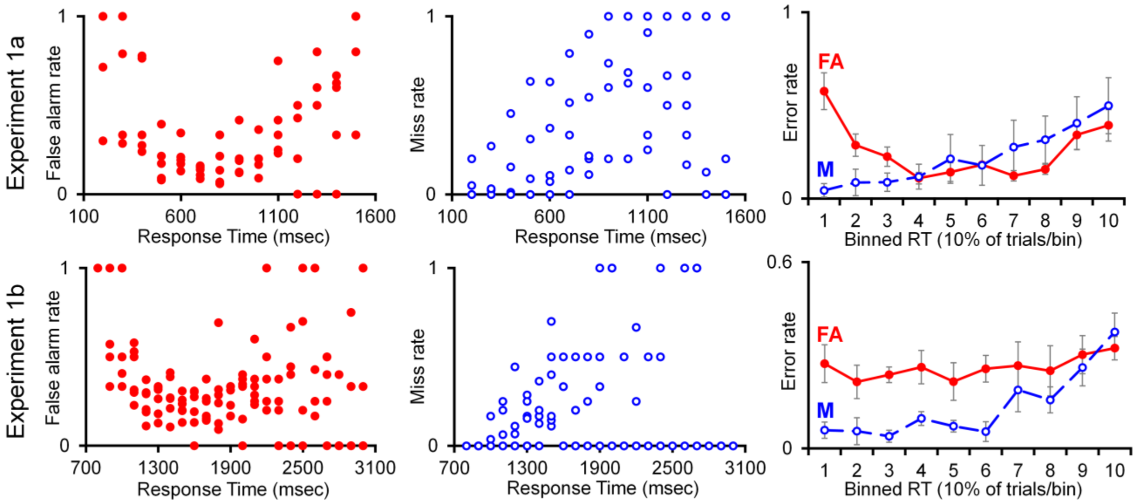


Figure 1. False alarms and misses plotted as a function of response latency. Quick errors were disproportionately false alarms, whereas slow errors were more likely to be guesses. Errors are depicted for Experiment 1a (top row) and Experiment 1b (bottom row). The left two panels depict absolute false alarm rates (# false alarms / # non-match trials) as a function of response time in 100msec bins. The middle two panels depict miss rates (# misses / # match trials) in the same way. Each dot represents all trials that fell into that bin from a single monkey; however, because not all monkeys made responses at all times, not all bins contain the same number of subjects. The right two panels depict the error rates (±SEM) as a function of response time binned such that each bin contains 10% of each monkey's trials.

Plots of accuracy as a function of response latency for each experiment produced an inverted U-shape, skewed towards the quicker response times. Again, we grouped performance into 10 bins based on latency with an equal number of trials. The average bins with the highest accuracies were bins four and three (Experiment 1a: mean = 4.00; Experiment 1b: mean = 3.20). Accuracies of the quickest responses, and the slowest responses, were significantly lower than the peak accuracies for each experiment (two-tailed paired t-tests; Experiment 1a: first vs. peak, t(4) = 5.36, *p* = .006, *d* = 2.40, last vs. peak, t(4) = 22.65, *p* < .001, *d* = 10.13; Experiment 1b: first vs. peak, t(5) = 2.64, *p* = .046, *d* = 1.08, last vs. peak, t(5) = 6.89, *p* < .001, *d* = 2.81). This peak in accuracy for the medium-latency responses was associated with superior rejection of familiar lures, suggesting the onset of a recollective process that could countermand responses based on the familiarity of the lures.

5.4 Experiment 2 – Targeted analysis of recognition errors

The results of the analyses described in Experiments 1a and 1b suggested that monkey recognition is composed of a quick familiarity process and a slower recollection process; however, these findings came from post-hoc analyses. The two paradigms that contributed data to Experiments 1a and 1b were designed to investigate unrelated questions, and consequently had features that were irrelevant to the current question, such as different types of stimuli, different memory delays, different numbers of studied targets, and different stimulus set sizes. The results of these analyses should therefore be considered tentative. In

Experiment 2, we evaluated the a priori hypothesis that this pattern of results would occur in a standard match/non-match recognition test designed to facilitate measurement of false alarms due to familiarity.

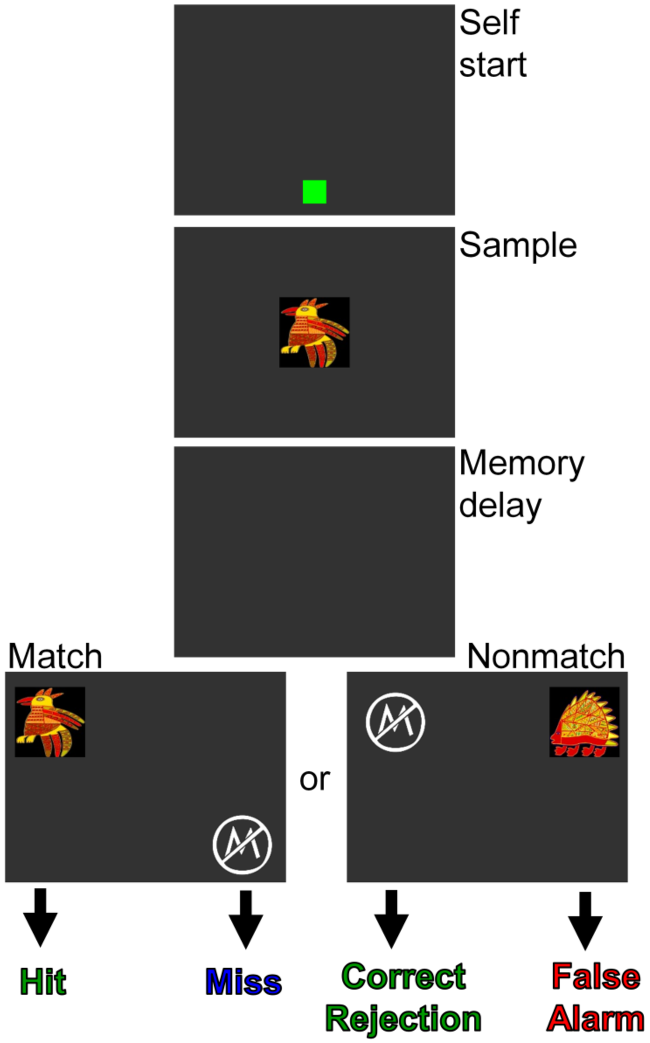


Figure 2. Diagram of a match/non-match recognition test used in Experiment 2. Monkeys initiated trials by touching the green square in the bottom center of the screen, saw and touched a

sample image presented in the center of the screen, waited during a memory delay, and then received either a match or a non-match test. Monkeys earned food by touching the test image if it matched the sample or by touching the non-match symbol if the test image did not match the sample. The test image and the non-match symbol appeared equally often in all four screen corners. Trials were separated by a 10-second interval during which the screen was black.

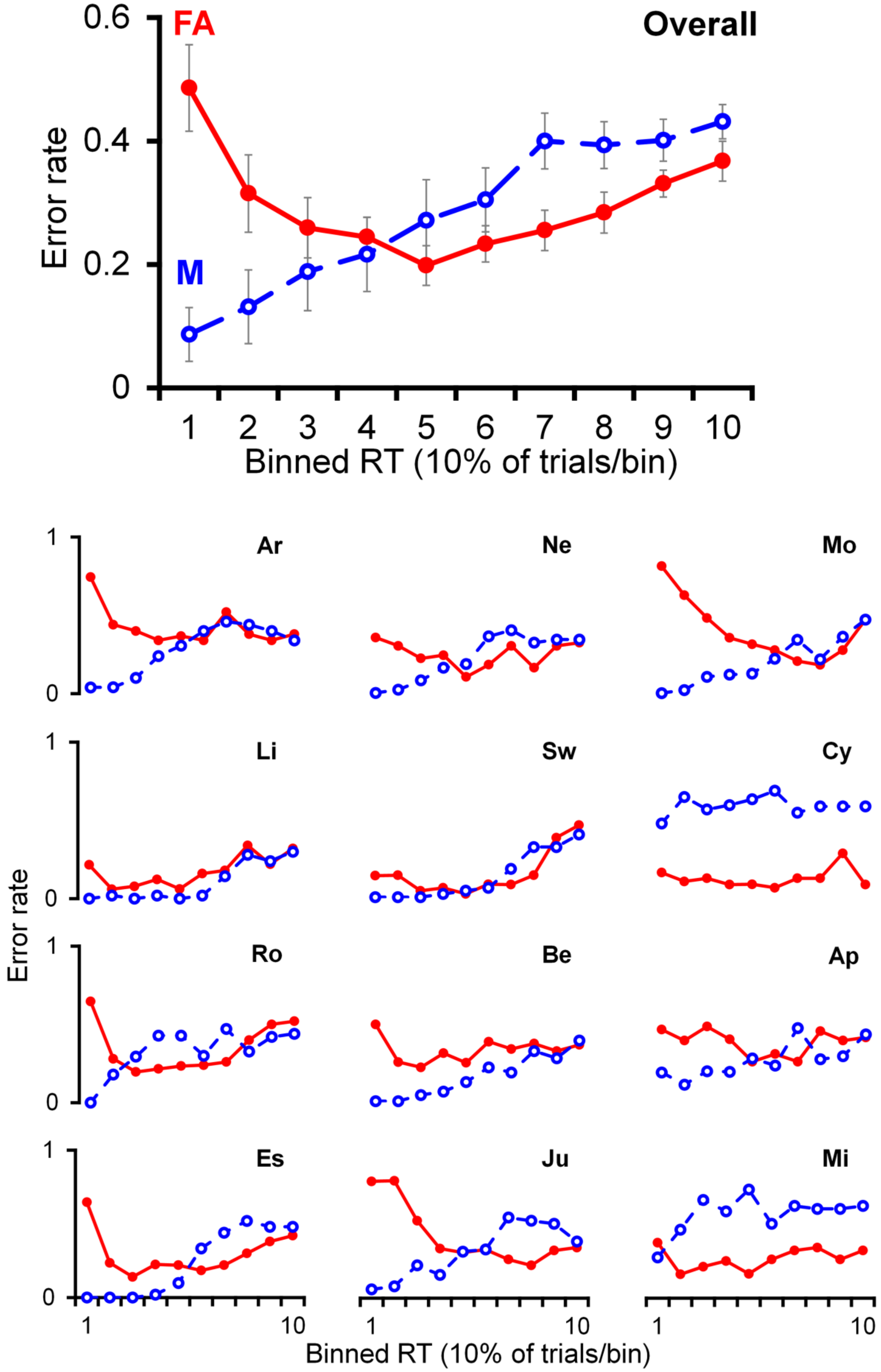
5.4.1 Results and Discussion

Performance for one monkey (Ju) fell to chance at the trained delay of four seconds and he was re-tested at a shorter memory delay of one second. Performance recovered and his data with the shorter memory delay were used in the group analysis.

Initial visual inspection of the error rates when plotted as a function of absolute reaction time again revealed two distinct patterns. False alarms showed a U-shape, with high rates in the quickest and slowest responses, whereas misses were most common with slow responses. For statistical analysis, we grouped trials from each monkey individually into 10 latency bins, each bin containing an equal number of trials. At the quickest response bin, monkeys made significantly more false alarms than misses (Figure 3; paired t-test; $t(11) = 4.15$, $p = .002$, $d =$

1.20), whereas the false alarm and miss rates did not differ for the slowest responses (Figure 3; paired t-test; t(11) = -1.32, *p* = .213).

Plotting accuracy as a function of response latency produced an inverted U-shape, skewed towards the quicker response times. Again, we grouped performance into 10 bins based on latency with an equal number of trials. The majority of monkeys showed the highest accuracy in bin 2 (mode = 2), and the average peak bin was bin 3 (mean = 3.08). Accuracy of the quickest responses, and the slowest responses, were significantly lower than the peak accuracy (two-tailed paired t-tests; first vs. peak: t(11) = 4.20, *p* = .001, *d* = 1.21; last vs. peak: t(11) = 5.64, *p* < .001, *d* = 1.63).


0.6
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Be
Ap
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0
Error rate
1
10
Binned RT (10% of trials/bin)

Figure 3. False alarms and misses as a function of response time. Quick errors were disproportionately false alarms, whereas slow errors were guesses. Each panel depicts the proportion (±SEM) of trials that were false alarms or misses (red solid dots with solid lines and blue open dots with dashed lines, respectively) as a function of response time binned such that each bin contains 10% of each monkey's trials. Data are shown averaged across all twelve monkeys (top panel) and for each individual monkey (bottom panels).

These results confirmed the post-hoc analyses from Experiments 1a and 1b under conditions designed for collection of these data. Quick errors were disproportionately false alarms, suggesting that responses were driven primarily by familiarity. At moderate response latencies, the absolute rate of false alarms was lower, the proportion of errors that were false alarms was lower, and accuracy was higher. This is consistent with the onset of a recollective process that could countermand the false familiarity of the familiar lures. At the longest response latencies, false alarms and misses occurred in equal proportion and accuracy was lowest, suggesting that monkeys had forgotten the target on those trials and were guessing.

5.5 Experiment 3 – Experimental manipulation of response speed

Experiments 1 and 2 provide compelling evidence that monkey recognition performance results from the combination of a quick familiarity process and a slower recollection process. However, the data presented so far are correlational. To provide a strong experimental test of this hypothesis, we directly manipulated processing time by training the monkeys to speed their responding on certain trials. If familiarity is available immediately upon re-presentation of the stimulus but recollection requires a longer interval to develop, then requiring monkeys to respond within a brief time window immediately after test onset should render recollection less-available and thus increase the proportion of responses controlled by familiarity. Greater dependence on familiarity should result in higher false alarm rates.

5.5.1 Results and Discussion

Performance of one monkey (Mi) fell to chance at the trained delay of four seconds and he was re-tested at a shorter memory delay of one second. Performance recovered and his data with the shorter memory delay were used in the group analysis.

Monkeys sped their responding in the initial 1000-trial block of training with the 1000-msec response deadline. The proportion of trials aborted due to slow responding decreased significantly within the initial 1000-trial sped session (first 100 trials: mean = .572, last 100 trials: mean = .334; two-tailed paired t-tests; $t(11) = 4.94$, $p < .001$, $d = 1.46$). In the critical test sessions, half of which had a response deadline of 800msec, monkeys responded more quickly in deadline trials than in normal trials (average median response latencies: sped =

700.7msec, normal = 824.6 msec; two-tailed paired t-tests; t(11) = 5.73, *p* < .001, *d* = 1.65). Together, these results indicate that our response deadline manipulation had the intended effect of speeding monkeys' responses.

Requiring monkeys to speed their responding caused a significant increase in the false alarm rate, but did not change the miss rate (Figure 4; two-tailed paired t-tests; false alarms: t(11) = 3.00, *p* = .012, *d* = 1.95; misses: t(11) = 1.71, *p* = .115). This indicates that speeding responses hindered recruitment of the slower recollection process and forced monkeys to respond primarily on the basis of familiarity.

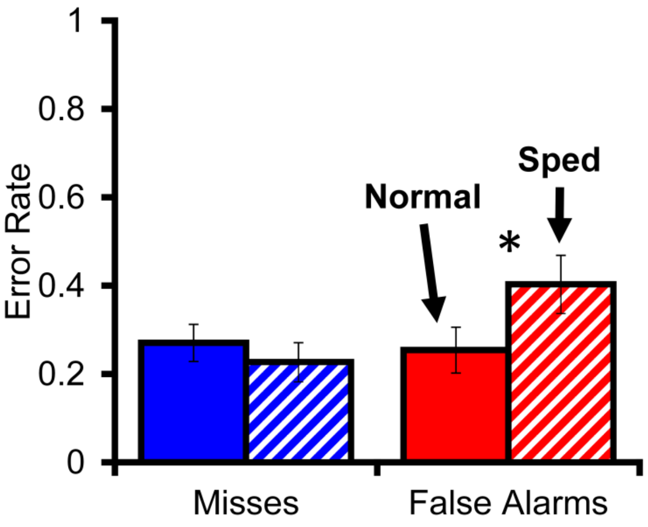

Figure 4. Error rates under normal and speeded responding. Speeding responding selectively increased false alarms. Mean miss and false alarm rates (±SEM) are depicted for both normal sessions and sessions in which responses were sped

using a response deadline. Asterisks denote statistically significant differences.

5.6 General discussion

The results of this study suggest that the time course of visual recognition in monkeys can be divided into three epochs with different characteristics. Very quick responses are controlled largely by familiarity, and are characterized by moderate accuracy and high levels of false alarms. Moderately-paced responses are controlled by both familiarity and recollection, resulting in a decrease in false alarms and the highest accuracy. Responding in this time window allows evaluation of the initial familiarity response and also the potential to countermand responses based on false familiarity if additional relevant information is recollected. Finally, the slowest responses occur when monkeys eventually guess. Because subjects are guessing on these trials, accuracy is lowest and errors are equally distributed between false alarms and misses.

This pattern of results suggests a “recollect to reject” strategy (often called “recall to reject” in humans), whereby recollection-based responses sometimes override familiarity-based responses. Evidence from humans suggests that subjects sometimes use a slower recollective process to countermand the familiarity produced by related, but unstudied, lures (Rotello and Heit 2000; Rotello et al. 2000). According to this account, when monkeys perceive either a recently-seen lure or a recently-seen target, a familiarity response results.

Responses controlled by familiarity will be to both targets and lures, resulting in high rates of false alarms. However, after a short interval, the slower-onset recollective process develops. The monkey can then correctly reject the familiar lure as unstudied if he recollects the studied target, fails to recollect the visible lure, or recollects that the lure was the target on a previous trial.

The performance of our twelve monkeys was strikingly similar to that of humans in similar tests. For both monkeys and humans, quick responses were disproportionately false alarms to familiar lures (Dosher 1984). In humans, a response deadline decreased estimates of recollection but not familiarity (Yonelinas and Jacoby 1994), and for monkeys, the response deadline increased the proportion of choices based on familiarity, suggesting a decrease in recollection but not familiarity. For humans, estimates of familiarity peaked around 700msec and estimates of recollection peaked around 1000msec (Yonelinas and Jacoby 1994), and in monkeys, a response deadline of 800msec was effective in increasing reliance on familiarity and increasing false alarms. These values suggest a broadly similar time course for recognition in both monkeys and humans, with most processing happening within the first second after stimulus onset.

The pattern of responses seen in these recognition tests is unlikely to be the result of a single memory process, impulsivity, or a response bias. If we assume a single memory process that is subject to forgetting, we would predict that monkeys would respond quickest when their memory is strongest and slowest when their memory is weakest. This would produce the highest accuracy at the shortest response-latencies, which was not observed. Alternatively, we might assume a single memory process, but assert that the monkeys sometimes impulsively choose a response, which they did. This would predict the inverted U-shape observed with accuracy because quick impulsive choices would be more likely to be errors. However, because the monkey could not predict the screen location of the test image and non-match symbol at test, impulsive choice of the first perceived stimulus at test would result in an equal number of false alarms and misses, which was not observed. Finally, we might assume that choice is guided by a single memory process in combination with impulsivity and a pre-existing response bias to choose the test image regardless of content. Behavior would then be controlled by the response bias when it was not being controlled by memory, such as when the monkey guessed or chose impulsively. This predicts that errors as a result of guessing would also be subject to the response bias and thus disproportionately false alarms, which was not observed. In the slowest response bins, when accuracy was near chance levels and monkeys were likely to be guessing, monkeys did not show a bias towards either type of error, suggesting that an overall response bias did not exist. In contrast to these single-process accounts, a dual-process account that posits quick familiarity and slow recollection readily explains our results.

These results are consistent with those of a recent study of ROC curves derived from speeded recognition tests in rats (Sauvage et al. 2010). Rats' normal ROC curves were curvilinear and asymmetrical, patterns that are often diagnostic of familiarity and recollection, respectively, in human recognition (Yonelinas and

Parks 2007). When a response deadline was added, by preventing access to the test options after a set time, rats' ROC curves became only curvilinear, suggesting control by familiarity only. Unlike the present study, no data from rats was reported to indicate whether the response deadline procedure actually succeeded in speeding the rats' responding, or whether rats responded at the same pace and the deadline effectively "threw out" all trials that would have taken longer. Similar results have also been found in humans using speeded recognition procedures and the same ROC estimates of recollection and familiarity (Koen and Yonelinas 2011). Finally, a recent study in monkeys has also found ROC curves that are curvilinear and asymmetrical under normal recognition conditions, suggesting that visual recognition in monkeys is also supported by recollection and familiarity (Guderian et al. 2011). However, because the interpretation of ROC curves is controversial, strong conclusions about the functional properties of recollection and familiarity should ideally include convergent findings from other methodologies (Wixted 2007; Wixted and Squire 2008). Therefore, the current results help inform our understanding of the dual-process model by contributing to the converging evidence, using multiple measures and species, that quick familiarity and slower recollection may be basic processes that underlie recognition in a wide variety of animals.

The growing literature on recollection and familiarity in nonhuman animals has broad practical and theoretical implications. Practically, it provides researchers with more valid animal models for the study of selective memory dysfunction. From these findings, which show that recognition in monkeys can be supported by familiarity or recollection or both, it is clear that reliance on simple recognition accuracy as a measure of memory will not meaningfully inform research into disorders that differentially affect recollection and familiarity. Theoretically, it indicates that recollection and familiarity are fundamental memory systems that have been conserved throughout much of vertebrate evolution. Based on the theory that different memory systems arise to meet functionally incompatible memory needs (Sherry and Schacter 1987), it may be that recollection and familiarity have been selected for because together they allow for recognition that is either quick but prone to false alarm, or slower but more detailed and accurate. Quick recognition may be called for when detecting predators or other threats, whereas slow accurate responses may be more appropriate in other situations, such as navigation or food choice.

5.7 Methods

5.7.1 Experiments 1a and 1b

Data from Experiments 1a and 1b came from Basile and Hampton (2011) and Basile and Hampton (2010), respectively. Detailed descriptions of the subjects, apparatus, stimuli, and procedures can be found in those articles, and are summarized below in an abbreviated form.

5.7.1.1 Subjects and apparatus

Data for Experiment 1a (n-=5) and 1b (n=6) came from adult male rhesus macaques (*Macaca mulatta*). All eleven monkeys had experience with various cognitive tests using a touchscreen computer. Subjects were tested six days per week, seven hours per day, in their home cages, using portable touchscreen testing rigs. One testing rig was attached to the front of each monkey’s cage allowing the monkeys to participate at their own pace in two or three different studies per day.

5.7.1.2 Stimuli

For Experiment 1a, stimuli were composed of two adjacent squares, one red and one blue, arranged in eight possible configurations (see Basile and Hampton 2011, Figure 1 bottom panel). For Experiment 1b, stimuli were six color photographs (see Basile and Hampton 2010, Figure 1).

5.7.1.3 Procedure

Data for both experiments come from match/non-match recognition tests (see Basile and Hampton 2010, Figure 1 ; and Basile and Hampton 2011, Figure 1 bottom panel). Monkeys initiated trials by touching a green box square at the bottom center of the screen, either a single target image was presented, or five target images were presented sequentially, in the center of the screen (in Experiments 1a and 1b, respectively) and monkeys touched them to progress the trial, an unfilled memory delay followed, and then monkeys were presented with one stimulus and a “non-match” symbol. If the test image was the same as the studied target image, monkeys could earn food by touching it. If the test image was an unstudied lure, monkeys could earn food by touching the non-match symbol. An unfilled ten-second intertrial-interval separated trials. Data from

Experiment 1a used a single studied target and a memory delay of 1second. Data from Experiment 1b used five studied targets, presented sequentially, and memory delays of 0.5 or 2 seconds. Only trials on which the fifth target was tested are included in the present analyses.

5.7.1.4 Data Analysis

For statistical analysis, each monkey's trials were split into trials on which the target was presented at test (match trials) and trials on which a lure was presented at test (non-match trials). Trials of each type were then ranked by response time and grouped into ten even bins. This ensured that each monkey contributed equally to each bin, which was not the case when data were binned by absolute response speed. Thus normalized, the data were suitable for repeated-measures statistical tests. False alarms and misses were then calculated using trials in each bin. Because only the last list item was used for Experiment 1b, there were five times more non-match trials than match trials, which resulted in five times more opportunities to make a false alarm than to make a miss. To provide an even number of match and non-match trials for analysis, one-fifth of non-match trials were selected by random number generator for inclusion in analysis. However, during testing, trials were evenly split between match and non-match trials to prevent monkeys from developing a bias.

5.7.2 Experiment 2

5.7.2.1 Subjects and apparatus

Subjects were twelve adult male rhesus macaques, eleven of which contributed the data for Experiments 1a and 1b. All housing conditions and testing equipment was the same.

5.7.2.2 Stimuli

Stimuli were two color clipart images, a hedgehog and a bird, measuring 300 pixels × 300 pixels. We used a small set of stimuli because Experiments 1a & 1b also used a small set of stimuli, because large sets of stimuli are easier to remember and do not produce enough errors for an error analysis (Mishkin and Delacour 1975; Basile and Hampton 2010), and because large sets of stimuli are more easily discriminable on the basis of relative familiarity which might encourage monkeys to always make familiarity-based choices.

5.7.2.3 Procedure

Monkeys were given one 1000-trial session of a standard match/non-match recognition test on a touchscreen computer (Figure 2). Monkeys initiated trials by touching a green “start box” on the bottom center of the screen, saw one of the two images as the target and touched it to progress the trial, received a four-second unfilled memory delay, and then were presented with one stimulus and a “non-match” symbol. If the test image was the same as the studied target image, monkeys could earn food by touching it. If the test image was the lure that had not appeared as the sample on that trial, monkeys could earn food by touching the non-match symbol. Correct trials always produced a positive secondary audio reinforcer (“woo-hoo!” or “excellent!”) and were accompanied by food reinforcement on 75% of correct trials. Incorrect trials produced a negative audio stimulus (“d’oh!”) and an unfilled 2-second time out. An unfilled ten-second interval separated trials. At test, the image and non-match symbol appeared pseudorandomly in two of the four screen locations, which prevented monkeys from being able to predict the location of either stimulus. To prevent registering of spurious choices, all responses required two consecutive touches to the same location.

5.7.2.4 Data Analysis

Data were binned and analyzed as described in Experiments 1a and 1b.

5.7.3 Experiment 3

5.7.3.1 Subjects and apparatus

All subjects and testing equipment remained the same as in Experiment 2.

5.7.3.2 Stimuli

All stimuli remained the same as in Experiment 2.

5.7.3.3 Procedure

The basic memory procedure remained the same as described for Experiment 2, with the exception that half of sessions were run with a deadline that required monkeys to respond at test within a set time window. A colored border (40 pixels wide) appeared 500msec prior to the test phase of each trial and remained on through completion of the trial. Borders were either blue or green with the color signaling normal or sped responding, counterbalanced across monkeys. Sped trials that were not completed within the deadline were aborted and repeated following the intertrial-interval.

To train monkeys to follow the cues, we first presented them with one 1000-trial session with a response deadline of 1000msec, followed by one 1000-trial session without a response deadline. This was followed by ten 200-trial sessions, alternating between sped and normal sessions. Because pre-testing suggested that a 1000msec deadline was not sufficient to increase the overall error rate, we used a response deadline of 800msec in the critical sessions.

5.8 Acknowledgements

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6. Introduction to paper 3

This paper originated as an investigation into the conditions under which short-term retention reflected active working memory. Active working memory is inferred when a concurrent cognitive demand interferes with memory retention (Phillips and Christie 1977; Logie 1986; Nimh 2010). In the paper, we contrasted active working memory with passive recognition that we thought might be based primarily on familiarity.

This paper is included in this dissertation, because it represents data on the characteristics of familiarity-based item recognition. Familiarity is usually assumed to represent a passive process that requires little or no cognitive control at encoding, retention, or retrieval (Jacoby 1991; Yonelinas 2002). If familiarity is passive in monkeys, then we expect that conditions that promote familiarity-based recognition should be largely unaffected by a concurrent cognitive demand.

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7. Paper 3

Dissociation of active working memory and passive recognition in rhesus monkeys

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7.1 Abstract

Active cognitive control of working memory is central in most human memory models, but behavioral evidence for such control in nonhuman primates is absent and neurophysiological evidence, while suggestive, is indirect. We present behavioral evidence that monkey memory for familiar images is under active cognitive control. Concurrent cognitive demands during the memory delay impaired matching-to-sample performance for familiar images in a demand-dependent manner, indicating that maintaining these images in memory taxed limited cognitive resources. Performance with unfamiliar images was unaffected, dissociating active from passive memory processes. Active cognitive control of memory in monkeys demonstrates that language is unnecessary for active memory maintenance.

Keywords: primate cognition, rehearsal, cognitive control, short-term memory, familiarity

7.2. Introduction

Human working memory can be compared to the display on an airport x-ray machine. Only a few bags can be viewed simultaneously and images of new baggage displace older images unless an operator exerts active control to freeze or manipulate the current view. Current models of human working memory differ in many aspects, but agree that the defining characteristic of working memory is active cognitive control (e.g., Baddeley 2003; Cowan 2008). Information is rapidly lost unless actively maintained, such as by verbal rehearsal in a "phonological loop" (Baddeley 2003). Because maintenance by top-down cognitive control consumes limited resources, cognitive operations that compete for these resources cause forgetting in a demand-dependent manner. For example, the comparatively difficult task of deciding whether two abstract shapes are identical impairs memory performance more than does passively viewing the same shapes (Logie 1986). Adding numbers impairs memory performance more than passively viewing numbers (Phillips and Christie 1977). Cognitive control over working memory is likely a major factor in general intelligence (Unsworth and Engle 2007), and may account for many cognitive differences between humans and nonhumans (Wynn and Coolidge 2004). Thus, cognitive control is a critical and defining feature of human working memory.

Researchers have made substantial progress characterizing the capacity (Elmore et al. 2011; Heyselaar et al. 2011) and neural substrates (Fuster and Alexander 1971; Miller et al. 1996; Constantinidis et al. 2001; Heuer and Bachevalier 2011b) of short-term memory in nonhuman primates. But it is unclear whether these studies characterize a cognitively-controlled system similar to human working memory (Washburn and Astur 1998). The definitions of working memory in humans and nonhumans often differ. In the human literature, definitions of working memory focus on cognitive control (Baddeley 2003; Cowan 2008). In the nonhuman literature, working memory is often operationalized as memory relevant only to the current trial, as opposed to reference memory for the rules of the task (Shettleworth 1998, chapter 6). Other criteria for identifying working memory can also lead to confusion. For example, working memory is not equivalent to short-term memory (Jeneson and Squire 2012). Humans can use working memory over relatively long delays if rehearsal is not interrupted (Milner 1970), and short-delay memory tasks can require long-term memory if the amount of to-be-remembered information exceeds working memory capacity (Hannula et al. 2006; Jeneson et al. 2011). Additionally, localized brain activity should not be uncritically equated with specific cognitive processes (Uttal 2001). Cells in the prefrontal cortex of monkeys fire when monkeys view to-be-remembered images and continue to fire during the memory interval (Fuster and Alexander 1971; Miller et al. 1996; Constantinidis et al. 2001). It is tempting to equate this monkey neural activity with human working memory based on fMRI studies that find activation of prefrontal cortex associated with active working memory in humans (D'esposito et al. 1999; Stern et al. 2001). But this equation ignores the potential for cognitive differences between species. It is possible that monkeys and humans remember information differently even when performance or neural activity is superficially similar. For example, the inference of active working memory based on prefrontal activity is empirically contradicted by the fact that prefrontal activity is also found in experimentally naïve monkeys during passive viewing of images (Meyer et al. 2007). Resolving these ambiguities will require more definitive behavioral methods for assessing cognitive control in monkey working memory.

Surprisingly, there is no strong behavioral evidence for cognitively-demanding memory maintenance in monkeys. In humans, memory performance is impaired by performing a distractor task and more cognitively-demanding distractor tasks produce more impairment (Phillips and Christie 1977; Logie 1986), demonstrating that working memory requires limited cognitive resources. In monkeys, distractors presented during the memory interval, such as flashing lights (Prendergast et al. 1998), irrelevant images (Miller and Desimone 1993; Miller et al. 1996), or a motor task (Washburn and Astur 1998), can impair memory performance. However, unlike the case in humans, distractor tasks that required sustained activity and attention produced no more impairment than ones that only required passive viewing (Washburn and Astur 1998). This indicates that the performance impairment in monkeys caused by these distractors was due to passive displacement of information rather than by competition for limited cognitive resources used to maintain information in working memory. Related investigations have tested for active control of memory in monkeys using directed forgetting paradigms or by providing opportunities for "rehearsal" of studied images. In humans, these approaches demonstrate cognitive control (Wright et al. 1990; Hourihan et al. 2009), but in monkeys they have not (Cook et al. 1991; Washburn and Astur 1998).

Previous tests may not have found evidence for active memory maintenance in monkeys because of the limited range of conditions under which these tests were conducted. Not all types of memory require active maintenance. For example, familiarity alone can support accurate recognition performance in many memory tests. Familiarity codes only whether stimuli have been seen previously (Yonelinas 2002), and is an automatic, effortless process (Jacoby 1991). In humans, the ability to distinguish items based on familiarity is unaffected by reduction in cognitive control by secondary tasks (Yonelinas and Jacoby 1994) or intoxication (Bisby et al. 2010). By contrast, when familiarity alone cannot support accurate performance, these manipulations do impair memory (Yonelinas and Jacoby 1994; Bisby et al. 2010). Accordingly, we gave monkeys two memory tests that differed in the extent to which they could be solved by familiarity alone. In tests using a small set of familiar, frequently-repeating images (hereafter, familiar images), target images from previous trials were reused as distractors in later trials. This made all images highly familiar and created a high level of interference among test images, presumably making it almost impossible to distinguish target images from distractors based on relative familiarity. We hypothesized that active maintenance of memory for the target image would be required in these tests. We also administered control tests using a large set of unfamiliar, infrequently-repeating images (hereafter, unfamiliar images) from which recently studied targets could easily be discriminated from distractors at test based on relative familiarity. Thus, the critical difference between the familiar and unfamiliar image sets was whether monkeys could discriminate studied images from unstudied images based on familiarity.

7.3. Experiment 1: Primary findings

We presented monkeys with visual matching-to-sample recognition tests on touchscreen computers and required them to complete one of three distractor tasks during the memory interval (Fig. 1). The three tasks required the same motor response but varied in cognitive demand: 1) touch a blue square that appeared in a randomly-selected corner of the screen (motor only), 2) touch a photograph that appeared in a randomly-selected corner of the screen (motor + image perception), or 3) classify a photograph as depicting a bird, fish, flower, or person by touching the appropriate symbol in one of the four corners of the screen (motor + image perception + classification). Touching a uniform blue square should require the least cognitive processing. Viewing unfamiliar photographs may elicit more cognitive processing than viewing a blue square because the photograph is more visually complex and presumably more interesting. Finally, classifying photographs should require the most cognitive processing because the monkeys had to accurately assign the images to one of four categories to proceed to the memory test. If remembering required active maintenance of the studied image during the memory interval, accuracy should be impaired least by the motor task and most by the classification task. Passive retention should be unaffected by these manipulations of concurrent cognitive demand.

7.3.1 Methods

7.3.1.1 Subjects and apparatus

Six adult, male rhesus monkeys (*Macaca mulatta*; mean age = 8.2 years) experienced in matching-to-sample and classification tasks (Basile and Hampton 2013b) were pair-housed except during testing, fed full food rations, and given ad libitum water access. Monkeys were tested in their home cages on portable touchscreen computers (Basile and Hampton 2010). Procedures were approved by the Emory Institutional Animal Care and Use Committee and complied with US law.

7.3.1.2 Stimuli

Stimuli were color photographs of exemplars from categories the monkeys had previously learned to classify as birds, fish, flowers, or people. The to-be-remembered stimuli consisted of two sets: a small set of four images, highly-familiar from previous testing, and a large set of 1400 relatively-unfamiliar images. Each category was equally represented within each set. For the concurrent task, images for the *classify* condition were drawn from the large set of 1400 images, and non-classifiable images for the *image* condition consisted of a set of 400 relatively-novel images.

7.3.1.3 Procedure

Monkeys completed four 300-trial sessions, two with the small set of familiar images and two with the large set of unfamiliar images, alternating and counterbalanced for testing order across monkeys. Half the trials in each session contained no secondary task; the other half were equally divided among motor, image, and classification tasks. The four levels of cognitive demand, the four categories, and the four possible response locations were intermixed pseudorandomly within each session. To-be-classified images were never from the same category as the sample and were not presented as distractors for that trial. Trials proceeded as in Fig. 1, separated by a 10-sec ITI. Because matching-to-sample accuracy in monkeys is typically higher with large sets of unfamiliar images than with small sets of familiar images (Mishkin and Delacour 1975; Basile and Hampton 2010), we matched baseline performance by testing the large set of unfamiliar images at a 30-sec delay and the small set of familiar images at a 1-sec delay (values determined during pre-testing). At test, selection of the sample produced a positive audio stimulus and a 75% chance of food, whereas selection of a distractor produced a negative audio stimulus and a 2-sec timeout. To ensure that monkeys were attending to, and processing, the concurrent task, incorrect responses in the concurrent tasks aborted the trial. Proportions were arcsine transformed prior to statistical analysis (Aron and Aron 1999).

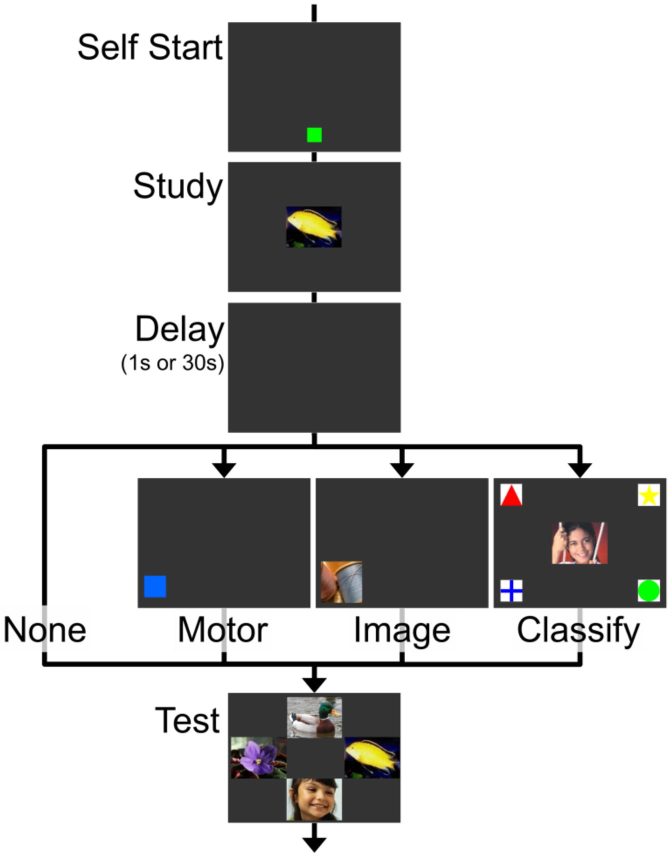

Figure 1. Memory tests with four levels of concurrent cognitive demand. Monkeys were required to remember an image over a memory interval that was either empty, or filled by one of three tasks: 1) *motor*: touch a blue square, 2) *image*: touch a non-classifiable image, or 3) *classify*: classify a central image as a bird, fish, flower, or person by touching the corresponding symbol. Motor and image stimuli could appear in any of the four screen corners. All three concurrent tasks required the same motor response.

7.3.2 Results and Discussion

The distraction tasks affected memory performance for the two image sets differently (Fig. 2; two-factor repeated measures ANOVA; interaction: $F_{(3,15)} = 57.83$, $p < .001$, partial $\eta^2 = .920$). Concurrent cognitive demand during the memory interval impaired performance for familiar images, but left performance for unfamiliar images intact (Fig. 2; one-factor repeated-measures ANOVA; familiar images: $F_{(3,15)} = 72.034$, $p < .001$, partial $\eta^2 = .935$; unfamiliar images: $F_{(3,15)} = 0.715$, $p = .558$). The classification task took longer to complete than did either the motor or image tasks, which did not differ from each other (paired t-tests, two-tailed, Bonferroni corrected $\alpha = 0.017$; motor vs classify: $t_5 = 6.11$, $p = .002$, $d = 2.50$; image vs classify: $t_5 = 6.20$, $p = .002$, $d = 2.53$; motor vs image: $t_5 = 0.59$, $p = .58$). Critically, the concurrent tasks that required more cognitive effort produced more impairment (paired t-tests, two-tailed, Bonferroni corrected $\alpha = 0.017$; none vs motor: $t_5 = 6.81$, $p = .001$, $d = 2.78$; motor vs image: $t_5 = 2.17$, $p = .083$; image vs classify: $t_5 = 9.05$, $p < .001$, $d = 3.69$; note that five of six monkeys performed numerically worse after image than motor interference, but the group difference was not significant). The differential impairment was not due to the familiar images being harder to remember than the unfamiliar images, because accuracy with the two sets was matched using different memory intervals and did not differ when concurrent cognitive demand was absent (Fig. 2, $t_5 = 1.37$, $p = .230$). Together, these results suggest that memory for familiar, but not unfamiliar, images was impaired by a concurrent cognitive demand in a demand-dependent manner.

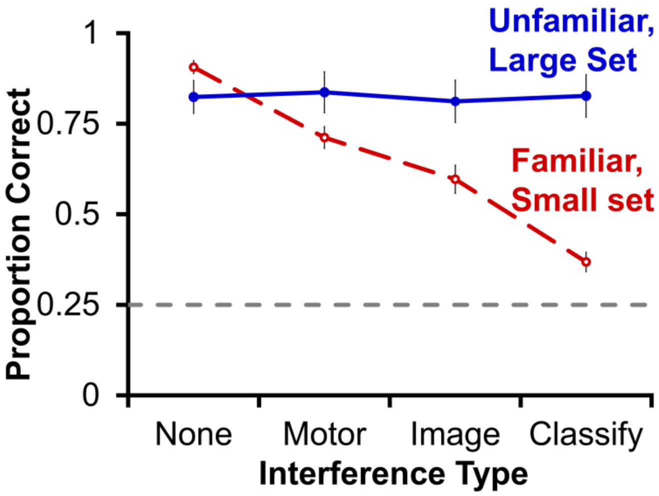

Figure 2. Memory performance for familiar but not unfamiliar images is impaired by concurrent cognitive demand in a demand-dependent manner in monkeys. Proportion correct (±SEM) on the final recognition test is graphed for both the familiar small image set (red dashed line) and the unfamiliar large image set (solid blue line) as a function of the four levels of concurrent cognitive demand imposed during the memory interval. The gray horizontal dashed line represents the proportion correct expected by chance.

7.4. Experiments 2a-2c: Alternative explanations

The results of Experiment 1 suggest that the concurrent tasks impaired performance because holding familiar, but not unfamiliar, images in memory required limited cognitive resources, and the concurrent tasks competed for those resources. Prior to accepting this interpretation, we investigated four alternative explanations. In Experiment 2a, we evaluated whether the decrement occurred because completing the concurrent task lengthened the memory interval. In Experiment 2b, we evaluated whether the decrement was due to the concurrent task occurring immediately after study in the familiar image condition, rather than after a relatively long interval in the unfamiliar image condition. In Experiment 2c, we evaluated whether the decrement occurred only when to-be-remembered samples were classifiable, and also whether the selective decrement was due to the two image sets being tested at different memory delays.

7.4.1 Methods

All subjects and apparatus were the same as in Experiment 1. All stimuli were the same as in Experiment 1, with the addition of a set of four non-classifiable photographs, already highly familiar from previous testing. For all three sub-experiments, half the trials contained no concurrent task and the other half contained the classification task, which was the most debilitating concurrent task. All other methods were the same as in Experiment 1 unless noted.

7.4.1.1 Experiment 2a: Lengthened memory interval

We ran one 100-trial session using the familiar set of images with a memory interval of 4 seconds. If the decrement in accuracy was due to the extension of the memory interval by the time taken to complete the secondary task (lengthened from 1 second to 2.5 seconds in the case of the classification task), then an unfilled 4-second interval should produce a decrement of similar or greater magnitude.

7.4.1.2 Experiment 2b: Timing of concurrent task

We ran two 100-trial sessions using the unfamiliar image set, one with the concurrent task at the end of the 30-second delay and one with the concurrent task at the start of the 30-second delay. If the decrement in accuracy with the small set of familiar items was due to the secondary task following quickly after the sample, then moving the secondary task to the beginning of the delay with the large set of unfamiliar items should produce a similar decrement to that found with the small image set.

7.4.1.3 Experiment 2c: Image content and constant memory interval

We ran two 100-trial sessions at a consistent memory interval of 4 seconds. The to-be-remembered images for the two sessions were the relatively unfamiliar set of 400 non-classifiable images used in the image condition of

Experiment 1 and the set of 4 highly-familiar non-classifiable images, respectively. If the classification task produced a large decrement because the samples were classifiable, then using samples that the monkeys were unable to classify should eliminate the effect. Additionally, if the difference between the two sets was due to them being tested at different memory delays, then testing them at the same memory delay should eliminate the effect.

7.4.2 Results and Discussion

7.4.2.1 Experiment 2a: Lengthened memory interval

The performance impairment seen with the familiar images in Experiment 1 was not due to elongation of the memory interval by the addition of time spent completing the concurrent tasks. On average, the concurrent tasks increased the memory interval of the familiar images from 1s to 2.5s in Experiment 1; however, memory performance following the unfilled 4s delay in Experiment 2a was significantly higher than the filled 2.5s delay from the Experiment 1 (mean proportion correct at 4s = .79, $t_5 = 8.47$, $p < .001$, $d = 3.46$).

7.4.2.2 Experiment 2b: Timing of concurrent task

The lack of performance impairment with the unfamiliar images in Experiment 1 was not due to the concurrent task following more quickly after the study phase with the familiar images than with the unfamiliar images in

Experiment 1. In Experiment 2b, memory performance with the unfamiliar images was equivalent when the classification task occurred at the end and at the beginning of the 30s delay (mean proportion correct: end of delay = 0.65, beginning of delay = 0.64; $t_5 = 0.39$, $p = .709$).

7.4.2.3 Experiment 2c: Image content and constant memory interval

The selective performance impairment seen in Experiment 1 was not due to the to-be-remembered images being classifiable by the monkeys. With non-classifiable images, we again observed selective impairment for the familiar stimuli but not the unfamiliar stimuli (non-classifiable familiar images mean proportion correct: none = .86, concurrent classification task = .51, $t_5 = 13.08$, $p < .001$, $d = 5.34$; non-classifiable unfamiliar images mean proportion correct: none = .95, concurrent classification task = .90, $t_5 = 1.45$, $p = .208$). Nor were the impairments in performance due to the two sets being tested at different memory delays in Experiment 1. The selective impairment seen with the non-classifiable image sets in Experiment 2c was observed at a constant 4s memory delay. Together, Experiments 2a-2c indicate that the concurrent tasks in Experiment 1 impaired performance for familiar images because they imposed different levels of concurrent cognitive demand.

7.5. General Discussion

Concurrent cognitive demands during the memory delay impaired performance for familiar, but not unfamiliar, images in a demand-dependent manner. This indicates that remembering familiar information is cognitively effortful for monkeys. This establishes a strong parallel with human working memory. It also raises the intriguing possibility that monkeys hold familiar images in working memory via an effortful maintenance process akin to human rehearsal (but see Washburn and Astur 1998). Primacy, or superior memory for items appearing early in a list, is often due to rehearsal in humans (Marshall and Werder 1972). We recently found that memory performance for lists of familiar, but not unfamiliar, images showed a primacy effect in monkeys (Basile and Hampton 2010), again suggesting a rehearsal-like process for familiar information (but see Cook et al. 1991). This difference between processing of familiar and unfamiliar memoranda parallels fMRI results from humans showing that the prefrontal cortex is more active when remembering familiar images (Stern et al. 2001).

The discrepancy of these results, which provide evidence of active maintenance of monkey memory, with previous results, which found no evidence of active maintenance (Cook et al. 1991; Washburn and Astur 1998), may be due to the relatively high familiarity of the images being remembered. In these previous studies, samples were either drawn from a medium-sized set of 32 photographs (Cook et al. 1991), or an unbounded set of algorithmically-generated grid patterns (Washburn and Astur 1998). Because target stimuli did not repeat every trial, it is possible that they could be discriminated from distractors at test on the basis of familiarity, and thus monkeys could perform accurately without needing to maintain them in working memory. Although set size appears to be a likely factor considering the current findings, there are too many differences between the current study and the previous ones to draw a firm conclusion without additional experiments.

It is a challenge to select appropriate language to accurately describe cognitive processes in nonhumans. Passive familiarity describes well the immunity to interference we saw in recognition of targets from the large set of unfamiliar images. With the large set, the target had been seen much more recently than the distractors and thus was presumably more familiar, memory for the target was unaffected by concurrent cognitive demands and thus primarily passive, and studies in humans have shown that familiarity judgments are primarily passive (Jacoby 1991; Yonelinas 2002). However, one could also describe this as a recency judgment or as a novelty judgment. We cannot distinguish between these descriptions in the current study, and it is not immediately clear whether these are different ways of describing the same type of judgment or different types of judgments. Future studies may help illuminate these distinctions.

Our results indicate that future studies of working memory in nonhumans should contrast performance with familiar and unfamiliar images. Because of the relative ease with which monkeys learn memory tasks with large sets of unfamiliar images (Mishkin and Delacour 1975), large sets have become the standard in primate memory research; however, the present results show that large and small sets are remembered differently. Failure to recognize this difference may have created the perception of inconsistencies between the nonhuman and human literatures, in which humans are often tested with familiar items and monkeys are often tested with relatively unfamiliar items (Stern et al. 2001). Secondary tasks that manipulate concurrent cognitive load can be used to identify instances of active working memory (Jeneson and Squire 2012) and may help resolve these apparent inconsistencies. Neurophysiological studies of working memory that contrast performance with large and small stimulus sets (Eacott et al. 1994) or that use other methods to contrast passive familiarity and active maintenance (Miller et al. 1996) will prove especially informative.

Humans often maintain information in working memory through verbal rehearsal, but our results with monkeys indicate that active memory maintenance does not require language. There is evidence that humans engage in nonverbal memory maintenance (Hourihan et al. 2009), but it is difficult to block the human tendency to name visual stimuli, and recoding unfamiliar visual stimuli into familiar words does facilitate memory (Wright et al. 1990). Based on these findings and ours, one intriguing possibility is that the capacity for active control of memory may have more to do with familiarity than with other properties of linguistic material. The ease with which humans recode unfamiliar memoranda into familiar words, an option unavailable to monkeys, may be one of the reasons that cognitive control over memory is more robust in humans than it is in monkeys.

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8. General discussion

The above papers represent a step forward in the study of recollection and familiarity in nonhumans, but it is a relatively small step compared to the ground yet to cover. I hope the studies presented in this dissertation, the methods that were developed for them, and the knowledge I have gained from conducting them, will serve as a solid foundation for future discoveries.

The three papers presented in this dissertation address different questions related to the distinction between recollection and familiarity. Paper 1 presents evidence that monkeys can recall and reproduce simple stimuli, and evidence that is consistent with the idea that recall tests primarily measure recollection while recognition tests measure both recollection and familiarity. Future studies will further explore performance on this shape reproduction test to determine the degree to which the test can assess recollection from long-term memory and is affected by selective hippocampal damage. Paper 2 provides evidence that item recognition does involve two retrieval processes, and is consistent with the involvement of a quick familiarity process and a slower onset recollection process. It also closely parallels similar findings from humans and rats (Sauvage et al. 2010; Koen and Yonelinas 2011) using a different species and method. Paper 3 provides evidence that familiarity-based recognition involves passive retention, in that it does not require cognitive control. Future studies may use a similar distractor paradigm at encoding or retrieval, as such manipulations have been used in humans to provide evidence that recollection is a more cognitively-demanding retrieval process than familiarity (Anderson et al. 1998).

In future studies, we will need to develop methods to distinguish between long-term memory and working memory. These experiments were conducted using relatively short memory delays ranging from 1 to 30 seconds; however, studies of recollection in humans often use much longer delays of minutes or days. The distinction between short-delay and long-delay memory tests is a concern because it is unclear whether recollection of information from short-term memory or working memory represents the same process as recollection of information from long-term memory. This is a difficult issue, and there is little agreement on the minimum delay length needed to test recollection. For example, one investigation of the forgetting rates of recollection and familiarity in humans excluded data from delays up to 8 seconds because they might represent working memory, but included delays of 16 seconds (Yonelinas and Levy 2002). A similar investigation included delays as short as 5 seconds (Hockley 1992). However, humans can use working memory over delays as long as 15 minutes (Milner 1970), and long-term memory can support performance in short-delay memory tasks if the amount of to-be-remembered information exceeds working memory capacity (Hannula et al. 2006; Jeneson et al. 2011). Thus, it can be misleading to equate a specific delay length with a specific memory process. The relation between delay length and memory process is further complicated by the practical consideration that nonhuman animals often remember stimuli for shorter durations than human subjects in laboratory tests. For example, studies of memory for lists have achieved similar performance levels by testing humans after a retention interval of 100 seconds, monkeys after 30 seconds, and pigeons after 10 seconds (Wright et al. 1985). Similarly, in tests comparing spatial memory across species, accuracy after a 15-second delay was approximately 98% for humans, 70% for rhesus monkeys, 56% for marmoset monkeys, and 51% for cats (Miles 1971). Thus, it may not be possible to test nonhumans on the same delays as humans, and it is unclear that the use of longer delays alone will meaningfully address the distinction between short- and long-term memory. Future studies might benefit from the use of distractor paradigms, such as that used in Paper 3, to suppress subjects' use of working memory.

Research into recollection and familiarity in nonhumans may make the most impact in our understanding of the neural substrates of the two processes. A major unanswered question is whether the hippocampus is equally important for recollection and familiarity (Eichenbaum et al. 2007; Squire et al. 2007). There is evidence to support multiple interpretations. Supporting the claim that the hippocampus is only necessary for recollection, some amnesic patients with damage limited primarily to their hippocampus perform normally on tests of recognition, despite severe impairments on tests of recall (Vargha-Khadem et al. 1997; Baddeley et al. 2001; Mayes et al. 2002). This spared performance on recognition tests following hippocampal damage has also been seen in rats (Fortin et al. 2002) and monkeys (Murray and Mishkin 1998; Heuer and Bachevalier 2011a); however, we lack comparable recall tests in these species. Alternately, supporting the claim that the hippocampus is necessary for both recollection and familiarity, most amnesic patients are equally impaired on tests of both recall and recognition (Manns and Squire 1999; Manns et al. 2003; Wixted and Squire 2004); however, the true extent of their brain damage cannot be characterized as fully as similar damage in nonhumans and it is possible that they also have extrahippocampal damage. Impaired performance on recognition tests following hippocampal damage has also been seen in rats (Clark et al. 2001) and monkeys (Zola et al. 2000), again without comparable recall tests. Thus, evidence for the role of the hippocampus in recollection and familiarity is conflicting and the topic is currently one of active research and controversial claims (Eichenbaum et al. 2007; Squire et al. 2007). Our ability to answer this question will benefit from an increase in the quality and variety of memory tests that can be used in nonhumans.

Recollection and familiarity are psychological constructs based in human memory theory and they carry theoretical baggage. The use of such constructs can sometimes be detrimental because they can constrain one's thinking and methods. One alternative approach is to describe memory using more narrow terms, such as by what is remembered (e.g., item vs. context), how long it is remembered (e.g., short-term vs. long-term), or what brain structures support it (e.g., hippocampal-dependent vs. perirhinal-dependent). At some point, it may be more advantageous to conduct investigations aimed at these more specific distinctions. However, a large body of literature supports the distinction between recollection and familiarity in humans (Yonelinas 2002), and the use of this as a framework has resulted in a wealth of knowledge about human memory. It is reasonable to expect that using a similar framework to study nonhuman memory will also result in productive gains.

8.1 Conclusions

The distinction between recollection and familiarity is longstanding in humans, but it has been difficult to test in nonhumans. In 1971, Eugene Winograd noted that it was interesting that the question was so commonly addressed with humans and yet so inappropriate with animals (Winograd 1971). Recent research has made much progress in this area. The current studies contribute to that recent research with the following findings:

1. Monkeys can reproduce simple shapes from memory in a test that parallels human visual recall tests.
2. The presence of two processes in recognition and one process in recall is suggested by higher recognition accuracy for the same stimuli under matched conditions.
3. In recognition tests, the high rate of false alarms at quick latencies and under speeded response requirements is consistent with a quick familiarity process and a slower recollection process.
4. Familiarity-based recognition performance is unaffected by a concurrent cognitive demand during retention, suggesting that familiarity does not require cognitive control.

Future studies will build on these findings by attempting to distinguish between long-term and short-term memory, testing the effects of concurrent cognitive load at encoding or retrieval, and combining these behavioral methods with selective hippocampal lesions. In conclusion, the study of recollection and familiarity will likely always remain more difficult in nonhumans than in humans, but it is no longer an inappropriate question.

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