

# Recognition errors suggest fast familiarity and slow recollection in rhesus monkeys

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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 for 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.

[Supplemental material is available for this article.]

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 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 (Doshier 1984). Similarly, false alarms to lures that are familiar to the target (e.g., if the target was “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 are 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

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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 requires 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 that seen in human recognition (Doshier 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, 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

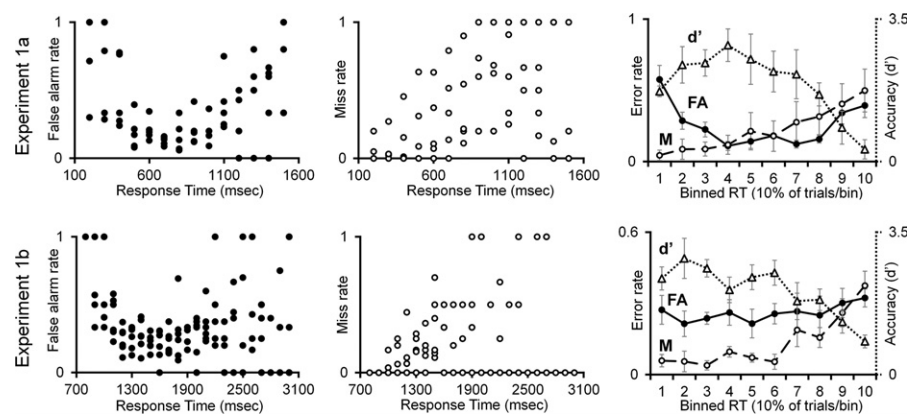
accuracy. Recognition based on a combination of familiarity and recollection should result in a higher probability of rejecting the familiar lures, evident in lower levels of false alarms and the highest level of accuracy. Failure to recognize the image either by familiarity or recollection should result 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.

## Experiments 1a and 1b: post-hoc analysis of recognition errors

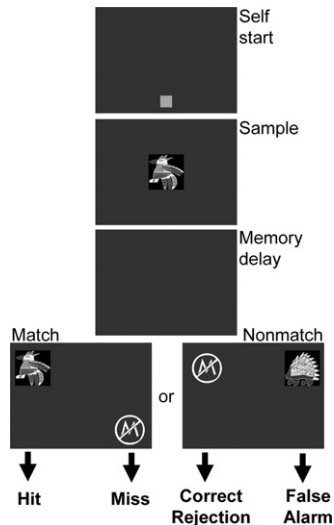
Experiments 1a and 1b are post-hoc analyses of recognition errors from two unrelated studies (Basile and Hampton 2010, 2011). The methodologies of the two studies differed in many aspects, but both used a computerized match/nonmatch recognition test presented on touchscreen computers (see Fig. 1 in Basile and Hampton [2010] and Fig. 1 bottom panel in Basile and Hampton [2011]). 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 nonmatch 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 nonmatch 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.

## Results and Discussion

Initial visual inspection of the error rates revealed two distinct patterns. False alarms plotted as a function of response latency formed



**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 (number of false alarms/number of nonmatch trials) as a function of response time in 100-msec bins. The middle two panels depict miss rates (number of misses/number of 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 errors and accuracies binned such that each bin contains 10% of each monkey's trials. (Solid line with solid dots) False alarms; (dashed line with open dots) misses; (dotted line with open triangles) accuracy ( $d'$ ). Error bars are  $\pm 1$  SEM.



**Figure 2.** Diagram of a match/nonmatch recognition test used in Experiment 2. Monkeys initiated trials by touching a 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 nonmatch test. Monkeys earned food by touching the test image if it matched the sample or by touching the nonmatch symbol if the test image did not match the sample. The test image and the nonmatch symbol appeared equally often in all four screen corners. Trials were separated by a 10-sec interval during which the screen was black.

a U shape, with relatively high levels occurring at the shortest and longest response latencies (Fig. 1, left two panels). In contrast, miss rates were low at the shortest response latencies and higher at the longer latencies (Fig. 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 (paired *t*-test; Experiment 1a,  $t_{(4)} = 4.10$ ,  $P = 0.015$ ,  $d = 1.84$ ; Experiment 1b,  $t_{(5)} = 3.05$ ,  $P = 0.028$ ,  $d = 1.25$ ) (Fig. 1, right two panels), whereas the false alarm and miss rates did not differ for the slowest responses (paired *t*-test; Experiment 1a,  $t_{(4)} = -0.46$ ,  $P = 0.672$ ; Experiment 1b,  $t_{(5)} = -0.63$ ,  $P = 0.558$ ) (Fig. 1, right two panels). 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 nonmatch trials to reduce response bias.

Plots of accuracy, measured as  $d'$ , as a function of response latency for each experiment produced an inverted U-shape, skewed toward the quicker response times (Fig. 1, right two panels). Again, we grouped performance into 10 bins based on latency with an equal number of trials. Accuracy peaked in different bins for different monkeys, with the average peak bins being bins 4 and 3 (Experiment 1a, mean = 4.00; Experiment 1b, mean = 3.20). Accuracies of the quickest responses were significantly lower than the peak accuracies for Experiment 1a, but not Experiment 1b (two-tailed paired *t*-tests, Bonferroni corrected  $\alpha = 0.00625$ ; Experiment 1a,  $t_{(4)} = 5.36$ ,  $P = 0.0058$ ,  $d = 2.40$ ; Experiment 1b,

$t_{(5)} = 2.64$ ,  $P = 0.046$ ). Peak accuracy was significantly higher than accuracy in the slowest response bin for both experiments (two-tailed paired *t*-tests, Bonferroni corrected  $\alpha = 0.00625$ ; Experiment 1a,  $t_{(4)} = 22.65$ ,  $P < 0.001$ ,  $d = 10.13$ ; Experiment 1b,  $t_{(5)} = 6.89$ ,  $P < 0.001$ ,  $d = 2.81$ ). 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.

## Experiment 2: targeted analysis of recognition errors

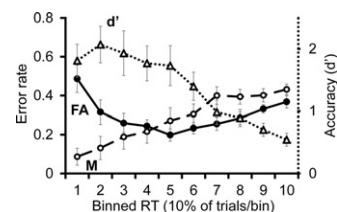
The results of the analyses described in Experiments 1a and 1b suggested that monkey recognition is composed of a quick familiarity process and a slower recollection process; however, these findings came from post-hoc analyses. The two paradigms that contributed data to Experiments 1a and 1b were designed 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/nonmatch recognition test designed to facilitate measurement of false alarms due to familiarity (Fig. 2).

## Results and Discussion

Performance for one monkey (Ju) fell to chance at the trained delay of 4 sec and he was re-tested at a shorter memory delay of 1 sec. 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 (paired *t*-test,  $t_{(11)} = 4.15$ ,  $P = 0.002$ ,  $d = 1.20$ ) (Fig. 3), whereas the false alarm and miss rates did not differ for the slowest responses (paired *t*-test,  $t_{(11)} = -1.32$ ,  $P = 0.213$ ) (Fig. 3).

Plotting accuracy, measured as  $d'$ , as a function of response latency produced an inverted U-shape, skewed toward the quicker response times (Fig. 3). 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). Accuracies of the



**Figure 3.** False alarms and misses as a function of response time. Quick errors were disproportionately false alarms, whereas slow errors were guesses. (Solid line with solid dots) False alarms; (dashed line with open dots) misses; (dotted line with open triangles) accuracy ( $d'$ ). Error bars are  $\pm 1$  SEM. Each bin contains 10% of each monkey's trials.



quickest responses, and of the slowest responses, were significantly lower than the peak accuracy (two-tailed paired *t*-tests, Bonferroni corrected  $\alpha = 0.00625$ ; first vs. peak,  $t_{(11)} = 4.20$ ,  $P = 0.001$ ,  $d = 1.21$ ; last vs. peak,  $t_{(11)} = 5.64$ ,  $P < 0.001$ ,  $d = 1.63$ ).

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.

### Experiment 3: experimental manipulation of response speed

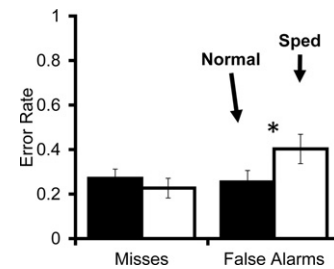
Experiments 1 and 2 provide preliminary evidence that monkey recognition performance results from the combination of a quick familiarity process and a slower recollection process. However, the data presented so far are correlational. To provide a strong experimental test of this hypothesis, we directly 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. Unstudied lures that would normally be rejected after recollection would now be accepted, resulting in higher false alarm rates. In contrast, studied targets can be correctly accepted on the basis of either familiarity or recollection, thus limiting reliance on recollection should not change miss rates.

### Results and Discussion

Performance of one monkey (Mi) fell to chance at the trained delay of 4 sec and he was re-tested at a shorter memory delay of 1 sec. 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 = 0.572; last 100 trials, mean = 0.334; two-tailed paired *t*-tests,  $t_{(11)} = 4.94$ ,  $P < 0.001$ ,  $d = 1.46$ ). In the critical test sessions, half of which had a response deadline of 800 msec, monkeys responded more quickly in deadline trials than in normal trials (average median response latencies, sped = 700.7 msec, normal = 824.6 msec; two-tailed paired *t*-tests,  $t_{(11)} = 5.73$ ,  $P < 0.001$ ,  $d = 1.65$ ). 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 (two-tailed paired *t*-tests, false alarms,  $t_{(11)} = 3.00$ ,  $P = 0.012$ ,  $d = 1.95$ ; misses,  $t_{(11)} = 1.71$ ,  $P = 0.115$ ) (Fig. 4). The failure to detect a decrease in misses was not the result of miss rates being at floor levels, as 11 of 12 monkeys had miss rates well above floor levels, even at quick responses (Supplemental Fig. S1). This indicates that speeding responses hindered recruitment of the slower recollection process and forced monkeys to respond primarily on the basis of familiarity. Accuracy was also lower in the sped condi-



**Figure 4.** Error rates under normal and speeded responding. Speeding responding selectively increased false alarms. Mean miss and false alarm rates ( $\pm$  SEM) are depicted for both normal sessions and sessions in which responses were sped using a response deadline. (\*) Statistically significant differences.

tion than in the normal condition ( $d'$ , sped = 1.18, normal = 1.52; two-tailed paired *t*-tests,  $t_{(11)} = 3.14$ ,  $P = 0.009$ ,  $d = 1.55$ ). That our experimental manipulation to decrease response time decreased accuracy and selectively increased false alarms further reinforces the findings from Experiments 1 and 2 that quick responses result in errors due to the inability to discriminate studied targets from familiar but unstudied lures.

### 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 12 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 (Doshier 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 700 msec and estimates of recollection peaked around 1000 msec (Yonelinas and Jacoby 1994), and in monkeys a response deadline of 800 msec 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. First, 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. Second, 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 nonmatch 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. Third, we might assume that choice is guided by a single memory process in combination with impulsivity and a preexisting 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 account 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 toward either type of error, suggesting that an overall response bias did not exist. Finally, we might assume that choice is guided by a single memory process in combination with impulsivity and a fluctuating response bias that quickly shifts from liberal to unbiased in the first few hundred milliseconds after stimulus onset. An early liberal bias would predict that quick responses would have an overall increased choice of the test image compared to slower responses, which would result in a higher proportion of false alarms and a lower proportion of misses. However, this is inconsistent with the results of Experiment 3, in which speeding responding selectively increased false alarms but had no effect on misses. This failure to detect a decrease in misses was not the result of miss rates being at floor levels, as 11 of 12 monkeys had miss rates well above floor levels, even at quick reaction times (Supplemental Fig. S1). In contrast to these single-process accounts, a dual-process account that posits quick familiarity and slow recollection readily explains all 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 were 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, the interpretation of ROC curves depends on the assumption that recollection represents a threshold process, and this assumption is contested (Wixted 2007; Wixted and Squire 2008). This controversy over whether ROC curves can be interpreted as a valid measure of recollection and familiarity highlights the need for convergent findings from other methodologies. Therefore, the current results inform our understanding of the dual-process model by contributing independent evidence, using a different method 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 the distinction between recollection and familiarity has 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, for example, whereas slow accurate responses may be more appropriate in other situations, such as navigation or food choice.

## Materials and Methods

### Experiments 1a and 1b

Data from Experiments 1a and 1b came from Basile and Hampton (2011) and from 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.

#### Subjects and apparatus

Data for Experiment 1a ( $n = 5$ ) and 1b ( $n = 6$ ) came from adult male rhesus macaques (*Macaca mulatta*). All 11 monkeys had experience with various cognitive tests using a touchscreen computer. Subjects were tested 6 d per week, 7 h 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.

#### Stimuli

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

#### Procedure

Data for both experiments come from match/nonmatch recognition tests (see Fig. 1 in Basile and Hampton [2010] and Fig. 1 bottom panel in Basile and Hampton [2011]). Monkeys initiated trials by touching a green 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 “nonmatch” 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 nonmatch symbol. An unfilled 10-sec intertrial interval separated trials. Data from Experiment 1a used a single studied target and a memory delay of 1 sec. Data from Experiment 1b used five studied targets, presented sequentially, and memory delays of 0.5 sec or 2 sec. Only trials on which the fifth target was tested are included in the present analyses.

#### 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 (nonmatch trials). Trials of each type were then ranked by response time and grouped into 10 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 (see Supplemental Table S1 for absolute latencies represented by each bin). 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 nonmatch 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 nonmatch trials for analysis, one-fifth of nonmatch trials were selected by random number generator for inclusion in analysis. However, during testing, trials were evenly split between match and nonmatch trials to prevent monkeys from developing a bias. Accuracy was calculated using  $d'$  (Macmillan and Creelman 2005). For the analysis of whether accuracy at the quickest and slowest response bins differed from accuracy in the middle response bins, the quickest and slowest response bins could theoretically be compared to any of the eight internal bins. Consequently, we used a Bonferroni corrected  $\alpha$  of  $0.05/8 = 0.00625$  to limit the familywise error rate.

## Experiment 2

#### Subjects and apparatus

Subjects were 12 adult male rhesus macaques, 11 of which contributed the data for Experiments 1a and 1b. All housing conditions and testing equipment were the same.

#### Stimuli

Stimuli were two color clipart images (a hedgehog and a bird) measuring 300 pixels  $\times$  300 pixels. We used a small set of stimuli because Experiments 1a and 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.

#### Procedure

Monkeys were given one 1000-trial session of a standard match/nonmatch recognition test on a touchscreen computer (Fig. 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 4-sec unfilled memory delay, and then were presented with one stimulus and a “nonmatch” 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 nonmatch 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-sec time out. An unfilled 10-sec interval separated trials. At test, the image and nonmatch 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.

#### Data analysis

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

## Experiment 3

#### Subjects and apparatus

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

#### Stimuli

All stimuli remained the same as in Experiment 2.

#### 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 500 msec 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 1000 msec, 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 1000-msec deadline was not sufficient to increase the overall error rate, we used a response deadline of 800 msec in the critical sessions.

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