Research

Greater dependence on working memory and restricted familiarity in orangutans compared with rhesus monkeys

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The prefrontal cortex is larger than would be predicted by body size or visual cortex volume in great apes compared with monkeys. Because prefrontal cortex is critical for working memory, we hypothesized that recognition memory tests would engage working memory in orangutans more robustly than in rhesus monkeys. In contrast to working memory, the familiarity response that results from repetition of an image is less cognitively taxing and has been associated with nonfrontal brain regions. Across three experiments, we observed a striking species difference in the control of behavior by these two types of memory. First, we found that recognition memory performance in orangutans was controlled by working memory under conditions in which this memory system plays little role in rhesus monkeys. Second, we found that unlike the case in monkeys, familiarity was not involved in recognition memory performance in orangutans, shown by differences with monkeys across three different measures. Memory in orangutans was not improved by use of novel images, was always impaired by a concurrent cognitive load, and orangutans did not accurately identify images seen minutes ago. These results are surprising and puzzling, but do support the view that prefrontal expansion in great apes favored working memory. At least in orangutans, increased dependence on working memory may come at a cost in terms of the availability of familiarity.

The prefrontal cortex is critical for a suite of cognitive control processes that are conspicuous in human cognition (Miller 2000; Rougier et al. 2005; Braver et al. 2009). One such process is working memory, which actively maintains representations in a state of heightened access for further processing (Baddeley and Hitch 1974; Engle 2010). Working memory and cognitive control are positively correlated with measures of general intelligence in humans, implicating the prefrontal cortex as a key neural structure in the evolution of human cognition (Gray et al. 2003; Unsworth and Engle 2007; Cole et al. 2012). Some neuroanatomical studies have found that the prefrontal cortex is larger than would be predicted based on body size and visual cortex volume in apes compared with monkeys (Rilling 2006; Passingham and Smaers 2014). These findings suggest that the prefrontal cortex expanded disproportionately in great apes during primate evolution. Disproportionate expansion of the prefrontal cortex in great apes may have resulted in greater capacity for cognitive control functions, such as working memory, compared with monkeys. Thus, studies directly comparing working memory in monkeys and apes are critical to understanding the evolution of intelligence in primates.

The role of cognitive control, and thus the prefrontal cortex, varies among memory systems. For instance, working memory relies heavily on cognitive control, consuming substantial cognitive resources, and is known to depend on frontal brain areas (Goldman-Rakic 1995; Fuster 1997). In contrast, familiarity, which is a strength-based memory signal that codes for whether or not a percept has previously been experienced (Kelley and Jacoby 1998;

Yonelinas 2002), relies substantially less on cognitive control, consumes fewer cognitive resources, and has been mostly associated with nonfrontal areas of the brain such as the perirhinal cortex (Bachevalier and Mishkin 1986; Brown and Aggleton 2001; Haskins et al. 2008; Tu et al. 2011; O'Neil et al. 2012). Thus, working memory and familiarity vary in the degree to which they rely on cognitive control, and the degree to which they rely on prefrontal areas of the brain.

If a relatively large prefrontal cortex enhances cognitive control and working memory, then we should expect recognition memory tests to engage working memory relatively more in apes than in monkeys. We evaluated this hypothesis by comparing the contributions of working memory and familiarity with recognition memory performance in orangutans and rhesus monkeys. Because the orangutans and monkeys here compared have different experience with cognitive testing, we aimed to compare the relative contributions of working memory and familiarity in each species, rather than the absolute accuracy of the two species in a particular memory test. This follows a logic similar to that used in many comparative anatomical studies; for example, those cited here that found the prefrontal cortex is larger in apes relative to body weight or visual cortex volume, rather than simply absolute volume.

The relative contributions of working memory and familiarity to behavior can be measured in visual recognition memory tests. In

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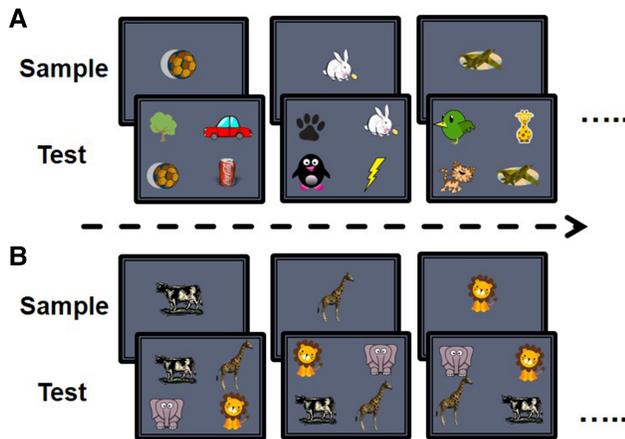
Figure 1. Recognition memory tests with repeating and trial-unique images. (*A*) In tests with trial-unique images, each image was only used once as a sample or a distractor within a session. (*B*) When tested with repeating images, the images were the same on each trial. The sample image was pseudorandomly selected each trial such that each image appeared equally often as the sample or as a distractor.

these tests subjects study a sample image at the beginning of each trial and after a delay they are presented with a test consisting of the recently seen sample image among distractors (Fig. 1). The images used in these tests can either be repeated, such that the subject's job is to determine which image in a set of familiar images was seen most recently, or the images can be trial unique, such that at test subjects need to discriminate a previously seen image from novel distractors. Working memory is critical for solving tests with repeating images, but much less so for tests using trial unique images, where familiarity plays a much greater role (Brady and Hampton 2018a). Monkeys (Jitsumori et al. 1988; Basile and Hampton 2013a) and apes (Harlow 1944; Hayes and Thompson 1953) are more accurate and better tolerate long delay intervals in tests with trial-unique stimuli, when familiarity can support performance. Experimentally naïve monkeys require comparatively little training to demonstrate proficient use of familiarity as a mnemonic cue, compared with the training required to become proficient in using working memory (Mishkin and Delacour 1975). Active working memory and passive familiarity are independent mnemonic processes that can be doubly dissociated. Working memory is impaired by a concurrent cognitive load imposed during the memory interval, while familiarity is not affected (Logie 1986; Jacoby et al. 1989; Basile and Hampton 2013a; Brady and Hampton 2018a). Completing the double dissociation, equating the familiarity of the sample and distractor images during study impairs choice based on familiarity, but not working memory (Brady and Hampton 2018a). Thus, recognition memory tests may allow us to compare the relative contributions of these two memory processes with recognition performance across species.

One might expect orangutans to show greater dependence on working memory compared with rhesus monkeys for at least two reasons. First, working memory is highly refined in humans and orangutans are more closely related to humans phylogenetically, sharing a common ancestor 13 million to 14 million years ago (Stewart and Disotell 1998), whereas rhesus monkeys and humans shared a common ancestor ~32 million years ago (Roos and Zinner 2015). Second, orangutans have a relatively larger prefrontal cortex compared with monkeys (Rilling 2006; Passingham and Smaers 2014). We compared the ability of rhesus monkeys and orangutans to maintain images from different sets in working memory. We also determined the extent to which familiarity contributed to rec-

ognition memory performance. Across three experiments, we observed striking species differences. We found that in orangutans, recognition memory performance for both repeating and trial-unique images was controlled by working memory. In contrast, monkeys relied on working memory for repeating images, and on familiarity for trial-unique images. Furthermore, monkeys dramatically outperformed orangutans in tests that exceeded the capacity and duration of working memory, and thus depended on familiarity.

Results

Experiment I: orangutans used active working memory under conditions in which rhesus monkeys used passive familiarity

In recognition memory tests using trial-unique images, monkeys can achieve high accuracy, even at relatively long delays, by selecting the image that is most familiar at test. This is because at test the sample is familiar from study, but the distractor images are unfamiliar. In contrast, monkeys use active working memory when tested with repeating images, and accuracy declines rapidly with a memory delay. Active working memory is required in tests with repeating images because all of the images that appear at test are familiar from preceding trials, making it difficult to discriminate the sample from distractors on the basis of familiarity (Jitsumori et al. 1988; Basile and Hampton 2013a; Brady and Hampton 2018a; Brown and Hampton 2020). In Experiment 1, we compared the extent to which orangutans showed a similar distinction in memory processes when tested with trial-unique and repeating images. We hypothesized that if working memory and familiarity both contribute to recognition performance in orangutans, then orangutans would show higher accuracy for trial-unique images, as do monkeys. Alternatively, if orangutans rely on working memory for both repeating and trial-unique images, then they would show similar performance in both types of memory test.

Accuracy of monkeys was higher in tests with trial unique images, while that of orangutans was not. Orangutans took an average 8.8 sessions of 80 trials with trial-unique images, and 5.6 sessions of 80 trials with repeating images, to pass criterion. Monkeys took an average of two sessions with 80 trials with trial-unique images and two sessions of 80 trials with repeating images. On test trials, orangutans and rhesus monkeys both performed well above chance and criterion (orangutans: repeating M = 75%, trial-unique M = 75%; monkeys: M = 82%, M = 97%). Rhesus monkeys were more accurate when tested with trial-unique images than with repeating images, whereas orangutans performed similarly with both types of images (two-factor ANOVA species × image set size interaction: $F_{(1,5)}$ = 13.2, P = 0.015, η_p^2 = 0.73; main effect species: $F_{(1,5)}$ = 85.7, P < 0.001, η_p^2 = 0.95; main effect image type: $F_{(1,5)}$ = 39.3, P = 0.002, η_p^2 = 0.89; post-hoc comparisons of arc sin transformed scores, orangutan repeating vs. trial-unique: MD = 0.02, P = 0.88; monkey repeating vs. trial-unique: MD = 0.552, P = 0.001) (Fig. 2). Performance with repeating images did not differ significantly between species whereas performance was different for trial-unique images between species (post-hoc comparisons repeating images orangutan vs. monkey: MD = 0.19, P = .089, trial-unique images orangutan vs. monkey: MD = 0.723, P < 0.001). Accuracy with trial-unique images is thought to be supported by the availability of familiarity as a mnemonic signal (Basile and Hampton 2013a; Brady and Hampton 2018a) and the release from proactive interference (Cook et al. 1991). The fact that orangutans were not more accurate with trial-unique images than repeating images suggests at least two possibilities. The first is that repeating and trial-unique images may engage working memory equally in orangutans. This would support the hypothesis
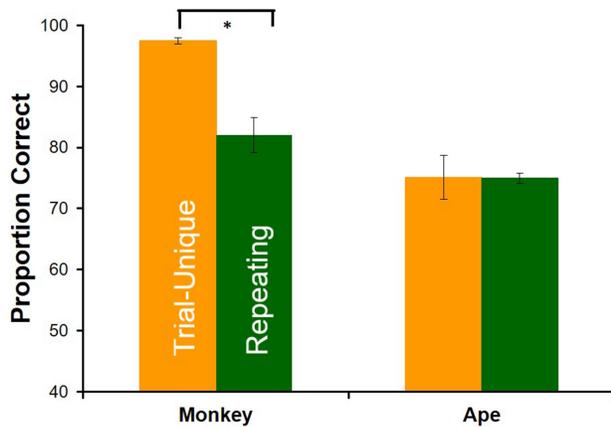
Figure 2. Rhesus monkeys showed significantly greater accuracy with trial-unique images, whereas orangutans did not. Orangutan memory performance was not significantly better when tested with trial-unique images.

that working memory is more prominent in orangutans than it is in rhesus monkeys. The second possibility is that familiarity may have occurred in the orangutans, but they are not as proficient at using familiarity as are rhesus monkeys, and thus performance was similar between the two conditions in orangutans. In order to discriminate between these possibilities, we directly tested for a dissociation of working memory and familiarity by manipulating concurrent cognitive load in Experiment 2 (Basile and Hampton 2013a; Brady and Hampton 2018a).

Experiment 2: concurrent cognitive load reduced accuracy with both repeating and trial-unique images in orangutans, but not rhesus monkeys

A defining characteristic of working memory is that it is cognitively taxing and thus vulnerable to competing cognitive load. If subjects using working memory simultaneously execute a second taxing cognitive task during the memory delay, retention will suffer (Logie 1986). This measure has been used as a defining criterion for working memory in both humans (Phillips and Christie 1977; Logie 1986; National Institute of Mental Health, Research Domain Criteria Database, https://www.nimh.nih.gov/research-priorities/rdoc/index.shtml), and nonhuman primates (Basile and Hampton 2013a; Brady and Hampton 2018a; Völter et al. 2019). In contrast, concurrent cognitive load during the delay interval does not affect memory performance that is supported by familiarity, because familiarity is an automatic process that does not depend on cognitive resources during the delay interval (Jacoby et al. 1989). Thus, response to concurrent cognitive load can be diagnostic of the extent to which choice at test depends on working memory or familiarity and constitutes a direct test of whether or not working memory is engaged (Basile and Hampton 2013a; Brady and Hampton 2018a). In Experiment 2, we tested the extent to which memory for repeating and trial-unique images was impaired by concurrent cognitive load in orangutans and rhesus monkeys. To the extent that working memory is critical for accurate choice, concurrent cognitive load should decrease accuracy. We hypothesized that if working memory is engaged for both repeating and trial-unique images in orangutans, we would observe a demand dependent memory impairment from concurrent cognitive load for both types of images. If orangutans rely on familiarity for trial-unique images, then we should observe a dissociation similar to what has previously been found in rhesus monkeys (Basile and Hampton 2013a).

Category training

All monkeys and four orangutans passed criterion after the first transfer test. Two orangutans did not achieve criterion in the category task in the time we had available for training and testing them. It was unfortunately necessary to complete as much of the other testing with these animals as possible, rather than exhausting our available testing time with the category task. We have no reason to expect these animals could not have learned this task with sufficient time.

Memory testing

Memory performance was analyzed in a three factor repeated measures design. Mauchly's test of sphericity indicated that the assumption of sphericity were not violated $\chi^2(5) = 0.464$, $P = 0.994$. Measures of skewness and kurtosis did not show values >2; however, a Shapiro–Wilk test of all eight combinations of related groups analyzed showed that two groups did violate normality (Shapiro–Wilk test of normality: trial-unique with category task: $W(10) = 0.83$, $P = 0.029$, repeating stimuli in the image task: $W(10) = .84$, $P = 0.044$). Repeated measures ANOVA only requires approximately normal data because it is robust to violations of normality, meaning that this assumption can be violated and still provide a valid result (Howell 2016).

Monkeys used working memory much more with the images from the small set than from the large set. Memory performance with the two sets of images was affected differently by concurrent cognitive load for rhesus monkeys, but not for orangutans (three factor repeated measures ANOVA, species × image type × concurrent cognitive load interaction: $F_{(3,9)} = 4.43$, $P = 0.036$, $\eta_p^2 = 0.60$, main effect of species: $F_{(1,3)} = 106.4$, $P = 0.002$, $\eta_p^2 = 0.97$; main effect of image type: $F_{(1,3)} = 40.7$, $P = 0.008$, $\eta_p^2 = 0.93$, main effect of concurrent cognitive load: $F_{(3,9)} = 45.9$, $P < 0.001$, $\eta_p^2 = 0.94$) (Fig. 3). We further tested whether this three way interaction demonstrated a difference in the use of working memory between the species by conducting follow-up within species ANOVAs. In rhesus monkeys, concurrent cognitive load caused a memory impairment for repeating images but not trial-unique images (separate two factor repeated measures ANOVA image type × concurrent cognitive load interaction: $F_{(3,15)} = 18.552$, $P < 0.001$, $\eta_p^2 = 0.79$; main effect of image type: $F_{(1,3)} = 171.76$, $P < 0.001$, $\eta_p^2 = 0.97$; main effect of concurrent cognitive load: $F_{(3,15)} = 58.71$, $P < 0.001$, $\eta_p^2 = 0.92$) (Fig. 3, left panel). These results indicate that working memory was critical for remembering the repeating images in monkeys, but not detectable for trial-unique images, likely due to the reliance on familiarity. The findings from monkeys replicate earlier work (Basile and Hampton 2013a; Brady and Hampton 2018a). Unlike monkeys, orangutans always used working memory. Concurrent cognitive load caused a memory impairment for both types of images for orangutans (two-factor repeated measures ANOVA; image type × concurrent load interaction: $F_{(3,9)} = 0.58$, $P = 0.64$, $\eta_p^2 = 0.16$; main effect image type: $F_{(1,3)} = 0.01$, $P = 0.927$, $\eta_p^2 = 0.003$; main effect concurrent load: $F_{(3,9)} = 27.5$, $P < 0.001$, $\eta_p^2 = 0.90$) (Fig. 3, right panel).

The results of Experiment 2 suggest that the lack of difference in performance with the two image set sizes observed in Experiment 1 was because orangutans did not use familiarity to identify studied images. Because memory failure from concurrent cognitive load is indicative of working memory, these results indicate that orangutan working memory was critical for maintenance of both repeating and trial-unique images in memory, unlike the case with rhesus monkeys. Monkeys only used working memory for repeating images. This finding supports the hypothesis that apes show a greater dependence on working memory compared with monkeys due to their relatively large prefrontal cortex.

Surprisingly, we found that orangutans did not use familiarity with the trial-unique set of images. Across Experiments 1 and 2,
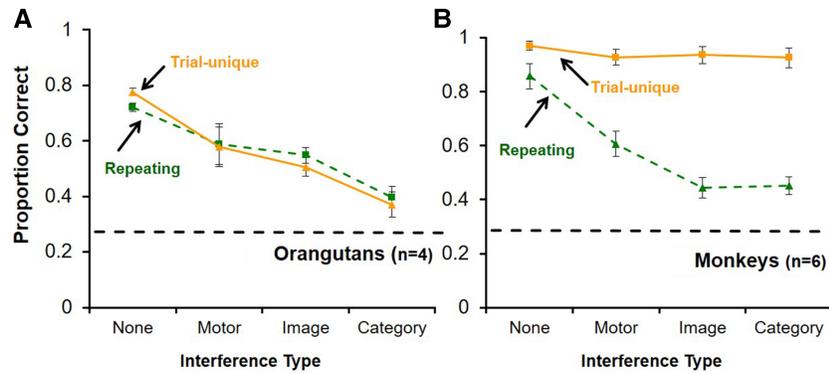
Figure 3. Familiarity in recognition memory performance by monkeys, but not orangutans. Concurrent cognitive load affected memory performance for both repeating (dashed line) and trial-unique images (solid line) in orangutans, demonstrating working memory for both types of memoranda. In contrast, concurrent cognitive load affected accuracy with repeating images but not with trial-unique images in rhesus monkeys, showing that monkeys relied on familiarity rather than working memory for recognition of trial-unique images. Proportion correct is graphed as a function of concurrent cognitive load from least (none) to greatest (categorization task). Dashed horizontal line indicates chance. These results reveal a striking and surprising difference in the use of working memory and familiarity between rhesus monkeys and orangutans.

tion, is not susceptible to concurrent cognitive load, and is not as constrained by capacity (Yonelinas 2002; Brady et al. 2008). To ensure working memory would not be used, we presented orangutans and rhesus monkeys with lists of up to 40 images to remember and tested their memory after a delay of many minutes after seeing the last image. While the capacity and duration of working memory cannot be precisely known, and varies with circumstances and individuals, these parameters are well outside normal capacity for monkeys and apes. In the case of capacity, rhesus monkeys do not reliably remember memory arrays greater than three images at once (Brady and Hampton 2018b), and their visual working memory capacity has been estimated to be about one item (Elmore and Wright 2015). In the case of duration, working memory has been found to degrade to near chance performance in under a minute (e.g., Eacott et al. 1994; Gazes et al. 2013). Therefore, working memory should not make a major contribution to performance in this experiment. If familiarity for the sample images is present, then subjects should select previously seen images over novel distractors.

familiarity was evident in the rhesus monkeys, but not orangutans, indicating that orangutans do not use familiarity to the same extent as monkeys. Because the lack of familiarity in orangutans was so surprising, we directly addressed two alternative explanations for the difference in performance between orangutans and monkeys in Experiment 3.

One possibility is that familiarity is available to orangutans, but they do not use it. Rather, orangutans, with a greater reliance on cognitive control, may use working memory and if that fails, they choose an image at random rather than selecting the most familiar image. By this reasoning orangutans may not respond based on familiarity because their heavy reliance on working memory overshadows familiarity. The second alternative explanation invokes the difference in delay interval used with the two species. We attempted to match the accuracy of orangutans and monkeys by using a 2-sec delay for orangutans and a 5-sec delay for monkeys. While this approximately equates accuracy, it may have introduced a confound in that working memory is most relevant for memory tests at short delay intervals. Thus, orangutans may have used working memory more than monkeys because the conditions under which they were tested favored working memory moreso for orangutans than monkeys.

To test these ideas, we designed a memory test that could not be solved by working memory, but could be solved by familiarity. This test virtually eliminates the possibility of successfully using working memory and strongly encourages dependence on familiarity. It provides an ideal opportunity to detect choices based on familiarity. If monkeys and orangutans differed in use of familiarity because of differences in delay interval, the species difference should disappear when both species are tested under conditions where working memory is not viable and familiarity is highly relevant.

Experiment 3: monkeys, but not orangutans, selected test images based on familiarity when working memory was not available

Experiment 3 was designed to measure familiarity exclusively, using a memory assessment that precluded working memory. In contrast to working memory, familiarity for a previously seen image can last for an extended period of time without sustained atten-

With no previous experience on this particular task, five of the seven monkeys met criteria within the first five sessions of the 40-image list condition ($M = 85\%$, $n = 5$). One of two monkeys passed criterion in the 20-image list condition, and the final monkey passed criterion in the eight-image list condition (Fig. 4). Because all monkeys passed criterion before moving to the final one-image list condition, none were tested in this condition. None of the orangutans met criterion within the allotted 10 sessions for either the 40-image ($M = 24\%$), 20 ($M = 28\%$), or eight-
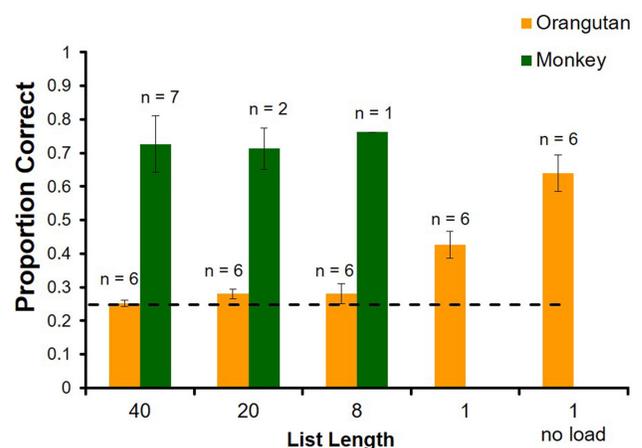
Figure 4. Orangutans only scored above chance when a single image was presented at a time. When memory load was outside of working memory capacity (lists of 40, 20, and eight images), performance was at chance. In contrast, five of seven rhesus monkeys passed criterion with 40 image lists within the first 10 test sessions with no prior training. The two remaining monkeys passed criterion with shorter lists. No orangutans reached criterion until the list was shortened to one image. In the final test, orangutans received lists of length one and no target finding tasks. The dotted line indicates chance. The "n" *above* each bar represents how many animals are included in the average.

image ($M = 26\%$) list length conditions. Orangutan performance did not differ from chance on any of the three conditions (40 list: $t_{(5)} = -0.56$, $P = 0.60$; 20 list: $t_{(5)} = 2.11$, $P = 0.09$; eight list: $t_{(5)} = 0.20$, $P = 0.85$). When orangutans were moved to the one image list condition, their performance resembled that observed in the preceding experiments where they were tested for memory for a single image (cf. Figs. 4 [one image—no load] and 3). Orangutans performed near criterion on one-image lists with no filler task between study and test, and accuracy was significantly worse with the filler task embedded between study and test, consistent with use of working memory (paired samples t-test one image vs. one image—no load: $t_{(5)} = 6.67$, $P = 0.001$) (Fig. 4).

These results provide a third converging indication that orangutans did not use familiarity in recognition memory tests. Rhesus monkeys performed above criterion almost immediately, whereas orangutans only performed above chance with a single sample image at a time, when working memory was apparently again in operation. Although the monkeys had no previous experience with this particular task, they did have considerable experience with other memory tasks. It is possible that monkeys' previous experience increased their motivation to remember images they saw presented on a screen, which might aid their performance in the experiments described here. However, differences in motivation are unlikely to account for the lack of evidence for familiarity in orangutans. When orangutans were tested with "lists" of just one image and a short delay, which is presumably within working memory range, accuracy immediately increased. Accuracy under these conditions demonstrates that orangutans did understand the task contingencies, and were motivated, so their failure was one of memory, not a failure to understand the task or a lack of motivation. Rhesus monkeys showed clear evidence of familiarity. Orangutans showed evidence of working memory, but did not show evidence of familiarity.

Discussion

Orangutans used working memory under a broader set of conditions than did rhesus monkeys, consistent with the relatively large prefrontal cortex of orangutans. In Experiments 1 and 2, orangutans engaged in working memory maintenance for both repeating and trial-unique images, whereas rhesus monkeys only used working memory with repeating images. Orangutan memory for both kinds of images was susceptible to concurrent cognitive load, which confirms that performance with images from both set sizes was supported by working memory (Basile and Hampton 2013a; Brady and Hampton 2018a). In contrast, rhesus monkeys were only susceptible to concurrent cognitive load with repeating images, which indicates that they engaged in working memory maintenance for repeating images, but relied on familiarity for trial-unique images.

Orangutans never selected sample images on the basis of familiarity in the current study. In Experiments 1 and 2, we saw the behavioral signature of familiarity in rhesus monkeys but not orangutans. In Experiment 3, we found that orangutans showed no evidence of familiarity even when working memory was made irrelevant, which should have highlighted the mnemonic value of familiarity. In contrast, rhesus monkeys recognized images from lists of up to 40 images, indicating strong familiarity.

One explanation for the lack of evidence of familiarity in direct tests of memory with orangutans is that the familiarity signal in orangutans is not strong enough to control explicit choice. Familiarity signals contribute to accurate choice in recognition memory tests to the extent that samples and distractors differ in familiarity. For example, in the recognition memory tests used in Experiments 1–3, a previously viewed sample was presented with three novel images. If the familiarity signal generated by the previously seen sample and by the distractors is similar when these images are perceived at test, then there is not a clear basis on which to identify the target image. An interesting possibility is that familiarity is present in orangutans, but may be more easily detected through memory tests that do not require explicit choice. It may be that familiarity in orangutans can be inferred indirectly from more implicit measures such as response latency or eye-tracking. Further work should compare direct versus indirect tests of memory in orangutans and the extent to which indirect tests would measure the same or different cognitive processes.

The results of these experiments contribute evidence for understanding the consequences of prefrontal cortex expansion in apes (Rilling 2006; Passingham and Smaers 2014). Our findings suggest that one functional consequence of the difference in prefrontal cortex volume between monkeys and orangutans is a greater proficiency in working memory function, as orangutans used working memory under a broader range of conditions than did monkeys. But because orangutans never actually performed more accurately than did monkeys, it is not certain that their working memory is more proficient. Orangutans do at least appear to depend on working memory more than do monkeys. It is much less clear why orangutans failed to use familiarity in our recognition memory tests, especially given that monkeys and humans use familiarity readily (Brady et al. 2008).

There are several potential confounds to consider in interpreting the absence of control of choice by familiarity in orangutans. First, orangutans had less experience with computerized testing than did the monkeys. It is possible that with more practice on our tasks, orangutans would switch from cognitively controlled working memory to more automatic familiarity. Indeed, a study claiming differences between chimpanzees and human children was later explained by effects of training (Inoue and Matsuzawa 2007; Cook and Wilson 2010). In the chimpanzee case, however, the memory system under investigation was working memory, a system known to benefit from expertise and training in specific problem types. There is no comparable body of evidence indicating similar effects of training on the ability to use familiarity. Extensive experience is not required for recognizing images based on familiarity. Experimentally naïve monkeys quickly learn to use the mnemonic cue of familiarity with trial-unique memoranda, but perform much less well with a small set of repeating memoranda, which requires working memory (Mishkin and Delacour 1975). Similarly, chimpanzees were found to perform well on recognition memory tests with trial-unique objects after little training, where they previously had shown poor memory for repeating objects (Harlow 1944; Hayes and Thompson 1953). These findings indicate that lack of experience is more likely to impact working memory than familiarity, and that experimental sophistication is not a prerequisite for control of choice by familiarity. We found in our experiments that orangutans performed well with repeating images, a condition that typically requires experimental sophistication, but did not make use of familiarity under conditions that favored this mnemonic signal.

The second potential confound in interpreting the failure of orangutans to use familiarity is that orangutans may not have been as motivated to obtain food rewards, or may have otherwise not been as interested in the memory tasks, as were the monkeys. It is widely recognized that working memory is effortful while familiarity is less so (Jacoby et al. 1989; Yonelinas 2002), yet our orangutans used working memory even under conditions that favored the use of familiarity. If orangutans were unmotivated or distracted, that would be all the more reason to use less effortful familiarity. Evidence from the current study clearly indicates sufficient motivation in orangutans. Orangutans signaled motivation through completing many training sessions in which they

achieved criterion level performance, and through completing the many experimental sessions included in our three experiments. This suggests that they were sufficiently motivated and understood the task rules. The clearest evidence of sufficient motivation comes from Experiment 3, where orangutans failed to perform above chance over many sessions in tests that could be solved only by familiarity, but they immediately performed well once memory load and delays were reduced to be within the capacity of working memory. This further suggests that what was lacking in orangutans was not motivation, understanding of the task rules, or experience with memory tests. More likely it was familiarity as a mnemonic cue that was missing.

A third concern is that there were differences in the conditions under which the two species were tested. Given constraints in our access to the two species, and differences in the housing conditions of the animals, there were some differences in testing we could not eliminate. Monkeys were tested while individually housed in a laboratory setting and had access to computers for ~7 h each day. Orangutans were tested in large enclosures that often housed more than one animal and could only be tested for ~1 h each day before going on exhibit. While these differences could arguably produce some differences in accuracy (for example, whether the orangutans were more likely to be distracted by another animal), two factors make it unlikely that these differences in housing and testing produced the large and robust difference we found in the use of familiarity. First, it is working memory that is especially vulnerable to distraction, not familiarity (Logie 1986; Jacoby et al. 1989; Basile and Hampton 2013a; Brady and Hampton 2018a). Distraction of orangutans would produce poor working memory and robust familiarity, but we observed the opposite pattern. Second, highly trained monkeys tested in laboratory settings performed quite similarly, across multiple tests, including matching to sample, to initially naïve monkeys living in large social groups that participated in shorter bouts than the laboratory monkeys (Gazes et al. 2013). It is therefore unlikely that differences in the social setting or duration of daily testing would substantially impact the current findings.

The prefrontal cortex of apes as a whole is disproportionately large compared with that of monkeys, but orangutans stand out among apes for having an abnormally small and undifferentiated ventromedial prefrontal cortex (Semendeferi et al. 2001; Schenker et al. 2005). This area is important for social cognition in humans, including perceiving facial expression, gaze direction, and social problem solving (Anderson et al. 1999; Frith 2007; Stout 2010). Orangutans differ from other apes, and rhesus monkeys, in life history as well as brain volumes. Orangutans live comparatively solitary lives and have less complex social organization compared with many other primates, including rhesus monkeys and the other apes (Knott 1999; Utami Atmoko et al. 2009). The relatively solitary life of orangutans might explain why an area of prefrontal cortex closely associated with social cognition is smaller in orangutans compared with other apes.

The ventromedial prefrontal cortex also plays important roles in memory. It is connected with the perirhinal cortex, which supports familiarity, and object recognition (Brown and Aggleton 2001; Haskins et al. 2008). Damage to ventromedial prefrontal cortex in monkeys causes deficits in recognition memory tests with large sets of images (Bachevalier and Mishkin 1986). These are exactly the tests that would readily be solved by familiarity. A related finding is that early-stage Alzheimer's disease patients show specific impairments in familiarity judgements (Schoemaker et al. 2016) and this deficit has been linked to the early degradation of the entorhinal/perirhinal cortices as well as the ventromedial/frontopolar cortices (Salat et al. 2001; Hornberger et al. 2014). This may be an interesting connection that lends support to the idea that the comparatively poor use of familiarity by orangutans is be relat-

ed to their relatively small ventromedial prefrontal cortex. Extrapolation of our findings to all orangutans and rhesus monkeys should of course be done with caution given the small sample sizes used here. However, it remains striking that we found a lack of familiarity in all the orangutans tested, while it is clearly present in all the monkeys. Whether ventromedial prefrontal cortex volume and the use of familiarity in recognition tests varies with sociality across other species certainly should be studied further before drawing firm conclusions.

We found that orangutans used working memory under conditions in which rhesus monkeys relied on familiarity, perhaps indicating that one consequence of a relatively larger prefrontal cortex in great apes is greater dependence on working memory. We also found that orangutans did not use familiarity in recognition memory tests, even under conditions that made it impossible to use working memory, suggesting that familiarity signals may be attenuated in orangutans compared with rhesus monkeys. Familiarity is widely reported in other animals including humans (Jacoby et al. 1989, Yonelinas 2002), monkeys (Basile and Hampton 2013a; Brady and Hampton 2018a), rats (Wan et al. 1999; Fortin et al. 2004), pigeons (von Fersen and Delius 1989; Cook et al. 1997), and dogs (Krichbaum et al. 2020), making its absence or weakness in orangutans puzzling. Our results suggest that relations between prefrontal cortex volume and the evolution of sophisticated cognition in primates may not be simple. Whether the lack of familiarity in orangutans can be explained evolutionarily by their solitary lifestyle, or anatomically by their relatively small ventromedial prefrontal cortex, will require further comparative studies.

Materials and Methods

Experiment 1 methods

Subjects and apparatus

We studied six adult male rhesus monkeys (*Macaca mulatta*) housed at Yerkes National Primate Research Center, and six orangutans housed at Zoo Atlanta (three Pongo abelii, three Pongo pygmaeus, three male and three female, see Table 1). Monkeys were individually housed, received a full daily food ration, and had ad libitum access to water. Orangutans lived in two groups of three, with access to outdoor habitats during the day. In both indoor and outdoor habitats, they received full daily food rations and had ad libitum access to water. The monkeys used in this study had extensive experience with recognition memory tasks, as well as categorizing images using touch-screen computers (Basile and Hampton 2013a,b). The orangutans also had previous experience using touch screen computers, albeit less than the monkeys (e.g., Diamond et al. 2016; Gazes et al. 2017). Monkeys and orangutans were trained and tested using portable touch-screen systems consisting of a 15-in color LCD touch-sensitive screen (Elo Touch

Table 1. Subjects

Subject name	Species	Sex	Age
Madu	*Pongo abelii*—Sumatran orangutan	F	36
Dumadi	*Pongo abelii*—Sumatran orangutan	M	13
Keju	*Pongo abelii*—Sumatran orangutan	F	4
Pelari	*Pongo pygmaeus*—Bornean orangutan	M	6
Miri	*Pongo pygmaeus*—Bornean orangutan	F	27
Satu	*Pongo pygmaeus*—Bornean orangutan	M	16
Albifrons	*Macaca mulatta*—Rhesus monkey	M	13
Geoffroyi	*Macaca mulatta*—Rhesus monkey	M	14
Byrd	*Macaca mulatta*—Rhesus monkey	M	11
Shackleton	*Macaca mulatta*—Rhesus monkey	M	11
Sylvanius	*Macaca mulatta*—Rhesus monkey	M	14
Volans	*Macaca mulatta*—Rhesus monkey	M	12

Systems) operating with a resolution of 1024 × 768 pixels, automatic food dispensers (Med Associates, Inc.) that delivered nutritionally balanced primate pellets (Bio-Serv) into food cups below the screen. Testing systems were mounted on animal habitats. Monkeys had open access to the touch screen via lifting a door, except for one monkey who touched the screen through the slots of his cage bars, and all orangutans touched the screen through holes in their cage mesh. Testing was controlled by laptop computers running custom programs written in Visual Studio 2013 (Microsoft Corporation). For monkeys, the calories from pellets earned during the day were subtracted from their total food ration, and they were given the balance of their ration in primate chow at the end of the day. Orangutans received no change in their daily food depending on how much they earned through pellets. Computers were available from 10 a.m. to 5 p.m. 6 d per week for monkeys. Computers were available for orangutans for ~1 h each morning from 8 a.m. to 9 a.m., as many days a week as possible, Monday through Friday, averaging 3 d per week.

Stimuli

We used 1284 images (200 × 200 pixels) collected from TUMBLR, using (BULKR software). From these, four were randomly selected to constitute the set of repeating images, the remaining 1280 were the trial-unique images.

Procedure

Monkeys and orangutans had previous experience in memory tests with both repeating and trial unique images. Because we intended to compare the relative use of working memory and familiarity, rather than absolute accuracy, we tested both species at delay intervals matched for accuracy. Based on previous training, orangutans could achieve 70% correct with repeating images at delay intervals up to 2 sec, whereas monkeys performed similarly at delays out to 5 sec. Thus, these delays were used with the two species. All animals had to achieve >70% correct responses for two consecutive sessions with a 500 msec delay before moving to test sessions at their respective longer delays. Half of the orangutans and half of the monkeys were tested with repeating images first, and the other half of the subjects were tested with trial-unique of images first. Subjects had to meet the accuracy criterion at 500 msec delay before participating in each condition. Each primate was tested on two sessions of 80 trials for each image condition. For repeating images, the same four images were used on each trial, and each image served as the sample or as a distractor the same number of times each session. For trial-unique testing, 320 images were drawn at random to be used at the beginning of the session, and were only seen once during the session, either as the sample or the distractor (Fig. 1). In both conditions, the location of the sample at test was pseudorandomly counterbalanced within each session such that each location was used equally often.

Subjects were rewarded at test with a single primate pellet and positive auditory feedback for choosing the image that had appeared as the sample in that trial. Selecting a distractor image at test produced a negative auditory signal and no pellet. Correct trials were followed by a 2-sec intertrial interval (ITI), and incorrect trials were followed by a 5-sec ITI.

Data processing

Proportion correct scores were arc sine transformed prior to analysis for all experiments (Aron and Aron 1994). Group differences were analyzed with repeated measures ANOVA and paired sample t-tests as appropriate. We tested for violations of sphericity and normality using Mauchly's test of sphericity and the Shapiro–Wilk test for normality. Any violations are reported.

Experiment 2 methods

Subjects

The same six rhesus monkeys and orangutans were used. However, the two youngest orangutans, Keju and Pelari, did not pass category training in the time available and therefore could not be used in the critical tests. The resulting data set for Experiment 2 included six rhesus monkeys and four orangutans.

Stimuli

The same image sets were used for repeating and trial-unique images. Different images were used for each of four levels of concurrent cognitive load, as described in the procedure.

Procedure

Animals completed two 300-trial sessions with the repeating and two with the trial-unique images. Sessions alternated after the completion of one, and the order of sessions was counterbalanced within each species. Half of the trials in one session were empty delay trials that contained no concurrent cognitive load, providing a baseline measure of accuracy, and the other half were divided equally among motor, image, and classification trials. On empty delay trials, the screen was blank during the delay interval. On motor trials, a blue square (200 × 200) appeared during the delay and subjects had to touch it to proceed to the memory test. On image trials one of 400 noncategorizable images was presented during the delay, and subjects had to touch it to proceed to the memory test. On category trials, one of 800 categorizable images appeared during the delay interval and subjects had to correctly categorize the image to proceed to the memory test. The eight category groups collected were guitars, shoes, cars, cats, frogs, horses, butterflies, and drums. Presentation of the concurrent cognitive loads within a session were pseudorandomly distributed. The progression of trials is illustrated in Figure 5. Incorrect responses to the concurrent task aborted the trial, and the same type of trial with a different sample image and category image followed. To equate the
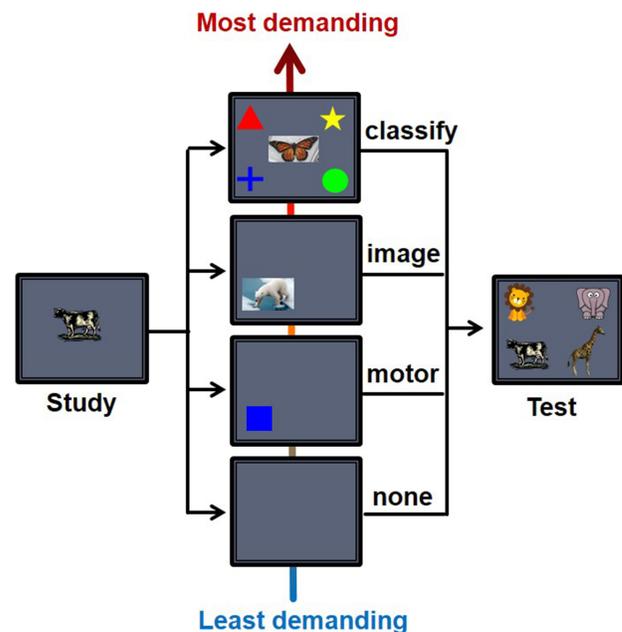
Figure 5. Recognition memory tests with concurrent cognitive load. During the delay interval, subjects experienced one of four conditions, from lowest concurrent cognitive load demand (none), to highest (classify). After completing the interference task, animals were given the recognition task.
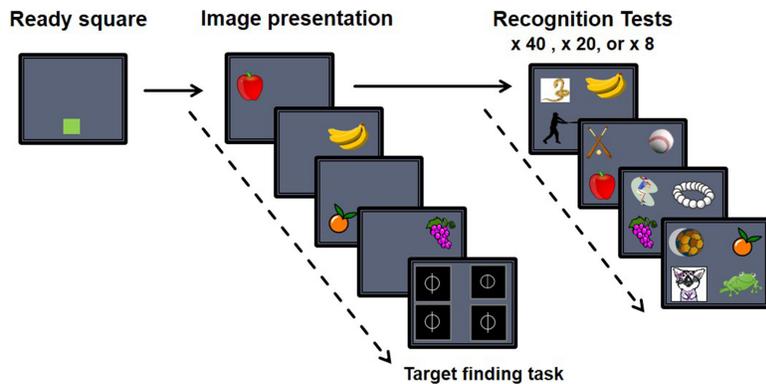
Figure 6. Isolating familiarity in recognition memory tests. During study, monkeys touched four images consecutively and then completed a filler task for a reward. This process continued until each image in the list had been viewed three times. Lists were of 40, 20, or eight images depending on the condition. After seeing each image three times, subjects were presented with one memory test for each image in the list, presented against novel distractors.

contribution of working memory to recognition memory performance between species, we matched the accuracy of orangutans and monkeys by using different delay intervals as in Experiment 1. The delay between sample and test was 2 sec for orangutans, and 5 sec for rhesus monkeys. If the distractor task was completed before this delay, the test would appear when the delay finished. If the distractor task took longer than this delay, the test would appear 250 msec after completing the distractor task and the total delay on that trial would be used for the following empty delay trial. This way, delays for trials with distraction and no distraction were matched. There was a 2-sec intertrial interval following correct trials, and a 5-sec intertrial interval following incorrect trials.

Motor and image task

The motor and image tasks required no training. The animals simply had to touch an image during the delay.

Category task

Monkeys and orangutans were trained to categorize four groups of images. Half of the monkeys and half of the orangutans were trained to categorize cars, cats, shoes, and frogs, and the other half of animals were trained to categorize butterflies, drums, guitars, and horses. Each category had a corresponding symbol that appeared in one of the four corners of the computer screen for subjects to select to categorized images (e.g., select heart for butterfly images; rectangle for cars; lightning bolt for cats; and moon for drums). Both species received the same training to learn categories. First the animals learned each category one by one. They received 100 trials where only images from category 1 were used, with all four category responses presented. Upon achieving >80% accuracy, they moved to training with only images from category 2. This process repeated until they achieved criterion with each of the four categories individually. They then received sessions of 200 trials with images from both categories 1 and 2 until achieving >80% accuracy. Next, they moved to 300 trial sessions of categories 1, 2, and 3. After passing this with 80% criterion, they moved to a 400 trial session with images of all four categories intermixed. After achieving 80% correct with all four categories concurrently, they moved to a transfer test in which they received a 100-trial session with 25 novel images from each of the four categories. The transfer test was to ensure that the animals learned a categorical representation, rather than memorizing the images. If the animal achieved >70% correct on the transfer test, they moved to the experimental sessions. If the animal did not pass criterion, they moved back to sessions of 400 trials with all four categories. After passing criterion again with all four categories, they repeated the 100-trial transfer test with 25 novel images from each category.

Experiment 3 methods

Subjects

The same six rhesus monkeys and six orangutans from Experiment 1, and an additional monkey that was available at the time of testing, were used in Experiment 3.

Stimuli

Six-thousand images were collected using the downloader software Bulkr, to use as trial unique memoranda for the memory test. White circles with a white line bisecting the middle and protruding slightly outside of the circle on both sides, presented on a black background (200 × 200 pixels) were used as distractors in the filler task. The target was the same image, except that the bisecting line did not protrude (Fig. 6).

Procedure

Subjects were presented lists of images of varying length, and were later rewarded for selecting these images rather than novel images. There were two phases: image presentation and recognition tests (Fig. 6). While the monkeys did have considerably more experience with touchscreen memory tasks, neither the monkeys nor the orangutans had experienced this particular paradigm.

Subjects started the image presentation phase by touching a green square. Four images were presented one at a time each in a different corner of the screen. Subjects touched each image before it would disappear and the next image would appear. They were not rewarded for touching the images. After every fourth image, a filler task appeared in which the subject had to touch a target image among distractors, which resulted in positive auditory feedback and food reinforcement. The distractors used in the filler task were identical circles with a line vertically through the middle extending beyond the border of the circle. The target was the same circle except the line stayed within the border of the circle (Fig. 6). The trial would not progress until the correct target stimulus was touched. The green square would then appear again and touching this started the presentation of four more images. Subjects touched all images in the list following this sequence, and then the order of the list was rerandomized, and the process repeated until the subject had seen and touched each image three times. Immediately following this study phase, subjects moved to the test phase. In the test phase, subjects were presented with the green square; touching of which was followed by the presentation of four images simultaneously. Three of the images were novel, and one was an image from the studied list. Touching the image from the studied list resulted in auditory and food reinforcement. Touching one of the distractor images resulted in a negative auditory stimulus and no food reinforcement. A 2-sec intertrial interval separated both correct and incorrect trials, after which the green square reappeared. A session was complete after all images from the list had been tested.

Up to four list lengths were used depending on performance: 40, 20, eight, and one. In the one-image list, half of the trials went straight to test after touching the image, and half of the trials had the filler task in-between study and test. Testing ended when a given subject reached the criterion of 70% or higher in two consecutive sessions. If a subject did not meet criterion in 10 sessions, they began testing with the next smaller list and this repeated until the subject either met criterion for a given list length, or had been tested with all the list lengths. For the 40- and 20-image list conditions, one session took place every morning. For the eight- and one-image list conditions, the 10 sessions were not limited to one per day. The subject was able to finish them one after another.

Acknowledgments

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