

Rhesus monkeys show greater habituation to repeated computer-generated images than do orangutans

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ARTICLE INFO

Keywords:

Attentional control
Familiarity
Primate cognition
Working memory

ABSTRACT

Humans and several other species of animals have demonstrated the ability to use familiarity to recognize that they have seen images before. In prior experiments, orangutans failed to show use of familiarity in memory tasks, even when other solutions were not available. We tested for evidence of habituation, a decreased response to repeated stimuli, as a behavioral indicator that repeated images were familiar to subjects. Monkeys and orangutans selected the smallest target out of four while computerized images were presented as distractors. Latency to complete the target-finding task was compared between conditions in which the distractor image was a familiar, repeating image, a novel, never-before-seen image, or no distractor was present. Rhesus macaques showed significant habituation, and significantly more habituation than orangutans, in each of four experiments. Orangutans showed statistically reliable habituation in only one of the four experiments. These results are consistent with previous research in which orangutans failed to demonstrate familiarity. Because we expect that familiarity and habituation are evolutionarily ancient memory processes, we struggle to explain these surprising, but consistent findings. Future research is needed to determine why orangutans respond to computerized images in this peculiar way.

1. Introduction

Memory is not a unitary phenomenon but instead is supported by multiple, dissociable systems that bear different functional characteristics (Cohen and Eichenbaum, 1993; Sherry and Schacter, 1987; Squire, 2004). Familiarity is a strength-based system that codes for whether a stimulus has been experienced before (Kelley and Jacoby, 1998; Yonelinas, 2002), and it is dissociable from some other memory systems on the basis of its relative passiveness and automaticity. For example, the maintenance of items in working memory requires limited cognitive resources, and those items are rapidly forgotten if not actively maintained (Oberauer et al., 2018; Rhodes and Cowan, 2018). In contrast, hours, and even up to years after a single exposure, humans are able to recognize large numbers of images as familiar, despite the fact that they were not actively or consciously thinking about the images in the interim (T. F. Brady et al., 2008; Larzabal et al., 2018; Mitchell, 2006). Similarly, monkeys can identify familiar images after delays that exceed the duration of working memory, and accuracy is not affected by concurrent cognitive loads (Basile and Hampton, 2013; R. J. Brady et al.,

2021; Brown and Hampton, 2020). Use of familiarity signals in recognition tests is widely considered to be automatic and phylogenetically widespread (Jacoby, 1991; Mandler, 1980; Yonelinas, 2002).

Surprisingly, in a series of experiments comparing the relative use of familiarity and working memory in monkeys and orangutans engaged in matching to sample tests, orangutans showed no evidence of using familiarity despite performing well above chance (R. J. Brady et al., 2021). In the first experiment, monkeys, but not orangutans, achieved higher accuracy on match-to-sample tests in which every trial used novel images from a large set as sample and distractors, compared to tests that used a small set of images, in which every trial used the same four images. This large-set advantage likely occurs because in tests with the large set, only the image seen as the sample produces a familiarity signal while the distractors are all novel. In contrast, in the small-set condition, in which all the images have been seen before, relative familiarity is a poor indicator of which image was seen as the sample on the current trial. Both the sample and distractor images produce familiarity signals. Absence of this advantage in orangutans suggested that they did not use familiarity.

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<https://doi.org/10.1016/j.beproc.2024.105011>

Received 10 October 2023; Received in revised form 23 February 2024; Accepted 23 February 2024

Available online 28 February 2024

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A second experiment dissociated familiarity from working memory using concurrent cognitive load, in this case a categorization task was presented during the memory delay, which interfered with working memory but not familiarity (Basile and Hampton, 2013; R. J. Brady et al., 2021; R. J. Brady and Hampton, 2018). Monkeys showed poor accuracy on trials with high competing cognitive load added to the retention interval in the small-set condition, suggesting the use of working memory, but did not show an accuracy drop in the large-set condition, consistent with the use of familiarity. In contrast, in orangutans, competing cognitive loads reduced accuracy in both large and small set conditions, suggesting that orangutans relied on working memory and not familiarity even in conditions in which familiarity could overcome the limitations imposed on working memory by competing cognitive load.

A final experiment tested monkeys and orangutans under conditions in which the use of working memory was not possible, further encouraging choices at test based on familiarity. Lists of images were presented to monkeys and orangutans, followed by recognition memory tests after comparatively long memory delays. In these tests, animals needed to identify images from the list against novel distractors. These tests could not be solved using working memory because the lists of 40 images, and memory delays over 10 minutes, exceed the working memory capacity of both humans and other primates (Cowan, 2010; 2022). For instance, in rhesus macaques in our laboratory, working memory performance drops to near chance within a few minutes at most (Gazes et al., 2013; Brown and Hampton, 2020). Five out of seven monkeys performed accurately on this test with lists of 40 images, the highest number tested, while one reached high accuracy with 20 images, and one with 8 images. Zero of six orangutans exceeded chance performance with any list length. However, orangutans did achieve high accuracy with single images. Accurate performance with single images shows both that orangutans understood the task was to match to the sample, and suggested that they used working memory and never familiarity, even when working memory was not a viable solution to the task (R. J. Brady et al., 2021).

The lack of evidence for familiarity in orangutans is surprising for several reasons. Familiarity is shared between humans and monkeys, and also plausibly present in animals including rats (Eacott and Easton, 2007), hummingbirds (Flores-Abreu et al., 2012), and ants (Baddeley et al., 2012). A true absence of familiarity in orangutans would entail that they lost a process that is presumably highly conserved in evolution. Familiarity likely serves basic ecological functions, enabling animals to respond appropriately to individuals, places, and objects that they have encountered before. Although orangutans are solitary for much of their lives, they do interact in loose fission-fusion societies with preferred individuals and in overlapping territories (Setia et al., 2009; Singleton and van Schaik, 2002), conditions in which familiarity would seem useful for remembering known locations and individuals. Indeed, orangutans have shown discrimination between familiar and unfamiliar individuals across multiple testing paradigms (Hanazuka et al., 2013; Talbot et al., 2015; Vonk and Hamilton, 2014). It therefore seems likely that orangutans have familiarity but for some reason do not use familiarity signals to solve the variety of memory tests used in our computerized tasks.

One possibility is that orangutans possess familiarity processes but are unable to, or simply do not, use that information in match-to-sample tests. If true, orangutans should show behavioral evidence that a repeated image is familiar under some conditions, even if they do not use that information in memory tests. One way to test this is to measure the related phenomenon of habituation, or a decrease in response to a repeated stimulus (Thompson and Spencer, 1966). Habituation is possibly the most evolutionarily widespread form of learning (reviewed in van Duijn, 2017). Electrophysiological studies with monkeys have revealed a possible basis for familiarity judgments in a decreased neuronal response in the perirhinal cortex as a result of repeated visual stimuli, which at a neural level looks very much like habituation (Aggleton and Brown, 1999; Eichenbaum et al., 2007; Voss et al., 2009).

Captive orangutans almost certainly habituate to new keepers, environments, and conspecifics when they are transferred between zoos or enclosures. For example, habituation might explain why aggressive behavior often diminishes over time after new individuals are introduced to each other (AZA Orangutan Care Manual, 2017). Furthermore, studies of wild orangutans regularly use ‘habituation’ procedures in order for researchers to observe orangutan behavior without signs of disturbance (Hardus et al., 2009; Lameira et al., 2013). However, it is unknown whether orangutans would show habituation to images of the kind used in prior memory tests. If they do habituate to images, then that evidence might support the idea that there is a disconnect between some implicit sense of familiarity and their ability to use familiarity on memory tests.

In the present study, we tested whether orangutans and rhesus monkeys habituate to repeated images. Subjects solved a series of target-finding tasks while potentially distracting images appeared on-screen. In each session, one image was presented many times, while other images were entirely novel. If orangutans habituate to images, then the repeated image should draw less attention over several presentations, resulting in shorter latencies to respond on the target-finding task on those trials relative to trials with novel images. As a positive control, we used the same paradigms to test for habituation in monkeys, who show familiarity and should show habituation if our tasks are sufficiently sensitive to that effect.

2. Experiment 1: Monkeys but not orangutans habituated to repeated images

2.1. Method

2.1.1. Subjects and apparatus

Subjects included 3 Bornean (*Pongo pygmaeus*) and 5 Sumatran (*Pongo abelii*) orangutans socially housed at Zoo Atlanta (see age and sex breakdown in Table 1). Orangutans were tested behind the scenes in their indoor habitats between 8 and 10 am, after receiving a breakfast of primate biscuits (and sometimes additional vegetables or training treats). The experiments were conducted using a portable touchscreen (Elo Touch Systems) attached to mesh on the enclosure. An automatic

Table 1
Age, sex, and species breakdown of subjects and the experiments they participated in.

Subject Name	Species	Sex	Age in Years	Experiments Participated In
Albifrons	<i>Macaca mulatta</i>	M	15	1–4
Byrd	<i>Macaca mulatta</i>	M	10	1–4
Geoffroyii	<i>Macaca mulatta</i>	M	20	1–4
Juan Carlos	<i>Macaca mulatta</i>	M	16	3–4
Shackleton	<i>Macaca mulatta</i>	M	13	1–4
Sylvanius	<i>Macaca mulatta</i>	M	16	1–2
Volans	<i>Macaca mulatta</i>	M	15	1–4
Biji	<i>Pongo abelii</i>	F	52	1–2
Blaze	<i>Pongo abelii</i>	F	27	1–4
Keju	<i>Pongo pygmaeus</i>	F	8	1–4
Madu	<i>Pongo abelii</i>	F	39	1–4
Pelari	<i>Pongo pygmaeus</i>	M	9	1–4
Pongo	<i>Pongo abelii</i>	M	10	1–4
Remy	<i>Pongo abelii</i>	M	12	1–4
Satu	<i>Pongo pygmaeus</i>	M	19	1

food dispenser (Med Associates, Inc.) delivered 190 mg pellet rewards (Bio-Serv). Testing was controlled by a personal computer with custom software written in Visual Studio 2021 (Microsoft Corporation). Subjects were not separated from their groups for testing, and orangutans from groups that contained more than one subject were tested simultaneously on individual computers. Subjects were free to come and go from testing and always had access to alternative enrichment.

Subjects also included 6 adult male rhesus macaque monkeys (*Macaca mulatta*) housed singly in cages in social proximity to each other at the Emory National Primate Research Center. Monkeys were tested on various cognitive experiments throughout the day between 9:30–5 pm, but they primarily completed this experiment at the beginning of the day, between 9:30–10 am. Their testing apparatuses were composed of the same components used with the orangutans, with a difference being that two food dispensers were available instead of one, although only one was used at a time, and pellets were only 97 mg. Computer testing was the first access to food the monkeys received that day, with additional primate chow, fruit, vegetables, and enrichment provided at the end of the day.

All orangutans had previous experience with cognitive testing via touchscreens (e.g. R. J. Brady et al., 2021; Diamond et al., 2016; Gazes et al., 2017), although monkeys had more extensive experience. All procedures used in the research are in accordance with the Guidelines for the Use of Animals in Research of the USA and have been approved by the Institutional Animal Care and Use Committees of Emory University (orangutan IACUC protocol 201700890; monkey IACUC protocol 201700700).

2.1.2. Procedure

2.1.2.1. Target training. Animals were initially trained on the target-finding task without any additional images appearing on-screen (Fig. 1). Subjects initiated a trial by touching a green self-start square (FR = 2 for all responses). Four white circles then appeared, one in each corner of the screen, three of which were the same size (diameter = 200 pixels) and one of which was smaller (diameter = 120 pixels). The smaller circle was the target. Selection of the target was rewarded with a single pellet and positive auditory reinforcement, followed by a 3-second intertrial interval. Selection of any other circle resulted in no reward and a negative auditory signal, followed by a 6-second timeout. The location of the target varied pseudo-randomly and was counter-balanced such that it appeared twice in each corner every 8 trials. 40-trial sessions repeated until subjects achieved an accuracy of $\geq 85\%$ in two consecutive sessions, or 100% accuracy in a single session. They then advanced to the habituation testing phase. Monkeys took an average of 1.3 sessions to reach criterion, while orangutans took an average of 4.4 sessions.

2.1.2.2. Habituation testing. Trials proceeded as they did in training, with the addition of a distractor image that appeared in the center of the screen during the target-finding task (Fig. 2A). A single repeated image

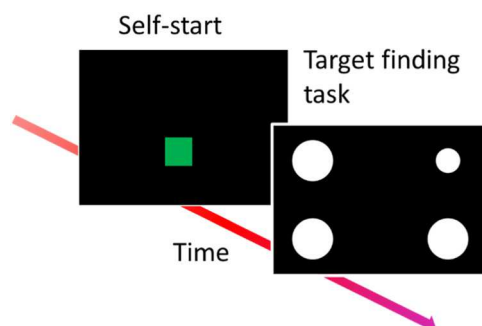


Fig. 1. Trial procedure for training on the target-finding task.

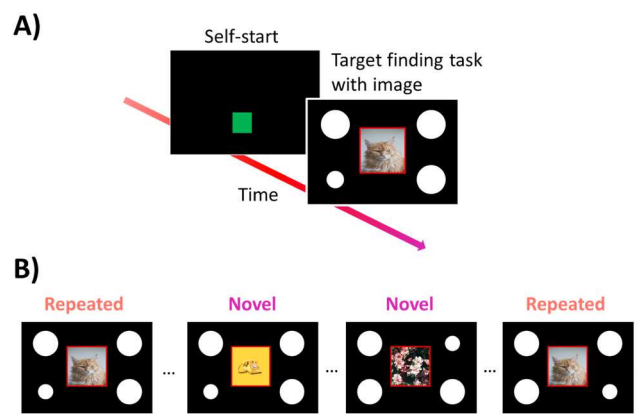


Fig. 2. A) Trial procedure for the habituation test. Following self-start, a distractor image appeared on-screen at the same time as the target finding task. B) Example organization of trial types in the habituation test. Distractor images were either Repeated, as in the first and last trials presented in this figure, or Novel, as in the second and third trials in this figure. Every bin of 4 trials included 2 Repeated images and 2 Novel images in a random order.

recurred multiple times in a session, with a different repeated image for each session. Novel images were presented once on a single trial and never recurred within or between sessions. Touching these distractor images had no effect, and the trial did not advance until the animal selected a circle as during training. All images were 300 × 300 pixels in size and were surrounded by a red border.

The order of trial types, *Repeated* or *Novel*, was counterbalanced such that every block of four trials included two *Repeated* images and two *Novel* images in a random order (Fig. 2B). In a 40-trial session, animals saw the *Repeated* image on 20 trials and *Novel* images on the other 20 trials. Both species completed a single session per day. Animals completed 20 sessions to finish the experiment.

2.1.3. Analysis

Only trials in which the animal correctly selected the target (smallest circle) were analyzed, to eliminate any trials in which subjects may have touched the screen without attending to either the image or the target-finding task. Accuracy on the target-finding task was high for both species (monkey accuracy = 99.8%; orangutan accuracy = 96.3%). In addition, latencies greater than 3 standard deviations from the average response time for subjects within each condition were removed to reduce the influence of extreme outliers. The first block of four trials (two *Repeated* and two *Novel*) were excluded, as *Repeated* images would appear novel until subjects had a chance to experience seeing them within a session. Analyses were conducted using generalized linear mixed models with an inverse-gaussian distribution in the lme4 package (Bates et al., 2015) in R version 4.2.1 (R Core Team, 2021) to account for any issues with normality, as is common with reaction time data (Lo and Andrews, 2015). We used likelihood ratio tests to compare a null model with random effects (subject) only to a full model with all fixed effects (trial type and species) plus random effects, and a model with interaction terms (trial type × species) plus random effects. Post-hoc pairwise comparisons were conducted using Tukey corrections.

2.2. Results and Discussion

Comparison between the full model with fixed effects and a null model for predicting reaction times was significant (GLMM: $X^2 = 163.20$, $p < .001$; see Table A1 for full model comparison). Additionally, the two-way trial-type × species interaction was significant (GLMM: $X^2 = 82.09$, $p < .001$), indicating species differences in reaction time to the different trial types (Fig. 3a). Overall, monkeys responded significantly faster than orangutans (monkey mean = 1.1 s; orangutan mean = 1.96 s). Pairwise comparisons further revealed that monkeys responded significantly

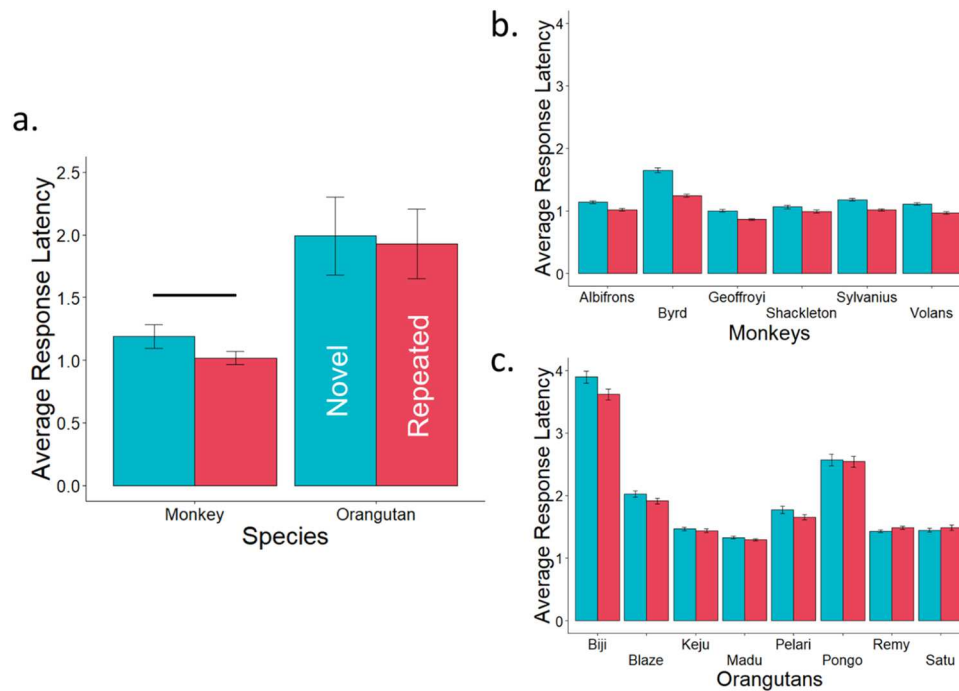


Fig. 3. a) Average latency (in seconds) to select the target in monkeys and orangutans in Experiment 1. Blue bars show response latencies on trials with novel image distractors, whereas pink bars show response latencies on trials with repeated, familiar images (with the first two presentations of the repeated image removed). Individual response latencies are shown for monkeys (b) and orangutans (c). Error bars reflect standard error of the mean. Lines indicate a significant difference in post-hoc pairwise comparisons, $p < .05$.

faster to repeated stimuli than they did to the novel stimuli ($\beta = 0.14$, $z = 15.41$, $p < .001$) while orangutans' response time did not significantly differ between the two trial types ($\beta = 0.02$, $z = 1.65$, $p = .10$).

Slower response to novel stimuli, as compared to repeated images, is consistent with a habituation response to the familiar, repeating, stimuli. The results are therefore demonstrating a significant habituation response in monkeys but not orangutans. A lack of statistical significance in response time between the two trial types does not prove an absence of a habituation effect in orangutans, and indeed the pattern of response overall in orangutans was the same as the monkeys. Looking at the individual latency response patterns does, however, indicate that monkeys may habituate more readily to these stimuli than orangutans, as all the monkeys show the pattern of response indicative of habituation (Fig. 3b), while there is some variation between individual orangutans (Fig. 3c).

One possibility for why we may not be seeing as strong of a habituation response in the orangutans could be that they have particularly good attentional control, allowing them to ignore the distractor image more effectively, whether it is a familiar or unfamiliar image. To test for this possibility, in Experiment 2, we included *Blank* trials in which there was no image at all presented with the target and distractors. An animal attending to the images (whether they are habituating to repeating images or not) should show a faster response on trials in which there is no distractor compared to either of the image conditions. Alternatively, if orangutans do not show a difference between blank trials and those with images, it may mean that they are somehow able to entirely ignore the distractors.

3. Experiment 2: Blank trials

3.1. Method

3.1.1. Subjects and apparatus

The same subjects (except for one less Bornean orangutan, Satu, who chose not to participate) were tested (orangutan $n=7$, monkey $n=6$) and the same apparatuses were used in Experiment 2 as in Experiment 1.

3.1.2. Procedure

Animals proceeded directly to habituation testing in Experiment 2 with no additional training. Trials proceeded as in Experiment 1, except that in addition to *Repeated* trials (one image presented repeatedly within a single session, differing between sessions) and *Novel* trials (never before seen images), *Blank* trials were added in which no distractor image appeared. Every block of six trials included two *Repeated* trials, two *Novel* trials, and two *Blank* trials in a random order (Fig. 4). Sessions consisted of 42 trials, including a total of 14 *Repeated* trials, 14 *Novel* trials, and 14 *Blank* trials. This modification of the procedure produces fewer repetitions of the familiar images per session (from 20 to 14), which could cause a reduction in habituation, but was chosen to match session length in Experiment 1. Animals completed 10 sessions.

3.1.3. Analysis

The same analytic strategy was used as in Experiment 1, with the exception that the first block of six trials (two *Blank*, two *Repeated*, and two *Novel*) was excluded, rather than just the first four trials, to account for the additional trial-type in Experiment 2 compared to Experiment 1. As in Experiment 1, accuracy on the target-finding task was high for both species (monkey accuracy = 99.9%; orangutan accuracy = 97.8%).

3.2. Results and Discussion

The full model with fixed effects (trial-type and species) was a significantly better fit than a null model (GLMM: $X^2 = 32.95$, $p < .001$; see Table A2 for full model comparison) and there was a significant interaction between trial-type and species (GLMM: $X^2 = 11.20$, $p = .004$). As in Experiment 1, monkeys generally selected the targets significantly faster than the orangutans (monkey mean = .94 s; orangutan mean = 1.69 s). Also similarly, post-hoc pairwise comparisons revealed significant contrasts for monkeys but not orangutans. Monkeys' responses were significantly faster on *Repeated* compared to *Novel* ($\beta = 0.09$, $z = 6.09$, $p < .001$) and *Blank* ($\beta = 0.04$, $z = 2.56$, $p = .03$) trials, and significantly faster on *Blank* compared to *Novel* ($\beta = 0.06$, $z = 3.46$, $p = .001$) trials, while orangutan responses did not significantly differ between conditions (Fig. 5a).

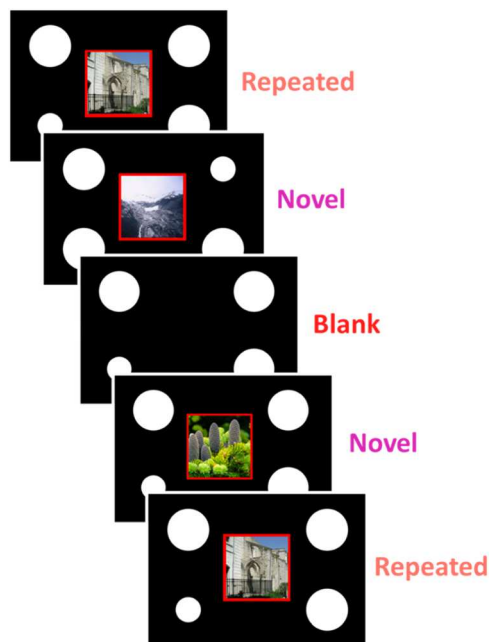


Fig. 4. Example organization of trial types in Experiment 2.

In Experiment 2, there is once again a significantly slower response in the presence of the novel stimuli relative to the repeated stimuli in monkeys, but not orangutans. The overall pattern of effect is the same in orangutans, but we again see substantial variation in the individual orangutan habituation effect (Fig. 5c), while the monkeys all show the expected direction of effect (Fig. 5b). Interestingly, although we see the same effect of response times to *Novel* versus *Repeated* stimuli for both monkeys and orangutans in Experiment 2 as we did in Experiment 1, we did not find the expected reduced latency to respond in the *Blank* trials relative to both the image-based trial types in either species. We

hypothesized that if subjects were attending to the images (*Repeated* or *Novel*), reaction times would be faster in the *Blank* condition in which there is no image to 'distract'. We did not, however, find that reaction times were fastest in this blank condition. One possible explanation for this is that the subjects may have hesitated on *Blank* trials as they waited for an image to appear as usual. While subjects were all initially trained in Experiment 1 on the target finding task alone (similar in appearance to a *Blank* trial in Experiment 2), no additional training was completed before Experiment 2, so it had been more than 20 sessions with every trial having an image in the center before they were suddenly exposed to *Blank* trials in this experiment, and two thirds of the trials still had images in the center.

While we replicated the habituation effect found in Experiment 1 of repeating stimuli on monkey reaction time, and similarly failed to find a significant effect in orangutans, we did not see the expected effect of our blank control trials. Since these trials were introduced as a means to examine attentional control, assuming that response time to *Blank* trials should be faster than any with a distracting image, it is difficult to conclude whether the greater habituation response of monkeys is the result of less attentional control than the orangutans. We therefore designed a third experiment that might better address this, in conjunction with additional measures that might increase attention to the images, and therefore presumably increase habituation to familiar images if that is occurring. Specifically, we moved the distracting images to *within* the target finding task, while simultaneously making the task somewhat harder by reducing the relative size difference between the target and distractor shapes.

4. Experiment 3: Images within targets

4.1. Method

4.1.1. Subjects and apparatus

The same apparatuses were used in Experiment 3 as in Experiments 1 and 2. As in the previous experiments, 6 macaques were tested, however one of the monkeys was a different individual due to loss (Juan Carlos

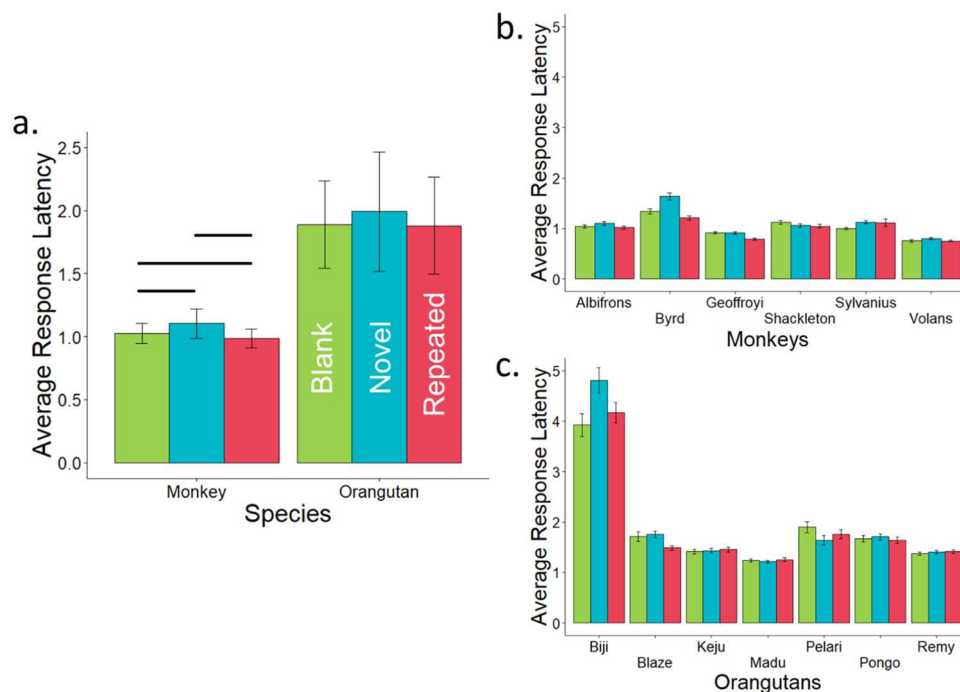


Fig. 5. a) Average latency (in seconds) to select the target in monkeys and orangutans in Experiment 2. Green bars show response latencies on trials with no distractor image present, blue bars show response latencies on trials with novel image distractors, and pink bars show response latencies on trials with repeated, familiar images (with the first two presentations of the repeated image removed). Individual response latencies are shown for monkeys (b) and orangutans (c). Error bars reflect standard error of the mean. Lines indicate a significant difference in post-hoc pairwise comparisons, $p < .05$.

replacing Sylvanius). In addition, only 6 orangutans were tested in this experiment (4 Sumatran and 2 Bornean orangutans) as one individual (Biji) did not pass training.

4.1.2. Procedure

The same general procedure was used in Experiment 3 as the previous experiments, but the targets were square (instead of circular), the images were located *within* the targets (as opposed to the center of the screen), and the target was closer in relative size to the distractors (Fig. 6). These changes were made to increase the likelihood that subjects would be distracted by the images while performing the target-finding task.

Subjects were first trained on the new task with 'blank' trials. After a self-start button was selected, black squares (240 × 240 pixels) with a thick white border (280 × 280 pixels) appeared in three corners, with a smaller target square in one corner. Subjects were required to touch the smaller stimulus to receive a reward. Subjects were first trained to criterion ($\geq 85\%$ accuracy across two consecutive sessions) on a target that was much smaller than the distractors (205 × 205 pixels), and then with a target size that was closer to the size of the distractors (215 × 215 pixels; relatively more difficult) to the same criterion. It took monkeys an average of 15.8 sessions to reach criterion across both sizes, and orangutans an average of 11.7 sessions.

After training, subjects advanced directly to testing. Trials proceeded as in Experiment 2. Every block of six trials included two *Repeated* trials, two *Novel* trials, and two *Blank* trials in a pseudo random order. Each 42-trial session included 14 *Repeated* trials, 14 *Novel* trials, and 14 *Blank* trials until they had completed 10 sessions with greater than or equal to 85% accuracy across image (*Novel* and *Repeated* combined) and *Blank* trial types. If after 10 sessions a subject had not yet performed with an accuracy greater than 85% on the image trials within a single session, subjects were placed on remedial training in which all the trials had an image instead of blanks, but the image only changed between *sessions* (the same image was used on all trials within a session). All six of the monkeys required this remedial training while only two of the six orangutans did. After two consecutive sessions with greater than 85% accuracy, subjects were placed back on testing. It took the monkeys an average of 67 sessions to reach this criterion, and orangutans 12.5 sessions.

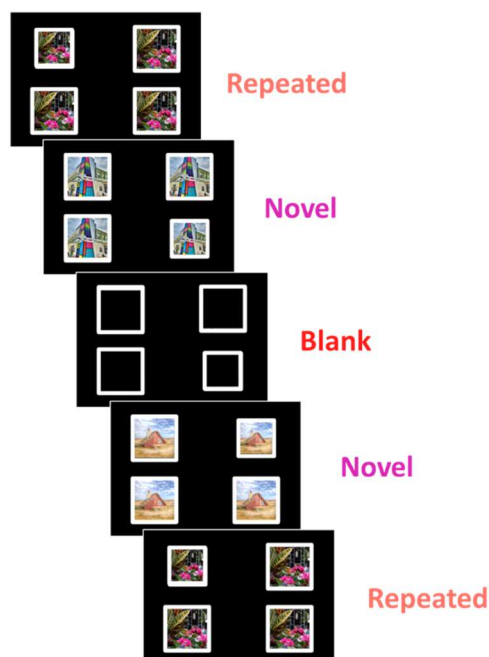


Fig. 6. Example organization of trial types in Experiment 3.

4.1.3. Analysis

The same analytic strategy was used in Experiment 3 as was used in Experiment 2. Accuracy on the target-finding task was high for both species (monkey accuracy = 92.8%; orangutan accuracy = 93.8).

4.2. Results and Discussion

The full model with trial-type and species was a significantly better fit than a null model (GLMM: $X^2 = 238.66$, $p < .001$; see Table A3 for full model comparison) and there was once again a significant interaction between trial-type and species (GLMM: $X^2 = 47.65$, $p < .001$). Unlike in Experiments 1 and 2, overall there was not a significant difference in species reaction times (monkey mean = 2.12 s; orangutan mean = 2.31 s). Post-hoc pairwise comparisons show, as in the previous experiments, that monkeys, but not orangutans showed significantly faster responding on *Repeated* trials compared to *Novel* trials (monkey: $\beta = 0.12$, $z = 5.76$, $p < .001$; orangutan: $\beta = 0.09$, $z = 2.01$, $p = .09$). Interestingly, in this experiment, both species show the expected effect of the *Blank* control trials, with significantly faster responding in these trials compared to either the *Repeated* (monkey: $\beta = 0.19$, $z = 10.32$, $p < .001$; orangutan: $\beta = 0.07$, $z = 3.78$, $p < .001$) or *Novel* trials (monkey: $\beta = 0.30$, $z = 15.85$, $p < .001$; orangutan: $\beta = 0.12$, $z = 5.88$, $p < .001$).

Blank trials in this experiment had no distracting image and we found the shortest reaction times on these trials in both species (Fig. 7a), indicating that these trials seemed to serve as the intended attentional control. Regardless of the content of the image (familiar or not), both species responded faster to find the target when there was no image at all to distract them. Furthermore, the monkeys again showed habituation to repeated, familiar images, showing shorter response times on trials with familiar images compared to trials with a novel image. Once again, however, while the direction of the effect was the same in orangutans in this experiment, it was not of a large enough magnitude to be statistically significant. We reiterate that the absence of statistical significance is not evidence of an absence of habituation, but we are consistently seeing that the apes appear to habituate less readily than the monkeys. Indeed, in this experiment there is a significant difference between the *Blank* trials and either image-type trial for the orangutans. Enhanced attentional control in the orangutans cannot fully explain the fact that they habituate less readily in this experiment, as they were still distracted by the images even though their behavior did not differentiate between image types. One possibility, however, is that the orangutans were able to attend primarily to the bright, distinctive, border around the images to solve the task, and avert their attention away from the image contents. This could still potentially result in the significantly faster response time to blank stimuli, as the overall popout effect of the smaller square in *Blank* trials may have been more obvious than in the image type trials. As a final test for this, we designed our last experiment identically to Experiment 3, with the exception that we reduced the brightness of the border around the images. Decreasing the brightness of the borders relative to the images might increase the relative amount of attention attracted by the images compared to the borders that defined their size.

5. Experiment 4: Images within targets, dimmer border

5.1. Method

5.1.1. Subjects and apparatus

The same subjects were tested, and the same apparatuses were used as in Experiment 3.

5.1.2. Procedure

The same procedures were used as in Experiment 3, although subjects were not first placed on any training. The primary difference in this experiment was a significantly lower brightness of the white border defining the size of the stimuli (Fig. 8). One monkey subject (Juan

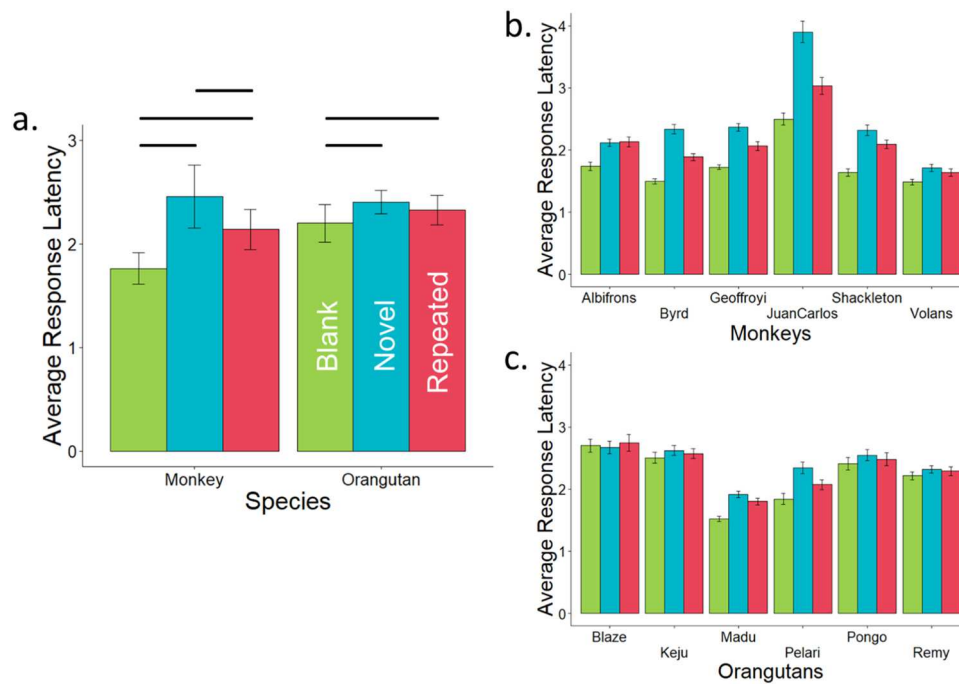


Fig. 7. a) Average latency (in seconds) to select the target in monkeys and orangutans in Experiment 3. Green bars show response latencies on trials with no distractor image present, blue bars show response latencies on trials with novel image distractors, and pink bars show response latencies on trials with repeated, familiar images (with the first two presentations of the repeated image removed). Individual response latencies are shown for monkeys (b) and orangutans (c). Error bars reflect standard error of the mean. Lines indicate a significant difference in post-hoc pairwise comparisons, $p < .05$.

Carlos) failed to reach the criterion of 10 sessions with accuracy greater than 85% on both blank and image trials after 130 sessions. We included data from his best 10 sessions instead (average accuracy of 90% for blank and 82% for image trials).

5.1.3. Analysis

The same analytic strategy was used in Experiment 4 as was used in Experiments 2 and 3. Accuracy on the target-finding task was high for both species (monkey accuracy = 91.2%; orangutan accuracy = 92.5%).

5.2. Results and Discussion

The full model with fixed effects was a significantly better fit than a null model (GLMM: $X^2 = 34.73$, $p < .001$; see Table A4 for full model comparison) and, as in all previous experiments, there was a significant interaction between trial-type and species (GLMM: $X^2 = 8.28$, $p = .016$). Unlike in the previous experiments, pairwise comparisons revealed significantly faster response times to the *Repeated* trials compared to *Novel* trials for both species (monkey: $\beta = 0.12$, $z = 5.14$, $p < .001$; orangutan: $\beta = 0.07$, $z = 3.07$, $p = .006$). We did not, however, replicate the results for responses to the control (*Blank* trials) as in Experiment 3. While the monkeys responded significantly faster on *Blank* trials compared to *Novel* trials ($\beta = 0.11$, $z = 4.67$, $p < .001$), they did not respond faster to *Blank* trials compared to *Repeated* trials ($\beta = 0.01$, $z = 0.44$, $p = .90$). Furthermore, orangutans actually responded significantly slower on these *Blank* trials than the *Repeated* trials ($\beta = -0.05$, $z = -2.42$, $p = .041$), and there was not a significant difference between *Blank* and *Novel* trials ($\beta = 0.01$, $z = 0.65$, $p = .79$).

Thus, in Experiment 4, we replicated the effects of the primary comparison (*Repeated* vs *Novel* trials) from the previous 3 experiments for monkeys, showing the habituation effect of decreased response time to familiar images (Fig. 9a). Interestingly, we do get the first statistically significant difference between these trial types in orangutans in this study, indicating habituation, although we still see more individual variation in the pattern of responding in orangutans compared to monkeys (Fig. 9b and c). We did not, however, find the expected response to

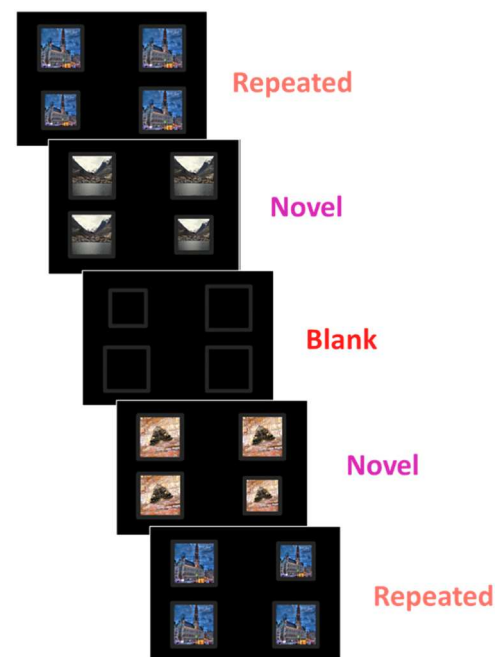


Fig. 8. Example organization of trial types in Experiment 4.

the *Blank* control trials. Our attempt to emphasize the image over the border in this experiment may have resulted in the task inadvertently being more difficult on *Blank* trials. The *Blank* trials with no image in the center were only discriminable on the basis of the now dim border and did not stand out against the black background as they did in prior experiments. This is presumably what led to the increase in latency for this trial type. Indeed, anecdotally, we found that viewing the screen at different angles had a disproportionate effect on these *Blank* trials, making the target more difficult to discern. While both species viewed the task on

identical model displays, the orangutans appeared more likely to view the screen from different positions, both within and between sessions, while the monkeys seemed to sit in a relatively constant location. This may account for the more variable effect of the *Blank* trials in orangutans.

Interestingly, we found the first statistically significant habituation in orangutans in this final experiment. While we cannot rule out the possibility that this was the result of orangutans taking longer to become accustomed to the task, monkeys and orangutans were matched for exposure to the tasks over the course of the experiments. One, potentially more likely possibility, is that while the dimmed border had an unexpected effect on the *Blank* trials, it did in fact have the desired effect on the image trials, increasing the emphasis on the image itself compared to the border, and therefore decreasing the ability of orangutans to exert their attentional control away from the contents. We reiterate, however, that the overall pattern of response to the image trials across all experiments was consistent with habituation in orangutans, and the lack of significance in the previous experiments does not indicate that there was no habituation. The emphasis on the image contents in this final experiment may have been enough to simply increase the magnitude of the effect. [Table 2](#)

6. General discussion

In a previous series of experiments, we found no conditions under which orangutans relied on image familiarity to solve a memory task, even when doing so was the only way to solve the task (R. J. Brady et al., 2021). Instead, the orangutans seemed to rely solely on working memory, despite working memory presumably being cognitively taxing and familiarity not so (Larzabal et al., 2018; Logie, 1986; Phillips and Christie, 1977). In contrast, monkeys in the same experiments used both working memory and familiarity, and performed well in the task that could be solved only by familiarity (R. J. Brady et al., 2021).

In the current study we tested for decreases in response or attention to repeated images. Evidence of such habituation would show that animals do register the fact that some images repeat, even if orangutans do not use that information in matching to sample tests. Although response latencies

Table 2
Summary of results from all experiments.

	Experiment 1	Experiment 2	Experiment 3	Experiment 4
<i>Species</i>				
Rhesus macaque	✓	✓	✓	✓
Orangutan	✗	✗	✗	✓

Note: Checkmarks indicate a statistically significant difference found between repeated and novel image types in post-hoc tests. X's indicate that there was no significant difference.

were in the direction expected if habituation occurred across all experiments, this effect was statistically significant for orangutans in only one of the four experiments. While experiments 2–4 involved fewer repetitions of the familiar image in each session (from 20 to 14 repetitions), monkeys nonetheless continued to show habituation in each experiment, and the orangutans showed significant habituation in only Experiment 4, so the exact number of repetitions does not appear to be a critical variable for obtaining effects in these experiments. Additionally, across all four experiments, the orangutans showed individual variation in response to the different image types. In contrast, rhesus monkeys habituated significantly to repeated images in all the experiments and, with exception of one monkey in Experiment 3, individual monkeys always showed the pattern of response expected with habituation. Together with previous findings (R. J. Brady et al., 2021), these results suggest that orangutans are less likely to show effects of image repetition than are rhesus monkeys.

It is possible that failure to find habituation in the orangutans in some of the studies was due to a lack of statistical power. In the first two experiments, the variability of response latencies was larger for orangutans than in monkeys, and response latencies in general were longer for orangutans. But invoking lack of statistical power as an explanation of the species differences should be done with caution given that at least as many orangutans as monkeys were used in each experiment. Additionally, in Experiment 3 and 4, identical numbers of monkeys and

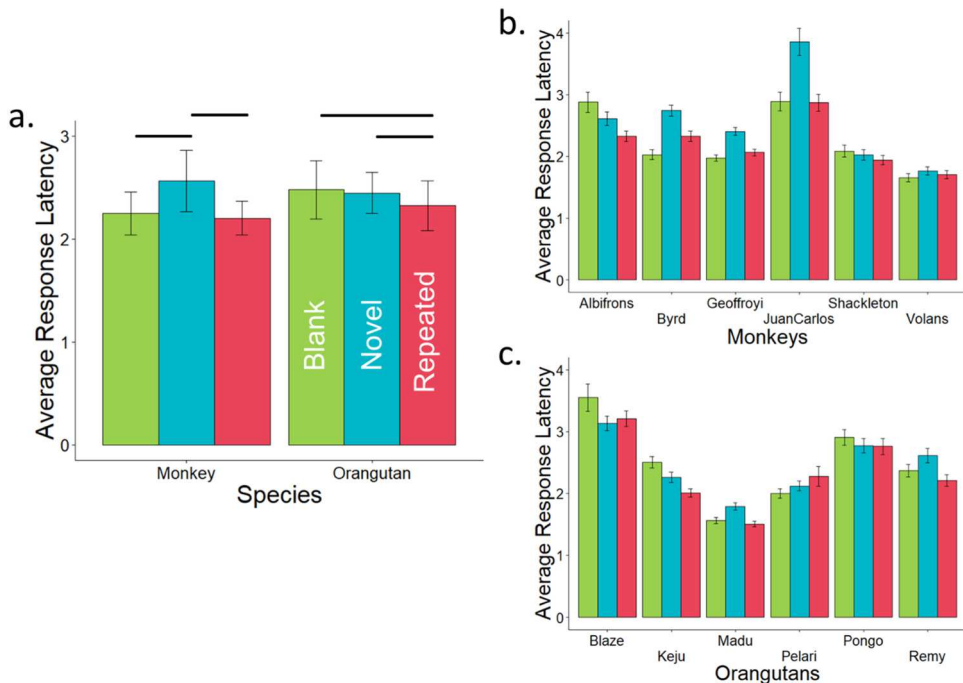


Fig. 9. a) Average response latency (in seconds) to selecting the target between monkeys and orangutans in Experiment 4. Green bars show response latencies on trials with no distractor image present, blue bars show response latencies on trials with novel image distractors, and pink bars show response latencies on trials with repeated, familiar images (with the first two presentations of the repeated image removed). Individual response latencies are shown for monkeys (b) and orangutans (c). Error bars reflect standard error of the mean. Lines indicate a significant difference in post-hoc pairwise comparisons, $p < .05$.

orangutans were well matched for latencies and variation. With this matching, monkeys, but not orangutans, clearly demonstrated habituation in Experiment 3. While lack of statistical power is a possibility if there was a very small effect for orangutans, it is worth noting that even if this is the case, we still see larger effects in monkeys.

We do not argue that orangutans do not habituate. Habituation has been argued to be one of the oldest forms of learning (van Duijn, 2017), and habituation, while not typically quantified, is noted when wild orangutans are observed over time (Hardus et al., 2009; Lameira et al., 2013). One possible explanation for finding less habituation in orangutans in these experiments is that the orangutans are somehow processing the computerized visual stimuli differently than macaques, which might account for minimal habituation found here as well as their inability to use cues of familiarity found in previous research (R. J. Brady et al., 2021). While the orangutans are obviously able to attend to computerized images, as they are successful on tasks in which they can rely on their working memory, it is possible that they disproportionately rely on localized cues to recall a sample image instead of the image as a whole, as may be more intuitive to humans. This hypothesis, however, is not supported by research on categorization in orangutans, which has demonstrated that orangutans can categorize within various biological categories (such as birds, reptiles, insects, mammals, and fish; Vonk, 2013), and can classify stimuli as birds, fish, flowers or people based on multiple attributes, including global features, in a manner very similar to monkeys (Diamond et al., 2016). Other research has, however, found that local features, such as color, can have a strong effect on orangutan categorization in some cases (Marsh and MacDonald, 2008).

It is possible, but unlikely, that motivational differences may have influenced the results. The orangutans in this study were housed at a zoological facility and participated in this research immediately following the first feeding of the day. The monkeys were similarly tested in their standard housing, but they were not fed before they began testing. It is possible that monkeys paid more attention due to higher motivation to get food rewards. It is also possible that there were different levels of distraction in the two housing environments. Monkeys were housed in social proximity to conspecifics, with other monkeys in adjacent cages, but with no physical access to each other. Human experimenters and husbandry staff were rarely in the room with them. Orangutans also had conspecifics nearby, but were not physically separated from one another. The experimenter was always present in the housing space during testing of orangutans, and husbandry staff were also sometimes present. There were also more potentially distracting objects in the orangutan space than in the monkey areas. Distraction could cause longer reaction times overall, as was observed for orangutans in Experiments 1 and 2. It seems less likely, but possible, that distraction selectively affected trials with repeated stimuli. It is more likely that distraction could have increased the variance in response times seen for the orangutans, which would reduce the chances of observing significant habituation. Greater variance in orangutans might therefore have affected Experiments 1 and 2 (in which the orangutans did not show habituation), but would not apply in Experiment 3, where the variance was less for orangutans than monkeys. In Experiment 3, monkeys but not orangutans showed significant habituation. These concerns about motivation and distraction are reduced, but not eliminated, by the requirement that both species had to perform at criterion levels of accuracy, and that we analyzed response latencies from correct trials only.

A final difference between species is that monkeys had substantially more experience with computerized testing. This additional experience could have made them more likely to actively attend to the images, perhaps anticipating a memory test, for example. On the other hand, the extensive testing experience of the monkeys might cause them to learn rapidly to ignore features of the test displays that are not relevant to the task, and ignoring the novel images altogether would attenuate measures of habituation. While differences in attention might affect the habituation scores reported here, this work was motivated by the finding that orangutans did not use familiarity, but did use attentionally

demanding working memory, in other tests (R. J. Brady et al., 2021). Inattention would be expected to have the opposite effects to those observed by Brady et al. (2021) and it is probably more parsimonious to seek a common explanation for both sets of findings. Weak familiarity signals in orangutans provides one such common explanation for the differences in matching-to-sample performance and habituation.

Interestingly, one major difference between monkeys and orangutans is the relative size of their prefrontal cortex, with apes having a larger prefrontal cortex relative to body size than do monkeys (Pas-singham and Smaers, 2014; Rilling, 2006). The prefrontal cortex is considered critical for working memory and cognitive control (Kane and Engle, 2002; Miller, 2000; Rougier et al., 2005). One possibility we were unable to rule out is that orangutans exert superior attentional control compared to the monkeys. Because the distractor images were always task-irrelevant, an ability to ignore the images might manifest in no response latency differences between trials with familiar and novel images. Indeed, this hypothesis may be supported by the fact that the only experiment in which we did find habituation at statistically significant levels in the orangutans was in the final experiment, specifically designed to limit the ability to ignore the distracting images.

Finally, whilst orangutans have a relatively larger prefrontal cortex than do monkeys, they also have a disproportionately small ventromedial prefrontal cortex relative to other apes (Schenker et al., 2005; Semendeferi et al., 2001). Damage to the ventromedial prefrontal cortex has been linked to recognition deficits with large image sets in monkeys (Bachevalier and Mishkin, 1986), and is connected to the perirhinal cortex which is implicated in encoding familiarity (Haskins et al., 2008). It is therefore possible that orangutans' relatively small ventromedial prefrontal cortex may contribute to their inability to recognize images as familiar (R. J. Brady et al., 2021) or habituate to repeated images in the current experiment as readily as macaques do. We do not know of any similar comparisons of familiarity to working memory in other apes, and so it will be important to test whether this apparent lack of familiarity occurs in other species, or is specific to orangutans. Additionally, dishabituation paradigms might shed more light specifically on the behavioral effects of repeated stimuli presentation in both orangutans and other apes.

We find here that orangutans habituate less than do monkeys to visual images presented on computer screens. This points to a need for further research on both habituation and familiarity processes in orangutans, and a deeper exploration of whether these effects are an artifact of computerized images and testing, or some underlying difference between monkeys and orangutans.

Funding

This research was supported by the NIH Office of the Director, Office of Research Infrastructure Programs, P51 OD011132. Additional support was provided by NSF BCS-1946767, and K12 GM000680/GM/NIGMS NIH HHS/United States (MFW).

Declaration of Competing Interest

none.

Data Availability

Data will be made available on request.

Acknowledgements

We thank Tara A. Dove-VanWormer for help testing the monkeys. We thank Jodi Carrigan, Marieke Gartner, Jennifer M. Mickelberg, Lynn Yakubinis, and all of the keepers and staff at Zoo Atlanta who made this work with the orangutans possible.

Appendix

Table A1
Model comparison used to predict reaction time in Experiment 1

Model	df	AIC _c	χ ²	p
Null		12962.88		
Species + Trial-type	2	12803.68	163.20	<.001*
Species x Trial-type	1	12723.58	82.09	<.001*

Note. AIC_c = corrected Akaike information criterion. *s indicate *p* < .05.

Table A2
Model comparison used to predict reaction time in Experiment 2

Model	df	AIC _c	χ ²	p
Null		4879.51		
Species + Trial-type	3	4852.58	32.94	<.001*
Species x Trial-type	2	4845.39	11.20	.004*

Note. AIC_c = corrected Akaike information criterion. *s indicate *p* < .05.

Table A3
Model comparison used to predict reaction time in Experiment 3

Model	df	AIC _c	χ ²	p
Null		8827.61		
Species + Trial-type	3	8594.97	238.66	<.001*
Species x Trial-type	2	8551.33	47.65	<.001*

Note. AIC_c = corrected Akaike information criterion. *s indicate *p* < .05.

Table A4
Model comparison used to predict reaction time in Experiment 4

Model	df	AIC _c	χ ²	p
Null		10239.57		
Species + Trial-type	3	10210.86	34.73	<.001*
Species x Trial-type	2	10206.60	8.28	.016*

Note. AIC_c = corrected Akaike information criterion. *s indicate *p* < .05.

References

Aggleton, J.P., Brown, M.W., 1999. Episodic memory, amnesia, and the hippocampal–anterior thalamic axis. *Behav. Brain Sci.* 22 (3), 425–444.

Bachevalier, J., Mishkin, M., 1986. Visual recognition impairment follows ventromedial but not dorsolateral prefrontal lesions in monkeys. *Behav. Brain Res.* 20 (3), 249–261. [https://doi.org/10.1016/0166-4328\(86\)90225-1](https://doi.org/10.1016/0166-4328(86)90225-1).

Baddeley, B., Graham, P., Husbands, P., Philippides, A., 2012. A model of ant route navigation driven by scene familiarity. *PLOS Comput. Biol.* 8 (1), e1002336 <https://doi.org/10.1371/journal.pcbi.1002336>.

Basile, B.M., Hampton, R.R., 2013. Dissociation of active working memory and passive recognition in rhesus monkeys. *Cognition* 126 (3), 391–396. <https://doi.org/10.1016/j.cognition.2012.10.012>.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.

Brady, R.J., Hampton, R.R., 2018. Nonverbal working memory for novel images in rhesus monkeys. *Curr. Biol.* 28 (24), 3903–3910.

Brady, T.F., Konkle, T., Alvarez, G.A., Oliva, A., 2008. Visual long-term memory has a massive storage capacity for object details. *Proc. Natl. Acad. Sci.* 105 (38), 14325–14329. <https://doi.org/10.1073/pnas.0803390105>.

Brady, R.J., Mickelberg, J.M., Hampton, R.R., 2021. Greater dependence on working memory and restricted familiarity in orangutans compared with rhesus monkeys. *Learn. Mem.* 28 (8), 260–269. <https://doi.org/10.1101/lm.053422.121>.

Brown, E.K., Hampton, R.R., 2020. Cognitive control of working memory but not familiarity in rhesus monkeys (*Macaca mulatta*). *Learn. Behav.* 48 (4), 444–452. <https://doi.org/10.3758/s13420-020-00432-7>.

Cohen, N.J., Eichenbaum, H., 1993. *Memory, amnesia, and the hippocampal system*. The MIT Press.

Cowan, N., 2010. The magical mystery four: how is working memory capacity limited, and why? *Curr. Dir. Psychol. Sci.* 19 (1), 51–57. <https://doi.org/10.1177/0963721409359277>.

Diamond, R.F.L., Stoinski, T.S., Mickelberg, J.L., Basile, B.M., Gazes, R.P., Templer, V.L., Hampton, R.R., 2016. Similar stimulus features control visual classification in orangutans and rhesus monkeys. *J. Exp. Anal. Behav.* 105 (1), 100–110. <https://doi.org/10.1002/jeab.176>.

van Duijn, M., 2017. Phylogenetic origins of biological cognition: Convergent patterns in the early evolution of learning. *Interface Focus* 7 (3), 20160158. <https://doi.org/10.1098/rsfs.2016.0158>.

Eacott, M.J., Easton, A., 2007. On familiarity and recall of events by rats. *Hippocampus* 17 (9), 890–897. <https://doi.org/10.1002/hipo.20325>.

Eichenbaum, H., Yonelinas, A.R., Ranganath, C., 2007. The medial temporal lobe and recognition memory. *Annu. Rev. Neurosci.* 30, 123–152. <https://doi.org/10.1146/annurev.neuro.30.051606.094328>.

Flores-Abreu, I.N., Hurly, T.A., Healy, S.D., 2012. One-trial spatial learning: Wild hummingbirds relocate a reward after a single visit. *Anim. Cogn.* 15 (4), 631–637. <https://doi.org/10.1007/s10071-012-0491-0>.

Gazes, R.P., Diamond, R.F.L., Hope, J.M., Caillaud, D., Stoinski, T.S., Hampton, R.R., 2017. Spatial representation of magnitude in gorillas and orangutans. *Cognition* 168, 312–319. <https://doi.org/10.1016/j.cognition.2017.07.010>.

Hanazuka, Y., Shimahara, N., Tokuda, Y., Midorikawa, A., 2013. Orangutans (*Pongo pygmaeus*) remember old acquaintances. *PLOS ONE* 8 (12), e82073. <https://doi.org/10.1371/journal.pone.0082073>.

Hardus, M.E., Lameira, A.R., Van Schaik, C.P., Wich, S.A., 2009. Tool use in wild orangutans modifies sound production: A functionally deceptive innovation? *Proc. R. Soc. B: Biol. Sci.* 276 (1673), 3689–3694. <https://doi.org/10.1098/rspb.2009.1027>.

Haskins, A.L., Yonelinas, A.P., Quamme, J.R., Ranganath, C., 2008. Perirhinal cortex supports encoding and familiarity-based recognition of novel associations. *Neuron* 59 (4), 554–560.

Jacoby, L.L., 1991. A process dissociation framework: Separating automatic from intentional uses of memory. *J. Mem. Lang.* 30 (5), 513–541. [https://doi.org/10.1016/0749-596X\(91\)90025-F](https://doi.org/10.1016/0749-596X(91)90025-F).

Kane, M.J., Engle, R.W., 2002. The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. *Psychon. Bull. Rev.* 9 (4), 637–671. <https://doi.org/10.3758/BF03196323>.

Kelley, C.M., Jacoby, L.L., 1998. Subjective reports and process dissociation: Fluency, knowing, and feeling. *Acta Psychol.* 98 (2), 127–140. [https://doi.org/10.1016/S0001-6918\(97\)00039-5](https://doi.org/10.1016/S0001-6918(97)00039-5).

Lameira, A.R., Hardus, M.E., Nouwen, K.J.J.M., Topelberg, E., Delgado, R.A., Spruijt, B. M., Sterck, E.H.M., Knott, C.D., Wich, S.A., 2013. Population-specific use of the same tool-assisted alarm call between two wild orangutan populations (*Pongopygmaeus*

- wurmbii) indicates functional arbitrariness. PLoS One 8 (7), e69749. <https://doi.org/10.1371/journal.pone.0069749>.
- Larzabal, C., Tramon, E., Murat, S., Thorpe, S.J., Barbeau, E.J., 2018. Extremely long-term memory and familiarity after 12 years. Cognition 170, 254–262. <https://doi.org/10.1016/j.cognition.2017.10.009>.
- Logie, R.H., 1986. Visuo-spatial processing in working memory. Q. J. Exp. Psychol. Sect. A 38 (2), 229–247. <https://doi.org/10.1080/14640748608401596>.
- Lo, S., Andrews, S., 2015. To transform or not to transform: Using generalized linear mixed models to analyse reaction time data. Front. Psychol. 6. (<https://www.frontiersin.org/journals/psychology/articles/10.3389/fpsyg.2015.01171>).
- Mandler, G., 1980. Recognizing: The judgment of previous occurrence. Psychol. Rev. 87 (3), 252–271. <https://doi.org/10.1037/0033-295X.87.3.252>.
- Marsh, H.L., MacDonald, S.E., 2008. The use of perceptual features in categorization by orangutans (*Pongo abelli*). Anim. Cogn. 11 (4), 569–585. <https://doi.org/10.1007/s10071-008-0148-1>.
- Miller, E.K., 2000. The prefrontal cortex and cognitive control. Article 1 Nat. Rev. Neurosci. 1 (1). <https://doi.org/10.1038/35036228>.
- Mitchell, D.B., 2006. Nonconscious priming after 17 years: invulnerable implicit memory? Psychol. Sci. 17 (11), 925–929. <https://doi.org/10.1111/j.1467-9280.2006.01805.x>.
- Oberauer, K., Lewandowsky, S., Awh, E., Brown, G.D.A., Conway, A., Cowan, N., Donkin, C., Farrell, S., Hitch, G.J., Hurlstone, M.J., Ma, W.J., Morey, C.C., Nee, D.E., Schweppe, J., Vergauwe, E., Ward, G., 2018. Benchmarks for models of short-term and working memory. Psychol. Bull. 144 (9), 885–958. <https://doi.org/10.1037/bul0000153>.
- Passingham, R.E., Smaers, J.B., 2014. Is the prefrontal cortex especially enlarged in the human brain? Allometric relations and remapping factors. Brain Behav. Evol. 84 (2), 156–166. <https://doi.org/10.1159/000365183>.
- Phillips, W.A., Christie, D.F.M., 1977. Components of visual memory. Q. J. Exp. Psychol. 29 (1), 117–133. <https://doi.org/10.1080/00335557743000080>.
- R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.R-project.org/>).
- Read, D.W., 2008. Working memory: A cognitive limit to non-human primate recursive thinking prior to hominid evolution, 147470490800600413 Evolut. Psychol. 6 (4). <https://doi.org/10.1177/147470490800600413>.
- Read, D.W., Manrique, H.M., Walker, M.J., 2022. On the working memory of humans and great apes: Strikingly similar or remarkably different? Neurosci. Biobehav. Rev. 134, 104496 <https://doi.org/10.1016/j.neubiorev.2021.12.019>.
- Rhodes, S., Cowan, N., 2018. Attention in working memory: Attention is needed but it years to be free. Ann. N. Y. Acad. Sci. 1424 (1), 52–63. <https://doi.org/10.1111/nyas.13652>.
- Rilling, J.K., 2006. Human and nonhuman primate brains: Are they allometrically scaled versions of the same design? Evolut. Anthropol.: Issues N. Rev. 15 (2), 65–77. <https://doi.org/10.1002/evan.20095>.
- Rougier, N.P., Noelle, D.C., Braver, T.S., Cohen, J.D., O'Reilly, R.C., 2005. Prefrontal cortex and flexible cognitive control: rules without symbols. Proc. Natl. Acad. Sci. USA 102 (20), 7338–7343. <https://doi.org/10.1073/pnas.0502455102>.
- Schenker, N.M., Desgouttes, A.-M., Semendeferi, K., 2005. Neural connectivity and cortical substrates of cognition in hominoids. J. Hum. Evol. 49 (5), 547–569. <https://doi.org/10.1016/j.jhevol.2005.06.004>.
- Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K., Van Hoesen, G.W., 2001. Prefrontal cortex in humans and apes: a comparative study of area 10. Am. J. Phys. Anthropol. 114 (3), 224–241. [https://doi.org/10.1002/1096-8644\(200103\)114:3<224::AID-AJPA1022>3.0.CO;2-I](https://doi.org/10.1002/1096-8644(200103)114:3<224::AID-AJPA1022>3.0.CO;2-I).
- Setia, T.M., Delgado, R.A., Atmoko, S.U., Singleton, I., Van Schaik, C.P., 2009. Social organization and male-female relationships. Orangutans–Geogr. Var. Behav. Ecol. Conserv. 245–253.
- Sherry, D.F., Schacter, D.L., 1987. The evolution of multiple memory systems. Psychol. Rev. 94 (4), 439–454. <https://doi.org/10.1037/0033-295X.94.4.439>.
- Singleton, I., van Schaik, C.P., 2002. The social organisation of a population of Sumatran orang-utans. Folia Primatol. ; Int. J. Primatol. 73 (1), 1–20. <https://doi.org/10.1159/000060415>.
- Squire, L.R., 2004. Memory systems of the brain: A brief history and current perspective. Neurobiol. Learn. Mem. 82 (3), 171–177. <https://doi.org/10.1016/j.nlm.2004.06.005>.
- Talbot, C.F., Mayo, L., Stoinski, T., Brosnan, S.F., 2015. Face discriminations by orangutans (*Pongo spp.*) vary as a function of familiarity. Evolut. Psychol. Sci. 1 (3), 172–182. <https://doi.org/10.1007/s40806-015-0019-3>.
- Thompson, R.F., Spencer, W.A., 1966. Habituation: A model phenomenon for the study of neuronal substrates of behavior. Psychol. Rev. 73 (1), 16–43. <https://doi.org/10.1037/h0022681>.
- Vonk, J., 2013. Matching based on biological categories in orangutans (*Pongo abelii*) and a gorilla (*Gorilla gorilla gorilla*). PeerJ 1, e158.
- Vonk, J., Hamilton, J., 2014. Orangutans (*Pongo abelii*) and a gorilla (*Gorilla gorilla gorilla*) match features in familiar and unfamiliar individuals. Anim. Cogn. 17 (5), 1089–1105. <https://doi.org/10.1007/s10071-014-0741-4>.
- Voss, J.L., Hauner, K.K., Paller, K.A., 2009. Establishing a relationship between activity reduction in human perirhinal cortex and priming. Hippocampus 19 (9), 773–778.
- Yonelinas, A.P., 2002. The nature of recollection and familiarity: a review of 30 years of research. J. Mem. Lang. 46 (3), 441–517. <https://doi.org/10.1006/jmla.2002.2864>.