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By

Wenying Zhu

Robert Hampton, PhD.
Adviser

Neuroscience and Behavioral Biology Program

Robert Hampton, PhD.
Adviser

Michael Crutcher, PhD.
Committee Member

Daniel Drane, PhD.
Committee Member

Ryan Brady
Committee Member

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a thesis submitted to the Faculty of Emory College of Arts and Sciences
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Abstract

Cognitive mechanisms of source memory in rhesus monkeys (*Maccaca mulatta)*

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In humans, successful recognition of context relies on source memory. However, in rhesus monkeys, evidence for source memory is scant, and little is known about the underlying cognitive mechanisms that support how monkeys might discriminate between contexts. Thus, through a series of experiments, we aim to investigate memory processes supporting source memory in rhesus monkeys. In Experiment 1, monkeys were shown images associated with two contexts, separated with a five-minute interval. After each of the context 2 images, they were presented a recognition test, and were rewarded for selecting context 1 images. Across sessions, all monkeys showed a shift from selecting context 2images at test, to selecting the context 1 images. This result demonstrates a discrimination between contexts, akin to source memory. To assess the extent to which this discrimination is supported by active, working memory-like mechanisms, or a more passive familiarity judgement, follow-up experiments investigated how cognitive load, extended delay intervals between context 2 and recognition test, and amount of exposure for context 1 images impact selection accuracy. Results show extending the delay between context 2 and test disrupts monkeys' performance. However, the exact roles of working memory, familiarity and recollection still remains to be further explored.

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Introduction:

In humans, successful recognition of a previously encountered object and the context related to it relies on the conjunction of item memory and source memory. It has been suggested that two processes, namely, familiarity and recollection, underlies both memory for the item itself and its associated source (Yonelinas, 1999; Wixted, 2007). Recognizing previously encountered objects, or item memory, can rely completely on familiarity, a mnemonic process that is automatic, fast, and codes for a feeling of knowing rather than details of context. Source memory, however, relies more heavily on recollection, a mnemonic process that is slower, more controlled, and allows for detailed and precise memory of source information (Yonelinas, 1999; Yonelinas, 2002). The ability to recollect the source of specific knowledge is a key characteristic of human episodic memory (Tulving, 1993). Thus, understanding mechanisms of recollection and familiarity in non-human primates is important to further our understanding of non-human episodic like memory.

Human memory paradigms have shown the separation of source memory and item memory (Yonelinas, 2002). For instance, when participants are presented with a list of non-famous names, the familiarity from having seen the names results in a relatively high item memory strength. With the fast decay of recollection memory, participants tend to misinterpret the non-famous names as famous after 24 hours (Jacoby, Kelly, Brown and Jasechko, 1989). However, if participants are presented with the non-famous names after a shorter interval, they can readily recollect seeing a name occurring in the non-famous name list, and successfully negate confounding influence of familiarity from the past experience of having seen the name (Jacoby, Woloshyn and Kelly, 1989). This paradigm, called the "False Fame paradigm", indicates that misattribution of sources can occur when source memory decays more rapidly than item memory (Jacoby, Kelly, Brown and Jasechko, 1989; Jacoby, Woloshyn and Kelly,1989).

Investigating source memory in non-human primates is critical for a better understanding of the evolution of primate memory and will allow us to compare the interaction between memory systems in different primate species. Additionally, it can also facilitate assessment for animal models aiming to provide translational results in both memory studies and pathology studies for memory impairments (Crystal, 2012). However, so far, the evidence documenting source memory in non-human animals is scant, and most studies have been performed with rats. For instance, rats distinguish between whether they had learned the location of food caches on their own, or under the guidance of researchers (Crystal et al, 2013). Such distinction can be regarded as a form of source memory, since it shows that the rats can tell the different means by which a location is known.

Rhesus monkeys have been shown to discriminate between two contexts separated by 10 or 20 seconds. Monkeys either simply viewed an image or categorized an image according to previously learned categories. If a 10 second or 20 second delay separated the two tasks, monkeys were able to distinguish between items encountered in different tasks, but had difficulty when the two tasks occurred at the beginning of the delay rather than separated. This suggests that rhesus monkeys’ ability to discriminate between two contexts may be limited to short time periods, and confusion of sources can arise when image recognition tasks are given with short intervals in between (Basile and Hampton, 2017). However, because a key characteristic of episodic memory in humans is that sources can be recalled over long-term periods of time, an important next step is to determine if context discrimination similar to what was observed in Basile and Hampton (2017) can be replicated when long time periods are used between two contexts.

In the current study, we first tested the degree to which monkeys can discriminate between images from two contexts that are separated by an extended period of time. Monkeys were first given a set of 40 pictures to be remembered. After five minutes, they were presented with 40 new images, each followed by a memory test. The test included four images: the one they just saw, one from five minutes ago, and two novel images. The monkeys were required to identify the image shown five minutes ago. We found that that monkeys were able to distinguish images from the earlier context. In follow-up experiments, we assessed the extent to which this discrimination was supported by active memory mechanisms such as working memory, or a more passive familiarity judgement.

Methods and Current Results:

Subjects:

Six adult male rhesus monkeys are participating in our experiment. The monkeys have access to water ad libitum, and receive full food rations each day after testing. All monkeys have previous experience with touchscreen based cognitive tasks such as target finding and match to sample tests for images. Testing procedures are approved by the Emory Institutional Animal Care and Use Committee. Experiments were conducted under the IACUC protocol YER-2003537-ENTRPR-A.

Apparatus:

Tests were conducted using portable testing systems consisting of a 15-inch LCD touchscreen, stereo speakers and two automatic pallet dispensers. The test equipment was available to monkeys from 10am to 5pm six days per week.

Stimuli:

The images used in this study were collected from three free open online image databases, Foter, Unsplash and Pixabay, using Scrapy, an open source python framework for website data extraction. In training phase, for each session, a set of 40 image stimuli were used as target images, and a set of 120 image stimuli were used as novel distracters during test. In Experiment I, II and III, for each session, a set of 40 images were used as context 1 images, and were presented the same way as the target images in training phase. Another set of 40 images were used as context 2 image stimuli, and 80 images served as novel distracters during the test. In

Experiment IV, the context 1 and context 2 image sets each contain 36 picture stimuli, while a set of 72 new images is used as novel image stimuli during the selection test. Across all training and experiment phases, images are never used repetitively.

Training:

<u>Procedure:</u> During training sessions, monkeys were presented with a set of 40 images that were used as target images in later testing. For each trial in this phase, monkeys self-initiated the image presentation by touching a green square on the screen twice. A sequence of four target images were then presented one at a time to the monkeys. Each target image appeared pseudo-randomly in one of the four corners of the screen, and monkeys again needed to touch each image twice to proceed to the next one. After every 4 pictures they touched, the monkeys received a target finding task, where four symbols occurred simultaneously in the four corners on screen. The monkeys were required to pick the one symbol that was different from the other three in order to receive a food reward. The symbols used in the target finding task were always the same, and the target symbol occurred pseudo-randomly at the four corners with equal frequency. The monkeys could only proceed to the next trial when they selected the correct symbol in target finding task. Selecting the other symbols would not elicit any responses from the program. This process was repeated such that monkeys were exposed to each of the 40 images 3 times (Figure 1).

Right after exposing monkeys to target images, test of matching to sample with four test stimuli was presented. The stimuli consisted of one image that was previously touched, and three novel images. Selection of the image from phase I was positively reinforced with auditory and food reward. Each testing session consisted of 40 trials, one trial for each image shown in the earlier sessions. Both the target image set and novel image set used in each session were different from the previous, and only one session of the training was performed each day in order to avoid interference caused by images from previous sessions. When monkeys reached an accuracy greater than 70% in this training for two consecutive days, the time between target finding task session and test session was increased to 5 minutes. After the monkeys again reached 70% accuracy in new training sessions for two consecutive days, Experiment I began.

Experiment I:

For Experiment 1, other than the original 40 images presented 5 minutes prior to the recognition task, a new image was presented at the center of the screen before each of the recognition tasks. As we considered features related to the item itself, the task design, as well as the passing of time to be components of the context that recognition tasks are based on, these new images were thus associated a different context than the original images (see General Discussion section for details). These image stimuli served as one of the distractors in image recognition tasks. All images were only used in one session, and there were no overlaps between images used in different days. We hypothesized that if monkeys were able to distinguish the contexts of these two image groups, then they would choose context 1 images above chance by the end of Experiment I

Procedure: In Experiment I, beside the original 40 target images (context 1), a set of 40 new images associated with different context was introduced to the monkeys (context 2 images). This was achieved by adding a new image before each recognition task trial, and monkeys had to touch the context 2 image in order to proceed (Figure 2). Five minutes after the presentation of all 40 context 1 images, the context 2 image presentation and recognition task would start. After touching each context 2 image twice, a recognition task would come up after 200msec of delay. While context 1 images would randomly occur at the four corners of the screen during presentation, the location of the context 2 images is fixed at the center of the screen during the presentation. For each recognition test, monkeys were again shown four test stimuli. The stimuli consisted of the image that was just touched, one image that was touched in earlier target finding task session, and two novel images. Selection of the context 1 image was positively reinforced with auditory and food reward. Each testing session consisted of 40 trials, one trial for each image used in context 1 sessions. We hypothesized that if monkeys were able to distinguish the contexts of two image groups separated by five minutes, then they would have above chance correct performance by the end of Experiment I.

Results: All monkeys indeed showed a shift from selecting more context 2 images at test, to selecting more context 1 images (Figure 3). The number of sessions that each monkey took to reach criteria varied drastically, with an average of 30 sessions, and a standard error of 7. This result suggests that monkeys are indeed able to distinguish between two images from different contexts separated by a 5-minute delay, just as observed for shorter delays. By placing 5 minutes of delay between context 1 and context 2 image presentations, as well as showing 40 different context 1 images repeated for three times in random sequence to monkeys, it was ensured that their memories for the context 1 images were well outside of the working memory range during recognition tasks. By presenting one image from context 1, one image from context 2, and two novel images in the recognition tasks, it was also ensured that the monkeys could not rely solely on familiarity strength to make the correct judgment. Although context 2 images were only shown once to the monkeys prior to the recognition task, yet context 1 images were shown three times, since the context 2 images were presented right before the recognition task, it would have the highest familiarity strength. Therefore, the monkeys could not accurately select the rewarded context 1 image by simply rejecting the image with highest familiarity (context 2 image), and the image with lowest familiarity (one of the novel images). Noticeably, at the beginning of Experiment I, the monkeys already had a very low selection percentage of novel images, indicating a clear distinction made between familiar and completely unfamiliar images. A switch of selection percentage only occurred between context 1 and context 2 images. There was a shift from selecting a higher percentage of context 2 images at the start of Experiment I to a higher selection percentage of context 1 images by the end of Experiment I. This indicates that monkeys switched from selecting an image only because it had the highest familiarity strength, to a more complex strategy. Experiment II was designed to investigate the exact cognitive mechanisms that enabled the monkeys to perform such context distinction.

Experiment II:

To explore underlying mechanisms that enabled monkeys to perform context distinction, we aimed to study whether working memory plays a role during the context discrimination process. One possibility is that monkeys achieve correct identification of context 1 images by holding the most recently seen context 2 images in working memory and rejecting it during recognition test. If this is true, then more confusion would happen between context 1 and context 2 images when the working memory for context 2 images are disrupted, but not with novel images. Thus, we hypothesized that if the monkeys distinguish different contexts by holding the most recently-seen image in working memory, then adding a cognitive load between image presentation and test will lead to a higher selection rate of context 2 image and a lower selection of context 1 image. On the other hand, adding a yoked delay interval should not have an effect on their performances.

Procedure: For this experiment, procedures were kept the same except that categorization tasks were added pseudo-randomly to half of the trials following context 2 image presentation, right before the test. The other half of the trials had un-filled delay intervals yoked to match the duration of the previous categorization trial (Figure 4). The categorization task required the monkeys to classify a given image into one of the four categories (fish, bird, flower, people), and has been previously shown to disrupt working memory (Basile & Hampton, 2013). We hypothesized that if the monkeys distinguish different contexts by holding the most recently-seen image in working memory, then adding a cognitive load between image presentation and test would lead to a higher selection rate of context 2 image and a lower selection of context 1 image.

Results: Counter to the hypothesis, when comparing the trials with and without additional cognitive load, although selection rate for context 1 significantly decreased (Figure 5, paired samples t test: $t_5 = 3.03$; $p = 0.029$), selection rate for novel images significantly increased (Figure 5, paired samples t test: $t_5 = 3.41$; $p = 0.019$). Selection rate for the context 2 images also did not significantly increase (Figure 5, paired samples t test: $t_5 = 0.966$; $p = 0.378$). Therefore, it is unlikely that the monkeys are holding context 2 image in working memory and rejecting it upon tests. On the other hand, a much more prominent difference in performance was found when comparing results of both trials with categorization tasks and delay-matched control trials in Experiment II to trials from Experiment I. The percentage of selecting context 1 images for both types of trials in Experiment II significantly decreased compared to Experiment 1 results (between control trials and Experiment I trials: paired samples t test: $t_5 = 6.92$, $p<0.001$; between categorical trials and Experiment I trials: paired samples t test: $t_5 = 11.2$, $p<0.001$). One factor that might have caused this is the elongated delay between context 2 presentation and recognition task for all Experiment II trials when compared to the original test. As the average time needed to complete the categorical task was around 3 seconds, a possibility is that the memory for context 2 images decreased significantly during both categorical tasks and empty delay intervals.

Experiment III:

Results from Experiment II showed a decrease in accuracy both in trials with added categorical tasks and yoked control trials. In Experiment III, we tested if this impaired performance was caused by elongated time between context 2 presentation and test. We hypothesized that if the monkeys could only remember the context 2 images within a very short period of time, then a decay in performance would occur as the empty delay interval between context 2 image presentation and test increases at a small scale.

Procedure: Procedures were kept the same as Experiment I except that instead of having a universal delay interval of 200msec between context 2 image presentation and the test, each session contained pseudo-randomly arranged trials with delay intervals of 200msec, 500msec, 1sec, 2sec and 4sec delays (Figure 6). Such manipulation was used to clarify the effect of an extended delay between seeing the context 2 image and completing the matching test on the performance of the monkeys, as observed in the result of Experiment II.

Results: By varying the empty interval between context 2 image presentation and the recognition task, the effect of delay length post context 2 presentation was confirmed. Selection percentages of context 1 and context 2 images were affected by time differently (repeated measures of anova: group*time interaction: $F_{4,20} = 28.1$; $p<.001$; main effect of group: $F_{1,5}=33.024$; $p = .002$; main effect of time: $F_{4,20} = 4.34$; $p=0.011$). As the Figure 7 shows, the longer the delay interval, the more likely that monkeys will confuse context 1 images with context 2 images, but not with the novel ones. At 200 msec interval, selection percentages of context 1 and context 2 images were significantly different (paired sample t test: $t_5 = 10.2$; $p<0.001$). However, at 4000 msec interval, the selection percentages between the two image groups were not significantly different (paired sample t test: $t_5=1.39$; $p=.222$). Noticeably, with mere 4 seconds of delay, the selection rate between context 1 image and context 2 image fell close to each other, even when given that context 1 images were seen for three times while context 2 were only seen once. As familiarity strength is highest right after an item is presented, the Experiment III result might reflect a decrease of context 2 image familiarity in the first several seconds after their presentation. If this is true, then the observed effect of elongated delay would be due to context 2 image familiarity strength dropping to near same level as context 1 image strength level, making it harder to distinguish between the two. Thus, manipulation of familiarity for images from either context should heavily impact the monkey performance by influencing the difference in familiarity strength between the two contexts.

Experiment IV:

In Experiment III, we found that as the empty delay between context 2 presentation and test increases, monkeys had decreased accuracy in selecting the context 1 images during test. Since a potential explanation is that the monkeys rely on difference in familiarity strength to make the distinction, in Experiment IV, we manipulated the familiarity of context I images to see if performances of the monkeys would be impacted. We predicted that the greater number of times that an image was shown to the monkeys in context 1, the higher its familiarity strength would be at the time of recognition task. Thus, it would be harder for the monkeys to distinguish between the context 1 images that are shown more times, and the context 2 images, which has the highest familiarity as it is most recently seen. Therefore, if the monkeys indeed rely on the difference in familiarity strength to distinguish context 1 and context 2 images, they will choose the context 2 images more if a context 1 image is shown for a higher number of times (Figure 8).

Procedure: In Experiment IV, procedures will be kept the same as Experiment I, except that the total number of trials will decrease to 36 trials. One third of the context 1 images will be only shown one time, rather than three times as before, and another one third of the context 1 images will be shown five times, with the remaining images still being showed for three times (Figure 9). Such manipulation will be used to explore the role of familiarity during the discrimination of images associated with two contexts. Selection of the context 1 image during test will be positively reinforced with auditory and food reward.

Preliminary Results: Although testing for Experiment IV has not finished yet, according to the preliminary data collected from 3 monkeys, it seems that the result was directly opposite of the hypothesis. That is, instead of increasing confusion between context 1 and context 2 images, the higher number of times that a context 1 image was presented, the more likely that monkeys can make the correct selection of context 1 images in the recognition task (Figure 10). This makes us question our initial presumption that no matter how many times an image is touched, the most recently seen image always possess a higher familiarity strength. If images presented for more times are actually more familiar than the images immediately shown before recognition task, then boosting context 1 image familiarity would instead increase the familiarity difference between images associated with the two contexts, thus causing the observed effect in selection percentage. Thus, although more data is needed for us to reach a more decisive conclusion for Experiment IV, the current result indicates a need to examine how familiarity strength is influenced by both number of times that an image is perceived, and the interval between its presentation to the recognition task.

General Discussion:

Our results showed that monkeys discriminate between images encountered in contexts separated by 5 minutes, akin to human source memory. In Experiment I, we found that monkeys initially selected a high percentage of the most recently seen context 1 image, but learned to switch their strategy, and selected a much higher percentage of context 2 image by the end of training. In Experiment II, we found that this process might not be affected by concurrent cognitive load. Rather, the context discrimination of the monkeys was more clearly susceptible to delay interval increase between context 2 image presentation and test. In Experiment III, we confirmed that even small-scale increase of the delay interval can make the monkeys more frequently confuse context 1 and context 2 images, but not the novel images, suggesting that the memory for context 2 fades quickly. In Experiment IV, preliminary results suggest that the more times context 1 images were presented to the monkeys, the less likely that the monkeys will confuse context 2 images with context 1 images, indicating an effect of familiarity strength. Taken together, these results suggest that monkeys indeed distinguish between different sources over a longer term, and may not rely on working memory to achieve this. However, more definitive roles of familiarity, recollection and working memory during context discrimination still need to be determined in future experiments.

The design of the paradigms used in this study is based on the False Fame paradigm (Jacoby, Kelly, Brown and Jasechko, 1989), a human paradigm that dissociates source memory and item memory over a relatively long term. In this paradigm, participants are presented with a list of non-famous names. A fame judgement test on mixed list of famous and non-famous names was then given either immediately or after a 24-hour interval. As the non-famous names were seen recently, they also have relatively high familiarity strength. During the fame judgement task, longer delay from presentation of non-famous names can cause recollection for non-famous names to fade. As a result, confusion between the familiar famous names and previously-seen non-famous names would arise, causing the participants to mistake non-famous names as famous more often at tests with 24-hour interval. In our experiments, the presentation of context 1 and context 2 images draws a parallel to the famous and non-famous names used in the False Fame paradigm. The context 1 images match the famous names used in the False Fame paradigm, as they are shown much earlier to the monkeys than the context 2 images and image recognition tasks. On the other hand, the context 2 images match the non-famous names, as it is shown in more proximity to the recognition task. Similar to the fame judgement task, in which the participants must recall sources from which they have encountered the non-famous names, the monkeys have to successfully distinguish between contexts in order to gain reward from the recognition tasks. In Experiment III, variation of the delay interval between context 1 images and context 2 images also matches the manipulation of time between viewing the non-famous names and receiving the test with mixed name list in human False Fame paradigm. (Jacoby et al., 1989) Nevertheless, the time scale used in the monkey study is significantly shorter than the human experiment to ensure that the monkeys are able to perform the tasks at a reasonable accuracy. By designing our paradigm to parallel the human False Fame paradigm, we hoped to enable comparison between performances of the monkeys to that in humans.

As a major component of source memory monitoring is the ability to retrieve contexts associated with a specific event (Smith and Vela, 2001), it is important to define the characteristics that constitute contexts in this study. In paradigms studying effects of contextual encoding, a variety of features have been considered as components of the context, such as the external environment, incidental features of the item itself, and even untested stimuli presented in between items (Smith and Vela, 2001; Manning et al, 2016; Eich, 1985). Meanwhile, the time at which an event occurs itself can be considered a form of context (Bouton, 1993; Schwartz et al, 2007), as it is likely for both intrinsic and external cues to change over an interval period. In our paradigm, both features related to the item itself and the passing of time serve to form the context that recognition tasks are based on. For example, by having the context 1 images presented pseudo-randomly at four corners of the screen, and context 2 images fixed at the center of the screen, the location of the images can serve as one aspect for context distinction. Also, the context 1 images were presented multiple times, and were interlaced with fixed target-finding symbols that were not tested in recognition tasks, while the context 2 images were presented only once before the recognition tasks with no target-finding symbols involved. These differences may also serve as reference for distinction between contexts for the monkeys. Besides, a five-minute delay interval separated context 1 presentation from context 2 / recognition task, which also served to make a clear distinction between images from context 1 and context 2. Thus, multiple features, either related to the conditions in which an image was presented, or the passing of time, can be regarded as cues that the monkeys rely on for context distinction in this paradigm.

Noticeably, the design of our test prevents monkeys from treating it as a simple match to sample test, and ensures that they are only able to obtain reward when contextual discrimination is applied. In this experiment, the images themselves were randomly grouped and assigned as context 1 image, context 2 image, or novel images. Across sessions, images were used non-repetitively. There are no features intrinsic to the images that would allow correct selection of the targeted image devoid of context information. The inclusion of two familiar images and two novel images during the recognition task also ensures that monkeys cannot treat the task as a simple item selection task and thereby avoid context discrimination.

Currently, evidence documenting existence of source memory in nonhuman animals is scarce. It has been found that rats are able to rely on information of food flavor, maze location, as well as whether a food location is learned on their own or with guidance of the researchers to successfully distinguish locations where food reward will be replenished, even after one week of the initial training (Crystal et al, 2013; Crystal & Smith, 2014). As the identification of replenished food location is retained over a long term and relies on features secondary to the food location itself, it can be considered as a form of source memory (Crystal 2016). Studies in chimpanzees and orangutans also showed that they are able to recall specific locations used in tool-finding tasks either from three years ago, or from two weeks prior to the test (Martin-Ordas et al, 2013). In studies with rhesus macaques, monkeys were presented two images that either requires touching, or a classification into one of four image categories (Basile and Hampton, 2017). It has been found that monkeys can readily distinguish between images associated with different tasks when they are separated by 10 seconds of interval. However, as recollection of the source of an event is most often associated with episodic memories in humans (Tulving, 1993), testing for source memory over longer terms in monkeys can further advance our understanding of similarities and differences in human and nonhuman memory systems.

The current study extends the results of the Basile & Hampton (2017). By moving one of the contexts outside of working memory range in our current experiment, we confirmed that the monkeys indeed retain the ability to discriminate between contexts over a longer delay. Compared to studies in rats and apes, we tested the context discrimination in monkeys with a visual task that lasts over a shorter interval period. We also presented the monkeys with more stimuli that need to be distinguished. Overall, our finding complements evidence found in Basile & Hampton (2017) study, and provides a way to look into longer term source memory in rhesus monkeys. It also allows for comparison of source memory-like mechanisms across different species for a better understanding of evolutionary basis of memory systems.

The paradigms developed in this experiment may have the potential to provide assessment of source memory performances for animal models used in clinical and pharmacological studies. For example, source memory and episodic memory have been known to be impaired by Alzheimer's disease and normal aging (Butters et al., 1987; Kessels et al., 2007; Barba et al., 2010). By evaluating the validity of animal models of dementia from both the aspect of anatomical and pathological similarities to the human disease, as well as from a behavioral aspect targeting source memory, we may draw better comparison between clinical studies conducted in animals and humans (Ridley & Baker, 1991).

In studies that aim to uncover neurological basis that supports different memory systems and decision makings, our behavioral paradigm may also be combined with neurological recordings, lesion studies or inhibition of specific brain regions to explore circuits and mechanisms underlying the cognitive processes. For example, by applying memory-guided reaching and saccade tasks along with inhibition of lateral intraparietal regions with drug injection in rhesus monkeys, the role of this region in oculomotor decisions was explored (Christopoulos et al., 2018). Simultaneous viewing of images of faces along with fMRI and single unit recording of the face patch region in rhesus monkeys also revealed how facial identity is coded in the primate brain (Chang & Tsao, 2017). With information on activation of the brain regions related to recognition and working memory, more evidence might also be gained on the cognitive mechanisms that support context discrimination in rhesus monkeys if these techniques were applied to our paradigm.

As a large quantity of non-repetitive images were used in this study (some monkeys have been trained and tested on over 30000 images already), an interesting future analysis would be applying data mining methods to identify features associated with the image itself that makes it more memorable to the monkeys. In humans, similar studies have been conducted (Isola, Xiao et al., 2011; Isola, Parikh et al., 2011; Jing et al., 2017). In one specific study (Isola, Xiao et al., 2011), testing results from 665 participants on a visual memory game was looked at. When support vector regression was applied to the dataset, it has been found that the model outputs predictions with reasonable accuracy when object and scene semantics of an image were taken into consideration. A potential future study may apply similar method to the data collected from monkeys in our study, and see if equivalent effect of object and scene semantics can be found.

In sum, our study provided evidence of context discrimination in rhesus monkeys between images separated by 5 minutes. Because previous experiments have only shown this in monkeys at 20 seconds, this longer time scale is significant, as it demonstrates existence of source memory in monkeys outside the range of working memory, which is more akin to human long-term memory. The finding allows for comparison of source memory-like mechanisms in rhesus monkeys with that in other animal species. The behavioral paradigm developed in this study may potentially facilitate the assessment of source memory in animal models for clinical and pharmacological testing that aim to either test or preserve the recognition process in subjects. In future experiments, features of the images shown to the monkeys can be analyzed to find out features that determine whether a picture is memorable through data mining techniques. Further exploration is also needed to determine the exact cognitive mechanisms that supports the monkeys' context discrimination ability.

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Figures

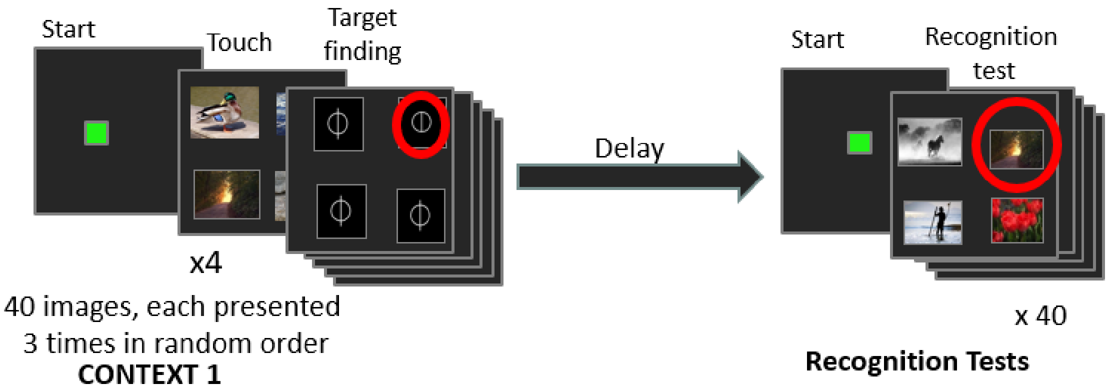

Figure 1: Flow chart demonstration of the training procedure, which constitutes only context 1 image presentation and recognition tests.

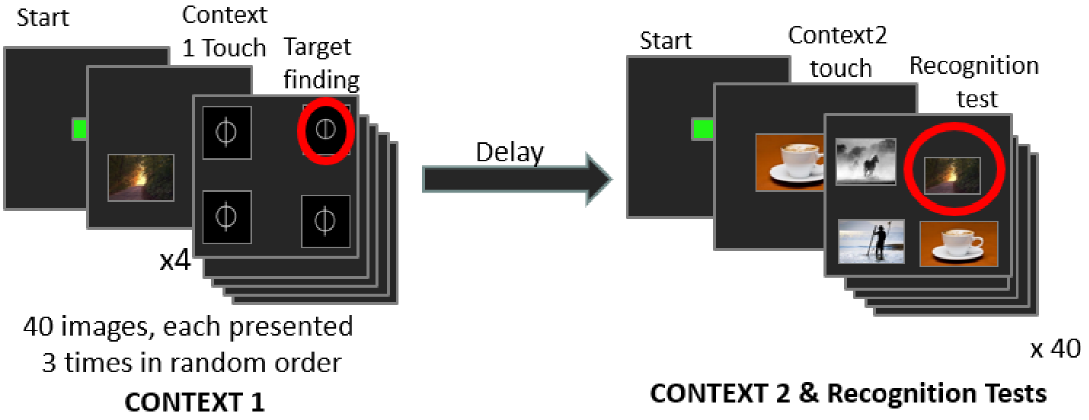

Figure 2: Flow chart demonstration of the Experiment I procedure, which has an added context 2 image presentation right before each trial of the recognition test.

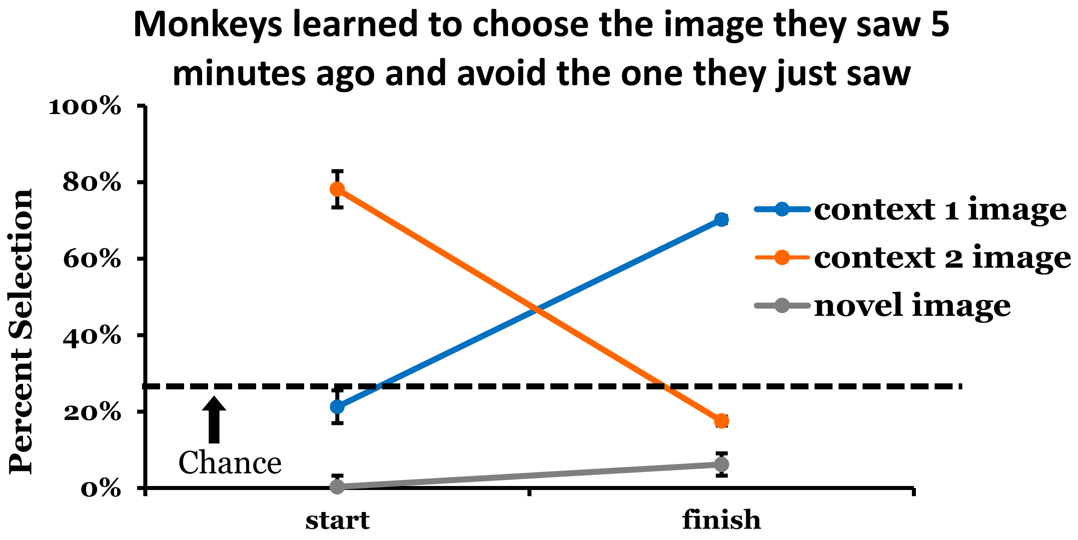

Figure 3: percent selection of context 1 images, context 2 images, and novel images at the start and end of the Experiment I. Note that as the stopping criteria is defined as reaching above 70% selection of context 1 images continuously for two sessions, the standard deviation is relatively small by the end of Experiment I.

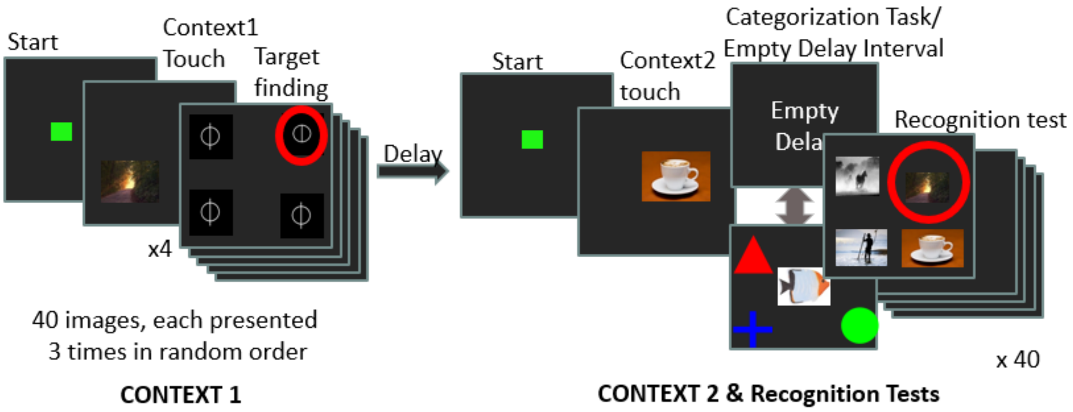

Figure 4: Flow chart demonstration of Experiment II procedure. Either a categorical task or an empty delay control with matched time length is inserted between context 2 presentation and the recognition test.

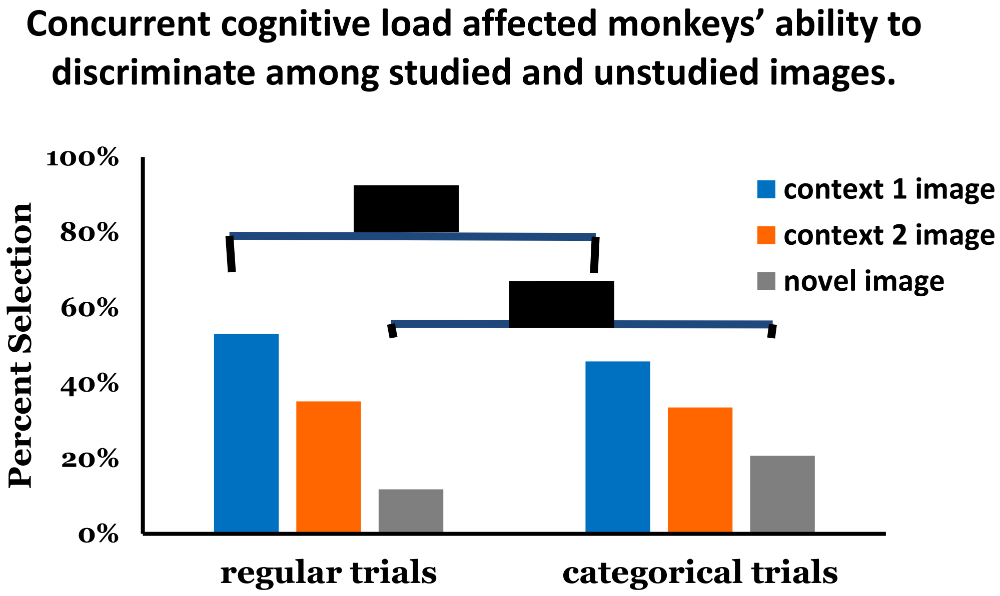

Figure 5: Percent selection of context 1, context 2 and novel images for regular trials and categorical trials. Noticeably, no significant differences in context 2 selection were observed (paired samples t test: $t_5 = 0.966$; $p = 0.378$), while significant changes were observed for context 1 (paired samples t test: $t_5 = 3.03$; $p = 0.029$) and novel images (paired samples t test: $t_5 = 3.41$; $p = 0.019$). However, selection percentages of context 1 images from both groups were significantly different from the result of the last five sessions of Experiment 1 (between control trials and Experiment I trials: paired samples t test: $t_5 = 6.92$, $p<0.001$; between categorical trials and Experiment I trials: paired samples t test: $t_5 = 11.2$, $p<0.001$).

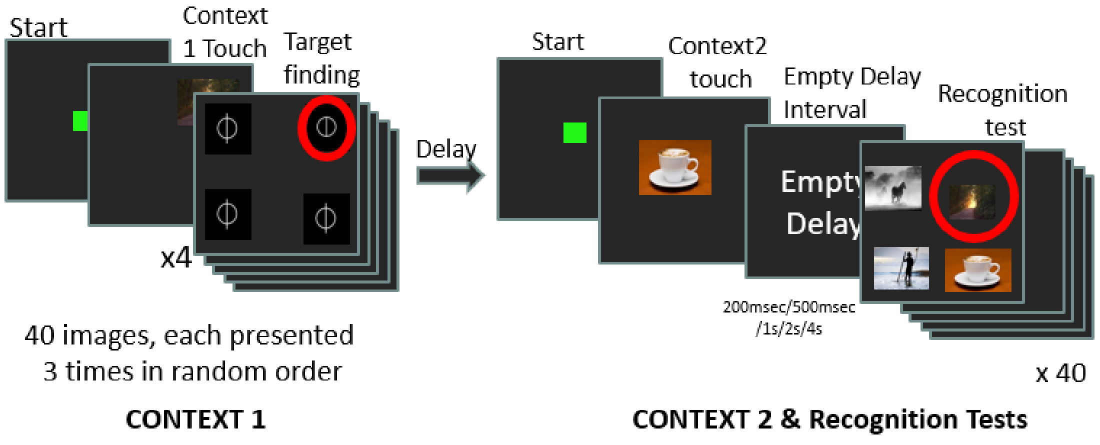

Figure 6: Flow chart demonstration of Experiment III procedure, with empty delays of various lengths inserted between context 2 images and the onset of recognition task.

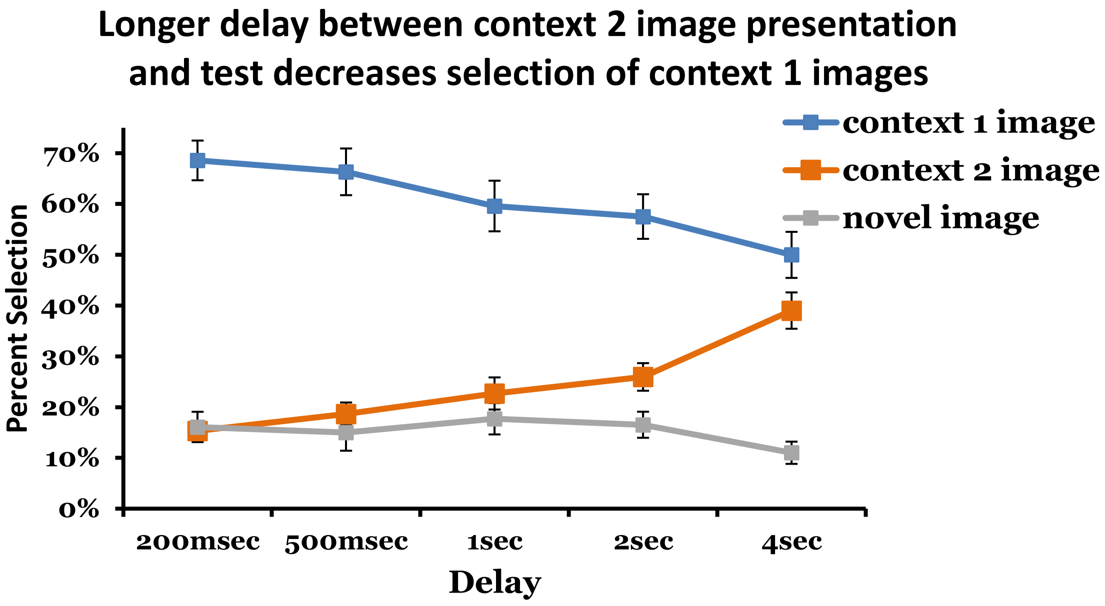

Figure 7: Percent selection of context 1, context 2 and novel images according to different lengths of delay interval between context 2 presentation and recognition task. As the interval

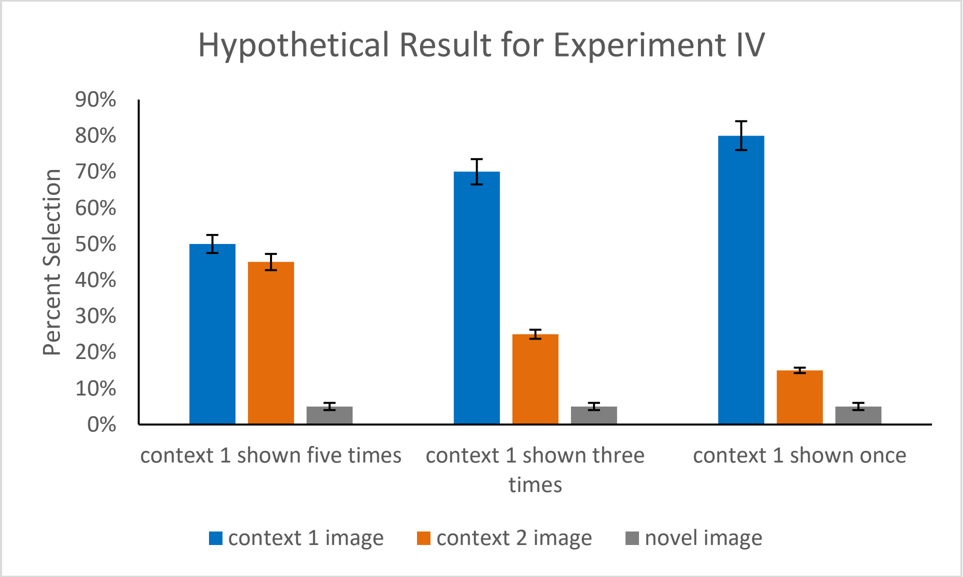

Figure 8: hypothetical result for experiment IV. It is hypothesized that the greater number of times that an image was shown to the monkeys in context 1, the higher its familiarity strength would be at the time of recognition task, leading to more confusions of the monkeys between context 1 and context 2 images

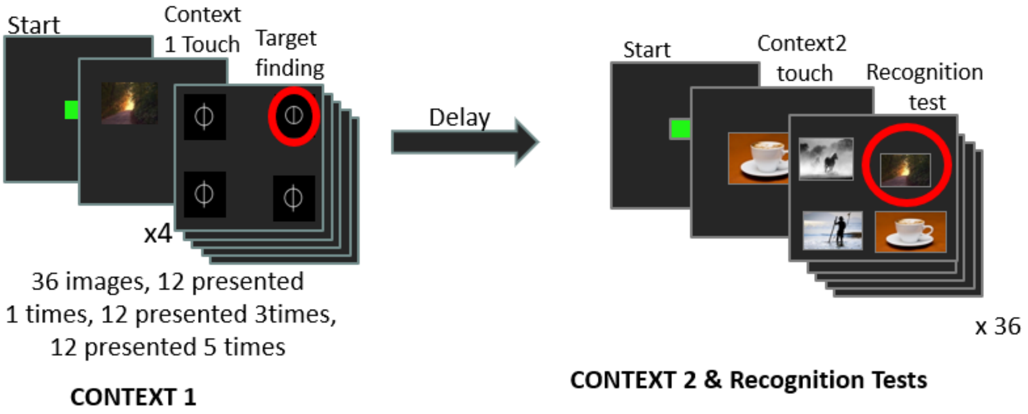

Figure 9: flow chart demonstration of Experiment IV procedures. Total number of trials were decreased to 36, with 12 trials presented randomly for one time, 12 trials presented randomly for three times, and 12 trials presented randomly for five times.

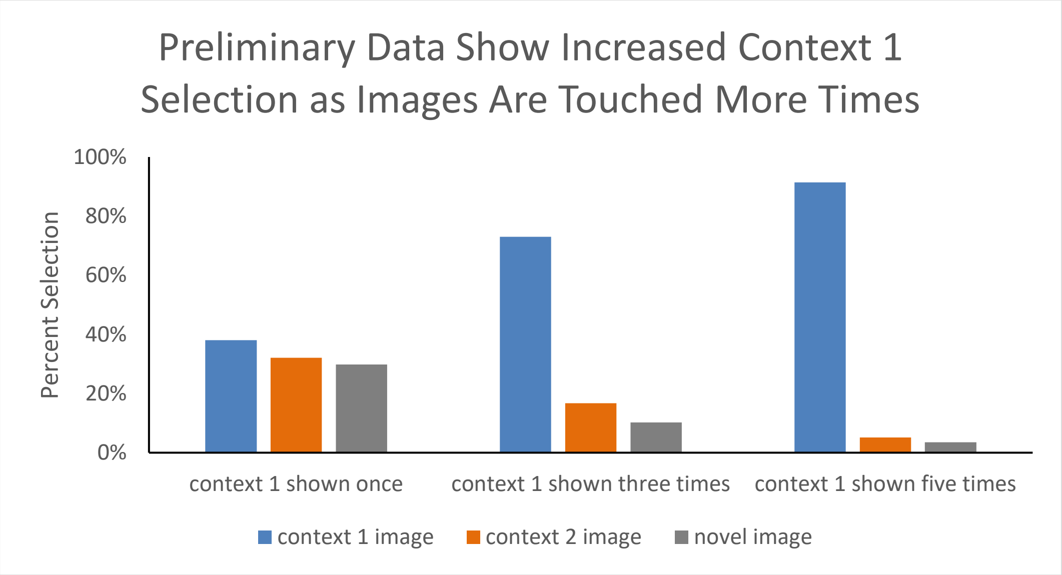

Figure 10: preliminary Experiment IV data from testing of three monkeys. Opposite from our hypothesis, the greater number of times that an image was presented, the higher the selection percentage for context 1 images.