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by

Lenora Hundertmark

Robert Hampton
Adviser

Neuroscience and Behavioral Biology

Robert Hampton

Adviser

Keith Easterling

Committee Member

Erica Craig

Committee Member

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An abstract of
a thesis submitted to the Faculty of Emory College of Arts and Sciences
of Emory University in partial fulfillment
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Abstract

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When humans are simultaneously presented with images in a list, they rely on spatial representations to memorize the order. Monkeys use the same strategy to learn the order of simultaneously presented images. This is indicated by the presence of the symbolic distance effect, in which accuracy is lower as the symbolic distance—or the number of images separating the two test images within the list—decreases. However, it is unknown whether these spatial representations in monkeys are a form of explicit memory—memory that an organism is aware of and can cognitively monitor. One approach to determine the memory system underlying a task is to add a metacognitive choice, consisting of the option to accept or decline a test trial. In the current study, three experiments were performed to test if the representations formed in the simultaneous chaining task, a task used to train monkeys on lists of images, are available to metacognition in monkeys. In Experiment 1 we ran a simultaneous chaining task in monkeys and found that representations of the lists of images are spatially organized, indicated by the presence of the symbolic distance effect. In Experiment 2 we tested monkeys on a circle-size discrimination task with a metacognitive choice and found that monkeys are capable of acting metacognitively, declining harder trials at a higher rate than easy trials. In Experiment 3 we combined Experiment 1 and 2 by adding a metacognitive choice to the simultaneous chaining paradigm. This final experiment provided preliminary evidence that representations formed in the simultaneous chaining task are both spatial and available to metacognitive monitoring. These modest results suggest that monkeys may rely on explicit memory to form representations of simultaneously presented images.

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Introduction

Human memory can be divided into two broad categories: explicit and implicit memory (Mullally & Maguire, 2014; Tulving, 2002; Zola-Morgan & Squire, 1993). Explicit memories are accessible to cognitive monitoring, meaning humans can be aware of them. For example, one can be aware of their own factual knowledge that Atlanta is the state capital of Georgia. Implicit memories, in contrast, control behaviors that humans are not aware of and therefore aren't accessible to cognitive monitoring—like the memory for how to ride a bicycle. Though there is evidence of the presence of explicit memory in nonhuman primates, a clear discrimination between the kinds of memory that are implicit and those that are explicit has yet to be established (for review see Hampton, Engelberg, & Brady, 2020). One method to classify different kinds of memory as explicit or implicit is through the use of a metacognition paradigm.

Metacognition is the ability to monitor and control one's own cognitive processes (Flavell, 1979; Smith, Couchman, & Beran, 2014). One function of metacognition is that it allows humans to discriminate between when they know something and when they don't know. For instance, Jessica has a final exam tomorrow that covers two large units of content. For the rest of the night Jessica could focus on both units equally, or she could dedicate most of her time to studying the second unit since she has only studied half of that content. The second option would be more beneficial to Jessica as she isn't caught up on all of the content from the second unit and she is comfortable enough with the content of the first unit to reduce the study time in that area. Jessica's ability to make the more advantageous decision stems from her awareness of her knowledge about the content and her ability to change her study behavior based on this awareness. The monitoring demonstrated when discriminating between known and unknown information as described in this scenario illustrates one example of the adaptive value of metacognition to behavior.

Monkeys also show metacognition (see Hampton, Brady, Engelberg, 2020). A typical test of metacognition in nonhuman primates is to give the monkeys the option to accept or decline trials in a task containing multiple levels of difficulty. For example, during a difficult trial on a circle-size discrimination task, where the circle the monkeys have to pick is nearly the same size as the distractor circles, monkeys are inclined to avoid the test. In contrast, monkeys readily choose to take an easy test (Brown, Templer, & Hampton, 2017). Thus, monkeys are able to metacognitively monitor whether or not they know the correct answer to the trial and, based on this assessment, are able to avoid trials they do not know in order to maximize reward. Such metacognition tasks can be used on monkeys to test which kinds of cognition and memory are being monitored, and thus can be used to determine which memory tasks involve explicit awareness (Hampton, 2019).

Metacognition tasks have recently been used to determine if organisms rely on explicit or implicit memory when memorizing the position of items in a list. Humans often memorize the order of a list by forming a spatial representation of the list in memory, with each item in the list represented in the same order as it occurred (Scarf & Colombo, 2008). For example, when memorizing a recipe, humans might remember step one from the recipe comes first, followed by step two, and so on, organizing these mentally in a spatial arrangement in which the steps are ordered from left to right. Evidence of this strategy comes from the symbolic distance effect (Colombo & Frost, 2001; Moyer & Bayer, 1976; Scarf & Colombo, 2008). When presented with two stimuli from a list of images they have learned belong in a sequence, humans are better at identifying which image comes first the “further apart” from each other the stimuli are in the sequence (Moyer & Bayer, 1976; Scarf & Colombo, 2008; see Figure 1). For instance, from a list that contains five images (A_1-A_5), humans will test with higher accuracy on pairs like A_1 and A_5 than on pairs like A_3 and A_4 (Moyer & Bayer, 1976). In the same way that two physical objects further apart in a line are easier to discriminate from each other than adjacent objects, images further apart in a spatial representation of a list are easier to discriminate despite the lack of physical distance separating them. The symbolic distance effect is also found in monkeys, providing evidence that constructing spatial representations for lists of stimuli is a strategy used by both humans and monkeys (Colombo & Frost, 2001; D'Amato & Colombo, 1990; McGonigle & Chalmers, 1992; Scarf & Colombo, 2008).

Memory for the order of events, which is subject to the symbolic distance effect, is available to metacognitive monitoring in monkeys. Monkeys were trained to touch a sequence of five individually presented images and then were tested on which of two images came earlier in the list. The results displayed the symbolic distance effect, suggesting that the images were represented spatially in the memory for the order of events task. This paradigm was then combined with a metacognition component. When the monkeys were presented with two images at test, they were given the option to take the test or decline the test before they could give their response. Monkeys were more likely to decline difficult tests—with the difficulty increasing as the number of images in the list separating the two test images, henceforth referred to as the symbolic distance, decreased. These findings suggest that the representations used to store the order of images are accessible to metacognitive monitoring. Thus, memory for the order of events in monkeys may rely on explicit memory (Templer, Brown, & Hampton, 2018).

Transitive inference is another task that displays the symbolic distance effect, but the limited evidence available indicates that monkeys do not display metacognition in this task

(Jessica Dugan, personal communication, May 15, 2019). The transitive inference task requires monkeys to learn a list of stimuli through inferring relationships between ranked pairs of stimuli. Monkeys were shown two images, referred to as a premise pair, and were positively reinforced when they picked which image was supposed to come first in the pairing (i.e. Image A > Image B). After the first premise pair was learned, another independent pair was trained (i.e. Image B > Image C). At test, the monkeys were presented with two images, some of the trials consisting of the premise pairs and others consisting of non-adjacent images (e.g. Image A > Image C), and the monkeys were to select which image came first in the list. It is believed that monkeys are able to combine the independent premise pairs into a synthesized list. This is shown through the presence of the symbolic distance effect, with performance on pairs separated by only one image being lower than pairs separated by five images (Gazes, Chee, & Hampton, 2012). When a metacognition test was added to the task to determine if the representations formed in transitive inference were accessible to metacognitive monitoring, similar to the choice paradigm given in the memory for the order of events task (Templer, Brown, & Hampton, 2018), the monkeys did not have a significant difference in their choice to decline the task across the varying levels of difficulty. This suggests evidence that transitive inference is not metacognitively-monitored (Jessica Dugan, personal communication, May 15, 2019).

The memory for the order of events task and the transitive inference task have contrasting metacognition results. Representations formed in the memory for order of events task are explicit while preliminary evidence suggests that the representations formed in the transitive inference task may be implicit. Due to the fact that monkeys seem to employ spatial representations in both of these two tasks, as indicated by the presence of the symbolic distance effect, it is surprising that the two are different in their access to metacognitive monitoring. It is possible that the two tasks are accomplished by using different memory systems in order to achieve the same goal, spatial representations. Further research is needed to determine why these two kinds of memory for spatial representations may be classified under separate memory systems.

Simultaneous chaining is a third task that is thought to require spatial representations, as indicated by the symbolic distance effect (Colombo & Frost, 2001; Templer, Gazes, & Hampton, 2019; Terrace, 2005; Terrace, Son & Brannon, 2003). Typically, in the simultaneous chaining task monkeys are presented with up to five images simultaneously. Through trial-and-error, the monkeys learn to touch the images in the correct order (Figure 2). On probe trials, the monkeys are presented with two images from the list and have to pick which image came first (Templer, Gazes, & Hampton, 2019; Figure 3). Though researchers are beginning to understand the extent to which monkeys are explicitly aware of their spatial representations in the transitive inference and memory for the order of events task, it is still unknown the extent to which monkeys are aware of the representations used for the simultaneous chaining task. An understanding of whether or not the representations formed by monkeys through simultaneous chaining are accessible to metacognitive monitoring may shed light on the contrasting results of the memory for the order of events task and the transitive inference task. Thus, further research is needed to determine if monkeys rely on multiple memory systems in order to form spatial representations.

The aim of the current study is to investigate the degree to which the mental representations formed by monkeys in simultaneous chaining are accessible to metacognitive monitoring. In Experiment 1, monkeys were trained on a simultaneous chaining task to determine whether the paradigm being used exhibits the symbolic distance effect. In Experiment 2, the monkeys were trained on a circle-size discrimination task with a metacognitive choice to confirm that the monkeys are capable of acting metacognitively when a task forms representations accessible to cognitive monitoring. Experiment 3 combined the simultaneous chaining task with a metacognitive choice to assess the extent to which the monkeys' metacognitive decisions align with their performances on simultaneous chaining.

Methods

Subjects

We used six adult male rhesus macaques (*Macaca mulatta*) housed within Yerkes National Primate Research Center in Atlanta, GA. All of the monkeys had at least eight years of computerized testing experience and have had experience with simultaneous chaining paradigms and metacognition paradigms prior to this experiment. The monkeys were housed individually, due to social incompatibility, and kept on a 12-hour light-dark cycle with light onset beginning at 7am. The monkeys received full rations of food each day and had access to water at all hours. All testing procedures were approved by the Emory Institutional Animal Care and Use Committee. Experiments were conducted under the IACUC protocol PROTO201700700.

Apparatus

The tests were administered using touchscreen computer systems with 15-inch LCD color displays and generic stereo speakers. Two automated food dispensers were attached to and controlled by the monitor, which released pellets into two food cups residing below the computer screen. The computer rigs themselves were secured on the front of the cages, overlaying the doors—which were lifted to provide full access to the screen. The rhesus macaques tested in their home cages from 10am until 5pm from Sundays through Fridays.

Stimuli

Fifty images, 25 for Experiment 1 and 25 for Experiment 3, of landscapes, flowers, objects, and non-primate animals were collected from Bulkr, an online image downloader (Antibody software, 2020). These images were visually checked to ensure that there were no duplications and that the content of the images spanned a wide array of details.

Experiment 1: Monkeys show the symbolic distance effect on the simultaneous chaining task

Hypothesis:

If lists of images that have been learned through simultaneous presentation are spatially represented in monkeys, then they will demonstrate the symbolic distance effect, being more accurate when tested with images that are presented further apart in a list than images that are presented close together.

Training:

All six monkeys were trained on the same five-image sequence through trial and error, with the sequence predetermined and held constant throughout the experiment (Figure 2). Each trial randomized the location of the images to one of ten possible spaces. Monkeys began the trials by touching a green start square—two touches were required for selection—which began the sequence. Training started with the simultaneous presentation of the first three images in the sequence (A_1, A_2, and A_3). After each correct touch, the border of the image was highlighted green for the duration of the trial and could not be selected again. Once a successful trial was concluded, a positive sound occurred along with a food reward. For any selections given in an incorrect order, the trial instantly terminated, concurrent with a negative sound. This was followed by a 5-second timeout in which the screen remained black. Criterion for the training sessions was defined as 40% correct responses within a 50-trial session. This is 23.33% higher than random chance, 16.67%, which represents the average percent accuracy if the monkey were to guess for each trial (33.3% chance for the first choice and 50% for the second). Once criterion was reached, a fourth image (A_4) was added to the simultaneous presentation, following A_1, A_2, and A_3 in order of touch. After criterion was reached again, the process was repeated until an image list of $A_1 > A_2 > A_3 > A_4 > A_5$ had been learned. When all five images were presented, there was a .83% chance that through guessing alone the monkeys could complete the full list, calculated from a 20% chance to select the first image correctly, a 25% chance for the second, 33% for the third, 50% for the fourth, and 100% for the fifth. After learning the first five-image list, a new five-image list was presented using the same procedure but starting with new images: B_1, B_2, and B_3. The procedure was then repeated until five unique five-image lists had been learned.

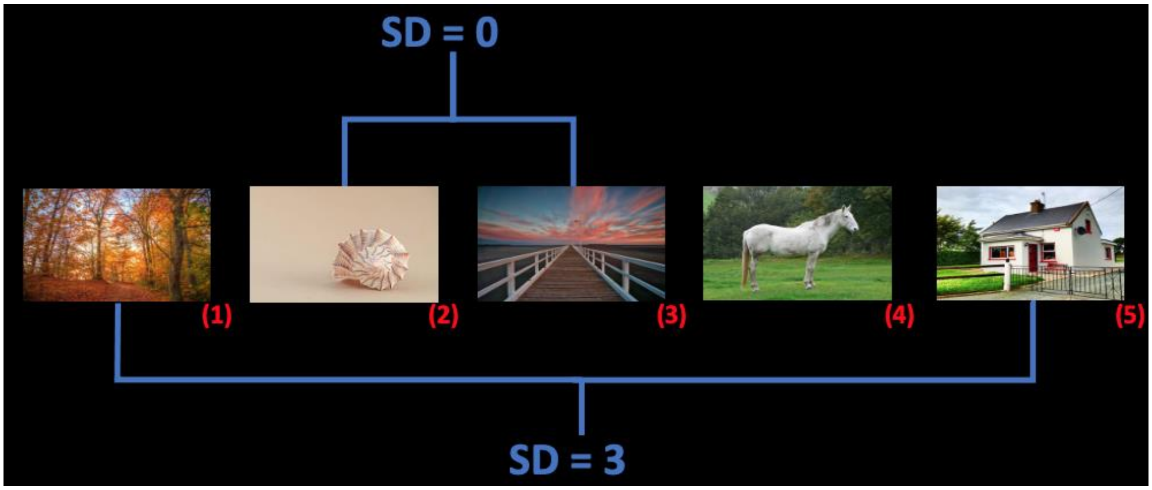

Figure 1: Visualization of Symbolic Distance. Symbolic distance refers to the number of images separating two test images from within a list. Two images adjacent to each other have a symbolic distance of zero. The first and last images have a symbolic distance of three.

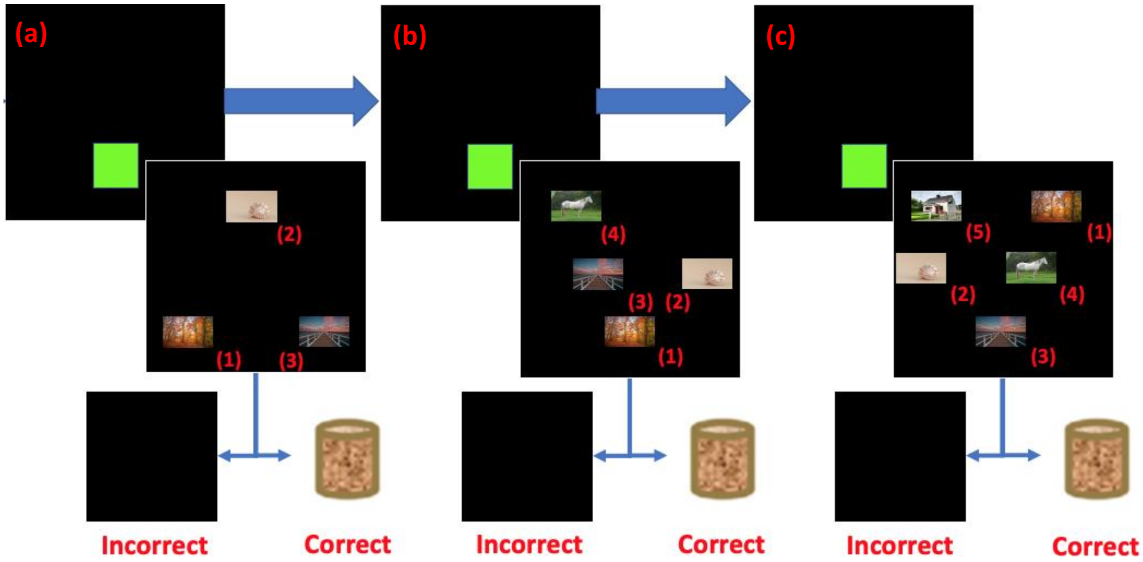

Figure 2: Simultaneous chaining training program. Monkeys touched the green start square, which opened up a training screen of three images from the first five-image list (a). The monkeys had to use trial-and-error to determine the correct order of the images by touching them one-by-one in sequence, with the image highlighting once it had been selected. If the images were touched in the correct order, one pellet was given along with a positive sound. If

the order was incorrect, a blank screen was shown for 5 seconds alongside the presentation of a negative sound. Once a criterion of 40% was reached with three images, a fourth image was added (b). After the criterion was reached for the four-image list, a fifth image was added (c). Once each training stage was completed with at least 40% accuracy, a new list of images was presented, starting with the first three images of list two. Each session contained 50 trials. Monkeys trained on five lists in total.

Testing:

Testing consisted of 300 probe trials in a session. In each trial, two random images from the same list were presented and the monkeys had to select which image came first in the list (Figure 3). Levels of difficulty in the simultaneous chaining probe test varied with the symbolic distance—with image pairs like 3 and 4 being one of the hardest and the image pair 1 and 5 being the easiest (Figure 1). Each image pair (ex. A_1 and A_4) was shown ten times over the course of the test session so that one image pair wasn't tested more often than another. Every 50 trials, trials with a symbolic distance of 3 were presented 5 times, trials with a symbolic distance of 2 were presented 10 times, trials with a symbolic distance of 1 were presented 15 times, and trials with a symbolic distance of 0 were presented 20 times. The monkeys received one testing session.

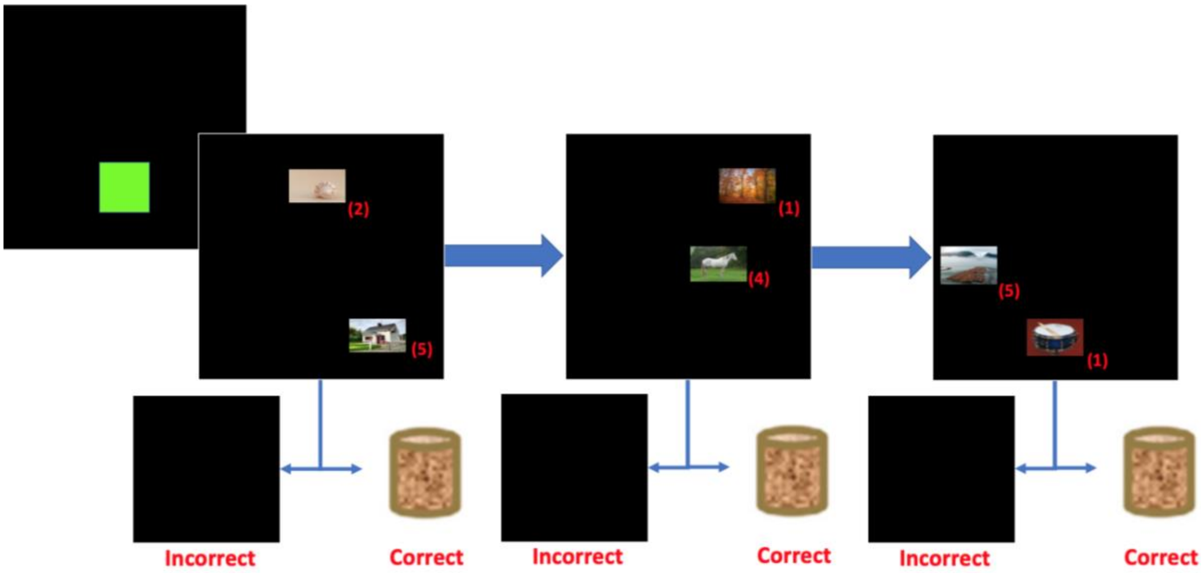

Figure 3: Simultaneous chaining probe test paradigm. Monkeys touched the green start square, and two random images from a previously learned list were presented. Correct selection of which image appeared first in the list resulted in one pellet with a positive sound while an incorrect selection resulted in a 5-second-long blank timeout screen alongside a negative sound. New trials randomized the location of the images, the list the images were being pulled from, and the image pairs. Monkeys completed one session, and the one session contained 300 trials.

Results and Discussion:

All proportions were arcsine transformed prior to analysis. Data were analyzed using repeated measures ANOVA with SPSS statistical software; any violations of sphericity are reported. Monkeys displayed the symbolic distance effect, which is consistent with previous experiments on simultaneous chaining in monkeys (Colombo & Frost, 2001; Scarf & Colombo, 2008; Templer, Gazes, & Hampton, 2019). Accuracy on trials was lower as the symbolic distance decreased (Figure 4; main effect of symbolic distance: $F(3,12) = 13.43$, $p < .001$). The monkeys performed well above chance, 50% accuracy, across each level of symbolic distance.

When the symbolic distance was 3, meaning that the probe images were separated by 3 images in the list, performance was at ceiling (M = 0.99, SD = 0.014).

The purpose of Experiment 1 was to train the monkeys on five-images lists through simultaneous chaining and test for the presence of the symbolic distance effect in this task. Previous literature has shown the existence of the symbolic distance effect in simultaneous chaining (Colombo & Frost, 2001; Scarf & Colombo, 2008; Templer, Gazes, & Hampton, 2019); however, it was crucial to replicate this finding in our monkeys. This replication confirms the condition needed for Experiment 3 that after exposure to the simultaneous chaining training, the monkeys represent the lists of images spatially. In Experiment 2, we aimed to replicate another previous finding in order to confirm that when representations are accessible to cognitive monitoring, the monkeys are capable of acting metacognitively (Brown, Templer, & Hampton, 2017).

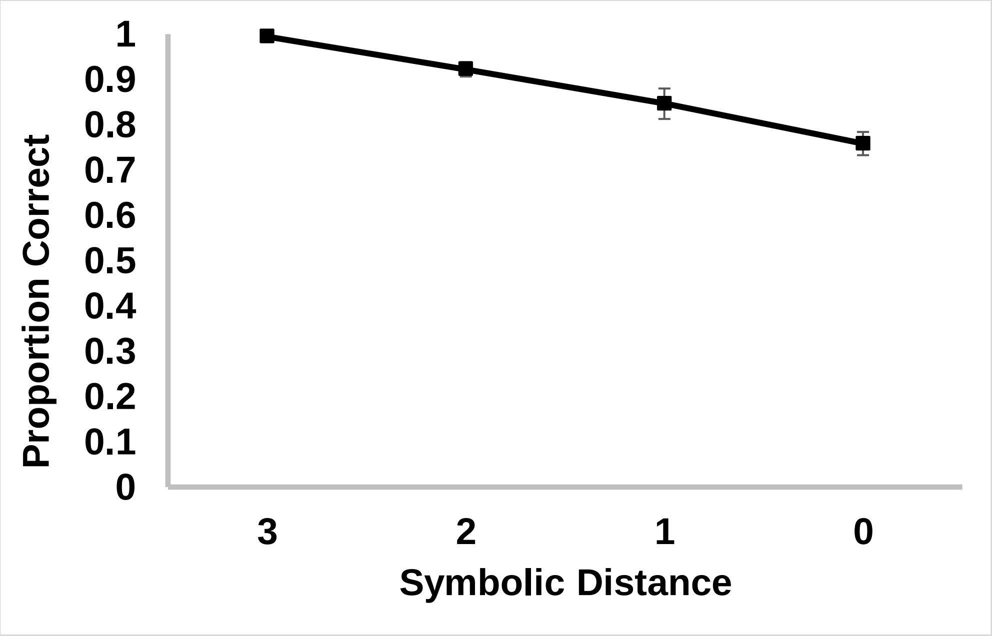

Figure 4: Accuracy on the simultaneous chaining probe test paradigm was lower for monkeys as symbolic distance increased.

Experiment 2: Monkeys show metacognition in the circle-size discrimination task

Hypothesis:

If the size discrimination between a target circle and distractor circles is accessible to metacognitive monitoring, then monkeys will decline tests containing a target circle with a smaller size difference more often than they will decline tests containing a target circle with a larger size difference.

Training:

Monkeys were trained on a circle-size discrimination task (Figure 5). After touching the green start square, a target circle and three distractor circles were presented. The monkeys had to select the target circle, which remained a constant size throughout the trials, in order to get the trial correct. Levels of difficulty for the circle-size discrimination task varied based on the deviation of the distractor circle sizes from the target circle. Criterion was 70% correct responses over an 80-trial session, well over random chance, which is 25%. This training set-up a subsequent test to determine whether the monkeys were acting metacognitively. Monkeys have shown metacognition on this paradigm prior to this experiment (Brown, Templer, & Hampton, 2017).

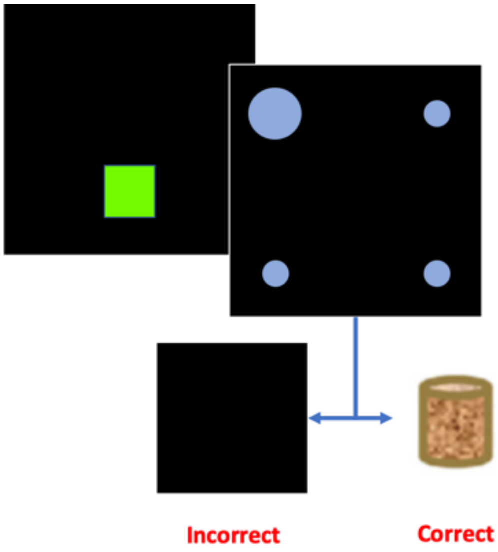

Figure 5: Circle-size discrimination training program. Monkeys touched the green start square, and four circles were presented—one target circle and three distractors. Correct selection of the target circle resulted in one pellet with a positive sound while an incorrect selection resulted in a 5-second-long blank screen timeout with a negative sound. One session consisted of 80 trials. After reaching a criterion of 70%, the monkeys proceeded to the test.

Testing:

Testing sessions contained 90 trials. The paradigm was similar to the training with the addition of a metacognitive choice (Figure 6). On two-thirds of the trials, the monkeys were given an option to accept or decline the test through an “accept test” and a “decline test” stimulus after being presented with the trial. If accepted, they proceeded with the test and received either the maximum number of pellets for a correct choice or no pellets for an incorrect choice. If declined, they automatically received the minimum number of pellets after touching a red bar stimulus five times to receive the next trial. The pellet ratio for each monkey was either 3:2 or 2:1 for correct choice and declined choice depending on what incentivized the individual monkey to use the decline button over at least 10% of the time. On one-third of the trials, the monkeys were forced to accept the test by tapping the “accept test” stimulus, allowing them to proceed with the trial. Criterion was defined as a 30% difference in decline rate between the easiest and hardest trials. The monkeys received 5 of these circle-size discrimination metacognition testing sessions.

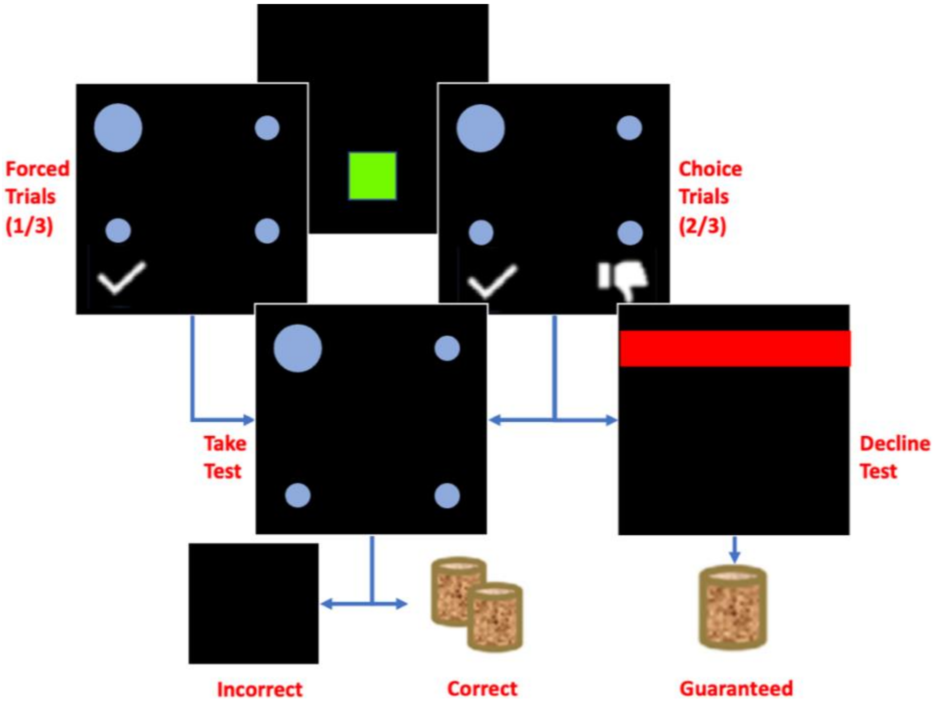

Figure 6: Circle-size discrimination metacognition paradigm. Monkeys touched the green start square, and four circles were presented—one target circle and three distractors. On 1/3 of these trials, the decline-test icon did not appear while the accept-test icon remained, forcing the monkey to take the test. Correct selection of the target circle resulted in a maximum number of pellets (2 or 3) with a positive sound while an incorrect selection resulted in a blank screen timeout of a varied time alongside a negative sound. The timeout period ranged from 6-60 seconds for different monkeys based on what incentivized the individual monkey to use the decline button over at least 10% of the time. On the other 2/3 of the trials, the decline-test icon appeared next to the accept-test icon. If the test was declined, the decline-test screen appeared along with a minimum number of food pellets (1 or 2), which was guaranteed after touching the red bar five times. If the test was accepted, correct responses resulted in a maximum number of pellets (2 or 3) and positive sound while incorrect responses result in a timeout and negative sound. One session consisted of 90 trials. Five sessions were performed. Monkeys had to reach a criterion of a 30% difference in decline rate between the hardest and easiest trials to proceed to Experiment 3.

Results and Discussion:

Four of five monkeys reached the criterion of a 30% difference in decline rate between the easiest and hardest trials. The sixth monkey from Experiment 1 was unavailable in Experiment 2 and Experiment 3 as it was completing a different project during the time of testing. The following is an analysis based on the final five criterion sessions of these four monkeys.

Monkeys acted metacognitively when presented with the circle-size discrimination task, consistent with previous findings (Brown, Templer, & Hampton, 2017). Accuracy on forced trials was lower as the difficulty level increased (Figure 7; main effect of difficulty level: $F(4,12) = 289.81$, $p < .001$). Accuracy on choice trials was lower as the difficulty level increased (Figure 7; main effect of difficulty level: $F(4,12) = 46.59$, $p < .001$). Decline rate increased as the difficulty level increased (Figure 7; main effect of difficulty level: $F(4,12) = 61.76$, $p < .001$).

The purpose of Experiment 2 was to test the second condition necessary for Experiment 3: monkeys are capable of acting metacognitively when a task involves representations that are accessible to cognitive monitoring. In Experiment 2, the representations that the monkeys monitored were whether they knew which circle was the target circle amidst the distractors. This experiment was then condensed into a 90-trial preparatory task given on the days of the simultaneous chaining metacognition task to show that the monkeys were acting metacognitively the day of testing in Experiment 3. As a result, if metacognition was not shown for simultaneous chaining, then the findings could be attributed to a lack of metacognitive monitoring in the simultaneous chaining task rather than the inability for monkeys to show metacognition in general.

The findings from Experiment 1 and Experiment 2 provided evidence that the two conditions required to progress into Experiment 3 were fulfilled. Experiment 1 indicated that the lists the monkeys learned through simultaneous chaining are represented spatially, described through symbolic distance. Experiment 2 indicated that if representations in a task are available to cognitive monitoring then the monkeys will act metacognitively by declining harder tasks significantly more than easy tasks. In Experiment 3, we aimed to combine these two findings to assess the extent to which representations used in simultaneous chaining are accessible to metacognitive monitoring in monkeys.

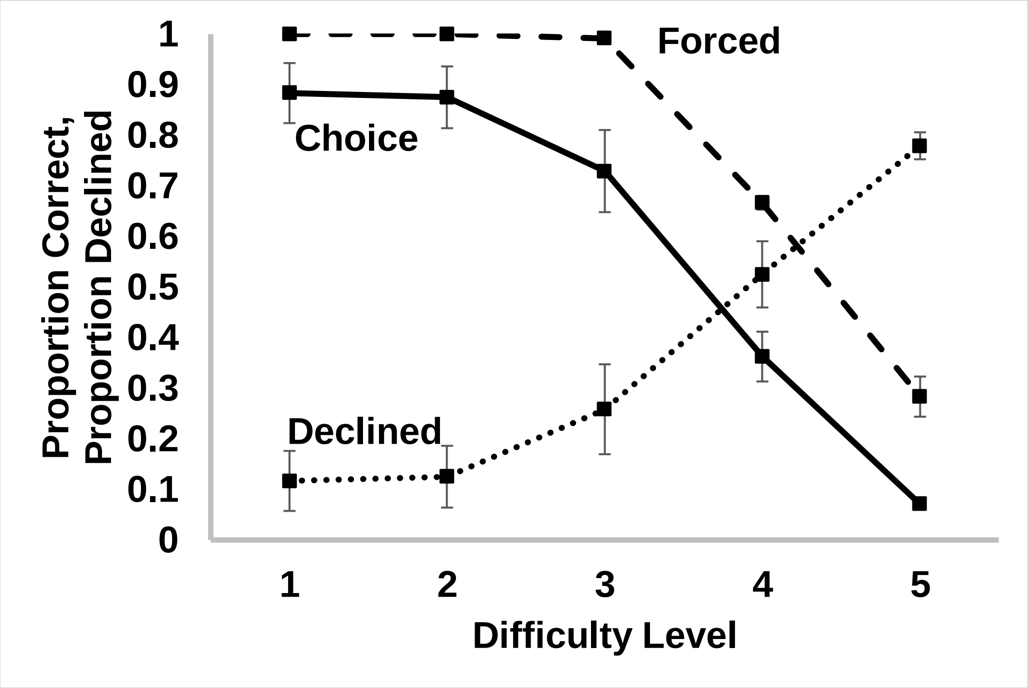

Figure 7: Decline rate of the monkeys increased on the circle-size discrimination metacognition task as the difficulty level increased.

Experiment 3: Preliminary findings

Hypothesis:

If memory for simultaneously presented sequences is accessible to metacognitive monitoring, then monkeys will decline tests containing pairs of images with a smaller symbolic distance at a higher rate than declining pairs with a larger symbolic distance.

Training:

Training proceeded in the exact same manner as Experiment 1 except with a new set of 25 images (Figure 2).

Testing:

The testing session consisted of two parts. At the beginning of every testing day, the monkeys completed 90 trials of the circle-size discrimination metacognition task. After reaching the criterion for metacognition on this task, a 30% difference in decline rate between the easiest and hardest trials, they moved on to the simultaneous chaining metacognition task (Figure 8). One session contained 300 of the metacognition trials, which used a similar paradigm as in Experiment 1 except with the addition of the metacognitive choice seen in the circle-size discrimination metacognition task (Figure 3 and 6). On 4/5 of the trials, there was an option to accept or decline the test through an “accept test” and a “decline test” stimulus (Figure 8). If accepted, the monkeys proceeded with the test and received either the maximum number of pellets if the answer was correct or no pellets if it was incorrect. If declined, they automatically received the minimum number of pellets after tapping a red bar five times to receive the next trial. The pellet ratio for each monkey was either 3:2 or 2:1 for correct choice and declined choice depending on the ratio used in Experiment 2. On 1/5 of the trials, the monkeys were forced to accept the test by touching an "accept test" stimulus, allowing them to proceed with the trial. The monkeys received one of these simultaneous chaining metacognition testing sessions.

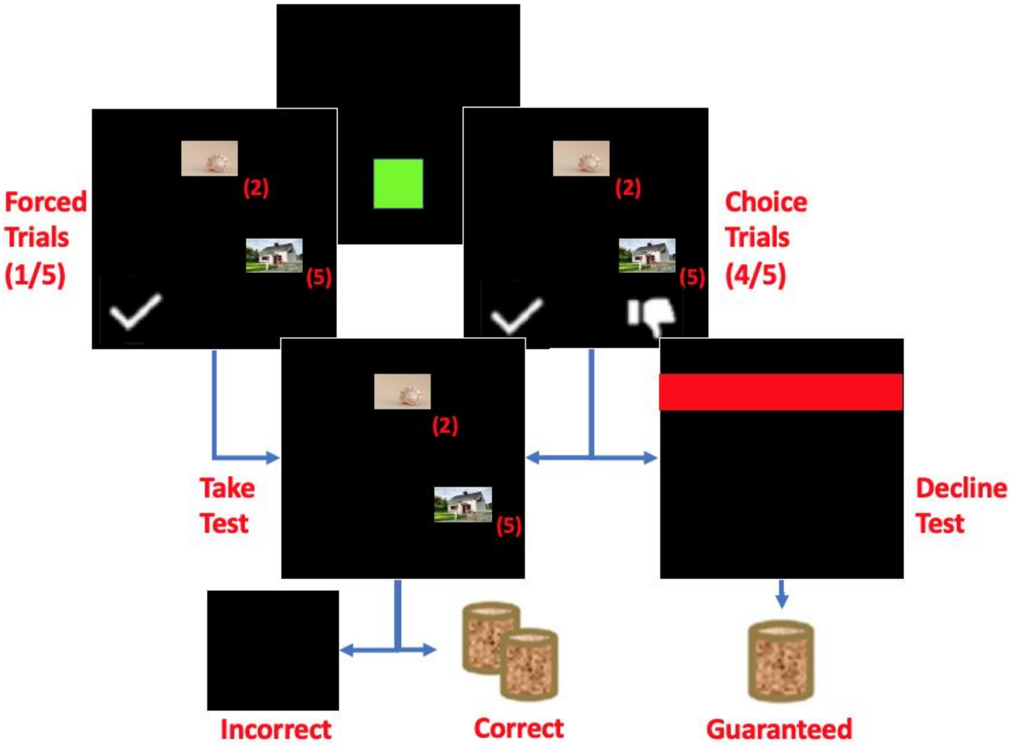

Figure 8: Simultaneous chaining metacognition paradigm. Monkeys touched the green start square, and two images from a previously learned list were presented. On 1/5 of these trials, the decline-test icon did not appear while the accept-test icon remained. Correct selection of which image came first resulted in a maximum number of pellets (2 or 3) with a positive sound while an incorrect selection resulted in a blank screen timeout of a varied time alongside a negative sound. On the other 4/5 of the trials, the decline-test icon appeared next to the accept-test icon. If the test was declined, the decline-test screen appeared along with a minimum number of food pellets (1 or 2), which was guaranteed after the red bar was touched five times. If accepted, correct responses resulted in a maximum number of pellets (2 or 3) and positive sound while incorrect responses result in a timeout and negative sound. One session consisted of 300 trials.

Results and Discussion:

All four monkeys reached criterion—a 30% difference between the decline rate of the easiest and hardest trials—on the session of the circle-size discrimination metacognition task and proceeded to the simultaneous chaining metacognition task. This showed that the monkeys were performing metacognitively right before the simultaneous chaining metacognition task began.

Monkeys showed modest evidence of metacognition when trained on lists of images using simultaneous chaining. First, the monkeys displayed the symbolic distance effect, replicating the findings of Experiment 1, for both the forced and choice trials. Accuracy on forced trials was lower as the symbolic distance decreased (Figure 9; main effect symbolic distance: $F(3,9) = 10.69$, $p = .003$). Accuracy on choice trials was lower as symbolic distance decreased (Figure 9; main effect of symbolic distance: $F(3,9) = 51.57$, $p < .001$). Second, monkeys suggested the presence of metacognition through their use of the decline button, though the evidence is not strong. Decline rate increased as the symbolic distance decreased (Figure 9; main effect of symbolic distance: $F(3,9) = 8.05$, $p = .006$). Though the difference in the decline rate between the easiest and hardest difficulty levels—a symbolic distance of 3 and a symbolic distance of 0 respectively—did not match the criterion of a 30% difference used in Experiment 2, there was a significant difference between the decline rate of the difficulty levels. This increase in decline rate paired with the lower accuracy is modestly consistent with classic findings of metacognition (Brown, Templer, & Hampton, 2017; Hampton, Brady, Engelberg, 2020; Templer, Brown, & Hampton, 2018).

The purpose of Experiment 3 was two combine the two findings in Experiment 1 and Experiment 2 in order to test the extent to which the representations used in the simultaneous chaining task were accessible to metacognitive monitoring. The results provide modest evidence that the spatial representations formed through training lists with simultaneous chaining are accessible to metacognitive monitoring. It is surprising that the largest increase in decline rate is between the symbolic distance of 3 and 2 due the accuracy lowering less in the forced trials between these two points; however, one monkey showed high accuracy across each difficulty level and thus did not show the symbolic distance effect. Unlike the other three monkeys, this monkey's decline rate showed no trend, which may have impacted the data. If these representations had not been available to metacognitive monitoring, then the monkeys would have shown no significant difference in decline rate between the easiest and hardest difficulty levels; when presented with the two test images, the monkeys would not have been able to assess whether they knew enough to accept the test. Because metacognition tasks can be used to determine which memories require explicit awareness, these initial findings provide modest evidence that the representations formed through simultaneous chaining are a form of explicit memory (Hampton, 2019).

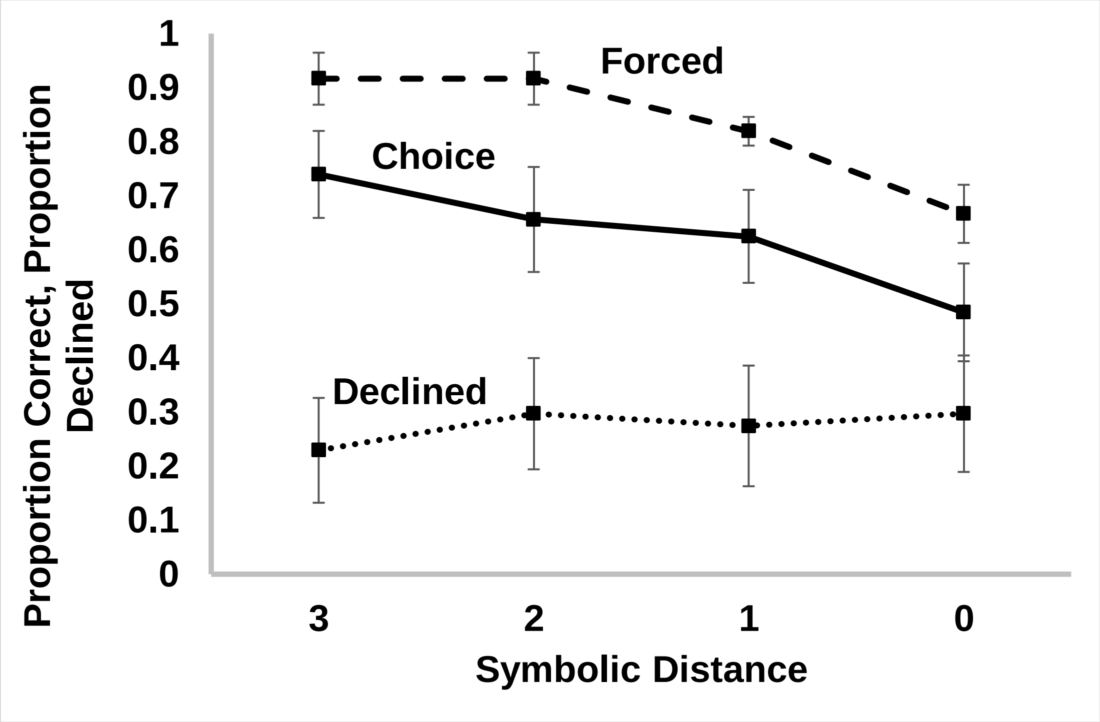

Figure 9: Accuracy on the simultaneous chaining metacognition task was lower for monkeys as symbolic distance decreased. Decline rate of the monkeys increased on the simultaneous chaining metacognition task as the difficulty level increased.

General Discussion

Monkeys displayed both the symbolic distance effect and preliminary evidence for metacognitive monitoring for lists of images learned through simultaneous chaining. In Experiment 1, accuracy was lower when symbolic distance decreased in the simultaneous chaining task, replicating previous findings that simultaneous chaining is subject to the symbolic distance effect (Colombo & Frost, 2001; Scarf & Colombo, 2008; Templer, Gazes, & Hampton, 2019). In Experiment 2, monkeys declined at a higher rate on difficult trials compared to easier trials in a circle-size discrimination task, consistent with previous literature on metacognition

(Brown, Templer, & Hampton, 2017; Hampton, Brady, Engelberg, 2020; Templer, Brown, & Hampton, 2018). In Experiment 3, monkeys showed the symbolic distance effect and declined harder trials more often than easy trials in the simultaneous chaining task. These initial results suggest that monkeys form spatial representations in the simultaneous chaining task that are accessible to metacognitive monitoring, though the evidence for metacognition is not strong.

In order to set up Experiment 3, two conditions had to be confirmed. The first condition was that lists learned through simultaneous chaining are represented spatially, with the images organized in the same order that they are presented to the monkeys. The second was that monkeys will decline harder trials more often than easy trials when the representations used in a task can be cognitively monitored. Experiment 3 combined these conditions in order to assess if the spatial representations formed in the simultaneous chaining task are accessible to metacognitive monitoring. The preliminary findings of these experiments provide modest evidence that the spatial representations used in simultaneous chaining are a form of explicit memory.

These findings may provide further information on the evolution of spatial representations in humans. Both humans and monkeys display the symbolic distance effect when trained on a simultaneous chaining task, meaning that both species use spatial representations during the task (Colombo & Frost, 2001; Templer, Gazes, & Hampton, 2019). Similar to how humans can express whether or not they know which step comes first in a simultaneously presented list like an unnumbered recipe, the preliminary findings of the current experiment suggest that monkeys may also have this capacity to monitor what they do and do not know about a simultaneously presented list. This potential presence of metacognition during simultaneous chaining in monkeys would mean that the representations formed by humans and monkeys through simultaneous chaining are a form of memory that both species are explicitly aware of. It is possible that this potential parallel is a result of convergent evolution. However, it is also possible that the kind of memory underlying the formation of the spatial representations used when a monkey or human encodes the order of simultaneously presented stimuli is shared by a common ancestor dating back to at least 32 million years ago (Roos and Zinner, 2015). Further testing for similar evidence in different primate species would help to confirm this claim.

One alternative interpretation is that these findings, and others that have been labeled as metacognition, can be explained in associative terms. It is possible that rather than the monkeys assessing how well they know the answer to the trial, they instead associate a specific trial with either the accept or decline button and the reward merely reinforces that association. However, associations alone do not explain the response patterns shown in the current study. If the monkeys were only using associations, then one might expect that the decline rate would stay the same across difficulty levels as the pellet reward is constant throughout the trials. The variable that changes throughout the trials is the probability that the monkey will get the answer correct based on the difficulty level. In order for the monkeys to show the increase in decline rate for harder trials, there must be some form of awareness that the probability of the monkey getting the trial correct is lower. The monkey must be able to monitor the information it knows about the list in order to gauge its chances of being correct—a key feature of metacognition. Furthermore, when associative models have been applied to the same accept and decline choices in previous literature as are used in this study, this low-level model wasn't able to encompass all of the findings that were labeled as the result of metacognition (see Smith, Couchman, & Beran, 2014).

This study contained at least two limitations. The first limitation was that the number of monkeys was small. The study started off with six monkeys but decreased to four by Experiment

3 due to scheduling and a monkey not reaching criterion in Experiment 2. Though this was unavoidable due to limited access to monkeys, the small sample size could make the results less generalizable than they have been presented as thus far. Second, using the circle-size discrimination task as a confirmation of the presence of metacognition could be considered a limitation as it is less similar to the simultaneous chaining task than another list-learning task would have been. This meant that the timeout periods and reward ratios determined in Experiment 2 may not have been as generalizable to Experiment 3, thus affecting the ratio of risk and reward that may incentivize the monkeys to use the most efficient, reward-maximizing rate of declining and accepting. However, one benefit of using the circle-size discrimination task is that the monkeys could never reach ceiling on all trials since visual discrimination could only be trained up to a certain threshold. This meant that multiple timeout periods could be tested even within the same day without the need to retrain entire new lists of images. Future experiments could benefit from replicating this study with a larger sample size and a new Experiment 2 task as a way to titrate the correct timeout period and reward ratio for Experiment 3.

The current study was motivated by potential contradicting results in nonhuman primate experiments. Two tasks, the memory for order of events task and the transitive inference task, both displayed the symbolic distance effect, showing that they both form spatial representations of lists (Gazes, Chee, & Hampton, 2012; Templer, Brown, & Hampton, 2018). However, when a metacognition component was added, the memory for order of events task suggested evidence of metacognition while the preliminary findings of the transitive inference task did not (Jessica Dugan, personal communication, May 15, 2019; Templer, Brown, & Hampton, 2018). This contrast is surprising as the two tasks appear to form similar representations in order to accomplish the similar task of encoding images in a list. A possible explanation for these findings is that the ability to do transitive inference exists in a more primitive form in monkeys, as research in humans shows that even though the presence of explicit memory leads to higher accuracy, transitive inference can be accomplished without conscious awareness (Titone et al., 2004). We added a metacognition component to an additional task that displays the symbolic distance effect, the simultaneous chaining task, to further investigate the intersection of spatial representations and metacognition. Given that the initial findings of this study provide modest evidence that the representations formed in simultaneous chaining are metacognitively monitored in monkeys, and therefore are a form of explicit memory, further research should be done on transitive inference and what may differentiate it from the other two tasks if it isn't metacognitively monitored.

The decision to use monkeys for this study was due to the gap in knowledge being specific to nonhuman primate research, as the referenced memory for order task and transitive inference task were both performed on monkeys. However, studies on spatial representations and metacognition are not specific to humans and monkeys. Though pigeons were able to learn a list of images through simultaneous chaining, they did not show the symbolic distance effect, which suggests pigeons do not use spatial representations on this task (Scarf & Colombo, 2008). However, previous literature has shown that pigeons can display the symbolic distance effect on numeracy tasks (Scarf, Hayne, & Colombo, 2011). These combined findings suggest that the use of spatial representations is both species- and task-specific. Pigeons have also been tested on a variety of metacognition tasks; however, none of the tasks could provide evidence that pigeons use metacognition (see Beran & Smith, 2011). The results of these metacognition studies provide evidence that metacognitive monitoring is species-specific.

The current study provides modest evidence suggesting that the representations of lists formed by monkeys through simultaneous chaining are spatially organized and are available to metacognitive monitoring. Thus, this preliminary evidence may indicate that representations learned through simultaneous chaining can be categorized as a form of explicit memory, though the current evidence is not strong. While these results potentially align with those of the memory for order of events task, further research needs to be done on the transitive inference task to confirm that the representations are not available to metacognitive monitoring and to determine why those representations may be unique. This information would advance the understanding of spatial representations in monkeys and thus may provide insight into the evolution of these representations in humans.

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