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April 3, 2023

A Test of Bias Towards Prototypical Features in Monkey Memory

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Abstract

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It is widely accepted that humans have evolved multiple memory systems to address different cognitive and behavioral demands. One such system is working memory, a form of short-term memory that temporarily holds information in readily accessible form, allowing us to perform tasks like reasoning, comprehension, and learning. Despite the vital importance of this type of memory it is limited to about 3-5 items. Humans overcome these limitations through the integration of working memory representations and prototypical knowledge. That is, when recalling well known items from working memory, we use prototypical knowledge to fill in missing information. The human literature demonstrates that this creates memory errors biased towards prototypes, yet it is not clear whether this is a uniquely human phenomenon, an evolved characteristic, or a fundamental property of memory. Studying non-human animals helps us understand this bias by providing insight into its evolutionary history. This study investigated this interaction and its evolutionary history in rhesus macaques because their extensive role in research has demonstrated that they have working memory and form prototypes. Specifically, we showed a monkey shape-specific features thousands of times, to incorporate the feature into a prototypical representation of the shape. We then had the feature vary from the prototypical value and tested the monkey's memory for the feature using the match to sample paradigm. Overall, we did not observe a significant bias towards the prototypical feature. Potential explanations for these findings and ways future research can improve on conceptual and methodological limitations are discussed below.

Keywords: working memory, semantic memory, evolution, prototype effect, monkeys

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A Test of Bias Towards Prototypical Features in Monkey Memory

Memory is a process that allows animals, both human and non-human, to acquire, store, and retrieve information about their environment. Thanks to this process, we can recognize the familiar, learn from experience, and predict the consequences of future behavior (Sherry & Schachter, 1987). In other words, organisms with memory systems can use earlier experiences to behave more appropriately at later times, an ability that would not be available to organisms without memory (Klein et. al., 2002; Tulving, 1995). This survival advantage leads to the likely conclusion that we evolved multiple memory systems through natural selection to address different cognitive and behavioral demands (Sherry & Schachter, 1987). To foreshadow, these memory systems do not perfectly preserve events as intact units of experience but are susceptible to decay and interference. To minimize these effects, humans use cognitive mechanisms to fill in missing details with information from other memory systems.

One such system is semantic memory, a type of long-term memory that stores our knowledge about the world without any context or information about the time of encoding (e.g., knowing that Paris is the capital of France or that dogs walk on all-fours, but not remembering when or in what context you learned those facts; Yee et. al., 2018). These memories create a large-scale knowledge system that we can draw on to interpret our experiences and determine appropriate actions. However, the vastness of our knowledge of the world can be difficult to navigate, resulting in difficulty conjuring the relevant information at the right time. To make this process easier, we often organize information into prototypes that group experiences with frequently cooccurring features together, allowing us to have one representation that summarizes the many different experiences (Gilboa & Maralatte, 2017). These constantly evolving representations incorporate common features as necessary, and uncommon features as optional

(Jitsumori, 2012). This helps us recall relevant information when needed and have potential knowledge about novel items, despite having no prior experience with the specific item (e.g., still being able to classify a purple dog as a dog; Rosch et. al., 1978).

Working memory, on the other hand, is a form of short-term memory that temporarily holds information in readily accessible form, allowing us to perform tasks like reasoning, comprehension, and learning (Baddeley, 2010). Through this system we are also able to rehearse, facilitating the organization of information into long-term storage (e.g., memorizing a phone number; Chai et. al., 2018). These critical functions, which account for around 50% of variance in general human intelligence, highlight the importance of working memory in daily functioning (Shipstead et. al., 2010). Despite the critical significance of this type of memory, it is quite limited in capacity, with a practical limit of about 3-5 items (Cowan, 2010; Brockmole & Logie, 2013). There are times when this limited working memory capacity is advantageous. That is, it can help humans, especially children, when learning imperfect rules like grammar, where exceptions are lost from working memory (Cowan, 2010). However, often, working memory capacity has a hindering effect: either it is necessary to hold more than 5 items in mind or the memory fades too quickly. Humans can overcome these limitations through the interaction of working memory and semantic memory networks.

One example of this interaction is chunking, a process that groups elements that have strong associations with each other, but weak associations with other elements (Gobet et al., 2001). For example, someone with knowledge about the Federal Bureau of Investigation and computer technologies would be able to encode “FBIIBM” as two items (FBI and IBM) instead of six (F, B, I, I, B, M; Guida et. al., 2012). The strength of associations that guide these groupings depend on preexisting knowledge from semantic memory. This integration of memory

systems allows experts (i.e., people with extensive prior knowledge) to have superior working memory for stimuli from their domain of expertise (Ericsson & Kintsch, 1995).

Another example of these mechanisms that limit information loss is the integration of working memory representations and prototypical knowledge. This process, thought to be adaptive, co-activates semantic memory networks when recalling well known items from working memory. This activation allows us to use relevant prototypes to fill in missing information in our working memory representations (Gilboa & Marlatte, 2017). However, this shortcut is imperfect. That is, the prototype may be activated when the item being recalled has characteristics that vary from the prototype. For example, in the popular Deese–Roedinger–McDermott illusion, after studying a list of associated words (bed, slumber, dream, etc.) people incorrectly identified a related lure (sleep) as being on the list, demonstrating how prototypes can cause false memories (Gallo, 2010).

A prototype may also be activated when there is no information missing, creating two conflicting sources of information. This conflict between representations in working memory and prototypical knowledge in semantic memory is reconciled through two processes: adaptation and assimilation. While adaptation adapts the prototype to incorporate new information, assimilation modifies working memory to fit existing prototypes (Gilboa & Marlatte, 2017). The latter often results in false memories biased toward typical experiences. For example, when holding object features in mind, humans make memory errors biased towards prototypical features, sizes, and angles, that an object is usually seen at (Konkle & Oliva, 2007; Olkkonen et. al., 2014)

The human literature provides a compelling argument for a bias in working memory towards prototypes, yet it is not clear whether this is a uniquely human phenomenon, an evolved characteristic, or a fundamental property of memory. Studying non-human animals can help us

understand this bias by providing insight into its evolutionary history. That is, if two different species demonstrate this bias, it is likely that it evolved in a common ancestor. Rhesus macaques are a particularly good species to investigate this evolutionary history because their extensive role in research has demonstrated that they have working memory (Brady & Hampton, 2018) and form prototypes (Jitsumori, 2012). They are also phylogenetically close enough to humans that it is unlikely that the bias evolved independently in the two species, but distant enough that it would be telling of its evolutionary history (Farris, 1973). Specifically, evidence of this bias in monkeys would suggest that a common ancestor of humans and rhesus macaques, some 25 million years ago (Disotell & Tosi, 2007), evolved under selective pressures favoring a memory system that supplements working memory representations with prototypical knowledge.

To investigate this interaction and its evolutionary history, the present study showed a monkey a shape-specific feature (i.e., color) thousands of times, to incorporate the feature into a prototypical representation of the shape. We then had the feature vary from the prototypical value and tested the monkey's memory for the feature. We hypothesized that if monkeys reconstruct working memory representations of objects using prototypes, then when object features differ from their typical values, they will make errors biased in the direction of the prototype. We also hypothesized that there would be a greater bias at longer delays because the more the memory decayed in working memory, the greater the influence of the prototype.

Method

Subjects & Testing Environment

We used one male rhesus macaque (*Macaca mulatta*, age at the start of the experiment = 14.4), housed at the Emory National Primate Research Center (ENPRC). Monkeys were reared outdoors in naturalistic family groups until they were relocated to a laboratory setting at the ENPRC at about 2.5 years of age. They were initially pair housed until they became socially incompatible, at which point they were moved to single housing, as advised by veterinary staff. The room in which they are housed allowed for visual and auditory contact with one another and was operated with an automated 12:12 (7:00 a.m. / 7:00 p.m.) light-dark cycle. Monkeys completed tasks for dietary pellets six days per week, and each monkey's caloric intake was subtracted from the daily caloric allowance determined by veterinary staff. The remainder of their allowance was given at the end of every day in the form of fruits, vegetables, and dietary chow. Water was available *ad libitum*.

The monkey had a long history of automated cognitive testing and was familiar with the delayed-match-to-sample paradigm. Testing was administered on 15-inch LCD touchscreens with a resolution of 1024 X 768 pixels, mounted to their home cage at the start of each testing day. The study used a Windows Forms Application (Microsoft .NET Framework, Version 4.8.04084), coded using Visual Studio (Version 17.1.0). The experimental apparatus was approved by the Emory Institutional Animal Care and Use Committee.

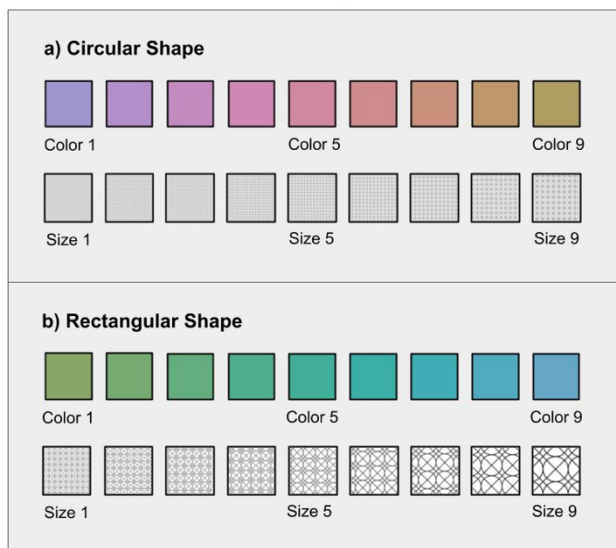
Experiment 1 Stimuli

Experimental stimuli were created using two novel shapes: the filled in outlines of Angola (a rectangular shape) and North Macedonia (a circular shape), stretched to fit a 300 X 300-pixel box. These shapes were selected to ensure that the monkey had no prior experience

with the experimental stimuli. Each shape was filled with a color and overlaid with a pattern of a particular size. These features, however, were shape specific, meaning the rectangular shape and the circular shape each had their own distinct color and pattern-size ranges (Figure 1).

Figure 1.

Possible Colors & Pattern-Sizes in Experiment 1



Colors

Color ranges were assigned using the perceptually equidistant HCL (hue-chroma-luminance) color space. Chroma and luminance values were held constant across shapes at 45 (+1) and 65, respectively. The hue range for the circular shape was 270 – 70 degrees (between purple, Color 1, and yellow, Color 9) with an average hue of 350 degrees (pink, Color 5), creating 9 equidistant colors spaced 20 degrees apart. On the other hand, the hue range for the rectangular shape was 110 – 230 degrees (between green, Color 1, and blue, Color 9) with an average hue of 170 degrees (teal, Color 5), creating 9 equidistant colors spaced 15 degrees apart. These HCL values were then converted to RGB, the color space used by the touchscreens and Visual Studio, using <http://hclwizard.org/>. For a review of this tool see Zeileis et al., 2020.

Pattern-Sizes

The pattern-overlay, created in Adobe Illustrator 2022, consisted of interlocked crosses and circles, repeated to create a square grid of 2500 reproductions (5003 X 5003 pixels). Size variations were created by resizing the pattern and cropping it to 300 X 300 pixels. These patterns were then overlaid over the appropriate shape. The central pattern-size for the circular shape was set at 900 X 900 pixels (Size 5), with 15% increases and decreases in both directions, creating 9 pattern-sizes ranging between 514.6 X 514.6 (Size 1) and 1574.1 X 1574.1 (Size 9) pixels. On the other hand, the central pattern-size for the rectangular shape was set at 3500 x 3500 pixels (Size 5), with 20% increases and decreases in both directions, creating 9 pattern-sizes ranging between 1687.9 X 1687.9 (Size 1) and 7257.6 X 7257.6 (Size 9) pixels.

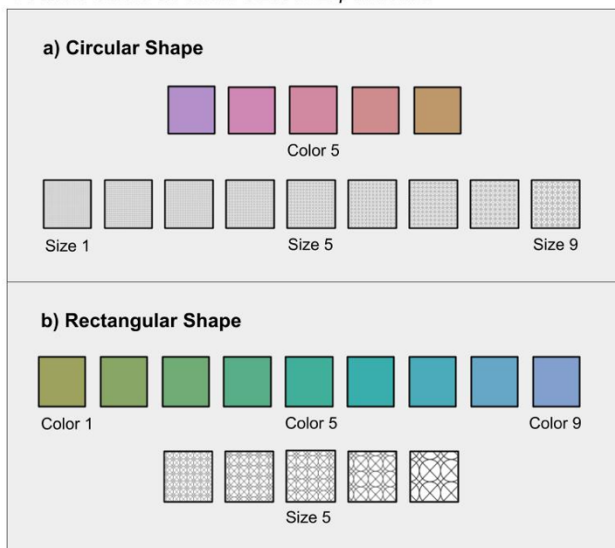
Experiment 2 Stimuli

More distinct versions of the stimuli were also created (Figure 2) with the goal of making the tasks easier to learn and increasing generalization between the two shapes that have completely different color and pattern-size ranges. In this iteration of the program, the hue range for the circular shape was 290 – 50 degrees (between pinkish-purple, Color 2, and orangish-yellow, Color 8) with an average hue of 350 degrees (pink, Color 5), creating 4 equidistant colors spaced 40 degrees apart. On the other hand, the hue range for the rectangular shape was 90 – 250 degrees (between green, Color 1, and blue, Color 9) with an average hue of 170 degrees (teal, Color 5), creating 9 equidistant colors spaced 20 degrees apart. The central pattern-size for the circular shape was set at 900 X 900 pixels (Size 5), with 20% increases and decreases in both directions, creating 9 pattern-sizes ranging between 434 X 434 (Size 1) and 1866.2 X 1866.2 (Size 9) pixels. On the other hand, the central pattern-size for the rectangular shape was set at

3500 x 3500 pixels (Size 5), with 69.4% increases and decreases in both directions, creating 4 pattern-sizes ranging between 2025.5 X 2025.5 (Size 2) and 6048 X 6048 (Size 8) pixels.

Figure 2.

Possible Colors & Pattern-Sizes in Experiment 2



Procedure

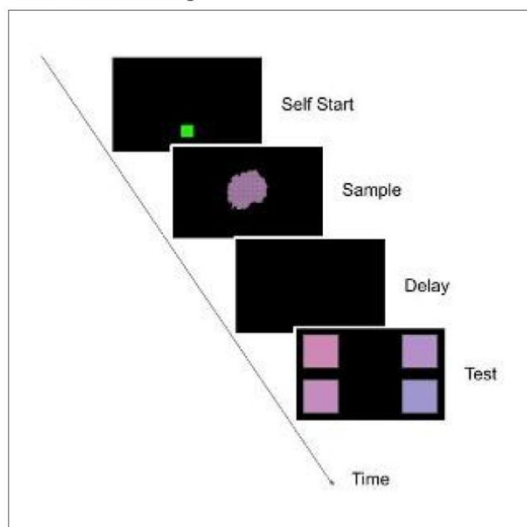
We used a delayed match-to-sample procedure. The sample shape and its features, however, varied in each of the six phases:

Color-Match Training

After tapping the green square twice (FR2), the monkeys saw the circular shape, with a pattern overlay constant at the central size (Size 5). The shape's color varied among the 8 colors surrounding, but not including the central pink (Color 5). The sample shape was seen in each of the 8 colors (Colors 1-4 and 6-9) once every 8 trials. Tapping the shape (FR2) resulted in a black screen and a 200ms delay, after which the monkey saw four response options in each of the four corners of the screen. All response options were from the same side of the central pink as the sample, presented as a square with just a color differentiating them (Figure 3). Each corner was

the correct response on 1 out of 4 trials and the incorrect options were randomized. Correct responses resulted in a dietary pellet reward, automatically dispensed to the cup at the bottom of the touchscreen. The pellet reward (or lack thereof) was accompanied by auditory feedback: an “excellent!” sound if correct, and a “d’oh” sound if incorrect. The correct responses resulted in a 3 second inter-trial interval, and incorrect responses resulted in a 12 second inter-trial interval. Each session consisted of 64 trials. Testing for this phase continued until the monkey reached 80% accuracy on two consecutive sessions. The goal of this training phase was twofold: 1) teach the monkey how to match colors, and 2) facilitate the formation of a prototype that includes the typical pattern-size for the circular shape.

Figure 3.
Color-Match Training

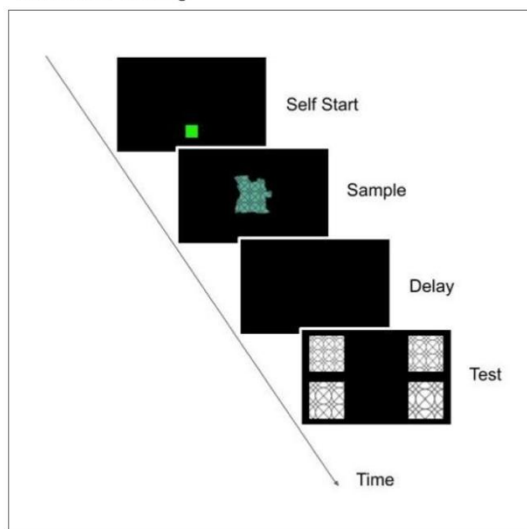


Size-Match Training

After tapping the green square (FR2), the monkeys saw the rectangular shape, in the central teal color (Color 5). The sample shape’s pattern-overlay was seen in each of the 8 sizes surrounding, but not including the central size (Size 5). The shape was seen in each of the 8

pattern-sizes (Sizes 1-4 and 6-9) once every 8 trials. Tapping the shape (FR2) resulted in a black screen and a 200ms delay, after which the monkey saw four response options in each of the four corners of the screen. All response options were from the same side of the central size as the sample, abstracted to create four boxes filled only with the black and white pattern (Figure 4). Each corner was the correct response on 1 out of four trials and incorrect options were randomized. Pellet rewards, auditory feedback and delays were administered in the same way as the Color-Match Training. Each session consisted of 64 trials. Testing for this phase continued until the monkey reached 70% accuracy on two consecutive sessions. The goal with this training phase was twofold: 1) teach the monkey how to match patter-sizes, and 2) facilitate the formation of a prototype that includes the typical color for the rectangular shape.

Figure 4.
Size-Match Training



Task Integration

This phase integrated the color-match training and size-match training tasks. Each task was presented twice every four trials. Each session consisted of 64 trials. Testing for this phase

continued until the monkey reached 70% accuracy for both tasks, on two consecutive sessions. The minimum number of sessions was set to 25.

Experiment 1 Testing: Short Delay

This phase repeated the Task Integration phase with one change: probe trials were introduced and presented on 2 out of every 18 trials. This phase consisted of 30 sessions, each with the following distribution: 64 regular color trials, 64 regular size trials, 8 size probes in which the shape previously associated with a color matching task resulted in a size matching task, and 8 color probes in which the shape previously associated with a size matching task resulted in a color matching task.

Half of the probes presented a *size-match* task for the circular shape, previously associated with the *color-match* task. In these trials, the color was held constant at the central pink (Color 5), and the shape was seen in each of the 8 probe pattern-sizes (Sizes 1-4 and 6-9) that had never been seen before. Each pattern-size appeared as the sample on 1 out of 8 probe trials featuring the circular shape. The response options were all from the same side of the central size (i.e., if the sample was Size 3, the response options were Size 1-4, in random order). Responses were abstracted, leaving only the black and white pattern, the same as in training.

The other half of the probes presented a *color-match* task for the rectangular shape, previously associated with the *size-match* task. In these trials, the pattern was held constant at the central size (Size 5) and the sample shape was seen in each of the 8 colors (Colors 1- 4 and 6-9) that had never been seen before. Each pattern-size appeared as the sample on 1 out of every 8 probe trials featuring the rectangular shape. The response options were all from the same side of the central size (i.e., if the sample was Color 7, the response options were Color 6- 9, in random order). Responses were also abstracted, leaving only a colored box.

Experiment 1 Testing: Long Delay

This phase repeated the first Testing phase, with one change: the delay interval between the sample and the response options was increased from 200ms to 2s. Like Probe Introduction, this phase consisted of 30 sessions each with the following distribution: 64 regular color trials, 64 regular size trials, 8 size probes and 8 color probes.

Experiment 2 Testing

Experiment 2 replicated all previous training and testing phases with one change: the more distinct versions of the stimuli described above were used, in an attempt to increase generalizability and transfer between tasks. The minimum length of each of the phases was set at 30 sessions, with a requirement of 70% accuracy on training trials.

Statistical Analyses

In our primary analysis, we hypothesized that if monkeys reconstruct working memory representations of objects using prototypes, then in probe trials in which object features differ from their typical values (Size 5, for the circular shape, and Color 5, for the rectangular shape), they will make errors biased in the direction of the prototypical feature. To test this, we compared the percent of errors made in the prototypical direction to chance (50%), using an exact binomial test. In our secondary analysis, we hypothesized that there would be a greater bias at the 2s delay (vs. the 200ms delay) because the more the memory decayed in working memory, the greater the influence of the prototype. To test this, we compared the percent of errors in the two delay conditions, using a Fisher's exact test. In Experiment 2, we thought that if the monkeys were having difficulty generalizing the task-related knowledge to the probes and differentiating the probe response options, then the more distinct stimuli would allow for the bias to be observed. We tested this using the first two statistical tests.

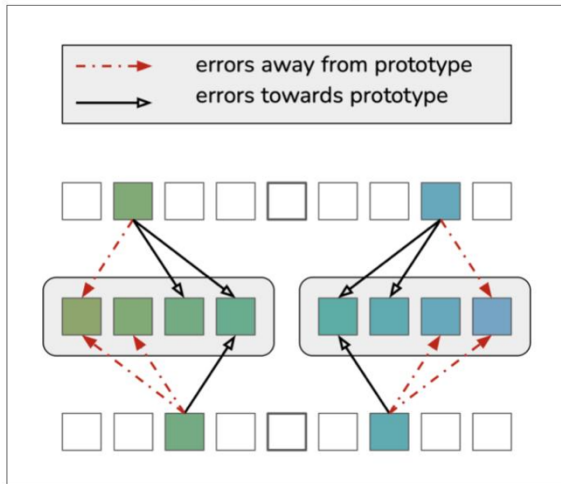
Results & Discussion

Experiment 1 Results

In the first phase, Color-Match Training, the monkey took 26,436 trials to reach the 80% criterion. For subsequent phases, the criterion was reduced to 70%, in an attempt to speed up the experimental timeline. In the next phase, Size-Match Training, the monkey took 70,311 trials to reach criterion, including 30,993 trials on a version of the program that presented the correct response option in predictable order. In the Task Integration phase, the monkey took 3,266 trials to reach criterion. All testing phases lasted for 4,320 trials.

To test the main hypothesis that a monkey's working memory is biased towards prototypical knowledge, we looked at the probe trials in which the samples were colors/sizes 2, 3, 7 and 8 (Figure 5). In these trials, we compared the percent of memory errors (i.e., incorrect selections) made in the direction of the established prototypical feature to chance (50%), using an exact binomial test. For analysis, the original probe trials (as opposed to the probe trials with the more distinct stimuli) were divided into four conditions: 1) color probes with short delays, 2) color probes with long delays, 3) pattern-size probes with short delays, and 4) pattern-size probes with long delays.

Figure 5.
Classification of Away vs. Towards Responses

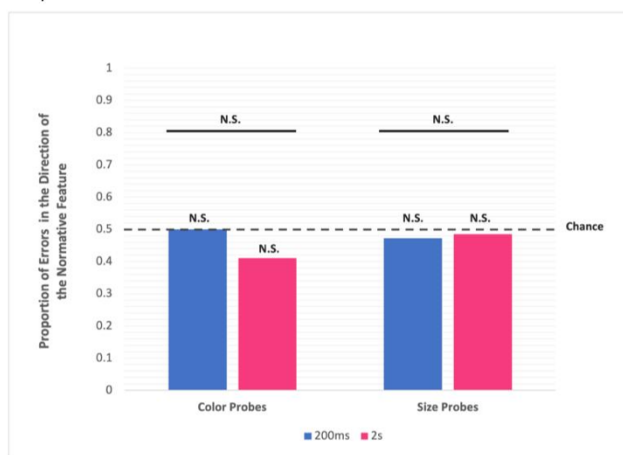


The analysis of these color probe trials revealed that neither condition had a bias significantly above chance (Figure 6): in the short delay condition exactly half of the errors (41 out of 82) were in the direction of the prototypical color (exact binomial test, $p = 1$), and in the long delay condition there were less errors (37 out of 90) in the direction of the prototypical color (exact binomial test, $p = .113$). Similarly, analysis of the pattern-size probes revealed that neither condition was different than chance: in the short delay condition there were less errors (42 out of 89) in the direction of the prototypical pattern-size (exact binomial test, $p = .672$), a pattern replicated in the long delay condition in which there were less errors (49 out of 101) in the direction of the prototypical pattern-size (exact binomial test, $p = .842$).

We also hypothesized that there would be more memory decay at a longer delay, resulting in more frequent bias in the direction of the prototypical feature. Testing of this hypothesis was carried out by comparing the long and short delays for color and pattern-size probes, separately, using a Fisher's exact test. Analysis of color probe data revealed that there was

no significant difference between the two delay conditions (Fisher's exact test, two-sided, $p = .284$). Similarly, no significant difference was found between the two delay conditions in the pattern-size probes (Fisher's exact test, two-sided, $p = .885$).

Figure 6.
Experiment 1 - Results



Experiment 1 Discussion

Contrary to our main hypothesis, the monkey did not show a bias in the direction of the established prototype in either the color-matching probe trials or the size-matching probe trials. We also did not find an effect of increased time on the bias, as the errors in the direction of the prototype were quite similar across the two conditions. A possible explanation for why we did not observe the hypothesized effect is that monkey was not generalizing his knowledge of the task (i.e., the feature matching rule) to the probe trials. This is supported by the finding that accuracy on the probe trials was near chance (26.46%) suggesting that the monkey did not know what he was doing and chose the response options at random. We thought that using more distinct training and probe stimuli would help mitigate this issue and allow for a prototypical bias

to emerge. This was in line with prior research that has found that increased variance of the training stimuli results in improved generalization to novel stimuli (Raviv et. al., 2022) and the intuitive reasoning that more distinct probe stimuli would be easier to differentiate at test. To test this, we introduced the more distinct, Experiment 2 stimuli and re-ran the tests above.

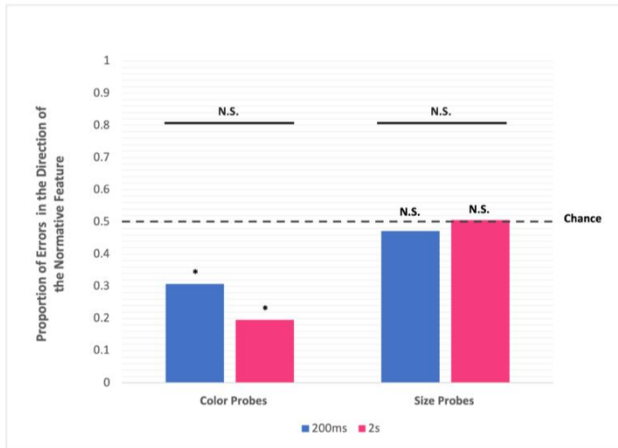
Experiment 2 Results

First, we compared the percent of memory errors made in the direction of the established prototypical color to chance (50%), using an exact binomial. This test revealed that in the color probes, there was no significant bias in the direction of the prototypical color (Figure 7).

However, the errors were significantly biased away from the prototypical color: in the short delay condition there were less errors (27 out of 88) in the direction of the prototypical color (exact binomial test, $p = < .001$), a pattern replicated in the long delay condition in which there were even less errors (18 out of 92) in the direction of the prototypical color (exact binomial test, $p = < .001$). We also compared the percent of memory errors made in the direction of the established prototypical pattern-size to chance (50%). In these probe trials, there was also no significant bias in the direction of the prototypical color: in the short delay condition there were less errors (42 out of 89) in the direction of the prototypical color (exact binomial test, $p = .672$), and in the long delay condition there were slightly more errors (40 out of 79) in the prototypical direction (exact binomial test, $p = 1$).

Finally, we compared the long and short delays for the more-distinct color and pattern-size probes, separately, using a Fisher's exact test. Analysis of color probe data revealed that there was no significant difference between the two delay conditions (Fisher's exact test, two-sided, $p = .089$). Similarly, no significant difference was found between the two delay conditions in the pattern-size probes (Fisher's exact test, two-sided, $p = .757$).

Figure 7.
Experiment 2 - Results



Experiment 2 Discussion

Contrary to the theorized effect of using more distinct stimuli in Experiment 2, the monkey's accuracy remained near chance (27.26%). Additionally, the monkey did not show a bias in either direction in size-matching probes, though his errors were biased away from the prototypical color in the color-matching probes. Increased time did not influence this bias, as the errors in the direction of the prototype were quite similar across the two delay conditions.

The significant findings in the color-matching probes are likely the result of a phenomenon called peak-shift, or the avoidance of stimuli similar to an unreinforced stimulus (Lynn et. al., 2005). Specifically, in the Size-Match Training, the monkey was attending to the pattern while inhibiting the processing of the color. While it was not our intention this may have trained the monkey to suppress the memory of the prototypical color. This would result in an avoidance of prototype-like colors, creating the observed response bias away from the prototype.

General Discussion

The current study investigated the effects of prototypes on working memory in one male rhesus macaque. Three hypotheses were examined: 1) memory of well-learned shapes will be biased towards prototypical features, 2) longer delays will increase the bias towards prototypical features, and 3) more distinct stimuli will facilitate generalization and increase the percent of biased errors. Overall, none of the hypotheses were supported by the study, as the bias towards the typical feature was not significantly above chance, a finding we observed across delay conditions and stimulus types. The lack of significant bias towards the prototype was particularly surprising at the longer delay given the human literature that reliably documents bias at delays of 2 seconds (Olkkonen et. al., 2014). However, these results must not be taken as proof for the lack of the phenomenon in the general population.

The lack of informative results of this study should be interpreted considering several limitations. Firstly, due to the small sample size ($N = 1$), the generalizability and power to detect an effect was low. The study was also not equipped to assess whether the prototypical feature had been acquired through indirect exposure. That is, during training they were never tested on the pattern size for the circular shape or the color for the rectangular shape, leaving open the possibility that they never attended to that feature. It is also possible that since the feature was never rewarded, the monkey learned to suppress its memory of it, a strategy that would accommodate more task-relevant information. Furthermore, the feature tested during training (i.e., color for the circular shape, and size for the rectangular shape) was held constant during probe trials at the central feature (i.e., Color 5 for the circular shape and Size 5 for the rectangular shape). The assumption was that the 8 features seen during training would be averaged to create a prototypical representation. However, if this did not occur as assumed, the

constant feature seen on probe trials may have stood out from training stimuli and therefore not invoked the prototype that would have caused the memory bias. Finally, transfer between training trials and probe trials during testing may have also been problematic. That is, it is possible that the monkey had difficulty generalizing what it learned with the yellow-purple color range, that it was trained on, to the very different looking blue-green color range, that it was tested on.

The current study contributes to the field of memory research by introducing new methodology to investigate the interaction of working and semantic memory in animals, namely monkeys. While the methods can be improved on, the experimental process highlights important considerations for the field. Specifically, this account of the intricacies of training a monkey on the matching of precise color hues, raises important considerations for the choice of stimuli in future research with non-human primates. Furthermore, the apparent inability of the monkey to generalize to another hue range highlights the potential disconnect between the way humans and monkeys conceptualize the match-to sample paradigm. Although the results did not provide insight on the evolutionary history of the interaction between working memory and semantic memory, the questions raised in this study highlight a gap in the literature. Ways future research can improve on both conceptual and methodological limitations are discussed below.

The results of the current study suggest specific actions future research can take to expand on both the methods utilized, and the field of reconstructive memory research. As discussed above, this study had various shortcomings that future research may be equipped to address. Firstly, it is possible that a larger sample size may yield informative results. In addition to a larger sample, the ability to assess whether the training phases successfully resulted in a prototype would be helpful. Additionally, the present study aimed to give the monkey as little

exposure to the probes as possible, to avoid the possibility of the probe features getting accommodated into the prototype. However, given the difficulty that the monkey faced generalizing between training trials and probe trials a different design that gives monkeys experience matching the probe response options before moving onto probes, may be helpful. Finally, in contrast to the present study that assessed directionality of bias, future studies might consider taking a step back to assess the non-directional influence of prototypes on monkey memory. This may be done by comparing the accuracy of prototype congruent shape-feature pairings and incongruent shape-feature pairings.

For the reasons outlined, it is our hope that future research builds on the methods and limitations of the present study and provides further insight into the interplay of prior knowledge and working memory.

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