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Kamin Bouguyon April 11, 2017

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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
of the requirements of the degree of
Bachelor of Sciences with Honors

Neuroscience and Behavioral Biology

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Abstract

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While non-human primates show evidence of having working memory, they lack language. In humans, language improves working memory. Some great apes have been trained to associate icons or gestures with objects and actions, a process often called language training. Whether this language training affects working memory in nonhuman primates the way language does in humans is yet to be explored. We first tested whether orangutans use working memory in a delayed matching-to-sample task by including trials in which orangutans had to touch an intervening image and trials in which they did not. We found evidence that orangutans use working memory in a delayed matching-to-sample task. We also tested Chantek, a language trained orangutan, with images for which he had previously learned signs and images for which he hadn't learned signs and compared his performance to that of the other orangutans. Chantek's accuracy for images for which he had signs was lower than those for which he did not. This suggests that language in orangutans, unlike in humans, does not improve working memory but rather impairs it.

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Acknowledgements

Thanks to Rachel Diamond and Rob Hampton for guidance. We would also like to thank Zoo Atlanta for their cooperation and assistance with subjects and testing.

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Humans use language to store and retrieve memories, even subconsciously (Munnich, Landau, & Dosher, 2001), so it is likely that language has an important role in the cognitive process of memory. In studying humans, however, it is almost impossible to separate language from thought to evaluate cognitive mechanisms independent of language (Martinich, 2013). Studying great apes allows us to examine primate cognition without the influence of language. Apes and humans share very similar cerebral anatomy and many evolutionary specializations (Rilling et al., 2008), but apes have no known form of language. Because they are not constantly exposed to language, apes do not have the strong tie between language and memory that humans do. However, an ape can be trained to make associations between icons or gestures and items or actions in a process called language training (Brakke & Savage-Rumbaugh, 1995; Miles, 1990). If language training improves memory, then a language trained subject should show increased performance on memory tasks for the trained items. By comparing performance on a memory task across a language-trained orangutan and non-language-trained orangutans, we can gain a better understanding of how language impacts memory.

Working memory is described as the process of holding and manipulating information in mind for a given context (Baddeley, 1992). According to Baddeley’s model, working memory consists of two components: a visuospatial component for manipulating vision-based input and a phonological component for maintaining auditory input. While Baddeley used behavioral experimentation with human memory to develop his model, later research employed fMRI to look at participant’s brain activation while performing working memory tasks (Cohen et al., 1997). Cohen and his colleagues discovered that the prefrontal cortex, an area in the brain involved in working memory, remains active even after the activating stimulus is no longer present. This maintenance of activation is thought to allow the brain to remember stimuli over a short delay. Using visuospatial working memory and the mental capacity for maintaining stimuli in mind for a short period of time, subjects can perform working memory tasks such as the delayed matching-to-sample (DMTS) task. For DMTS tests, the subject is presented with a sample stimulus to hold in mind for a brief delay before selecting the sample stimulus among a number of distractor stimuli (Lind, Enquist, & Ghirlanda, 2015). Non-human primates like rhesus monkeys have been shown to have visuospatial working memory and are capable of performing well on a DMTS task (Washburn & Astur, 1998). Though the literature does not contain any evidence, it is reasonable to infer that orangutans would also be able to perform well in a DMTS task because they are more closely related to humans than rhesus monkeys.

Another defining characteristic of working memory is that its resources are limited in comparison to other systems such as long-term memory. The amount of information working memory systems are capable of maintaining during a delay seems to be limited to around 4 items (Cowan, 2001; Luck & Vogel, 1997). This limited capacity for maintaining stimuli suggests that one's brain can only devote so many of its resources to any one working memory task. Forcing the brain to redistribute working memory resources to another task by including an intervening item during the DMTS delay could affect the accuracy of the working memory task. Measuring performance with and without such a competing task allows researchers to determine whether the intervening task consumes working memory resources needed for the DMTS task (Jeneson, Mauldin, Hopkins, & Squire, 2011; Jeneson & Squire, 2011). Impaired performance in the presence of a competing cognitive load indicates that the subject is likely using working memory. However, simply including a competing cognitive load does not necessarily guarantee that the subjects are using working memory. When given a DMTS task with either a large (1400) or small (4) set of images in the sample stimulus pool, rhesus monkeys' performance was impaired by a competing load in the small set condition but not in the large set condition (Basile & Hampton, 2013). Because deficit in the presence of a competing cognitive load is a characteristic of working memory, the rhesus monkeys seem to use working memory for the small set of images but not the large set. In light of this, we used a small set of 5 images in a DMTS task with and without a competing cognitive load to determine if orangutans are using working memory in DMTS, which is a question that has not yet been answered.

After answering the question of whether orangutans use working memory for a DMTS task, we aim to determine what effect, if any, language-training may have on orangutan memory processes. For the purposes of this study, language is defined as associations between symbols and concrete ideas, such as the association between the word "ball" and a spherical object. These associations are stored in long-term memory, a brain-wide system devoted to storing information for later recall (Atkinson & Shiffrin, 1968; Jeneson & Squire, 2011). In memory recall, items stored in long-term memory can interact with working memory. In certain situations, specifically with regard to words and objects, these associations can enhance a person's ability to retain information in working memory (Hulme, Maughan, & Brown, 1991; Lanfranchi & Swanson, 2005). Adult, English speaking participants remember words better than word-sounding non-words (e.g. swijit) when asked to immediately recall lists of words and non-words (Hulme et al., 1991). Similarly, English speaking participants remembered lists of Italian words better after learning their meanings. This study suggests that the representation of words in language can augment memory for those words in humans. However, it is impossible to completely remove the influence of language in humans because language is so deeply ingrained in our cognition (Martinich, 2013). By testing great apes, we avoid any language predisposition found in humans.

Thus, comparing Chantek's performance with that of the other orangutans will allow for a clearer representation of language's effect on working memory.

As one of our closest living relatives, orangutans share much of our neuro-anatomical structure, including regions in the brain believed to be important for human language. One such region is the arcuate fasciculus, a white matter tract connecting the frontal and temporal lobes. In neuro-anatomical studies of the arcuate fasciculus, researchers found similarities between humans and non-human primates that suggest language-like abilities are theoretically possible for non-human primates (Rilling et al., 2008). However, early attempts to teach young chimpanzees to speak like humans were unsuccessful (Kellogg, 1968). This is likely due to the lack of proper vocal cord structure and control necessary to produce the complex sounds required for human speech (but see also: Fitch, de Boer, Mathur, & Ghazanfar, 2016). Some of these studies did reveal that the chimps spontaneously used gestures in an attempt to convey their thoughts and could even be taught to use a set of symbols to dynamically communicate (Kellogg, 1968; Premack, 1971). Later researchers were more successful in fostering great apes' ability to learn a set of symbols and communicate with their handlers (Brakke & Savage-Rumbaugh, 1995; Miles, 1990). Bonobos and chimpanzees learned to use a table of written symbols to which they pointed to communicate specific words and ideas (Brakke & Savage-Rumbaugh, 1995). Chantek, who currently resides at Zoo Atlanta, learned to associate hand gestures, or signs, with objects when he was young (Miles, 1990). In each case, symbols represented both words and concepts, creating a repertoire of signs stored in long-term memory. In his training, Chantek acquired an extensive vocabulary of signs for a variety of semantic categories from food items such as "banana" to animals like "cat". Chantek's enculturation also allows him to understand and use a pointing gesture more flexibly than his non-enculturated counterpart when communicating with his human handlers (Call & Tomasello, 1994), which suggests a more complex understanding of communication. Chantek's knowledge and flexibility with expressing these signs seems to mimic language and could change the way he holds stimuli in mind during working memory tasks involving images for which he has a sign. Having access to Chantek offers the opportunity to test the interaction between language and working memory. Because apes do not innately have language as we would recognize, the other orangutans at Zoo Atlanta provide an intra-species comparison. Testing a language trained ape and comparing him to counterparts who are not may provide insight into the importance of language's role in memory without the confounding factor of language predisposition that humans have.

In the current study, we first seek to determine whether orangutans use a working memory system similar to that of humans and rhesus macaques on a DMTS task. We then specifically examine how language training affects the maintenance of information in working memory. We test two hypotheses. Hypothesis 1: If the orangutans use working memory on the DMTS task, then accuracy will be lower on trials that include a competing cognitive load during the delay. Hypothesis 2: If language improves working memory in a DMTS task, then Chantek's accuracy will be greater for trials with images for which he has a sign than trials with images for which he does not, but the other orangutans will perform equally well with both types of sample images.

General Methods

Subjects

The subjects were: two Sumatran orangutans (*Pongo abelii;* Dumadi, 10-year-old male and Madu, 33-year-old female), one Bornean orangutan (*Pongo pygmaeus;* Satu, 14-year-old male), and one hybrid (Chantek, 39-year-old male). These four orangutans lived in social groups at Zoo Atlanta and were tested while off exhibit. They had regular access to food and water throughout the testing period. All of these individuals have had some form of experience with the matching-to-sample paradigm.

Apparatus

The testing apparatus consisted of a 15-inch LCD color touchscreen monitor, laptop computer, speakers, and automated reward dispenser (MedAssociates Inc. St. Albans, VT) in a metal case hung on the indoor housing enclosures. The orangutans had access to the apparatus for approximately 1 hour in the morning 5 days a week before going on exhibit for the day. All testing occurred indoors and food reinforcement was given by an automated pellet dispenser which dispensed nutritionally balanced fruit-flavored pellets into a food cup located below the touch screen.

Experiment 1

Stimuli

Stimuli were 200x200 pixel images of objects separated into two sets, one small set of 5 unique images (cherry, phone, plate, glasses, and rock) and one large set of 200 unique images. The images featured an object displayed against a white background. None of these stimuli depicted objects for which Chantek had learned signs and were specifically chosen to not resemble anything on his list of vocabulary provided by Zoo Atlanta.

Procedure

DMTS Training. First, each orangutan was trained on DMTS trials with a delay of 2000 milliseconds (ms). The animals initiated a trial by touching a green start square (150x150 pixels) in the bottom middle of an otherwise black screen (Figure 1). After touching the start square, an image from the small set appeared in the center of the screen. The assignment of images to trials

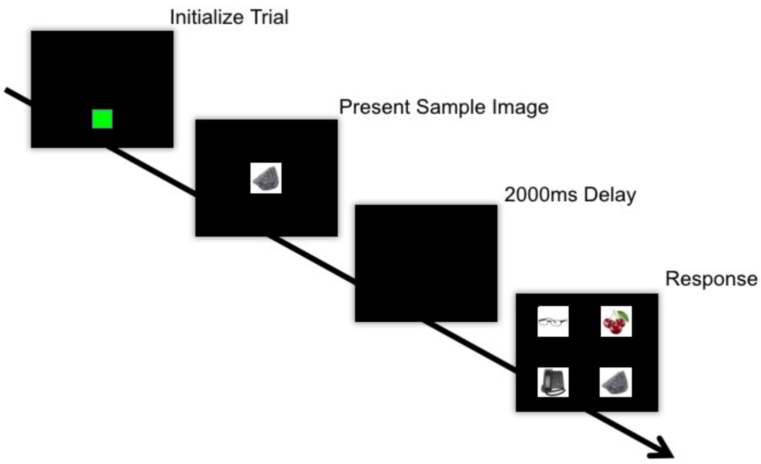

Figure 1. General outline of the DMTS task without interference. The trial began when the green start square was touched and the sample image appeared. Once touched, the sample image disappeared for 2000 ms before four response images were presented. The subjects then chose one of the images on the response screen. After the response images disappeared, an inter-trial interval of 2000 ms separated each trial.

was pseudo-random such that in every 5 trials each of the five images appeared once, and no image could be repeated more than twice in a row. When the orangutan touched this sample image, the screen went black for a 2000 ms delay before four choice images appeared in the four corners of the screen. One of these choice images matched the sample image while the other three were distractors chosen at random from the small set. The location of the correct choice image was pseudo-randomly assigned such that in every 4 trials the sample image appeared in each of the four choice locations once and in the same location no more than twice in a row. The distractor images were randomly assigned to the remaining locations. For all trials, the orangutans had to touch the image that matched the sample image. Correct responses were rewarded with a positive auditory stimulus and a fruit flavored pellet. Incorrect responses led to a negative auditory stimulus and no food reward. An inter-trial interval of 2000 ms followed each trial. Sessions consisted of 40 trials where each image appeared a total of 8 times and the sample image appeared in each response location a total of 10 times. The orangutans completed training sessions until they reached the criterion of 85% accuracy on one session or 100 completed sessions with a final accuracy significantly above chance (25%), then moved on to the test phase.

Competing Cognitive Load Test. The test trials were similar to the training trials except that half of these trials included a competing cognitive load during the delay. Each trial was assigned to have either an empty delay or an intervening item. Trials were pseudo-randomly assigned such that for every 4 trials, each type appeared twice and the same trial type could occur no more than 4 times in a row. For the cognitive load trials, as with training, after touching the start square the orangutans saw a sample image presented in the center of the screen. After the subject touched the sample image, it disappeared and a novel image was presented in one of twenty non-overlapping locations in a 5x4 grid on the screen, randomly assigned before each trial (Figure 2). These novel images were assigned from the

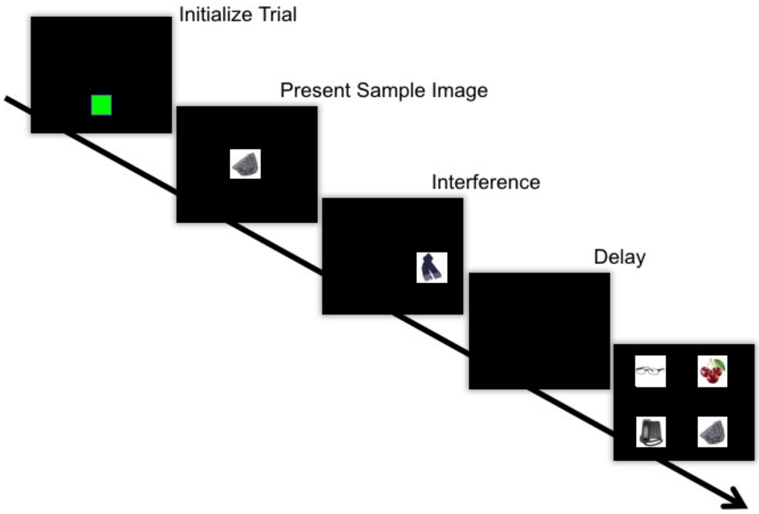

Figure 2. General outline of the DMTS task with competing cognitive load. The trial began when the green start square was touched, then the sample image was presented until touched. The subjects were then presented with an intervening image that remained until it was touched. The time taken to touch the intervening image was subtracted from the 2000 ms delay and the subjects waited the remaining time with a blank screen before the response screen was revealed. The subjects then chose one of the response images. After the response images disappeared, an inter-trial interval of 2000 ms separated each trial.

large set of images at the beginning of the test such that the subjects only saw each image a single time. To control the delay length, the program measured the time until the subject touched this intervening image and subtracted it from 2000 to calculate the remaining delay before revealing the response images. If the time taken to touch the intervening image exceeded 2000 ms, that trial was noted and was not included in data analyses. After the delay, the subjects saw the response screen with four images and touched one of the images. The reinforcement criteria for correct and incorrect responses were the same as above. The subjects completed five 80-trial sessions. At the beginning of the first session, the array of 200 images was randomized. It was not re-shuffled at the end of each session, so that a novel image was shown for each cognitive load trial.

Data Analysis

A one-tailed binomial statistical test was used to compare each subject's final accuracy in the training paradigm with a chance level of 25%. Chi-squared tests with 1 degree of freedom were run for each subject to determine if their accuracy differed significantly between empty delay and competing cognitive load conditions. A one-tailed t-test with 2 degrees of freedom was performed for the combined data between the subjects to determine if the difference in accuracy was evident at the group level.

Results and Discussion

Dumadi and Satu reached the criterion of 85% accuracy on their 78th and 94th sessions, respectively, while Chantek and Madu completed 100 sessions, ending with an accuracy of 62.5% and 70% on the final session, respectively (Figure 3). The latter two orangutans performed above chance on their final training sessions (Chantek: $p < 0.001$; Madu: $p < 0.001$). By these criteria, all orangutans completed the training trials and moved on to testing.

The competing cognitive load impaired performance on the DMTS task for all three of the non-language-trained orangutans (Figure 4; Dumadi (A): M(empty) = 71, $SD = 7.20$; M(cog. load) = 53.9, $SD = 7.35$; X^2 (1, $N = 1$) = 12.32, $p < 0.001$; Madu (B): M(empty) = 72, $SD = 3.71$; M(cog. load) = 36.3, $SD = 4.98$; X^2 (1, $N = 1$) = 50.06, $p < 0.001$; Satu (C): M(empty) = 73.5, $SD = 6.02$; M(cog. load) = 56.5, $SD = 7.91$; X^2 (1, $N = 1$) = 12.23, $p < 0.001$) but not for Chantek, the language trained orangutan (Figure 4D; M(empty) = 63, $SD = 4.11$; M(cog. load) = 62.2, $SD = 9.86$; X^2 (1, $N = 1$) = 0.0075, $p > 0.5$). Because the images within the matching task were identical across the two trial types, the accuracy impairment from the cognitive load suggests that most of the orangutans used working memory to complete this task. Chantek performed equally well on both trial types, suggesting that either the cognitive load did not impair his memory in the DMTS task or he used a different cognitive mechanism than

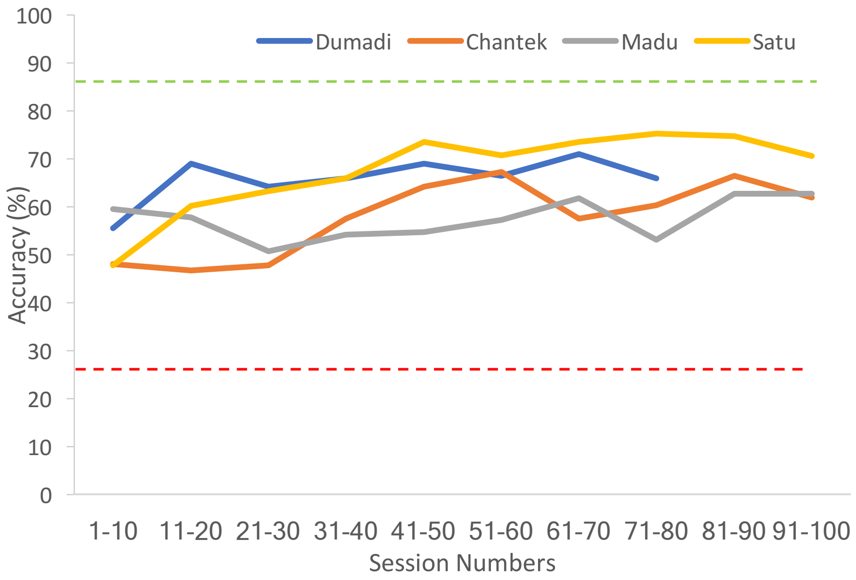

Figure 3. Learning curves for each orangutan on the delayed matching-to-sample task. Accuracy for each session is graphed relative to the session numbers (binned every 10 sessions) to track how the orangutans learned the task over time. The red dotted line indicates chance level performance (25%). The green dotted line denotes the criterion for completion (85%). All orangutans reached criterion.

the control orangutans to complete the DMTS task. When the data from all subjects were combined, the orangutans showed a deficit in accuracy when presented with a competing cognitive load ($t(4) = 2.913$, $p < 0.05$). Interestingly, even though Chantek showed no individual difference between the two trial types, his data were not enough to overcome the difference

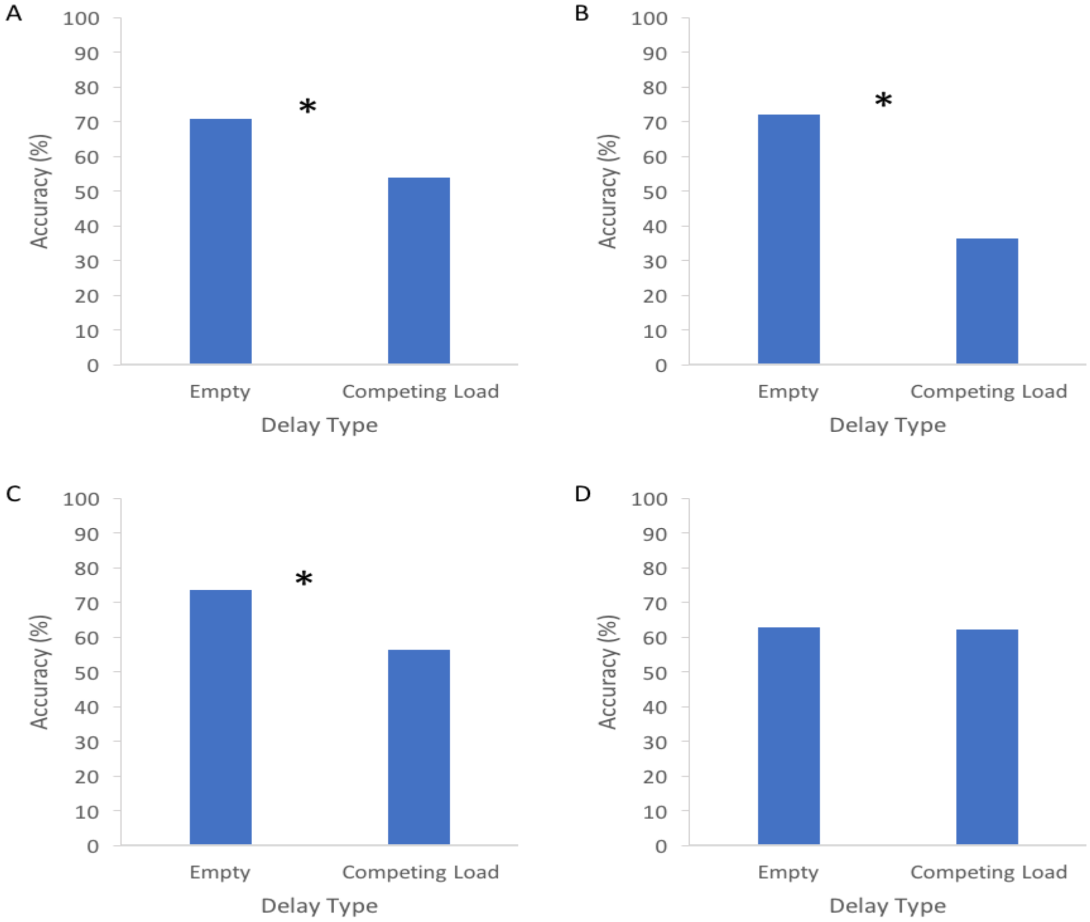

Figure 4. Effect of competing cognitive load on accuracy in delayed matching-to-sample task. Accuracy on DMTS task was impaired for three of the orangutans (Dumadi: A, Madu: B, and Satu: C) but not for the language trained orangutan (Chantek: D). Accuracy is graphed as the average proportion of correct trials across all 5 sessions separated by the two delay types. The empty condition includes the trials in which there was no intervening image and the competing load condition includes the trials that had an intervening image during the delay. Chi-squared statistics with $p < 0.05$ indicated (*).

shown by the other subjects. Overall, these data show that cognitive load strongly impairs memory performance in orangutans, indicating that they use working memory. It is important to note, however, that Chantek did not actually show impairment with the given conditions.

Experiment 2

Based on the results in Experiment 1, orangutans showed evidence of using working memory in a DMTS task. Interestingly, Chantek did not show the expected deficit in the presence of a competing cognitive load. Keeping this in mind, we operated under the presumption that all the orangutans used working memory in the DMTS task. In Experiment 2, we focused on the impact of language training on memory performance.

Stimuli

Stimuli were ten new images divided into two sets corresponding to whether Chantek had a sign for the given image. The “represented” set (R) consisted of images for which Chantek, prior to testing (Miles, 1990), learned to associate a sign with the item depicted in the image and the “unrepresented” set (U) consisted of images for which Chantek had not explicitly learned a sign. The 5 represented images (cheese, toothbrush, cat, q-tips, car) were taken from a list of vocabulary provided by Zoo Atlanta and the 5 unrepresented images (biohazard bin, wrench, computer mouse, hippo, wheat) were specifically chosen to not be close to anything on that list.

Procedure

The orangutans did not complete a new set of training trials, but began with Experiment 2 test trials following the completion of Experiment 1 test trials. Each trial began when the subject touched the green start square and was presented with a sample image. The sample images were assigned pseudo-randomly from one of the two sets of images. First, the image set was chosen such that every 4 trials each set was selected twice and no more than 4 times in a row. Next the sample image was pseudo-randomly assigned from the selected set so that for every 20 trials, each image in each set appeared twice and no image appeared more than 4 times in a row. Once the sample image was touched, it disappeared for a 2000 ms delay during which the subject saw only a black screen. After the delay, the response screen appeared, containing four images. One of these images matched the sample image and the remaining images were randomly selected from the same image set as the sample image. Thus, all four choice images were either "represented" or "unrepresented'. The location of the sample image was pseudo-randomly assigned such that for every 8 trials the sample image appeared in each corner twice and did not appear in the same corner more than 4 times in a row. After one of the images was touched, the reinforcement criteria for correct and incorrect responses were the same as in Experiment 1. The subjects completed five 80-trial sessions.

Data Analysis

Chi-squared tests with 1 degree of freedom were run for each subject to determine if their accuracy differed between the R and U conditions. These tests were also run for Chantek to compare the change in his accuracy from the first to last session each for R and U conditions.

Results and Discussion

The control orangutans showed no difference between the R (Dumadi: $M = 78.5$, $SD = 5.18$; Madu: $M = 54.5$, $SD = 4.11$; Satu: $M = 64.5$, $SD = 5.12$) and U (Dumadi: $M = 80.5$, $SD = 6.94$; Madu: $M = 62$, $SD = 10.4$; Satu: $M = 69.5$, $SD = 7.58$) conditions (Figure 5; Dumadi: $X^2 (1, N = 1) = 0.2454$, $p > 0.05$; Madu: $X^2 (1, N = 1) = 2.313$, $p > 0.05$; Satu: $X^2 (1, N = 1) = 1.131$, $p > 0.05$). The lack of difference in accuracy suggests that Dumadi, Madu, and Satu remembered the images from each set equally well. Chantek, however, performed more accurately on the U ($M = 78$, $SD = 12.04$) than the represented ($M = 61.5$, $SD = 9.78$) trials (Figure 5; $X^2 (1, N = 1) =$

12.90, $p < 0.001$). These data suggest that there was a difference in how Chantek remembered the represented images, but this cognitive difference seems to have impaired rather than aided his ability to remember these images. One explanation for the deficit may lie in the increased interference created by the distractor images in the R trials as compared to the U trials. In the R trials, Chantek, saw several images with which he has made associations, whereas in the U trials he saw several images with which he has no special associations. This may have distracted him during the test phase in the R condition and led to a decrease in accuracy. In examining this possibility, we looked at the images Chantek touched on the incorrect trials in both the R and U

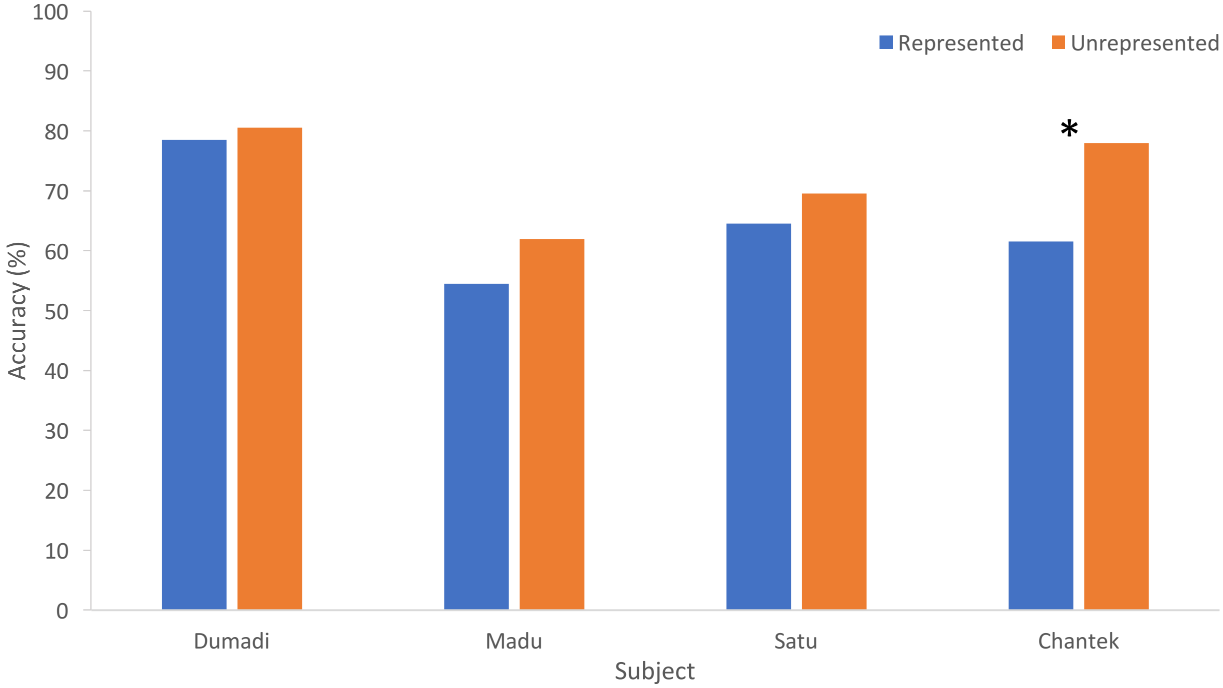

Figure 5. Difference in accuracy for represented and unrepresented images in a delayed matching-to-sample task. Accuracy is graphed as the average proportion of correct trials across all 5 sessions separated by trial type. The performance of the control orangutans (Dumadi, Madu, and Satu) was no different whether the sample image was represented or unrepresented. Chantek's accuracy was lower when presented with represented samples than unrepresented samples. Chi-squared statistics with $p < 0.05$ indicated (*).

conditions. We might expect to see higher overall accuracies for images he touched more often when he was incorrect. Of the images Chantek touched in incorrect R trials (cheese: 2.6%, toothbrush: 41.6%, cat: 14.3%, q-tips: 14.3%, car: 27.3%), there did not seem to be any correlation with accuracy for the specific images (cheese: 75%, toothbrush: 77.5%, cat: 50%, q-tips: 47.5, car: 57.5%). The same is true for the U trials (incorrect touches of biohazard bin: 9.1%, wrench: 50%, computer mouse: 18.2%, hippo: 13.6%, wheat: 9.1%; accuracies of biohazard bin: 92.5%, wrench: 90%, computer mouse: 65%, hippo: 55%, wheat: 87.5%). In light of this result, distraction may not be a complete explanation for Chantek's impairment with represented images. Another interesting point to note is that Chantek's accuracy with R trials is about the same as his accuracy in Experiment 1. He performed much more accurately in U trials than both R trials and trials in Experiment 1. Because the subjects were not given a training session with the new sets of images, it is possible that Chantek became more accustomed to the U images than the R images over the course of testing. We looked at Chantek's first (initial accuracy) and last (final accuracy) sessions for represented and unrepresented images to examine this effect. The difference between Chantek's initial and final accuracies was negligible for R trials (initial: 52.5%, final: 65%; X^2 $(1, N = 1) = 1.290$, $p > 0.05$), but his accuracy substantially increased for U trials (initial: 65%, final: 85%; X^2 $(1, N = 1) = 4.267$, $p < 0.05$). This improvement for U images seems to be the source of the overall difference in accuracy between R and U trials for Chantek. This suggests that there is something about the specific images in the U image set that makes them easier for Chantek to learn.

General Discussion

Competing cognitive load impaired DMTS performance for three out of the four orangutans. Because working memory is sensitive to a competing cognitive load (Basile &

Hampton, 2013), these results indicate that the orangutans who performed less accurately during the cognitive load trials used working memory in a DMTS task. The language trained orangutan did not show the same decrease in accuracy, which could indicate either that he was using a cognitive mechanism other than working memory to complete the matching task or that the cognitive load was not taxing enough to impair his accuracy. All of the sample images in Experiment 1 were unrepresented by Chantek, which is the same category with which he performs more accurately in Experiment 2. Thus, Chantek may have had an easier time holding the unrepresented images in mind, which could have lessened the effect of the intervening task on his accuracy. Giving Chantek a more taxing intervening task might impair his accuracy as compared to empty delay trials without a cognitive load. Such an increased load might involve a type of categorization task like the one in the Basile and Hampton study, which led to much greater impairment of DMTS accuracy in rhesus macaques (Basile & Hampton, 2013).

Another possibility is that Chantek is distributing his cognitive functions in such a way that would resist interference. In humans, elderly (ages 58-74) individuals recruit more brain areas when presented with greater working memory load than younger (ages 21-32) participants (Vellage et al., 2016). The young and old participants showed no difference in performance, but the older participants routinely recruited additional brain areas to achieve a similar accuracy. This distribution of brain function that seems to accompany age may enable more resistance to certain types of cognitive load. Older adults also seem to be better able to encode visual information under a competing load (Peterson & Naveh-Benjamin, 2016). Participants remembered a set of shapes filled with colors for a delay period and at test had to determine if a given stimulus appeared in the set or if it was new. When presented with these tasks, older participants (ages 65-85) showed little change between load and no load conditions, while younger participants (ages 18-22) showed a decline in accuracy with the addition of a load. Because orangutans generally live no more than 40 years in the wild, it is possible that Chantek, who is quite old at 39, recruited more brain areas or more effectively encoded the visual stimuli to complete the DMTS task with a cognitive load. This could explain why his accuracy on the cognitive load trials did not differ from the empty delay trials. Giving another old orangutan a DMTS task with and without competing cognitive load could provide further evidence to support the claim of age being a factor in Chantek's performance.

In the second experiment, the control orangutans showed no difference in accuracy between the represented and unrepresented trials while the language trained orangutan performed less accurately when presented with represented stimuli than unrepresented stimuli. We hypothesized that if language improved his working memory, then Chantek would show greater accuracy for represented images. The results suggest that there is a difference in how Chantek processes the images for which he has been given signs, but language training seems to have impaired his working memory rather than improved it. One possible explanation for the impairment in accuracy for represented images is increased interference from having represented images as distractors. Seeing several identifiable images alongside the remembered image might be more distracting than seeing irrelevant images alongside the remember image. If the extra interference is causing the deficit, a similar experiment could be performed using a yes/no discrimination task. Such a task would involve the same set up as in Experiment 2 but in the response phase, the subject would be presented with a single image that either matches or does not match the sample image. Additionally, two icons on the screen would allow the subject to indicate if the image on the screen matched the sample or not. By removing the distractor images from the response screen, the interference would be reduced and could allow us to measure a more apparent effect of language training.

The impairment in accuracy for represented images could also suggest that Chantek's internal representation of the images for which he has learned signs impeded his ability to remember those images. This challenges the notion that language aids working memory in orangutans the same way it does in humans. When humans are given objects in a DMTS task, having names to represent the objects makes the objects easier to remember over the given delay (Santa & Ranken, 1972). It is possible that Chantek is storing and accessing his signs differently than humans store and access words. If Chantek is accessing his signs with the same resources needed to maintain the image, then we would expect to see the above results. Humans have dedicated neural circuitry for language independent of the working memory circuitry (Rilling et al., 2008). If Chantek is relying more on circuitry involving working memory to maintain his sign associations, this could also decrease accuracy with represented images, and this could be a major difference between how apes and humans use language. An fMRI study of Chantek or another language-trained orangutan comparing their brain activation during signing versus during the maintenance interval of a DMTS task might shed light on the difference between how the signs and images are being stored and accessed. If the orangutans are using the same areas of the brain for each task, then that would help explain why language impaired working memory in Chantek, but aided it in humans. We cannot say for certain that Chantek remembers the signs or represented images in a way that would be relevant for working memory because we did not directly test for it. However, if there was no connection between his internal representations of the represented images, then his accuracy on the two trial types should look more like the control orangutans.

An entirely different take on Chantek's results in Experiment 2 is that Chantek showed an improved accuracy for unrepresented images rather an impaired accuracy for represented images. Results indicate that Chantek's performance for unrepresented images improved between the first and last session while his performance for represented images remained unchanged. His overall accuracy for unrepresented images in Experiment 2 even surpasses his accuracy for the images in Experiment 1, which were also unrepresented. One possible explanation is that the images used in Experiment 2 were easier for Chantek to learn and retain over the course of testing.

Overall, these results suggest that orangutans use working memory in a delayed matching-to-sample task. Furthermore, language seems to impact working memory. Interestingly, our results suggest that in orangutans, unlike in humans, language impairs working memory. One of the orangutans did not show evidence of working memory, but he might if presented with a more difficult intervening task. Alternatively, his age may have contributed to his difference in performance, so testing another similarly aged orangutan might yield results like Chatnek's. We cannot say for certain that Chantek stores his sign associations in a way that resembles human language, but fMRI studies of Chantek or another language trained great ape may shed light on how they are storing and accessing the associations learned in language training. Alternatively, Chantek's impairment in the DMTS task with represented images may be indicative of additional interference from seeing several images for which he can sign. Training Chantek on and then giving him a simpler yes/no discrimination task may yield results that more accurately show the interaction of language and working memory.

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