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INFERENTIAL REASONING IN THE VISUAL AND AUDITORY MODALITIES IN COTTON TOP TAMARINS (*SAGUINUS OEDIPUS)*

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ABSTRACT

Inferential reasoning by exclusion is defined as the choice of an accurate option by rationally eliminating all other possibilities. Multiple experiments have been run testing the ability of non-human primates to show inferential reasoning, with mixed results. In this experiment, we attempt to extend these studies to a new species, the cotton-top tamarin. Cotton top tamarins were tested to see if they could demonstrate inferential reasoning in either the visual or the auditory domains. The experiments consisted of baiting a cup out of sight of the tamarins, then using different types of cuing to indicate which of two cups contained the food. The food was shown to the tamarins in the visual condition and shaken in the auditory condition. Most tamarins performed better in the positive condition, where they could see the food than negative condition, when they were only given information from an empty cup, when asked to choose the cup with food. This result was expected given the negative condition actually tests for inferential reasoning. Although results varied between individual tamarins, overall, the experiments show tamarins as a species are capable of inferential reasoning in the visual domain, similar to other primate species. While results were not significant in the auditory domain, there is still a possibility that tamarins are capable of inferential reasoning in this domain, but likely at a lesser degree.

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Chapter 1

Introduction

Inferential Reasoning

Inferential reasoning has been defined as "the ability to use available information to draw conclusions about circumstances that are not directly observable" (Heimbauer, Antworth, & Owren, 2012, p. 2). Although Streumer (2007) argues there may be other ways to distinguish this type of reasoning from reasoning that does not involve inference, this is a commonly used definition to study the ability in both humans and animals. One specific type of inferential reasoning is termed inferential reasoning by exclusion, defined as the choice of the accurate option by rationally eliminating all other possibilities (Aust, Range, Steurer, & Huber, 2008). Empiricist David Hume (1910) implied that inferential reasoning is a purely human ability, and that any seemingly similar ability in animals is not due to reasoning but other factors including past observations or instincts. Since Hume's time, many experiments have been conducted with the purpose of testing this theory on the ability of animals to use inferential reasoning by exclusion. Pigeons, dogs, monkeys, and great apes have all been tested in this aspect (Aust et. al., 2008; Hill, Collier- Baker, & Suddendorf, 2011). If inferential reasoning is indeed an ability that is not unique to humans, in any capacity, it could have great significance in terms of both evolutionary relationships as well as how animals perform certain behaviors.

In humans, inferential reasoning is considered crucial, because it is involved in predicting and organizing events that may occur in one's environment (Vandorpe, De Houwer, & Beckers, 2005). It also leads to further learning, which can then affect multiple aspects of life, such as language and an understanding of relations (Ogawa, Yamazaki, Ueno, Cheng, & Iriki,

2010). Similarly, inferential reasoning could also be used in the daily life of animals. For example, inferential reasoning could be used by primates in the wild in tasks such as foraging (Heimbauer et. al., 2011). One specific example is that visual cues could be used to find insects in plant stems (Paukner, Huntsberry, & Suomi, 2009). If the primates do not see any indication of an insect in one plant stem, they could infer that they should look elsewhere.

Parts of the brain, which differ in size and complexity in different species, are believed to play a significant role in inferential reasoning. Brain size varies between species, with carnivorous or fruit eating species and animals with larger social groups tending to have a large brain size. Likewise, ecological niches and various behavioral domains may also have a correlation with brain size (Lefebvre, Reader, & Sol, 2004). The hippocampus is thought to be involved in storing memories that can later be used in new situations to come up with the information necessary for inferential reasoning (Zeithamova, Schlichting, & Preston, 2012). In birds, this area has been studied in terms of complex bird song and food storage abilities (Lefebvre et. al., 2004). Other areas of the brain, such as the parietal and prefrontal cortices become highly activated when humans perform a task that involves inferential reasoning. These parts of the brain, including the inferior parietal lobe unique to humans, are also involved in vocabulary learning and language. Some researchers hypothesize, then, that these parts of the brain may determine the difference between a human and an animal's ability to use inferential reasoning (Ogawa et. al., 2010).

Studies in Other Species

Animals have been tested in various experiments studying their results in various non-inferential reasoning-based tasks in the visual and auditory sensory modalities. For example, in a match-to sample test performed by D'Amato and Colombo (1985), tufted capuchins (*Cebus*

apella) were proficient in a visual matching task but not in an auditory one. In this task, the capuchins were trained to press a lever if they were given the same stimuli. In contrast to capuchin's performance in visual tasks, only half of the capuchins tested in this study could even progress past the first stage of testing involving matching tones. In another experiment also using a similar match-sample task, Rhesus macaques (*Macaca mulatta)* improved performance faster in the visual domain than in an auditory domain (learning to master the task in hundreds of trials in the visual domain as compared to nearly 15,000 trials in the auditory domain) (Ng, Plakke, & Poremba, 2009). These findings indicate that similar results likely may also carry over into inferential reasoning tasks. If this is the case, we would expect the animals to perform better in the visual tasks than auditory tasks.

Over the years, multiple methods have been used to test for inferential reasoning in humans and animals. One early animal experiment tested dogs and pigeons (Aust et. al., 2008). In this experiment, inferential reasoning was tested using photographs. The animals were trained to discriminate between two randomly assigned set of 4 photographs (given the arbitrary names of S+ and S-), and were rewarded for choosing the S+ set. After this training, the animals were given the choice between a novel photograph and a photograph that was in the S- category. If they used inferential reasoning, it would be logical for the animal to choose the novel object instead of the S-. Once the choice was made, other tests were performed using a second set of novel stimuli (S") in order to determine whether the choice was made using inferential reasoning or for other reasons such as preference or novelty. The results of this experiment revealed that dogs were shown to be capable of inferential reasoning, at least in the visual modality. However, the pigeons were not shown to be capable of this, as they were shown to only choose based on novelty (Aust et. al., 2008).

A more commonly used method to test for inferential reasoning is the cups task. In this task, out of view of the subject, food is placed in an opaque cup while a second cup remains

empty. The animal must then choose between these cups after being given an indication of which cup the food is in, by either being shown one of the cups or having one of the cups shaken. If the animal is shown or hears an empty cup being shaken, then, if capable of inferential reasoning, it should know the food is in the other cup and choose that cup. Both humans and animals have been tested using this task. This method, while the most widely accepted method of testing inferential reasoning, does have its flaws. Concerns include lack of application to real situations in the wild, lack of complexity of the task, use of a straightforward associative rule, and the possibility that the animal may avoid an empty shaken cup due to its being aversive (Hill et. al., 2011).

Results in the cups task have varied among species and even between animals of the same species. One animal that has been tested using this experimental procedure is the African grey parrot (*Psittacus erithacus*). The parrot has been tested in both the visual and auditory domains. Results of these experiments show that at least some of the parrots are capable of choosing the baited cup based on seeing or hearing an empty cup, thus indicating that this species is capable of inferential reasoning in both domains (Mikolasch, Kotraschal, and Schloegl, 2011, Schloegl, Schmidt, Boeckle, Weib, & Kotraschal, 2012). This is a significant finding, as this is the first time a non-primate has been found to be capable of inferential reasoning in both domains (Schloegl et. al., 2012).

Non-human primates and humans have also been tested in the cups task with varied results across individuals and species (e.g. greater apes, lesser apes, Old World monkeys, New World monkeys, and prosimians). Using the cups task with a jigsaw puzzle piece as a reward instead of food, Hill et. al. (2012) tested human children for inferential reasoning. Based on these studies, children have been found capable of inferential reasoning as early as three years of age. The three year olds were found to perform significantly better in the visual condition than the auditory condition. However, their performance improves with age, a factor that has also been

significant in the performance of great apes (Hill, Collier-Baker, & Suddendorf, 2012; Call, 2006).

Several studies have indicated that most nonhuman primate species are more proficient in the visual modality, as was indicated in previous research on other topics, such as the match-to-sample task, where performance seems to be better and learning faster in the visual over the auditory modality. Call (2004) reports that while some of the gorillas and bonobos were capable of inferential reasoning in both domains, chimpanzees were unsuccessful in the auditory domain, and orangutans were unsuccessful in both modalities. However, all the great ape species were found to be capable of inferential reasoning in the visual domain in a different experiment using the same cups task performed by Hill et. al. (2011), although only a small percentage of the animals tested showed this ability. Lesser apes have also been tested. Although gibbons would not complete the task, siamangs (*Symphalangus syndactylus*) were capable of inferential reasoning in the visual, but not auditory, modality (Hill et. al., 2011).

New World primates have also been tested using versions of the cups task. In the Hill et. al (2011) experiment, New World spider monkeys (*Ateles geoffroyi)* were also tested using a modified procedure, baiting the food inside the experimenter's hands instead of cups, yielding the same result as the siamangs. Capuchins also have been tested extensively. In this species, results varied between experiments. Sabbatini and Visalberghi (2008) found that all capuchins tested could choose correctly in the visual domain, while half of the monkeys tested performed above chance in the auditory condition. However, later studies showed that the capuchins choose correctly in the visual domain, but only make the correct choice in the auditory positive (shake cup with food) but not the auditory negative condition (Paukner, Huntsberry, & Suomi, 2009; Heimbauer et. al., 2012).

It is interesting to note the African grey parrot has seemingly outperformed most of these non-human primates except for the great apes in the auditory domain (Schloegl et. al., 2012). On

the other hand, lemurs were shown to be more successful in the auditory than the visual negative condition, a result opposite to that of other primates (Maille & Roeder, 2012). One possible explanation for this difference is that lemurs live in the forest and tend to use auditory cues in order to find food (Maille & Roeder, 2012). The differences in performances between these species of primates led to the question of how tamarins would perform in inferential reasoning tasks in either domain based on their evolutionary relationships and foraging behaviors.

Experimental Background Information and Theory

Cotton-top tamarins are a critically endangered species that primarily live in the tropical forests of Colombia (Mittermeier, 1988). Cotton-top tamarins have a wide variety of foods in their diets. These foods include, but are not limited to, nectar, fruit, insects, bird eggs, and possibly small birds, amphibians, and reptiles (Lang, 2005). Because they eat insects and other small animals, they may use sound to find their prey when foraging. Therefore, auditory cuing, which could facilitate inferential reasoning, may be an important mechanism for tamarins in the wild (Neyman 1980). It could thus be questioned whether tamarins are better at their ability of inferential reasoning in the auditory domain than other primates such as great apes or other New World monkeys.

The cotton-top tamarin is a New World monkey, meaning that its continent of origin is the Americas. Evolutionarily, New World monkeys are the second farthest group of primates from humans. The great apes (chimpanzees, bonobos, gorillas, and orangutans) are the closest to humans, followed by the lesser apes (gibbons and siamangs), Old World monkeys (macaques, etc), New World monkeys (such as squirrel monkeys, capuchins, and tamarins), and then the prosimians (lemurs, for example), which are the most distantly related. With this knowledge, it could be expected that, the great apes, as they are the most closely related to humans evolutionarily,

would exhibit behaviors most similar to the humans (the behavior in this case would be inferential reasoning). This expectation, as mentioned previously, has been proven, as the great apes are one of the few groups of animals who show inferential reasoning in both the visual and auditory modalities. However, the lemurs, which are the most distant evolutionarily, perform better than the lesser apes and the New World monkeys in the auditory domain, indicating that other factors, such as habitat and/or foraging methods, or even brain/neural mechanisms may play a significant role in determining an animal's performance in experiments testing for inferential reasoning. It would thus be informative to see where the cotton-top tamarin fits within this relationship, to determine which factors (evolutionary relationships versus ecological behaviors) play a bigger role in determining the tamarin's capacity for inferential reasoning.

The purpose of this study was to determine if cotton-top tamarins (*Saguinus oedipus*) are capable of inferential reasoning in either the visual or auditory domains. It was hypothesized that if tamarins are capable of using inferential reasoning in either of these two domains, then they should be able to correctly choose a baited cup when shown either the empty cup or when the empty cup is shaken. In order to test this hypothesis, the tamarins were tested by baiting a cup out of the tamarin's sight, and then having them choose a cup after being shown either the baited or empty cup, or having the baited or un-baited cup shaken. By studying the tamarins' performances in the cups task, we are able to compare their abilities to those of the other animals and see how different factors such as evolutionary relationships, foraging behaviors, and physical/physiological differences may play a role in inferential reasoning abilities between species.

Chapter 2

General Methods

Subjects

The subjects were six adult cotton top tamarins. These monkeys were born in the New England Regional Primate Research Center and since 2005 have been housed at The Pennsylvania State University. The tamarins were pair-housed, and lived in adjacent cages, although Homer and George were single-housed for part of the experiment due to the death of their cage-mates. Four monkeys went through a familiarization phase but were not used in the experiments. The monkeys used in the experiments were three females (Susan, Elaine, and Mulva) and three males (Jerry, Homer, and George). The monkeys were fed a meal each evening as well as small treats such as raisins used for catching. These tamarins have been tested in multiple behavioral studies, including choice tests, but have not been tested on any inferential reasoning tasks. The study has been approved for use of animals under IACUC protocol.

Materials, Stimuli, and Apparatus

The food reward used in this experiment consisted of yogurt-covered raisins, cut in quarters. One tamarin, Mulva, was switched to blue- and green-colored yogurt chips, as she would not eat the raisins. The monkeys were tested in isolation in their transport box, sized 30 cm x 23 cm x 30 cm, which was placed on a table in a testing room. The box's metal door was replaced with a transparent piece of Plexiglas containing two holes that the tamarins could stick

their hands through (Figure 1). The apparatus used to hide the food was handmade and consisted of a black cardboard base with two inverted yogurt cups affixed to it. The cups were wrapped in paper so that they were a solid, opaque color. In the visual conditions, a white piece of cloth was attached as a cover for the cup, which could appear either covered or held open. For the auditory condition, the yogurt cups were covered with an opaque plastic lid. Trials were recorded using a video camera.

Figure 1. The Apparatus

Procedure

This study consisted of a total of four experiments to test inferential reasoning in the tamarins.

Familiarization

Before the experiments began, a familiarization phase was conducted to acquaint the tamarins with the apparatus. In the familiarization session there were three conditions: cups baited in front of the tamarins and held open (the See Both), cups baited in front of the tamarins and then opened and closed at the same time, and cups held closed with no information given. In the See Both condition, one quarter of the yogurt raisin was placed in one of the cups in front of the monkeys. Both cups remained uncovered by the cloth, and the monkey simply had to

reach through one of the Plexiglas holes to grab the food. Once the monkeys consistently chose the baited cup at least three times in a row, testing in the next two conditions began. In the second condition, one randomly predetermined cup was baited such that the tamarin could see which cup contained the raisin. The cups remained uncovered for three seconds at the same time. After placing the cloth back over the cups, the tamarins were given the opportunity to choose the cup with the raisin. If the correct cup was chosen (determined by contact with the cover of the cup), the monkey was allowed to access the food. In the control condition, a quarter of a yogurt raisin was placed in the cup out of view from the monkeys, and both cups were covered. Then, the tamarin had the opportunity to choose a cup, and received the food if the correct choice was made. On each familiarization day, these conditions were repeated for approximately 10 minutes. As subjectively measured by the experimenter, once proficient at these conditions, the tamarins were able to progress to the actual experiments. No results were recorded for these sessions. If the tamarins were unwilling or unable to complete these tasks, they did not progress to the experimental phases.

Experimental Procedure

Four general types of cuing were used in the experiments: Control (no cue), Visual or Auditory Both, Visual or Auditory Positive, and Visual or Auditory Negative. Positive cuing consisted of the monkey being given information pertaining to the cup with food. This was accomplished by either showing the tamarin the food in the baited cup or by shaking the baited cup, depending on which experiment was conducted. Negative cuing was accomplished by showing the inside of the empty cup or shaking it. In both the Positive and Negative conditions, only one cup was manipulated, while the other remained untouched. In the Visual and Auditory Both conditions, the insides of both cups were shown sequentially (Visual) or both cups were shaken sequentially (Auditory).

There were several of the above conditions in each experiment. The order of individual

trials was randomized, but constrained in that no side or condition could occur more than twice in a row. Each session lasted no more than 15 minutes. In each trial, cups were baited with the food (1/4 yogurt raisin) under a table so that the monkey could not see which cup was baited. The covered cups were then placed on the table approximately 7 inches in front of the transport box. In the control trials, the cups remained covered with the experimenter's hands placed over the tops of the cups for a total of 3 seconds. For the experimental trials, the experimenter either lifted the cover off the cup or shook the cup horizontally for 3 seconds each. The cups were then covered again and the cups were moved to 2 inches from the transport box so the monkey was given the opportunity to choose a cup. Once a choice was made, the tamarin was permitted to see the inside of the cup and to take the food inside the cup when a correct choice was made. The experimenter would then remove the cups from the table and bait a cup for the next trial. The next trial began as soon as the monkey's attention was focused on the apparatus.

Results were manually recorded as choices were made. These results were verified by a review of the videos. If a choice was not made within 30 seconds after being presented with the cups, the trial was repeated. If a choice was not made a second time, the trial was aborted. If two trials in one session had to be aborted, the test session was terminated. Aborted trials and sessions were made up after all other sessions of that particular experiment were completed.

Statistical Analysis

For each monkey, the number of correct choices in each condition were calculated and divided by the total number of possible correct choices to find the percentage correct in each condition for each experiment. Also, for each condition, binomial *t*-tests were performed to check for performance above chance. The comparison was to the number correct if chance was the only

contributing factor (50%). In addition, two-tailed independent *t*- tests were conducted to ascertain if unsuccessful monkeys may have been side-biasing when making their choices.

Chapter 3

Experiment 1: Choosing Food Location Under Conditions of Visual Certainty

Subjects

All six tamarins (Elaine, George, Homer, Jerry, Mulva, and Susan) were tested in this experiment.

Procedure

The two conditions in this experiment were "Visual Both" and "Control." In this experiment, the cups were either not manipulated (Control), or both cups were shown sequentially, each for three seconds, and then re-covered (Visual Both). Each session consisted of eight randomized trials (4 Control and 4 Visual Both). Each tamarin was tested in 6 sessions. Two monkeys, Homer and Jerry, were unable to choose the correct cup in the Visual Both condition significantly above chance. To ascertain if they would succeed in this condition after more time, they were run for an additional four sessions.

Results

One control trial and one session were aborted for Elaine based on the aforementioned criteria. This aborted session was re-run, but the aborted trial was not re-run. Two trials for Mulva were also aborted because she would not choose during them.

The percent correct scores can be seen in Figure 2. Elaine and George had the highest

percentage of Visual Both correct at 91.7% All tamarins were at or below chance in the control condition.

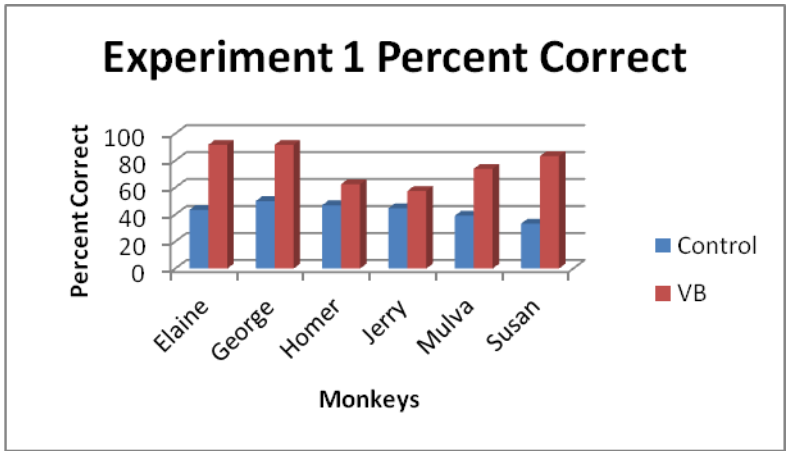

Figure 2. Experiment 1 Percent Correct Scores

This figure depicts the total percent correct over all of the sessions of Experiment 1 for each condition (control and showing both a baited and empty cup).

One-tailed, binomial *t*-tests were conducted to test for statistical significance above chance in the Visual Both condition. Homer and Jerry did not perform significantly above chance (62.5%, $p = 0.11$ and 57.5%, $p = 0.22$, respectively). However, the remainder of the monkeys did perform significantly above chance in the Visual Both Condition (Elaine, 91.7%, $p<0.0001$; Susan, 83.3%, $p<0.001$; Mulva, 73.9%, $p=0.017$, and George, 91.7%, $p<0.0001$). George, Jerry, and Susan were shown to have a significant amount of side-biasing in their sessions ($p<0.0001$, $p<0.04$, and $p=0.012$, respectively.

Performance over time across the sessions was looked at to check for evidence of learning. These results can be seen in Figure 3.

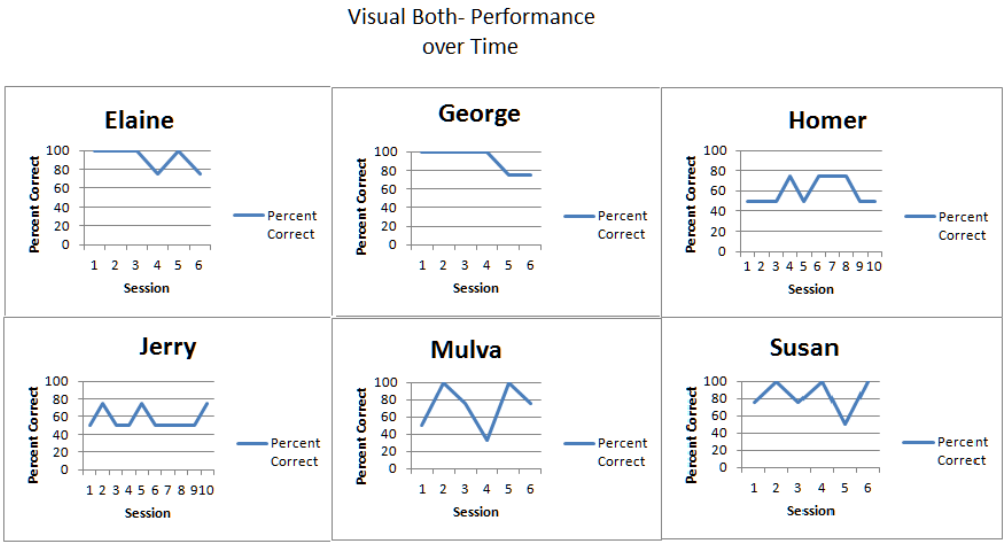

Figure 3. Visual Both Performance over Time

The percentage of correct choices in which the baited cup was chosen when the insides of two cups were shown to the monkeys is depicted for each successive session.

Discussion

Results varied among the monkeys, even in the Visual Both condition meant primarily to test the tamarin's basic understanding of food location when they were able to see into both cups. In this condition, the tamarins were shown both the empty cup and the cup with food, so they did not need to infer to make the correct choice. Most of the monkeys, with the exception of Homer and Jerry, were able to make a correct choice when shown the inside of both cups. This outcome indicates that they understood the task and preferred the cup with food.

Results of Experiment 1 demonstrate that some tamarins will use visual cues to obtain food, although the exact extent of this ability varied between individuals of the same species. Overall, the results of this experiment revealed the same general outcomes as the cups task with different species of primates, with the exception of lemurs, as the tamarins are capable of using obvious visual cues to find food. However, in contrast to some of the other experiments using the

cups task with non-human primates, some tamarins did not perform significantly above chance (Call, 2004; Hill et. al., 2011, Heimbauer et. al., 2012; Maille & Roeder, 2012). Their failure could be due to a variety of reasons, such as incomplete understanding of the task, lack of hunger or other motivation, or side biasing. While Susan and George performed significantly above chance despite the apparent side-biasing, the side-biasing could explain Jerry's performance below chance. Another reason for the lack of significance is that in a number of sessions, Jerry continuously chose the side that the food was located on in the previous trial. Overall, however, the lack of statistical significance in choosing the correct side even when both sides were shown indicates a possible lack of understanding or a lack of ability to make a choice based on what was cued. This was a serious concern in the subsequent experiments, as any insignificant results may not necessarily indicate a lack of inferential reasoning. On the other hand, the difference shown by these monkeys compared to other primate species could be a product of the divergence indicative of important branching points in the phylogenetic tree (see General Discussion).

As seen in Figure 3, none of the monkeys showed evidence of learning across the trials. Interestingly, when a monkey was at 100% by session 2, they did perform above chance in Experiment 1. If a monkey was not above chance by this point, as with Homer and Jerry, they did not perform above chance in the experiment.

The monkeys that did perform significantly above chance immediately moved on to the next experiment. Because Homer and Jerry were below statistical significance they did not immediately move to the next experiment. However, after three months, we decided to test Homer on the subsequent experiments to see if performance improved or if he revealed an ability to infer in the auditory modality. Jerry did not participate in further experiments due to his death from cancer one month after he completed Experiment 1.

Chapter 4

Experiment 2: Inferential Reasoning in the Visual Modality

Subjects

Five tamarins (Elaine, George, Homer, Mulva, and Susan) participated in Experiment 2.

Procedure

The conditions in this experiment were Control, Visual Positive, and Visual Negative. The Control condition was the same as in Experiment 1. In the Visual Positive condition, after baiting a cup, the experimenter only showed the cup with the food to the monkey. In the Visual Negative condition, only the empty cup was shown to the monkey. Each session was comprised of 12 trials (4 Control, 4 Visual Positive, and 4 Visual Negative, in randomized order, with no side or trial repeating more than twice in a row). Each monkey was tested in eight sessions, for a total of 96 trials. The same criteria that were used in Experiment 1 for aborted trials and sessions were used in this experiment.

Results

Four of the tamarins had to make up sessions because their session was aborted when they did not make choices. Elaine, Susan, and Mulva each had one session aborted, while George had to make up four aborted sessions.

Percentages were calculated for the Visual Positive, Visual Negative, and Control conditions. These results can be seen in Figure 4.

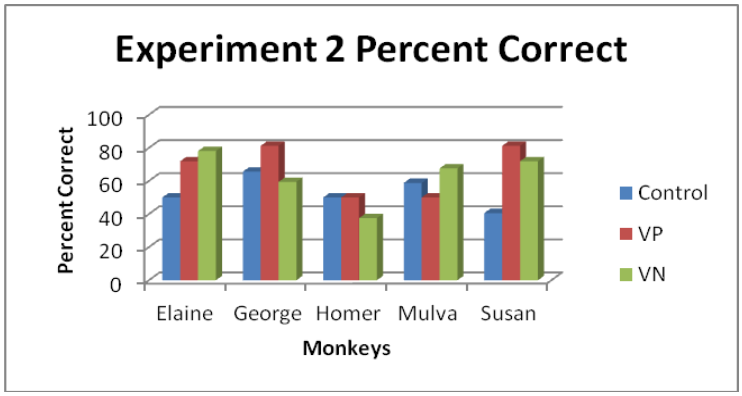

Figure 4. Experiment 2 Percent Correct Scores

This figure depicts the total percent correct over all of the sessions of Experiment 2 for each condition (control, showing just a baited cup, and showing just an empty cup).

No monkey was significantly above chance in the Control condition. George and Susan had the highest percent correct score in the Visual Positive condition, while Elaine had the highest percent correct score in the Visual Negative condition. Susan and George (81.2%, $p<0.001$) and Elaine (71.9%, $p<0.01$) performed significantly above chance in the Visual Positive condition. Homer and Mulva (50%, $p=0.57$) did not show evidence of performing differently from chance. Interestingly, Mulva performed with a higher percentage correct on the Control condition that the Visual Positive condition. In the Visual Negative condition, Susan (71.9%, $p<0.01$), Mulva (67.6%, $p=0.029$), and Elaine (78.1%, $p<0.001$) all performed significantly above chance, while Homer (37.5%, $p=0.11$in the opposite direction) and George (59.4%, $p=0.19$) did not. Homer was the only monkey shown to side-bias in this experiment ($p<.0001$).

Performance over time across the sessions was looked at to check for evidence of learning. These results can be seen in Figure 5.

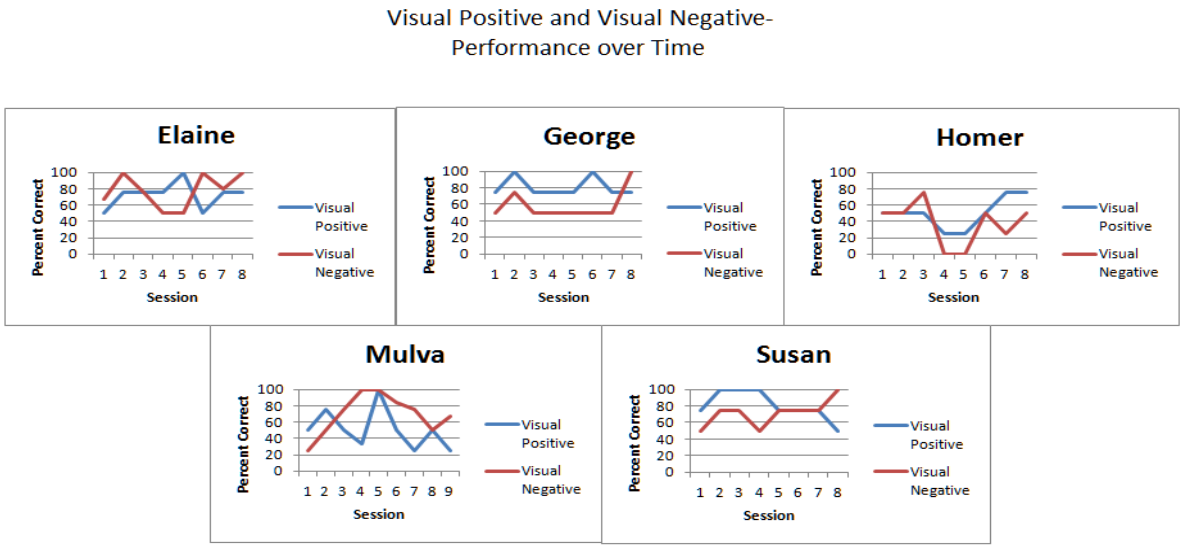

Figure 5. Visual Positive and Visual Negative Performance over Time

The percentage of correct choices in which the baited cup was chosen when the inside of only one cup (baited or empty) was shown to the monkeys is depicted for each successive session.

Discussion

As in Experiment 1, the results in this experiment varied for each individual monkey. The purpose of this experiment was to test the actual inferential reasoning capability of these tamarins in the visual domain, as shown especially in their performance of the Visual Negative trials. Because the results in the control condition were not significantly above chance, it shows that there was no external cueing from the demonstrator that may have influenced the tamarin's choice.

Overall performance in this task indicates that tamarins as a species at least have the capability to use inferential reasoning in the visual domain, as half of the monkeys performed at a level significantly above chance. Interestingly, one monkey, Mulva, performed above chance in the Visual Negative trials, when shown the inside of an empty cup, but not the Visual

Positive trials, where she was directly shown the food. Multiple reasons for this strange result are possible, but one possibility is that she simply was not hungry or didn't like the food during the sessions, and thus had no desire to take the food. Another possibility is that she viewed the experimenter as a competitor, and thus was avoiding the cup that was manipulated (see General Discussion for further explanation).This could explain why her performance in the Visual Positive task was also lower than in the Control condition, but also points to an understanding of the Visual Negative task.

Reasons for lack of success with some of the other monkeys could be similar to those in Experiment 1, including lack of understanding of the task and side biasing. Homer's inability to perform above chance in both the Visual Positive and Visual Negative conditions could relate back to his inability to perform above chance in Experiment 1, which was used just to measure the tamarins' understanding of the task. His results in this experiment (2) could indicate that he never fully grasped the task in the first place, rather than him not being capable of inferential reasoning. There is significant evidence of side-biasing in the task, which could also correspond to his inability to perform above chance in either the Visual Positive or Visual Negative conditions.

As shown in Figure 5, most of the tamarins showed no evidence of learning across sessions. However, Susan did show a positive learning trend in the Visual Negative condition.

Chapter 5

Experiment 3: Choosing Food Location Under Conditions of Auditory Certainty

Subjects

Four monkeys (Elaine, Homer, Mulva, and Susan) were tested as subjects in this experiment. George did not complete this and subsequent experiments due to his inability to be caught on a regular basis and three consecutive sessions that had to be aborted because he would not make a single choice.

Procedure

In this experiment, the tamarins were tested in the auditory domain, with Control and Auditory Both trials. The Control condition was the same as in Experiments 1 and 2. The Auditory Both condition was similar to the Visual Both condition, where both cups were shown sequentially, but instead of showing the cups to the monkey, both the baited and empty cup were horizontally shaken sequentially for 3 seconds each. Each session had an average of 12 trials, with 5 control and 7 auditory both trials. Each monkey was tested in 10 sessions. More sessions were run than in Experiment 1 in order to try to get more monkeys significantly above chance before moving to the next experiment. All other procedures were identical to the visual task.

Results

Percent correct scores were calculated for the Control and Auditory Both conditions (Figure 6).

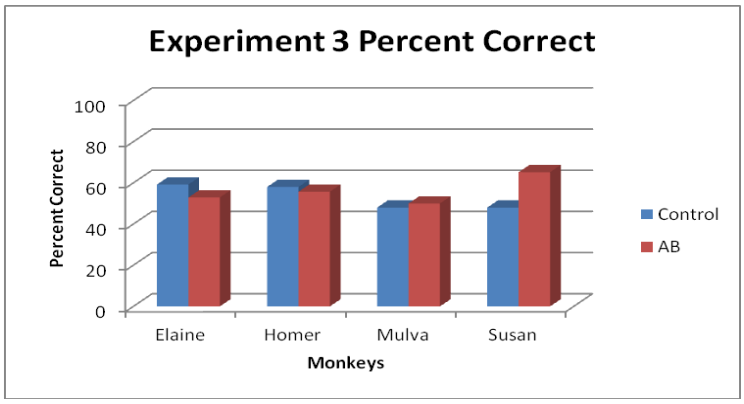

Figure 6. Experiment 3 Percent Correct Scores

This figure depicts the total percent correct over all of the sessions of Experiment 3 for each condition (control and shaking both a baited and an empty cup).

No tamarin performed significantly above chance in the Control condition. Only Susan performed significantly better on the Auditory Both condition than chance (65.2%, p=0.008). Mulva, in terms of percentages, performed slightly better in the Auditory Both condition than the Control, but this result did not give evidence that the difference was due to anything but chance (50%, p=0.55). In fact, she actually had the lowest percentage correct in the Auditory Both condition. The other two tamarins, Elaine and Homer, performed with a higher percent score correct in the Control condition than the Auditory Both condition. Percent correct scores and p-values for the Auditory Both results for these monkeys were 52.9%, p=0.36 and 55.7%, p=0.20, respectively. Elaine, Homer, and Mulva all showed evidence of side-biasing (p<0.01, p<0.0001, and p<0.0001, respectively.

Performance over time across the sessions was evaluated for evidence of learning. These

results can be seen in Figure 7.

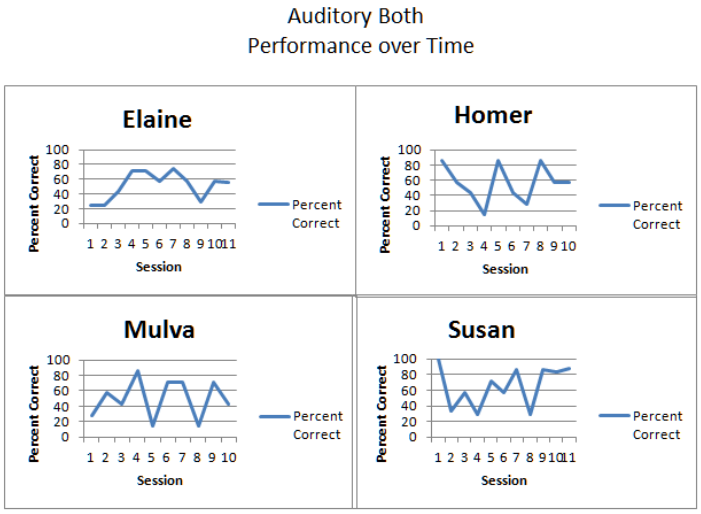

Figure 7. Auditory Both Performance over Time

The percentage of correct choices in which the baited cup was chosen when two cups (one baited, one empty) were shaken is depicted for each successive session.

Discussion

As with the previous two experiments, the results varied among individual monkeys, although a majority of the tamarins did not perform well in the task. However, the statistically significant performance of one monkey, Susan, indicates that tamarins as a species are, to some extent, capable of understanding and completing this task properly. The purpose of this task was to make sure that the tamarins could make a correct choice when given all of the information (hearing both the empty and the baited cup). No inference was needed in this experiment, so there should have been less difficulty in this task. Four possibilities for the poor performances are likely: 1) because they were not shown there was food before the cup is shaken, they did not realize the noise they heard came from the food, 2) they found either the empty cup "sound" or the baited cup sound aversive, and thus would not choose it, 3) the rate of reinforcement was high

enough to keep them choosing randomly, or 4) there was some reason for side-biasing. Only the tamarin that was not shown to side-bias performed at a level significantly better than chance. Regardless of the exact reasoning for the poor performance in this task, results from this experiment are a preliminary indication tamarins perform better in the visual than in the auditory domain. This is consistent with the results from most other non-human primates.

As indicated in Figure 7, there is no evidence of learning across sessions for any of the monkeys. Only the monkey who performed at 100% in the first session demonstrated success in the Auditory Both condition. This indicates that inferential reasoning is an innate ability of which the tamarin species is capable.

Chapter 6

Experiment 4: Inferential Reasoning in the Auditory Modality

Subjects

Four tamarins (Elaine, Homer, Mulva, Susan) participated in this experiment.

Procedure

In this experiment, there were two experimental conditions (Auditory Positive and Auditory Negative) and a Control condition. The Control condition was the same as in the first three experiments. In the Auditory Positive condition, only the cup with food inside was shaken, while the empty cup remained covered on the table. In the Auditory Negative condition, only the empty cup was shaken, while the baited cup was not manipulated. Each of eight sessions consisted of 12 trials (4 Control, 4 Auditory Positive, and 4 Auditory Negative), for a total of 96 trials. All other procedures, including criteria for aborted sessions, are identical to those used in the visual condition.

Results

Based on the criteria for aborted sessions, Elaine and Susan each had to make up one session, while Mulva had to make up three.

Percents correct were calculated for the Auditory Positive, Auditory Negative, and Control conditions (Figure 8).

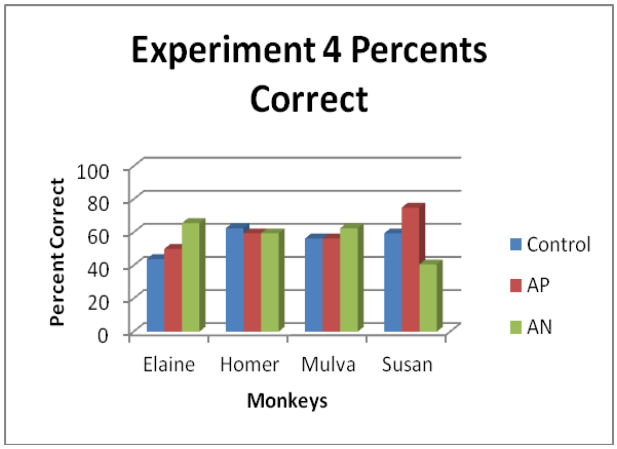

Figure 8. Experiment 4 Percent Correct Scores

This figure depicts the total percent correct over all of the sessions of Experiment 4 for each condition (control, shaking just a baited cup, and shaking just an empty cup).

No results in the Control condition were significantly above chance. Only Susan's results in the Auditory Positive condition produced a statistically significant value (Susan, 75%, p=0.004; Elaine, 50%, p=0.57; Homer, 59.4%, p=0.19; Mulva, 56.3%, p=0.3). In the Auditory Negative condition, no monkey performed significantly above chance. However, Elaine's performance yielded a p-value of 0.055 (65.6%) just above the alpha cutoff of .05. (Homer, 59.4%, p=0.19; Mulva, 62.5%, p=0.11; Susan, 40.6%, p=0.19 in the opposite direction). Homer and Susan were shown to have significant side-biasing.

Performance over time across the sessions was evaluated for evidence of learning. These results can be seen in Figure 9.

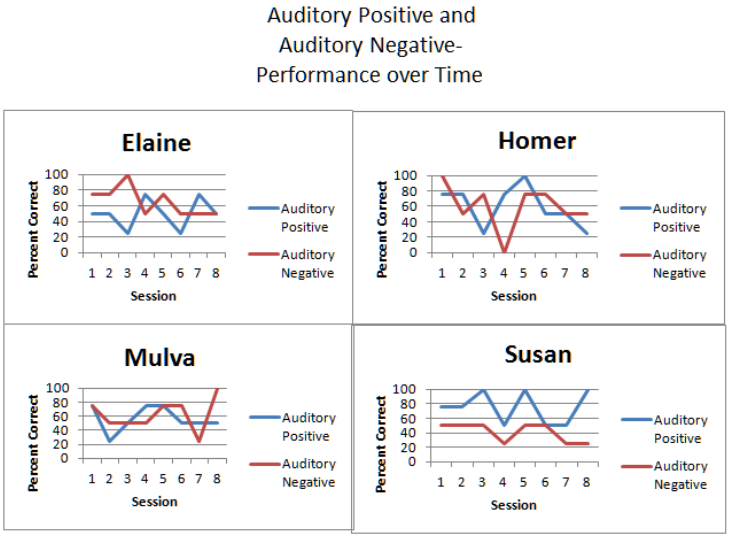

Figure 9. Auditory Positive and Auditory Negative Performance over Time

The percentage of correct choices in which the baited cup was chosen when only one cup (baited or empty) was shaken is depicted for each successive session.

Discussion

In this experiment, only one monkey performed significantly above chance in the Auditory Positive condition, and no monkeys performed above significantly above chance in the Auditory Negative condition, which was the condition used to truly test for inferential reasoning in the auditory domain. Side-biasing was correlated with poor performance, especially in the Auditory Negative condition.

As with Experiment 2, Mulva performed better in the negative condition than the positive condition, again possibly indicating that she was not interested in the food or that she was avoiding the cup that was manipulated by the experimenter. Elaine, while her results were marginally significant, did perform above chance (above 65%) in the Auditory Negative condition. This indicates that Elaine may be capable in some respect of inferential reasoning in the domain, and the lack of full statistical significance may be due to side-biasing or lack of interest in the later

sessions. As such, looking at the first six sessions in the experiment, Elaine performed statistically above chance (70.8%, p=.032). In the last two sessions, Elaine was found to be significantly side-biasing (p<.005). Thus, her performance actually decreased over time. There was no evidence of a significant trend in learning for any of the other monkeys.

It is important to consider these results in terms of performance in the previous experiment. Susan was the only tamarin who performed significantly above chance in Experiment 3, and this was the same for the Auditory Positive condition of Experiment 4. This lends to an increased likelihood the tamarins had difficulty understanding the task or the sound of the shaken cup may have been aversive to them. Thus, while no monkey performed marginally significantly above chance in the Auditory Negative condition, and only one performed significantly above chance in the Auditory Positive condition, this does not necessarily mean they are incapable of inferential reasoning in this domain. Instead, further experiments should be performed to test this hypothesis, possibly by training the monkeys to associate the sound with food before testing.

Chapter 7

General Discussion

Overall, results of this experiment show tamarins are indeed capable of inferential reasoning, although the degree to which this occurs varies between individual monkeys. The findings in these experiments verify that, unlike Hume's suggestion, this ability is not just a human trait, but instead can occur in most species of non-human primates.

One aspect of this experiment to consider is a comparison of the monkeys' performances in the visual and negative conditions. Two monkeys performed better in the Visual Positive than the Auditory Positive condition, indicating that the monkeys may understand the task better when they see the food versus when they hear a noise coming from shaking the food. However, interestingly, both Homer and Mulva performed better on the Auditory Positive condition. In the actual test for inference, the Visual and Auditory Negative conditions, only Homer performed better in the auditory domain, although this performance was still not significantly above chance. Elaine, Mulva, and Susan performed better in the visual condition than the auditory one. This difference may be due to chance alone, or may stem from some sort of biasing, or lack of understanding of the task. Overall, since the remaining monkeys performed better in the Visual Negative than the Auditory Negative condition, this indicates they are better at inferential reasoning in the visual domain.

While the majority of the tamarins (n=3) performed better when given positive cues (see/hear baited cup) than negative cues (see/hear empty cup), two tamarins (Elaine and Mulva) performed better with negative cues in both the visual and auditory modalities. While Elaine still performed above chance in the visual modality, Mulva did not perform above chance when given positive cueing in either modality. One possible reason for this performance is the competition

effect. Mulva may have been viewing the experimenter as a competitor, and thus avoiding whichever cup the experimenter manipulated. Viewing a task as a competition versus a cooperative experience has had a heavy influence on performance in other domains, especially theory of mind (a concept dealing with the ability to understand the differences between your own mental state and that of others). For example, Santos, Nissen, & Ferrugia (2006) found when given the opportunity to choose between two boxes, if the experimenter was viewed as the competitor, Rhesus macaques would choose the box the experimenter could not see or hear. In the visual modality, the macaques were more likely to steal food from a box when the experimenter was unable to see them. Likewise, in the auditory modality, if the experimenter was not looking, the macaques were more likely to choose a box that made no noise over a box with bells on it that would make a sound when manipulated. By looking at the present experiment in the context of the experimenter being a competitor, Mulva's results would make more sense, as she would simply choose the container not being manipulated by the experimenter. For the other monkeys, however, the competition effect did not seem to override their ability for inferential reasoning.

Performance of the tamarins in this inferential reasoning cups task can be compared to the performance of other species (bonobo, chimp, gorilla, siamang, spider monkey, capuchin, lemur, and African grey) (Call, 2004; Heimbauer et. al., 2012; Hill et. al., 2011; Maille & Roeder, 2012; Mikolasch, Kotrschal, &, Schloegl 2011, Schloegl et. al. 2012). Table 1 shows the proportions of correct responses in the Visual Both, Visual Positive, Visual Negative, Auditory Both, Auditory Positive, and Auditory Negative conditions. While a smaller percentage of tamarins performed above chance in the visual condition than most other species, further experiments with a larger sample size could help indicate whether this difference is truly significant between species (Taborsky, 2010). Of interesting note, however, is that percent of tamarins that performed above chance in the Auditory Both condition was actually higher than in chimps, which could indicate a difference in

foraging styles or food selection between the species (Lang, 2005; Lang, 2006).

Table 1. A Comparison Between Species

Species	**Proportion of Animals Tested that Achieved Statistically Significant Results**					
	Visual Both	Visual Positive	Visual Negative	Auditory Both	Auditory Positive	Auditory Negative
Great apes						
Chimps	12/12	2/2	2/2	2/12	2/2	0/2
Bonobos	4/4	2/2	2/2	2/4	2/2	1/2
Gorillas	8/8	5/5	5/5	5/8	5/5	2/5
Lesser apes						
Siamangs	3/3*	2/3*	3/3*	**	**	**
New World Monkeys						
Spider	1/1*	0/1*	1/1*	**	**	**
Capuchins	8/8	8/8	8/8	5/8	6/8	0/8
Tamarins	4/6	3/5	3/5	1/4	1/4	0/4
Prosimians						
Lemurs	0/6	1/3	0/3	2/6	1/4	1/4
Non-Primate						
African Grey	1/7	**	**	3/6	5/6	4/6

*using modified hands task
** no specific numbers given
***results from Call, 2004; Heimbauer et. al., 2012; Hill et. al., 2011; Maille & Roeder, 2012; Mikolasch, Kotrschal, &, Schloegl 2011, Schloegl et. al. 2012
****highlighted results are from present experiment

Most results from this experiment are comparable to results seen in other New World monkeys. Both capuchins and squirrel monkeys have been shown to be capable of inferential reasoning in the visual domain, but are relatively unsuccessful in the auditory domain (Hill et. all, 2011; Heimbauer et. al., 2012). Like the capuchins, some tamarins were able to perform above chance in the Auditory Positive, but not the Auditory Negative, condition. In fact, the mean performance in this condition in both the capuchins and the tamarins was just under 60% in both of these species, indicating similar capabilities in this domain. However, the mean performance in the visual domain was much lower in the tamarins than the capuchins (62.9% vs over 94%,

respectively) (Heimbauer et. al., 2012). This could indicate a more developed visual sense or capability for inference in this domain. On the other hand, the differences could also be due to lack of interest in the task or another similar reason. Results in these experiments did not follow those of the lemurs, which were shown to use inferential reasoning in the auditory but not visual domain (Maille & Roeder, 2012). No lemurs were shown to be capable of inferential reasoning in the visual domain, while one of four lemurs (25%) was shown to perform above chance in the auditory modality. This difference in results disproved the prediction that tamarins may perform similarly to lemurs based on related foraging styles. Various species of lemurs, like tamarins, have been known to eat fruits, plants, and insects, and have been shown to rely on auditory cues in the wild (Clutton-Brock, 2012; Sussman, 1999; Piep, Radespiel, Zimmermann, Schmidt, & Siemers, 2008).

Inferential reasoning in the visual, domain seems to be more important to tamarins than inferential in the auditory domain. Most of the tamarins' diet consists of insects and plants, both of which likely require some form of inferential reasoning in order to determine where to look for food. Indeed, they at least must consider visual cues to determine the food's location (Paukner et. al., 2009). In contrast, it may not be a necessity to use inferential reasoning in the auditory domain, as tamarins could rely solely on visual or olfactory cues, as they usually come in conjunction with or prior to the auditory cues (Paukner et. al., 2009). Inferential reasoning in the auditory domain thus may be useful to improve foraging performance but not required to find some food, which could explain the non-significant but above chance (>50%) in the auditory domain for some of the monkeys in this experiment. It is possible that the lemurs rely on auditory cues more often in the wild, especially since their visual acuity is considerably worse than other primate species (6 c/deg compared to >40 c/deg in other species of primates) (Kirk & Kay, 2004). A possible reason for this difference may be due to the evolutionary lineage of the different primate species.

Evolution has led to the development of a branching tree that starts with a common

ancestor and spreads out to the different species of primates. The branch points arise when a new trait develops that separates this species (and future species down the line) from previous species. Thus, the different primate species share various traits with their common ancestor (homologies) but also have diverged from each other with new/different traits and characteristics. The different subsets of primates (humans, great apes, Old World monkeys, New World monkeys, and prosimians) diverge at various points, with the prosimians branching off first, then the New World monkeys, then the Old World monkeys, then the great apes, which are the closest related to humans (Figure 10, Disotell, 2008). This branching order, and the relative distance between the each of the branches from the human branch, seems to play a role in performance overall. The great apes seem to have the highest capabilities in inferential reasoning, while most New World monkeys perform similarly to each other.

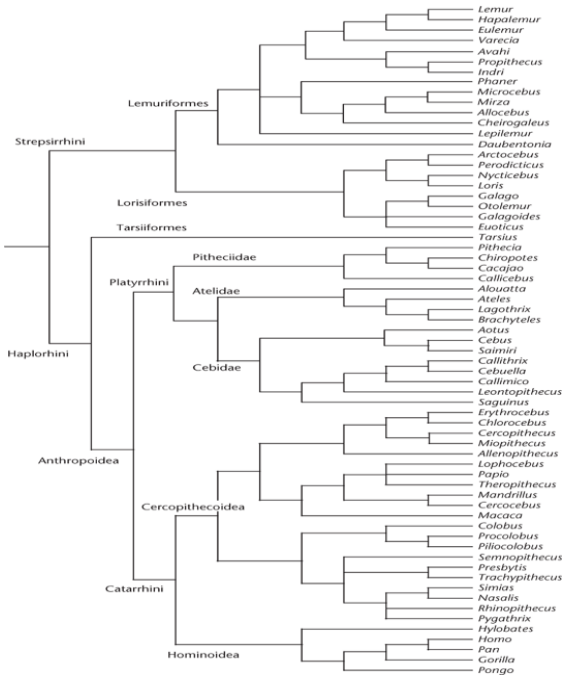

Figure 10. A phylogenetic tree depicting the evolutionary relationship of different primate species (Disotell, 2008)

A variety of different factors may have influenced the performance of the tamarins and thus

the results of this experiment. First of all, individual differences between members of the same species have been shown to play a role in various aspects of behavior. For example, Clarke & Boinski (1995) reported primates have intraspecies and interspecies variation in temperament and personality on an individual, population, and species level. These differences, stemming from factors such as age, sex, life history, hormones, genetics, physiology, social groups, and environment, lead to variation in an individual's to new situations. In addition, these differences can lead to a variation in foraging styles, manipulation of objects, and more (Clarke & Boinski, 1995). These differences could explain the variation in behavior and results obtained from each tamarin, as well as the variation between the tamarin species and other species of primates.

Other factors that may have affected performance of the tamarins include side-biasing and lack of motivation or understanding of how to complete the task. Based on the statistical analysis from the *t*-tests, side-biasing appeared to correlate to lack of statistically significant performances in the various conditions. Side-biasing has been shown to be prevalent in primate species overall. For example, tamarins have been demonstrated to have a particular handedness. Because of this, they tend to reach for food on a particular side, usually the right (Mandal, Bulman-Fleming, & Tiwari, 2000). This may be a factor in this case, although a majority of the tamarins in this experiment actually biased to the left (in 6/8 cases where statistically significant side-biasing was correlated with non-statistically significant results). Another possible cause of this side-biasing could be the position of the experimenter or it could simply be a strategy the tamarin used if they could not figure out the task (Schloegl, Waldmann, & Fischer, 2013). Whether this biasing in the case of this experiment was simply due to lack of understanding of the task or whether it was actually the cause of the below chance performance needs to be studied further.

Aspects of the experimental procedure could also be adjusted to give us a more concrete picture of the extent of the capability for inferential reasoning in the species. First of all, lack of a more structured familiarization or learning phase may have impacted the results. The tamarins

may not have fully understood the task or known that a shaking noise indicated food. In this experiment, a familiarization phase was only given for the visual condition and not the auditory condition. It would be interesting and perhaps useful to compare the current results with results of the experiment after giving the tamarins a chance to manipulate a similar apparatus. In one experiment using the cups (box) task, after testing capuchins without a training phase, Sabbatini &Visalberghi (2008) allowed the capuchins to explore the properties of both empty and filled containers. After given this opportunity, the capuchins were again tested in the same task. While this did not improve performance in the visual condition, two additional monkeys were able to perform above chance in the auditory condition. By changing the apparatus/ test to something more related to what actually occurs in the wild, we might gain a more accurate picture of how inferential reasoning may be relevant to survival in that situation. Giving the monkey a chance to manipulate the object may begin to resemble opportunities and experience a monkey has in the wild (Paukner et. al., 2009). However, by studying tamarins in conditions more similar to their natural environment with a more ecologically relevant task, the tamarins may be more likely to show behavior that parallels behavior in the wild. Further studies could be performed in order to learn more about this subject, and these may help us understand the exact neural mechanism of the behavior and how it developed evolutionarily. At this time, however, all that can be said with certainty is that the ability to use inferential reasoning exists in these monkeys, and this behavior could play a role in many different aspects of life.

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Education

Pennsylvania State University, Schreyer Honors College, University Park, PA
BS in Veterinary and Biomedical Sciences w/ Honors in VBSC
Expected date of graduation: May 2014

Honors and Awards

Dean's List from Fall 2010-Fall 2013
Top 1% of all baccalaureate degree students in College of Agriculture
Awarded $3500 Schreyer Honors Scholarship (for 4 years)
Awarded $1625/semester in agricultural college scholarships (for 4 years)
Awarded the Evan Pugh Scholar Award (Senior)

Memberships/Activities

Reproduction Research Team- Member — *Spring 2014*
Small and Exotic Animals Club- Scrapbooking Chair — *Fall 2010-Present*
Pre-vet Club- Member — *Fall 2010-Present*
Earth House- Member — *Fall 2010- Present*
Club Track- Triple Jumper — *Fall 2010- Fall 2012*

Work Experience

Comparative Communications Lab — *Spring 2014*
University Park, PA
- Lab Opening and Closing
  - Inspected tamarin colony rooms
  - Cleaned floors and surfaces

Exeter Grooming and Doggie Daycare — *June – Sept 2010*
Reading, PA
- Assistant Groomer
  - Groomed dogs by brushing, bathing, clipping fur, and removing ticks
  - Cleaned floors and surfaces daily
  - Helped care for dogs in day care and recorded sessions

St. Catharine of Siena Parish — *2008-2012*

Reading, PA
- Organist/ pianist

Research Experience

Comparative Communications Lab- studying behaviors of tamarins
Principal Investigator- Dan Weiss
Techniques: Weigh out and distribute medications to monkeys
: Catch and weigh the tamarins
: Perform behavioral research experiments with tamarins
: Carry out VBSC honors thesis project testing inferential reasoning in tamarin monkeys

Other Experience

Shadowing/Volunteering at Local Veterinary Hospitals
Exeter Veterinary Hospital *Summer 2010-2013*
Reading, PA
- Shadowed for 20+ hours a week (Summer 2012-Summer 2013)
- Learned about diagnostic techniques for turtles, dogs, cats, birds. and pocket pets
- Observed physical exams, surgeries, and other veterinary procedures

Wyomissing Animal Hospital *Summer 2012*
Wyomissing, PA
- Worked 4 hours a day, 5 days a week
- Learned restraint techniques for cats and dogs
- Observed approximately 4 surgeries per day

Quakertown Veterinary Clinic *Fall 2013*
Quakertown, PA
- Observed physical exams, diagnostic procedures, and surgeries on large animal species