

THE CHOICE EFFICIENCY OF CAPUCHIN MONKEYS (*CEBUS APELLA*) IN A LASER
POINTER TRAVELING SALESMAN TASK

by

ALLISON HOWARD EURY

(Under the Direction of Irwin Bernstein)

ABSTRACT

Non-human primates have demonstrated a preference for efficient route choices in the wild and in simulated foraging experiments. This experiment tested the preferences of two adult male capuchin monkeys (*Cebus apella*) for efficient route choices while stationary using a joystick-controlled laser pointer apparatus. In Experiment 1, subjects were presented with two identical food items in Egocentric (one item nearer to the subject) or Allocentric (both items equidistant from the subject) conditions with the laser dot between the food items. One subject demonstrated an Egocentric bias, preferring the item closest to himself even when this was not the most efficient choice. The other subject did not always demonstrate this Egocentric bias. In Experiment 2, subjects directed the laser dot at three identical food items in Egocentric and Allocentric conditions. Subjects did not demonstrate a clear Egocentric bias in Experiment 2, and did not significantly prefer the most efficient route to retrieve all three foods.

INDEX WORDS: Traveling Salesman Problem, Route Choice, *Cebus*, Spatial Cognition, Egocentric, Allocentric

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BA, Appalachian State University, 2003

BS, Appalachian State University, 2003

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment
of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2010

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December 2010

DEDICATION

To my mother, the hardest working woman I know, for teaching me the value of persistence. To my father, for my toy microscope set and all the late night science projects. I never had a chance, did I? To my love, for your affection, your unrelenting support, and for all the tomorrows that come.

ACKNOWLEDGEMENTS

Many thanks are due to Dr. Irwin Bernstein for his insightful support throughout the development and execution of this project. Also, thank you to Dr. Dorothy Frigaszy and Dr. René Bobe for their guidance and comments on this work.

Several fellow students have been instrumental in the execution of this project. Thank you to Brian Stone for his generous contribution of advice and help in the lab. In addition, the many hours of data collection would not have been possible without help from Joanna Watkins, Marjolein De Nijs Bik, Erin Colbert-White, and Taylor Vance.

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THE CHOICE EFFICIENCY OF CAPUCHIN MONKEYS (CEBUS APELLA) IN A LASER POINTER TRAVELING SALESMAN PROBLEM TASK

Animals moving from one resource to another expend time and energy even as they attempt to fulfill their energetic requirements. As organisms are in part time and energy limited and, since time and energy conserved while traveling can be applied to other important activities such as reproduction or predator avoidance, animals should benefit from choosing energy-efficient routes because they increase an animal's reproductive fitness. It is therefore expected that animals should have evolved some mechanism for minimizing distance to reach food resources.

The Traveling Salesman Problem

Traveling between a series of resource sites while minimizing distance traveled is a problem that humans and nonhuman animals face. In an application of optimal foraging theory to animal behavior, Kamil and Roitblat (1985) present life as a maximization problem in which organisms are required to maximize the rate of rewards among competing demands. The Traveling Salesman Problem (TSP) is a theoretical mathematical problem consisting of choosing a minimum distance path through a series of destinations or nodes and then returning to the origin, much like a traveling salesman might choose a path through a series of cities before returning home at the end of the day. This maximizes the rate of rewards while minimizing distance traveled. The TSP is considered highly difficult to solve given large numbers of destinations, but solutions to the problem are easier to check. In addition, the problem has been intensely studied in the fields of mathematics and computer science, as finding an algorithm to

solve the TSP would signify that similar algorithms exist to solve all other problems in the same category (Wilf, 1994).

Despite the complexity of creating an algorithm to solve the TSP, humans in experimental scenarios find optimal or near-optimal routes in situations where simple algorithms often fail (e.g., $n \leq 60$) (MacGregor & Ormerod, 1996). Known strategies that produce efficient routes for the TSP include the nearest neighbor and convex hull models. The single heuristic of the nearest neighbor model assumes that the traveler always chooses the next closest node in the experimental set, and the solutions from this model rank high in terms of efficiency. However, although the results of the nearest neighbor model reduce distance traveled, they do not take into account the global problem set and tend to produce results that are less efficient than human performance (Ormerod & Chronicle, 1999). The convex hull strategy refers to creating an imaginary hull around the boundary points of the problem set, and entering between boundary points to reach the interior points of the set. This heuristic more closely approximates human performance on the TSP. A model of human performance on the TSP proposed by MacGregor, Ormerod, & Chronicle (2000) combined known strategies such as the nearest neighbor and the convex hull models, and was found to approximate human performance on the TSP quantitatively and qualitatively.

Rats (*Rattus norvegicus*; Long-Evans) performing a modified version of the TSP were shown to use a distance reducing strategy that resembled the nearest neighbor model (Bureš, Burešová, & Nerad, 1992). When performing a simplified version of the Traveling Salesman task in which a reward was received only after visiting all of a series of goal sites, rats took the shortest route in 20% of trials, and the second-shortest route in 21% of trials.

Gibson, Wasserman, & Kamil (2007) studied the performance of humans and pigeons (*Columba livia*) in finding efficient routes between a series of points. Traveling Salesman tasks of three, four, or five nodes were presented in a single horizontal line on a computer screen. The subjects were required to click all nodes using a mouse, or in the case of the pigeon, by pecking the screen. The TSP was considered one-way, as subjects were not required to return to the start node in order to complete the trial. Human participants were more efficient than a Monte Carlo model. People were also more efficient than the nearest neighbor model, yet less efficient than the optimal route. Pigeons were more efficient than the Monte Carlo model, yet less efficient than the nearest neighbor model. Yet, when required to choose routes that were in the top 66% of all possible solutions, the pigeons learned to perform more efficiently and their routes became more comparable to the nearest neighbor solutions. This result indicates that when the costs of inefficiency are high, pigeons can learn to choose efficient routes.

Primate Route Efficiency in the Wild

Previous studies of primate ranging patterns have demonstrated that monkeys and apes appear to minimize distance when foraging in the wild. Garber (1988) demonstrated that tamarin monkeys (*Saguinus mystax* and *Saguinus fuscicollis*), like other non-primate nectar foragers (e.g., *Hymenoptera*: Ackerman, Messler, Lu, & Montalvo, 1982; Heinrich, 1976), exhibit a behavior resembling trap lining in which they appear to attempt to minimize the distance traveled between food patches when foraging, and travel in repeated straight-line paths between flowering trees. Noser and Byrne (2007) demonstrated that wild Chacma baboons (*Papio ursinus*) use linear route segments when traveling towards sparse fruit resources and waterholes during the dry season. Janson (1998) experimentally demonstrated that capuchin monkeys

(*Cebus apella*) moved toward 15 feeding platforms more linearly than could be predicted by several random models of their movement. They also preferred the closest feeding platforms more frequently than a random model would predict. Similarly, black capuchin monkeys (*Cebus nigrinus*) were shown to travel more linearly toward resource sites that had been previously visited than new resources (Presotto, 2009).

Primate Route Efficiency in the Laboratory

In an experimental context, Menzel (1973) examined the route efficiency of juvenile chimpanzees (*Pan troglodytes*) in a simulated foraging environment and demonstrated that chimpanzees are capable of choosing efficient routes. In this experiment, a single chimpanzee was carried around an outdoor enclosure as food items were hidden by an experimenter using a random path. Following the hiding phase, the subject was released into the outdoor enclosure with his group, and allowed to retrieve the hidden foods. The path the subject used to retrieve the hidden food was more efficient than random and did not resemble the path used when the items were hidden. Chimpanzees also maximized the rate at which they received the hidden rewards by first visiting the side of the enclosure with the greatest number of hidden food items when one side of the enclosure had more hidden items than the other.

Yellow-nosed monkeys (*Cercopithecus ascanius whitesidei*) demonstrated an ability to remember the locations of food items hidden within eight plastic cups and to retrieve those food items using a distance-minimizing route (MacDonald & Wilkie, 1990). Conversely, gorillas (*Gorilla gorilla gorilla*) tested in a similar food search task in which food items were hidden and retrieved after a delay did not use a distance-minimizing strategy between food containers (MacDonald, 1994). Capuchin monkeys (*Cebus apella*) retrieving food from opaque containers

were more efficient when those containers were arranged in a straight line or a circle than in a matrix array (DeLillo, Aversano, Tucci, & Visalberghi, 1998).

Vervet monkeys (*Cercopithecus aethiops*) retrieving food from baited opaque containers used a retrieval path that minimized the distance traveled (Cramer & Gallistel, 1997). The foods were hidden in one of two configurations. In the diamond configuration, monkeys visited baited containers configured as the four vertices of a diamond. The start location was baited after the subjects had moved to the second vertex in one condition, and not baited in a second condition. In the baited condition, the optimal path was a diamond-shaped route through the four vertices, and returning to the start container. In the non-baited condition, the optimal path was a zigzag route through the four vertices. Vervet monkeys were found to choose their routes preferentially based upon the baiting of the start container. In the unequal sides configuration, the subjects visited six baited containers split unequally into four containers to one side of the start location and two containers to the other side. The monkeys were allowed to make a complete tour through all six food items, and yet, on every trial, they traveled first to the side of the array with four baited containers. This maximized the rate of reward and required the subjects to look ahead at least two choices into the future.

The current experiment will investigate the preferences of capuchin monkeys (*Cebus apella*) for efficient one-way routes through a series of goal sites, and also investigate any evidence of planning these routes at least two choices in the future. However, unlike the vervet monkeys of the previous experiment, subjects will not locomote through the array of goal sites, a limitation that is expected to affect their preference for efficient routes.

An Egocentric Bias

The ability of animals to choose efficient paths as they move between resource sites may depend upon their ability to reason about the distance between those resource sites, allocentrically, and about their current position in relation to those resource sites, egocentrically. The present study investigates the role of allocentric and egocentric reasoning in choosing an efficient path between a series of resource sites.

In previous tasks, capuchin monkeys have demonstrated a bias for coding the location of hidden items using an egocentric frame of reference. Poti (2000) observed the use of spatial reference frames of four capuchin monkeys (*Cebus apella*) in a test of spatial memory. In this study, a food item was hidden within one of two identical opaque containers placed on a rotating platform. The monkeys were stationary, yet they had visual access to the rotating platform while the food item was being hidden. The platform was then obscured and rotated (90, 180, 270, or 360°). Capuchin monkeys responded in a pattern consistent with a preference for use of the egocentric reference frame instead of using the small-scale allocentric frame of reference provided by a landmark cue placed near the baited platform in Experiment 1. The subjects showed the greatest degree of difficulty with the 180° rotation condition, likely due to the fact that the arrangement of containers in the choice phase closely resembled the container arrangement in the baiting/observation phase. The possibility exists that the monkeys used an allocentric frame of reference at the wrong scale. Instead of relating the position of the reward container to the position of the proximal landmark, the monkeys may have associated the position of the reward container to the other larger scale landmarks in the experiment room. If the monkeys were using the incorrect scale of allocentric reference frame in this study, it may indicate that capuchins prefer to use the external reference frame that aligns with their egocentric

reference frame. Either through their choice of the egocentric reference frame or the allocentric frame at the scale that concurred with their egocentric frame, these results indicated a predisposition of capuchins toward use of the egocentric frame of reference (Potì, 2000).

In a previous experiment, capuchins (*Cebus apella*) used a laser pointer to indicate desired food items of different sizes, types and distances from self (Stone, 2008). These monkeys remained stationary and, after making their choice, a human researcher delivered their chosen food item. Capuchins in this study significantly preferred proximal food items to foods placed at a greater distance from themselves, although they did not locomote to the food's location. The subjects demonstrated an ability to judge the distance between the food and self, and their preferences incorporated distance, food type, and size.

The primary goal of the present study was to investigate the efficiency of capuchin monkeys solving a TSP without the perspective of locomoting throughout the array of goal sites. I predicted that holding a subject stationary while it completed a Traveling Salesman task would compromise their ability to minimize the distance of their route, due to an egocentric bias for objects closer to self. Two identical food items were placed at a distance from the subject, with a laser dot between the two foods. Since the efficiency of choice without the added challenge of remembering the location of the food item was the question of interest, the food items were in full view of the subject throughout testing. When the laser dot was initially placed in the center of the space between these two food items, the length of the tour was not affected by which food item was chosen first. The two possible tours were of equal length. When the laser dot began closer to one food than the other, a distance minimizing route consisted of first choosing the food closer to the laser dot. Capuchin efficiency was investigated when egocentric and allocentric reasoning were congruent, that is, both food items were equidistant from the subject himself.

Their efficiency was also investigated when these two strategies led to conflicting solutions to the TSP, or when one food item was closer to the subject than the other. When both food items were equidistant from the subject, I expected their responses to correspond with the least distance path. However, when allocentric and egocentric cues were placed in conflict, the responses of the subjects were expected to be biased towards objects closer to self.

A further goal of this experiment was to investigate the effect of the capuchins' egocentric bias when the number of food items was increased to three. When these items were arranged in a horizontal line perpendicular to the body axis of the subject, I predicted that capuchins would be able to use a least distance route that incorporated all three food items. However, when these food items were arranged in a straight line directly in front of the subject, I expected capuchins to be more likely to choose inefficient routes based upon their egocentric bias. The choice of a least distance path in this experiment required subjects to consider the global problem set, looking ahead two choices in the future to plan their route and choose the most efficient path.

EXPERIMENT 1

METHOD

Subjects

Two adult male capuchins (*Cebus apella*), Leo and Xenon (ages 18 and 25), from the Primate Cognition and Behavior Laboratory at the University of Georgia participated in this experiment. These individuals were pair housed, however their cage mates did not participate in this experiment. Leo and Xenon had been previously tested in various behavioral experiments, including computerized maze tasks (e.g., Frigaszy et al, 2009) and laser-pointer tasks (Stone, 2008). The subjects were fed a consistent diet of monkey chow and fruit twice a day throughout the experiment, and water was available *ad libitum*.

Apparatus

The subjects were transported from their home cages to a transparent acrylic testing cage (64x47x78 cm cage, sitting 84 cm above the floor) located in a hallway (2.2x12.2 m) of the Primate Cognition Laboratory. Subjects sat on a metal perch (30 cm above the cage floor) while working, and extended their arm through a hole in one side of the testing cage to contact a joystick apparatus (Figure 1). The metal joystick controlled a projected laser dot by directing a motorized pan-tilt head (Bescor, MP-101b) attached to a laser pointer (Figure 2). The red laser dot was projected onto the gray cement floor of the hallway. The motorized pan-tilt head stood on a tripod 108cm above the floor on the right side of the testing cage.



Figure 1. Subject manipulating joystick-controlled laser apparatus

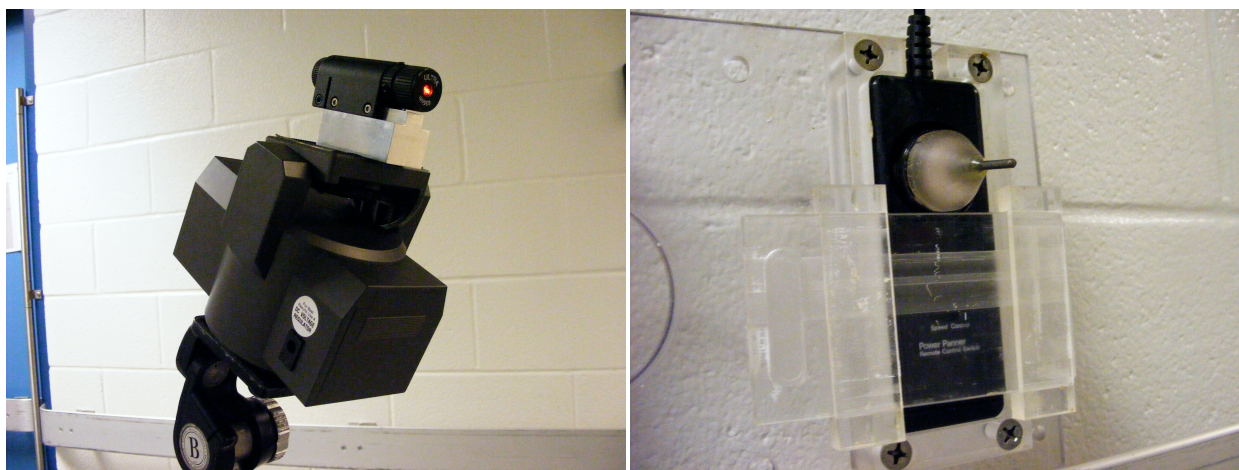


Figure 2. Motorized pan-tilt head and joystick apparatus

Procedure

Two food items of equal size and type (e.g., peanut halves, white chocolate chips, multigrain cereal, fresh fruit) were placed on the floor of the hallway in front of the testing cage. The food type was varied throughout testing to increase motivation, but in any given trial, the food items presented simultaneously were identical. The laser dot was placed between the two food items, such that the distance ratio between the dot and the two food items was equal to 1:1,

1:2, 1:3, or 1:4. The metric distances of these ratios are provided in Table 1. There were two arrangements of food items, resulting in two conditions for Experiment 1, allocentric and egocentric (Figure 1). The distance ratios between those items and the laser dot were the same in both conditions. In the allocentric condition, the two food items were placed at equal distances (2.7m) from the subject. In the egocentric condition, the two food items differed in their distance from the subject, at 0.5 and 2.3 meters from the aperture in the front of the testing cage. Figure 2 illustrates the location of the laser dot for each of the distance ratios in the allocentric and egocentric conditions.

Table 1

Ratios and Metric Distances Between Food and Laser Dot

Ratio	Distance
1:1	0.75 m: 0.75 m
1:2	0.5 m: 1 m
1:3	0.375 m: 1.125 m
1:4	0.3 m: 1.2 m

A trial began with both food items placed on the floor. A human experimenter stood to the right of the subject, removing and replacing the joystick apparatus from the front of the acrylic testing cage. A second human experimenter stood by the initial location of the laser dot. The subject manipulated the joystick controlling the laser dot to contact the food item. When the laser dot came within 2.5 cm of the food item, the subject was verbally praised and the joystick was withdrawn. Following each choice, the chosen food item was delivered to the monkey

subject. Once the subject had consumed the food item, the joystick was returned to him. The subject completed the trial by retrieving the second food item in the same manner as the first. Trials in which the subject did not retrieve the second food item were discarded.

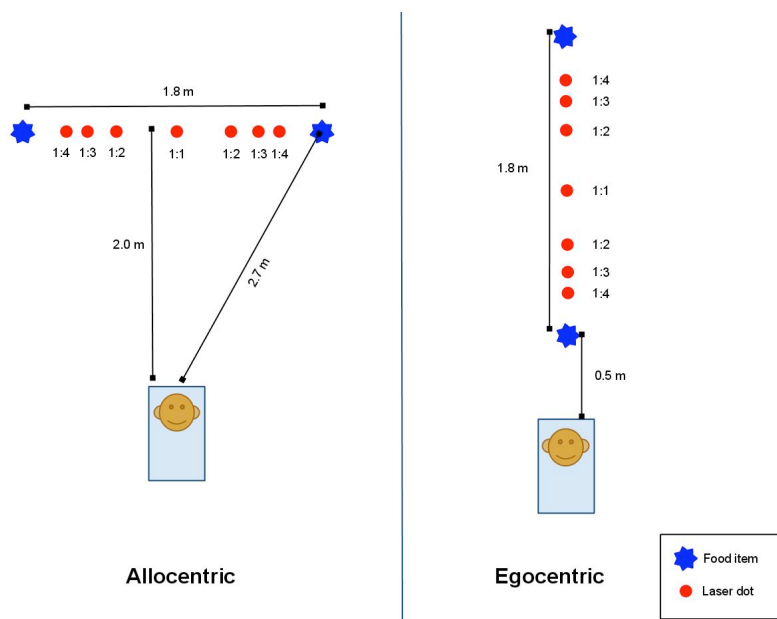


Figure 3. Allocentric and Egocentric Conditions and Distances

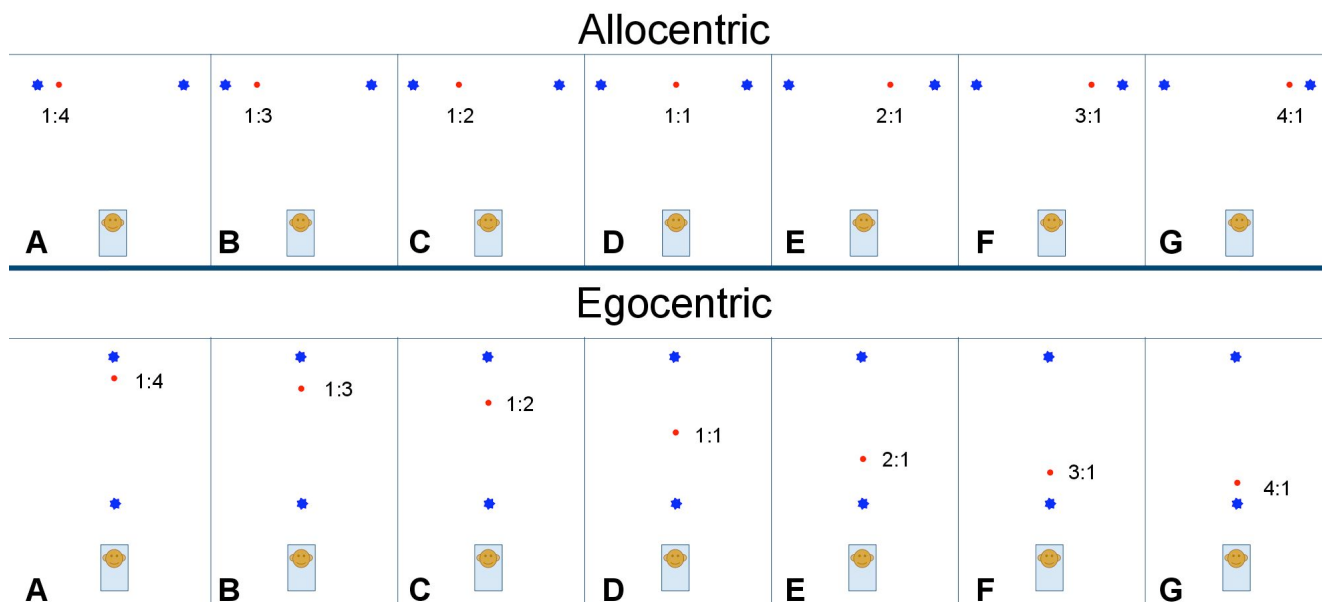


Figure 4. Allocentric and egocentric conditions and locations of laser dot

The distance traveled by the laser dot was the independent variable of this experiment. It was therefore important that the manner in which the food was delivered to the subject did not confound the distance traveled by the cursor. As such, the distance traveled by the experimenter in delivering the food was designed to replicate the distances between the food choices made by the subjects. An experimenter stood directly behind (in the egocentric condition) or beside (in the allocentric condition) the laser dot as the subjects made their food choice. After the subject's choice, the experimenter walked in a straight line path from her start location to the location of the first food item, retrieved the food item, and then took a straight-line path to deliver the food to the subject (Figure 3). The experimenter knew these delivery routes, however, they were not marked on the floor of the array to prevent the subjects from directing the cursor to these marks. The experimenter then stood directly behind or beside the laser dot again, in the location where the subjects paused the cursor after their first choice. Occasionally, the subject continued to manipulate the joystick after their first choice and before the joystick was removed from their reach. These manipulations of the joystick did not appear to be visually guided, as the subjects were watching the experimenter walk toward the food item, and not watching the laser dot. In the allocentric condition, this often resulted in the laser dot being left on the wall of the hallway. In these trials, the experimenter placed the laser dot back upon the floor of the experimental space before the joystick was returned to the subject.

A single least distance path existed for each distance ratio, direction, and condition. This least distance path consisted of a first choice of the nearest food item, followed by a second choice of the further food item. For example, in an allocentric B trial (i.e., 1:3 ratio, closest food left), the least distance path was to direct the laser dot 37.5 cm to the left in the first choice, followed by 1.5 m to the right in the second choice. An inefficient first choice (e.g., directing the

laser dot to the right in the previous example) caused an increase in total trip length proportionate to the ratio of the trial. In the previous example, a first choice of the food item on the right would mean an increase in total trip length of 0.75 m. In egocentric trials, the least distance path required the subject to direct the laser dot toward and away from himself. For example, the least distance path for an egocentric-B trial (i.e., 1:3 ratio, closest food back) required the subject to direct the laser dot 37.5 cm away from himself, followed by 1.5 m toward himself. This response was expected to be more challenging for the capuchins, as it placed the proximity of the laser dot to the back food item in conflict with the proximity of the front food item to self. The most efficient path was always to choose the food item closest to the laser dot first, regardless of the proximity of any other food to the subject himself.

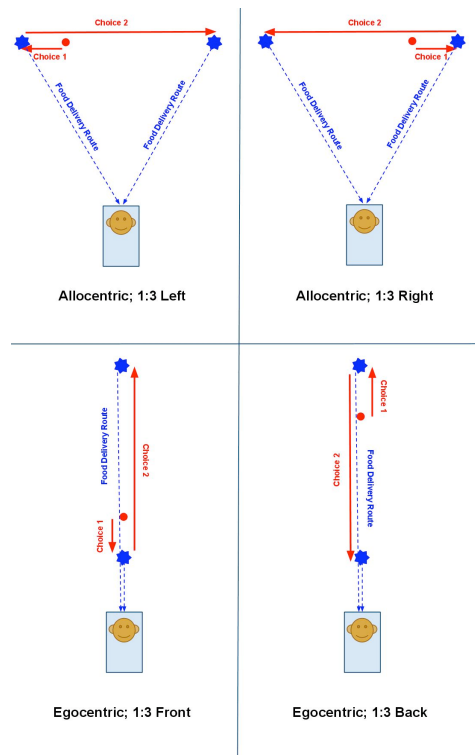


Figure 5. Least Distance Paths and Food Delivery Routes for Egocentric and Allocentric 1:3 Trials

For the subject, the only disadvantage to an inefficient route was the time delay in receiving the food reward. However, subjects were apparently sensitive to the time required to complete the task. Over the testing period, batteries in the pan-tilt unit controlling the laser dot had to be changed every three testing days. When the batteries were used for longer, the subjects often refused to participate in the task, apparently noting the difference in speed of the movement of the laser dot.

Analysis

A binomial test was conducted to analyze the frequencies of the subjects' preferences for food items proximal to the laser dot and proximal to the subject himself. For distance ratios 1:2, 1:3, and 1:4, a one-tailed binomial test was performed to determine if the frequency of efficient choice was significantly greater than the null hypothesis of 0.5. For the 1:1 distance ratio, a two-tailed binomial test was performed to test whether subjects significantly preferred either of the two equidistant food items.

EXPERIMENT 1

RESULTS

In the Allocentric condition, Leo chose the food item closer to the laser dot for both the 1:3 (Left, $p = 2.00 \times 10^{-5}$; Right, $p = 0.0207$) and 1:4 (Left, $p = 0.0059$; Right, $p = 2.01 \times 10^{-4}$) distance ratios, and did not significantly more often choose the food item closer to the laser dot in the 1:2 distance ratio (Left and Right, $p = 0.05766$) (Table 2). In the 1:1 distance ratio, although neither food item was closer to the laser dot, Leo showed a significant preference for the left-most food item ($p = 0.002577$) (Table 3).

In the Allocentric condition, Xenon significantly preferred the food items closest to the laser dot in all distance ratios: 1:2 (Left, $p = 0.02069$; Right, $p = 0.0059$), 1:3 (Left, $p = 0.0059$; Right, $p = 9.54 \times 10^{-7}$), and 1:4 (Left, $p = 2.01 \times 10^{-4}$; Right, $p = 2.00 \times 10^{-5}$) (Table 2). In the 1:1 distance ratio, Xenon did not show any preference for the left or right food item ($p = 0.2632$) (Table 3).

In the Egocentric condition, Leo significantly preferred the closest food item in every distance ratio when the food closest to the laser was also closest to himself. In fact, Leo chose efficiently in all 20 trials of the 1:2, 1:3, and 1:4 distance ratios ($p = 9.54 \times 10^{-7}$) (Table 2). In the 1:1 distance ratio, neither food choice was more efficient, but Leo showed a significant preference for the food item closer to himself ($p = 0.01182$) (Table 3). When the laser dot was closest to the back food item, Leo did not significantly prefer the most efficient first choice.

In the Egocentric condition, Xenon chose the food item closest to the laser dot in every distance ratio when this food item was also closest to himself (1:2 Back, $p = 2.01 \times 10^{-4}$; 1:3

Back, $p = 9.54 \times 10^{-7}$; 1:4 Back, $p = 9.54 \times 10^{-7}$) (Table 2). In addition, Xenon chose efficiently in the 1:3 and 1:4 distance ratios (1:3 and 1:4 Front, $p = 9.54 \times 10^{-7}$) when the food item closest to the laser dot was further from the subject. Xenon did not, however, choose efficiently in the 1:2 condition (1:2 Back, $p = 0.1316$) when the laser dot was closer to the back food item (Table 2). In the 1:1 Egocentric condition, Xenon did not have a significant preference for either food item, although the front food item was closer to the subject himself ($p = 0.1153$) (Table 3).

Table 2

Frequency of Choosing the Closer Food Item Across Trial Types for 1:2, 1:3, and 1:4 distance ratios

Condition	Subject	1:2		1:3		1:4	
		Left	Right	Left	Right	Left	Right
Allocentric	Leo	14	14	19**	15*	16*	18**
	Xenon	15*	16*	16*	20**	18**	19**
		Front	Back	Front	Back	Front	Back
Egocentric	Leo	20**	13	20**	10	20**	9
	Xenon	18**	13	20**	18**	20**	20**

Note. All trial types n=20

* $p < 0.05$. ** $p < 0.001$

Table 3

Frequency of Choosing Equidistant Food Items for the 1:1 Distance Ratio

Condition	Subject	1:1
		Left
Allocentric	Leo	17*
	Xenon	7
Egocentric		Front
	Leo	16*
	Xenon	14

Note. All trial types n=20

* $p < 0.05$

EXPERIMENT 1

DISCUSSION

Previous research indicated that capuchin monkeys and other primates are capable of choosing efficient routes between resource sites both in the wild and in captive settings with simulated foraging experiments. However, experiments with stationary subjects demonstrated that capuchin monkeys have an egocentric bias for coding the location of an object in relation to themselves, as opposed to using landmarks as allocentric cues. It was therefore hypothesized that when using a laser pointer apparatus, stationary capuchin subjects would choose efficient routes between two food items when the allocentric and egocentric cues were congruent. However, when the allocentric and egocentric reasoning systems were in conflict, I expected that capuchins would demonstrate a bias towards objects closer to themselves, even when this bias yielded a less efficient route.

Leo's choice patterns conformed to preferences hypothesized for the allocentric and egocentric conditions of this experiment. His choices in the allocentric condition indicated that when there was a large difference between the efficient and inefficient routes (i.e., 1:3 and 1:4 distance ratios), he was capable of choosing the item closest to the laser dot significantly more often. When the inefficient and efficient choices were similar (i.e., 1:2 ratio), he did not show a significant preference for the item closer to the laser dot, although he preferred that item 70% of the time. This result conforms to Weber's Law as discrimination of the distances between food items becomes more difficult as the ratio becomes more similar.

In the Egocentric condition, Leo did not choose efficient routes in any distance ratios when the food closest to the laser dot was more distant from the subject himself. However, Leo also did not significantly prefer the food item closest to himself in these trials. These results support evidence of an egocentric bias, yet not an absolute preference for items close to self. In trials in which the laser dot was close to Leo and to his nearest food item, Leo chose the efficient route in all 60 trials. When egocentric and allocentric reasoning were congruent, Leo chose efficient routes between food items at a distance from himself. However, when the two reasoning systems were opposed, Leo demonstrated a bias towards objects closer to himself.

Xenon chose efficient routes significantly more often in almost every distance ratio tested. His preference for efficient routes demonstrated an ability not only to reason egocentrically about the distance between food items and himself, but also allocentrically, about the distance between food items and the laser dot. The only condition in which Leo did not significantly prefer the most efficient route was the 1:2 Egocentric condition in which the laser dot was nearer to the food item that was farther from the subject. This indicates the slight influence of an egocentric bias, as Xenon was capable of choosing the most efficient route in both 1:2 Allocentric conditions (left and right). However, it is clear that the placement of the food items nearer and farther from the stationary subject did not greatly inhibit Xenon's ability to choose an efficient route between the two food items.

When the laser dot was equidistant from both food items, there was no least-distance path, since choosing either of the two food items would have resulted in the same path length. However, it was expected that subjects would demonstrate a preference for the item closest to self in the Egocentric condition, and show no preference for either direction in the Allocentric condition. In the 1:1 distance ratio, Leo preferred the food item to his left in the Allocentric

condition, and the food item closest to him in the Egocentric condition. The preference for the food item closest to self was predicted by the Egocentric bias hypothesis. The left side bias demonstrated by Leo in the Allocentric condition was not expected, but was only seen in this 1:1 distance ratio. Although Leo may have directional biases, they were not absolute, as he was able to choose efficient routes in some other ratios. In addition, the left direction bias was not as strong as his bias for objects closer to self, as Leo only demonstrated a preference for items to his left in the 1:1 Allocentric condition, and was unable to choose the most efficient route in any of the back Egocentric ratios. Xenon, however, was not influenced by a bias in either the Egocentric or Allocentric condition, as he did not prefer either of the two food items when they were equidistant from the laser pointer.

The results of Experiment 1 conform to the observation by Frigaszy and colleagues (2003) that capuchins performing a computerized maze task were less likely than chimps to take a route that eventually led to the goal, but initially led away from that goal. In this experiment, the initial movement of the laser pointer away from themselves may have interfered with the capuchins' ability to choose a route that would eventually efficiently retrieve all the food items of the array.

EXPERIMENT 2

METHOD

This experiment tested the influence of the egocentric and allocentric layouts in selecting an efficient route with three, rather than two goal locations and the ability of capuchin monkeys to plan an efficient route at least two goal sites in the future. The choice of either of the two food items closest to the laser dot would yield an equal rate of reward for the first and second choices. However, choosing the most efficient path through all three food items required the subjects to look ahead to the third food choice.

In addition to retrieving more food items, the subjects had to complete the entire route before receiving a food reward. In this way, the experiment modified the traditional TSP, in which rewards are attained at each goal site. However, this design allowed the movement of the experimenter delivering the food items to duplicate the movement of the laser pointer, and avoided the problem of the experimenter's path differentially increasing the time to food delivery for any of the distance ratios.

Subjects and apparatus

The subjects and apparatus of Experiment 2 were the same as Experiment 1. The trials took place in the same test space described in Experiment 1.

Procedure

Following completion of Experiment 1, both subjects completed 24 training trials in which they were required to contact first two, then three food items with the laser dot before these items were given to the subject. These training trials increased in distance from 60 cm up to

the final testing distance. From the very first training trial, subjects were contacting all available food items, despite the delay in reward.

In the testing phase of Experiment 2, three food items of equal size and type were placed in a straight line on the floor in the hallway in front of the testing cage. The laser dot was placed between two of the three food items, equidistant (76 cm) from two, and further (1.5m) from the third food item. There were two arrangements of the food items, resulting in two conditions for Experiment 2, allocentric and egocentric. For each condition, the laser dot was positioned equidistant between both possible food item pairs. In the egocentric condition, this meant that the laser dot was either closer to the subject (i.e., front) or farther (i.e., back). In the allocentric condition, the laser dot was between the two left-most food items, or the two right-most food items. Thus, there were four possible arrangements of the food items and the laser dot: egocentric-front, egocentric-back, allocentric-left, allocentric-right. The arrangements of the food items and locations of the laser dot are depicted in Figure 4.

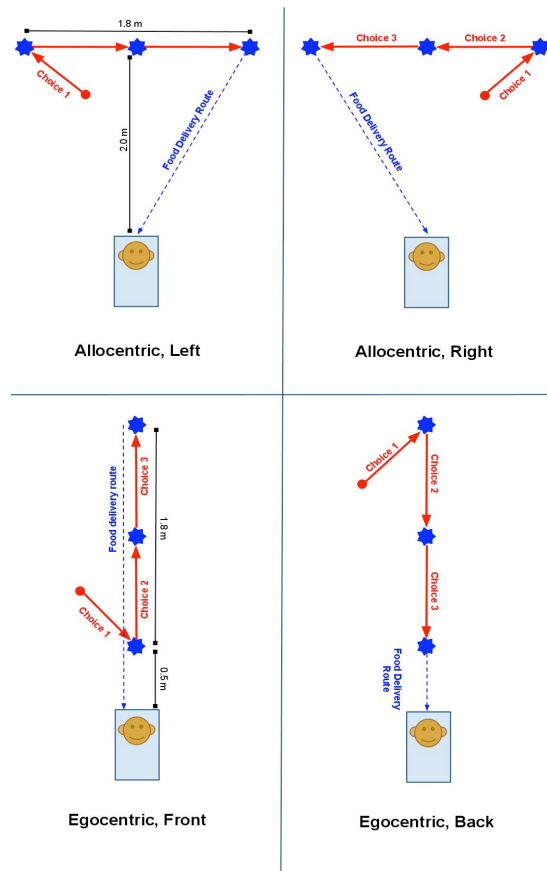


Figure 6. Experiment 2 Layouts, Least Distance Paths and Food Delivery Routes

The subject manipulated the joystick controlling the laser dot to contact the food item. When the laser dot came within 2.5 cm of the food item, the subject was verbally praised and Experimenter 1 withdrew the joystick. Experimenter 2 immediately walked along a predetermined route (Figure 5) to collect the food item, but no food was delivered until the end of the trial. Once Experimenter 2 was standing stationary at the location where the first food item had been retrieved, Experimenter 1 returned the joystick, and the subject made the second choice. This procedure was repeated for the third food item. Following the third choice, Experimenter 2 walked along the predetermined route to deliver all three food items to the subject. Subjects completed all three choices in every trial of Experiment 2.

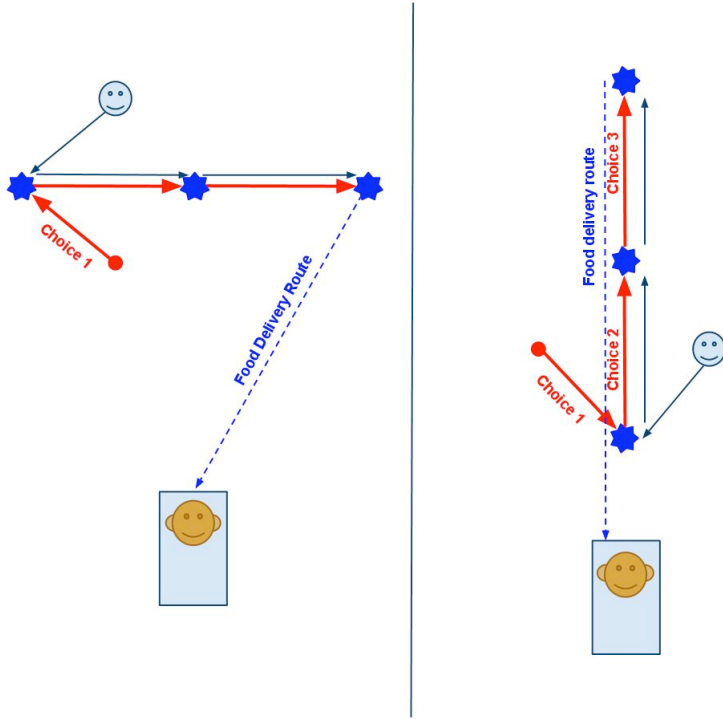


Figure 7. Layout of allocentric and egocentric conditions with position and food delivery path of the experimenter

For the allocentric left and allocentric right conditions, the first choice of the three foods consisted of two foods equidistant from the laser dot and one food item further away. Considering only the first choice, the left or right closest food items would have maximized the rate of reward equally. However, the first choice of the subject impacted the second and third choices, such that there existed a single least distance path to collect all food items (Figure 4). A single, straight-line path across the plane of food items minimized the distance of the route. For example, the most efficient first choice considering the entire array in the allocentric-left condition would be the left-most food item. A choice of the center food item would cause an increase in the length of the total route by 0.9 m. This was also true for all the other tested conditions.

Analysis

A one-tailed binomial test was used to evaluate the alternate hypothesis that subjects would prefer a first food choice that would minimize the total route distance. Although there were three possible first food choices, the two of interest were the two food items closest to the laser dot. Thus, the null hypothesis stated that the frequency of choosing the most efficient first food item would not be significantly greater than 0.5.

EXPERIMENT 2

RESULTS

Leo did not prefer the most efficient first choice significantly for any of the trial types. It is notable that in the Egocentric condition, Leo did not significantly prefer the food item closer to himself ($p = 0.146$) (Table 4). However, Leo significantly preferred the inefficient first choice that was further from himself ($p = 0.03857$) in the Egocentric condition. Xenon preferred the most efficient first choice in the Egocentric condition when the most efficient first choice was closest to himself (Front, $p = 0.0002441$), and in the Allocentric condition when the most efficient first choice was to the subject's left ($p = 0.006348$).

Table 4

Frequency of Efficient First Choices in the Egocentric and Allocentric Conditions

	Leo	Xenon
Egocentric		
Front	9	12**
Back	2*	0**
Allocentric		
Left	8	11*
Right	5	3

Note. All trial types $n=12$

* $p < 0.05$. ** $p < 0.001$

Following a choice of the most efficient first food item, subjects most often chose the nearest neighbor second food item (Table 5).

Table 5

Frequency of Choosing an Efficient Second Food Item After the Choice of an Efficient First Food Item

	Leo	Xenon
Egocentric		
Front	9(9)*	12(12)*
Back	2(2)	0(0)
Allocentric		
Left	7(8)	11(11)*
Right	4(5)	2(3)

Note. Numbers in parentheses represent the total number of trials in which the subject made the correct first choice for that condition. Numbers before the parentheses represent the number of second choices

* $p < 0.05$

Table 6 illustrates the subjects' preferences for one of the two food items closest to the laser dot (i.e., the nearest neighbor choices) over the farther food item. Both Leo and Xenon chose the farthest food item first on one trial out of twelve in the Egocentric Back condition. In addition, Xenon chose the far left food item first on three of the twelve trials in the Allocentric Right condition.

Table 6

Frequency of Nearest Neighbor First Choices in the Egocentric and Allocentric Conditions

	Leo	Xenon
Egocentric		
Front	12*	12*
Back	11	11
Allocentric		
Left	12*	12*
Right	12*	9

Note. All trial types $n=12$

* $p < 0.05$

EXPERIMENT 2

DISCUSSION

It was hypothesized that capuchins using a laser pointer apparatus would choose a route between three food items that would minimize travel distance. It was also expected that this preference would be inhibited when the most efficient route required a first choice that was further away from the stationary subject himself.

In this experiment, Leo did not significantly prefer the most efficient first choice item of the three in any of the tested conditions. In the Egocentric back condition, Leo significantly preferred the less efficient middle food item. These results may indicate that Leo had a bias for objects located closer to self. However, this bias was not consistent, as Leo did not significantly prefer the most efficient first food item in the Egocentric front condition.

Xenon was significantly influenced by a bias for items closer to himself in the Egocentric conditions of Experiment 2, as he significantly preferred items closer to himself in both the front and back conditions. However, he was also significantly influenced by a directional bias in the Allocentric condition, as he significantly preferred items to his left in the left Allocentric condition. This result was not predicted by the Egocentric bias hypothesis.

The performance of the subjects in this experiment was not as expected, as subjects did not choose efficient routes consistently when egocentric and allocentric strategies were congruent. These results indicate that the capuchin subjects did not make efficient first choices in their route on the basis of the entire path, planning future choices. The subjects did, however, significantly prefer the two nearest neighbor goal sites over the further goal site in their first and

second choices. The strategy of capuchins in this experiment was apparently to choose randomly between the two nearest neighbor goal sites, without considering the global problem set, and to proceed through the problem set using the nearest neighbor strategy. However, future experiments with a larger number of goal sites are necessary in order to more effectively describe subjects' strategies, as subjects may consider the global problem set when it includes clumping of goal sites or greater relative distances between goal sites.

The results of Experiment 1 indicated that subjects prefer efficient routes, although some choices are affected by an Egocentric bias. However, the results of Experiment 2 indicate that subjects did not plan their routes considering their future choices. Therefore, the execution of efficient routes by primates in the wild and in previous simulated foraging experiments may reflect a strategy that does not look forward more than one choice in the future, or, alternatively, the stationary nature of the subjects in this experiment may have prevented them from planning their future choices. Vervet monkeys locomoting through an array of hidden food items appeared to plan these routes looking two steps into the future (Cramer & Gallistel, 1997). The lack of planning demonstrated by capuchin subjects in this experiment may be due to a species difference, or to the effect of holding subjects stationary in the current experiment. The vervet monkeys in the previous experiment not only locomoted through the array to retrieve hidden food items, but they were carried through the experimental space as the food items were hidden using a random path. This prior experience with traveling the distances between the goal sites may have enhanced their ability to plan an efficient route. The lack of prior experience, and the lack of continuously updating perceptual cues through locomoting between goal sites may have contributed to the observed lack of planning in Experiment 2.

GENERAL DISCUSSION

Choosing efficient routes between two goal sites while stationary is within the range of abilities of the species of *Cebus apella*, even when an efficient route means first choosing an item further away from the subject himself, as evidenced by Xenon's performance in Experiment 1. However, individual variability was evident in reasoning allocentrically in this way. The egocentric bias for items closer to self, even when those items do not yield the most efficient route, influenced the choice patterns of Leo in Experiment 1.

The influence of the egocentric bias for objects closer to self was also apparent when capuchin subjects chose a route to three goal sites while remaining stationary. However, the influence of this egocentric bias is less clear, and a directional bias also seemed to influence the choices of subjects in the Allocentric condition. Both individuals in this experiment preferred the food item closer to themselves in at least one of the conditions. However, Xenon also preferred the item to his left in the allocentric condition, a bias he did not demonstrate in Experiment 1, and Leo did not demonstrate a directional bias for left or right in the Allocentric condition of Experiment 2, despite demonstrating a bias for objects to his left in the 1:1 condition of Experiment 1.

The stationary nature of this task may have interfered with subjects' ability to reason allocentrically about the distances between multiple goal sites, as well as interfering with their ability to plan an efficient route between three goal sites. While foraging in the wild, capuchins move toward real food rewards; however, they locomote independently instead of being held stationary, as they were in the present study. Presumably, the ability to locomote in their

environment enhances reasoning about the spatial relationships between subjects themselves and goal sites, as well as the spatial relationships among multiple goal sites. Previous experiments with human infants indicate that experience with self-produced locomotion enhances their spatial cognitive abilities (Uchiyama et al, 2008). Experience locomoting through the experimental array may enhance the abilities of capuchins to reason allocentrically about their routes between goal sites.

The laser pointer apparatus allows experimenters to ask new research questions about the spatial cognition of animals. Choices made with the laser pointer are from a distance, and as resources are often distant from animals in their natural environment, this format may allow us to more accurately represent many theoretical spatial problems. In addition, the movement of the laser dot is not equivalent to the energetic demands placed on the subject manipulating the joystick. Therefore, it is possible to disassociate the preferences of subjects from the energetic costs of locomotion. Finally, as seen in this experiment, subjects manipulating the joystick are stationary, while the laser dot moves through the environment. Therefore, the perspective of the subject is not updated as each subsequent choice is made and the egocentric and allocentric frames of reference of the subject can be disassociated, allowing experimenters to investigate the effects of each frame of reference independently.

Future experiments with larger numbers of goal sites are now possible with the subjects of the present study. The effects of their egocentric biases are known, and experimental arrays with more complex geometries with goal sites at varying distances from one another and from the subjects themselves should be tested. Testing the preferences of subjects with large numbers of goal sites will better allow us to describe the choice strategies or algorithm used by subjects to choose between a group of goal sites, and to compare these strategies to those used by humans.

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APPENDIX

LITERATURE REVIEW

Non-human primate cognition is of interest because monkeys and apes are highly intelligent animals that perform well in various cognitive tasks, and also because of their phylogenetic proximity to humans. Capuchin monkeys are of particular interest to researchers studying primate cognition. They are largely considered the most intelligent of the new world primates due to their use of tools and complex social behavior. However, capuchins as new world monkeys are relatively phylogenetically distant from humans, having diverged from the human lineage at least 25 million years ago (Fleagle, 1998).

Animals moving from one resource to another expend energy even as they attempt to fulfill their energetic requirements. According to optimal foraging theory organisms are ultimately energy-limited and, since energy conserved while foraging can be applied to other important activities such as mating or predator avoidance, animals should benefit from choosing energy-efficient routes. Thus, natural selection should favor efficient behaviors as this would increase an animal's genetic fitness. In an application of optimal foraging theory to animal behavior, Kamil and Roitblat (1985) present life as a maximization problem in which organisms are challenged to maximize the rate of rewards among competing demands. It is therefore expected that animals should have evolved some mechanism for minimizing distance to reach food resources.

The Traveling Salesman Problem (TSP) is a theoretical mathematical problem consisting of choosing a minimum distance path through a series of destinations or nodes and then returning

to the origin, much like a traveling salesman might choose a path through a series of cities before returning home at the end of the day. The problem is in a category of difficult problems known as NP-complete (Nondeterministic-polynomial Complete) (Wilf, 1994). The amount of time required to find a solution to a NP-complete problem such as the TSP is greater than any polynomial expression of the number of cities in the tour. This means that finding a least-distance solution may require an exhaustive search through all the possible routes. An exhaustive search is significantly restrictive with large problem sets, as the number of possible solutions to a TSP is equal to $(n-1)!/2$, with n equal to the number of cities in the tour. However, approximation algorithms for the TSP can find approximate solutions to it and other optimization problems more quickly. The complete designation of the TSP means that all NP-complete problems reduce to the same basic problem. Therefore, if it can be determined that an algorithm exists to solve any one NP-complete problem in polynomial time, an algorithm exists for all NP-complete problems. Likewise, if it can be determined that no algorithm exists to solve any one NP-complete problem in polynomial time, no algorithm exists for any of them (Wilf, 1994). As such, the TSP has been intensely studied in the fields of computer science and mathematics (e.g., Applegate, Bixby, Vasek, Chvátel, & Cook, 2006).

Despite the complexity of creating an algorithm to solve the TSP, humans in experimental scenarios find optimal or near-optimal routes where simple heuristics often fail (i.e., $n \leq 60$) (MacGregor & Ormerod, 1996). The ability to solve the TSP and other optimization problems has also been found to correlate with cognitive processing speed, fluid intelligence, and visuo-spatial ability in humans (Burns, Lee, & Vickers, 2006). Known strategies that produce efficient routes for the TSP include the nearest neighbor, convex hull, and crossing avoidance models. The single heuristic of the nearest neighbor model assumes that the traveler always

chooses the next closest node in the experimental set, and the solutions from this model rank high in terms of efficiency. However, although the results of the nearest neighbor model do reduce distance traveled, they do not take into account the global problem set and tend to produce results that are less efficient than human performance (Ormerod & Chronicle, 1999). The convex hull strategy refers to creating an imaginary hull around the boundary points of the problem set, and entering between boundary points to reach the interior points of the set. This heuristic more closely approximates human performance on the TSP. Crossing avoidance, another distance-reducing strategy involves avoiding crossing over previously traversed routes. This heuristic has been proposed as a less complex cognitive strategy that yields routes resembling the convex hull solutions (van Rooij, Stege, & Schactman, 2003). However, human performance is more efficient than solutions produced by the crossing avoidance heuristic alone (MacGregor, Chronicle, & Ormerod, 2004).

A model of human performance on the TSP proposed by MacGregor, Ormerod, & Chronicle (2000) was found to quantitatively and qualitatively approximate routes generated by human participants. This model combined known strategies such as the nearest neighbor and convex hull models. For humans, Macgregor and Ormerod found the complexity of Traveling Salesman tasks increased with the number of nonboundary point, not with the total number of points in the problem set (1996). In the foveating pyramid model of the TSP (Pizlo, Stefanov, Saalweachter, Li, Haxhimusa, & Kropatsch, 2006) the focal point of the model moves sequentially through clusters of nodes in the problem set. The theoretical basis for this model is the decreasing visual acuity and attention at increasing distances from the focal point of the fovea of the human eye. In this model performance declines (i.e., tour lengths increase) slowly as the number of cities increase. A strength of this model is that it solves the TSP as humans do,

sequentially, unlike the MacGregor-Ormerod model which solves the TSP from its perimeter inward.

Human proficiency on the TSP may reflect selection for an ability to find least distance routes. However, it is also plausible that natural selection may have favored general spatial intelligence rather than an ability to minimize routes. Chronicle, MacGregor and Ormerod (2006) tested the hypothesis that human proficiency on the TSP reflected an inherent capacity to minimize distance by asking participants to find least-distance and greatest-distance routes between a series of points. Humans were significantly better at finding short routes than finding long routes, supporting the hypothesis of an inherent ability to route minimize.

Rats (*Rattus norvegicus*; Long-Evans) performing a simplified version of the TSP were shown to use a distance reducing strategy that resembled the nearest neighbor model (Bureš, Burešová, & Nerad, 1992). When performing a simplified version of the Traveling Salesman task in which a reward was received only after visiting all of a series of six to eight goal sites, rats took the shortest route in $20.2 \pm 4.0\%$ of trials, and the second-shortest route in $20.7 \pm 4.0\%$ of trials. In addition, their efficiency was inhibited by drugs (i.e., ketamine and scopolamine) previously demonstrated to interfere with working memory of rats in a radial maze. Presumably, the decrease in efficiency following the administration of these drugs was related to rats' inability to recall previously visited goal sites.

Gibson, Wasserman, & Kamil (2007) studied the performance of humans and pigeons (*Columba livia*) in finding efficient routes between a series of points. Traveling Salesman tasks of three, four, or five nodes were presented in a single horizontal line on a computer screen. The subjects were required to click all nodes using a mouse, or in the case of the pigeon, by pecking the screen. The TSP was considered one-way, as subjects were not required to return to the start

node in order to complete the trial. Human participants were more efficient than a Monte Carlo model for a random solutions. People were also more efficient than the nearest neighbor model, however less efficient than the optimal least distance route. Pigeons were more efficient than the Monte Carlo model, yet less efficient than the nearest neighbor model. Yet, when required to choose routes that were in the top 66% of all possible solutions, the pigeons learned to perform more efficiently and their routes became more comparable to the nearest neighbor model solutions.

Previous studies of primate ranging patterns have demonstrated that monkeys and apes appear to minimize distance when foraging in the wild. Garber (1988) demonstrated that tamarin monkeys (*Saguinas mystax* and *Saguinas fuscicollis*), like other non-primate nectar foragers (e.g., *Hymenoptera*: Ackerman, Messler, Lu, & Montalvo, 1982; Heinrich, 1976), exhibit a behavior resembling trap lining in which they appear to attempt to minimize the distance traveled between food patches when foraging, and travel in repeated straight-line paths between flowering trees (Garber, 1989).

Noser & Byrne (2007) demonstrated that wild Chacma baboons (*Papio ursinus*) use linear route segments and increase their velocity when traveling towards sparse fruit resources and waterholes during the dry season. Linearity and velocity of routes are common measures used to infer route minimization and spatial memory of ranging animals in the wild. Linear travel between goal sites increases efficiency and may indicate knowledge of the goal site's location. The increased velocity of travel segments as animals approach a goal may also indicate spatial memory of the goal location (Janson & Byrne, 2007). However, Noser & Byrne (2008) noted that linearity and velocity did not always mark goal-directed behavior since the baboons in this study had only one sleeping site, yet they approached this site slowly and indirectly. Janson

(1998) experimentally demonstrated that capuchin monkeys moved toward 15 feeding platforms more linearly than could be predicted by several random models of their movement. They also preferred the closest feeding platforms more frequently than a random model would predict. Janson and DiBitetti (1997) had also previously determined the distance at which the monkeys in this study could visually detect the feeding platforms, eliminating the possibility that the speed and linearity of routes and nearest platform choices could be explained by visual detection of the feeding platform (Janson, 1998). Similarly, black capuchin monkeys (*Cebus nigratus*) were shown to travel more rapidly and more linearly toward resource sites that had been previously visited (Presotto, 2009).

In an experimental context, Menzel (1973) examined the route efficiency of juvenile chimpanzees (*Pan troglodytes*) in a simulated foraging environment and demonstrated that chimps are capable of efficient foraging choices. In this experiment, a single chimpanzee was carried around an outdoor enclosure as food items ($n = 18$) were hidden by an experimenter using a random path. Following the hiding phase, the young chimpanzee was released into the outdoor enclosure with his group, and allowed to retrieve the hidden foods. The path the chimpanzee used to retrieve the hidden food was more efficient than random and did not resemble the path used when the items were hidden. In addition, the chimpanzees incorporated food preference in their route choice when preferred and non-preferred foods were available. In another experiment of this study, chimpanzees also maximized the rate at which they received the hidden rewards by first visiting the side of the enclosure with the greatest number of hidden food items when one side of the enclosure had more hidden items than the other.

Yellow-nosed monkeys (*Cercopithecus ascanius whitesidei*) demonstrated an ability to remember the locations of hidden food items and to retrieve those items using a distance-

minimizing route (MacDonald & Wilkie, 1990). In the first condition of this experiment, all eight of eight containers placed in an outdoor enclosure were baited with food. In a second condition, four of the eight containers were baited, and after a delay the monkeys were allowed to retrieve the food items from the same four containers. The third condition was similar, except in the retrieval phase, the four containers previously empty were baited with food. Yellow-nosed monkeys learned these contingencies and chose food retrieval routes that reduced travel distance. Conversely, gorillas (*Gorilla gorilla gorilla*) tested in a similar food search task did not use a distance-minimizing strategy between food containers (MacDonald, 1994). An adult male gorilla was released into an outdoor enclosure with eight opaque containers, four of which contained food. The gorilla was allowed to search until all four food items had been retrieved from the containers. After a 24-hour delay, the gorilla was released into the enclosure, and again allowed to search the containers for food. The subject learned the contingency when the containers baited on the previous day were rebaited on the following day. The subject also notably used some technique for quantity discrimination since, on every trial, after finding the four pieces of food, he ended his search. In a second phase of this experiment, a juvenile male was tested in a similar fashion. In this experiment the containers not previously containing food were baited during the testing phase. This gorilla also learned the locations of the hidden food items. However, in choosing routes to retrieve the hidden objects, neither gorilla used a least-distance strategy. The use of quantity discrimination by the adult gorilla may have been a strategy for minimizing energy expended during foraging.

The spatial memory and path efficiency of vervet monkeys (*Cercopithecus aethiops*) were tested in a simulated foraging task using baited opaque containers (Cramer & Gallistel, 1997). The monkeys observed from outside the experimental space as the containers were baited,

and were then released to retrieve the food. The foods were hidden in one of two configurations. In the diamond configuration, monkeys visited baited containers configured as the four vertices of a diamond. The start container of the vertex was rebaited after the food had been retrieved in one condition, and not rebaited in a second condition. In the rebaited condition, the optimal path was a diamond-shaped route through the four vertices, and returning to the start container. In the non-rebaited condition, the optimal path was a zigzag route through the four vertices. Vervet monkeys were found to choose their routes preferentially based upon the rebaiting of the start container. In the unequal sides configuration, the subjects visited six baited containers split unequally into four containers to one side of the start location and two containers to the other side. The monkeys were allowed to make a complete pass through all six food items, and yet, on every trial, they traveled first to the side of the array with four baited containers. Their choices reflect an ability to maximize the rate of reward as well as to remember the locations of the hidden food. In addition, the choice to maximize reward rate required the subjects to look ahead at least two choices into the future.

In a similar experiment using opaque baited containers, the search efficiency of capuchin monkeys (*Cebus apella*) was affected by the geometry of the search environment (DeLillo, Aversano, Tucci, & Visalberghi, 1998). Capuchins were more efficient in searching for hidden food items when the containers to be searched were arranged in a straight line or a circle, than when the search environment was a matrix configuration. The authors propose two explanations for the interaction effect of the search environment. The monkeys may have wished to minimize distance traveled while foraging. Alternatively, the use of the environmental cues of the search space might minimize the cognitive costs in remembering each previously visited container.

In previous tasks, capuchin monkeys have demonstrated a bias for coding the location of hidden items using an egocentric frame of reference. Poti (2000) tested the reference frames of four capuchin monkeys (*Cebus apella*) in a test of spatial memory. In this study, a food item was hidden within one of two identical opaque containers placed on a rotating platform. The monkeys were stationary, yet they had visual access to the rotating platform while the food item was being hidden. The platform was then obscured and rotated (90, 180, 270, or 360°). In Experiment 1, a landmark close to the correct container indicated the location of the hidden food item in every trial. In Experiment 2, the monkeys observed the placement of the food in a container near to or far from the landmark cue. This experiment required the monkeys to learn a more complex rule concerning the location of the food item. That is, the landmark might have indicated the presence or the absence of food. Three scales of reference frame were available to the monkeys in these experiments. The self-referenced frame would dictate that the monkey used the location of the container in relation to himself (i.e., his left or his right) in making the choice. The small-scale external reference frame would indicate the location of the container in relation to the landmark. The large-scale external reference frame would indicate the location of the container in relation to other objects in the room.

In experiment 1, capuchins solved the task in all degrees of rotation, although they experienced the greatest difficulty with the 180°-rotation condition. This result indicates capuchin monkeys are able to overcome the use of the self-reference frame and to use the small-scale external frame in this task. The difficulty with the 180°-rotation condition most likely relates to the bias that capuchin monkeys have for using the self-referenced frame. In other words, when the two containers were presented in a left-to-right arrangement during the baiting phase, and then rotated 90°, the container arrangement changed dramatically, and the subjects

were able to use the small-scale external frame of reference provided by the landmark cue. However, when the containers were rotated 180°, the container arrangement was very similar to the baiting phase, and the bias toward using the egocentric frame of reference overcame their use of the landmark. (Potì, 2000)

In Experiment 2, the monkeys were unsuccessful in all test conditions (90°, 180°, 270°, and 360°). This failure persisted with invisible rotations even after the experimenters conducted a visible rotation phase, giving the subjects an opportunity to observe that the rotation of the platform does not impact the relation between the landmark and the baited container. If the subjects had applied a flexible allocentric association of the reward location with the landmark, the monkeys would have succeeded in this task. The possibility exists that the monkeys used an allocentric frame of reference at the wrong scale. Instead of relating the position of the reward container to the position of the proximal landmark, the monkeys may have associated the position of the reward container to the other larger scale landmarks in the experiment room. This use of the incorrect scale of allocentric reference frame might have led to the failures of the monkeys in this experiment. If the monkeys were using the incorrect scale of allocentric reference frame in this study, it may indicate that capuchins prefer to use the external reference frame that aligns with their egocentric reference frame. Either through their choice of the egocentric reference frame or the allocentric frame at the scale that concurred with their egocentric frame, these results indicated a predisposition of capuchins toward use of the egocentric frame of reference (Potì, 2000).

In a previous experiment, capuchin monkeys (*Cebus apella*) from the Primate Cognition and Behavior Laboratory were shaped to use a joystick-controlled laser apparatus to indicate desired food items at a distance (Stone, 2008). The individuals trained in this study participated

in the current experiment. The shaping procedure for this apparatus required a gradual transition away from computerized stimuli, as subjects had previous experience with joystick-controlled computerized tasks. In the baseline condition of the shaping procedure, stimuli were presented on a CRT-monitor. Capuchin subjects manipulated a joystick to control a cursor and received a reward when the cursor came in contact with the goal stimulus on the screen. This gradually progressed from stimuli presented on a CRT-monitor to similar stimuli being projected on an open wall, and then to a combination of laser pointer and computerized stimuli. Subjects were required to complete the tasks at increasing distances from the stimulus array, and goal locations were transitioned from computerized stimuli to real food items at a distance. The final stages of the shaping procedure used real food items and the laser pointer with no computerized stimuli. Following the shaping procedure, the subjects used the laser pointer to indicate desired food items of different sizes, types and distances from self. Capuchins in this study preferred proximal food items to foods placed at a greater distance from themselves, demonstrating their ability to judge the distance between food and self, egocentrically. This incorporation of distance into food preference is notable since subjects were not required to locomote to the food's location. The experiment did not examine, however, the efficiency of the routes subjects used to retrieve the desired food items.