CAPUCHIN MONKEYS (CEBUS APELLA) USE A LASER POINTER TO INDICATE DISTAL OBJECTS

by

BRIAN WILLIAM STONE

(Under the Direction of Dorothy Fragaszy)

ABSTRACT

Given the limitations inherent to two popular cognitive testing paradigms used with captive non-human primates – reaching tasks and computerized tasks – a complementary methodology that circumvents these limitations would be helpful in increasing ecological validity. We trained monkeys to use a joystick-controlled laser pointer to indicate distal objects and locations. Subjects were five male capuchin monkeys (Cebus apella), two of which acquired skillful control of the laser pointer in experiment 1 and demonstrated efficient control in numerous generalized conditions in experiment 2. In experiment 3, subjects used the laser pointer to make genuine choices between an array of distal food items varying in terms of type, size and distance. Subjects failed to show evidence of during-task gaze alternation, suggesting the laser pointer was not used as an imperative point. Finally, we discuss the applications and limitations of the laser pointer setup, including fruitful areas of future testing.

INDEX WORDS: Laser pointer, Indicating, Cebus, Primates, Foraging distance

# CAPUCHIN MONKEYS (CEBUS APELLA) USE A LASER POINTER TO INDICATE DISTAL OBJECTS

by

BRIAN WILLIAM STONE

B.S., Washington State University, 2006

B.A., Washington State University, 2006

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

2008

CAPUCHIN MONKEYS (CEBUS APELLA) USE A LASER POINTER TO INDICATE DISTAL OBJECTS

by

BRIAN WILLIAM STONE

Major Professor: Dorothy Fragaszy

Committee: Irwin Bernstein
Jonathon Crystal

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
August 2008

# DEDICATION

To my family, my friends, and my love, for their infinite support. To my mentor Dorothy Fragaszy, for guidance and patience. To Charles Menzel and Theodore Evans, for inspiration and collaboration.

# ACKNOWLEDGEMENTS

Charles Menzel and Theodore Evans at the Language Research Center of Georgia State University inspired this study, and our labs collaborated on simultaneous replication with different subjects and slightly different conditions. Extensive undergraduate testing assistance was provided by Jennifer Benoit and Christopher Bates. Thanks to Dorothy Fragaszy, Irwin Bernstein and Jonathon Crystal for comments on an earlier draft. Thanks to the University of Georgia facilities and lab staff. Work supported by HD38051 and HD056352 to Georgia State University.

# TABLE OF CONTENTS

# SECTION 1

# INTRODUCTION

Primates foraging in the wild must choose among many potential resources and paths located at a significant distance from the forager. This involves cognitive processes such as memory, spatial perception and navigation, and distance may interact with all of these. Remembering a relatively large number of dispersed locations is crucial to navigating a large environment with varying but predictable food patches (Di Fiore & Suarez 2007; Cunningham & Janson 2007). Perceiving and choosing among resources and environmental layouts can take place visually even before the animal physically enters and explores the area (Dominy et al. 2001). Wild capuchins, for example, visually detect novel food locations at ranges up to 20 or 30 m when traveling at normal rates, and alter their path accordingly (Janson & Di Bitetti 1997). Baboons, spider monkeys and woolly monkeys rely on out-of-reach but in-sight topographical features of the environment to orient during travel and to choose among familiar or alternate paths (Noser & Byrne 2007; Di Fiore & Suarez 2007). Selecting between food choices may involve weighing not only the type or quantity of a food, but also how far away it is (Janson 1996, 2000, 2007; Bicca-Marques 2006). Furthermore, the distance at which resources are visually detected varies across resource types (Noser & Byrne 2007) and sizes of the same resource (Janson & Di Bitetti 1997), further supporting a distance-payoff interaction. When weighing dimensions such as size, food type and distance during foraging, primates tend to optimize their food intake against the energetic costs of their foraging (Perry & Pianka 1997). This also implies a weaker claim, that they are generally rational foragers, insofar as they tend to choose the larger, closer or more-preferred type of food (all else being equal, including energy expenditure) when multiple options are available (Perry & Pianka 1997; Janson & Di Bitetti 1997).

Unfortunately, testing choice, memory, spatial perception and navigation in captive primates often leaves out distance as a relevant variable. For example, reaching tasks typically involve the subject extending an arm toward one of two or more objects placed nearby, within or just out of reach (e.g. Barth & Call 2006; Anderson et al. 2007; Genty & Roeder 2007). They have been used to study food and object choice (Vick & Anderson 2000; Padoa-Schioppa et al. 2006; Genty & Roeder 2007), as well as memory in both simple circumstances (Harlow et al. 1932; Funahashi et al. 1993) and more complicated situations involving rotational and transpositional displacements of a nearby linear array (Beran et al. 2005; Barth & Call 2006). As can be expected, reaching tasks almost invariably take place within the close distance that a subject can extend its arm through a testing cage (Table 1), usually to select an item from an equidistant array of nearby items. The limited distance to the items in reaching tasks has tended to keep the number of items or item locations simultaneously presented relatively low because only so many items easily fit in reach in front of a subject. Likewise, those items tend to be placed close together. That is, not only is the distance to the items small, but the distance between them is small (Table 1).

Similar limitations are common to computerized tasks, which involve directly touching a monitor or controlling a cursor on one (with a joystick, for example). This paradigm has been used to study choice (Washburn et al., 1991), memory (Hopkins & Washburn 1994; Inoue & Matsuzawa 2007), spatial perception (Rumbaugh et al. 1989; Iversen & Matsuzawa 2003; McGonigle et al. 2003), and navigation (Washburn 1992; Fragaszy et al. 2003). Unfortunately, all tasks involve perceiving and manipulating (directly by touch or indirectly by joystick) items which are up-close. Thus the distance to the stimuli is short, and the screen on which they are presented limits both the size and spread of the items (Table 2). No monitor can match the distances of the full three-dimensional (3D) world. The largest screen used so far was 254 cm diagonal (Sato et al. 2004), far short of the natural distances primates deal with in perceiving, remembering and choosing among resources and spatial features (Garber 1989; Di Fiore & Suarez 2007; Janson 2007).

Table 1 Representative examples of the number of, and the distance to and between, items or item locations in reaching studies.

| STUDY | SPECIES | # ITEMS OR LOCATIONS | DIST. TO ITEM/LOCATION | DIST. BETWEEN |
|---|---|---|---|---|
| Anderson et al. 2007 | Squirrel monkeys | 2 | 20 cm, just beyond reach | 22 cm |
| Barth & Call 2006 | Great apes | 3 | Within reach | < 36 cm |
| Beran et al. 2005 | Chimpanzees | 3, 5 or 7 | Within reach | 5 cm |
| Blaschke & Ettlinger 1987 | Rhesus monkeys | 2 | Just beyond reach | 30 cm |
| Genty & Roeder 2007 | Black/brown lemurs | 2 | Within reach | < 70 cm |
| Harlow 1932 | Apes, monkeys, a lemur | 2 | < 8 cm, within reach | 30 cm |
| Kaminski et al. 2004 | Great apes | 2 | Beyond reach | 50 cm |
| Mitchell & Anderson 1997 | Capuchin monkeys | 2 | Just beyond reach | 30 cm |
| Padoa-Schioppa et al. 2006 | Capuchin monkeys | 2 | Within reach | < 30 cm |
| Vick & Anderson 2000 | Capuchin monkeys | 2 | Within reach | 20 cm |

Table 2 Representative examples of the distance to computer screen, maximum number of distinct items presented on-screen (including any cursor controlled by subject), and screen size (diagonal) in computer-based studies. NA means the measurements are not available for that study.

| STUDY | SPECIES | DIST. TO SCREEN | # ITEMS | SCREEN SIZE |
|---|---|---|---|---|
| Andrews 1993 | Squirrel monkey | 8.9 cm | 2 | 20.5 cm |
| Hopkins et al. 1989 | Chimpanzees, rhesus | 20 cm | 2 | 33 cm |
| Hopkins & Washburn 1994 | Rhesus monkeys | 20 cm | 3, or 2 in maze | 33 cm |
| Inoue & Matsuzawa 2007 | Chimpanzees | NA, in reach | 9 | NA |
| Iversen & Matsuzawa 2003 | Chimpanzees | 30 cm | 2, or 2 in maze | 53 cm |
| Kawai & Matsuzawa 2000 | Chimpanzee | NA | 5 | NA |
| Leighty & Fragaszy, 2003 | Capuchin monkeys | 25 cm | 2 | 34 cm |
| McGonigle et al. 2003 | Capuchin monkeys | NA, in reach | 9 | 36 cm |
| Rumbaugh et al. 1989 | Rhesus monkeys | 20 cm | 2 | 32 cm |
| Sato et al. 2004 | Japanese monkeys | 57 cm | Virtual maze | 254 cm |
| Smith et al. 1998 | Rhesus monkeys | 33 cm | 4 | 20 cm |
| Vauclair & Fagot 1993 | Guinea baboons | 47 cm | 2 | 36 cm |
| Washburn et al. 1989 | Rhesus monkeys | 20 cm | 9 | 33 cm |
| Washburn et al. 1991 | Rhesus monkeys | 20 cm | 6 | 33 cm |

Menzel (2005) presents a new approach that circumvents the distance limitations of reaching and computerized tasks. He used a single captive chimpanzee (*Pan troglodytes*) subject that had extensive experience with a lexigram system for communicating with humans. The subject mastered use of a joystick to control a tripod-mounted laser pointer in order to indicate targets in the distal environment. Even outdoors in a full 3D environment with an area of potential error over 100 square meters (not including the possibility of moving the dot up into the sky), she could pinpoint targets with incredible spatial specificity. Extending previous results with raised-arm pointing (Menzel 1999), the laser study involved Panzee witnessing an experimenter hide items in the forest around her outdoor cage. After a delay ranging from a few minutes to over 90 hours, and without prompting, Panzee recruited a naive experimenter, led the person outdoors, and subsequently used the laser to pinpoint the hidden item (always within 1 m, usually within 15 cm), which the experimenter retrieved.

As the laser pointer setup has only been used with one subject so far, it is possible that other captive primates – especially those without such a special rearing and training history (Brakke & Savage-Rumbaugh 1995, 1996) – will not be able to use a joystick-controlled laser pointer to target items in the distal environment. However, given the success of many primate species on previous tasks using a joystick interface, and given Panzee's immediate success with the laser pointer, we hypothesize that the ability to control a laser pointer is common to all primates. Capuchin monkeys make an ideal candidate for testing the hypothesis, as they are highly proficient tool users both in captivity and the wild (Fragaszy et al. 2004), and some have already mastered using a joystick to move a cursor to a target in a wide variety of computerized tasks (Fragaszy et al. 2003).

Thus we predicted that joystick-trained capuchin monkeys would use a joystick to move a laser dot onto a target in the full 3D environment. More specifically, we predicted that they would consistently and efficiently contact both generic flat targets as well as 3D targets such as food. Furthermore, given that acquiring the initial computerized joystick skill required a lot of training and shaping for these monkeys (Leighty & Fragaszy, 2003), and given the differences between tasks (especially added distance to the stimuli and removal of the computer monitor), we predicted that some shaping would be required to bridge the gap between computer-based joystick tasks and the laser pointer. These predictions were tested in experiment 1.

Further, we hypothesized that the laser pointer would serve not just as a cursor for simple instrumental responding (i.e. move cursor to an arbitrary target for reward), but would function as a proxy for physically contacting an object; thus, given food as a target, we hypothesized that their use of the cursor would model foraging behavior. We predicted, then, that their pattern of responding when presented with multiple simultaneously-available food items in the distal environment would be rational.

That is, they should prioritize the items according to some salient dimensions such as food type, size and distance away. We predicted that they would select larger items over smaller (all else being equal), more-preferred food type over less-preferred (all else being equal), and near items over far (all else being equal). In other words, a rational forager would not consistently select an item that is worse than an alternative along some dimension(s), unless it was better along some other dimension(s). On the other hand, if the monkeys were not choosing rationally among the items as food resources, but instead simply treated them as arbitrary targets to be contact for reward, then their pattern of responding would be different. For example, they should not immediately demonstrate a bias toward targeting higher quality items (given the other dimensions are controlled for). In that case, some irrational choices would be expected regularly; they should choose a less-preferred food type about as often as the more-preferred food type, given equal size and distance. Thus, rational choice and simple instrumental responding provide different predictions, and we tested these predictions in experiment 2.

Thus, the purposes of this study are two-fold: (1) to test whether capuchin monkeys can use a laser pointer to target distal objects in the environment around them; (2) to test whether they use the laser pointer to make rational choices among food resources varying in size and type, and available at different distances from the subject.

# SECTION 2

# EXPERIMENT 1

This experiment tests two predictions: (1) joystick-trained capuchin monkeys will adapt that skill to use a joystick-controlled laser pointer to target objects in the general 3D environment; and (2) some shaping will be necessary, given the differences between familiar computerized tasks on a nearby monitor and laser use at a further distance with no monitor.

## Method

### Subjects and housing

The subjects of this study were five male tufted capuchins (*Cebus apella*), age 15-22: Leo, Nick, Solo, Xavier and Xenon. They were members of four pairs housed in indoor cages at the University of Georgia, and were fed a diet of monkey chow and mixed fruit. All subjects had previous experience over a 10-year period with various computerized joystick tasks displayed on a nearby CRT monitor, and all had participated in a variety of other behavioral experiments.

### Apparatus

See Table 3 for measurements of apparatus described below. We tested the subjects in a small room near the home cage or in the adjoining hallway. During testing, the subject was inside a mobile testing cage made of clear acrylic sides with a mesh floor. The subject sat on a perch while working. An armhole (5.8 cm diameter) centered on the front Plexiglass panel allowed access to one of two joysticks which slid into place 10 cm in front of the armhole. The joystick in early, computer-based conditions was a Kraft KC3 joystick, while later, laser-based conditions used a metal joystick handle attached to the wired remote control for a motorized pan-tilt head. All tasks involved the subject moving a small red cursor to a larger stationary target. The exact dimensions and nature of the cursor, target and background varied across the conditions (Table 3).

For computer-based conditions, we presented a program called Geomjoy, developed at the Language Research Center of Georgia State University. The program presented stimuli on a black background on a CRT monitor at eye level or it projected the stimuli at eye level on a nearby wall. For the computer task, subjects used the joystick to move a red cursor to a green target for a small food reward (a quarter of a peanut or a half of a small raisin). As the cursor moved, speakers behind the monitor provided continuous beeps, and when the cursor contacted the target the speakers played a louder beep. For each trial, the target appeared near the edge of the screen, placed randomly among eight positions: the middle top of the screen, the middle bottom, the middle left, the middle right or one of the diagonal corners of the screen. The cursor started directly opposite the target (e.g. upper left cursor for lower right target).

For later conditions, the joystick controlled a red laser pointer attached to the top of the motorized pan-tilt head. Deflection of the joystick in any of eight directions (up, down, left, right or diagonal) rotated the pan-tilt head on top of a camera tripod such that the laser dot moved in the corresponding direction on whatever surface it was aimed at. Except for the final condition, the target in laser conditions consisted of a flat circle of green cardboard; the final condition used a sticky, translucent candy. Unless mentioned otherwise, the laser cursor always started in a fixed, central position and the target was placed pseudo-randomly within the working area described for each condition, at varying distances and directions from the cursor, and never in the same quadrant more than twice in a row.

The Geomjoy program recorded time to completion for computer trials, while experimenters measured laser trials with a stopwatch or coded the time later from video. We video-taped all laser trials. Cursor speed on the Geomjoy program was constant, while the speed of the laser dot increased with the distance to target (Table 3). Additionally, the changing battery level within-session decreased the laser speed at a given distance a negligible amount. Given the variation in speed, trial completion times for tasks at different distances are not necessarily directly comparable.

The subject's cage mate was present for all trials, but stayed in a small transport box behind and to the side of the testing cage. Cage mates were typically silent throughout the task.

Table 3 Description and measurements of experiment 1 apparatus.

| APPARATUS | DESCRIPTION/MEASUREMENTS |
|---|---|
| Testing Room | 3.2 x 2.9 m floor space; pale cream paint on cement wall |
| Hallway | 2.2 x 12.2 m floor space; pale cream paint on cement wall; grey cement floor |
| Mobile Testing Cage | 64 x 47 x 78 cm cage; sitting on an 84 cm tall cart; perch 30 cm above cage floor |
| CRT Interface | Kraft KC3 joystick on a Windows 98 computer and 33 cm diag. CRT monitor (CRX) |
| Projection Interface | Kraft KC3 joystick on a Windows 98 computer and 64 cm diag. projection (Epson PowerLite 50c) |
| Laser Interface | Metal joystick handle 5 cm long x 0.25 cm diameter; MP-101 motorized pan-tilt head (Bescore) |
| Computer Cursor | 0.9 cm diameter red circle on CRT; 1.8 cm diameter red circle projected |
| Computer Target | 2.7 cm diameter green circle on CRT; 4.5 cm diameter green circle projected |
| Computer Cursor Speed | 3 cm/s left-right, 3.7 cm/s up-down |
| Laser Cursor | Red dot 0.6 cm diameter when 110 cm from surface; 1.3 cm diameter when 11.5 m from surface |
| Laser Target | Most conditions: flat green cardboard circle, 3.8 cm diameter; last condition: 1 $cm^3$ sticky candy |
| Laser Cursor Speed | At 110 cm: 22 cm/s left-right, 6 cm/s up-down; at 11.5 m: 100 cm/s left-right, 26 cm/s up-down |

## **Procedure**

Trials in all conditions began when the subject first displaced the joystick, and ended successfully when the cursor contacted the target (be it a computerized cursor/target or the laser dot contacting a physical target) within 180 s. Subjects failed a trial if the cursor did not contact the target within 180 s of first moving the joystick (TIME FAIL) or, in the case of the laser pointer, if the cursor left the relevant working area for greater than 15 seconds (OUT FAIL). For example, when target and cursor were on the wall in front of the subject, then moving the laser 90 degrees to the side so that it was completely out of sight counted as a fail, and we began a new trial.

All five subjects began on a baseline condition (labeled CRT 20) running Geomjoy on the familiar monitor located 20 cm away from eye level until they reached criterion (Fig. 2). Moving on to subsequent conditions required completing a session of 20 trials with at least 16 correct. Table 4 lists the distance to target, size of the working area in which the target could appear, and a brief description of all conditions. On subsequent testing days, some subjects received review trials of previously passed conditions before trying a new condition. Only the first successful session for any condition was used in the analysis.

Following baseline testing, we split subjects into two groups, independent of their baseline performance and prior to any other testing. These groups received a slightly different order of conditions (Fig. 1). A subset of the subjects (Leo, Nick, Solo) were immediately presented with the PROJECTION condition. This involved the subjects facing an area of open wall where the Geomjoy program was projected; the condition was otherwise identical to using a monitor (Fig. 3). That is, the boundary of the projection was also the boundary of the program, so subjects could not move the cursor beyond it. The darker background of the projection on the light wall potentially provided a screen-shaped contextual cue to the monkeys. This condition involved a significant increase in distance between the subject and the cursor-target area, and it removed the CRT monitor while otherwise retaining similar stimuli (same program, sounds, background color/shape, cursor color/shape, and target color/shape).

If these subjects met criterion in the first two sessions, we moved them on to the LASER/PROJECTION condition described below. If they failed to meet criterion on the first two sessions, or if they completely failed to engage the joystick for three trials in a row, then we presented them with a series of conditions aimed to shape joystick use at a distance. We gave the remainder of the subjects (Xenon and Xavier) these distance shaping conditions directly after baseline so as to avoid experience with the projection setup until after mastering the distance aspect (Fig. 1).

For distance shaping, we incrementally pulled the subject's cage back from the computer monitor while keeping everything else the same as the baseline condition (presenting the Geomjoy task using the same joystick). These conditions were CRT 35, CRT 50, CRT 80, and finally CRT 110 (Fig. 4), corresponding to how many cm back they were from the screen. This gave the subjects experience with completing joystick tasks at the distance used in later conditions.

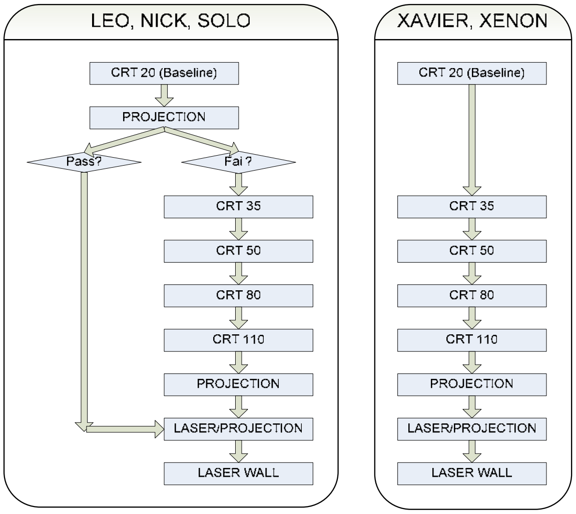

Fig. 1 Condition order for laser acquisition (exp. 1)


Fig. 2 CRT 20 condition


Fig. 3 PROJECTION condition


Fig. 4 CRT 110 condition

Table 4 Measurements and brief description for experiment 1 conditions. Distance is between subject and target. Work area corresponds to the area in which the target could be placed (see text).

| CONDITION | DISTANCE | WORK AREA | BRIEF DESCRIPTION |
|---|---|---|---|
| CRT 20 | 20 cm | 33 cm CRT | Baseline; computer running Geomjoy on familiar, up-close monitor |
| CRT 35 | 35 cm | 33 cm CRT | Same as baseline but pulled back |
| CRT 50 | 50 cm | 33 cm CRT | Same as baseline but pulled back |
| CRT 80 | 80 cm | 33 cm CRT | Same as baseline but pulled back |
| CRT 110 | 110 cm | 33 cm CRT | Same as baseline but pulled back |
| PROJECTION | 110 cm | 64 cm diag. | Geomjoy program projected on an empty wall space |
| LASER/PROJECTION | 110 cm | 64 cm diag. | Laser and flat green target on projected blank background on wall |
| LASER WALL | 110 cm | 110 x 75 cm* | Laser and flat green target on empty wall space |
| FLAT | 85 cm diag. | 58 x 38 cm | Laser on a flat tray below and in front of test cage |
| IRREGULAR | 170 cm | 3.75 x 1 m* | Laser on large wall space, including an irregular room corner |
| DISTANCE 1 | 3.2 m | 0.75 x 2.1 m | Laser aiming out of test room onto opposing hallway door |
| DISTANCE 2 | 6.1 m | 2.1 x 1.2 m | Laser on wall at far end of hallway, with subject in hallway too |
| DISTANCE 3 | 11.5 m | 2.1 x 1.2 m | Laser on wall at far end of hallway, with subject in hallway too |
| GRID CONTROL | 115 cm | 2.9 x 1.2 m* | Laser to bait randomly affixed to one among a grid of 20 locations |

*See Fig. 5 for a depiction of the testing room layout for these conditions.

Subjects meeting criterion on all of the distance conditions moved on to PROJECTION. This included any of the subjects who received earlier PROJECTION trials, if they failed initially and had to do distance shaping. Passing the PROJECTION condition led to the LASER PROJECTION condition. In the LASER PROJECTION condition, we projected a blank grey background of the same size onto the wall area. The laser dot was centered in the grey area and the experimenter placed the green cardboard target circle within the projection area, after which the subject was given access to the laser joystick. Unlike the cursor in previous conditions, the laser dot could freely move out of the projected background. If the subject moved the dot out of that area for greater than 15 seconds, we considered the trial an OUT FAIL and began a new trial. A second experimenter using a stopwatch measured time the dot spent outside of the boundary, and the primary experimenter later verified these times on video.

Subjects succeeding at the LASER PROJECTION condition moved on to the LASER WALL condition. We removed the projected background, and the entire open area of wall became a space on which the target could be placed and the laser dot could move. If the subject moved the laser dot out of the working area, the dot was often obscured from view; thus if the subject moved the dot out for more than 15 seconds without returning into the working area, we considered the trial an OUT FAIL. We considered subjects that completed this condition to have acquired use of the laser pointer (albeit in a limited context) and moved them on to a set of generalization conditions.

First, for the FLAT condition we put the target on a flat tray 78 cm above the ground, the center of which was 60 cm below eye level and 60 cm in front of the testing cage (Fig. 6). Again, the laser cursor started in the center and was not allowed to travel outside of the tray surface for more than 15 s.

The next condition, IRREGULAR, tested the subjects on an irregular, 3D surface. We aimed the laser at a corner of the testing room where the wall jutted out at the corner (Fig. 7). The working area extended across both adjacent walls as well as the jutted out wall area, and it included the room door.

Subjects then moved on to three long-distance conditions. DISTANCE 1 directed the laser out the open door of the testing room onto the opposing hallway door, with 3.2 m between subject and target. For the DISTANCE 2 condition we moved the subject's testing cage into the hallway outside the testing room to allow for distance not possible in the normal testing room. We placed the target on the far wall 6.1 m away. In the DISTANCE 3 condition we used the same working area, but located the subjects 11.5 m away from the target and cursor (Fig. 8). Because of the increased speed of the cursor and decreased relative size of the target at this distance, we gave a 0.6 cm grace area around the target which counted as contacting it.

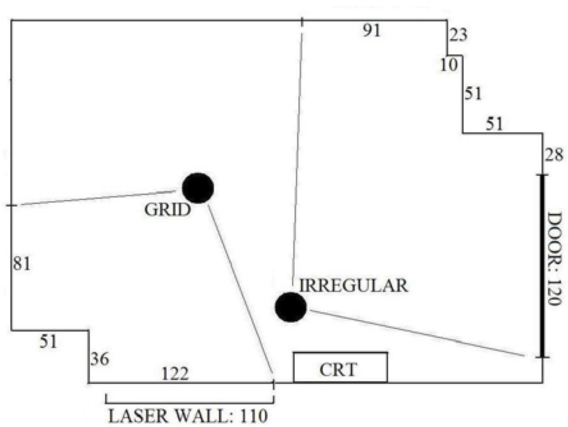


Fig. 5 Testing room dimensions (in cm)

Fig. 6 TRAY condition

Fig. 7 IRREGULAR condition

Fig. 8 DISTANCE 3 condition

Finally, we implemented a control condition to establish that performance was not due to random joystick movement. For this condition, GRID, we set out a grid of 20 locations, five across by four down, each marked as a black dot on the wall. We separated each of the 20 locations from its neighbors by 53 cm horizontally or 22 cm vertically, and staggered the locations on the bottom and second-from-top levels rightward by 12 cm to minimize accidental contacts (Fig. 9). Over 20 trials, we selected one of the locations randomly, without replacement, and baited it by affixing half of a sticky, translucent candy to the wall (approximately 1 x 1 x 1 cm). To complete a trial, subjects had to contact the candy with the laser within 180 s. If they did so, we immediately provided verbal feedback ("good boy") and gave them the candy from the wall. We considered the trial a failure if the subject failed to contact the target in 180 s, or moved the dot within 1 cm of any five of the unbaited locations (including repeats of the same location). The laser dot always started in the same position near the center of the grid. Furthermore, we scored successful trials by video according to how many and which unbaited locations the laser came within 1 cm of before contacting the bait. Moving directly to the baited location, and contacting zero unbaited locations or minimal adjacent ones, would suggest efficient, non-random targeting. This 20-trial test was repeated twice for each subject, on separate days.

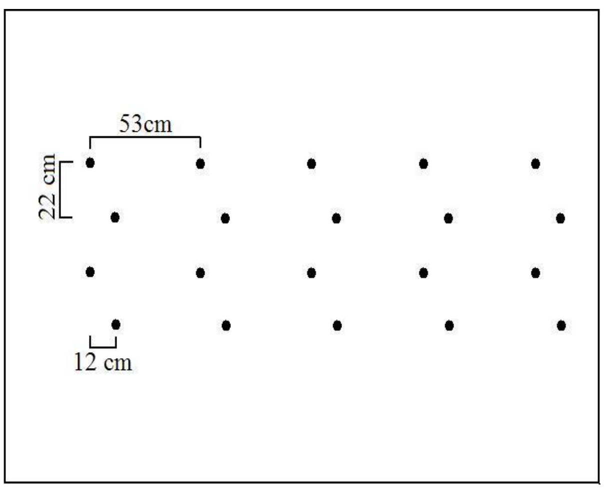


Fig. 9 GRID condition layout. Dots represent potential bait locations.

**Analysis**

We report the number of 20-trial sessions required to reach criterion, as well as the number of successful trials per session. We also present the median time to completion for all successful trials in the first successful session per condition. For the last condition, GRID, we applied a binomial test to test against the theoretically expected results if the locations were contacted randomly.

The primary experimenter coded laser movement times from video, and a second experimenter coded 289 trials for reliability. Mean deviation between coders was 0.61 s, less than 7.8% of the mean completion time on those trials. The primary experimenter's times were used for analysis.

**Results**

All subjects completed the baseline condition on their first session. None of the subset of subjects that received PROJECTION immediately after baseline completed any trials in the first session, and they all completely stopped contacting the joystick by the third trial. Thus we moved all five subjects on to the distance shaping conditions. All subjects completed each distance shaping condition on the first session, with the single exception of Xavier at 80 cm (completed on the second session). Table 5 lists the session on which each subject succeeded, how many trials they passed each session, and the median trial time measured from initial displacement of the joystick until successful completion.

Every subject moved on to the PROJECTION condition after distance shaping. Three subjects – Nick, Solo and Xavier – failed to complete the first PROJECTION session. Nick succeeded on a single trial by holding the joystick down without looking at the wall. All other trials for these three subjects were failures due to TIME. By the tenth trial, all three subjects completely stopped contacting the joystick for at least three trials in a row, so these subjects did not test any further.

Two subjects – Xenon and Leo – succeeded at the PROJECTION condition on their first session. Xenon required two sessions to pass the LASER/PROJECTION condition, due to five failures in the early trials of the first session. Leo started one session, in which he failed his first trial and completed the next two. A technical malfunction rendered the projector inoperable immediately after the third trial. However, given his quick and efficient completion of trial three, we presented him with LASER WALL condition. He immediately succeeded on the first session. Xenon also succeeded on his first session of the LASER WALL condition.

Table 5 The session number in which criterion was met for each condition for each subject, with number of successful trials for each test session in parentheses. Median time to completion taken from all successful trials in the first successful session.

| CONDITION | LEO | NICK | SUBJECT<br>SOLO | XAVIER | XENON |
|---|---|---|---|---|---|
| CRT 20 (Baseline) | | | | | |
| Successful Session | 1 (20) | 1 (20) | 1 (17) | 1 (20) | 1 (20) |
| Median Time | 13 s | 10 s | 30 s | 11 s | 11 s |
| PROJECTION (Early) | | | | | |
| Successful Session | FAIL (0)* | FAIL (0)* | FAIL (0)* | ---- | ---- |
| Median Time | ---- | ---- | ---- | ---- | ---- |
| CRT 35 | | | | | |
| Successful Session | 1 (20) | 1 (20) | 1 (20) | 1 (20) | 1 (20) |
| Median Time | 10 s | 10 s | 11 s | 9 s | 13.5 s |
| CRT 50 | | | | | |
| Successful Session | 1 (20) | 1 (20) | 1 (20) | 1 (20) | 1 (20) |
| Median Time | 10 s | 9.5 s | 12.5 s | 13.5 s | 18 s |
| CRT 80 | | | | | |
| Successful Session | 1 (20) | 1 (20) | 1 (19) | 2 (13,19) | 1 (20) |
| Median Time | 10 s | 10 s | 11 s | 12 s | 10 s |
| CRT 110 | | | | | |
| Successful Session | 1 (20) | 1 (20) | 1 (20) | 1 (20) | 1 (20) |
| Median Time | 11.5 s | 10 s | 13 s | 21 s | 17 s |
| PROJECTION | | | | | |
| Successful Session | 1 (20) | FAIL** (1) | FAIL** (0) | FAIL** (0) | 1 (16) |
| Median Time | 12.5 s | 6 s | ---- | ---- | 14.5 s |
| LASER/PROJECTION | | | | | |
| Successful Session | *** | ---- | ---- | ---- | 2 (15, 20) |
| Median Time | 55 s | ---- | ---- | ---- | 3 s |
| LASER WALL | | | | | |
| Successful Session | 1 (20) | ---- | ---- | ---- | 1 (20) |
| Median Time | 5 s | ---- | ---- | ---- | 5 s |

*Failed to contact joystick on first session, moved to distance shaping beginning with CRT 35.
**Failed to contact joystick on first session, did not move on to laser conditions.
***Due to technical problems, only 3 trials given before moving on. Succeeded on 2. See text for details.

Both subjects succeeded on their first session for conditions FLAT, IRREGULAR, DISTANCE 1, DISTANCE 2, and DISTANCE 3. Table 6 lists the number of sessions required to reach criterion, the number of completed trials in each session, and the median trial time measured from initial displacement of the joystick until successful completion. Subjects immediately generalized their use of the laser to novel situations and surfaces, including a hallway environment they had never been tested in. Even at a distance of 11.5 m, the subjects could quickly pinpoint the laser dot onto a small target of 3.8 cm diameter.

Table 6 The session number in which criterion was met for each condition for each subject, with number of successful trials for each test session in parentheses. Median time to completion taken from all successful trials in the first successful session. Contact Bait First gives the number of trials in each 20-trial session where the baited location was the first one contacted.

| | SUBJECT | |
|---|---|---|
| CONDITION | XENON | LEO |
| FLAT | | |
| Successful Session | 1 (20) | 1 (18) |
| Median Time | 4 s | 2.5 s |
| IRREGULAR | | |
| Successful Session | 1 (20) | 1 (18) |
| Median Time | 7 s | 6.5 s |
| DISTANCE 1 (3.2 m) | | |
| Successful Session | 1 (20) | 1 (20) |
| Median Time | 3.5 s | 4.5 s* |
| DISTANCE 2 (6.1 m) | | |
| Successful Session | 1 (20) | 1 (20) |
| Median Time | 2 s | 4 s |
| DISTANCE 3 (11.5 m) | | |
| Successful Session | 1 (20) | 1 (20) |
| Median Time | 3 s | 3 s |
| GRID CONTROL | | |
| Contact Bait First | 13/20, 18/20 | 16/20, 20/20 |

*Based on trials 9-20, due to a faulty video tape.

For the GRID control condition, both subjects contacted the baited location before any other significantly more often than predicted by chance (Xenon Day 1: Binomial test, $P < 0.001$; Xenon Day 2: Binomial test, $P < 0.001$; Leo Day 1: Binomial test, $P < 0.001$; Leo Day 2: Binomial test, $P < 0.001$). On the first day, Xenon contacted the baited location before any other on 13 of 20 trials. On three trials he contacted one unbaited location first; on two trials he contacted two unbaited locations first; and on another trial he contacted four unbaited locations before finishing. He failed one trial, having contacted the same unbaited location five times. On the second day of Xenon's testing, and for both days of Leo's testing, we made a much lighter and less visible mark on the wall for each location. On Xenon's second day of GRID testing, he went straight to the baited location on 18 of 20 trials, and on the other two trials he hit only one unbaited location first. On Leo's first day, he went to the baited location immediately on 16 of 20 trials, while he hit a single unbaited location first on the other four trials. On day 2, Leo contacted the baited location first on 20 of 20 trials.

For Xenon, half (9 out of 18) of the instances of contacting an unbaited location happened on locations adjacent to the baited location, or in a direct line between the cursor's starting location and the baited location. For Leo, all (4 out of 4) contacts to the unbaited location were from adjacent locations or one directly on the way to the bait. Thus the errors were non-random. Fig. 10 presents the path of Xenon's first five trials of day 1, and Fig. 11 gives the same information for Leo's first five trials of day 1. The laser paths taken by each monkey were non-random and appear reasonably efficient from the beginning.

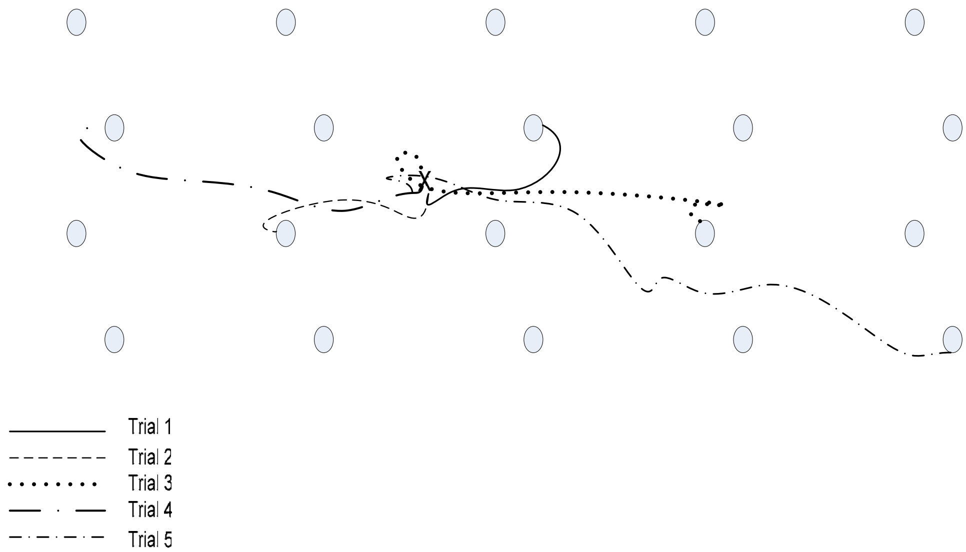


Fig. 10 Xenon, GRID condition: laser path, first five trials. X marks the laser starting point.

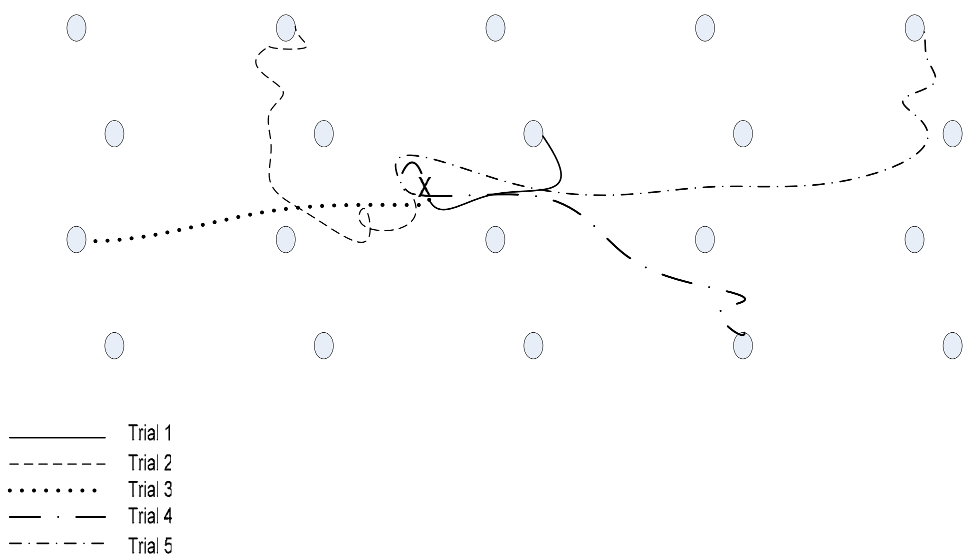


Fig. 11 Leo, GRID condition: laser path, first five trials. X marks the laser starting point.

**Discussion**

Experiment 1 shows that capuchin monkeys can use a joystick to move a laser pointer onto a target object on many different surfaces in the 3D distal environment, confirming our prediction. However, not all subjects succeeded, suggesting this is likely a challenging skill for monkeys or it may simply require adjusted training with some subjects.

The three subjects that were given the PROJECTION condition directly after baseline failed to complete any trials. With shaping, one of the subjects subsequently succeeded at the PROJECTION condition and all further conditions. So the second prediction was partially supported, insofar as no subject that was given a chance could immediately and without shaping complete any trials at the new distance without a monitor.

Finally, the GRID condition introduced a new target in the form of food (a 3D object), rather than a flat green circle. Both subjects immediately generalized their use of the laser to contact the food target. Xenon did fail one trial, and hit some non-food locations before the food on seven trials of his first session. However, this may be explained by the fact that on this first day of GRID testing the 20 locations had been marked thickly with a black permanent marker. The novel target might not have stood out obviously as a target compared to the black dots. On the second day of Xenon's testing, and for both days of Leo's testing, we made a much lighter and less visible mark on the wall for each location, and performance was much better.

However, in all cases we could describe their performance as a fairly straightforward instrumental response akin to the baseline computer task: moving a cursor to a target resulted in reinforcement. Is that all that is happening when the monkeys use the laser tool, or is it possible the monkeys could use the device to make rational choices among distal food items? To answer this question, we moved both subjects on to experiment 2.

## SECTION 3

## EXPERIMENT 2

Given that the monkeys were able to target food items, we hypothesized that they would use the laser to choose in a rational manner between multiple simultaneously presented food items, receiving the items they selected. Rational foraging would mean consistently choosing the more desirable (or avoiding the less desirable) among the foods available, in terms of dimensions such as food size, type and distance. To test this, we laid an array of food items on the floor in front of the monkeys. This procedure allowed us to control three dimensions of each potential target: (1) size: large or small, (2) food type: banana or cucumber, and (3) distance: near or far. A rational forager would take a larger item over a small one, all other dimensions being equal between available items; likewise for a more-preferred food type (banana) over a less-preferred food type (cucumber), and a close item over a far one. Irrational choices – such as choosing a small, far away cucumber when a large, nearby cucumber is available – should be uncommon for a rational forager.

Alternately, the subjects might treat the simultaneously-presented foods simply as arbitrary targets to be contacted for reward, akin to moving a computer cursor onto a computer target for a food reward. If so, then their expected pattern of responding would differ from our hypothesis. They would presumably still show a bias for near items over far, all else being equal (because near items enter the field of view sooner when tracking the laser dot visually). Likewise, they would still show a bias for large items over small, all else being equal (because larger surface area makes them stand out more as potential targets, and also increases the chance of random contact). However, unlike our hypothesis, we would not expect a bias for the more-preferred food, bananas, over the less-preferred food, cucumbers, all else being equal. For example, we would not expect the subjects to consistently choose a near large banana over a near large cucumber; nor would we expect the subjects to consistently choose a far banana when nearby cucumbers of the same or larger size are available. If anything, we would expect cucumbers to be targeted preferentially, since their color is very close to that of the green cardboard target used for most previous laser tasks; but if color is not a salient cue then no difference would be expected.

**Method**

**Subjects and housing**

Xenon and Leo, the same two monkeys that succeeded in acquiring laser pointer use in experiment 1, were the subjects of experiment 2.

**Apparatus**

The testing cage, joystick and laser pointer remained the same as in experiment 1. Testing took place in the hallway adjoining their normal testing room (2.2 m x 12.2 m). For this test, an array of eight food items was set out on the floor in front of the subject at the beginning of each trial. The items varied along three dimensions: type, size and distance. Food type was either banana or cucumber, the former a preferred food for both subjects. Size was manipulated by varying between large (16 grams, 2.5 x 2.5 x 5.5 cm) and small (2 grams, 2 x 1.5 x 1.5 cm) pieces. Bananas and cucumbers have similar enough density that the size and weight could both be matched. Finally, the foods were placed either 0.6 m beyond the starting location of the laser dot ("near"), or 2.4 m beyond it ("far"). At each distance level we placed a large and small item of each food type (four items total), and these were spaced so as to maintain equal distance from the laser dot and equal distance from the nearest neighbor item (Fig. 12). The near foods were spaced 45 cm apart from each neighboring item, and the far foods 61 cm apart. The laser dot itself started each trial on the floor centered 1.2 m in front of the testing cage, and was reset to that position after each item selection. Thus, the near items were located 1.8 m from the subject, and the far items 3.6 m.

**Procedure**

A trial involved the subject contacting with the laser pointer, and immediately receiving, each of the eight items in turn, without replacement (Fig. 13). Subjects completed only one trial (i.e. eight selections) per testing day. Trials started when subjects first touched the joystick. If they targeted one of the food items, they were immediately verbally praised and the item was quickly retrieved and given to them (taking care that it was in sight the entire time). We reset the laser pointer to its starting location and then gave subjects access to the joystick again. The trial continued until all of the items had been selected, or until three minutes had elapsed without selecting a food item. When not retrieving food, the experimenter stood to the side of the cage, behind the monkey, and looked straight ahead. We gave each subject a total of ten trials, and recorded their selections on video.

The layout of the food items was balanced across trials, but within each trial there was always a large and small item of each food type on the near row, and a large and small item of each food type on the far row (not necessarily in the same place on the row). Food was always baited from left to right, from the subject's perspective, and trials were balanced between baiting the near or far row first. The subject's cage mate was present for all trials, but stayed in a small transport box behind and to the side of the testing cage. Cage mates were typically silent throughout the task.

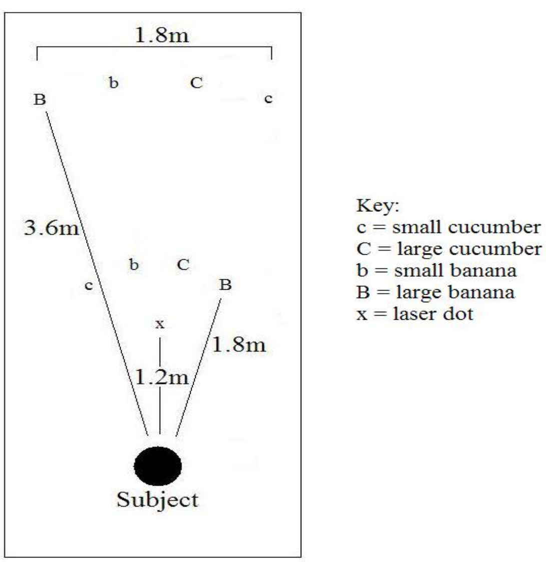


Fig. 12 CHOICE condition, example layout.

Fig. 13 Experiment 3: CHOICE condition

**Analysis**

We report a summary of the selections made by each subject, presenting how often each item was selected first, second, third and so on during the 10 trials. The first four selections per trial are considered early selections and the last four are considered late selections. We use a Chi-square test to test among early selections for significant difference between large and small items, bananas and cucumbers, and near and far items. We also report the number and trial of irrational choices for each subject. An irrational choice is defined as choosing an item when there is still available another item that is better along one or more dimensions and no worse along any dimensions.

**Results**

Both monkeys showed orderly and generally rational item selection. Table 7 presents a summary of Xenon's choices listing the frequency of trials on which each item type fell at a particular position in the selection order. Table 8 lists the same information for Leo. Note that, in all but one trial, the nearby large banana was selected first. The far away cucumbers were always chosen late in the trial, among the last four items selected (always the final two picks for Xenon, in fact).

Table 7 Results of choice task for Xenon. Number of trials on which each item was picked first, second, third and so on to the eighth and final pick for each trial.

| ITEM | Pick 1 | Pick 2 | Pick 3 | Pick 4 | Pick 5 | Pick 6 | Pick 7 | Pick 8 |
|---|---|---|---|---|---|---|---|---|
| Near Large Banana | **10** | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Near Small Banana | 0 | **7** | **2** | 0 | 0 | **1** | 0 | 0 |
| Near Large Cucumber | 0 | **2** | **4** | **3** | 0 | **1** | 0 | 0 |
| Near Small Cucumber | 0 | **1** | **1** | **2** | **4** | **2** | 0 | 0 |
| Far Large Banana | 0 | 0 | **3** | **5** | **1** | **1** | 0 | 0 |
| Far Small Banana | 0 | 0 | 0 | 0 | **5** | **5** | 0 | 0 |
| Far Large Cucumber | 0 | 0 | 0 | 0 | 0 | 0 | **7** | **3** |
| Far Small Cucumber | 0 | 0 | 0 | 0 | 0 | 0 | **3** | **7** |

Table 8 Results of choice task for Leo. Number of trials on which each item was picked first, second, third and so on to the eighth and final pick for each trial.

| ITEM | Pick 1 | Pick 2 | Pick 3 | Pick 4 | Pick 5 | Pick 6 | Pick 7 | Pick 8 |
|---|---|---|---|---|---|---|---|---|
| Near Large Banana | **9** | 0 | 0 | **1** | 0 | 0 | 0 | 0 |
| Near Small Banana | 0 | **6** | **2** | **2** | 0 | 0 | 0 | 0 |
| Near Large Cucumber | **1** | **2** | **3** | **3** | 0 | **1** | 0 | 0 |
| Near Small Cucumber | 0 | 0 | **1** | 0 | **3** | **2** | **3** | **1** |
| Far Large Banana | 0 | **2** | **4** | **3** | 0 | 0 | 0 | **1** |
| Far Small Banana | 0 | 0 | 0 | **1** | **3** | **2** | **4** | 0 |
| Far Large Cucumber | 0 | 0 | 0 | 0 | **4** | **5** | **1** | 0 |
| Far Small Cucumber | 0 | 0 | 0 | 0 | 0 | 0 | **2** | **8** |

The subjects' selections show a bias for near items over far items. Of the 80 selections made early in a trial (the first four picks), 62 were near items and only 18 were far. The difference was significant, $\chi^2_1$ = 24.200, P < 0.001. Note that all 18 far selections made early in a trial were of bananas; 17 of them were large bananas, and in 16 of those cases the near large banana had already been selected.

Subjects also showed a bias for bananas over cucumbers. Of the 80 early selections (the first four picks per trial), 57 were bananas and 23 cucumbers. This is significantly unlikely under random selection, $\chi^2_1$ = 8.450, P = 0.004. Of these 23 early cucumber selections, all were for near items, 18 were for large rather than small, and 19 occurred when there was no obviously better item left nearby (i.e. of nearby items, the large banana was gone when the large cucumber was selected, and all the other items were gone when the small cucumber was selected). In other words, when the less preferred food type was selected early, it was typically because no better item was left within that distance.

Furthermore, there was a bias for large items over small ones early in the trials. Of the 80 early selections (the first four picks per trial), 55 were large items and 25 were small. Again the difference was significant, $\chi^2_1$ = 11.250, P = 0.001. Of those 25 early small items, 24 were nearby items, and 19 were bananas. So when the smaller food was chosen early, it was because it was spatially close or of the preferred food type.

Between trials and between subjects, there was variation in the priority among dimensions. That is, no one factor automatically overrode all of the others. However, even with the variation, only rarely (8 of 80 selections per subject) were there direct reversals of what would be expected for rational foraging (Table 9). That is, very rarely did the subjects pick an item if there was available an item that was better along one or more of the three dimensions but no worse along the other dimensions. Examples of such an irrational choice would be choosing a far small banana when a small (or large) banana was left nearby, or selecting a small near cucumber when any other item was nearby, or selecting a far large cucumber when a near large cucumber or a near or far large banana was still available. On the other hand, examples that would not be irrational would be choosing a far large cucumber when a small banana was nearby (since this might just indicate a weighting toward valuing size) or choosing a near small cucumber when all far items are left (since this might just indicate a weighting toward valuing nearby items).

Table 9 Number of irrational choices per trial for each subject. See text for explanation.

| | SUBJECT | |
|---|---|---|
| TRIAL | XENON | LEO |
| 1 | 1 | 4 |
| 2 | 1 | 3 |
| 3 | 0 | 0 |
| 4 | 0 | 0 |
| 5 | 1 | 1 |
| 6 | 0 | 0 |
| 7 | 0 | 0 |
| 8 | 2 | 0 |
| 9 | 2 | 0 |
| 10 | 1 | 0 |

**Discussion**

These results suggest that the subjects were choosing among the items in front of them in a rational manner. Simple instrumental responding (treating the food as arbitrary targets) is not consistent with our results. The strong bias toward bananas over cucumbers, the rare reversals of rational choice, and the non-random selections when passing up nearby items to select far ones early on all support the contention that the subjects were making rational choices. Irrational choices happened only eight times per subject, out of 80 choices. For Xenon, five of those times he was distracted (by calls from the home room, for example) and looking away from the floor while the dot moved; by the time he looked back, the dot was very close to an item, which he then selected. For Leo, seven of those times were in the first two trials. However, even during those two initial trials, his selections were non-random and followed the general pattern, with 75% of near items and 75% of bananas chosen in the first four picks, and 75% of far items and 75% of the cucumbers chosen in the last four picks.

## SECTION 4

## GENERAL DISCUSSION AND CONCLUSION

We demonstrated in experiment 1 that capuchin monkeys can use a joystick to control a laser pointer in the distant environment, including multiple surfaces and 3D as well as flat targets. Thus, we can conclude that the laser pointer setup is not just relevant to a single, special ape subject (Menzel 2005), but may in fact be extended to other captive primates, including monkeys. Our results further suggest that some shaping, particularly with regards to distance, may be required to extend the skill of joystick-trained monkeys to a joystick-controlled laser pointer. However, those subjects that mastered use of the laser in one condition quickly and easily generalized to other conditions. Their movement of the laser dot was not random; rather the path taken was efficient, as demonstrated in the GRID control condition.

The failure of some subjects to pass the PROJECTION condition in spite of distance training suggests there are other relevant factors. Most PROJECTION trial failures occurred because the subject was not attending to the wall, and quickly lost interest in contacting the joystick without reinforcement. We suspect that the presence of the computer monitor itself, as opposed to just the program stimulus on the screen, may be a crucial contextual cue to the subjects that their joystick movements are controlling something in front of them. For example, one subject, Xavier, was able to complete trials of Geomjoy projected onto the turned-off CRT monitor, and he even used the laser to target the green cardboard disk on the turned-off monitor. It seems that moving away from the computer monitor itself interrupted his attention to the task. Alternate or complementary shaping routes, such as projecting their original joystick training programs, might allow more subjects to master use of the laser pointer.

The results of experiment 2 demonstrate that the monkeys chose rationally among multiple simultaneously presented food items, weighing the parameters of size, food type and distance. At the food types, sizes and distances used, none of these dimensions took complete priority over the others, but rather they were balanced against one another. These results mirror those found in field studies (Janson 1996, 2000, 2007; Bicca-Marques 2006).

The laser pointer method allows the integration of significant distances to captive testing conditions, avoiding some of the inherent limitations in popular testing paradigms such as reaching tasks and computerized tasks. In experiment 2, the monkeys chose among eight food items up to 3.6 m away, with 45 to 61 cm between neighboring items and roughly 2.4 m between items at the extremes. These distances are much greater than those used in typical reaching tasks (Table 1), and far exceed both the distance to screen and the dispersion possible on a screen in computerized testing (Table 2). The laser pointer allows subjects to target real items – by no means limited to food objects – in the full, 3D environment, much richer than any simulation on a screen. Obviously, this method can easily be extended to systematic tests of more and different items, with further distance to and between the items; thus the number of items we used and the distances we used should by no means be seen as an upper limit. Overall, the laser pointer method allows researchers to evaluate a richer model of rational foraging than is available in shorter-distance captive testing.

## REFERENCES

**Anderson, J. R., Kuwahata, H. & Fujita, K.** 2007. Gaze alternation during "pointing" by squirrel monkeys (Saimiri sciureus). *Animal Cognition*, **10**, 267-271.

**Andrews, M. W.** 1993. Video-task paradigm extended to Saimiri. *Perceptual and Motor Skills*, **76**, 183-191.

**Barth, J. & Call, J.** 2006. Tracking the displacement of objects: A series of tasks with great apes (Pan troglodytes, Pan paniscus, Gorilla gorilla, and Pongo pygmaeus) and young children (Homo sapiens). *Journal of Experimental Psychology: Animal Behavior Processes*, **32**, 239-252.

**Beran, M. J., Beran, M. M. & Menzel, C. R.** 2005. Spatial memory and monitoring of hidden items through spatial displacements by chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, **119**, 14-22.

**Bicca-Marques, J. C.** 2006. Distance influences the foraging decisions of emperor and saddleback tamarins. *Journal of Zoology*, **269**, 221-224.

**Blaschke, M. & Ettlinger, G.** 1987. Pointing as an act of social communication by monkeys. *Animal Behavior*, **35**, 1520-1523.

**Brakke, K. E. & Savage-Rumbaugh, E. S.** 1995. The development of language skills in bonobo and chimpanzee: I. Comprehension. *Language and Communication*, **15**, 121-148.

**Brakke, K. E. & Savage-Rumbaugh, E. S.** 1996. The development of language skills in Pan: II. Production. *Language and Communication*, **16**, 361-380.

**Cunningham, E. & Janson, C.** 2007. Integrating information about location and value of resources by white-faced saki monkeys (Pithecia pithecia). *Animal Cognition*, **10**, 293-304.

**Di Fiore, A. & Suarez, S. A.** 2007. Route-based travel and shared routes in sympatric spider and woolly monkeys: Cognitive and evolutionary implications. *Animal Cognition*, **10**, 317-329.

**Dominy, N. J., Lucas, P. W., Osorio, D. & Yamashita, N.** 2001. The sensory ecology of primate food perception. *Evolutionary Anthropology*, **10**, 171-186.

**Fragaszy, D., Johnson-Pynn, J., Hirsh, E. & Brakke, K.** 2003. Strategic navigation of two-dimensional alley mazes: Comparing capuchin monkeys and chimpanzees. *Animal Cognition*, **6**, 149-160.

**Fragaszy, D. M., Visalberghi, E. & Fedigan, L. M.** 2004. *The complete capuchin*. Cambridge University Press: Cambridge, pp 173-201.

**Funahashi, S., Inoue, M. & Kubota, K.** 1993. Delay-related activity in the primate prefrontal cortex during sequential reaching tasks with delay. *Neuroscience Research*, **18**, 171-175.

**Garber, P. A.** 1989. Role of spatial memory in primate foraging patterns: Saguinus mystax and Saguinus fuscicollis. *American Journal of Primatology*, **19**, 203-216.

**Genty, E. & Roeder, J. J.** 2007. Transfer of self-control in black (Eulemur macaco) and brown (Eulemur fulvus) lemurs: Choice of a less preferred food item under a reverse-reward contingency. *Journal of Comparative Psychology*, **121**, 354-362.

**Gust, D. A.** 1989. Uncertain availability of a preferred food affects choice in a captive group of chimpanzees (Pan troglodytes). *American Journal of Primatology*, **17**, 165-171.

**Harlow, H. F., Uehling, H. & Maslow, A. H.** 1932. Comparative behavior of primates: I. Delayed reaction tests on primates from the lemur to the orang-outan. *Journal of Comparative Psychology*, **13**, 313-343

**Hopkins, W. D., Washburn, D. A. & Rumbaugh, D. M.** 1989. Note on hand use in the manipulation of joysticks by rhesus monkeys (Macaca mulatta) and chimpanzees (Pan troglodytes). *Journal of Comparative Psychology*, **103**, 91-94.

**Hopkins, W. D. & Washburn, D. A.** 1994. Do right- and left-handed monkeys differ on cognitive measures? *Behavioral Neuroscience*, **108**, 1207-1212.

**Inoue, S. & Matsuzawa, T.** 2007. Working memory of numerals in chimpanzees. *Current Biology*, **17**, R1004-5.

**Iversen, I. H. & Matsuzawa, T.** 2003. Development of interception of moving targets by chimpanzees (Pan troglodytes) in an automated task. *Animal Cognition*, **6**, 169-183.

**Janson, C. H.** 1996. Towards an experimental socioecology of primates: Examples for Argentine brown capuchin monkeys (Cebus apella nigritus). In: *Adaptive radiation of neotropical primates* (Ed. by Norconk, M., Rosenberger, A. L. & Garber, P. A.), pp. 309-325. New York: Plenum Press.

**Janson, C. H.** 2000. Spatial movement strategies, theory, evidence, and challenges. In: *On the move: How and why animals travel in groups* (Ed. by Boinski, S. B. & Garber, P. A.), pp. 165-203. Chicago: University of Chicago Press.

**Janson, C. H.** 2007. Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Animal Cognition*, **10**, 341-356.

**Janson, C. H. & Di Bitetti, M. S.** 1997. Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. *Behavioral Ecology and Sociobiology*, **41**, 17-24.

**Kaminski, J., Call, J. & Tomasello, M.** 2004. Body orientation and face orientation: Two factors controlling apes' begging behavior from humans. *Animal Cognition*, **7**, 216-223.

**Kawai, N. & Matsuzawa, T.** 2000. Numerical memory span in a chimpanzee. *Nature*, **403**, 39-40.

**Leighty, K. A. & Fragaszy, D. M.** 2003. Joystick acquisition in tufted capuchins (Cebus apella). *Animal Cognition*, **6**, 141-148.

**McGonigle, B., Chalmers, M. & Dickinson, A.** 2003. Concurrent disjoint and reciprocal classification by Cebus apella in seriation tasks: Evidence for hierarchical organization. *Animal Cognition*, **6**, 185-197.

**Menzel, C.** 1999. Unprompted recall and reporting of hidden objects by a chimpanzee (Pan troglodytes) after extended delays. *Journal of Comparative Psychology*, **113**, 426-434.

**Menzel, C.** 2005. Progress in the study of chimpanzee recall and episodic memory. In: *The missing link in cognition: Origins of self-reflective consciousness* (Ed. by Terrace, H. S. & Metcalfe, J.), pp. 188-224. New York: Oxford University Press.

**Menzel, E. W. Jr.** 1973. Chimpanzee spatial memory organization. *Science*, **182**, 943-945.

**Mitchell, R. W. & Anderson, J. R.** 1997. Pointing, withholding information, and deception in capuchin monkeys (Cebus apella). *Journal of Comparative Psychology*, **111**, 351-361.

**Noser, R. & Byrne, R. W.** 2007. Mental maps in chacma baboons (Papio ursinus): Using inter-group encounters as a natural experiment. *Animal Cognition*, **10**, 331-340.

**Padoa-Schioppa, C., Jandolo, L. & Visalberghi, E.** 2006. Multi-stage mental process for economic choice in capuchins. *Cognition*, **99**, B1-B13.

**Perry, G. & Pianka, E. R.** 1997. Animal foraging: past, present and future. *Trends in Ecology and Evolution*, **12**, 360-364.

**Rumbaugh, D. M., Richardson, W., K., Washburn, D. A., Savage-Rumbaugh, E. S. & Hopkins, W. D.** 1989. Rhesus monkeys (Macaca mulatta), video tasks, and implications for stimulus-response spatial contiguity. *Journal of Comparative Psychology*, **103**, 32-38.

**Sato, N., Sakata, H., Tanaka, Y. & Taira, M.** 2004. Navigation in virtual environment by the macaque monkey. *Behavioral Brain Research*, **153**, 287-291.

**Smith, J. D., Shields, W. E., Allendoerfer, K. R. & Washburn, D. A.** 1998. Memory monitoring by animals and humans. *Journal of Experimental Psychology: General*, **127**, 227-250.

**Vauclair, J. & Fagot, J.** 1993. Manual and hemispheric specialization in the manipulation of a joystick by baboons (Papio papio). *Behavioral Neuroscience*, **107**, 210-214.

**Vick, S. & Anderson, J. R.** 2000. Learning and limits of use of eye gaze by capuchin monkeys (Cebus apella) in an object-choice task. *Journal of Comparative Psychology*, **114**, 200-207.

**Washburn, D. A.** 1992. Analyzing the path of responding in maze-solving and other tasks. *Behavior Research Methods, Instruments & Computers*, **24**, 248-252.

**Washburn, D. A., Hopkins, W. D. & Rumbaugh, D. M.** 1989. Video-task assessment of learning and memory in macaques (Macaca mulatta): Effects of stimulus movement upon performance. Journal *of Experimental Psychology: Animal Behavior Processes*, **15**, 393-400.

**Washburn, D., Hopkins, W. D. & Rumbaugh, D. M.** 1991. Perceived control in rhesus monkeys (Macaca mulatta): Enhanced video-task performance. *Journal of Experimental Psychology: Animal Behavior Processes*, **17**, 123-129.