PLANNING IN CAPUCHIN MONKEYS (*CEBUS APELLA*): MAZE CHARACTERISTICS AND EXPERIENCE AFFECT NAVIGATION IN TWO-DIMENSIONAL SPACE

by

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(Under the Direction of Dorothy M. Fragaszy)

ABSTRACT

Planning was examined in four capuchin monkeys that completed a series of 192 two-dimensional computer mazes. These mazes differed in number of choice points (0-5) and "non-obvious" choices (0-3). Non-obvious choices were those in which the incorrect choice appeared to lead more directly to the goal than the correct choice. The number of choices varied randomly throughout testing. Planning abilities were measured in terms of the type of errors made by subjects while solving the mazes. Results of this study were compared to those of a previous study in which three capuchins solved the same mazes in order of increasing difficulty. The current study aimed to determine to what extent performance was influenced by properties of the mazes and by general experience solving these problems. The results of this study suggest that both of these factors affect the extent to which capuchins learn to plan when navigating through two-dimensional space.

INDEX WORDS: Planning, Spatial navigation, Mazes, Capuchin monkey, *Cebus apella*

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CHAPTER 1

INTRODUCTION

The ability to plan one's actions is an integral component of efficient problem-solving and navigation through space. Haith (1994) defines planning as "future-oriented problem-solving". The degree to which non-human primates plan their actions remains a source of controversy. The purpose of the current study is to expand on findings from a study conducted by Fragaszy, Johnson-Pynn, Hirsh and Brakke (2003) that investigated the planning abilities of capuchin monkeys and chimpanzees as they solved two-dimensional computer mazes. The current study specifically aims to determine to what extent maze characteristics and individual experience affect the ability of four capuchin monkeys (*Cebus apella*) to navigate through two-dimensional space.

Various evidence suggests that non-human primates have the capacity to plan movements of themselves and objects in three-dimensional space. Efficient foraging and travel require some degree of planning. Many primate species have shown evidence of using a "least-distance" strategy when traveling between two foraging locations (Menzel, 1973; MacDonald, 1994; Kuhlmeier & Boysen, 1999). In these cases, the animals choose the route between two locations that minimizes travel distance and thus energy expenditure. Some degree of planning also appears evident in transporting objects to use as tools. For instance, some chimpanzees in the Tai forest select different tools based on their appropriateness for opening different kinds of nuts. The chimps will select a wooden tool to crack open the relatively soft coula nut but will search for heavy stone hammers to crack open the harder panda nut (Boesch & Boesch, 1984). Of particular interest, the chimps in these cases have been observed to transport heavy stone hammers some distance to be used to crack open panda nuts that were located in another location. This finding suggests that the animals are able to determine that the stone tool, although useless in its current location, would be useful in another context and thus transport it to a place that has panda nuts. Capuchins have also been witnessed to engage in similar transport of tools in captivity (Fragaszy & Visalberghi, 1989). It would appear that both species are engaging in some degree of future-oriented problem solving as they are able to anticipate what tool will be needed to solve a problem outside of the immediate context.

As in studies with children, planning in non-human primates has been investigated experimentally by examining the kinds of errors that are made while attempting to solve multiple-step problems. One such study by Davis and Leary (1968) investigated the ability of lemurs and seven species of monkeys to solve bent-wire detour problems. In this task, subjects were required to manipulate a circular Life Saver candy through a series of different bent-wire patterns in order to retrieve the candy. The wire patterns varied in complexity, with some configurations requiring that the candy be pulled toward the subject and others requiring that it be pushed away from the subject in order to be retrieved. The results showed that Old World monkeys solved significantly more detour problems than New World monkeys, although all species improved with experience. Differences were also found in subjects' ability to successfully use strategies that involved pushing the candy away from them. Capuchin monkeys utilized this strategy more effectively than lemurs and squirrel monkeys but less effectively than spotnose monkeys and macaques. It could be argued that this strategy involves a greater degree of planning as it requires that the subjects move the reward in a direction away from the goal (themselves).

Of particular interest relating to the current study is the degree to which non-human primates use planning in their attempts to navigate through two-dimensional space. Washburn (1992) has provided evidence that rhesus monkeys using a joystick solve two-dimensional computer mazes by traveling along an optimal path rather than completing the mazes through random movements. The monkeys in the Washburn (1992) study were required to use a joystick to move a cursor through a series of choice points in simple two-dimensional mazes in order to reach a goal point. The study conducted by Fragaszy et al. (2003) investigated species differences in the planning abilities of chimpanzees and capuchin monkeys in a two-dimensional maze task similar to that used by Washburn (1992). In this case, four chimpanzees and three capuchins solved 192 two-dimensional mazes that varied systematically in number of choices (1-5) and number of "non-obvious" choices (0-3). Non-obvious choices were correct choices that required traveling away from the goal. Both species were presented with mazes in order of perceived difficulty, with mazes later in the presentation order containing the greatest number of choices and non-obvious choices.

The authors investigated the planning abilities of both species by measuring the type, frequency, and location of errors made while solving these mazes. The performance of the subjects was then examined in terms of a model of planning developed by Fragaszy et al. (2003). According to this model, absence of planning results in random movements of the joystick while solving mazes. Level 1 planning is represented by "bodily planning" which is defined as, "controlled directional movement of the joystick coupled with random selections at choice points" (Fragaszy et al., 2003). The next level (2) involves a "forward search" strategy which produces choices that appear to lead directly to the goal and involves correcting errors when the goal is not reached. Level 3 planning is "integrated" in that decisions made at each choice point are made on the basis of two properties in hierarchical relation (such as directness to the goal or continuation of an alley). The highest level of planning (4) involves subgoaling. This level involves planning the entire route through the maze (either in forward or reverse order), and would be manifest as routinely navigating mazes without error.

Fragaszy et al's (2003) results revealed that individuals of both species solved more mazes without error than expected by chance (Fragaszy et al., 2003). Apes corrected 44% of their errors and capuchins corrected 42% of their errors by reversing the direction the cursor was moving before reaching the end of an incorrect alley. The percentage of choices that were errors declined after the presentation of the second maze set for chimps and remained low. However, the percentage of capuchins' choices that were errors was greatest during the presentation of maze sets containing additional non-obvious choices in comparison to the previous sets (Fragaszy et al., 2003). The presentation of non-obvious choices had a significant effect on the performance of the capuchins, but not on the performance of the apes. The errors of both species were not related in an orderly manner, however, to number of choices or number of non-obvious choices, as the authors had expected. Overall, the results of this study were seen as evidence that both chimpanzees and capuchin monkeys have some ability to plan. Both species showed "planful" (*sensu* Willatts, 1989) behavior in that they made decisions at each maze choice point based on at least one element (directness to the goal) (Fragaszy et al., 2003). Specifically, it was argued that both species showed evidence of level 2 planning and the apes and one monkey appeared also to show planning at level 3.

The present study expands on the findings of the Fragaszy et al. 2003 study by closely examining the effects that maze characteristics and presentation order have on the ability of capuchin monkeys to plan their route through two-dimensional mazes. In this study, four maze-naïve capuchin monkeys encountered the same 192 computer mazes that were used in the Fragaszy et al. study. In the previous study, these mazes were presented in order of increasing perceived difficulty, with mazes presented later containing the greatest number of choices and non-obvious choices. Therefore, the effect of the properties of the mazes on performance was confounded with the animal's general maze-solving experience. The main goal of the present study was to disentangle the effects of experience and maze characteristics by means of random presentation of the mazes without regard to maze properties (number of choices and non-obvious choices). This study compares the performance of four capuchin monkeys given the random presentation of mazes to that of the three animals that completed the mazes in increasing order of difficulty.

Two additional aims of the current study are to evaluate how monkeys are affected by the specific elements of a complex problem (i.e. maze characteristics), and whether the way in which they are exposed to these elements alters the microdevelopment of planful behavior. It is unclear whether the unexpectedly consistent performance of capuchins across mazes of increasing complexity in the ordered group reflected general experiential effects. The development of planful action may be facilitated throughout the course of solving numerous multi-step problems, or more specifically by experience with gradual increases in more difficult elements. It is hypothesized that if the performance of capuchins in the ordered condition was improved by the gradual increase in task complexity over time, then the development of planful actions of capuchins in the random condition should be hindered by the absence of this gradual increase in complexity. Learning to plan at even the most basic level (i.e., forward search; level 2) should be more difficult (i.e., require more experience) for capuchins in the random condition than for capuchins in the ordered condition.

This hypothesis leads to five predictions concerning the kind and number of errors that the monkeys would commit when presented with the mazes in random order and when compared with the performance of the ordered presentation condition. 1) Monkeys in the random condition should make more choices resulting in error in comparison to those in the ordered condition. 2) Self-correction of errors represents the ability of subjects to anticipate that their current actions will not lead to the goal and they therefore reverse the direction of the cursor. As this ability requires "looking-ahead", it is predicted that subjects in the random condition should self-correct their errors less often than subjects in the ordered condition. Levels of self-corrects should gradually increase with experience for both groups, but remain lower for the random group. 3) Monkeys in the random condition should show improved performance (fewer errors, more self-corrects) over blocks of trials (as trials do not increase in difficulty and experience contributes to the development of planful activity). 4) For monkeys in the random group, mazes containing the greatest number of non-obvious choices should result in the greatest number of errors. 5) Monkeys in the random condition should show increased dead-end errors and loops (both measures of general confusion) when solving mazes containing non-obvious choices.

Level of planning was measured in terms of the number and kinds of errors committed while navigating through a maze, and the frequency with which the monkeys "self-corrected" their errors before reaching a dead-end. Overall, the primary goals of this study were to determine the extent to which maze characteristics affect the ability of naïve capuchins to efficiently navigate through two-dimensional space and to further our general understanding of the degree to which non-human primates plan their actions.

CHAPTER 2

METHOD

Design

The design and procedure used for this study replicated that used by Fragaszy et al. (2003) except for order of maze presentation and re-presentation of uncompleted mazes. The previous study presented the mazes to the subjects in order of increasing difficulty and mazes that were not solved after the first presentation were presented to the subject one additional time before the subject continued to the next maze library. In the current study, subjects were presented with mazes in random order and mazes that were not solved after the first presentation were re-presented to the subject up to two additional times (see procedure). All subjects had previous training to master the use of a joystick (Leighty & Fragaszy, 2003). In the current study, monkeys were required to complete a series of two-dimensional mazes on a computer monitor through use of a joystick. Their task was to move a cursor from its initial location through a series of binary choice points to a distinctively marked goal point. The mazes varied according to the number of choice points and the number of choice points that were non-obvious. In a non-obvious choice-point, the correct choice appeared to lead less directly to the goal than the other (incorrect) choice. In the Fragaszy et al. (2003) study, capuchins completed a series of 192 mazes in order of perceived difficulty, with mazes presented later containing the greatest number of choices and non-obvious choices. In the current study, maze-naïve subjects were presented with the same mazes in random order, without regard to maze characteristics.

Subjects

Four male capuchin monkeys (*Cebus apella*) participated in this study. These monkeys (Leo, Nick, Mickey and Solo) ranged in age from 8-13 years old. The monkeys were pair-housed at the University of Georgia. None of the animals were food deprived during testing. The monkeys received a diet of Purina monkey chow in addition to fruit twice a day. During testing subjects were rewarded with a food item (nuts, cereal, or dried fruit) upon successful completion of a maze. Subjects were transported to a room adjacent to their housing area for testing. The care and experimental treatment of the monkeys followed local and federal regulations concerning humane care and treatment.

Test apparatus

The mazes were presented to the subjects in a two-dimensional format on a computer screen (46 cm wide x 28 cm high). Subjects had to manipulate a joystick (5 cm below the screen) in order to move the cursor (a white cross) on the monitor from the start of the maze to the goal (a blue circle). The cursor could be moved anywhere within the alleys on the screen by the joystick. The mazes used for this study were those created and used for the Fragaszy et al. 2003 study. The mazes appeared as black pathways (approximately 2.5 cm in width) against a white background on the computer screen. All angles in the maze pathways were 90 degrees. For this task, the cursor traveled approximately 20 cm in 5 seconds.

Mazes

Each maze presented a novel layout of paths, start and end points, and choice points. Mazes were grouped into sets of 16 (12 maze sets total). The first set consisted of 12 “L”-shaped training mazes that were designed to familiarize subjects with moving the cursor in alleys and around corners and in moving the cursor from the start to the end point. This maze set was the same as that used for training of the ordered group. Mazes in this set contained no choice points. All subjects were exposed to this library (>100 trials) prior to the start of testing with mazes containing choice points.

The number of choice points in the test mazes varied between one and five. The number and nature of choice points in each maze characterized the libraries in the ordered condition (see Table 1). The start and end points of the mazes appeared equally often in the four quadrants of the screen, and the choices were spatially distributed evenly across quadrants insofar as was possible given the constraints of path widths (Fragaszy et al., 2003). At a choice point, the subject had to choose between one of two possible pathways. Some points offered a choice between paths that differed in how directly they led to the goal, either in terms of Euclidean distance or the angle one would have to make from movement along that path to reach the goal. Choices that resulted in apparently traveling a longer distance to the goal or a greater angle away from the goal were categorized as "non-obvious" choices (NOC).

Procedure

The four capuchins in the random group were exposed to 12 maze sets each composed of 16 mazes per set that were originally members of the ordered libraries presented to the subjects in the Fragaszy et al. (2003) study (see Table 1). One maze from each of the libraries as defined in Table 1 was assigned to each of the maze sets used in the current study. Each set therefore contained a mixture of mazes representing the range of choices (1-5) and non-obvious choices (0-3). The mazes within the set appeared in a different random order for each subject (although the mazes comprising the set remained the same). Each of the four naïve subjects was presented with the 12 maze sets in a different predetermined (random) order.

Table 1. Properties of the mazes for the ordered condition

Library	No. of choice points	Non-obvious choices
1 (training)	0	0
2	1	0
3	2	0
4	3	0
5	1	1
6	2	1
7	3	1
8	2	2
9	3	2
10	4	2
11	3	3
12	4	3
13	5	3

*Note that in Fragaszy et al. 2003, the training library was given the number 0 and the other libraries were numbered 1-12.

Completion of a maze was signaled by a tone and the display of a black screen for a three second inter-trial interval. If a subject did not complete an entire set of 16 mazes during testing, the remaining mazes that had not been solved were placed into a new file so that the subject would begin with these mazes during its next testing session. A subject was permitted to work on each maze for a maximum of five minutes. If a subject did not complete a given maze in this amount of time, the next maze appeared after a three second inter-trial interval. The mazes that a subject did not complete were presented again at the end of each maze set. If the subject did not complete a maze in a second five-minute presentation, then it was exposed to a third and final five-minute presentation of the same maze. If the subject did not complete the maze after the third exposure, then this maze was designated as "unsolved" and the subject was permitted to progress to the next maze set. The testing procedure otherwise remained the same as that used with the subjects in the ordered group (Fragaszy et al., 2003).

Maze Scoring

Throughout testing, the maze software program (developed by C. & E. Menzel) automatically stored the movement of the cursor (in terms of pixel jumps) for future play-back. The maze play-back program allowed us to trace the movement of the cursor as it moved through the maze alleys for scoring purposes. This program provided the option of having the cursor leave a visible trail of its movement and also allowed for varying speeds of play-back. We scored each first choice made by subjects as they navigated through the mazes through play-back. An error occurred when the monkey continued an existing path of movement 2.5 cm past the correct alley. An error also occurred when the cursor was moved 2.5 cm down an incorrect alley. Errors resulted in one of two outcomes: "Dead-end" or "Self-correct". When the cursor made contact with the end of an incorrect alley, the error resulted in a Dead-end. It was possible for a subject to make repetitive Dead-end errors within the same alley. The frequency of these Dead-end repetitions was scored. Repetitive Dead-ends occurred when the cursor struck the end of the alley, reversed direction (see below) and then struck the end of the same alley again. In a Self-correct, the monkey moved the cursor away from the end of an incorrect alley before reaching it. Looping of the cursor within maze alleys was also scored. A "Loop" occurred when the cursor moved at least 2.5 cm in a direction 180 degrees from the original path of motion and then returned to the original path of motion. It was possible for consecutive Loops to occur. The initial movement of the cursor away from a dead-end alley was not counted as a Loop. Loops were coded in terms of the location within the maze in which they occurred: (A) within a correct or incorrect alley, (B) within 2.5 cm of the goal, (C) before the first choice, and (D) "during" a choice (at an alley junction-point). The frequency of the various kinds of Loops was tallied.

Analysis

The data collected from the current study investigating performance of capuchins in the random condition were compared with data from three capuchins that completed the same mazes in order of perceived difficulty (Fragaszy et al., 2003). The kind and frequency of errors made by monkeys in both conditions were compared for the subjects' first choice as they encountered each maze choice-point (repeat choices were not compared). Type and frequency of loops were not scored by Fragaszy et al. 2003 for monkeys in the ordered condition and therefore no comparison between the groups could be made for this variable.

The performance of the four subjects in the random condition was compared to that of three subjects who were exposed to the same mazes in order of increasing difficulty (results obtained from Fragaszy et al., 2003) by means of analysis of variance. All analyses were conducted using SPSS statistical software. Arc-sine transformations were performed on the data to normalize the distribution prior to analysis. As this transformation had no effect on the significance levels of the performed tests, all reported results were obtained from analysis of non-transformed data. Mauchly's test of sphericity was performed for each analysis, revealing that the homogeneity of variance assumption was not violated for tests reported here.

Analysis of variance (ANOVA) was performed for the percentage of first choices resulting in error as a function of experience using a 2 x 5 (group x percentage of completed trials) mixed factorial model. In all cases experience was measured in terms of percentage of completed trials which was divided into five levels (20, 40, 60, 80, and 100% trials completed). A separate analysis examined the percentage of first choices resulting in error as a function of maze library (incorporating changes in both number of choices and non-obvious choices) using a 2 x 12 (group x maze library) mixed factorial ANOVA. Maze characteristics were represented by maze library number as listed in Table 1. Mazes from higher numbered maze libraries contain a greater number of choices and non-obvious choices. The percentage of errors that were self-corrected as a function of experience was also compared for the two presentation conditions using a 2 x 5 (group x percentage of completed trials; 20, 40, 60, 80, and 100) mixed factorial model. A 2 x 12 (group x maze library) mixed factorial ANOVA was used to compare the two groups in terms of percentage of self-corrected errors as a function of maze library.

A repeated measures ANOVA was used to evaluate the effects of experience (percentage of completed trials; 20, 40, 60, 80, and 100) on the percentage of choices resulting in error for subjects within the random condition. In addition, a repeated measures ANOVA was used to compare the proportion of errors that were self-corrected as a function of maze library (12 levels) for monkeys in the random group. A repeated measures ANOVA was also performed to examine the effects of experience (five levels, see above) on the proportion of errors that were self-corrected within the random condition.

Separate analyses were conducted solely on the random group data in order to determine the effects that non-obvious choices (NOC's) had on performance and also to determine the extent to which dead-end errors and reversals varied as a function of maze library and experience. A repeated measures ANOVA was conducted on percentage of NOC's resulting in error as a function of percentage of trials completed (five levels; 20, 40, 60, 80, and 100) for subjects within the random group. A repeated measures ANOVA was also calculated for the proportion of NOC's resulting in error as a function of maze library (for the nine libraries containing non-obvious choices). In addition, separate repeated measures ANOVA's were conducted to examine the proportion of NOC's resulting in error for maze libraries containing one NOC (libraries 5, 6, and 7), two NOC's (libraries 8, 9, and 10), and three NOC's (libraries 11, 12, and 13). In a separate analysis, the percentage of error-free mazes was compared to levels expected by chance within subjects using binomial tests.

The proportion of errors resulting in dead-ends as a function of experience (percentage of completed trials; 20, 40, 60, 80, and 100) was examined by means of repeated measures ANOVA. The proportion of dead-end errors that were repeated was also calculated as a function of experience and maze library using repeated measures ANOVA. In addition, the frequency of loops was examined as a function of maze library and also as a function of location within the maze (five possible locations) using repeated measures ANOVA.

CHAPTER 3

RESULTS

Effect of ordered versus random presentation

Effects of experience

Analyses revealed no significant difference between the overall proportion of choices resulting in error as a function of presentation condition (ordered vs. random), $F(1,5)=5.37$, $p=.068$. There was, however, a significant interaction between experience (in terms of percentage of trials completed) and presentation order on the percentage of choices resulting in error, $F(4,20)=8.84$, $p<.001$. As shown in Figure 1, the random group initially produced a greater proportion of errors than the ordered group, but differences between the groups lessened with experience. Separate analyses revealed that the ordered group did not show a significant effect of experience on error rates, F(4,8)=2.83, $p=.098$. Experience did, however, have a significant effect on the proportion of choices resulting in error for the random group, $F(4,12)=10.82$, $p=.001$.

The percentage of errors that were self-corrected increased significantly as a function of experience in both groups considered together, $F(4,20)=3.27$, $p=.032$. As seen in Figure 2, there was a significant main effect of presentation group on percentage of self-corrected errors, with the ordered group ($M= .408$, $SE=.038$) revealing higher overall levels of self-corrected errors in comparison with the random group ($M=.225$, $SE=.033$), $F(1,5)=13.21$, $p=.015$. There was no interaction between group and experience on the percentage of self-corrected errors, $F(4,20)=.466$, $p=.760$. However, a separate analysis revealed a significant effect of experience on the proportion of self-corrected errors for monkeys in the random group, with subjects self-correcting more with increased experience, $F(4,12)=3.68$, $p=.035$.

Effects of maze characteristics

Maze characteristics (represented in terms of maze library number; see Table 1) significantly affected percentage of choices resulting in error for subjects in both groups in very similar ways, $F(11,55)=11.91$, $p<.001$. As seen in Figure 3, there are increased error rates for the ordered and random conditions for maze libraries that contain an additional non-obvious choice in comparison to the previous library (note libraries 5, 8, and 11 in comparison to 4, 7, and 10). Tukey's LSD post hoc comparisons revealed significant differences in error rates for maze libraries containing increased non-obvious choices in comparison to previous libraries where the mazes have no or fewer non-obvious choices. The proportion of choices resulting in error was significantly higher for maze libraries in which the choices were only non-obvious (libraries 5, 8 and 11; containing 1, 2, and 3 non-obvious choices respectively). There was no significant difference in error rates revealed by pair-wise comparisons of these three maze libraries.

Maze characteristics also had a significant effect on percentage of errors that were self-corrected, with lower rates of self-corrects occurring in libraries containing non-obvious choices, $F(11,55)=3.11$, $p=.003$. There was a significant interaction between presentation group and maze library number, $F(11,55)=2.49$, $p=.013$. As shown in Figure 4, the ordered group self-corrected proportionally more often in later libraries suggesting effects of experience for the ordered group. A separate analysis revealed that maze library did significantly affect proportion of self-corrected errors for subjects within the ordered group, $F(11,22)=3.52$, $p=.006$. Maze library did not significantly affect the proportion of self-corrected errors for subjects within the random group, $F(11,33)=2.12$, $p=.047$. As seen in Figure 4, the proportion of self-corrected errors remained relatively low across maze libraries for the random group.

Performance of random group

Error-free mazes

The proportion of mazes completed without error upon initial exposure was compared to the number expected by chance as a function of number of maze choice points (1-5). The number of error-free mazes did not significantly differ from chance levels for three of the subjects Leo, Nick, and Mickey ($p>.05$) for mazes containing 1-5 choices. Solo, however, completed mazes without error at levels above chance for mazes containing 2, 4, and 5 choices ($p<.05$). For mazes containing two choices (libraries 3, 6, and 8), the probability of solving mazes without error as the result of chance responding is .25. Chance level responding by any one subject would result in 12/48 error-free mazes for these libraries. Solo solved 20/48 mazes without error for libraries containing two choices. The probability of error-free mazes as the result of chance for mazes with four choices (libraries 10 and 12) was .0625 (resulting in 2/32 error-free mazes expected by chance). For mazes with four choices, Solo solved 5/32 mazes without error. There was only one maze library containing five choices (library 13), and it was expected that 1/16 error-free mazes would be the result of chance responding (.03125) for this library. Solo solved 4/16 mazes without error for mazes with five choices.

Non-obvious choices

Experience (percentage of trials completed) had a significant effect on the percentage of non-obvious choices resulting in error for subjects in the random presentation condition, $F(4,12)=3.48$, $p=.042$. As seen in Figure 5, these results primarily reflect changes in Solo's performance. For the first trial block, 88% of non-obvious choices resulted in error for Solo, while 40% of non-obvious choices resulted in error for Solo during the last trial block. The mean proportion of non-obvious choices resulting in error for the other three subjects for the first trial block was 88% and this value only decreased to 75% for the final block of trials (see Figure 5). There was no significant difference in the percentage of non-obvious choices resulting in error as a function of maze library properties, $F(8,24)=1.39$, $p=.25$. We analyzed the proportion of non-obvious choices resulting in error as a function of number of choices contained in the mazes. There was no significant difference in the percentage of non-obvious choices resulting in error as a function of number of choices (1-3) for mazes with one non-obvious choice (libraries 5, 6, 7), $F(2,6)=1.82$, $p=.241$. For mazes containing two non-obvious choices (libraries 8, 9, 10), there was no significant difference in the percentage of non-obvious choice errors as a function of the number of choices (2-4) contained in the maze, $F(2,6)=3.68$, $p=.091$. There was also no significant difference in the percentage of non-obvious choices resulting in error as a function of number of choices (3-5) for mazes containing three non-obvious choices (libraries 11, 12, 13), $F(2,6)=1.00$, $p=.421$.

Loops and dead-end errors

The proportion of errors resulting in dead-ends was not significantly affected by experience (percentage of completed trials), $F(4,12)=1.192$, $p=.364$, nor was the proportion of dead-end errors that were repeated, $F(4,12)=1.865$, $p=.181$ (see Figure 6). Although the proportion of dead-ends that were repeated varied across maze libraries, there was no significant effect of maze characteristics on this variable, $F(11,33)=2.059$, $p=.054$ (see Figure 7).

The number of choices and the number of non-obvious choices occurring within a maze both had a significant effect on the overall frequency of loops (all types combined) for the random group, $F(11,33)=11.51$, $p<.001$ (see Figure 8). There was also a significant effect of location within the maze (i.e., correct alley, incorrect alley; see Methods) on the frequency of loops, $F(4,12)=89.92$, $p<.001$. The majority of loops (94%) occurred in incorrect alleys (71%) (*M*=39.06, *SE*=3.73) while the second greatest amount occurred in correct alleys (23%) (*M*=12.75, *SE*=2.12).

Overall, nineteen ANOVA's were conducted. Ten of these analyses produced F values that were significant with an alpha level of .05. A Bonferroni correction was used to adjust the error rates for each test in order to control for inflation of experimentwise error. With the Bonferroni correction, six of the nineteen comparisons were significant with an alpha level of .003 (with the experimentwise alpha set at .05). With an experimentwise alpha level of .05, it would be expected that one of the 19 tests would be significant as the result of chance. Although it is noted that large numbers of tests result in increased experimentwise error, it is believed that the pattern of these results is robust.

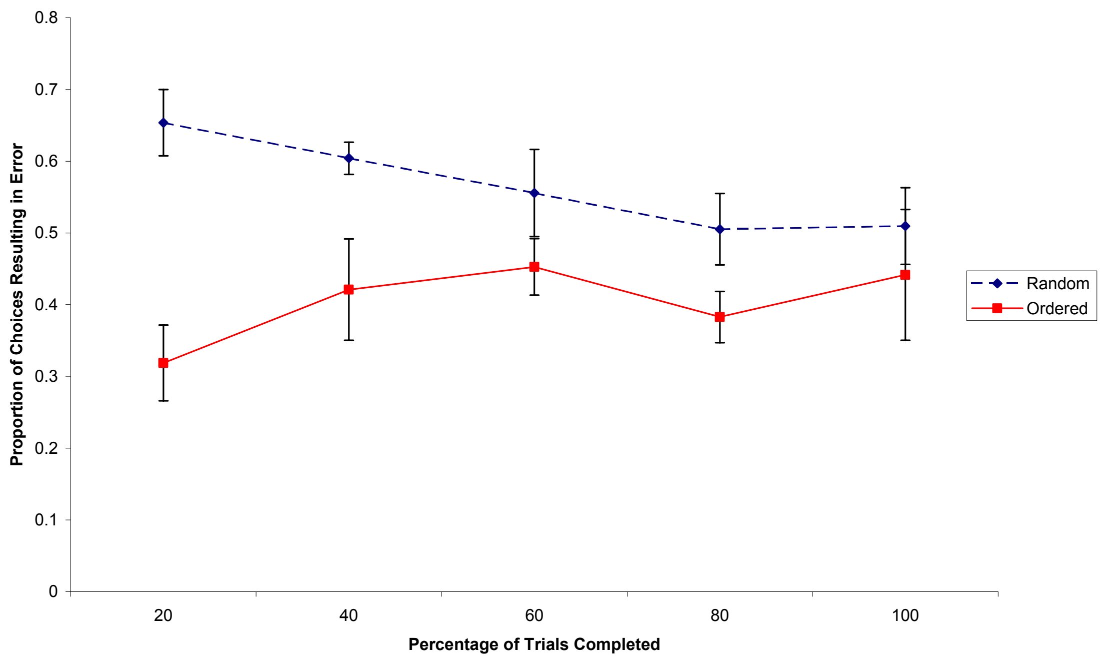

Figure 1. Proportion of choices resulting in error as a function of percentage of completed trials.

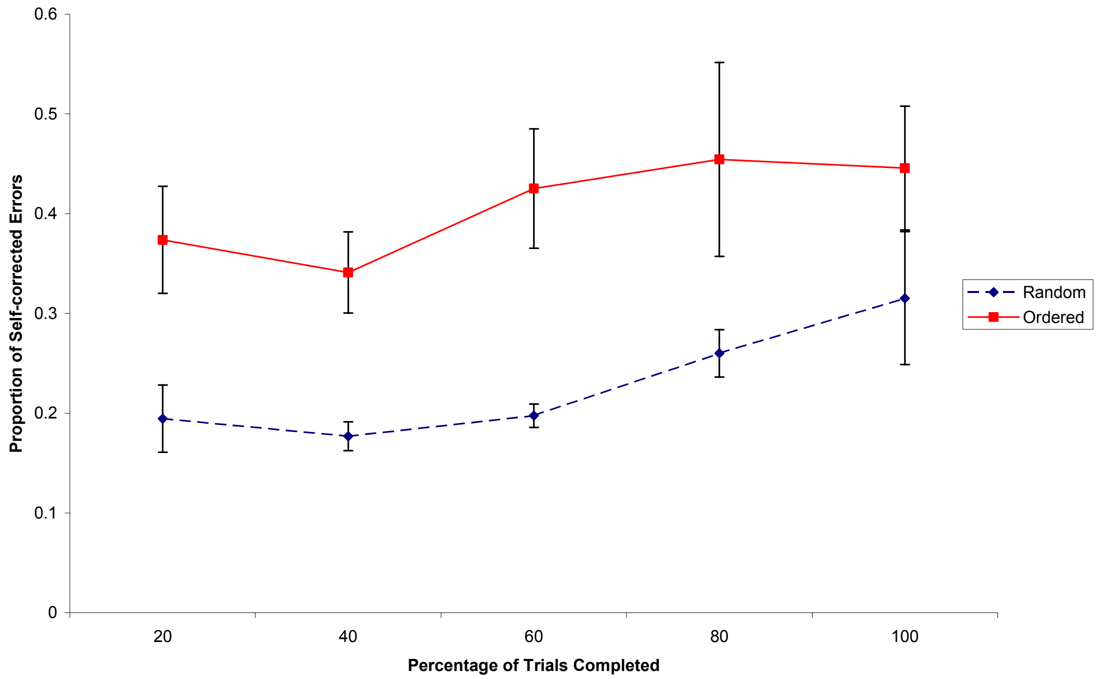

Figure 2. Proportion of self-corrected errors as a function of percentage of trials completed.

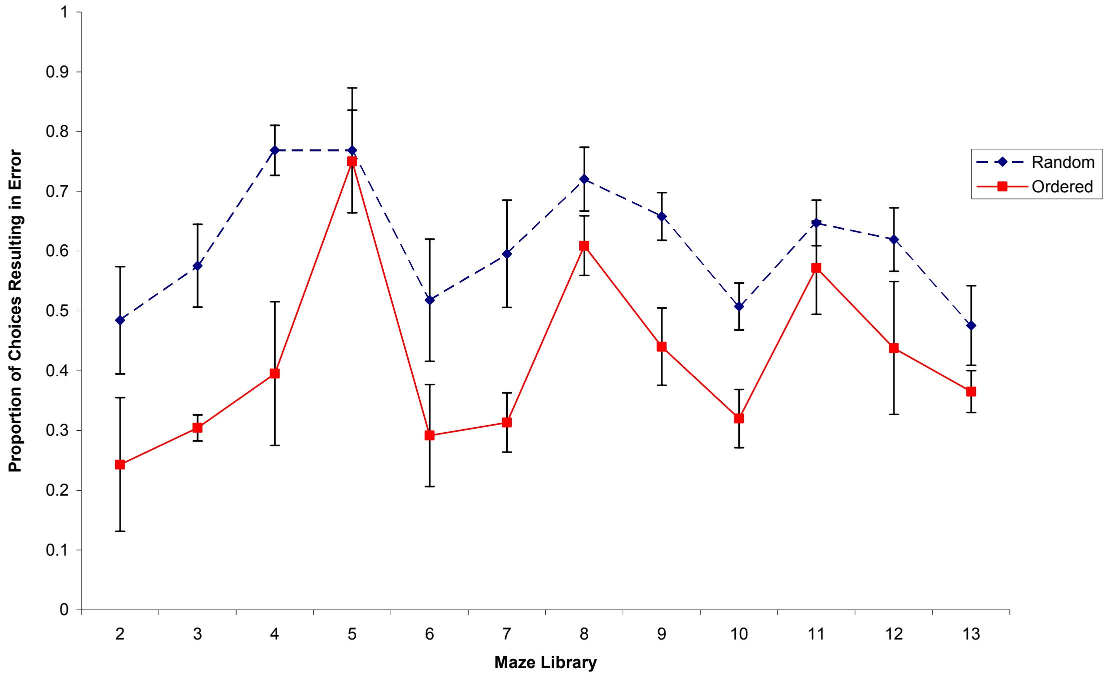

Figure 3. Proportion of choices resulting in error as a function of maze library.

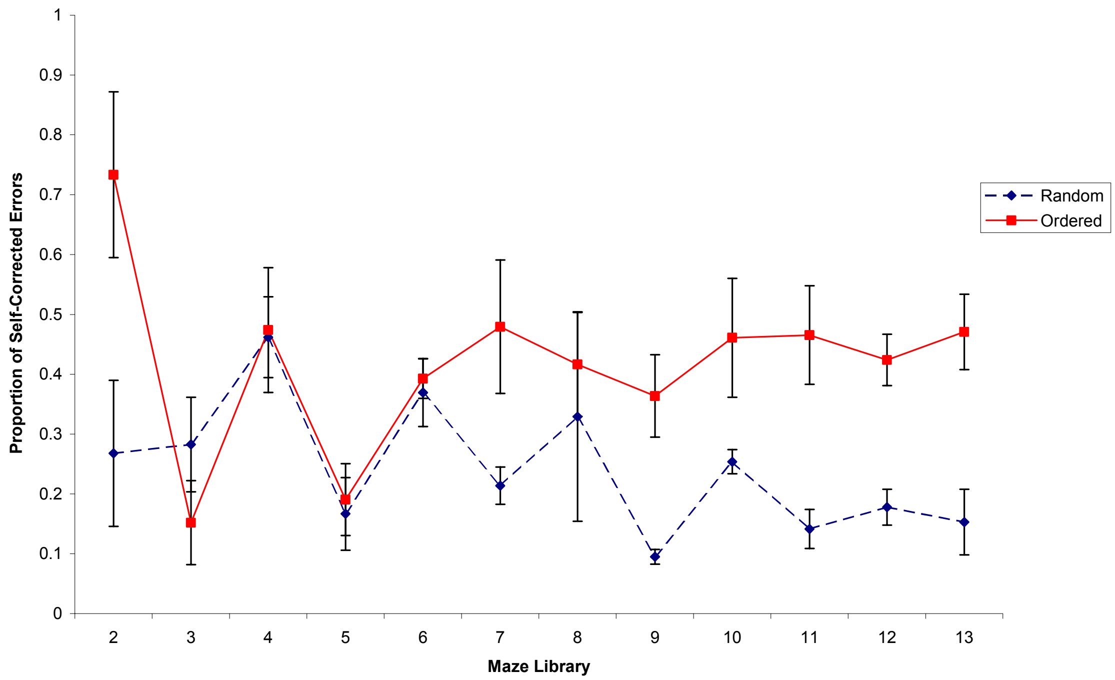

Figure 4. Proportion of self-corrected errors as a function of maze library.

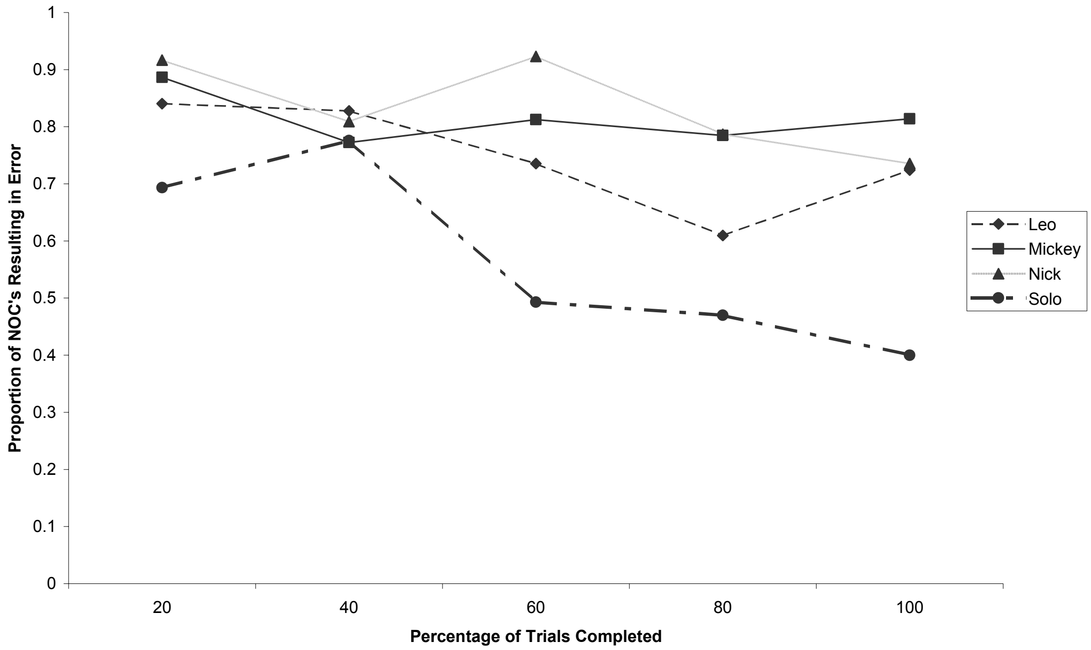

Figure 5. Proportion of non-obvious choices resulting in error as a function of percentage of trials completed.

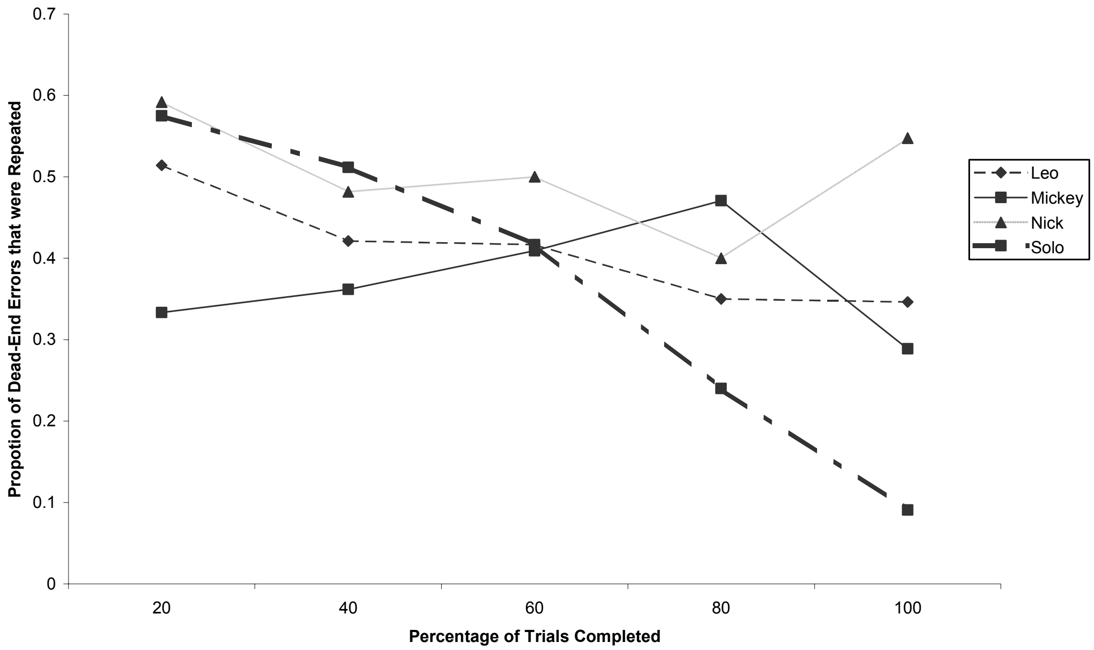

Figure 6. Proportion of dead-end errors that were repeated as a function of percentage of trials completed.

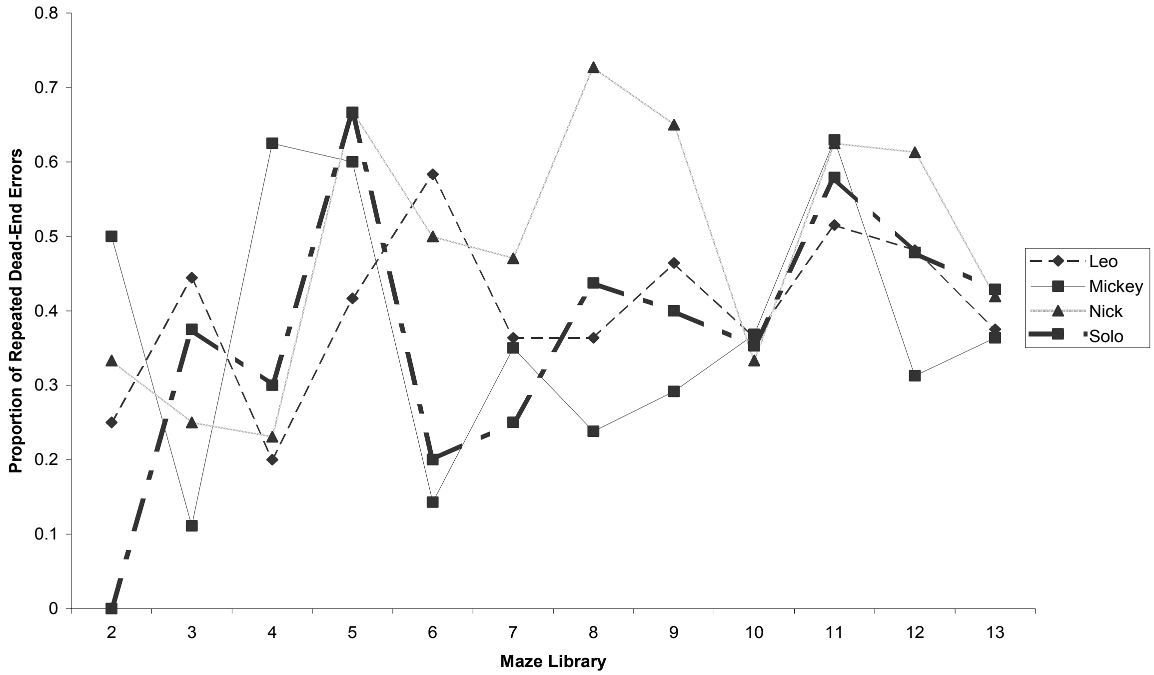

Figure 7. Proportion of dead-end errors that were repeated as a function of maze properties.

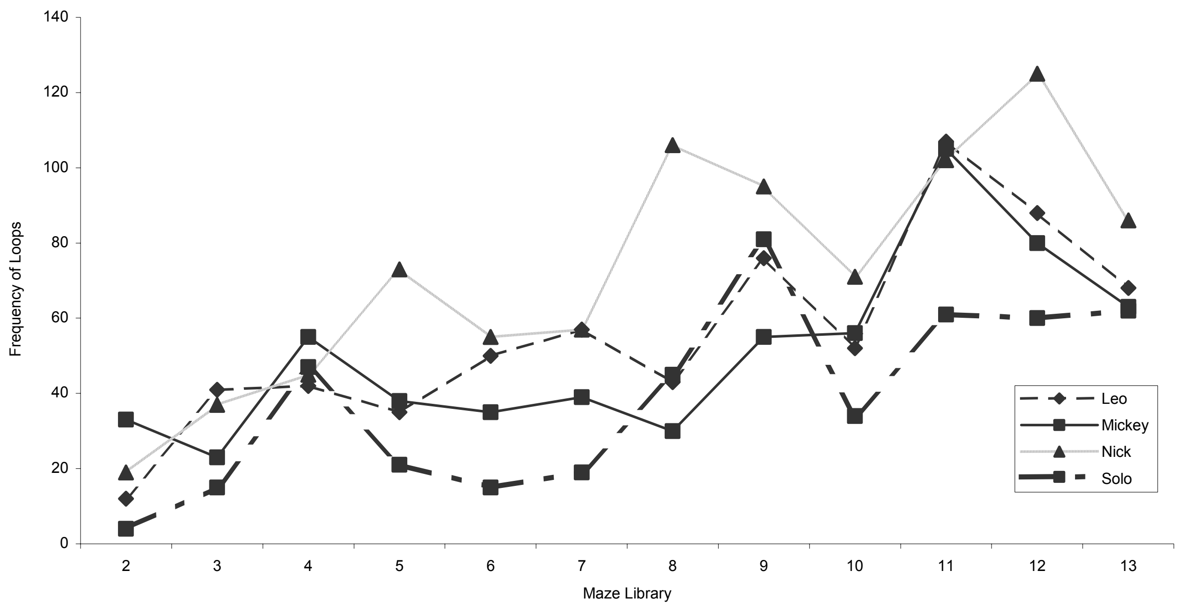

Figure 8. Frequency of loops as a function of maze library.

CHAPTER 4

DISCUSSION

Comparison of random and ordered groups

Overall, as predicted, capuchins in the random group showed an impaired ability to plan their actions while navigating through two-dimensional mazes when compared to capuchins in the ordered group. Subjects in the random group self-corrected their errors less often than those in the ordered group. As the self-correction of errors demonstrates the ability to "look-ahead", this suggests that completing the mazes in order of increasing difficulty may have facilitated the development of planful behavior in the ordered group. However, despite the difficulty they encountered, capuchins in the random group were able to complete most of the mazes in 1-3 presentations and their performance improved with experience. Thus, although the gradual increase in maze complexity aids strategic navigation, it is not necessary for completion of these problems.

In addition to looking at differences in planning as a function of type of maze presentation, we were also interested in disentangling the effects of experience and maze characteristics on the performance of the ordered group, as reported in Fragaszy et al. (2003). By exposing subjects to mazes without regard to maze characteristics we were able to determine experiential effects in the random group more clearly. The significant interaction between presentation type and experience on the percentage of choices resulting in error reveals that both of these factors play a role in maze performance. The errors of the random group decreased significantly with experience demonstrating that monkeys in this group improved despite the difficulty of the task. Thus, this study clarifies the results of Fragaszy et al. (2003) by a) showing that the type of presentation affects the ability of capuchins to solve multi-step spatial problems and b) that capuchins became more strategic in novel problems with practice.

Although there were differences in the performance of the random and ordered groups, there were similarities. First, maze characteristics influenced errors of monkeys in both conditions in similar ways. The addition of non-obvious choices resulted in increased in errors in comparison to mazes with no or fewer non-obvious choices. This suggests that non-obvious choices are inherently more difficult than other choices regardless of the monkeys' experience with such choices. Second, the frequency of self-corrected errors increased with experience for both groups. Thus, it appears that the overall increase in exposure to mazes resulted in increases in planning behavior (in terms of self-corrected errors) for monkeys in both groups. Non-obvious choices, however, proved to be difficult obstacles for monkeys in both conditions across all sessions.

Performance of random group

Comparisons of number of error-free mazes to that expected by chance revealed that only one monkey (Solo) solved mazes without error at levels significantly greater than chance for mazes containing two, four, and five choices. Maze sets containing four and five choices also contain 1-3 non-obvious choices, suggesting that Solo in some way developed an ability to look one step ahead, or to inhibit the dominant movement towards the goal at every choice. Future studies could further investigate the development this ability by presenting subjects with mazes containing only non-obvious choices and by measuring the rate of decline in repeated dead-end errors over the course of testing. It may also be informative to examine capuchins' ability to inhibit their errors while navigating through virtual three-dimensional mazes. It is possible that the cues associated with dead-end errors in two-dimensional mazes are not salient enough to hinder repeated incorrect choices. A virtual three-dimensional maze, however, may provide monkeys with additional perceptual cues (such as more realistic "walls") that may help them to avoid making repeated errors.

Measures of confusion

Capuchins in the random group produced high levels of dead-end errors. Subjects in this group were also prone to make repeated dead-end errors within a single incorrect alley. Overall, the high frequency of dead-end errors is evidence of the general confusion of the monkeys while attempting to navigate through the mazes. Moreover, repeated dead-end errors within an incorrect alley suggest that the monkeys have difficulty inhibiting the use of incorrect strategies when solving these problems. The majority of capuchins persisted in using strategies that did not permit them to reach the goal and therefore prevented them from receiving a food reward. It is possible that the monkeys were drawn by the "perceptual lure" of the apparent nearness of the goal in non-obvious choices, and were unable to inhibit using a "least-distance" strategy despite encountering a barrier. It could be argued that one of the primary maze-solving strategies learned by the monkeys in the random group was not to make the same error more than once.

Monkeys in the random group also produced many loop errors. These errors are also indicators of uncertainty and the lack of a single planned strategy. The majority of loops occurred in alleys rather than at choice points. If the monkeys were planning their actions at each choice point, it would be expected that the monkeys should show highest levels of loops at the choice point itself, rather than in the alleys. Instead, it appears that the monkeys commit an error, attend to cursor's location in relation to the goal, and then reverse direction. Thus, loops within incorrect and correct alleys are evidence of a general lack of planning within the random group.

Extent of planning

According to the Fragaszy et al. (2003) model, monkeys in the ordered group showed evidence of level 2 planning. Planning at this level involves a "forward search" strategy which produces choices that appear to lead directly to the goal and involves the correction of errors when the goal is not reached. Overall error rates did not significantly differ between the ordered and random groups suggesting that the actions of subjects in the random group may also be categorized as level 2 planning. Percentage of self-corrected errors did differ for the two groups, however, which suggests that there may be differences in planning within a given level that are not accounted for by the model of planning proposed by Fragaszy et al. (2003). Whereas three of the four monkeys in the random group (Leo, Nick, and Mickey) showed relatively low levels of planning within level 2 described by the model, one monkey (Solo) showed levels of planning comparable to monkeys in the ordered group. Solo produced error-free mazes at above-chance levels for mazes containing the greatest number of choices (four and five choices) suggesting that he had mastered the forward-search strategy and perhaps showed some evidence of integrated planning evident in level 3 planning. Overall, all four monkeys in the random group showed increases in self-corrected errors as a function of experience, providing evidence for the microdevelopment of planning despite the negative effects of random maze presentation.

Further effects of random presentation

An additional effect of the random presentation of mazes was observed in the motivation of the monkeys while performing this task. Whereas monkeys in the ordered condition had a history of being reinforced for the completion of relatively simple mazes as testing progressed, monkeys in the random group did not have the same history of reinforcement. It was possible for monkeys in the random group to be presented with the most complex mazes (those with the greatest number of choices and non-obvious choices) upon their initial exposure to the task. The lack of an initial history of reinforcement stemming from the completion of mazes with few choices produced behavior suggestive of frustration and low motivation. For example, after many unsuccessful attempts to reach the goal using the same incorrect strategy, the monkeys would often show aggressive displays (i.e., shaking the bars of their cage) and stop attending to the task (face the opposite direction). Despite this apparent lack of motivation, however, the monkeys in this group were eventually able to complete the task. In future studies, it would be informative to measure the behavioral responses of subjects as they progress through the series of mazes to determine more clearly the effects that presentation type has on general motivation.

Conclusions

Overall, random presentation did have a negative effect on the microdevelopment of planning of capuchins in the random group. Although the maze-solving strategies of both the random and ordered groups could be classified as level 2 planning according to the Fragaszy et al. (2003) model, the lower percentage of self-corrected errors in the random group suggests that it would be useful to further differentiate differences in planning within the levels proposed in the original model. In particular, the ability to inhibit incorrect responses appeared to be a crucial component of improved maze performance that is not accounted for by the model. It may be useful in future studies to further define the levels of planning and possibly include “sub-levels” that account for inhibition of errors in order to more accurately describe potential differences in planning abilities.

In addition to investigating the effects that random presentation had on the ability of capuchins to navigate strategically through two-dimensional mazes, this study was also useful in clarifying the results of the Fragaszy et al. (2003) study. As previously discussed, the effects of experience and maze characteristics on the performance of the ordered group were confounded as a result of the way in which the mazes were presented. The current study aimed to disentangle the effects of these two factors by means of random presentation of the same mazes. Overall, the results showed that both experience and maze characteristics played a role in maze performance.

Despite the increased difficulty associated with the random presentation of the mazes, capuchins in the random group were still able to complete the task and did improve with experience. The improvement of capuchins in the random group over the course of testing suggests that the microdevelopment of planning did occur to some degree within the task. However, the differences in the performance of monkeys in the ordered and random groups suggest that planning may not be a characteristic that is static for any given species. The differences between the groups also provide evidence that the way in which complex problems are presented can have an effect on the extent to which subjects "learn to plan" over the course of their experience with a particular kind of problem. Additional research would be useful in order to determine the effects that presentation type has on motivation and also to further differentiate the varying levels of planning that can be observed while solving multi-step problems.

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APPENDEX A

REVIEW OF THE LITERATURE

The ability to plan is fundamental to human life. Planning can be generally defined as, "future-oriented problem solving" (Haith, 1994). This ability is needed for creating tools, building shelter, getting food, and avoiding obstacles. In human society, planning is used for everything from determining the most efficient travel route from the Atlantic to the Pacific Ocean to deciding the best way to find all of the items on one's grocery list. Complex problem solving is not possible without planning. Human society would be drastically different if individuals were unable to envision a goal and take steps to bring their current state closer that goal. This review aims to examine different ways of defining planning and to briefly investigate how planning develops in children. Of primary interest, however, is the investigation of the degree to which non-human primates plan their actions.

There are multiple ways to define planning, and there has been some debate as to which definition most accurately describes what behaviors are necessary or sufficient to be labeled "planning". For example, Bidell and Fischer (1994) argue that planning involves, "the ability to hold action sequences on line in working memory so as to anticipate and guide performance". DeLisi (1987) provides an alternate definition of plans, claiming from a more cognitive view-point that they are, "units of procedural knowledge that coexist with propositions, which are units of declarative knowledge". He defines declarative knowledge as "knowing what" and procedural knowledge as "knowing how". Thus, according to this definition, planning involves utilizing these special units of procedural knowledge in order to attain a goal.

Choosing a definition for planning can be controversial, as certain definitions may potentially exclude certain groups from having the ability to plan. For example, if it is necessary that an individual be able to communicate their plans or an awareness of their goals to others, this would exclude young children and animals from being capable of planning (DeLisi, 1987). If however, the definition is broad and involves any behavior that may be viewed as goal-directed, then the definition may become overly inclusive. For the purposes of this paper, I will define planning according to Haith's (1994) definition as future oriented problem-solving, because this definition does not place an emphasis on the ability to communicate one's goals but also is not widely inclusive.

One solution to the dilemma of determining a single definition for planning is to divide the process into varying levels of complexity. DeLisi (1987) divides planning into four levels based on four different types of plans. At the most basic level, a type 1 plan involves a sequence of behaviors that are performed to attain a goal. At this level, plans are not conscious and require no representational or communicative component (DeLisi). At the next level, type 2 plans involve a more deliberate sequencing of the actions required to attain a goal. These plans differ from type 1 plans because they involve anticipating the actions that will be needed to reach a goal prior to performing those actions. These plans are limited as they are only used to achieve short-term goals (DeLisi, 1987). Type 3 plans, however, involve the ability to anticipate future problems and develop methods to solve them well in advance. This level of planning involves evaluation and monitoring of the effectiveness of plans and allows for their revision.

Type 4 plans are the most complex as the plan becomes an end unto itself in this case (DeLisi, 1987). These plans are representational in nature and may attempt to solve purely hypothetical problems. This categorization of plans into different levels of complexity allows for greater flexibility in the investigation of planning in both humans and animals. Thus, instead of studying whether an individual is capable of "planning", it is possible to examine to what extent, or at which level, an individual plans their actions.

Planning in children is typically studied by examining the number and kinds of errors made while a child performs a problem-solving task that involves multiple steps for completion. One such problem is the "Tower of Hanoi" task (Siegler, 1998). This problem involves moving a stack of three seriated disks (arranged on a rod) into the same configuration as the experimenter's set of seriated disks. The child must move their disks from the starting rod (on their left) to the goal rod (on their right), with one rod located between the start and the goal. They are told that they can only move one disk at a time, and can not place a larger disk on a smaller one. They are also told that their goal is to move their stack of disks into the same arrangement as the experimenter's disks in the least amount of moves. It has been found that younger children (3 year olds) have difficulty in solving this task as it requires the use of subgoals. Older children (6 year olds) show better performance on these relatively long problem-solving tasks and in their ability to form subgoals in order to reach the goal (Siegler, 1998).

The development of planning abilities in children can also be examined by noting the kind of strategies children of different ages use to solve problems. Willatts (1989) defines two primary problem-solving strategies, "forward search" and "means-ends analysis". The forward search strategy involves performing a series of actions by trial-and-error until the goal is reached. It can be noted that this strategy is relatively inefficient and can involve a large demand on memory as previous incorrect actions need to be remembered and avoided in the future. Means-ends analysis, however, involves noting the differences between one's current state and a goal state and attempting to create a solution that will reduce the difference between the two states (Willatts, 1989). This strategy often involves the formation of subgoals which are intermediary goals that must be achieved in order to reach the larger goal. This kind of strategy also relies heavily on memory as the overall plan to reach the final goal must be remembered as the individual works toward each of the subgoals. These two strategies vary greatly in terms of the amount of planning that is involved with each. With the forward search method, planning is not required as the individual does not need to look beyond the first step in the problem in order become closer to the goal. It is possible to progress only through trial and error. Means-end analysis does involve planning, however, as it requires that the individual solving the problem have a sequence of subgoals established before even attempting to solve the problem (Willatts, 1989).

There is currently some debate as to when these different forms of problem-solving strategies emerge in young children. For instance, Piaget believed that intentionality was needed in order to solve problems, and that infants weren't capable of this level of thinking until they have reached stage IV of sensorimotor development (between 8-12 months). Willatts, however, argues that there is evidence of goal-directed behavior in children as young as 4.5 months, as seen in the behavior of one of Piaget's own subjects (Laurent) who appeared to show goal-directed actions in order to make a toy move with use of a stick as a tool (1989). Piaget claimed that true goal-directed behavior did not actually occur until infants are able to search for hidden objects and remove obstacles blocking a goal. Willatts argues that children at this developmental level use unplanned forward search strategies, and that problem-solving at this stage is relatively limited in that infants are not able to try new methods in order to solve a problem (1989). At this stage, infants commit the "A not-B error" in which a child will continue to search in a location where they have previously found an object (site A), even though they have seen the object being hidden in a new location (site B). Piaget claimed that the ability to engage in novel problem-solving strategies does not emerge until stage V (between 12-18 months) (Willatts, 1989; Berk, 2000). At this point, infants show flexibility in their problem-solving and no longer commit the A not-B error. Problem-solving at this level would still not be considered "planful", however. Piaget argued that true planning was not possible until children were able to form mental representations, and he argued that this did not occur until stage VI (between 18 months and 2 years). It was argued that, once a child is able to represent the world symbolically, they no longer have to solve problems by trial-and-error (they can form solutions in advance). At this point it would appear that children are able to switch from a forward-search strategy to means-end analysis in order to reach a solution (Willatts, 1989).

Although Piaget's theory relating to the stages of infant sensory-motor development has been widely used to explain the emergence of problem-solving abilities, there are problems with relying on these stages. In particular, there appears to be evidence to suggest that infants are capable of "higher-level" problem-solving at younger ages than Piaget believed. For instance, there appears to be evidence that infants show intentionality prior to stage IV (Willatts, 1989). A study by Lamb and Malkin (1986) on the effect that infants' crying has on attention from parents suggests that infants as young as five months may be able to link their behavior to events in their environment. In addition, a study by Hood and Willatts (1986) has shown evidence that 5 month old infants will reach in the direction of an object that they were previously prevented from reaching when the lights are turned off. This has been seen as evidence that these young children show intentionality because they persist at trying to obtain a goal even when it is not visible. Piaget also argued that problem-solving at the stage IV level is not flexible and that children will persist with the same ineffective methods. There is some evidence, however, that children can make changes to their strategies prior to stage IV (as early as 7 months) (Willatts, 1989).

There is also some debate as to whether children at Piaget's stage VI truly showed planned solutions to problems. It has been argued that children at this stage who successfully complete a task usually have had much prior experience with the task and tend to not solve problems without first trying solutions that fail. Piaget also used speed of problem completion as evidence for planning. It has been argued that speed is not a good criterion for planning because an unplanned strategy is not necessarily slower than a planned one (Willatts, 1989). Therefore, both the evidence suggesting that children show more complex problem solving strategies at a younger age, and Piaget's questionable criteria used to define planning suggest that alternatives to Piaget's theory of sensory-motor development should be used to understand the development of planning in children.

The ability to plan is not only useful for solving novel problems (such as those studied by Piaget), but is also crucial for efficient navigation through space. Several studies have attempted to determine how route-planning develops in children. One such study specifically examined how forward search strategies develop within the context of a route-planning task (Fabricius, 1988). In this case, 4 and 5-year-olds were asked to search for "baby animals" (small stuffed animals) that were hidden in buckets and return these "babies" to the mother animal in the quickest way possible. There were three buckets, each containing "babies" that were arranged in an array, with the "mother" animal being closest to only one of the buckets (the "endpoint" location). The children were required to search and collect the animals and take them to the mother using the shortest possible route. Fabricius argued that use of a forward search strategy would involve three different processes: forming a representation of a route, evaluating the route's efficiency (in terms of amount of backtracking), and then repeating the first two steps in the event that backtracking occurs. It was suggested that the children may choose to search a given location on the basis of perceptual features (such as always searching the right-most bucket first) rather than relying on a forward search strategy. The results showed that children improved with age in their ability to avoid backtracking, and overall the 5 year-olds showed greater evidence of using the components of a forward search strategy in comparison with the 4 year-olds (Fabricius, 1988). In addition, 5 year-olds were more likely to self-correct errors, although there was evidence of self-monitoring of performance by the 4 year-olds. Overall, this study showed that the development of route planning could be examined by dividing problem-solving strategies into component parts and by investigating differences in the frequency of use of these component processes.

Planning in children can also be studied by examining their ability to navigate through two-dimensional space. One such study investigated the planning strategies of children 4 to 9 years of age as they solved mazes (Gardner & Rogoff, 1990). In this study, children were asked to complete two-dimensional concentric circle mazes under three different task conditions. One condition involved instructions for children to solve the maze quickly, one used instructions to solve the maze accurately, and the third condition instructed the children to solve the mazes quickly and accurately. In this case, the authors wanted to determine if the children would alter their planning strategies based on the specific demands of the task (related to the instructions given). The results showed that children used more advanced planning when accuracy was emphasized in comparison with when the instructions emphasized speed. The results also revealed that older children tended to be better at adapting their maze solving strategies based on the specific requirements of the task (Gardner & Rogoff, 1990). Thus, this study shows evidence of planning by children as they navigate through two-dimensional space and also that task circumstances can alter the use of problem-solving strategies.

To what extent do non-human primates share the capacity to plan with humans? It would appear that the ability to plan would be adaptive in the wild, as it would allow animals to forage more efficiently (by avoiding backtracking and revisiting depleted food sites) and also in terms of travelling from one destination to another while expending the least amount of energy (Janson, 2000). In addition, planning could be useful in terms of solving relatively complex problems related to obtaining food (such as using a stone tool to open a hard nut) (Shettleworth, 1998). Solving problems by trial-and-error is expensive both in terms of time and energy expenditure. Thus, if an animal has the ability to remember the correct solution to a previously solved problem (or anticipate potential obstacles before solving a problem), this can potentially give an animal an advantage in terms of food acquisition over animals who do not plan.

Several studies suggest that non-human primates have at least some capacity to engage in future-oriented problem solving. In one such study, a female chimpanzee ("Ai") was required to select a series of three numerals (0-9) in correct ascending order on a touch-screen monitor (Biro & Matsuzawa, 1999). At the start of a trial, three numerals (consecutive and nonconsecutive) were presented in a random array on the monitor, and upon touching the each number correctly in an ascending order, the numbers would disappear from the screen. Ai was rewarded after all three numerals had been touched in the correct order. In "switch" trials, the lowest number was chosen and then disappeared, but then the remaining two numbers automatically switched positions on the screen. These trials required that Ai select the position where the highest numeral had previously been located following her initial response. The results revealed that Ai was overall very proficient at ordering the numbers (both consecutive and nonconsecutive), but her performance was greatly disrupted by the introduction of the “switch” trials. It was also noted that, on non-switch trials the amount of time Ai required to make her first response was greater than that required for her to make her second and third responses. The authors suggested that this, along with Ai’s difficulty with the “switch” trials, was evidence that she planned her selection of numerals prior to physically selecting them on the touch-screen. It was argued that the “switch” trials hindered performance because they interfered with Ai’s “preplanned motor sequence” which she had chosen before making her first selection. If this is the case, then this study provides evidence that chimpanzees have the ability to plan their solution to a problem before actually attempting to solve it (Biro & Matsuzawa, 1999).

Further evidence of planning in primates can be seen in strategies used to combine seriated cups (Johnson-Pynn, Fragaszy, Hirsh, Brakke, & Greenfield, 1999). In this particular study, three primate species (chimpanzees, bonobos, and capuchin monkeys) were required to combine “nesting” cups that differed in size. There were three primary strategies that were used in combining these cups. The simplest method was the “pairing” strategy in which two cups were nested together. The “potting” strategy involved placing two or more cups individually into a single cup (Johnson-Pynn, et al, 1999). The third and most complex strategy, known as “subassembly”, involved combining two or more cups and placing these cups as a unit into another cup. It is argued that this strategy is the most complex of the three as it requires a hierarchical combination of the cups. During testing, subjects were given five different-sized cups to combine. If the subjects successfully combined the five cups, they were given a sixth cup to insert into the middle of their already combined set. Unlike the ape species, the capuchin monkeys did not spontaneously attempt to combine the cups and thus were exposed to a series of training trials prior to the start of testing. It was expected that the apes would show greater use of the subassembly strategy in comparison with the monkeys. The results showed, however, that the apes and monkeys did not differ in their preferential use of a particular strategy. The relatively complex “subassembly” method was used by all species, but was not the predominately used strategy. It can be argued that the “subassembly” method requires the greatest amount of planning because this strategy is hierarchical in nature and thus requires the use of subgoals for efficient completion. Although neither apes nor monkeys used this as the dominant means of solving this task, all three species revealed the capacity to use this strategy when combining these seriated cups. This suggests at least some capacity for planning, although not at the more advanced levels shown by children when completing the same task (Johnson-Pynn et al., 1999).

There is also evidence of planning in non-human primates as seen in their ability to efficiently navigate through large-scale space. One instance of apparent planning is evident in the tool-transport behavior of chimpanzees in the Tai National Forest (Boesch & Boesch, 1984). In this case, chimps are known to use stone or wooden “hammers” to crack open hard nuts. Different nuts require the use of different tools, however. The panda nut has a very hard shell and requires the force from a stone hammer to open while the somewhat softer coula nut can be opened through use of a wooden club. Panda trees and nuts are relatively rare in comparison to coula nuts, and the appropriate tools to open these nuts are often not in direct proximity to the trees. Thus, the chimps have been observed to transport the appropriate tools a relatively long distance in order to use them with the nuts. In particular, chimps have been shown to transport heavier stones longer distances to crack open panda nuts as heavier stones make more optimal tools and can be difficult to find. The fact that these apes find the appropriate tool some distance from the nuts and then take the tool to a location where it can be used appears to be evidence of future-oriented problem solving. The goal (opening the nuts) can only be achieved if they have the appropriate tool (a stone). Transporting the tool to the location of the nuts would appear to be a subgoal in relation to the overall goal of cracking the nuts. There is also evidence that the chimps use a "least distance rule" when transporting their tools. In other words, they travel the most efficient, shortest route between two points. As was discussed, choosing the most efficient route between locations has been used as evidence of planning in children (i.e., Fabricius, 1988). There are numerous studies with non-human primates that have documented the use of least-distance strategies in both natural and artificial foraging situations (Menzel, 1973; MacDonald, 1994; DeLillo, Visalberghi, & Aversano, 1997). The results of these studies are generally used as evidence that primates possess some form of "cognitive map" that aids in their navigation of space. It could also be argued, however, that the reliance on least distance strategies in travel can be seen as a rudimentary form of planning, as the choice of the most direct route is often not achieved by energetically expensive trial-and-error.

Planning in primates has also been investigated in terms of how they solve problems in smaller-scale space. Davis and Leary (1968) investigated the ability of several species of monkey (including lemurs, pigtail and stumptail macaques, capuchin, squirrel and woolly monkeys) to solve detour problems. These detour problems consisted of a bent wire arranged in different patterns (varying in complexity) with a Life Saver candy located in the center. The monkeys were required to manipulate the candy over the wire in order to retrieve the reward. Some of these problems required that the animal push the candy away from them in order to retrieve it. The results showed that animals "higher on the phylogenetic scale" were more efficient at solving these problems (Davis & Leary, 1968). Lemurs and New World monkeys had the more difficulty with problems that involved pushing the candy away from them in order to obtain it in comparison with the Old World monkeys. This study reveals clear species differences in the ability to solve detour problems in small-scale space.

Planning in primates is also studied by examining strategies used to navigate through two-dimensional space. As was previously discussed, planning in children has been studied by examining performance in completing two-dimensional mazes (Gardner & Rogoff, 1990). This same method has been extended to non-human primates. In one such study, rhesus monkeys were required to complete a series of two-dimensional computer mazes by moving a cursor through alleyways toward a goal by means of a joystick (Washburn, 1992). The monkeys were exposed to five maze templates that varied in terms of arrangement of alleyways and could not be solved by moving the cursor directly toward the goal. The author argued that the monkeys could successfully complete the mazes by means of two primary strategies. First, it was possible for the monkey to move the cursor directly toward the goal, and then by moving randomly when an obstacle was encountered and they were otherwise prevented from advancing (Washburn, 1992). The second possible strategy involved moving along a path of "optimal maze solution" without direct regard for the location of the goal. The paths that the monkeys chose while completing the mazes were analyzed in order to determine if the animals were using a strategy based on trial and error or one based on determining the "optimal path" toward the goal. The results revealed that the monkeys did travel along the optimal path in these mazes rather than using random movements in the direction of the goal. Although the mazes used in this study were relatively simple, these results suggest that rhesus monkeys engage in some level of planning behavior in order to solve the mazes using the most efficient method.

Further studies have been conducted to investigate planning abilities in non-human primates through use of the two-dimensional computer maze paradigm. Of primary interest was a study that compared the performance of chimpanzees and capuchin monkeys on a series of two-dimensional computer mazes that varied in terms of level of difficulty (Fragaszy, Johnson-Pynn, Hirsh, & Brakke, 2003). In this study, four chimpanzees and three capuchin monkeys were presented with 192 novel mazes that varied in terms of perceived difficulty. As in the Washburn (1992) study, subjects used a joystick in order to move a cursor through a series of alleyways in order to reach a goal. Mazes differed in terms of number of choice points and number of "non-obvious" choices. A maze choice point was defined as an area of the maze in which the subject must choose between one of two pathways. The number of choices contained in each maze ranged from one to five. "Non-obvious" choices were defined as those, "that resulted in apparently traveling a longer distance to the goal or a greater angle away from the goal" (Fragaszy et al., 2003). The number of non-obvious choices ranged from zero to three. Mazes were grouped into sets (or "libraries") composed of 16 mazes. Each maze library contained mazes with the same number of choices (1-5) and non-obvious choices (0-3). Libraries were presented to the subjects in order of perceived difficulty, with mazes later in the series containing the highest number of choices and non-obvious choices. Performance was scored in terms of the kind and number of errors subjects made while navigating through the mazes.

The authors purposed a model with five levels to describe the amount of planning that was evident in the subjects' maze performance (Fragaszy et al., 2003). At the lowest level (0), the subjects would navigate through the mazes using random movements of the joystick. Level 1 involved controlled directional movement but random selections at choice points. At level 2, subjects would choose paths that appeared to lead directly to the goal (a "forward search" strategy). The third level involved evidence of subgoaling in that subjects would make a choice on the basis of whether a potential path would lead more directly to the goal or whether a choice would result in a "dead-end" or another path. The highest level strategy (4) involved planning the entire sequence of choices prior to navigating through the maze. This highest level of planning should result in the completion of mazes without errors. Performance of both the capuchins and chimpanzees was analyzed in terms of the number and type of errors made at each choice point and was then compared to this model to determine the degree to which each species planned their solutions. The results revealed that both chimps and capuchins solved more mazes without error than expected by chance. There was a significant difference between the error rates of the two species, with 14% of all choices being incorrect for chimpanzees and 41% incorrect for capuchins. Contrary to the authors' predictions, the number of errors decreased as the number of maze choices increased for chimps, but remained unchanged for capuchins. In addition, the appearance of "non-obvious" choices had a significant effect on the performance of capuchins but not on the error rate of the chimps. Also of importance, both species were more likely to travel to the end of an incorrect alley ("dead end") than to self-correct their errors, although self-correction was evident in both species.

These results were taken as evidence that apes and monkeys plan their actions at least at level 2 as defined by the model. At this level, individuals plan ahead on the basis of one element, in this case the directness of the path in leading to the goal (Fragaszy et al., 2003). It was argued that the apes may have shown evidence of higher level planning abilities because they showed higher error rates for choices farther away from the goal, which would be consistent with memory demands relating to planning several steps ahead (evident in stages 3 and 4). It is also noted that the overall performance of the chimpanzees was better than that of the capuchins, as the monkeys made significantly more errors and were negatively affected by "non-obvious" choice points. The authors also note, however, that the worst performances of the two species overlapped, suggesting that the chimps may not necessarily be better at planning, but may be quicker at learning how to navigate through the mazes strategically (Fragaszy et al., 2003). Overall, this study provides evidence that both monkeys and apes possess the ability to plan at least one step ahead while navigating through two-dimensional space. This study also illustrates that the computer maze paradigm is useful for testing species differences in relation to planning.

One factor that this study was not able to examine, however, was whether the changes in performance throughout the course of testing were due to changes in the characteristics of the mazes (i.e., number of choice points and non-obvious choices), or if these changes were the result of acquired experience solving mazes. Thus, because the experience of the subjects increased as the perceived difficulty of the mazes increased, it is not possible to clearly determine the effects that the characteristics of the mazes had on performance. The purpose of the current study is to disentangle the effects of experience and maze presentation order in attempt to determine which factor is most influential in affecting performance throughout the course of testing. In this study, four maze-naïve capuchin monkeys were exposed to the same 192 mazes that were used in the Fragaszy et al. (2003) study, but in random order. Thus, mazes in each library (or set) no longer increased in number of choices and non-obvious choices as testing progressed, but rather varied randomly in level of difficulty based on these characteristics. In this case, it was possible that a subject could receive a maze with the greatest number of choices (5) and non-obvious choices (3) as the first maze that they were exposed to. Overall, this study hopes to add to the findings obtained by Fragaszy et al. (2003) by further investigating the effects that presentation type, experience, and problem characteristics (maze properties) have on the planning abilities of non-human primates.