Development of maze navigation by tufted capuchins (*Cebus apella*)

Jing Pan[a], Erica H. Kennedy[b], Tomas Pickering[a], Charles R. Menzel[c],
Brian W. Stone[a], Dorothy M. Fragaszy[a,*]

[a] *Department of Psychology, University of Georgia, Psychology Building, Athens, GA 30602, USA*
[b] *Department of Psychology, Frostburg State University, 101 Braddock Road, Frostburg, MD 21532, USA*
[c] *Language Research Center, Georgia State University, 3401 Panthersville Road, Decatur, GA 30034, USA*

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ABSTRACT

Theories of spatial navigation hypothesize that animals use vector or topological information to choose routes, often including detours, to move objects or themselves to goals. We assessed adult capuchin monkeys' (*Cebus apella*) navigation through 192 virtual two-dimensional mazes that incorporated detour problems. Six monkeys initially were significantly less likely to choose the correct paths when detours were required than when not. Three of the six monkeys repeatedly practiced the 192 mazes to asymptotic mastery; the other three did not practice the mazes again. In a subsequent transfer test, each monkey made correct choices equivalently often on familiar and novel mazes, which suggests that they used general planning skills for maze navigation. Of the three monkeys that practiced the 192 maze-set repeatedly, one efficiently detoured and the other two significantly improved detouring compared to their initial performance. Two monkeys, contrary to their performance when completing the 192 maze-set for the first time, made correct choices at the same rate as chimpanzees. Some evidence suggested that two monkeys used topological information, but utilization of vector information was obvious for all monkeys. Our findings suggest that the boundaries of any individual's navigational abilities are not predicted by species, but depend on experience.

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1. Introduction

This study reports how capuchin monkeys (*Cebus apella*) become skilled at navigating two-dimensional mazes. Animals in many orders (Collett, 2002), including primates (Janson and Byrne, 2007), show strategic goal-oriented navigation. Testing how non-human primates move a cursor from a start to a goal on computerized mazes provides insights on how they plan paths (e.g., Fragaszy et al., 2003; Iversen and Matsuzawa, 2001; Menzel and Menzel, 2007; Sato et al., 2004). Planning is defined as formulating in advance an organized method for action (Friedman and Scholnick, 1997, p. xi).

Based on how the future action is stored in memory, planning can be dichotomized into two forms, planned solutions and planful solutions (e.g., Willatts, 1990). In a planned solution, the solver retains the whole sequence of moves in working memory. In a planful solution (also called forward search), each step is solved

independently (Willatts, 1990). As choices constitute steps in the maze problem, we can test whether the number and the order of choices will influence a subject's choice of path to evaluate if the subject uses planned solutions (Aim I). If a planned solution is used, the subject will make a higher proportion of correct choices when there are fewer choices in a maze because it is easier to remember fewer choices (Baddeley, 2005; Fragaszy et al., 2003), and a higher proportion of correct choices at choice points that are nearer to the start because it is easier to remember the earlier elements in a sequence of future movements (i.e., the proximity effect in prospective memory) (Hitch and Ferguson, 1991). If these patterns are not evident, the subject does not use a planned solution and may use a planful solution.

A planful solution can make use of multiple heuristic visuospatial cues at each choice point concurrently. We consider two potential cues: vector information and topology. These two properties are readily perceptible to individuals with a bird's-eye view of a computerized two-dimensional maze with binary choices (as our subjects had). With regard to topology, the property of connectivity is the most important for planning paths through a two-dimensional maze. Connectivity is a mathematical concept first described by Euler in his famous analysis of "the Seven Bridges of Königsberg" problem as the existence of an edge (bridge) linking two vertices (land masses) (Gross and Tucker, 2001). Euler showed

* Corresponding author. Tel.: +1 706 542 3036; fax: +1 706 542 3275.
E-mail addresses: ustcpanjing@gmail.com (J. Pan), ehkennedy@frostburg.edu
(E.H. Kennedy), tomas.pickering@gmail.com (T. Pickering), lrccrm@langate.gsu.edu
(C.R. Menzel), brianwstone@gmail.com (B.W. Stone), dfragaszy@gmail.com
(D.M. Fragaszy).

that connectivity is the critical property governing possible routes. The angle of the path with respect to the goal and the proximity of the current location to the goal constitute the vector information of each path at the current location.

To evaluate which spatial structures of the maze were used as heuristic cues (Aim II), we incorporated detouring in the mazes such that correct alleys sometimes temporarily led away from the goal. Because capuchin monkeys made more errors at binary choice points where the correct alley pointed away from the goal (i.e., a detour) than at choice points where the correct alley pointed directly towards the goal (Fragaszy et al., 2003, 2009), we predict that the angle of the path with respect to the goal will serve as a strong heuristic cue for our subjects. Another visuospatial feature in a maze serving as a candidate heuristic cue is the termination of the incorrect alley (an end vertex of the edge). Subjects can plan a path efficiently by noticing and subsequently avoiding the termination (hereafter, dead end) of the incorrect alley before they make a choice at a choice point. This could be measured directly via eye-tracking methods. Alternatively, we can examine whether subjects avoid striking the end of the incorrect alley with the cursor after they make an incorrect choice.

Development of planning can be described as learning at the strategy level. Children can shift from inefficient to efficient strategies for planning in a variety of tasks (Bidell and Fischer, 1994; Siegler and Jenkins, 1989). The upper limit or static stage of the learned performance is often referred to as asymptote (Bouton, 2007). In a previous study (Fragaszy et al., 2009), capuchins were biased towards choosing the alley that pointed directly to the goal, choosing this path 61% of the time when it was the incorrect path. We asked in this study if they can overcome their initial bias and develop more efficient path planning (Aim III).

Assuming monkey can learn relatively efficient strategies for planning in maze navigation, we further asked whether the learned strategies are general to all mazes or specific to the trained mazes (Aim IV). Learning general strategies for planning a route through an unfamiliar maze is different from encoding and retrieval of an optimal path in a familiar maze. Testing on new versions of the same problem can reveal whether the asymptotic performance can be generalized to new mazes (Katz et al., 2002).

2. Methods

2.1. Subjects and housing

Six adult male capuchin monkeys (*C. apella*), 14–22 years old in 2007, completed this study. They were randomly assigned to two experimental groups, three monkeys per group. They resided at the University of Georgia. None of them were food-deprived during the course of testing. They were transported to a room adjacent to their housing area for testing no more than once per day. All the subjects learned to manipulate a joystick on a computer (Leighty and Fragaszy, 2003) before this study. Shortly after they demonstrated mastery of a joystick this study began, which was the first experiment in which they used a joystick.

2.2. Test apparatus

Two-dimensional alley mazes were presented to each subject. Each subject manipulated a joystick to move a white cross-shaped cursor from the start point to the end point within the alleys of a maze (see Fragaszy et al., 2003; Fragaszy et al., 2009). Upon bringing the cursor into the goal region (completion of the maze), subjects heard a tone and received a small food reward by a pellet dispenser (for Group 1 in Phase A) or by hand (for the rest of the study).
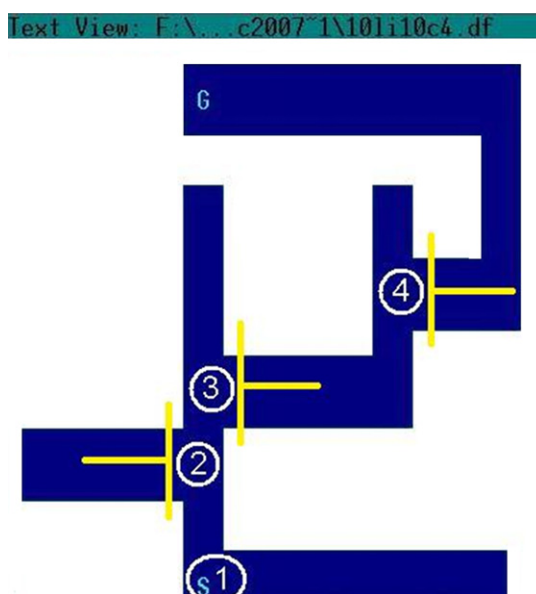

Fig. 1. Illustration of maze properties. "S" indicates the start; "G" indicates the goal. Numbers 1–4 indicate the four choice points in a sequential way on the path from the start to the goal in a maze. For the choice point with respect to the structure of the alleys, the first choice point is a forced choice point; the second choice point is a straight alley correct choice point and it is a "T" (marked yellow in the picture) rotated 90 degrees clockwise; the third and the fourth choice points are turned alley correct choice points and they are "T"s (marked yellow in the picture) rotated 90 degrees counter-clockwise. For the choice point with respect to the goal position, the first and second choice points are turns towards the goal (obvious choice points); the third and fourth choice points are non-obvious choice points.

Table 1
Maze library properties.

Library	Number of choices in a maze	Number of non-obvious choices
1	1	0
2	2	0
3	3	0
4	1	1
5	2	1
6	3	1
7	2	2
8	3	2
9	4	2
10	3	3
11	4	3
12	5	3

Each maze represented a unique organization of pathways, choice points, start and end. Fig. 1 illustrates the layout of the mazes. All the alleys were horizontal or vertical, so that all turns in the pathways were 90 degree angles. Every choice point presented one correct alley and one incorrect alley[1]. Each incorrect alley was a single straight segment and at least 2.5 cm long. Thus, choices could be in a "T" shape as the 2nd, 3rd and 4th choices shown in Fig. 1. The choice could also be in a "L" shape as the 1st choice point shown in Fig. 1, in which the incorrect alley and correct alley formed a 90 degree angle, or in a "-" shape, in which the two alleys formed a 180 degree angle, if the start was the 1st choice point.

The original mazes were grouped into 12 libraries (Table 1) of 16 mazes per library according to the total number of choice points and the number of "non-obvious" choice points. A non-obvious choice

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[1] In one maze, one choice unintentionally had two incorrect alleys and one correct alley. This maze was presented to subjects in Phase A, but not in Phase C. In the probes of Phase B, it was presented to Nick twice, Leo once and Solo once.
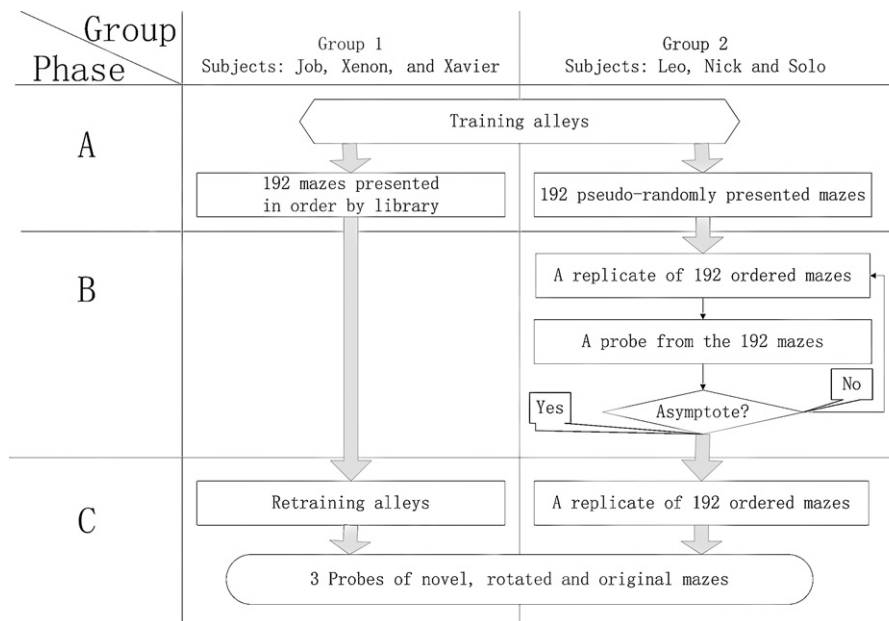
Fig. 2. Flowchart of the procedure.

point occurred where the line from the choice point to the goal point formed a greater angle with the correct alley than with the incorrect alley. A correct response at a non-obvious choice point required the cursor to "turn-away-from-goal". All other choice points were "obvious" and the correct response is to "turn-towards-goal". Within each library of the original mazes, the first 10 mazes were uniquely designed, and two of these 10 mazes were selected randomly and flipped in upside-down, left-to-right, and both directions to generate the last 6 mazes in the 16-maze library.

We also classified choice points based on the three layout combinations of previous path, correct path and incorrect path at the "T" shaped choice point. If the previous path began at the bottom of the "T" so that the subject was required to turn one way or the other, the choice point was "forced". If the choice point was at the start point, it was also "forced" as the 1st choice point shown in Fig. 1. If the previous path was at one of the arms of the "T" and the correct path was at the other arm of the "T" so that the subject had to move the cursor straight ahead to be correct, the choice point was a "straight alley" choice point as the 2nd choice point shown in Fig. 1. If the previous path was at one of the arms of the "T" and the correct path was at the bottom of the "T" so that the subject had to turn the cursor to be correct, the choice point was considered a "turned alley" choice point as the 3rd and 4th choice points in Fig. 1. Collectively, the "straight alley" and "turned alley" choice points allowed facultative choices (i.e., the cursor could go straight on or could turn 90 degrees).

Finally, we classified choice points in relation to horizontal and vertical planes. The correct alley could lead towards left, right, up or down (for example, the correct alley of the 1st choice point in Fig. 1 leads up). An imaginary horizontal axis and a vertical axis crossing at the center of a maze divide the maze into four quadrants. The correct alley could lead towards the inside of the maze (i.e., the adjacent quadrant if the choice point was in one quadrant or the center of the maze if the choice point was on one of the axes) as the 1st, 2nd and 3rd choice points shown in Fig. 1. Alternatively, it could lead to the periphery of the maze as the 4th choice point in Fig. 1, or it could be directionally neutral (towards either side of the quadrant if the choice point was on one of the axes).

The mazes were designed so that the start and end points appeared equally often in each of the four quadrants of the mazes and the choice points were spatially distributed across four quad-

rants as evenly as possible. The novel mazes in Phase C had the same properties as the original mazes. Collectively the novel mazes in Phase C had 18 non-obvious and 15 obvious choice points, 17 forced and 16 facultative choice points which were comprised of eight straight alley choice points and eight turned alley choice points.

2.3. Procedure (Fig. 2)

2.3.1. Phase A. Initial exposure

We trained each subject to move the cursor through alleys without a choice point towards the goal and to move the cursor through 90 degree turns and across the length of the monitor. After completing the training, 192 unique mazes (hereafter, original mazes) were presented to each subject.

2.3.1.1. Group 1.
Subjects in Group 1 (Job, Xenon and Xavier) were presented with the maze libraries in numerical sequence (i.e., library 1 followed by library 2) (hereafter, ordered presentation). The experimental procedure and the performance of Group 1 in Phase A was reported previously (Fragaszy et al., 2003). Group 1 did Phase A in 1994 and then did not experience mazes or joystick for 13 years but were involved in other routine testing.

2.3.1.2. Group 2.
From July 2002 to April 2003, subjects in Group 2 (Leo, Nick and Solo) completed the original mazes in 16 sets, each composed of 12 mazes. To construct these sets, one maze was pseudo-randomly selected without replacement from each of the 12 libraries. The process was repeated to select exhaustively every original maze, generating 16 sets. The 16 sets were presented to each subject in a different pseudo-random order and the mazes within each set appeared in a different pseudo-random order for each subject. This procedure is referred to as "random presentation" hereafter. The experimental procedure and the performance of Groups 1 and 2 in Phase A was reported in Fragaszy et al. (2009).

2.3.2. Phase B. Replication to mastery

Testing in Phase B began in December 2003, nine months after monkeys in Group 2 completed Phase A, and the testing was completed over 3.5 years, with several pauses of one to two months in testing. In Phase B, monkeys in Group 2 completed a replication of

the 192 original mazes (i.e., 1584 choices) using the ordered presentation described in Section 2.3.1.1 for Group 1 in Phase A. After completing each replication, the monkeys completed two mazes pseudo-randomly selected without replacement from each of the 12 libraries of the original mazes (a total of 24 mazes; hereafter, a probe set). The process was repeated until monkeys achieved an asymptotic level of correct choices on probe sets. The asymptote for each subject was defined that for five consecutive probes, the slope of best linear fit to Y (proportions of choices that were correct) against X (the ordinal number of probes) is smaller than 0.01. Subjects in Group 2 in Phase B took on average 12 testing days to complete one replication of the original 192 mazes (i.e., about one library per testing day).

2.3.3. Phase C. Transfer testing

Phase C was completed in June 2007, one month following the completion of Phase B by Group 2, and 13 years following completion of Phase A by Group 1. Group 1 had not experienced any computerized maze or joystick task in the 13 years prior to the testing stage in Phase C.

2.3.3.1. Preparation.

As preparation for Phase C, subjects in Group 2 completed their final replicate of the original 192 mazes presented in order by library. Subjects in Group 1 completed four sets of training alleys (with no choice). The first, second, third, and fourth sets of alleys contained alleys with zero, one, two, and three turns respectively. Each training set had six unique patterns of alleys and each pattern was flipped upside down, left to right, and in both planes to generate three additional patterns so that each set had 24 alleys. Subjects completed each alley by moving the cursor from the start to the goal. The subjects were given the first set on the first day of retraining, and the second set on the second day, etc. Subjects completed each retraining alley within 1-min except that Job and Xavier each took longer than 1 min to complete one alley in the fourth set.

2.3.3.2. Testing.

Following completion of the preparation, subjects from both groups were given the same common test of 3 probes, each composed of 24 mazes (72 in total). The 72 mazes in Phase C came from three sources. First, two unique mazes (i.e., flipped mazes in the original set were excluded) per library from the original mazes were selected for Phase C. Second, eight of the 24 original mazes selected for Phase C were then flipped in upside-down, left-to-right, and both directions to form the set of 24 flipped mazes for Phase C. Finally, 24 novel mazes in Phase C were constructed using the same rules as the original mazes. Each test session had an equal number of original, flipped, and novel mazes and an equal number of mazes from each library.

2.4. Analysis

2.4.1. Coding

For subjects in Group 1 during Phase A, all testing was videotaped and the videos were played back in slow motion for scoring. For the rest of this study, software programs stored the movements of the cursor in terms of pixel jumps for playbacks, and provided a visible cursor "trail" in a play-back. Dependent variables scored in playback in all phases included choice (correct or error) and if error, the outcome (self-correction or dead-end). At a choice point, a choice was made when the cursor traveled into one of the two alleys in which the cursor had not traveled. An error was coded if a subject's initial response at a choice point was to move the cursor into the incorrect alley for more than 2.5 cm on a full screen replay on a desktop CRT monitor (33 cm long × 24 cm wide); otherwise, the initial response was a correct response. An error was followed
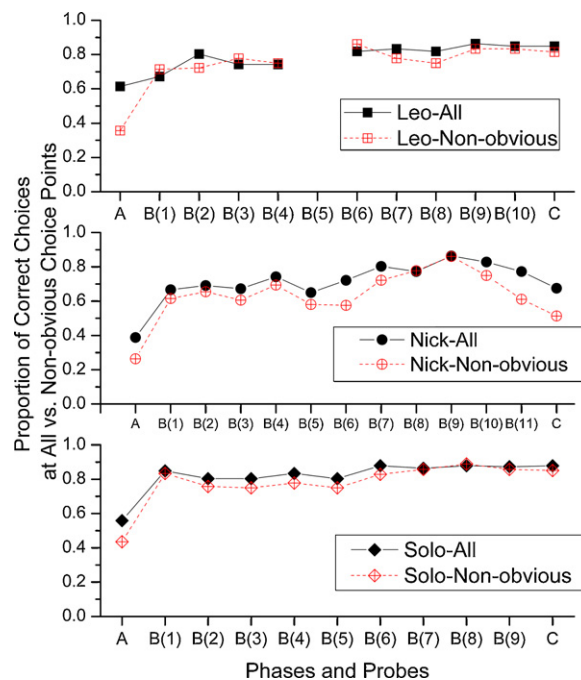

Fig. 3. Forward learning curves of correct choices at all choice points and non-obvious choice points for each individual in Group 2. Leo's data for probe 5 was inadvertently lost.

by one of two outcomes: (1) "dead-end" (DE), when the cursor contacted the end of an incorrect alley, or (2) "self-correction" (SC), when the cursor moved away from the end of an incorrect alley before contacting it.

2.4.2. Data processing

The goals of the analysis were to evaluate whether and how maze performance (measured by the choice at a choice point and/or the outcome following an error) differed as a function of individual experience and the familiarity and spatial structure of the mazes. The first step in the analysis was to examine learning curves, followed by stepwise logistic regressions. Forward learning curves for Group 2 in Phase B, starting from the first probe series, were constructed for proportion of correct initial choices out of total initial choices and proportion of correct initial choices out of total initial choices at non-obvious choice points (Fig. 3). The forward curves were used to examine individual performance. To examine group performance for Group 2, we constructed backward curves for the same two proportions (Fig. 4). Backward learning curves started with performance in Phase C as the 0 point and probes in Phase B were counted backwards from the 0 point.

Stepwise logistic regressions calculated in SPSS 15 and 16 (SPSS Inc.) were applied separately to the binary dependent variable: error vs. correct of all choices. The 10 predictor variables were (1) phases (A or C), (2) groups (1 or 2), (3) the number of choice points in a maze, (4) the order of choice points in a maze, (5) dichotomy of current choice points with regard to the goal (obvious or non-obvious), (6) directions the correct alley led towards (left, right, up or down), (7) convergence of the correct alley (inward vs. outward), (8) layouts of alleys at current choice points (straight alley choice points, turned alley choice point or forced), (9) categories of final responses at the immediately previous choice with regard to the goal (turned-away-from-goal vs. turned-towards-goal response for the 2nd and subsequent choice points), "final response" hereafter, and (10) combinations of turned-away-from-goal vs. turned-towards-goal

responses at the immediately previous two choice points for the 3rd and subsequent choice points, "previous two responses" hereafter.

For an overall test of the model, we used the data from both groups pooling Phases A and C together. To evaluate individual patterns in Phase A, the analysis was applied to each of the six monkeys. To evaluate individual patterns in Phase C, one test was applied to each of the six monkeys. The predictor variable set used in Phase C was the nine predictor variables described above excluding phases plus the source of the mazes (original, flipped and novel), producing a set of 10 predictor variables.

The criteria for all the stepwise logistic regressions were, following Hosmer and Lemeshow (2000), p-value for a variable to be entered into the model (P_e) = 0.15, p-value for a variable to be removed from the model (P_o) = 0.20 and maximum iteration = 20. The method for variable entry was forward stepwise. Dummy variables were constructed for all categorical variables with more than 2 categories. A stepwise method was appropriate because the predictor variables were assumed to be relatively orthogonal to each other by the design of the mazes. If not otherwise stated (such as in the stepwise logistic regression analysis), α level was set at 0.05, two-tailed.

3. Results

The data set was composed of 6005 choices in completed mazes by both groups across three phases. For Phases A and C, there was approximately the same number of choices for each monkey at each Phase for data analysis (for Phase A, from 440 to 528; for Phase B, from 529 to 682; for Phase C, from 162 to 198).

3.1. Development of performance during practice with mazes

Subjects met the asymptote criteria at the 9th (Solo), 10th (Leo) or 11th (Nick) probe. For correct responses at all choice points and at non-obvious choice points (Fig. 4), there were two waves in the curve defined by an inflexion point. Seven probes before Phase C seemed to be a common inflexion for the development of correct responses at all choice points and six probes before Phase C seemed to be an inflexion for the development of correct responses at non-obvious choice points. The high performance cluster began at the beginning of Phase B for Solo, which was earlier than the other two subjects. For all subjects, the lower limits of performance were located in Phase A and the upper limits were never located at the last probe in Phase B.
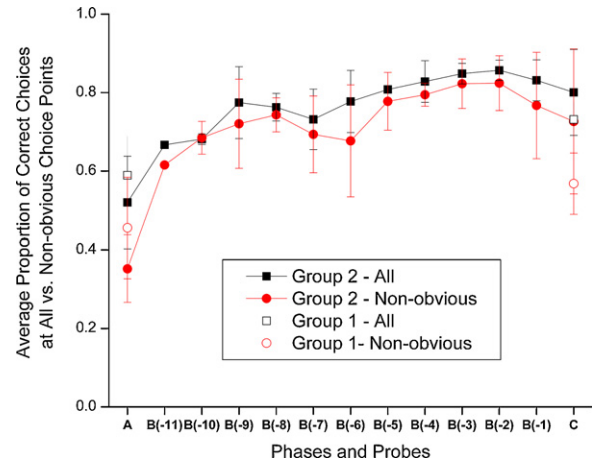

Fig. 4. Backward learning curves of correct choices at all choice points and at non-obvious choice points using mean value. The last probe is on the far right (noted as −1) and the first probe is on the far left.

3.2. Effects of repeated practice with the mazes on performance during transfer testing (Aim III)

As shown in Table 2, each individual achieved significantly more correct choices than chance (50%) in Phase C. As shown in Table 3, both groups made significantly more correct choices in Phase C than Phase A (p < 0.001 for each group, Fisher's exact test). In Phase C, Group 2 had a significantly larger proportion of correct choices than Group 1 (p = 0.0046, Fisher's exact test). Group 1 self-corrected the same proportion of errors in Phase A and Phase C (p = 0.71, Fisher's exact test); Group 2 self-corrected a significantly greater proportion of errors (p < 0.001, Fisher's exact test) in Phase C than in Phase A.

3.3. Variables affecting choice

As shown in Table 4, stepwise regression analysis on the data from Phases A and C for all the monkeys revealed that choice (correct or error) at each choice point was significantly influenced by phase, group, spatial configuration of the current choice and configuration of previous choices. Neither the number of total choices nor the order of choices in a maze influenced choice. At the last step, the Nagelkerke R square for the model was 0.22 and the p-value for Hosmer and Lemeshow Test was 0.072 (note: p > 0.05 implies that the model's estimate fits the data at an acceptable level). Phase and obvious vs. non-obvious choice point yielded the smallest p value.

Table 2
Individual's choices as a function of non-obvious vs. obvious choice points in Phase C.

Group	Individual	Correct/non-obvious choices	Correct/obvious choices
1	Job	55/103	81/87[*]
	Xavier	42/82	71/80[*]
	Xenon	69/105[*]	71/87[*]
2	Leo	88/108[*]	80/90[*]
	Nick	55/107	78/90[*]
	Solo	91/107[*]	82/90[*]

[*] Distribution of correct vs. incorrect choices significantly different from chance, one-way Chi-square test, d.f. = 1, p < 0.05.

Table 3
Performance in Phases A and C.

		Phase A	Phase C
Proportion of choices that were correct	Group 1	845/1425 = 0.59	399/544 = 0.73
	Group 2	734/1584 = 0.46	477/592 = 0.81
Proportion of errors that were self-corrected	Group 1	244/580 = 0.42	58/145 = 0.40
	Group 2	174/850 = 0.20	68/115 = 0.59

Table 4
Stepwise logistic regression model for predicting whether the choices were correct using data from both groups in Phases A and C.

Variables remained	Categories of the variable	Number of choices	Number of correct choices	Proportion of choices that were correct	Wald Chi-square	d.f.	Sig.
Phase	A	3009	1579	0.52	2.2×10^2	1	<0.0001
	C	1136	876	0.77			
Group	One	1969	1244	0.63	30	1	<0.0001
	Two	2176	1211	0.56			
Non-obvious choice	Obvious	1890	1389	0.73	2.9×10^2	1	<0.0001
	Non-obvious	2255	1066	0.47			
Directions	Down	1049	697	0.66	43	3	<0.0001
	Left	912	484	0.53			
	Right	1217	697	0.57			
	Up	967	577	0.60			
Convergence	In	2190	1355	0.62	6.8	2	0.034
	Neutral	380	208	0.55			
	Out	1575	892	0.57			
Layout	Turned alley choice point	1089	619	0.57	31	2	<0.0001
	Forced	1665	972	0.58			
	Straight alley choice point	1391	864	0.62			
Final response	First choices	1530	979	0.64	35	2	<0.0001
	Turned-towards-goal	1178	752	0.64			
	Turned-away-from-goal	1437	906	0.63			
Previous two responses	Turned-towards-goal/turned-towards-goal	250	143	0.57	3.0×10	4	<0.0001
	Turned-towards-goal/turned-away-from-goal	319	192	0.60			
	Turned-away-from-goal/turned-towards-goal	368	265	0.72			
	Turned-away-from-goal/turned-away-from-goal	416	267	0.64			
	First two choices	2792	1588	0.57			
Overall choice distribution		4145	2455	0.59			

The monkeys were more likely to make correct choices in Phase C, and were more likely to make errors at non-obvious choice points.

The direction of the correct alley significantly influenced the monkeys' choices in the following manner. Subjects were significantly more likely to make correct choices when the correct alley led downward rather than upward ($p < 0.0001$) but significantly less likely to make correct choices when the correct alley led to the left rather than upward ($p = 0.041$). They made equivalent proportions of correct choices when the correct alley led to the right and upward. Subjects were significantly more likely to make correct choices when the correct alley led inward rather than outward ($p = 0.011$), and subjects were significantly less likely to make correct choices when the correct alley led in a neutral direction rather than outward ($p = 0.15$).

Subjects were more likely to make a correct choice if previous choices were turned-towards-goals than if previous choices were turned-away-from-goals ($p = 0.052$), and also more likely to make a correct choice if there were no previous choices (current choice points were the first choice points) than if previous choices were turned-away-from-goals ($p < 0.0001$). Subjects were more likely to make a correct choice if the immediately previous two choices were a turned-away-from-goal followed by a turned-towards-goal than all other conditions ($p < 0.0001$, see Table 4). Subjects were less likely to make a correct choice at turned alley choice points than straight alley choice points ($p < 0.0001$), but the probability of making a correct choice did not differ between forced choice points and straight alley choice points ($p = 0.33$).

Subjects showed individual differences in their strategies to solve the mazes, and their strategies changed from Phase A to Phase C (Table 5). Only Solo (from Group 2) in Phase C managed to make choices without respect to non-obvious vs. obvious structure of the choice points (88% correct choices). The remaining two monkeys from Group 2 improved making correct choices at non-obvious choice points significantly (for Nick, χ^2 (1, $N = 391$) = 22, $p < 0.001$; for Leo, χ^2 (1, $N = 394$) = 64, $p < 0.001$). In Phase C, each monkey made correct choices in equal proportions on novel and original mazes. Each monkey except Solo also made correct choices in equal proportions on original and flipped mazes. Solo made significantly fewer correct choices in flipped mazes than original mazes, $p = 0.049$. This comparison is known as a transfer test (Katz et al., 2002). Monkeys in Group 1 were influenced by the number or the order of the choice points. Xenon and Xavier in Phase A but not in Phase C made more correct choices when there were more choice points in a maze (Fig. 5); Job in Phase A and C consistently made more correct choices for choice points that were nearer to the goal.

4. Discussion

We determined that capuchin monkeys in Group 2, with extended practice on a large set of two-dimensional mazes, improved on reducing their initial bias to select the more direct route to the goal, and instead chose the detour path when necessary. The bias disappeared for one monkey (Solo) and lessened significantly for the other two. Following practice, they performed better than another group of three monkeys (Group 1) that did not have this practice, reversing an advantage on initial testing held by Group 1, as reported by Fragaszy et al. (2009). In that report, Group 1 was labeled "ordered group" and Group 2 was labeled "random group". We further demonstrated that the monkeys' learned strategies generalized to novel mazes. In the transfer test, all monkeys smoothly transferred their terminal performance in the original mazes to novel mazes, as measured by the proportion of choices

Table 5

Individual patterns by stepwise logistic regression model for predicting correct responses across Phases A and C.

Variables remaining in the model	Values or categories of the variable	Group 1						Group 2					
		Job		Xavier		Xenon		Leo		Nick		Solo	
		Phase A	Phase C	Phase A	Phase C	Phase A	Phase C	Phase A	Phase C	Phase A	Phase C	Phase A	Phase C
Number of choice points	1			0.48	N.S.	0.42							
	2			0.50		0.66							
	3	N.S.[b]	N.S.	0.43		0.57	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
	4			0.49		0.69							
	5			0.58		0.67							
Order of choice points	1st	0.56	0.60										
	2nd	0.67	0.66										
	3rd	0.77	0.87	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
	4th	0.87	1.00										
	5th	0.61	1.00										
Non-obvious choices	Obvious	0.85	0.93	0.67	0.89	0.74	0.93	0.55	0.92	0.53	0.87	0.70	N.S.
	Non-obvious	0.53	0.53	0.31	0.51	0.53	0.66	0.36	0.82	0.26	0.51	0.44	
Directions	Down		0.77	0.58				0.85			0.96	0.69	
	Left	N.S.	0.56	0.53	N.S.	N.S.	N.S.	0.53	N.S.	N.S.	0.78	0.43	N.S.
	Right		0.68	0.41				0.79			0.85	0.56	
	Up		0.82	0.40				0.902			0.86	0.52	
Convergence	In							0.47			0.66		0.90
	Neutral	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.42	N.S.	N.S.	0.78	N.S.	1.00
	Out							0.41			0.69		0.84
Layout	Turned alley choice point	0.56		0.51	0.73	0.63	0.76	0.34		0.28	0.63		0.87
	Forced	0.64	N.S.	0.53	0.74	0.63	0.71	0.38	N.S.	0.40	0.70	N.S.	0.83
	Straight alley choice point	0.77		0.40	0.60	0.61	0.91	0.58		0.45	0.68		0.96
Final response	turned-towards-goal		0.76			0.68	0.80	0.49	0.94	0.44			0.91
	First Choices	N.S.	0.59	N.S.	N.S.	0.53	0.67	0.32	0.83	0.34	N.S.	N.S.	0.79
	Turned-away-from-goal		0.82			0.68	0.89	0.53	0.83	0.39			0.94
Previous two responses	Turned-towards-goal/turned-towards-goal	0.87		0.32		0.59		0.44		0.42	0.60		
	Turned-towards-goal/turned-away-from-goal	0.59	N.S.	0.48	N.S.	0.57	N.S.	0.53	N.S.	0.30	0.76	N.S.	N.S.
	Turned-away-from-goal/turned-towards-goal	0.85		0.58		0.67		0.67		0.52	0.75		
	Turned-away-from-goal/turned-away-from-goal	0.81		0.41		0.81		0.51		0.33	0.89		
	First 2 choices	0.61		0.49		0.60		0.39		0.39	0.63		
Sources	Flip												0.82
	Novel	N.A.[c]	N.S.	N.A.	N.S.	N.A.	N.S.	N.A.	N.S.	N.A.	N.S.	N.A.	0.89
	Original												0.92

Notes:

[a] Only for variables that are significant for predicting correct responses, the proportion of correct responses are given in the body of the table.

[b] Not significant for predicting correct responses.

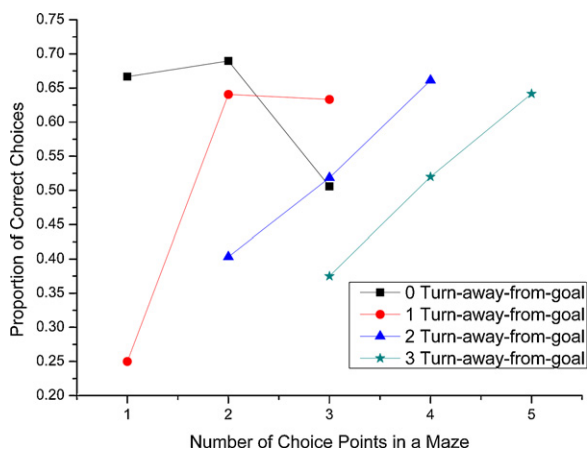[c] Not applicable, because in Phase A, all the mazes are original mazes.

Fig. 5. Xenon and Xavier's average correct choices in Phase A grouped by number of non-obvious choices in a maze. For mazes with an equal number of non-obvious choice points, the more choice points in a maze, the lower the proportion of non-obvious choice points and the higher the proportion of obvious choice points.

that were correct out of the total number of choices made. These findings show that the monkeys used general strategies to solve maze problems rather than remembered routes in specific mazes. We discuss these findings in relation to models of spatial planning in navigation, models of learning, and findings with chimpanzees on similar spatial problems.

4.1. Models of planning: planful solutions vs. planned solutions

We found little evidence that the monkeys memorized a sequence of movements before they started to move the cursor in a maze (i.e., used a planned solution). Monkeys were as likely to make errors on choice points nearer to the start point as farther away. They were also as likely to make errors in mazes with fewer choice points compared to mazes with more choice points. Instead of using planned solutions, subjects apparently used planful solutions. If the monkeys used planful solutions, their choices should not have been affected by either number or order of choice points but instead by other spatial features of the mazes. Three forms of evidence suggest that they used planful solutions. The strongest evidence for planful solutions is that all subjects in all phases, except for Solo in Phase C, made proportionally more errors at non-obvious choice points than at obvious choice points. Further evidence that the monkeys used planful solutions comes from Xenon and Xavier's performance in Phase A. In this phase and in mazes that contained at least one non-obvious choice point, these two monkeys made proportionally more correct choices at mazes with proportionally more obvious choice points (see Fig. 5). The final piece of evidence that the monkeys used planful solutions is that Job made proportionally more correct choices at choice points nearer to the goal, showing that he did not store in memory the full sequence of choices to the goal location before beginning to move the cursor in a maze.

4.1.1. A vector strategy for planful solution

A planful solution does not require memorizing routes. Instead, it requires paying attention to the spatial features at each choice point, such as the location of the goal. Capuchin monkeys most often moved directly towards the goal (made turn-towards-goal choices) regardless of whether the chosen alley led to the goal and consequently they made more errors at non-obvious choice points than at obvious choice points. We name this strategy the "vector strategy". If the cursor is free to move on the screen without restriction by the alleys, the shortest path to the final goal would be along a Euclidean radial from the current choice point to the final goal. The vector towards the goal is what seemed to guide the monkeys'

choices: they preferred the alley associated with the longer of the two components of the vector. When the choice point is obvious, this strategy produces a correct choice. But when the choice point is non-obvious, the same strategy produces an error.

The "vector strategy" as displayed by the monkeys in this study can be compared to a model that explains efficient detouring in insects: the vector accumulator in path integration (Collett, 2002). For insects that are forced to take detours, path integration enables or enforces detours. An accumulator keeps vector information of its current distance and direction from the insect's nest, and at any point, the insect can use this vector information to navigate by path integration until it has reached its nest. There is both similarity and difference between the path integration in insects and the "vector strategy" in the monkeys in this study. The similarity is that the direction of the vector is used. The difference is that capuchins do not need to accumulate directional information from past routes to update their heading, because all the information required to make a correct choice is visible at each choice point.

Overall, capuchins prefer the shorter path even when it cannot lead to the goal. Chimpanzees showed the same preference in finger mazes (Iversen and Matsuzawa, 2001) but not while solving mazes by moving a cursor with a joystick (Fragaszy et al., 2009). In the former case, when the familiar short path in a finger maze was blocked but a longer path was available, chimpanzees kept choosing the blocked short path. The difference in the chimpanzees' relatively impaired performance in the touch-screen vs. joystick mode of presentation could reflect the immediacy of interaction with the display in the case of the touch-screen compared to the joystick. Using abstract symbols (Arabic numerals representing the quantity of food instead of real food) improved chimpanzees' performance in a reversed contingency task in which they received the quantity of the food they did not choose (Boysen and Berntson, 1995). Perhaps the touch-screen version of the mazes presents chimpanzees with the same difficulty of reversing their actions when the hand approaches the goal as was present in Boysen and Berntson's (1995) task. One could investigate how individuals perceive the path in 2D virtual mazes in different modes of interaction (cursors controlled by joysticks vs. discs controlled by finger on touch-screens). One could argue that it is more abstract to control a cursor on a 2D screen through the movement of a joystick in three dimensions (a hand (3D) → a joystick (3D) → a cursor (2D)) (Leighty and Fragaszy, 2003) than to control a disc on a touch screen (a hand (3D) → a disc (2D)). If the joystick presentation is indeed more abstract than touch screens for chimpanzees, and if abstract stimuli help chimpanzees to override a predisposition to move directly to the goal, then it make sense that chimpanzees chose the turned-away-from-goal path (long path) efficiently on a joystick work platform (Fragaszy et al., 2009) but did not choose the long path on the touch screen platform (Iversen and Matsuzawa, 2001). Capuchins needed extensive practice to reach this same point with the cursor presentation, suggesting that capuchins have greater difficulty in shifting from a strongly biased behavior to another behavior, compared to chimpanzees.

4.1.2. Attending to continuity of the alleys for planful solution

Alternatively, an efficient planful solution can be to pay attention to the continuity of the alley. If monkeys had learned to pay attention to the continuity of the alley to the goal, their performance would not have been affected by non-obvious choice points. Paying attention to the continuity of the alley would produce perfect performance, and that is what Solo nearly achieved in Phase C. In Phase C, Solo achieved a proportion of 85% correct choices on non-obvious choice points. This performance was not significantly different from his performance on obvious choice points (91% correct choices) and is the best performance among the 6 subjects on obvious choice points.

If a monkey is able to note continuity of the path, and is more motivated to complete the maze the closer it gets to the goal, it might make more correct choices at choice points nearer to the goal. Perhaps that is what one monkey (Job) did. In Phase A and Phase C, regardless of the number of choice points in a given maze, the nearer the choice points to the goal, the more likely Job was to make a correct choice (as seen in Table 5).

Paying attention to the alley continuity may be related to the topological spatial cognition model that explains detouring in rodents. Place cells in the hippocampuses of rodents fire maximally when the animals are in a particular location. These cells are described in terms of networks of interconnected place cells that can link a start point to a goal site (Collett, 2002). When barriers are introduced into an arena, place cells with fields close to the barrier become silent, and effectively remove themselves from the network of interconnected cells and thus form a neural version of the planning process. Consequently, the rat would detour around the barrier (Collett, 2002). Neurons displaying place-related activities like those of the place cells in rodents are also found in primates' hippocampuses (Hori et al., 2005; Hori et al., 2003). If capuchin monkeys have similar neural capacities as rhesus monkeys, which can have different neural representations for the final goal and the current goal in a maze (Saito et al., 2005), they should be capable of choosing an alley going to the next choice point (the current goal) instead of choosing an alley pointing to the final goal. In Phase C, capuchins did this to some extent and Solo clearly did so.

4.1.3. Attention to continuity towards the end of the alley (but after choices)

We could not test whether the subjects looked ahead along either alley before they made a choice. Instead, we showed that subjects looked ahead after making an error (i.e., they self-corrected). Each subject in Group 2 clearly learned to do this, making significantly more self-corrections, proportionally, in Phase C than in Phase A (overall mean, 59% vs. 20%, respectively. To avoid hitting the dead end, they must notice it, and this could happen before or after passing through a choice point. If subjects continuously visually monitored a certain distance ahead of the cursor's current position, they would not hit the dead end because as soon as it was within the distance that they monitored ahead of the cursor, they would notice it. Our results, however, showed that they hit the dead end at a measurable rate. Thus, we propose that subjects looked ahead of the cursor intermittently, not continuously. We assume that the positions where they looked ahead were randomly and discretely distributed around the choice points. When the position where they looked ahead was before the choice point, and the dead end was within the distance they monitored, they made a correct choice before the choice point. When they looked ahead after passing the choice point and the dead end was within the distance they monitored, they made self-correction after the choice point. This is evidence of planning at least at least within the distance of a single segment of the alley. Diminishing errors and increasing rates of self-correction could reflect an extension of the monitored distance, or more frequent visual monitoring. Further tests should use eye-tracking techniques to verify our hypothesis.

4.1.4. Alternative planful strategy based upon goal location

An alternative planful strategy guiding choice at each choice point would be choosing inward alleys. Although in our design we distributed goal locations evenly across four quadrants to keep subjects from developing a preference for moving in any of the four directions (up, down, left and right), we did not control whether the correct alleys led inward or outward. There were more correct alleys leading inward (2190 choice points) than in other directions (380 neutral choice points and 1575 choice points leading outward;

see Table 4). Thus the dead ends are more likely to be located on the peripheries of the mazes, and subsequently consistently choosing an alley leading inward at any choice point will result in a better-than-chance performance. As shown in Table 5, the "choosing an alley leading inward" strategy is evidently influenced by experience because no animals in Group 1 were influenced by the correct alley leading in or out, but animals in Group 2, following extensive experience with the original mazes, were influenced differentially to move inward in Phase C compared to Phase A.

4.2. Learning

The data have shown that capuchin monkeys' planning strategies can be improved and transferred to novel mazes. Both the proportion of overall choices and non-obvious choices that were correct and proportion of errors that were self-corrected improved over the course of the study. This improvement cannot be attributed merely to improved control of the cursor, as the monkeys controlled the cursor well at the start of the study, and improved control would not differentially impact the proportion of correct choices at a particular kind of choice point.

Fragaszy et al. (2009) suggested that capuchins could master the maze problem with practice. This study confirmed Fragaszy et al.'s suggestion. Initially, both groups of capuchins in Phase A made significantly more errors when compared to chimpanzees in the same maze tasks (Fragaszy et al., 2009). The performance of capuchins in Group 2 (the group that practiced the original series to asymptote) in Phase C, however, was significantly better than that of all capuchins in Phase A (Fragaszy et al., 2009). The two best capuchins' performances (84% and 87% correct choices) in Phase C fall into the range of the performance by chimpanzees on their first exposure to the same original mazes used in this study (average 82% correct choices for ordered presentation and 81% correct choices for random presentation; reported in Fragaszy et al., 2009). Thus, the difference in chimpanzees and capuchins' initial performance is not a fixed feature of cognitive capacity, but rather is a dynamic feature of cognitive development. Lacking practice, no monkey in Group 1 achieved the chimpanzees' level of performance. Practice permitted capuchins in Group 2 to perform in Phase C as efficiently as chimpanzees in this task. A similar argument for the dynamic nature of cognitive skill has been made concerning chimpanzees' spatial memory for numbers briefly presented on a touch screen. After extensive practice (over several years), a chimpanzee outperformed adult humans naïve to the task (Kawai and Matsuzawa, 2008).

The mazes we presented to the monkeys required altering a prepotent action (traveling directly towards the goal) in favor of an alternative action (taking a detour). Another problem where monkeys show difficulty in altering a prepotent action is the "gravity bias" task. In the gravity bias task, tamarin monkeys preferred to search for a dropped object directly beneath the release point even when the trajectory of the object was altered by a tube to another place (Hauser et al., 2001; Hood et al., 1999). The gravity bias in tamarins, unlike in human children or dogs, persisted despite "extensive" training, which lasted several days for each of three phases in total (Osthaus et al., 2003; Hood et al., 1999). In both the gravity bias task and the maze problem, the problems are spatial; the prepotent actions are to take the shortest Euclidean path (to the ground or to the goal); monkeys are biased even after a certain amount of training. Because of those similarities in the tasks and the performance capuchins in Group 2 finally achieved, we predict more extensive and longer training will allow tamarins to diminish their gravity bias in the gravity bias task significantly. More generally, when investigating whether an individual of any species, including our own, can alter prepotent behaviors, we should allow practice to asymptote on a large set of exemplars before we reach a

conclusion. Effective strategies for spatial problem-solving, including detouring, can be learned.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.beproc.2010.11.006.

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