Anim Cogn (2003) 6:149–160
DOI 10.1007/s10071-002-0137-8

ORIGINAL ARTICLE

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Strategic navigation of two-dimensional alley mazes: comparing capuchin monkeys and chimpanzees

Received: 14 December 2001 / Revised: 16 May 2002 / Accepted: 6 June 2002 /

Abstract Planning is an important component of cognition that contributes, for example, to efficient movement through space. In the current study we presented novel two-dimensional alley mazes to four chimpanzees and three capuchin monkeys to identify the nature and efficiency of planning in relation to varying task parameters. All the subjects solved more mazes without error than expected by chance, providing compelling evidence that both species planned their choices in some manner. The probability of making a correct choice on mazes designed to be more demanding and presented later in the testing series was higher than on earlier, simpler mazes (chimpanzees), or unchanged (capuchin monkeys), suggesting microdevelopment of strategic choice. Structural properties of the mazes affected both species' choices. Capuchin monkeys were less likely than chimpanzees to take a correct path that initially led away from the goal but that eventually led to the goal. Chimpanzees were more likely to make an error by passing a correct path than by turning onto a wrong path. Chimpanzees and one capuchin made more errors on choices farther in sequence from the goal. Each species corrected errors before running into the end of an alley in approximately 40% of cases. Together, these findings suggest nascent planning abilities in each species, and the prospect for significant development of strategic planning capabilities on tasks presenting multiple simultaneous or sequential spatial relations. The computerized maze paradigm appears well suited to investigate movement planning and spatial perception in human and nonhuman primates alike.

Keywords Planning · Spatial relations · Sequential actions · Nonhuman primates · Microdevelopment

Introduction

This report concerns evidence of planning in capuchins and chimpanzees as they used a joystick to move an icon through successive choice points in two-dimensional space. Specifically, they moved a cursor through alley mazes presented on a computer screen. We address (1) the extent of planning, (2) the relation between efficacy of planning and properties of the mazes or of the choices within the mazes, and (3) the microdevelopment of strategic action with experience at the task. We also consider differences in these domains between the subjects of the two genera and what these differences imply.

Planning is an essential aspect of human activity that deservedly has received much attention from cognitive developmental researchers (e.g., Friedman et al. 1987; Friedman and Scholnick 1997; Haith et al. 1994). Friedman et al. (1987) provide a broad definition of planning as a set of conceptual activities that anticipate and regulate behavior. Planning incorporates memory in that the goal of the activity must be kept in mind (i.e., in working memory, or prospective memory) as the activity is carried out. Planning includes monitoring actions to determine if the outcome leads one closer to the goal, and if not, restructuring activity. This aspect of planning is also characterized by the term "problem solving" (e.g., Klahr 1994).

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In general, contemporary theories proposed from an information-processing perspective treat planning and problem solving in young children as a challenge in relating multiple elements to each other sequentially or simultaneously to achieve a goal (e.g., Bidell and Fischer 1994; Case and Okamoto 1996; Siegler 1998). Planning can further be conceived as a process unfolding in time as an activity proceeds (Roberts and Ondrejko 1994). Skill in planning encompasses "planning in advance of action or during action according to the circumstances, flexibly anticipating constraints and opportunities, and adapting to circumstances" (Rogoff et al. 1994, p. 354). This conception of planning emphasizes that planning is improvisational in character; it occurs not only in advance of action but also during the course of activity.

Willatts (1989) characterizes two forms of problem solving in human infants and toddlers. In "forward search," the individual pursues a sequence of actions until the goal is reached, responding to ineffective actions by choosing a different course. Each individual choice is made independently of subsequent choices. Willatts (1989) uses the term "planful" to capture the "one move at a time" character of this kind of activity; Klahr (1994) calls it "generate and test."

In a more advanced form of problem solving, "subgoaling," individual decisions are taken in series in service of the one overarching goal (Willatts 1989). For example, Fabricius (1988) examined route planning in 4- and 5-year-old children as they collected several toy dolls in a large space. He concluded that 5-year-olds were able to consider multiple courses of action and in this way avoid errors, whereas 4-year-olds' planning was more rudimentary and more prone to errors. As conceived by many developmental researchers, the improving coordination of elements in working memory (evident, for example, in subgoaling) is what drives advances in planning efficiency in young children (Bidell and Fischer 1994; Case and Okamoto 1996).

Previous work with children and with nonhuman animals indicates that the direction of a possible choice with respect to the position of the goal in a maze or detour problem powerfully affects decision making at that choice point. For example, Davis and Leary (1968) showed that individuals of a variety of nonhuman primate species showed limited initial propensities to move a lifesaver candy threaded onto a wire (bent into a series of L turns in three dimensions) away from themselves, even when this direction of movement was necessary to get the candy to the end of the wire and thus retrieve it for themselves. Whitecraft et al. (1959) reported that 2-year-old children had the same initial problems as the monkeys in moving the lifesaver away from themselves, although older children had no such problems.

Rhesus monkeys, chimpanzees, and orangutans can solve two-dimensional alley mazes (Lethmate 1977; Washburn 1992; Menzel et al. 1999). These studies have varied in the nature of the mazes presented (e.g., how many choice points, how the choice points were structured, how many times the subject saw each pattern), and how the subject physically solved the problem (using a joystick to move a visual icon, moving an object along a path). Together, these studies provide compelling evidence that nonhuman primates can navigate through two-dimensional spaces. However, they do not provide an assessment of maze properties that we predict will affect performance (such as the number and the directional properties of choices) if the subjects are making strategic choices at decision points. Such assessments are needed to evaluate planning abilities of nonhuman primates in conceptual terms.

Concepts associated with planning are readily adapted to tasks that involve moving a visual icon, or cursor, through a two-dimensional maze. We identify five levels of planning activity in our maze task (see Table 1). We used level 0 for random movements of the joystick. Level 1 represents controlled directional movement of the joystick coupled with random selections at choice points. A "planful" or "forward search" strategy (level 2) would lead one to choose paths that appear to lead directly to the goal. Using a forward search strategy should lead to corrective actions when the path ends short of the goal. "Subgoaling" (level 3) would result in a different pattern of decisions depending on to which properties of the choice points in a maze the subjects were attending and how well they could integrate or prioritize the properties. For example, at each choice point in a maze the subject might evaluate which of the possible paths led to another choice, versus those that led to a dead end (i.e., evaluate the property of continuation). Alternatively, the subject might evaluate whether one path led more directly toward the goal compared to the other path (i.e., evaluate the property of directness). Directness might affect choice more than continuation, but when directness was equivalent among the choices, then continuation might guide choice. A more sophisticated (and memory-intensive) strategy

Table 1 Levels of planning in a two-dimensional maze task

Level	Planning activity
0	Absence of planning: movements of the joystick or other instrument are guided only by encountering a barrier (either the wall of the alley or the end of an alley)
1	Bodily planning: moving the body in such a way as to make the cursor or other agent follow a specific direction (i.e., move the cursor along a straight line or through a turn), but selections at each choice point are made randomly
2	One-element planning: making decisions at each choice point on the basis of one property (e.g., directness to the goal); monitoring the outcome one choice at a time (Encompasses "planful" and "forward search" strategies)
3	Integrated planning: deciding at each choice point on the basis of two (integrated or prioritized) properties (e.g., continuation first, and directness second)
4	Sequential integrated planning: implementing a sequence of choices devised in advance and based upon two or more integrated or prioritized properties (e.g., planning backward from the end point to the start point, and subsequently making these choices in the forward direction)

would be to check the property of continuation first, and the property of directness second. An even more memory-intensive subgoaling strategy (level 4) would be to plan through the entire route, either forward or backward, keeping in mind the sequences of choices to be made. This strategy, if used effectively, would lead to error-free solutions.

Tufted capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*) are vastly different in size (4 kg vs 80 kg, average adult male) and are phylogenetically distant. Tufted capuchin monkeys are in the family Cebidae, from South and Central America; this family of primates has been separate from African and Asian primates for approximately 40 million years (Kinzey 1997). Nevertheless, intriguing behavioral, ecological, and life history parallels exist between capuchin monkeys and chimpanzees (see Visalberghi and McGrew 1997, for a series of papers highlighting these parallels). Some of the most striking parallels involve how these animals interact with objects in near space (i.e., within arm's reach). Both chimpanzees and capuchin monkeys are noted for using tools in their feeding activities (McGrew 1992; Visalberghi 1997) and, in fact, are the most frequent spontaneous users of tools among all the nonhuman primates.

Navigating two-dimensional mazes in near space involves some of the same skills as using a tool, such as anticipation of movement of objects in space, acting to make these movements happen, and responding to feedback from actions (Bidell and Fischer 1994; Case and Okamoto 1996; Lockman 2000). For example, using a tool and solving a maze can involve visual scanning, moving the body, and holding in working memory a sequence of planned goal-directed actions. Visual scanning and moving the body might be considered "on-line planning" in Bidell and Fischer's (1994) terminology. These activities correspond to levels 1 and 2 in our scheme (see Table 1). Holding a sequence of actions in working memory might be considered equivalent to Bidell and Fischer's category of "coordinating represented actions" and corresponds to levels 3 and 4 in our scheme.

Evaluating skills in planning sequential actions while solving mazes, and determining how readily these skills develop, provide independent assessments of cognitive abilities tapped jointly by maze-navigation tasks and object-manipulation tasks. Maze tasks also provide additional opportunities to compare the integration of perception and actions across circumstances (cf., Lockman 2000). The maze task requires integrated perception and action to control the joystick. It lacks, however, the motor demands of achieving a specific positional relation of one object to another (as when a stone must be positioned precisely to crack a nut) inherent in a tool-using task. The maze task has many fewer degrees of freedom than a task in which the subject must produce (as opposed to recognize) the relation among elements. The two-dimensional mazes have fewer degrees of freedom than coordinating body, objects, and surfaces in three-dimensional space (as in seriating nesting cups – Johnson-Pynn et al. 1999). The maze task also provides a convenient means to compare capuchin monkeys and chimpanzees to other species that do not share the propensities of these two genera to use tools, such as rhesus monkeys.

We currently have some information on capuchin monkeys' abilities to organize sequences of movements with spatial elements (at least at level 2 in our scheme of planning). McGonigle et al. (2002) have shown that capuchin monkeys are able to accomplish an exhaustive search, hitting each displayed icon once, with up to nine items distributed on a touch-sensitive computer monitor. More impressively, the monkeys are able to coordinate their selection of icons in accord with a hierarchical scheme of two properties (e.g., selecting all icons of a particular shape, and by ascending order of size within shape, then selecting all the icons of the next shape, again by size, etc.).

Using a larger three-dimensional space, DeLillo et al. (1997) showed that capuchin monkeys conducted spatially strategic searches of food containers arrayed in a two-dimensional plane on the mesh roof of their cage. Their searches were coordinated in space in a manner suggesting memorial "chunking" of nearby elements. These findings suggest that capuchin monkeys are able to organize multiple choices strategically. However, they do not speak to the structural properties of the spatial relations capuchin monkeys can handle, nor whether they "look ahead" while making a choice.

We have more data for chimpanzees than for capuchin monkeys on many cognitive tasks (as reviewed in Anderson 1996), including serial ordering of numbers and strategic search (Kuhlmeier et al. 1999; Boysen and Halberg 2000; Beran et al. 2001; Biro and Matsuzawa 2001). Recent studies involving sequential selection of ordered items from known spatial locations (using computerized testing methods) indicate that chimpanzees can organize in advance a sequence of choices. On the basis of available data, chimpanzees appear to be able to organize at least two choices in sequences of this type (Beran et al. 2001; Biro and Matsuzawa 2001) and, with extensive practice, up to five (Kawai and Matsuzawa 2000). By comparison, Klahr (1994) reports that two-thirds of children at about 5 years of age faced with spatial problems posing four to seven steps (the "dog-cat-mouse" problems) managed to stay on the "minimum path" to solution when they were no more than two moves away from the goal; one-third could do so three moves away from goal. The dog-cat-mouse problem precluded the use of strictly spatial subgoals. Five-year-old children, according to Klahr, were able to plan farther ahead in a sequence of choices in another task that did support subgoals (the "tower of Hanoi" problem) when the subgoals were unambiguous.

The take-home message from these studies, and their comparison with findings from studies with chimpanzees, is that planning two or three steps into the future is possible for these subject groups, but the nature of the task profoundly impacts the nature and effectiveness of planning. We can expect that the same caveat will hold for capuchin monkeys: their abilities to plan sequences of actions will be profoundly affected by the nature of the tasks they are given. For this reason, directly comparative studies are particularly illuminating when the goal is to understand how species compare in this domain.

In this study, we presented novel mazes to capuchins and chimpanzees. We constructed the mazes to present varying numbers of choice points, and two kinds of correct choices (obvious and non-obvious) that would lead to the goal. Obvious choices were those in which the correct path led in the direction of the goal. Non-obvious choices were those in which the correct path initially led away from the goal, or in which the incorrect path ended a short distance from the goal, so that the goal served as a perceptual "lure" to that incorrect path. We presented the mazes to the subjects in an order we hypothesized went from "easy" to "difficult" on the basis of the total number of choice points and the number of non-obvious choices within a maze. With this design, evidence of planning can be sought by comparing the number of mazes completed without error to the number expected by chance using binary probability at each choice point. Evidence that maze or choice-point properties affect planning can be sought by comparing error rates as a function of the number of choice points per maze, comparing errors on obvious and non-obvious choices, and comparing errors as a function of proximity to goal, or recency.

We expected that the monkeys and apes would, at minimum, be planful in their navigation of mazes, that is, that they would be able to correct errors and complete the mazes. We further expected some degree of looking ahead while navigating mazes, and some degree of planning actions ahead of performance. If the subjects looked ahead, they would reverse direction following an error before striking the end of the alley. If they prepared a series of choices in advance of action, they would make proportionally more errors on mazes with more choices because these mazes would present greater memory demands than mazes with fewer choices. Similarly, if they planned choices in the forward direction, they would make proportionally more errors on choices appearing later in the maze rather than early in the maze. If they planned choices by tracing the route backward from the goal, they would make more errors on choices appearing early in the maze. Finally, we expected that the subjects would be more attentive to Euclidean direction to the goal than continuation of the path, that is, that they would make proportionally more errors at non-obvious choices than at obvious choices.

One weakness of presenting the mazes in order of presumed difficulty is that presentation order is confounded with maze properties, making assessment of microdevelopment problematic. With the current design, the relation between performance and testing order can only be considered suggestive evidence concerning microdevelopment. We adopted this design, however, because we expected to run into the boundaries of capuchins' abilities to solve mazes. We anticipated that we would generate better effort on the part of subjects encountering their limits with this design if they were rewarded with consistent correct performance early. In general, improved performance with testing is taken as evidence of microdevelopment. However, given that in our design the difficulty of the mazes increased concurrently with testing (and many measures validate that assumption), maintaining the same level of performance is suggestive of microdevelopment in this study. We report some general indices of performance with respect to testing order as suggestive evidence of microdevelopment in both species.

Methods

Subjects and housing

Four chimpanzees (*Pan troglodytes*), two males and two females, and three male capuchin monkeys (*Cebus apella*) participated in the study. The male chimpanzees, Sherman and Mercury, were 22 and 9 years old, respectively. The two females, Lana and Panzee, were 26 and 10 years old, respectively. The three male capuchins, Jobe, Xavier, and Xenon, were young adults between 6 and 11 years old. The chimpanzees resided at the Language Research Center of Georgia State University, and the capuchins resided at the University of Georgia. None of the subjects were food deprived at any time over the course of testing; all remained in their normal social housing arrangements except during the brief testing sessions. Capuchin monkeys moved to a test room adjacent to their housing area for testing; chimpanzees moved to a specific part of their home cage.

Test apparatus

We presented the mazes to subjects in a two-dimensional format on a computer screen (46 ×28 cm, W×H). Subjects had to manipulate a joystick positioned below the screen to move the cursor on the monitor from the start of a maze to the end point. The cursor could be moved anywhere within the alleys on the screen by the joystick. In this task, the cursor traveled approximately 10 cm in 5 s. All subjects had several years of previous experience with this computerized test system on tasks that required joystick manipulation (Rumbaugh et al. 1993; Filion et al. 1994) using software developed by Richardson et al. (1990).

The maze task

The three capuchins had practiced repeatedly solving a barrier task with a fixed layout (an H shape) and randomized location of start and end points prior to this study. The four chimpanzees had extensive experience solving alley mazes, including mazes with more choice points than we presented in this study (Menzel et al. 1999). The mazes in this study had a different visual appearance (e.g., the color of the maze pathways and background) than those the chimpanzees had seen before, as well as different layouts.

In the current study, each maze presented a novel layout of paths, start and end points, and choice points. With only a few exceptions that occurred because of technical problems or mazes left unfinished at the end of a session, each maze was presented just once to each subject. Three sample mazes are shown in Fig. 1. The mazes appeared as black pathways against a white background on the computer screen. The cursor appeared as a white cross in the black pathway, and the goal appeared as a pink square that fit just within the width of the path. All angles in the maze pathways were 90°. Mazes were grouped into sets (hereafter, libraries) of 16 (13 libraries total). The first library (library 0) consisted of 12 training mazes that were designed to familiarize subjects with the action of moving the cursor in alleys and around corners, and with the goal of the maze task – that is, to move the cursor from the start to the end point. Mazes in this library contained no choice points. The remaining 12 sets (libraries 1–12) constituted the test libraries.

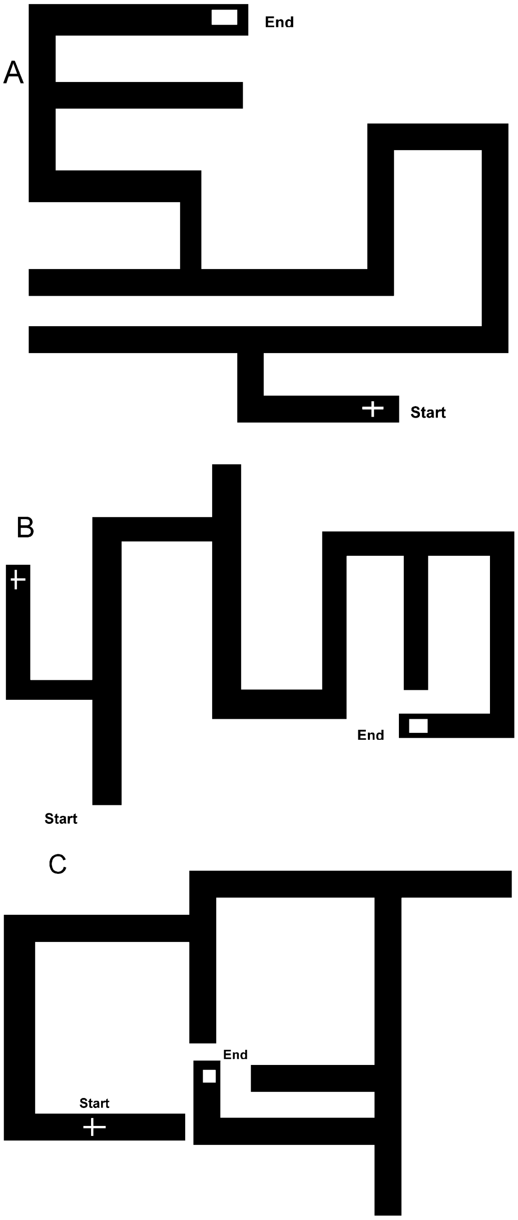

Fig. 1A–C Three sample mazes. The endpoint in each maze is represented as a *white square* in this figure; however, it appeared bright pink to the subjects. The first two mazes contain three choice points. In the first maze (**A**), the third (and final) choice is non-obvious; an incorrect path leads nearly directly to the goal. In the second maze (**B**), the first choice requires moving the cursor in a direction away from the goal; the second choice is neutral, and at the third choice the incorrect path goes nearly directly toward the goal. Thus choices one and three in this maze were non-obvious according to our criteria (see text). We classed maze B as more difficult than maze A because B contains two non-obvious choices, versus one non-obvious choice in maze A. The last maze (**C**) requires five choices (four at choice points and one at the start, where the cursor is positioned in the middle of the alley). The first, second, and fourth choices in this maze are non-obvious choices. Maze C belongs to library 12, the most difficult group of mazes we presented

Table 2 Properties of the mazes

Library	No. of choice points	Non-obvious choices
0	0	0 (Training)
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 test library contained 10 unique mazes. The remaining 6 mazes that made up each library were varied presentations of 2 (randomly selected) of the 10 mazes. For each of the 2 repeated mazes, the repeated presentations were flipped vertically, horizontally, or both. We presented varied versions of 2 mazes to determine if performance on flipped mazes improved from previous navigation of the maze in a different orientation. As it turned out, performance on the flipped mazes was indistinguishable from performance on the other mazes on all variables. We will hereafter ignore this aspect of the mazes and consider all 16 mazes per library as unique for the purposes of our analyses.

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 possible given the constraints of path widths. The number and nature of choice points in each maze characterized libraries (see Table 2). The number of choice points in the test mazes varied between one and five. At each 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.

Correct choices that resulted in apparently traveling a longer distance to the goal or a greater angle away from the goal we categorized collectively as non-obvious choices (NOC). This occurred, for example, when the incorrect choice presented an angular displacement from the goal 60° less than the other choice (i.e., the correct choice appeared to lead farther away than the incorrect choice). Most NOC were of this form, because they required that the subject move the cursor in a direction away from the goal. However, if the incorrect choice ended far from the goal, even if the angles were more than 60° different, we did not designate the choice as non-obvious. A second form of NOC occurred where the two paths formed roughly the same angle with the goal (i.e., not more than 60° different), but the incorrect path was relatively near the goal (in the same quadrant) and the end of the incorrect path was within two path widths of the goal. In these circumstances the incorrect path appeared to lead nearly directly to the goal, and the goal worked perceptually as a "lure." Figure 2 illustrates the two forms of NOC.

The order in the sequence of choices for NOCs was counterbalanced within each library. The distance of the goal from each choice point varied from 1.5 to 10.5 cm. The distances of the choice points from the goal were normally distributed, with a slight skew to closer distances. We included the distance of the choice from the goal as an independent variable in analyses. Choice points were further identified as forced or facultative. A forced choice point occurred when the path ended at a T intersection and the subject was required to turn one way or the other. A facultative choice occurred when the subject traveled along a path that continued past an intersection, so that the subject had the option to turn or to continue in the same direction. Overall, the four apes made choices at 785 forced turns out of 2,037 total turns

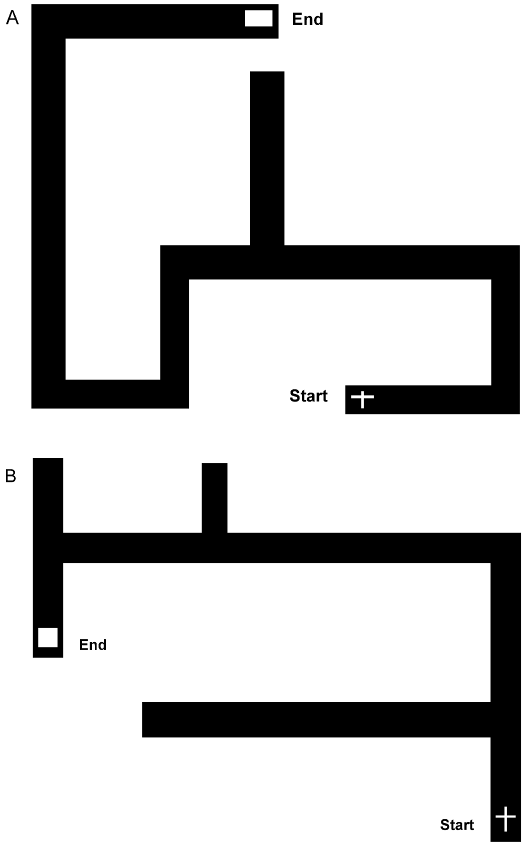

Fig. 2A, B Illustrations of non-obvious choices. The endpoint in each maze is represented as a *white square* in this figure; however, it appeared bright pink to the subjects. **A** Both angle and distance between end of incorrect path and goal combined make the correct choice non-obvious. **B** Angles are similar but path lengths make the incorrect choice attractive

(39% forced turns); the numbers and proportions were similar for the three capuchin monkeys (543 forced of 1,421 total turns, or 38%).

Procedure

We presented the test mazes to each subject beginning with library 1. Subjects moved through the libraries in numerical sequence (e.g., library 1 followed by library 2) if they solved 12 or more of the 16 mazes in each library (with one exception: one subject advanced to library 12 after completing only eleven mazes in library 11). Subjects were given approximately 2 min to solve a maze. Completing a maze required bringing the cursor into contact with the pink square "goal." Subjects received the next maze in the series upon completion of a maze or after 2 min elapsed without activity. We re-presented once any maze that the subject had not completed before proceeding to the next library. This occurred approximately six to eight times per subject due to the computer prematurely ending a trial while the subject was still working.

Subjects typically took 1–2 min to complete a single maze. Capuchin monkeys completed each of the libraries 1–9 in 20–30 min in a single test session; they occasionally required more than one session to complete libraries 10–12. A few times during presentation of these last three libraries to the capuchins, a maze not completed at the end of one test session was re-presented as the first maze the next day. Apes typically completed two to three libraries per 60-min test period. Testing occurred over approximately 2 weeks for both groups. We videotaped the subject's monitor, capturing the cursor moving through the maze pattern. All subjects received food treats intermittently upon completion of one or more mazes during the course of testing.

Scoring

For each maze that the subject completed, we scored movements made at each choice by viewing video playbacks in slow motion. The primary dependent variable was choice of path (Correct or Error). Movement of the cursor 2.5 cm into one path past the choice intersection constituted a choice. We also scored several other dependent variables. After an Error, we noted if the subject reversed the cursor's direction of movement before contacting the end of the alley (noted as Self-correcting) or after hitting the end of the alley (noted as Dead-ending). Errors were further identified as Overshoot (when the subject incorrectly bypassed the correct choice and continued on a linear path) or Wrong Turn (when the subject made a turn down an incorrect path when the correct choice was to stay on the continuing path at a facultative choice point, or to turn in the opposite direction at a forced choice point). Subjects frequently reversed the direction of cursor movement backward through choice points they had previously navigated. They could produce ten choices, for example, while taking the cursor through a maze pattern with only three choice points. In this report we present only the actions made during each subject's first pass through each choice point.

The 192 test mazes presented 528 choices to each subject, for a potential data pool of 3,696 choices. Through a combination of video recording problems and non-completion of some mazes, we scored slightly fewer than 192 mazes for each subject. The chimpanzees each lacked 3–7 mazes; the capuchins lacked 9, 15, and 21 mazes, respectively. We scored between 439 choices and 481 choices per capuchin monkey, and between 504 and 516 choices per ape (3,460 total; 94% of the maximum).

Analysis

We looked for evidence of planning within subjects using chi-square tests to compare expected frequencies to observed frequencies of error-free mazes within libraries. To examine our other predictions concerning the properties of mazes and the microdevelopment of strategic actions and to compare the genera, we used stepwise logistic regression, a form of generalized linear models, using SAS (SAS Inc.). This model assumes a binomial distribution of binary data. We examined the fixed effects of the seven variables of interest listed below on the frequency of errors. We used Wald's chi square to evaluate the probability of the observed distributions. The model included the variables Genus (*Pan* or *Cebus*), Library (1–12), Choice (Correct or Error), Non-obvious choice (Yes or No), Total number of choices (1–5), Category of choice point (Forced or Facultative), Type of error (Wrong Turn or Overshoot), and Outcome following the error (Self Correct or Dead End). Separately, we evaluated the effects of distance (in centimeters) from each choice to the goal, and the order of the choice in the choice sequence on the probability of making an error. The variable Distance was not associated with significant effects for either group and will not be discussed further in this report.

Results

Error-free performance and overall error rates

All the subjects of both species completed 11 or more mazes in each of the test libraries. All four chimpanzees and two of the capuchins completed more mazes without error than expected by chance. Apes completed 53–78%

of the mazes without error; capuchin monkeys completed 24–35% of mazes error-free. Only 20% of mazes would be error-free if choices were made randomly on the full set of 192 mazes.

The probability of error-free solution varies across libraries as a function of the number of choice points per maze in that library. For libraries with a single choice point, random choices would result in 8 mazes solved without error out of 16 mazes presented (0.5×16=8); for libraries with four or more choices, 1 maze would be solved without error on a random basis (0.0625×16=1). One capuchin monkey solved more mazes without errors than expected by chance in 10 of the 12 libraries. The two libraries at chance or below were 4 and 7, in which NOCs were introduced. The second monkey was below chance on library 4 and at chance on libraries 8 and 10. The last monkey solved more mazes without errors than expected in 5 of the 12 libraries, and solved mazes without error at chance rates or below in 7 libraries (3, 4, 6, 7, 8, 10, and 12).

Two of the four apes solved more mazes without error in each library than expected by chance. The other two apes did so on 11 of 12 libraries; each of their performances on a single library (library 2; a second choice point introduced) was at chance levels. These results provide strong evidence that all the subjects planned and/or monitored their movements through sequential choices in some way with respect to reaching the goal, but there is considerable variation in effectiveness of planning across individuals.

Overall, 14% of chimpanzees' choices and 41% of monkeys' choices were incorrect, a significant difference [χ^2=325.85 (*df*=1, *n*=3,460), *P*<0.001]. As we shall see, the structure of the choices impacted the capuchin monkeys' and the apes' performance in different ways.

Effects of maze parameters

The number of choices per maze significantly impacted the commission of errors [apes, χ^2=14.37 (*df*=4, *n*=2,037), *P*=0.006; monkeys, χ^2=11.54 (*df*=4, *n*=1,423), *P*=0.021] but in a direction opposite to expectations. We found that subjects produced fewer errors, not more, on mazes with more choices; adjusted residuals were consistently negative, indicating fewer errors than expected, for mazes with four or five choices. As shown in Fig. 3, for capuchin monkeys, errors declined from a maximum of 50% on choices in libraries with one choice point (libraries 1 and 4) to 36% in libraries with four or five choice points (libraries 9, 11, and 12). Chimpanzees' errors declined from a peak of 19% errors in libraries with two choice points to 10% in the last library, which had five choice points, three of which were NOCs.

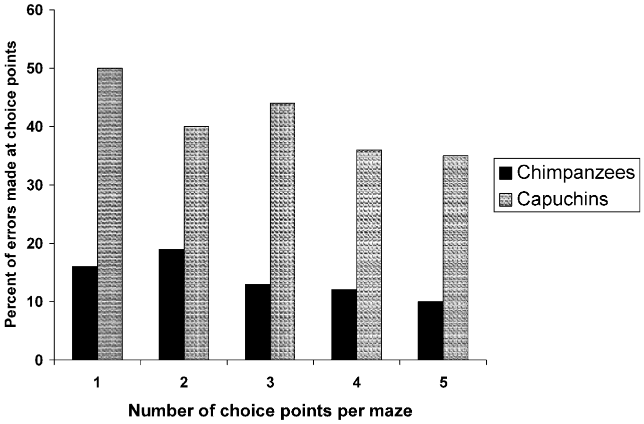

Fig. 3 Percentages of all choices that were errors by number of choices in the maze

Effects of choice parameters

Over the 192 mazes in the test series, each subject could encounter 288 choice points that presented NOCs, and 240 other choice points in which the correct path led to the goal. Thus, NOCs constituted potentially 55% of all choices across all libraries. In actuality, apes did encounter this percentage of NOCs (1,114 out of 2,037 total choices). However, because of incompletion of some (particularly later) mazes, only 45% of choice points that capuchins encountered presented non-obvious correct choices (635 out of 1,423 total choices). Analyses within genera indicated that encountering NOCs disrupted the performance of monkeys [χ^2=124.91 (*df*=1, *n*=1,423), *P*<0.001], but not that of chimpanzees [χ^2=0.22 (*df*=1, *n*=2,037), *P*=0.643]. Overall, capuchin monkeys made errors at 54% of choice points that were non-obvious, versus errors on 24% of other choices. The comparable figures for apes are errors at 13% of non-obvious choice points and errors on 14% of other choices.

The position of the choice point relative to the end of the maze significantly impacted the probability of making an error in chimpanzees [χ^2=12.24 (*df*=4, *n*=2,037), *P*=0.016], with choices farther in sequence from the goal often associated with more errors (Fig. 4). Capuchins as a group did not reveal the same pattern [χ^2=5.17 (*df*=4, *n*=1,423), *P*=0.270]; however, further analyses of individual capuchin subjects (Fig. 4) indicated that one monkey made significantly fewer errors at the final choice point than at prior choice points [χ^2=15.23 (*df*=4, *n*=481), *P*=0.004]. Figure 4 presents individual values for proportions of choices that were errors, plotted by number of choices remaining before reaching the goal.

With respect to movement of the cursor, two types of errors could be made at choice points. These were "wrong turns" (WTs), at which the subject altered the direction of the cursor incorrectly at an intersection, or "overshoots" (OSs), for which the subject maintained forward cursor direction when it should have turned. At forced choices, all errors were necessarily wrong turns. Monkeys committed WT errors on 216 of 556 forced turns (39%); apes committed 65 WTs during 794 forced turns (8%). Either WTs or OSs could occur at facultative turns, depending on the direction of the correct path. Monkeys were equally likely to commit both types of errors at facultative turns, and they made an error of some kind at 41% of facultative turns.

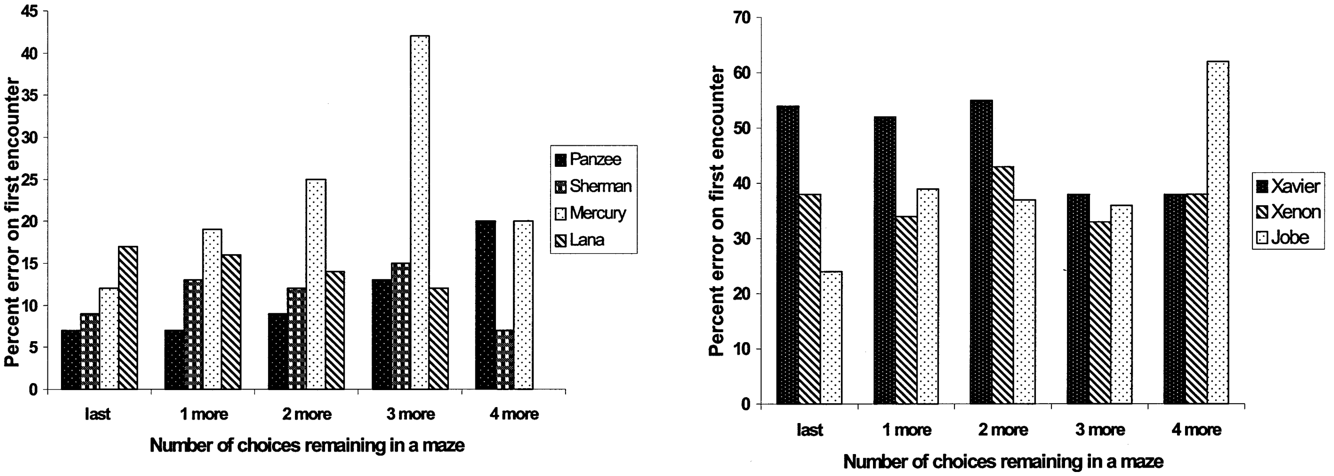

Fig. 4 Individual values for the proportion of choices that were errors, sorted by the number of choices remaining in the maze. *Left* chimpanzees' performance; *right* capuchins' performance

Apes committed far fewer WTs at these intersections [apes made WTs at 4% of facultative turns; χ^2=268.38 (*df*=1, *n*=1,255), *P*<0.001]. Apes, however, committed OSs on 36% of facultative turns, a rate comparable to that of the monkeys [χ^2=1.74 (*df*=1, *n*=815), *P*>0.10, n.s.]

Responses to errors

Both monkeys and apes were more likely to travel to a dead end than to self-correct after any error, although the difference was significant only for monkeys [58% dead end; 42% self-correct; χ^2=14.01 (*df*=1, *n*=578), *P*<0.001] and not for apes [56% dead end, 44% self-correct, χ^2= 3.44 (*df*=1, *n*=279), *P*=0.06]. Apes, but not monkeys, were significantly more likely to self-correct after WTs than after OSs [apes: χ^2=25.32 (*df*=1, *n*=279), *P*<0.001; monkeys: χ^2=2.07 (*df*=1, *n*=575), *P*=0.150; see Fig. 5].

Extensive individual variation in self-correcting existed within each genus. The ape with the fewest errors overall (Panzee: 42 errors) was the most likely to self-correct (following 71% of errors), and the ape with the second-most errors (Lana, 78 errors) was the least likely to self-correct (following 18% of errors). All of Lana's dead ends, and indeed most of those committed by apes, occurred after overshoots, suggesting a strong forward-movement bias. The three capuchins fell within the middle of the apes' range on proportion of self-correcting (ranging from 33% to 52% of errors); the individual with the most errors (Xavier, 230 errors) had the lowest proportion of self-corrections.

Microdevelopment

Proportional rate of errors across libraries declined for apes after library 2 and remained consistently low. This was not the case for monkeys. As shown in Fig. 6, the monkeys' error rate scalloped upward each time an additional NOC appeared in the library (libraries 4, 7, and 10) and remained rather consistent otherwise.

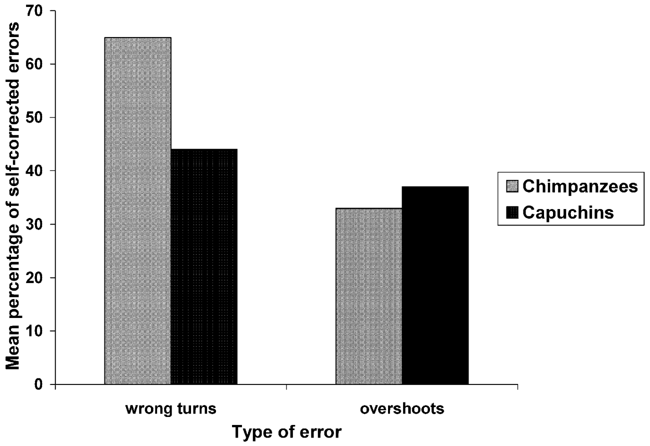

Fig. 5 Mean percentage of errors that were self-corrected, according to whether the errors occurred by taking a wrong turn or by overshooting

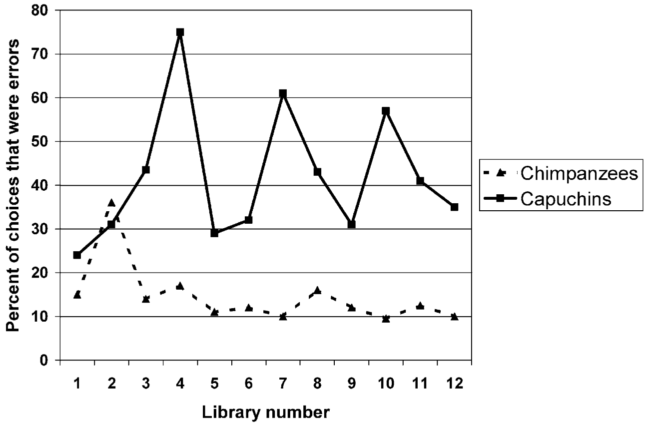

Fig. 6 Percentages of choices that were errors, plotted by library. Libraries were presented in ascending numerical order. Expected error rates across all libraries if subjects were making choices randomly would be 50%

Discussion

Evidence for planning

Overall, our subjects performed surprisingly well on the battery of novel two-dimensional mazes that we presented to them. Both capuchin monkeys and chimpanzees solved more mazes without error than expected by chance, and subjects of both species made fewer errors per maze than expected by chance in most libraries of mazes. Subjects of both species corrected their path after making an error (self-correction), although they more often reached the end of an alley before turning around. Some subjects made proportionally fewer errors than expected at choices closer in sequence to the goal, and proportionally more errors than expected at choices farther in sequence from the goal. All of these findings indicate that the subjects employed some aspect of planning as they navigated the mazes, although they were not consistently successful. Others have found that nonhuman primates can search with varying degrees of efficiency in larger three-dimensional settings, such as when searching for food in multiple locations (cf., Menzel 1973; Gallistel and Cramer 1996; DeLillo et al. 1997; Janson 1998). We recognize that processes supporting navigation in the near space of two-dimensional mazes and in larger three-dimensional spaces may differ; our discussion focuses on the former. However, we believe that there are parallels between the two settings that warrant further consideration. For example, both settings involve the integration of vision, movement, and memory, even though specific task demands may differ across spatial scales.

Properties of mazes and of choice points affect performance

Apes maintained low rates of committing errors as testing progressed, regardless of the properties of the mazes and choice points. The capuchin monkeys, on the other hand, made errors at rates that varied across testing in a patterned way, and this pattern reflected properties of the choice types rather than of the number of choices in the mazes. That is, capuchin monkeys made more errors on choices that were designated as non-obvious than on other kinds of choices (whereas the apes did not). To review, NOCs included choices where the correct path initially led away from the goal, and where the incorrect path appeared to go nearly directly to the goal, so that the goal served as a perceptual "lure." Capuchin monkeys made errors at higher rates on libraries in which the mazes had more of such NOCs, and most especially, when NOCs first appeared (library 4), and when they increased again from one per maze to two per maze (library 7). Apparently the capuchin monkeys encountered difficulty in inhibiting the tendency to move the cursor in the direction of the goal. Chimpanzees did not show this pattern.

Extent of planning

It would be possible to make a correct choice at every choice point in our mazes by looking ahead to the end of both alleys and selecting the one that presented another choice (versus a dead end). The task can be characterized as requiring just one "look ahead" with respect to one property of the alleys. However, none of our subjects made only correct choices. The monkeys were most likely to make an error by incorrectly choosing the "obvious" (but wrong) direction at NOC points. Monkeys appear to use the direction of the paths in relation to the goal as the first priority in making a decision about where to move the cursor. Thus they looked to a location relevant to solving the maze, but not in the most efficient manner (i.e., they "looked ahead," but did not look very far down the alleys to see where they led). This pattern of behavior fits the characterization of "planful" behavior, where decisions at each choice point are made on the basis of one element, directness to the goal. This behavior represents level 2 in our scheme (see Table 1).

The apes more consistently attended to the continuation of the alley to make a selection (as indicated by equivalent error rates at NOC points as at other choice points). Their behavior was thus also at least "planful" (level 2). The apes, however, appeared to have a bias toward moving the cursor straight ahead rather than turning at an intersection; they made many more overshoot errors than wrong turns at facultative choices and they made very few errors at forced choices. When an overshoot was made it often resulted in a dead end. We suspect that many of these overshoot errors, as well as the dead ends that accompanied them, resulted from momentary inattention to the task rather than inability to perceive the correct choice at those intersections.

The apes and one monkey appeared to look ahead in a manner relating future choice points to the end of the maze, as indicated by significant differences in error rates for these subjects for choices farther in series from the goal (e.g., the first choice) than nearer in series to the goal. A higher error rate on choices farther from the goal than on those closer to the goal (the last, most recent choice) would be expected if subjects are planning more than one choice ahead (level 3) or visually scanning the entire image on the screen and remembering a sequence of decisions at choice points (level 4). This outcome would be expected if an individual were practicing level 4 planning because the memory demands for sequential choices increase with the number of moves to be remembered.

The full spectrum of results suggests that apes and monkeys are able to monitor one choice at a time, and sometimes more, when they make decisions at choice points. At the same time, they often look ahead less than one step immediately *after* making a choice, as suggested by their relatively high rate (60%) of striking the end of the alley after making a wrong choice, especially with overshoot errors. The common occurrence of striking the end of an alley suggests that either the subjects' forward search was quite limited during testing, or that their attention was not consistently on the task at hand (e.g., they may have taken their eyes off the computer monitor to look around). Given that they do usually select correct paths, they do self-correct, and at least some individuals improve performance as they approach final choices, we view inconsistent attention as an important part of the explanation for their varying performance on different measures. On the other hand, in support of the suggestion that our subjects' errors reflected limited forward search, Beran et al. (2001) report similar findings with macaques and chimpanzees (including some of the same subjects that participated in this study). In Beran et al.'s (2001) study, the subjects were able to look one move ahead, but not more, in a sequential selection task that involved moving the cursor via a joystick to make a selection, as did our mazes. It is likely that both inattention and limited forward search contributed to incorrect choices in our nonhuman subjects, but we are not yet able to determine the relative contributions of each factor.

Relations between planning movements in two-dimensional mazes and planning movements of three-dimensional objects

Planning movements through alley mazes in two-dimensional space can involve several different perceptual and attentional skills, including detection of choices, looking ahead to avoid a dead end, and the ability to inhibit continuation of movement toward the goal to make a detour. All of these skills permit planning sequential movements in a multi-choice task as reflected in levels 2–4 in our scheme. We have firm evidence for level-2 planning in our maze task, and some suggestions of level-3 or even level-4 performance. One might ask whether the format of presentation (two-dimensional space) impacted our subjects' performance. Would monkeys and apes plan sequences of actions differently with real objects in three-dimensional space?

We have studied how apes and monkeys organize sequential actions while seriating nesting cups (Johnson-Pynn et al. 1999; Johnson-Pynn and Fragaszy 2001). We found that, as in their behavior with two-dimensional mazes, monkeys and apes are able to seriate nesting cups rather well from the point of view of success, even to the point of inserting a middle cup into an already-seriated set, although they are not necessarily very efficient at the task from the point of view of the number of moves made to seriate a set of cups. They often compose incorrect combinations that must be dismantled or otherwise altered to achieve a nested arrangement.

One can consider the degree of planning evident in combinatorial activity with nesting cups with the same conceptual scheme developed in this report to classify decisions at choice points in a multi-choice maze. The most common problem encountered by monkeys and apes while seriating multiple cups is placing a cup that is too large onto a smaller cup. The obstruction produced by this action is immediately evident to the actor (as is striking the end of the alley in the maze task). The most common reaction to this error is to take the larger cup off the stack, put it down, and then either dismantle the existing stack or start working with a different stack of cups. This pattern qualifies as "planful" (level 2 in our scheme): after an error they use a different cup; one element is altered (as when a different direction is chosen following a dead end in navigating a maze).

We also asked our nonhuman primate subjects to insert a middle sixth cup into an already-seriated five-cup set. Some subjects (three apes, one capuchin) achieved this with a minimum of three actions: removing the top two cups as a nested pair and putting them into the middle third cup, followed by moving this three-cup set as a unit into the bottom two cups. The direct manner in which some subjects succeeded in inserting a cup into the middle of a series suggests that they might incorporate relational properties of the cups in their planning, which corresponds to level 4 in our scheme.

Like nesting cups, the mazes presented multiple elements that had to be handled sequentially, but unlike the cups, hierarchical combinations (that reduce degrees of freedom of future actions) were not possible. Both monkeys and apes commonly "chunked" two cups into one unit (by placing two together, and then moving the set as a unit) when combining cups. There is no physical way to "chunk" two sequential choices in a maze in the same manner – the actions remain temporally individuated. However, sequential movements can be chunked in prospective (or working) memory, and we have good evidence that capuchin monkeys can do this when the visual exemplars remain visible. McGonigle et al. (2002) indicate that capuchin monkeys become impressively quick and accurate at selecting by sampling without replacement all exemplars of a class in an ordered sequence, each of several classes in turn, from a two-dimensional display.

Chunking multiple spatial locations in prospective memory may be more difficult than chunking sets of icons in a predetermined order, as suggested by Beran et al.'s (2001) findings that chimpanzees were able to produce accurately only the next choice following disappearance of the visual icons that had to be selected in order. That is, having looked at the display and having selected the first item in the series, they were able to select the second item even when its numerical label was removed, but they could not accurately select additional items past the second under these circumstances. They were looking one item ahead. Biro and Matsuzawa (2001), however, found that chimpanzees could look ahead several steps in a sequence in a conceptually similar ordinal ordering task using a touch-screen format rather than a joystick. The touch-screen format allowed faster movements between locations than the joystick system and direct "contact" of the hand with the target objects in a tagging action. Perhaps these features of the task enabled more effective "chunking" or look-ahead skills than the task presented by Beran et al. (2001).

The message here is that perceptual skills involved in "looking ahead" are no doubt context sensitive in nonhuman primates, as they are in humans (e.g., Bidell and Fischer 1994). Further exploration of the particular demands imposed by different computer-interactive formats in these tasks is warranted.

Mastering multiple simultaneous and/or sequential relations is also an intrinsic part of using a tool proficiently (Lockman 2000). Using an object as a tool requires producing a specific spatial relation between one object and another, and at the same time performing a specific action with one object. Working within our model of relational complexity, we would predict that both chimpanzees and capuchin monkeys would have no difficulty mastering an instrumental action that required a single relation, as in pounding something open by banging it directly on the substrate, so long as they could readily accomplish the necessary actions (i.e., were strong enough and accurate enough). These are, after all, the normal conditions they face in real life. Mastering two relations simultaneously challenges both monkeys and apes, as demonstrated by performance in these mazes. However, they apparently can succeed at this level (level 3–4 in Table 1). Mastering three relations at one time (as in arranging an object in a specific orientation on a substrate, and another object in a specific orientation in the hand, and then combining the two objects in a particular alignment) will challenge both of them even more, as it does young children (Lockman 2000). In fact, we do not yet have a paradigmatic example for capuchin monkeys solving a problem like this, although we do for chimpanzees (e.g., cracking nuts with stones as described by Inoue-Nakamura and Matsuzawa 1997). Probing the outer boundaries of each genera's abilities to master problems with specific relational demands – and the microdevelopmental processes that support mastery – with three-dimensional objects and with two-dimensional displays can provide a principled basis for comparative understanding of their physical cognition.

Comparing apes and monkeys

There were obvious differences in performance between monkeys and apes. Apes made significantly fewer errors, especially wrong turns, than did the monkeys, and were as accurate at NOC points as at other points (whereas the monkeys were more likely to make an incorrect choice at NOC points vs other choice points).

It is important to keep in mind, however, that the best and worst performances in monkeys and apes overlapped. Thus it is more parsimonious to assume that apes learn more quickly than monkeys how to navigate mazes strategically rather than to posit that apes possess a qualitatively different means of planning movements of objects through space. To come to the latter, stronger conclusion, we need to examine asymptotic performance of both species, particularly on more difficult mazes that require looking ahead more than one step at a choice point to make a correct choice. A two-step problem taps what Bidell and Fischer (1994) refer to as a representational mapping, where a prior action is dependent on its follow-up action.

Replication of the current study with naïve apes would also be informative. If naïve apes do indeed arrive at this task with a greater propensity to look ahead to the end of the two alleys at each choice point, or are faster to learn to do so than the monkeys, the difference between the genera observed in this study will be sustained. Alternatively, perhaps prior experience with similar mazes at an earlier time permitted the apes in this study to approach these mazes with an established perceptual strategy that the monkeys lacked. In this case, we would find smaller or no differences between naïve apes and naïve monkeys. We are conducting these follow-up studies now.

Value of interactive computer tasks for studying planning as a process

In closing, we would like to point out that the detailed records of movements through time and space afforded by interactive computerized tasks are an important resource for researchers interested in spatial cognition (cf. Menzel et al. 1999; Washburn and Astur 2002), including those interested in cognition as an embodied process. Concomitant with their analytical power, however, must come the recognition that the challenges of organizing movement in two dimensions in computerized tasks are no doubt different from the challenges of organizing movement in three dimensions, because the degrees of freedom of movement that the actor must integrate or manage are necessarily different between two- and three-dimensional formats, as is the sensory feedback one receives while acting. Comparison of performance on two- and three-dimensional tasks can tell us much about how an actor integrates perceptual search and manual action (Roberts and Ondrejko 1994; Ballard et al. 1997).

Acknowledgements We thank Li Jianrong and Jaxx Reeves of the Department of Statistics, University of Georgia, for initiating us into the community of generalized linear modelers, James Fuller for programming the maze tasks, SiGui Li and Nadine Schroeder for assistance with statistical analysis, Ron Davis and members of the UGA Instrument Shop for superb craftsmanship in fabrication of our test stations, Charles Menzel and Sarah Cummins-Sebree for many fruitful discussions about mazes, David Washburn for excellent advice about all things relating to joysticks, John Kelley for assistance in testing the chimpanzees, Karen Parnell for scoring assistance, and Christine Filion Orman for continuing collegial help while these data were collected and afterward. This work was supported by Grants HD06016 and HD38051 from the National Institutes of Health (USA) to Georgia State University. Studies were conducted at the University of Georgia and Georgia State University and complied with the laws regulating animal care and use in the United States.

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