Anim Cogn (2001) 4 : 179–192
DOI 10.1007/s100710100101

ORIGINAL ARTICLE

Iver H. Iversen · Tetsuro Matsuzawa

Acquisition of navigation by chimpanzees (*Pan troglodytes*) in an automated fingermaze task

Received: 14 August 2000 / Accepted after revision: 30 July 2001 / Published online: 19 September 2001

Abstract These experiments investigated how chimpanzees learn to navigate visual fingermazes presented on a touch monitor. The aim was to determine whether training the subjects to solve several different mazes would establish a generalized map-reading skill such that they would solve new mazes correctly on the first presentation. In experiment 1, two captive adult female chimpanzees were trained to move a visual object (a ball) with a finger over the monitor surface toward a target through a grid of obstacles that formed a maze. The task was fully automated with storage of movement paths on individual trials. Training progressed from very simple mazes with one obstacle to complex mazes with several obstacles. The subjects learned to move the ball to the target in a curved path so as to avoid obstacles and blind alleys. After training on several mazes, both subjects developed a high level of efficiency in moving the ball to the target in a path that closely approached the ideal shortest path. New mazes were then presented to determine whether the subjects had acquired a more generalized maze-solving performance. The subjects solved 65–100% of the new mazes the first time they were presented by moving the ball around obstacles to the target without making detours into blind alleys. In experiment 2, one of the chimpanzees was trained using mazes with two routes to the target. One of the routes was blocked at one of many possible locations. After training to avoid the blind alley in different mazes, new mazes were presented that also had one route blocked. The subject correctly solved 90.7% of the novel mazes. When the mazes had one short and one long open route to the target the subject preferred the shorter route. When the short route was blocked, the subject solved only 53.3% of the mazes because of the preference for the shorter route even when blocked. The overall results suggest that with the training methods used the subjects learned to solve specific mazes with a trial-and-error method. Although both subjects were able to solve many of the novel mazes they did not fully develop a more general "map-reading" skill.

Keywords Fingermaze · Maze learning · Navigation · Touch monitor · Chimpanzees

Electronic supplementary material to this paper can be obtained by using the Springer Link server located at http://dx.doi.org/10.1007/s100710100101.

I.H. Iversen (✉)
Department of Psychology, University of North Florida, Jacksonville, FL 32224, USA
e-mail: iiversen@unf.edu,
Tel.: +1-904-6202807, Fax: +1-904-6203814

T. Matsuzawa
Section of Language and Intelligence, Department of Behavioral and Brain Sciences, Primate Research Institute, Kyoto University, Inuyama, 484 Japan

Introduction

The fingermaze has a long tradition in human experimental psychology (Woodworth and Schlosberg 1954; Golledge 1999) and also serves diagnostic purposes (e.g., Grosse et al. 1991). The fingermaze is used to examine navigational or spatial orientation skills because the subject has to be able to move a finger spatially based on immediate cues that are either visual or tactile (as when solving a maze blindfolded) and based on prior experience in solving mazes. Regarding learning of mazes by non-human subjects, there is a considerable body of literature on animals (particularly rodents) traversing various spatial arrangements (e.g., Reid and Staddon 1998). In general, terms such as "cognitive map" and "insight" are frequently used in the context of maze studies, as when performance is said to be insightful or show evidence of a cognitive map (e.g., Tolman and Honzik 1930). The term "cognitive map" does not, of course, refer to a real tangible map that the subject examines prior to performance in the maze. Rather, the term is used as a metaphor or summary label for a certain kind of performance. An interesting question, though, is whether a non-human subject could indeed learn to use a real map. Appropriate map use would indicate correct negotiation of a novel maze by avoiding all blind alleys.

Surprisingly little research on fingermaze acquisition has been done using non-human subjects. An early study by Spragg (1936) used a stylus maze with hidden stops in blind alleys that were not indicated visually; a single chimpanzee learned to move a stylus to a target while avoiding blind alleys, even while blindfolded. In an impressive study also using a single chimpanzee, Rensch and Dohl (1968) showed that the subject could learn to move a metal ring to a target along a path in a maze on a wooden board. The mazes used were quite complex and usually had two possible routes from the start location to the target, only one of which led to the target. The subject learned several fingermazes in various progressions of complexity. The subject apparently spent a long time looking at each maze prior to moving the ring. However, the authors did not provide information about performance each time new mazes were introduced, and actual paths of movement were not presented because the method used did not allow for storage of movement paths. Using a joystick method, Washburn (1992) demonstrated that rhesus monkeys could learn to negotiate mazes presented on a computer monitor. The joystick controlled the movement direction of a cursor that had to be steered to a target but could not pass obstacles that formed a maze. Subjects were given 100 trials of each of five mazes and learned to steer the cursor along an optimal path to the target. The focus of Washburn's study was neither acquisition of this skill nor generalization to new mazes. The studies by Spragg (1936), Rensch and Dohl (1968), and Washburn (1992) suggest that the fingermaze is a tool that has great potential for research on spatial navigation in non-human primates. With the computerized method used by Washburn (1992), the movement path can be examined on individual trials to provide detailed information about the acquisition of maze navigation.

In the present experiments, visual mazes were presented on a touch-sensitive monitor. Using a finger the subject moved a small graphical symbol, a "ball", to a stationary target. The maze consisted of various graphical barriers that the ball could not pass through. The task was fully automated with storage of the ball's movement path on each trial. Figure 1 shows one subject moving the ball (the disk near the right hand) to the target (the open square in the upper left corner); the ball could not pass through the obstacles (see also electronic supplementary material, ESM: Fig. S1 shows the same image in color, and Figs. S3, S4 show video clips of the maze perforrmance). The subjects were taught this skill by an automated training method, which was based on response and stimulus shaping (e.g., Gleeson 1991; Iversen and Matsuzawa 2001). In general, maze complexity was increased in graduated steps in accordance with progress of the subjects' skills in moving the ball around the obstacles. We based our training method on the principle that to establish a generalized skill involving discrimination of complex stimuli one must present a variety of stimulus exemplars during training (Stokes and Baer 1977).

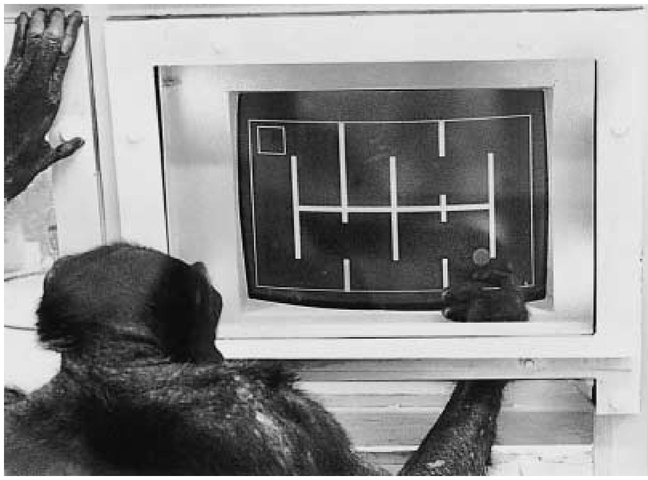

Fig. 1 Photographic representation of the experimental situation with the *chimpanzee* (Pendesa) sitting in front of the *touch monitor* during a trial from maze set 14 in experiment 2. The *screen* shows a *maze* of *red obstacles*, a *blue ball* (near *Pendesa's right index finger*), and a *small open white target box* (*upper left corner*). The task is to bring the blue ball to the target box by moving it with a finger on the touch monitor. The perimeter of the maze is indicated by the *large open rectangle* near the rim of the monitor. The ball cannot move through the obstacles that form the maze or pass the perimeter. During a session each trial featured a different maze. Reinforcement (bits of fruit) was presented in a tray under the monitor (not visible on the photo). A clear Plexiglas front (30 cm from the monitor surface) served to protect the monitor. The subject reached the monitor by placing the arm in the *slot under the Plexiglas front*, as shown in the photo. Electronic supplementary material, ESM: Figure S1 shows the same image in color. Figures S3 and S4 show video clips of maze performance in two single trials

The purpose of the present experiments was to examine in some detail how chimpanzees acquire the skill of navigating in fingermazes. In addition, we examined the extent to which the subjects would be able to navigate correctly in novel mazes without moving into blind alleys. First we trained the subjects on a variety of different mazes. Then we tested them on novel mazes to determine whether they had acquired a more general "map-reading" skill that would enable them to solve new mazes the first time they were presented.

Methods

Subjects

We used two adult, female chimpanzees (Ai, age 18 years, Pendesa, age 17 years), who had considerable prior laboratory experience. Both subjects had used a touch monitor in matching-to-sample tasks (e.g., Fujita and Matsuzawa 1990; Matsuzawa 1985a, 1985b; Tomonaga and Matsuzawa 1992) and in automated drawing tasks (Iversen and Matsuzawa 1996, 1997, 1998, 2001). Subjects were not food deprived and received 50–150 daily training trials in the present experiment. The chimpanzees lived in a group of 11 chimpanzees in an outdoor enclosure with an attached indoor residence.

Apparatus

From the outdoor enclosure, subjects entered an experimental booth (150×180×200 cm), which was equipped with a Mitsubishi FHC Vex color-display 21-inch (53 cm) monitor on one wall. A Microtouch transparent touch screen (for capacitance detection) was integrated with the monitor surface to enable automatic recording of the location of a touch directly on the monitor surface. Bits of fruit were delivered automatically as reinforcement into a tray under the monitor; delivery was accompanied by a 0.5-s beeping sound. An Epson (PC-386 ES) personal computer was used for programming using the QuickBASIC language. With the monitor used, 100 pixels equaled 5.83 cm. The experiment was fully automated.

Pretraining

Iversen and Matsuzawa (1996, 1997, 1998, 2001) used the same apparatus and subjects. Both subjects were trained to draw on the monitor surface.

Sweeping the finger over the monitor surface left a finger-tip wide trace of blue "electronic ink" exactly when and where the finger touched. The subjects had learned to aim the finger at one small stimulus shown on the monitor and then to move the finger across the monitor, without lifting it, to another small stimulus. Because this movement left a trace on the monitor the subjects were in reality drawing a line that connected the two stimuli. Thus, the subjects had already learned the prerequisite behavior of placing the finger at a specific visual object and then moving the finger across the monitor to another object. In the present experiments, finger movement did not leave any visual trace on the monitor.

Experiment 1

The purpose of experiment 1 was to establish movement of an object from one location to another within a maze of obstacles. Once the subjects had learned to move the ball to the target without moving it into blind alleys on the way, we introduced novel mazes of equal or higher complexity to determine whether the subjects had acquired a generalized skill. A blue fingertip-sized ball had to be moved into a white open square target. The ball was moved by placing the finger on the ball and then dragging it on the monitor surface around the obstacles to the target. Touching the target with the ball produced reinforcement. Successful performance in this task entails visual identification of the ball and the target as separate stimuli and requires the sequential motor components of first touching the ball and then dragging it to the target around the obstacles. The subjects received continuous visual feedback of the finger movement in terms of the displacement of the ball on the screen, which was strictly isomorphic with finger movement; if the subject stopped moving the finger or lifted it from the monitor, the ball stopped moving and remained stationary until touched again.

Method

Subjects

Both subjects participated in experiment 1. Pendesa was trained first, and Ai was trained 1 year later.

Procedure

On each trial in a session, the subject had to move the ball to the target. The ball was a blue disk 25 pixels (1.46 cm) in diameter and the target was an open white square (30×30 pixels). The obstacles (red) that formed the maze were various configurations of filled bars and squares. All stimuli were presented on a black monitor surface. Each maze was shown within a thin frame (640×400 pixels) which served as a perimeter. The ball could be moved freely on the monitor and followed finger movement instantaneously; the ball stopped moving when the finger stopped moving, and if the subject lifted the finger from the monitor the ball remained at its current location. However, when the edge of the ball touched an obstacle or the maze perimeter, the ball froze in its forward movement on the monitor and a 2000-Hz, 0.2-s tone sounded. The subject could dislodge the ball from its frozen position by moving it away from the barrier it had hit. Finger movement left no trace on the screen. When the ball hit the target the subject received a small piece of fruit as reinforcement. A trial could be abandoned at the discretion of the experimenter if the subject was not able to move the ball to the target within a reasonable time (usually about 60 s); on abandoned trials, the subject did not receive reinforcement. Trials were separated by a 1-s inter-trial interval.

Table 1 outlines the general procedure. Each session presented a series of mazes, one maze per trial. All mazes were different within a session. A maze set refers to the series of mazes that was presented in one session; for example, a maze set of 12 trials presented 12 different mazes in one session, one maze for each trial. Training was divided into five logical steps. Figure 2 presents examples of individual mazes for each step.

Table 1 Steps of training in experiment 1. A touch monitor showed a maze of visual obstacles. With a finger the subject had to move a „ball" to a „target" on the monitor while avoiding the obstacles. The procedural steps describe the increasing complexity of the maze beginning with no maze in step 1. Steps 3 and 5 tested for generality of the maze-solving performance established in earlier steps. The number of trials per session was 24 in steps 1–4 and 12 in step 5. Each trial in a session featured one maze, and each session presented one set of different mazes

Step	Description	Sessions for each subject	
		Ai	Pendesa
1	Train moving the ball to the target with no obstacles	10	14
2	Train ball movement with gradually increasing obstacle interference, maze sets 1–7	13	15
3	*Test* new maze set 8	2	2
	For Ai only, train new set 9	6	N/A
4	Train ball movement with the more complex maze set 10	6	10
5	*Test* new maze sets 11–12	4	4

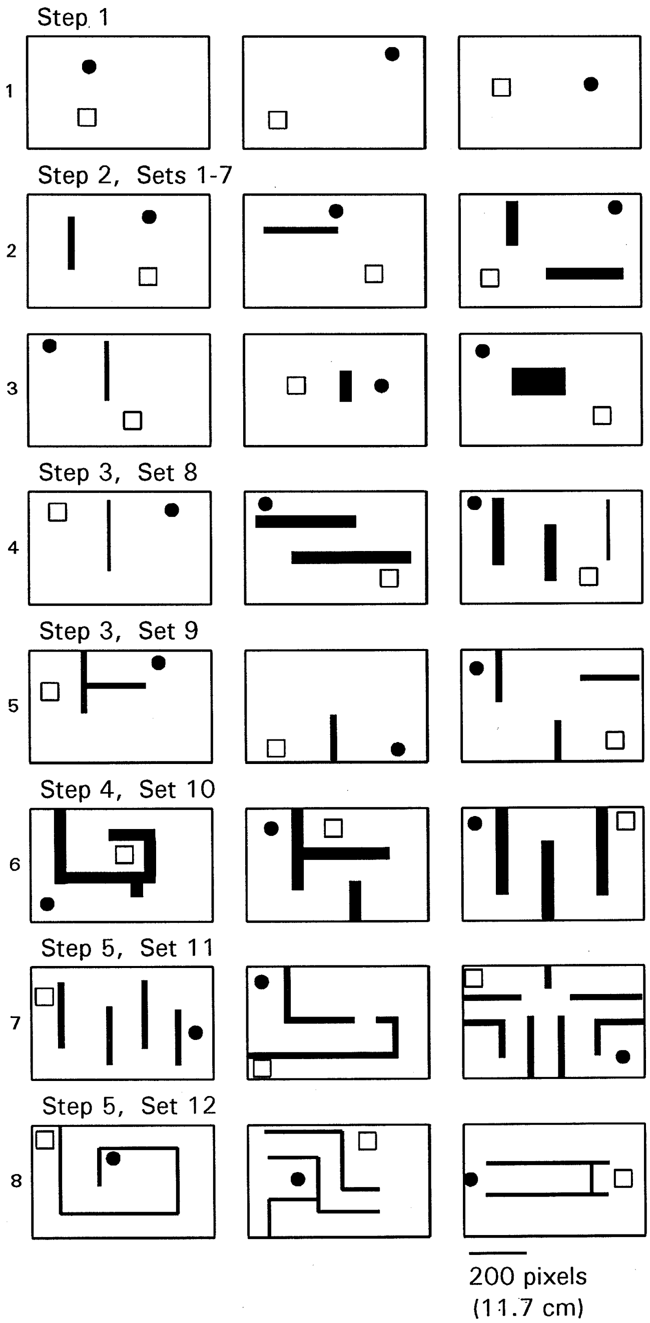

Fig. 2 Samples of individual trials from maze sets 1–12. Each *frame* illustrates what the monitor looked like at trial start. The *filled circle* is the start ball, the *small open square* is the target, and *dark lines and bars* are the obstacles that formed the maze. The *frame* represents the perimeter of the maze. Figure S2 (ESM) shows all individual mazes for maze sets 7, 8, 10, 11, and 12

Step 1. The screen showed only the ball and the target, and the subject had to move the ball to the target. When a trial began, the ball was at some distance from the target and could appear on any side of the target (as shown in three examples of individual trials in row 1 in Fig. 2).

Step 2. Using an automated shaping procedure, the subjects were taught to move the ball around obstacles to get it to the target. Thus, obstacles that the ball could not pass through were introduced in graduated steps ranging from obstacles far away from the shortest path between ball and target to obstacles that blocked this path (first very little and then considerably). On trials where an obstacle blocked a straight path to the target, the ball had to be moved around the obstacle. Trials with obstacles were mixed with trials without obstacles; these obstacle-free trials served as „easy“ trials to keep the subjects motivated to stay with the task. Seven different maze sets (1–7), each with 24 different mazes, had a gradually increasing number of mazes with obstacles and a gradually increasing number of obstacles that blocked a straight path to the target. Rows 2 and 3 in Fig. 2 show examples of mazes used in step 2. Each of the seven maze sets can be characterized as number of trials with obstacles (*a*) and number of trials where the obstacle(s) required a curved movement path (*b*). This information is given here as *a*/*b* for each set (set 1: 5/0, set 2: 7/0, set 3: 13/4, set 4: 13/6, set 5: 18/5, set 6: 18/11, and set 7: 21/14). For example, for set 6, 18 of the 24 trials showed one or more obstacles on the screen, and on 11 of these trials the subject had to move the ball in a curved path because a straight route from the ball's start location to the target was blocked by one or more obstacles.

Step 3. To establish the generality of the performance of avoiding obstacles, step 3 presented new mazes (maze set 8) in two test sessions that each featured 24 mazes with one, two, or three obstacles; 20 of these mazes required curved paths for the ball to reach the target. Row 4 in Fig. 2 shows three examples of mazes from this test set. After one test session for Ai it was clear that she needed more training to avoid obstacles, and she was given additional training in six sessions on a separate maze set (9), where all trials required that she moved the ball around one or more obstacles. Row 5 in Fig. 2 shows three mazes from set 9. Ai then received an additional test session with set 8.

Step 4. Maze complexity was increased further in a new set (10) of 24 mazes. All mazes featured from one to four obstacles, and 23 of the mazes required considerable curvature of the movement path, as can be seen in the three maze examples from this set presented in row 6 in Fig. 2.

Step 5. Again, as in step 3, the generality of moving the ball around the obstacles was tested in the new maze sets 11 and 12. Each set featured 12 different mazes, which each had from two to seven obstacles. Each maze set was presented twice. Rows 7 and 8 in Fig. 2 show examples of mazes from these two test sets. Notice that the leftmost maze in row 8 required a spiral movement path; set 12 presented three different mazes that required such a movement path. Because of the increased complexity of the mazes in set 12, the obstacles were closer to each other and thinner than for mazes in earlier sets.

Progression in maze complexity and the number of sessions for each maze set was determined by a general impression of progress for sets 1–7. Sets 9 (Ai only) and 10 were repeated until each subject had two or fewer trials per session where the ball was moved in a path directly toward the target even though that path was blocked by an obstacle. Figure S2 (ESM) presents all mazes from sets 7, 8, 10, 11, and 12.

Results

Acquisition: steps 1 and 2

With just the ball and the target on the screen in the first session both subjects failed to move the ball to the target; they just touched the two stimuli alternately. Although both subjects were familiar with moving the finger over the monitor in other tasks with the same equipment, as described under pretraining, neither subject spontaneously moved the ball to the target in this new task. To induce this movement, we connected the ball and the target with a thin line in the next session. Because both subjects readily traced lines with the finger in other tasks, they immediately „drew“ on this line and thereby moved the ball to the target. In the third session we eliminated the connecting line, and both subjects now moved the ball to the target, as the three frames of individual trials in row 1 of Fig. 3 show. The movement path on each trial is indicated as a continuous series of small black dots that represent the locations of screen contact during movement (these dots did not appear on the monitor during the movement). Thus, the paths shown in individual frames in this and subsequent figures present snapshots of the cumulative moment-to-moment path changes that took place within a single, individual trial; no averaging across trials was used for these displays. Because the subjects moved the ball from its initial position to the target, the ball was on top of the target by the end of the trial. However, the frames show the ball in its initial position to illustrate the spatial relationship between ball, target, and obstacles that the subjects faced when a given trial started.

On trials where the ball was located to the left of or under the target, both subjects often touched the target first and then tried to move it to the ball. The thinner movement paths in rows 2 and 3 in Fig. 3 illustrate this finger movement without ball movement for two such trials. An arrowhead between frames indicates that the two frames are successive for the same trial; first the subject tried to move the target to the ball, next the subject moved the ball to the target. Attempting to move the target from top to bottom or from right to left has its origin in the prior experiments on drawing (e.g., Iversen and Matsuzawa 1996) where both subjects had learned to move the finger from the top of the monitor and downwards and from the right

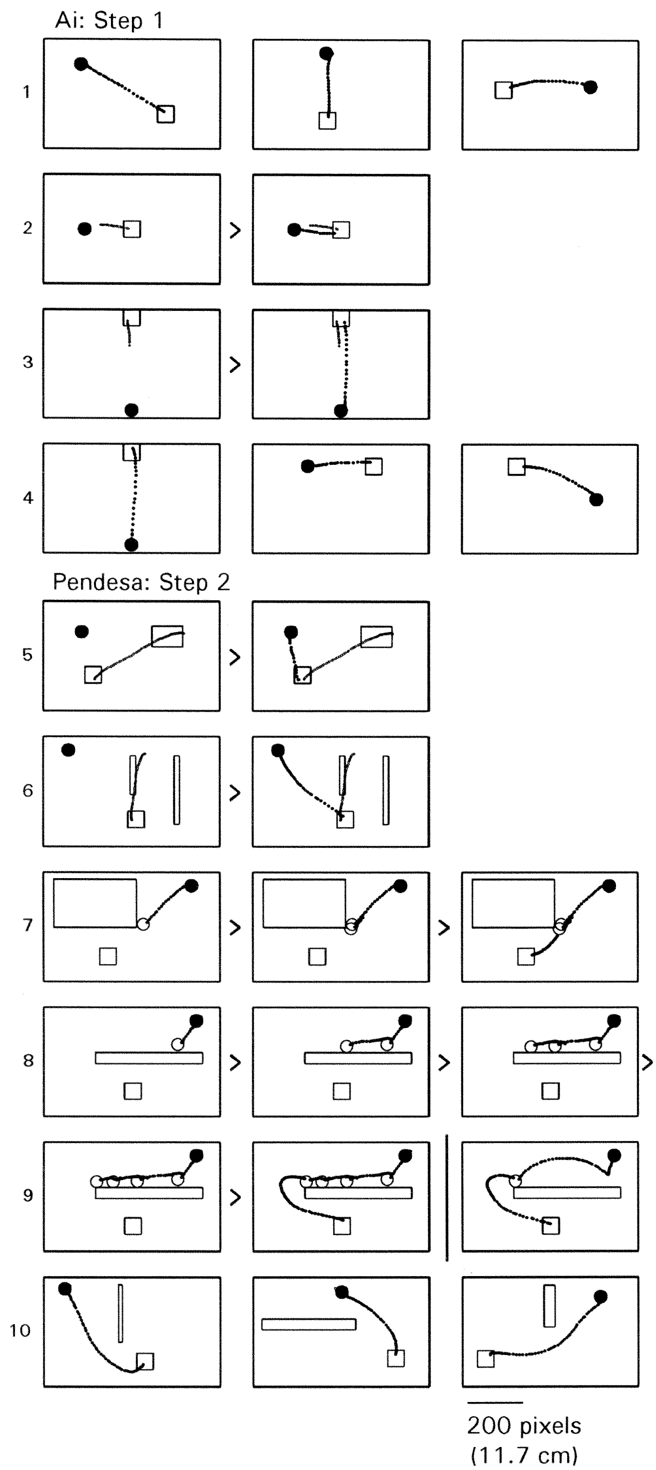

Fig. 3 Selected individual trials show the stepwise behavior changes that took place as the subjects learned to move the ball to the target in a smooth path. The *ball* is shown in its initial position at trial start. A *string of small dots* indicates the path of finger movement that transported the ball from its start location to the target. These dots did not appear on the monitor during the task. In *rows 2, 3, 5, and 6*, finger movement that did not produce ball movement is shown as a *thinner movement path* that begins elsewhere than at the ball. Obstacles are shown in *outline* in this figure to allow for presentation of finger movement unrelated to ball movement, such as in *row 6* where the subject moved the finger from the obstacle to the target before moving the ball to the target. An *arrowhead* between frames indicates that the frames are successive cumulative images from the same trial. For example, *rows 8–9* show five successive steps of performance in just one trial; the *third trial in row 9* is from the same maze in the next session

side to the left side. Both subjects acquired the new directions of movement (bottom to top and left to right) within a few sessions in step 1; additional examples of correct ball movement are shown in three trials in row 4.

With obstacles presented on the monitor in step 2, both subjects first tried to move the obstacle to the target or to move the finger along the obstacle, as if "tracing" it, before they moved the ball to the target. This behavior is illustrated in two successive frames from each of two trials in rows 5 and 6 in Fig. 3 (obstacles are shown in outline so that one can see the movement of the finger over an obstacle, and this movement is shown as the thinner path of dots). This ineffective behavior produced no changes on the monitor or reinforcement and disappeared within a few sessions. When obstacles blocked a straight path to the target, both subjects at first "bumped" the ball into the obstacles, as illustrated in three successive cumulative frames from one trial in row 7 (a large open circle indicates where the ball got stuck on an obstacle and had to be moved slightly backwards to be freed from the obstacle). Rows 8 and 9 show in five successive cumulative frames from one trial how the subject first moved the ball in a path directly toward the target, then hit the obstacle, and then moved the ball around the obstacle in several steps of bumping into the obstacle. The last frame in row 9 shows performance on the same maze in the next session; the subject stopped the movement before the ball hit the obstacle and then managed to move it almost all the way around the obstacle in one sweeping motion. Row 10 shows in three mazes from set 7 how the subjects developed curvature of ball movement so that the ball could be moved to the target in a sweeping movement without hitting an obstacle on the way. By the end of training on set 7, both subjects avoided obstacles as shown in these three trials.

Test new mazes, step 3

Rows 1–4 in Fig. 4 show examples of performance by both subjects for the first test session of maze set 8 after training with sets 1–7. To compare the two subject's performances, Fig. 4 shows the same mazes for the subjects; hence, the mazes in row 3 are identical to those in row 1, and the mazes in row 4 are identical to those in row 2. Rows 1 and 3 show mazes where ball movement did not collide with obstacles for Ai and Pendesa, respectively. Rows 2 and 4 show mazes where both subjects collided with the obstacles. In the second maze for Ai in row 2, the experimenter had to abandon the trial because she seemed unable to move the ball past the second obstacle; she kept moving the ball back and forth between the left sides of the two obstacles. For the same maze, Pendesa similarly hit the lower edge of the second obstacle but managed to get the ball past the obstacle to the target. On the third maze in rows 2 and 4, both subjects also selected a path under the middle obstacle; Pendesa managed to get the ball past the obstacle, but Ai did not and instead moved the ball back to near its start position and then to the target. These trials illustrate that neither subject was prepared to move the ball upward over an obstacle in the new test mazes. Because Ai did not reach the target on several trials, the experimenter terminated the test session prematurely for her. Ai then received six sessions of training with maze set 9, which featured more trials that required movement around obstacles than did set 8. Rows 5 and 6 in Fig. 4 show three selected trials from the first and sixth session of this maze set. The travel paths in row 5 show that Ai at first moved the ball directly toward the target

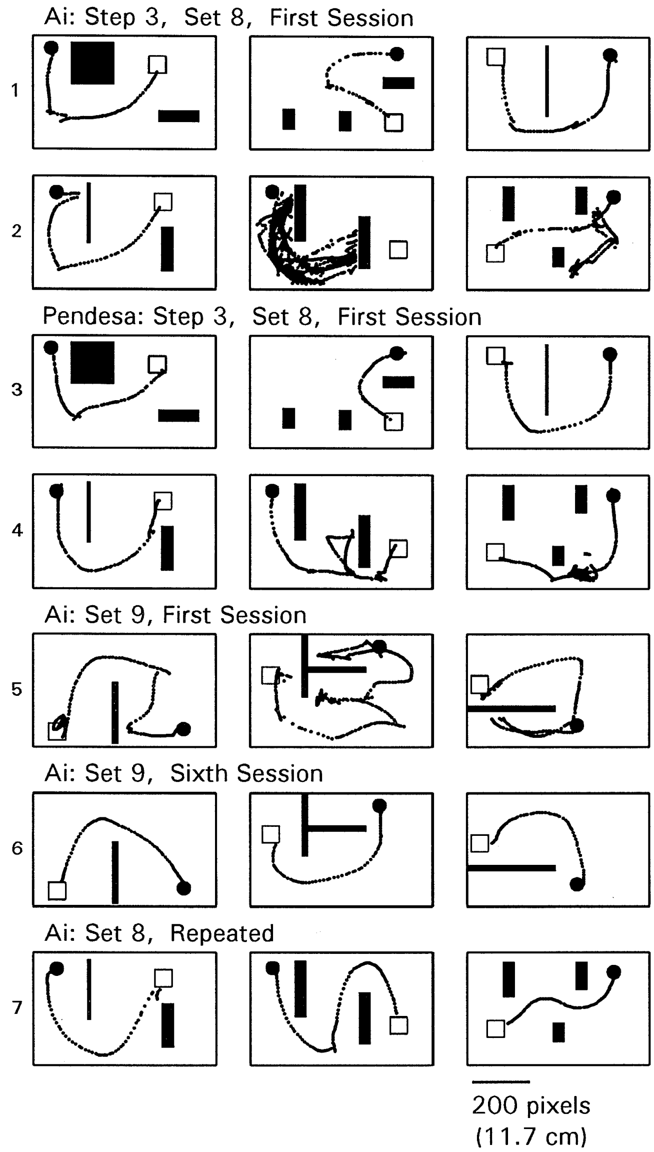

Fig. 4 Selected individual trials for the first test session of maze set 8 in step 3 are shown in *rows 1–4*; the same mazes are selected for both subjects so that their performances can be compared. The *filled circle* is the start ball, the *small open square* is the target, and *filled objects* are the obstacles that form the maze. Movement paths are indicated as a *series of small dots*, which did not appear on the monitor. *Rows 5 and 6* shows examples for maze set 9 for Ai only from the first session (*row 5*) to the sixth session (*row 6*). *Row 7* shows a repeat of maze set 8 for Ai, using the same trials as in row 2 for comparison. The *second trial in row 2* was abandoned by the experimenter

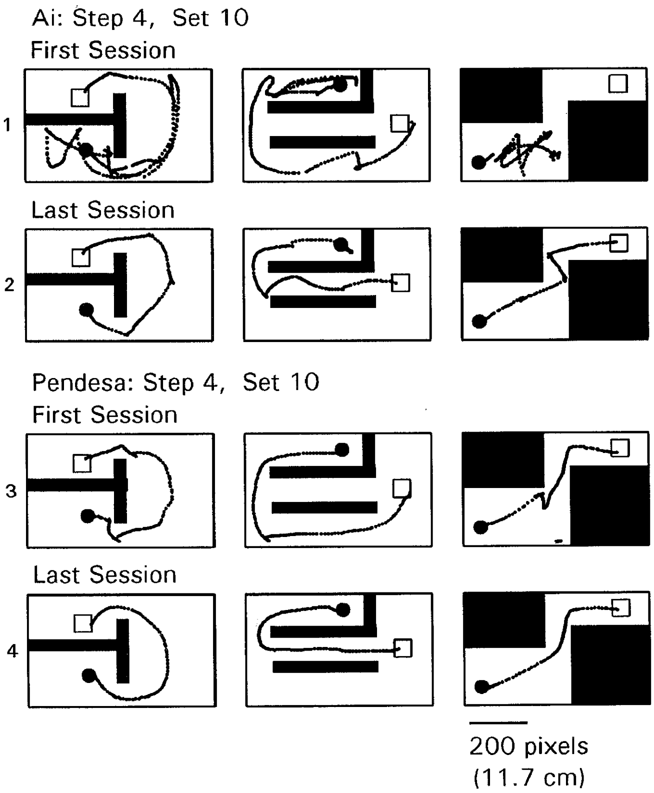

Fig. 5 Selected individual trials for the first and last session of training with maze set 10 in step 4. The same mazes are selected for both subjects so that their performances can be compared. The *filled circle* is the start ball, the *small open square* is the target, and *filled objects* are the obstacles that form the maze. *Small dots* show the travel path, which did not appear on the monitor

without regard to the obstacle that blocked the path. After a few sessions with this maze set, Ai avoided the obstacles and even moved the ball in a very wide path around the obstacles, as shown in row 6 for the same mazes as in row 5. When retested on maze set 8 (row 7), Ai now moved the ball to the target in a correct curved path without colliding with an obstacle and without first attempting to move it in a path directly toward the target (cf. row 2).

Training mazes in step 4 and testing new mazes in step 5

Maze set 10. Training with the more complex maze set 10 in step 4 resulted in further improvement in obstacle avoidance and travel path efficiency. Figure S3 (ESM) shows a video clip of maze performance by Pendesa for a single trial from maze set 10; the maze is the second in row 6 from Fig. 2. For a within- and between-subject comparison, Fig. 5 shows examples of improvement in three selected trials for each subject for the first and last session. In the first maze, Ai initially moved the ball in a path directly toward the target and thereby collided with the obstacle, but in later sessions she avoided the obstacle. In the second maze, both subjects initially avoided the narrow middle path to the target but eventually selected this shorter route. In the third maze, Ai did not manage to pass the narrow corridor in the first session (the trial was abandoned by the experimenter) and never went through smoothly as did Pendesa, as seen for the third maze in row 4.

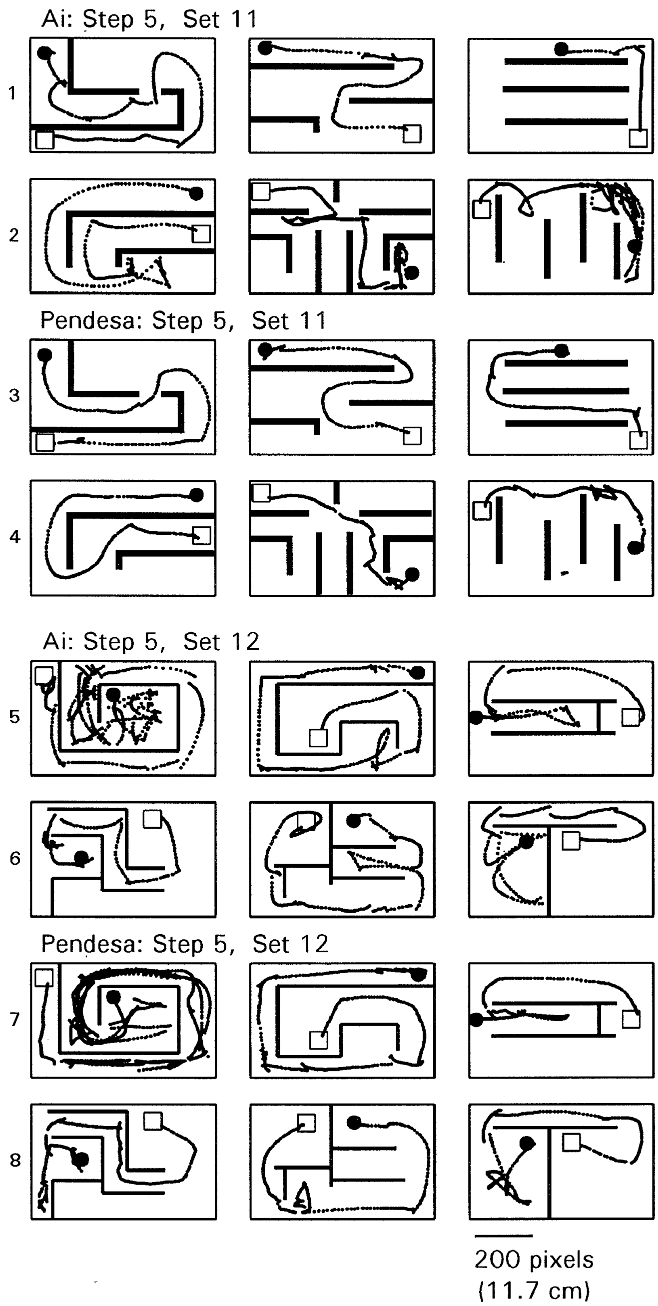

Fig. 6 Selected individual trials for the test sessions with maze sets 11 and 12 in step 5. For each maze set, the same mazes are selected for both subjects so that their performances can be compared. The *filled circle* is the start ball, the small open square is the target, and *filled objects* are the obstacles that form the maze. *Small dots* show the travel path, which did not appear on the monitor

Maze set 11. When tested with the two new maze sets in the final step 5, both subjects moved the ball to the target while avoiding obstacles for most mazes. The top half of

Fig. 6 displays six selected mazes for each subject for maze set 11, and the bottom half displays six selected mazes for maze set 12. In a between-subject comparison of the first three mazes (rows 1 and 3), Ai and Pendesa did about equally well, and in the third maze in row 1 Ai, in fact, selected a shorter path to the target than did Pendesa. However, in the next three mazes (rows 2 and 4), Ai moved the ball directly toward the target and into the obstacle in the lower part of the first maze and on the left side of the second maze, and she had considerable trouble moving the ball past the second obstacle in the third maze in row 2. Pendesa, on the other hand, did not move the ball directly toward the target and into an obstacle on any trial and had only minor problems getting past the obstacles in the second and third maze shown in row 4.

Maze set 12. Maze set 12 featured thinner and more complex obstacles, as shown in the lower part of Fig. 6. Both subjects had considerable trouble with the first spiral-shaped maze, moved the ball into the blind alley in the third maze, and tried to move the ball through the lower part of the obstacle in the sixth T-shaped maze. Ai attempted to move the ball in a shortcut path directly toward the target in the second, third, fifth, and sixth mazes, and Pendesa did so for the third, fifth, and sixth mazes. Pendesa tried to move the ball through the lower part of the obstacle in the fourth and sixth mazes. Thus, even after exposure to several maze sets, neither subject could move the ball to the target on all mazes in the new sets 11 and 12 without first moving into obstacles or moving toward the target via a blind alley.

Quantitative analysis of maze performance

Table 2 presents quantitative performance measures for maze sets 2–12. Data were analyzed as:

1. *Efficiency*, which is defined as the path length divided by the length of an ideal shortest path to the target (determined by the experimenter); a score of 1.0 thus indicates that the subject selected the shortest path possible.
2. *Obstacle collision* is the number of times the ball collided with an obstacle.
3. *Path error* is how many times the subject moved the ball a distance of 50 pixels or more in a path directly toward the target even though that path was blocked by an obstacle; path errors are shown relative to the number of trials where an obstacle prevented a direct path.

For Ai the efficiency improved from 1.7 for the early maze sets 2 and 3 to 1.1 for maze set 7. For Pendesa the efficiency was about 1.2 from the start and improved only slightly. When maze sets 3 and 4 were first introduced, both subjects made several path errors by moving the ball in a route directly toward the target. But when the more complex maze sets 6 and 7 were introduced, both subjects made only a few such path errors. On the new set 8, Ai fared poorly and collided with obstacles 80 times and made 6 path errors out of 14 opportunities (the session was abandoned after 18 trials). For Pendesa on set 8, the efficiency ratio increased slightly, and the number of collisions also increased, but she made only 2 path errors out of 20 opportunities. When Ai received training on set 9, her performance improved considerably within six sessions. This improved performance led Ai to fare much better on the second test of set 8, where her performance now was similar to that of Pendesa on her first encounter with set 8.

On the first session of maze set 10 both subjects increased the number of collisions with obstacles but only Ai made path errors, which virtually disappeared after additional training sessions on this maze set. On the last two maze sets (11 and 12) both subjects increased the number of collisions compared to the last session for set 10, and Ai made several path errors while Pendesa made three on set 12 only.

The quantitative measure of travel efficiency can be exemplified by a comparison of performance change for individual maze trials. For example, for Ai for the same three mazes from maze set 9 shown in rows 5 and 6 in Fig. 4 from sessions 1 and 6, respectively, the efficiency ratio improved from 1.8 to 1.1, from 3.4 to 1.1, and from

Table 2 Qualitative measures of maze performance. *The efficiency ratio* is the total path length of ball movement divided by the ideal, shortest possible movement path between the ball's start location and the target location (determined by the experimenter for each maze); the ratio shown here is a grand average for each maze set. *Obstacle collision* gives the raw number of times the ball collided with an obstacle per session (several collisions could happen in one trial). The *path errors* indicate the number of trials in which a route was selected that moved the ball directly toward the target but with an obstacle blocking that route (data are given as the number of trials with such paths:number of opportunities for such paths). Maze set 8 was tested twice (1 and 2). For Ai, maze set 9 data are presented for the first (*F*) and the last (*L*) session. For maze set 10, data are presented for the first (*F*) and the last (*L*) session of training. For sets 11 and 12, data are from the first session of each set

Maze set	Ai			Pendesa		
	Efficiency ratio	Obstacle collision	Path errors	Efficiency ratio	Obstacle collision	Path errors
2	1.6	11	0:0	1.1	2	0:0
3	1.7	9	2:4	1.2	6	2:4
4	1.4	7	2:6	1.3	12	4:6
5	1.5	7	0:5	1.1	3	0:5
6	1.1	4	2:11	1.2	3	2:11
7	1.1	8	2:14	1.2	9	2:14
8 (1)	2.2	80	6:14[a]	1.3	38	2:20
9 (F)	1.5	54	9:24	N/A	N/A	N/A
9 (L)	1.1	6	1:24	N/A	N/A	N/A
8 (2)	1.3	23	4:20	1.2	15	2:20
10 (F)	1.5	105	7:24	1.1	32	0:24
10 (L)	1.2	27	1:24	1.1	12	0:24
11	1.5	67	3:24	1.1	35	0:24
12	1.7	79	8:24	1.1	77	3:24

[a]This session was terminated after 18 trials for Ai

2.7 to 1.2, reading the mazes from left to right. For the mazes in row 6, Ai moved the ball with an excessive curvature away from the obstacle yielding a path that was slightly longer than the ideal shortest path to the target. Across maze sets, Pendesa's efficiency ratio was relatively constant and near 1.1–1.2. For Ai, however, the efficiency ratio increased (i.e., performance became less efficient) each time a new maze set was introduced, yet her performance efficiency improved within a few sessions each time a maze set was repeated, as for sets 9 and 10.

The efficiency, obstacle collision, and path error measures provide a way to assess performance improvement for a given maze and for a set of mazes, and these measures can also be used to compare the subjects. The efficiency measure in particular is useful because it is calculated relative to the ideal travel path and hence can be used freely in a comparison across mazes and subjects. Obstacle collisions and path errors obviously depend on maze complexity and are, therefore, useful mainly for comparisons of performance on a given maze across sessions and subjects. Maze performance can also be analyzed in terms of how long time the subject takes to complete a given maze. However, this measure obviously depends on the length of the required minimum travel path and on the speed of movement, which is slowed down in complex mazes that require many turns. In general, the time to complete a given maze shortened as the subjects improved their performances by reducing the number of obstacle collisions and by making the path more efficient. For example, for Ai for the six sessions with maze set 9, the average time to complete a maze was 5.4 s for the first session and 2.2 s for the sixth session. At the level of individual trials, the times to complete the three mazes shown for Ai in row 5 in Fig. 4 were, from left to right, 4.8 s, 19.2 s, and 8.8 s for the first session and 1.5 s, 4.8 s, and 1.0 s for the sixth session (row 6).

One may consider a maze free of path errors to be a correctly solved maze even if the subject makes some obstacle collisions on the way to the target. Thus, the percent of mazes solved correctly was 91.6% for each subject in step 7 (for two path errors in 24 mazes, see Table 2, the percent correct equals 100×22/24). For the first session of set 8, the percent correct was 66.7% for Ai and 91.6% for Pendesa. For set 9 (Ai only) the percent correct improved from 62.5% to 93.8% in six sessions. For the new set 11, Ai's percent correct was 75.0% and Pendesa's was 100%. For the new set 12, Ai's percent correct was 66.7% and Pendesa's was 87.5%. However, because of its dynamic nature the maze performance cannot easily be converted to a single measure of percent correct for all maze types. For example, for the first presentation of a maze with a spiral pattern (e.g., the first maze in row 7 in Fig. 6) both subjects obviously did not know how to solve the maze and reached the target only after considerably aimless ball movement. Because of the spiral maze shape, which did not allow for any path errors, this maze would be counted as correctly solved if one considered only path errors in the assessment of maze performance. Hence, the measure of percent correct based on path errors (as used above) is a somewhat inflated measure because it does not fully capture the dynamic nature of the maze performance.

The efficiency ratio does seem to capture the totality of the maze performance quite well since it decreases (i.e., performance improves) when path errors or detours into blind alleys disappear. Similarly, the efficiency ratio decreases as the number of obstacle collisions decreases as well as when performance becomes smooth and nearly optimal, as seen, for example, for the mazes in row 4 in Fig. 5.

Discussion

Experiment 1 demonstrates that the chimpanzee can relatively easily learn to negotiate an automated, electronic visual fingermaze presented on a touch monitor. Progress in solving the mazes was seen in several aspects of the performance. Both subjects first tried to move the obstacles. Second, they moved the ball directly into obstacles that blocked a straight route toward the target. Many object collisions occurred before each subject learned to steer the ball around or away from an obstacle. Even though both subjects had learned to avoid the obstacles in the training sets, they nonetheless readily moved the ball into the obstacles for some of the novel mazes. Apparently, learning that *any* red obstacle had to be avoided was not acquired very rapidly. For example, for some of the mazes presented in the last set 12, both subjects moved the ball directly toward an obstacle, as for the third maze in rows 6 and 8 in Fig. 6, or into blind alleys, as for the third maze in rows 5 and 7 in Fig. 6. Ai did not move the ball very efficiently in most new mazes, but Pendesa managed to move efficiently in most new mazes, especially in maze set 11. Both subjects showed considerable progress when the same set of mazes was presented repeatedly in steps 3 and 4. The results indicate that the subjects learned to move the ball in the most efficient path for each individual maze. The more generalized performance of being able to move efficiently in any new maze was only evident to some extent.

Experiment 2

This experiment examined route selections more formally in mazes with only two routes to the target. The mazes were designed such that one route could be blocked by a closed "door" at various distances from the target. The objective of the experiment was to determine whether such an obstacle would influence the selection of transport route. That is, if the subject consistently selects the open route without first making a detour down the blocked route, then the closed door must be a stimulus that makes the subject select the opposite, open route. Pendesa was trained with 18 mazes each with a different closed door that blocked one of the two routes. When she consistently selected the open route, new mazes with a similar design but with different closed doors were presented to test whether she had learned a more general maze-solving skill. Additional tests were designed to determine whether Pendesa had learned to examine the maze prior to ball movement. In one test we assessed the effects of presenting insoluble mazes that blocked both routes to the target; if she had learned to not move in the direction of a closed door maybe she would not engage the maze at all because both routes were blocked. In mazes that had one long and one short open route to the target, we tested whether she would learn to select the shorter of the two routes. Once she had learned this skill, we blocked the shorter route to examine whether she would immediately select the alternative, open route.

Method

Subject

Only Pendesa was used in this experiment.

Procedure

Each session had 12 trials that each presented one maze. Each trial began with the presentation of a 100×100 pixels solid, red, square in the middle of the dark screen. When the subject pressed this square the screen cleared and a maze was presented with a ball and a target. The time from this trial-initiation response to the first touch on the ball was defined as the start latency. On each trial, the subject had to transport the ball to the target by moving it with a finger across the screen while avoiding the obstacles, which the ball could not pass through. The ball was 20 pixels in diameter and the target was 25×25 pixels. Trials were separated by a 1-s inter-trial interval. When the subject moved the ball to the target she received a small piece of fruit as reinforcement. Table 3 outlines the general procedure, and the top two rows in Fig. 7 present sample mazes. Training was divided into six logical steps. Pendesa usually had five to ten sessions each training day.

Table 3 Steps of training in experiment 2 (Pendesa only). Each session presented 12 different mazes. Each maze had two routes from the ball to the target. Some mazes had one route blocked. In maze sets 1–8 the ball and target were always located on the left or right side alternating randomly from trial to trial; in maze sets 9–14 the ball and target locations varied

Step	Description	Sessions
1	Maze set 1, no blocked routes	1
2	Maze sets 2–4, 6 mazes each session had one blocked route, the other 6 mazes were as in set 1	42
3	*Test* of maze sets 5–7, 6 mazes each session had one blocked route (different from maze sets 2–4), the other 6 mazes were as in set 1	9
4	*Test* of maze sets 5 and 6 with 2 mazes changed with both routes blocked	
5	Maze set 8 with varying ball and target locations with no blocked routes	5
6	*Test* of maze sets 9–14, 5 mazes each session had one route blocked, the other 7 mazes were as in set 8	9

Step 1: pretraining. The pattern of obstacles shown in frame A in Fig. 7 was presented on all 12 trials with the ball and target switching position randomly from trial to trial in maze set 1. The two possible routes from ball to target were of the same length and had the same patterns of obstacles. Prior to step 1, Pendesa had received eight sessions with the same general maze pattern as in frame A but without the middle horizontal obstacle.

Step 2: training with one blocked route. Six mazes each session were as in step 1. Six additional mazes had one route blocked by an additional obstacle that was either horizontal (e.g., frame B) or vertical (e.g., frame C); the block was either at the upper half (top) or at the lower half (bottom) of the maze. The block was the same color (red) and thickness as the other obstacles. There were 11 possible blocks (5 vertical and 6 horizontal) that could be filled at the top of the maze and 11 at the bottom. Combined with the location of the ball and target on either side, this yields 44 different mazes with one blocked route. In step 2, we presented 18 of these possible 44 different mazes on trials with one blocked route. Each set (2–4) of 12 mazes thus had 6 different mazes with one blocked route and 6 mazes with both routes open; each of the three maze sets was presented 14 times yielding a total of 42 training sessions.

Step 3: test for generalization of maze performance on new mazes. Six trials each session presented a new maze that was different from but structurally similar to those presented in step 2. Each new maze set (5–7) was presented three times. Thus, 18 new mazes with one blocked route were tested in step 3. Six trials each session had both routes open, as for maze set 1.

Step 4: test for performance in impossible mazes with no open route to the target. Maze sets 5 and 6 were each presented once with one trial in each set having both routes blocked (e.g., frame D in Fig. 7). After about 30 s in each of these two test trials, the experimenter pressed a key which removed the block so that the subject could eventually bring the ball to the target.

Step 5: training to select the shortest path. In maze set 8, the ball and the target appeared at varying locations within the maze yielding one long and one short route to the target; both routes to the target were open on all trials (e.g., frame E in Fig. 7).

Step 6: test for generalization of maze performance on new mazes. The ball and target locations varied as in step 5 but the shorter route to the target was blocked in some mazes to force the subject to take the longer route. Six

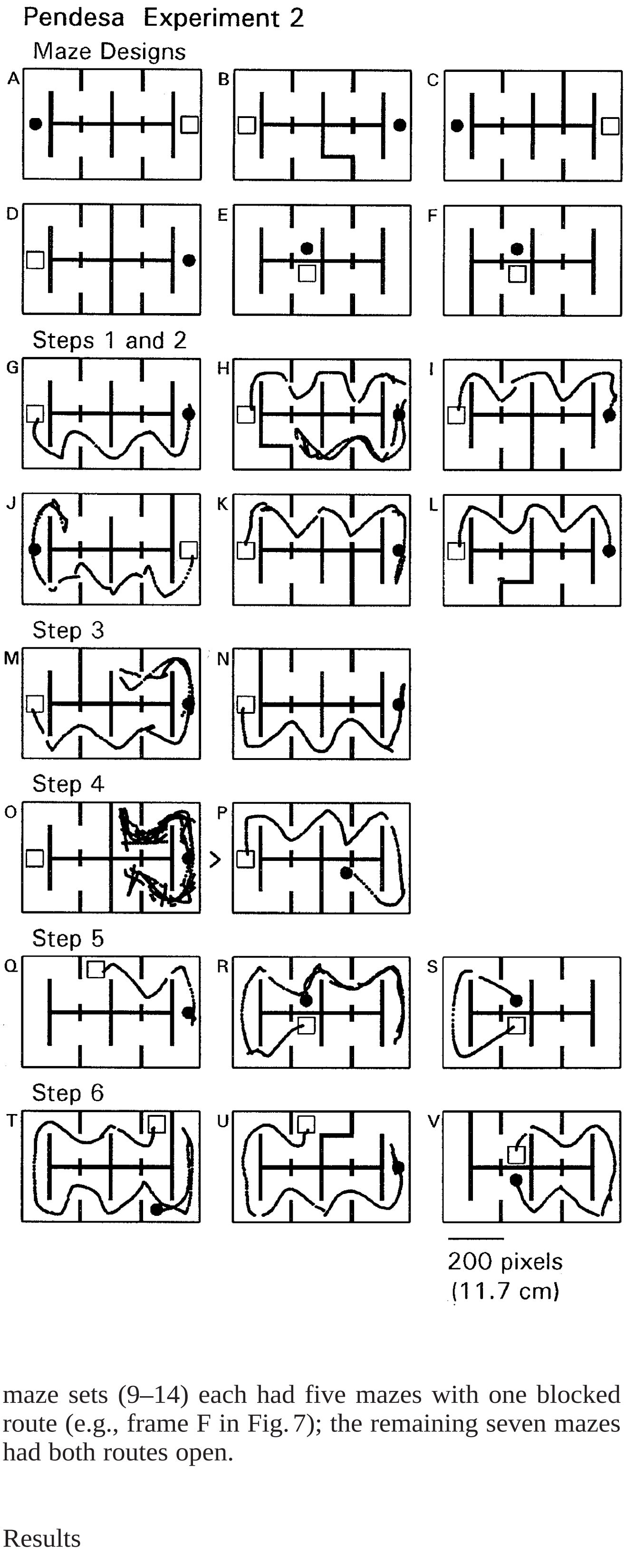

Fig. 7 Two-choice maze designs used in experiment 2. The *filled circle* is the start ball, the *small open square* is the target, and *filled objects* are the obstacles that form the maze. *Small dots* show the travel path, which did not appear on the monitor. *Frames A-F* show sample mazes used for training or testing. In *frame A*, there are two possible routes to the target, and ball and target are always located left or right varying from trial to trial. *Frames B* and *C* are as *A* but one route is blocked by a „closed door" the location of which varied from trial to trial; the door was the same color as the other obstacles. In *frame D* two single maze trials featured an impossible maze with both routes blocked. In *frame E* the ball and the target had varied locations producing one short and one long route to the target. *Frame F* was as *E* except that one route was blocked by a closed door. *Frames G–V* illustrate the performance in the mazes at each procedural step, see text. (Occasional brief „gaps" in the travel path resulted from the subject moving the ball into the edge of an obstacle, as seen, for example, in the *lower left corner in frame M*)

maze sets (9–14) each had five mazes with one blocked route (e.g., frame F in Fig. 7); the remaining seven mazes had both routes open.

Results

Pendesa readily moved the ball to the target in the two-choice mazes from the first session in step 1; frame G shows performance on one trial. With one route blocked in step 2, Pendesa at first sometimes moved the ball down that route and in such cases usually moved it up to the block, the „closed door", and then moved the ball back again all the way around to the target, as shown in frame H in Fig. 7. On other trials, Pendesa selected the open route apparently by chance, as in frame I. Pendesa went into the blind alley on 66% of the trials with one closed route in the first three sessions of step 2. Over sessions the distance traveled into a blind alley became shorter and shorter, as illustrated in frames J and K. In general, Pendesa first learned to avoid routes where the block was near the ball's start position. By the end of step 2 training, Pendesa practically never selected a blocked route. Thus, for the last three sessions of step 2, she moved the ball a short distance into a blind alley on one trial only. Frame L illustrates the final performance.

In step 2, Pendesa showed considerable improvement in movement efficiency within the maze. In a quantitative analysis of all mazes with one blocked route, the average number of collisions with obstacles decreased from the first six to the last six sessions from 2.7 to 1.6 per trial, and the proportion of trials without a single collision (such as in frame L) increased from 3% to 18%. One consequence of the improved smoothness of movement was a reduction in the time it took to complete the maze. Thus, from the first six to the last six sessions in step 2, the time to complete a trial (from first touching the ball to contacting the target with the ball) decreased from 4.7 s to 3.2 s for mazes with both routes open and from 8.4 s to 3.4 s for mazes with one route blocked. On trials without any collisions in the last six sessions, the average completion time was 2.6 s; the shortest recorded completion time for one trial was 1.9 s. Similarly, the path efficiency (defined as for experiment 1) improved from 3.2 for the first six sessions to 1.1 for the last six sessions for mazes with one closed route.

When new maze sets 5–7 were introduced in step 3 using mazes with blocks at different locations from those used in step 2, Pendesa made a detour into the blind alley on only 5 of 54 opportunities for all nine sessions. Frame M shows the trial with the longest detour, which occurred in the first test session in step 3. The remaining four detours were very short, as shown in frame N. If a detour is considered to be an error, Pendesa showed a 90.7% (49/54) accuracy in the transfer test to mazes with novel closed doors. Thus, Pendesa to a large extent generalized the performance learned in step 2 to similar mazes with different closed doors; the performance indicates that for most mazes Pendesa must have looked for the block that closed one route or for the open route before she began moving the ball. Figure S4 (ESM) shows a video clip of maze performance in a single trial from maze set 6.

As an additional test of the role of the block that closed one route we presented two single test trials in step 4 with an impossible maze where both routes to the target were blocked. After about 30 s the block was removed when the experimenter pressed a key on the computer's keyboard to allow Pendesa to move the ball to the target. Frames O and P show two successive frames from the first of these trials; the second frame begins the moment one of the two blocks was removed and shows the location of the ball at that moment. With the impossible maze, Pendesa moved the ball back and forth as if looking for an opening. When the block was removed she immediately moved the ball through the opening to the target (frame P). She repeated this performance on the second trial with another impossible maze on the next sessions. This performance indicates that although Pendesa had learned to avoid moving the ball into a blind alley, she did not generalize this skill to the new situation with two blocked routes; a perfect generalization conceivably would result in no movement of the ball. Instead, faced with these impossible mazes, Pendesa apparently moved the ball to one of the blocks and then, as in earlier sessions, moved the ball in the opposite direction because this movement had always led the ball to the target through the other open route. Because both routes were blocked, this established behavior resulted in the "back and forth" movement seen in frame O.

For step 5, with the ball and target presented in varying locations with no blocked routes, frame Q shows a trial with selection of the shorter route on the first session. Frame R shows a detour and a correction of the route back to the start point and continuation to the target the long way around, which also occurred on the first session. Pendesa went the long way around for this particular maze on the next three sessions but eventually selected the shorter route (frame S). Pendesa consistently selected the shorter route on all mazes for the last two sessions.

In step 6, one door was closed to prevent Pendesa from using an established short route from ball to target. In the first three test sessions in step 6, Pendesa moved into the open but longer route on only 8 of 15 opportunities (a 53.3% accuracy of solving novel mazes). Frame T in Fig. 7 shows the first trial with ball movement up to the closed door. Pendesa at first initiated the preferred shorter path for this particular maze, which had the target relatively close to the ball's start location. When the ball reached the closed door she redirected the path and moved the ball to the target the other way around. The path into a blind alley became very short after a few more sessions, as illustrated in frame U. For all nine sessions combined, Pendesa correctly avoided the blind alley on 32 of 45 opportunities (71.1% correct). By the last three sessions in step 6, Pendesa went into a blind alley on only 2 of 15 opportunities. Thus, on most trials, Pendesa avoided the blind alley, as illustrated in frame V, and she learned to avoid blind alleys much faster than in steps 2 and 3.

In experiment 2, each trial began with just a small square on the monitor. When Pendesa pressed this square the screen cleared, and the maze was presented with the ball and the target. The time that passed from the press on the square to the first touch on the ball was defined as the latency or reaction time and was measured for each trial. This reaction time was almost always 0.5–1.0 s (85% of all latencies were less than 1.0 s) and did not depend on whether a given trial featured two open routes to the target or one open route and one blocked route. For example, in step 3 the mazes with one blocked route had an average latency of 0.78 s and mazes with both routes open had an average latency of 0.76 s (this small 0.02 s difference was not statistically significant). Similarly, in step 6 with the shorter route to the target blocked, the mazes with one blocked route had an average latency of 0.89 s and mazes with both routes open had an average latency of 0.86 s (this small 0.03-s difference was not statistically significant).

Discussion

In the first sessions with one route blocked in the two-choice mazes, Pendesa often moved the ball all the way to the point where the route was blocked. Her performance looked almost as if she was „seeing“ the locked door only when it was close to her fingertip. Over sessions, Pendesa must have learned to look ahead of her finger movement as the travel paths into blind alleys became shorter and shorter. Eventually, Pendesa avoided all blind alleys. With new doors closed in the same maze pattern, she at first did move the ball into a few blind alleys but this performance disappeared quickly. Similarly, when the preferred shorter route to the target was blocked, she at first moved the ball into the blind alley on some trials but again she quickly began to avoid the blind alley. The overall performance seems to be a matter of learning specific maze displays. Once a display is learned, she solves that maze the same way each time. A generalized map-reading performance of avoiding any blind alley in new mazes was not fully established in this experiment. The best evidence of such map-reading was the 90.7% accuracy on new mazes in step 3. But for the new mazes in step 6, the transfer was only at 53.3% accuracy. Similarly, with both routes blocked simultaneously in two test trials in step 4, Pendesa did not refrain from moving the ball back and forth in an apparent attempt to search for an opening. Such futile movement would seem unnecessary if a generalized map-reading skill had been acquired. However, in general, her performance of avoiding blind alleys improved as she was exposed to more mazes, and she learned to avoid blind alleys more quickly as the experiment progressed.

An analysis of time spent looking at the maze prior to moving the ball to the target (latency) did not reveal any differences for mazes with one blocked route and for mazes with both routes open. Latencies were generally less than 1 s and the subject therefore decided quickly which route to take.

General discussion

Both subjects acquired the skill of moving the ball to the target in a path that approached the optimal shortest path between ball and target in a maze of obstacles that had to be avoided. The acquisition of this skill progressed from moving the ball straight to the target with no obstacles present to bumping into obstacles that blocked this path, and to moving the ball in a curved path around obstacles. Once movement curvature had developed, both subjects became very proficient in avoiding several obstacles. A measure of performance efficiency, which was a simple ratio of path length divided by optimal path length, proved very useful for both within- and between-subject comparisons at the level of individual trials as well as at the level of an entire set of mazes. For maze sets the subjects had worked with for several sessions, the performance became very proficient, with avoidance of blind alleys and very few collisions with obstacles. But each time new mazes were introduced both subjects often moved the ball into blind alleys or into obstacles that blocked a straight route to the target and thereby increased the number of collisions with obstacles. These results suggest that the subjects had not yet acquired a generalized map-reading skill. Evidently, both subjects learned each maze with a trial-and-error type method. However, the performances were far from random for new maze sets. The subjects' performances on many new mazes reflected previous successful movements in the trained mazes. Both subjects adjusted their movement paths very quickly when the previously acquired paths proved unsuccessful. The overall performance can perhaps best be characterized simply as moving the ball toward the target in the shortest and quickest, most economical path possible.

Pendesa in experiment 2 showed very promising progress by only rarely moving into blind alleys on new mazes. Yet, even for the last set of novel mazes, she still moved straight into the blind alley on a few trials. And when impossible mazes with no open routes to the target were presented she did not pause or walk away; instead she tried to move the ball the other way around as she had done in early steps of acquisition when novel mazes were presented.

The most positive finding of the present experiments was the rapidity with which both subjects improved their performance each time new maze sets were introduced. After just a few sessions with each new set, the subjects improved the efficiency of ball movement and reduced the number of collisions with obstacles. This suggests that the subjects' performance is very much influenced by their experiences. Some of the problems evident in the subjects' performance during test sessions suggest that the training method may have established performance patterns that were not optimal for new situations. For example in experiment 1, both subjects failed to move the ball upwards over obstacles for some mazes in the novel maze set 8 (last two frames in rows 2 and 4 in Fig. 4), and both subjects tried to move through the same spot at the bottom side of an obstacle (last frame in rows 6 and 8 in Fig. 6). These examples indicate that in training with maze sets 1–7 we probably had not presented sufficient exemplars of mazes that required upward ball movement over obstacles; similarly, we had probably presented to many exemplars of mazes where the optimal path was a U-shaped movement. Hence, when the subjects could not readily solve a novel maze, they instead often did what they had done successfully in the past, such as attempts at U-shaped movement paths. Similar performance problems in test situations were seen with the same two subjects in other experiments on drawing one line parallel to another (Iversen and Matsuzawa 1997). In general, the results indicate that the chimpanzee's performance in test situations is very much influenced by prior experiences.

The present experiments extend previous findings of maze learning in rhesus monkeys and chimpanzees (Spragg 1936; Rensch and Dohl 1968; Washburn 1992) and suggest that the fingermaze is a very promising method to examine wayfinding in non-human primates in experimental situations. The rapid progress in performance seen in the present experiments suggests that the chimpanzee subjects might quite conceivably learn a more generalized maze-solving or map-reading skill in future experiments after extended training with maze sets that are considerably more varied than those used in the present experiments.

Acknowledgements The authors wish to thank Mr. Sumiharu Nagumo for his technical assistance. The chimpanzees were cared for according to the *Guide for the care and use of laboratory primates* of the Primate Research Institute, Kyoto University. The experiments comply with the current laws of Japan, where the research took place. The first author was supported by a Center of Excellence (COE) fellowship from Kyoto University, and the research was financially supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science, Sports, and Culture, Japan.

References

Fujita K, Matsuzawa T (1990) Delayed figure reconstruction in a chimpanzee (*Pan troglodytes*) and humans (*Homo sapiens*). J Comp Psychol 104:345–351

Gleeson S (1991) Response acquisition. In: Iversen IH, Lattal KA (eds) Techniques in the behavioral and neural sciences:experimental analysis of behavior, part 1. Elsevier, Amsterdam, pp 63–86

Golledge RG (1999) Wayfinding behavior: cognitive mapping and other spatial processes. The Johns Hopkins University Press, Baltimore

Grosse DA, Wilson RS, Fox JH (1991) Maze learning in Alzheimer's disease. Brain Cogn 15:1–9

Iversen IH, Matsuzawa T (1996) Visually guided drawing in the chimpanzee (*Pan troglodytes*). Jpn Psychol Res 38:126–135
Iversen IH, Matsuzawa T (1997) Model-guided line drawing in the chimpanzee (*Pan troglodytes*). Jpn Psychol Res 39:154–181
Iversen IH, Matsuzawa T (1998) Automated training of line drawing and object movement (in fingermaze and sorting tasks) on a touch-sensitive monitor in captive chimpanzees (*Pan troglodytes*). Presentation at Measuring Behavior 1998, Groeningen, The Netherlands, August (abstract available at http://www.noldus.com/events/mb98/abstracts/iversen1.htm)
Iversen IH, Matsuzawa T (2001) Establishing line tracing on a touchmonitor as a basic drawing skill in chimpanzees (*Pan troglodytes*). In Matsuzawa T (ed) Primate origin of human cognition. Springer, Berlin Heidelberg New York, pp 235–268
Matsuzawa T (1985a) Use of numbers by a chimpanzee. Nature 315:57–59
Matsuzawa T (1985b) Color naming and classification in a chimpanzee (*Pan troglodytes*). J Hum Evol 14:283–291
Reid AK, Staddon JER (1998) A dynamic route finder for the cognitive map. Psychol Rev 105:585–601
Rensch B, Dohl J (1968) Choice behavior between two mazelike pathways that can be overlooked by a chimpanzee. Z Tierpsychol 25:216–232.
Spragg SDS (1936) Anticipatory responses in serial learning by chimpanzee. Comp Psychol Monogr 15, no 7
Stokes TF, Baer DM (1977) An implicit technology of generalization. J Appl Behav Anal 10:349–367
Tolman EC, Honzik CH (1930) „Insight“ in rats. Univ Calif Publ Psychol 4:215–232
Tomonaga M, Matsuzawa T (1992) Perception of complex geometric figures in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*): analysis of visual similarity on the basis of choice reaction time. J Comp Psychol 106:43–52
Washburn DA (1992) Analyzing the path of responding in maze-solving and other tasks. Behav Res Meth Instrum Comput 24:248–252
Woodworth RS, Schlosberg H (1954) Experimental psychology (revised edition). Holt, Rinehart and Winston, New York