FACTORS IN TWO-DIMENSIONAL MAZE NAVIGATION BY PIGEONS

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DISSERTATION ABSTRACT

FACTORS IN TWO-DIMENSIONAL MAZE NAVIGATION BY PIGEONS

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Navigation of two-dimensional mazes in a computerized environment has been used to assess and compare spatial cognition in human and nonhuman primates. Recent technology advances have led to the extension of these maze tasks to pigeons. To determine the extent to which the joystick and touch screen technologies can be used to compare these species, the effect of various manipulations on the touch screen task should be accomplished and the results compared to those of the primate literature. If the sources of control for each task are not equated across species, possible quantitative differences (i.e., level of a process) may by explained as qualitative differences (i.e., absence of process). The overall goal of these studies was to assess stimulus control by various maze parameters inherent in two-dimensional maze navigation. The first experiment assessed how two types of choice points (i.e., forced and facultative) affected performance. The results indicate full transfer (i.e., maze navigation) after training with facultative-choice mazes, and partial transfer after training with forced-choice mazes. Experiment 2 addressed the effect of proximal but unavailable paths on performance. The results indicate that at a short distance to the goal, control by path characteristics (i.e., wall) decreases. Expanding on the implications of distance, Experiment 3 assessed distance discrimination in both simple and complex (i.e., curved) paths. The results indicate that the distance to the goal affects responses when the difference in distance between two paths is large. Experiment 4 expanded the analysis on path complexity by comparing performance across various ratios of directional changes within a path while holding the Manhattan (i.e., actual path distance to the goal) and Euclidean (i.e., shortest path to the goal assuming no limitation in direction) distances constant. The results indicate that path complexity does not affect performance. The results suggest that under certain manipulations the pigeons may reach the same levels of path-planning as primates. However, the analyses also suggest that higher levels of planning may require redefining in order to account for sources of behavioral control.

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Style Manual used

Publication Manual of the American Psychological Association, 5th Edition

Computer Software used

Microsoft Word

Microsoft Excel

SPSS

Sigma Plot

Visual Basic

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I. INTRODUCTION

Successful navigation of the environment involves the subject's determination of its current location with respect to environmental cues and the goal location. Such cues may be physical features, landmarks, sun position, or internal mechanisms. The ability to navigate an environment allows organisms to approach or avoid food, mate, or predators. If an organism moves randomly in its environment the likelihood of not finding food or a protected area decreases while the likelihood of becoming prey increases. Alternatively, the organism may learn the exact pattern of responses necessary to reach food and safe areas. This would allow it to survive as long as these were permanent sources of food and safety. Optimally, the organism may learn to move in any environment by using old and novel cues to return to old locations and move into new locations.

Maze-navigation has been extensively studied with human subjects across a variety of media (point mazes: Martin & Bevan, 1963; paper mazes: Sweller, 1983; surface mazes: Barker, 1932; open physical mazes: Ericksen, 1962; Newman & Kasniak, 2000; physical mazes: Chouinard, Briere, Rainville, & Godbout, 2003; and virtual mazes: Kirschen, Kahana, Sekuler, & Burack, 2000; Sandstrom, Kaufman, & Huettel, 1998). In the case of point, paper, and surface mazes, the task could allow an overview of the maze, including the start and goal locations. These tasks assess path-finding behaviors but not goal-finding behaviors. Open physical mazes, physical mazes, and virtual mazes assess goal-finding behaviors. Goal-finding behaviors have usually been measured in nonhuman animals. Because of the controls required to diminish the effect of extraneous variables these behaviors were not measured extensively with humans until recently. Buel (1935) summarized ninety-three factors affecting maze navigation in rats into 13 categories, including route and path preferences, goal functions, maze structure and pattern, and general orienting factors. He concluded that these factors were not independent of each other and that analyzing behavior based solely on the independent variables proposed in the hypothesis of an experiment ignores other factors that may actually control behavior. The result of such a minimal scope in the analyses could predict performance for groups under different conditions but not individual performance. A similar overview of the factors affecting two-dimensional maze navigation was not found by this author.

Recently, two-dimensional mazes in computerized environments have been used with human and nonhuman primates to assess the properties that control maze navigation (i.e., path-finding) and the emergence of path-planning behaviors (Fragaszy, Johnson-Pynn, Hirsh, & Brakke, 2003; Mushiake, Saito, Sakamoto, Sato, & Tanji, 2001; Washburn, 1992; Washburn & Rumbaugh, 1992). The combined control by various maze properties in relation to current and goal locations has been regarded as evidence of planning. Recent use of touch screens with pigeons offer the opportunity for species comparison on the factors affecting learning and transfer to novel mazes and the possible emergence of path-planning behaviors (Miyata, Ushitani, Adachi, & Fujita, 2006).

The development of tasks that make use of joysticks and touch screens to control motion have allowed other species to be tested in tasks similar to the two-dimensional tasks used to assess path-planning in humans. However, an extensive assessment of the factors controlling performance similar to Buel's attempt with goal-finding tasks in rats has not been completed in these new tasks. An attempt to assess path-planning behavior across species with novel instruments should address the possible factors controlling performance in addition to the known manipulations of the study. The studies proposed here begin to assess how factors commonly manipulated to increase maze novelty and difficulty may also affect performance and thus any conclusions about path-planning.

Maze Properties

Maze navigation consists of motions performed through a series of paths to reach a goal location. Performance at each intersection, or choice point, can be conceptualized as a sub goal given that correct responding at these locations ultimately leads to the goal location. Although the same could be argued about every location within a path, inside the path the target can only be moved forward or backwards. If the target is moved forward and backwards inside a path, that performance could be explained as control by the goal location or, alternatively, it could also be said that the subject has not learned to reach the intersections. Thus there is no clear distinction between the two explanations.

Choice points could offer the possibility of a forced response or a facultative response (see Figure 1). Forced-choice points occur when the target reaches an intersection where the previous direction of motion is no longer available. This type of choice point may only require control by the goal location when the previous response is no longer available. After training, subjects may come to be under control of the goal location at choice points (when a wall interrupts motion) but not while moving inside the path. Facultative-choice points occur when an additional path branches off from the current path direction without physically interrupting responses. This type of choice point may increase control by the path characteristics because a path may be missed if a response is produced continuously in one direction (e.g., if the hand is inclined to the right in the joystick task until the target cannot be moved in that direction any further).

A comparison of the type of errors on each type may provide evidence of the properties controlling maze navigation. In forced-choice points errors occur in the form of wrong turns or moving back. In facultative-choice points errors may occur in the form of wrong turns, overshoots, and moving back. Provided that the paths do not curve into different directions between choice points and the specific location of the goal, wrong turns and moving back errors could suggest that directness to the goal has a higher priority than continuation of the path. Overshoots in facultative-choice points would suggest that either the choice point was not detected or that repetition of the same response has a higher priority.

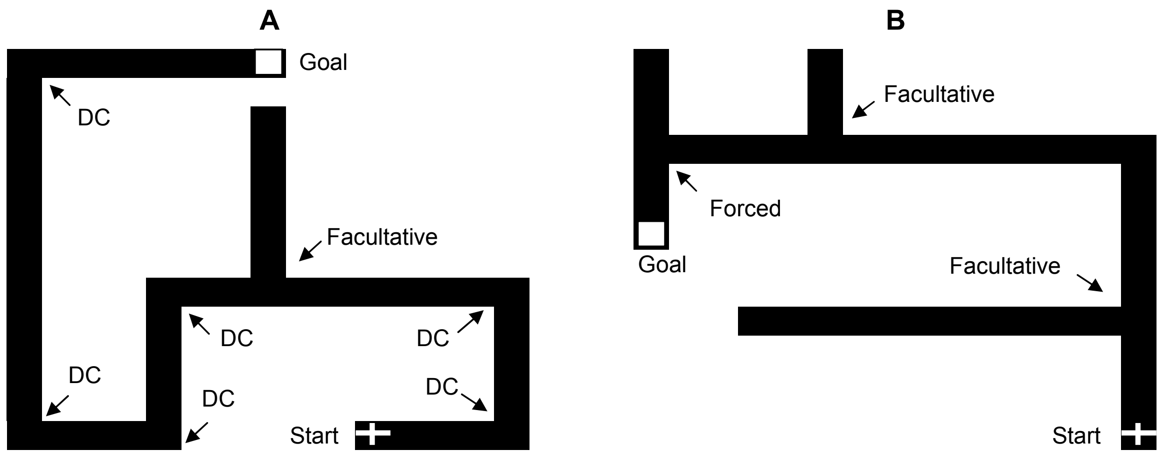


Figure 1. Maze navigation task used with primates in Fragaszy, et al. (2003). Panels A and B recreate two mazes from the experiment. Using the joystick, subjects moved the white cross from the start location to the goal location. Panel A shows a maze composed of one choice point and various directional changes (DC) before and after the choice point. Panel B illustrates a maze with three choice points. Panels A and B also illustrate the difference between a forced-choice point (current direction is no longer available) and a facultative-choice point (current direction is available).

Fragaszy, et al. (2003) assessed performance on both types of choice points. However, because this was not the main manipulation of the study, the mazes were made by presenting one or both types of choice points within each maze. In addition, the paths before and after each choice point could be of various distances and have one or more directional changes before reaching the next choice point or goal (see Figure 1). A change in the direction within the path could alter the possible control by the original direction of the path, the direction at the middle of the path, and the direction at the end of the path. The task in Fragaszy, et al. (2003) required apes (*Pan troglodytes*) and monkeys (*Cebus apella*) to reach the goal on 12 out of 16 mazes of any given set of mazes before the difficulty level was increased. Because each maze was novel the number of choice points of each type varied across subjects, with forced-choice points accounting for 38-39% of the total number of choice points in the study depending on the species. There was, however, no information on the distribution of these choice points across all phases of training. At forced-choice points, wrong turn errors accounted for 8% of the apes' responses, while for the monkeys they accounted for 39% of the responses. On facultative-choice points, monkeys were equally likely to make wrong turns and overshoots, for a combined total of 41% of the responses. However, apes were more likely to commit overshooting errors (36% of the responses) than take wrong turns (4% of the responses) at the facultative-choice points. Although the data suggest that both types of choice points have distinct effects on both species, this conclusion cannot be completely justified given the possible differences in training of both types of mazes and the possible effects of distance and directional changes between choice points for each type. In addition, moving back errors at the choice points were not reported. These errors may indicate, depending on the maze, if directness to the goal controlled responding more than continuity of the path.

In addition to choice point type, other maze characteristics that are manipulated to increase novelty and difficulty and whose effect has not yet been assessed in touch screen and joystick tasks include the distance between paths, the number of choice points, distance to the goal, and path shape. Increasing the number of choice points, and thus paths within the maze, may place various paths close enough to be perceived as part of the same path. Differences in the distance toward two choice points and the complexity (i.e., number of directional changes) of the available paths may control the direction in which the target is moved.

Distance to the goal location in two-dimensional mazes is usually analyzed in terms of path distance to the goal (Manhattan distance). However, the actual distance from the start location to the goal (Euclidean distance) may affect performance (see Figure 2). Euclidean distance may exert more control during training, while the task is being learned. Mushiake, et al. (2001) measured the paths selected by monkeys (*Macaca fuscata*) on a two-dimensional computerized maze with various paths of equal Manhattan (2 or 3 blocks) and Euclidean distance to the goal but at different angles (see Figure 3). In this task, control of the target's motion was achieved through the supination and pronation of two knobs, one for left and right motions, and the other for up and down motions. The directions assigned to each knob were switched throughout the study. Their findings indicate that monkeys develop a series of 'preferred' paths to specific goal locations on the four quadrants of the maze because they repeated the steps of a path irrespective of the directional assignment of the knobs. For example, they may have always moved to B in order to reach goal 1 regardless of which knob moved the target left and right. Thus, although more than one path offered the same Manhattan distance to the goal, the monkeys in this study used one of the paths more often than the others.

However, because path preference was analyzed in terms of response at the first choice point of the maze, it is not clear if the monkeys had developed a preference for one or two directional changes (see Figure 3). For example, a goal located diagonally to the right and above the start location and at a Manhattan distance of three responses can be reached with three responses in three different paths: a) up, up, right; b) up, right, up; and c) right, up, up. The first two paths require the same first response and would be categorized as using the same path. However, path 1 requires one directional change while path 2 requires two directional changes. In addition, path 1 requires a change in direction near the goal location whereas path 3 requires a change in direction near the start location. Thus, at the same goal location and with the same Manhattan distance, the shape of the available paths may have different effects on performance.

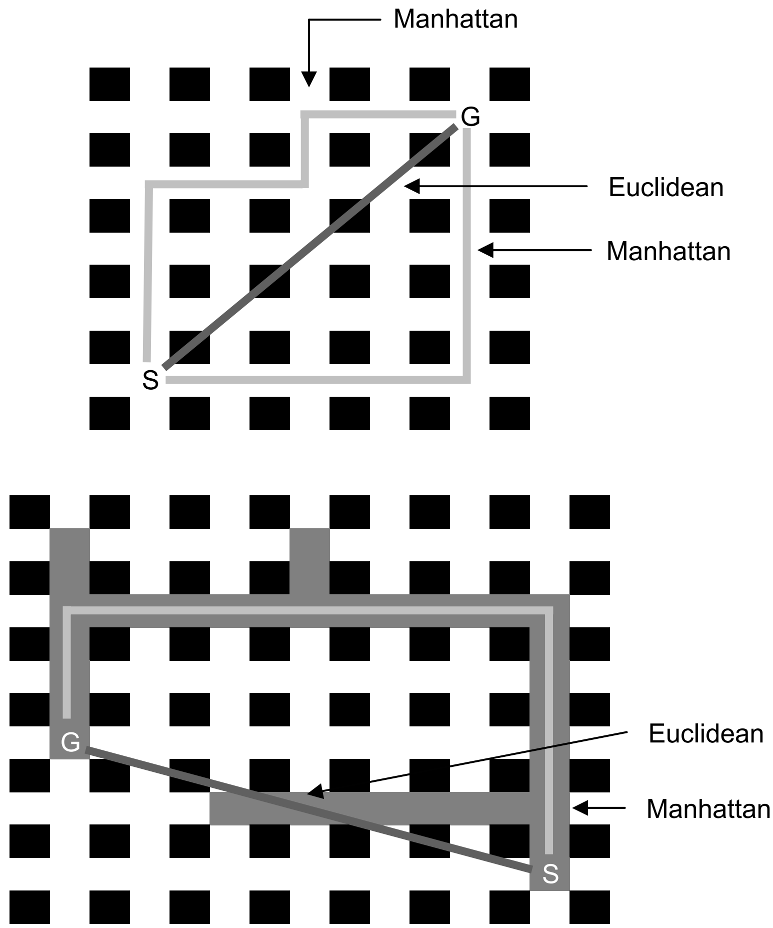


Figure 2. Euclidean distance (dark grey) and Manhattan distance (light grey) for the possible paths traveled within a city block environment where movement is possible inside the white paths. The Euclidean distance represents the shortest path if no limitations to direction were present. The second panel represents one of the mazes used in Fragaszy, et al. (2003) within the city block environment. While the Euclidean distance offers a direct route from the start location (S) to the goal location (G), the correct path has a longer distance and moves away from the direction of the goal.

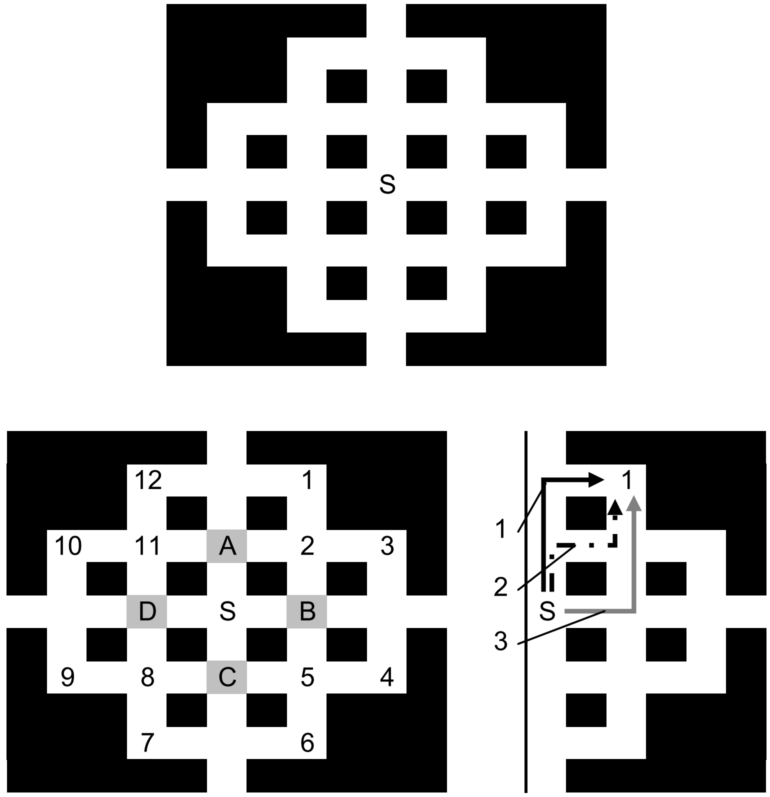


Figure 3. Maze used in Mushiake, et al. (2001). After viewing the maze for one second, the target (S) was shown in the middle of the maze for another second. Then, the goal appeared in one of the 12 alternative locations for half a second before disappearing. After one second the subject was allowed to begin moving the target towards the location were the goal used to be. Each movement of the knobs moved the target one full space. That is, the target could not occupy the middle position between black squares. Preference for a specific path was assessed by the number of trials for which the same initial intersection (A, B, C, D) was used for a given goal location. However, after the first intersection three paths of equal Manhattan distance (black line and dotted line) were available for goal locations 1, 3, 4, 6, 7, 9, 10, and 12.

Planning

The ability to move in an environment must be differentiated from path-planning. An organism may be capable of motion that eventually leads into the goal location without performing path-planning behaviors. Path-planning behaviors are part of the larger construct of planning. Optimal planning incorporates control by the current and goal states with the continuous analysis of how each response has affected the relationship between those states (Friedman, Scholnick, & Cocking, 1987). Thus, planning is proposed to occur before and during responding. This last property poses a test problem because the original planning cannot be differentiated from the current planning unless some form of verbal protocol is in place. This difficulty extends to the distinction between emission of a previously learned sequence of responses and planning at the beginning of each trial.

Pea and Hawking (1987) described the properties that must be present within a task for path-planning behaviors to emerge. First, the organism must have experience with the objects in the test environment and have learned their properties (e.g., the target will not move through a wall). Second, the task must be difficult and novel enough that learning a specific sequence of responses to reach the goal location will decrease the reinforcer value or delay the reinforcer. And third, the organism must be able to come under control of alternate cues. For example, if planning occurs before the first response of the trial, the value of the goal must be reduced for the organism to delay responding. Another cue, such as the closest choice point, must have a temporarily higher value than the final goal. Otherwise the organism will respond in the direction of the goal regardless of path characteristics (i.e., directness).

In the area of motor activities, Fragaszy, et al. (2003) offered five levels of path-planning behaviors dependent on maze performance (see Figure 4). The requirements for each level were dependent, with the exception of level 4, on the possible behaviors in the apparatus. In Fragaszy's task, monkeys and apes used a joystick to move a target (i.e., the icon or cursor being moved) across a monitor screen and their performance at the choice points was analyzed for evidence of path-planning behaviors. Level 0, absence of planning, was defined as navigation where the direction of the movement of the target occurred at random through the paths and at choice points. For example, the joystick may have been repeatedly moved towards a wall. Performance at this level indicates that the path characteristics of the maze have not been learned (e.g., the target moves only inside the path area). Level 1, bodily planning, involved directional movement of the target along the path but random responding at choice points. Performance at this level indicates that the characteristics defining a path have been learned, but either the task (i.e., move the target into the goal location) has not been learned or sufficient control by other properties is not present (e.g., path continuation). Level 2, one element planning, was defined as responses that were controlled by one property of the maze at each choice point. For example, if the property used was directness to the goal, then at each choice point the target would be moved toward the path that intersected the goal or seemed to pass the closest to the goal location. Performance at this level indicates that the task has been learned, but responses at each choice point will be correct as long as the correct path can be derived from only one path property present at each choice point. In addition, this level of planning does not involve control by upcoming choice points. Thus, it involves planning in the sense of control by the goal location but not in the sense of processing the available paths at a future location. This may be because the choice point falls outside the organism's visual angle (i.e., the visual area in which a subject can detect stimuli). Level 3, integrated planning, involved control by two maze properties at each choice point. For example, if a choice point presented one path that lead away from the goal and another that lead toward the goal but ended before reaching the end (Panel D, Figure 4), a subject may have responded more often toward the path that was directed toward the goal (level 2) unless the path was not complete (level 3). This would suggest an integration of two maze properties. Performance at level 3 indicates that the path characteristics and task have been learned and that a secondary property can be used to improve responses based on a prioritized maze characteristic. It is not clear if planning at this level is still based on the current target location and not based on possible future locations and paths. Finally, level 4 or sequential integrated planning, was defined as selecting a series of choice point responses before the first response in the maze based on two or more properties. It is not clear in the definition if reevaluation occurs at each choice point once the target has actually moved to that location or if the responses are emitted in order regardless of the maze characteristics. Performance at this level would indicate that the path characteristics and task have been learned, that information obtained from two or more properties can be integrated, and that a sequence of responses can be stored and managed in memory until they are performed.

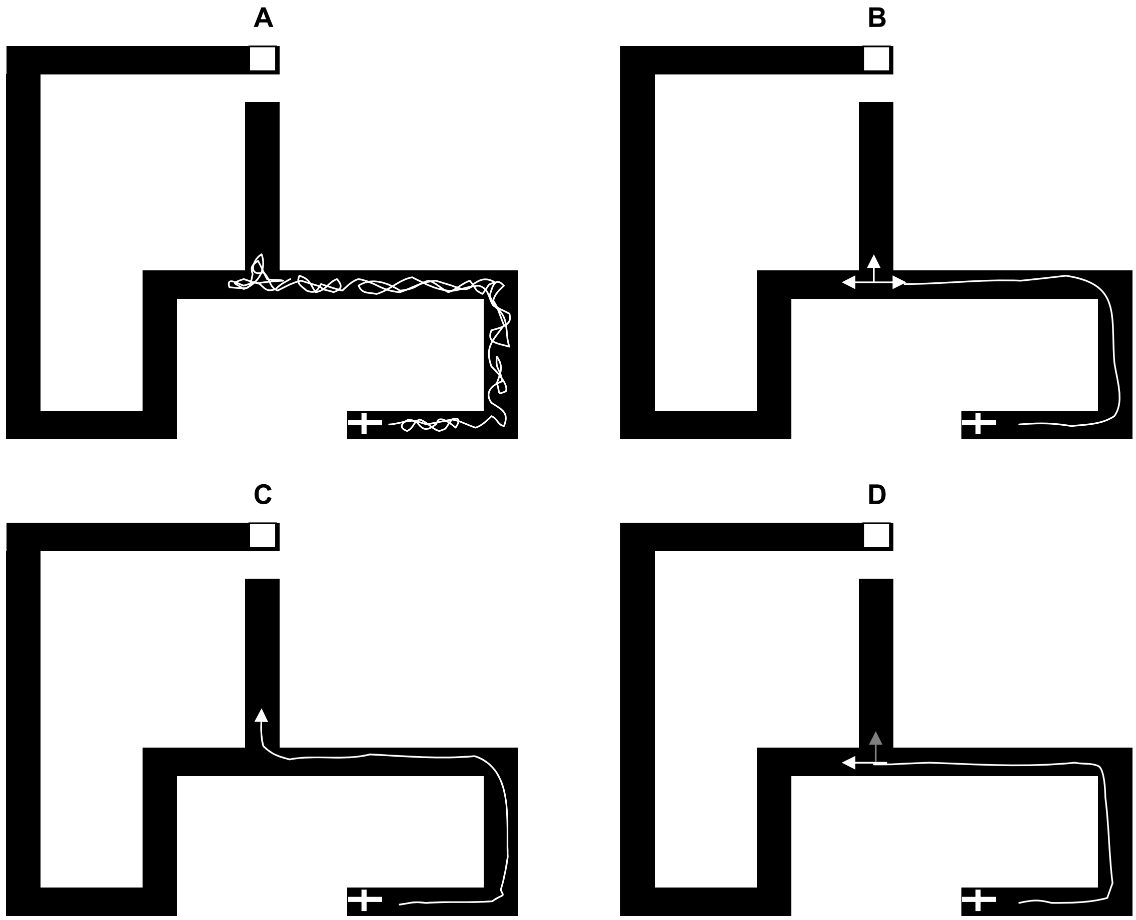


Figure 4. Levels of planning proposed by Fragaszy, et al. (2003). The levels of planning in the study include absence of planning (A), bodily planning (B), one element planning (C), and integrated planning (D). In panel D the grey arrow indicates a decrease in control by directness because the path is not complete.

Path Properties and Maze Navigation in Touch Screen Tasks

Unlike three-dimensional mazes, two-dimensional mazes allow for the continuous presence of the current and goal locations, and the location and direction of all paths. This means that the influence of the goals and paths on responding may be continuous throughout the trial or that their behavioral control may increase or decrease depending on the current location of the target. Choice point characteristics, alternate path proximity, and distance and angle to the goal vary across training and testing mazes, but also vary as a result of the thickness of the path and the number of choice points. Because they are usually side effects of the main manipulations, their effect on responding has not been addressed. However, these factors may control responding depending on their relationship to the subject's visual angle of the maze or with the global and local properties currently controlling responding.

The visual angle is established by the subject's visual capacities (and those of the species) and the distance from the stimuli. Although optimally the subjects learn to search the entire maze before responding (level 4 of planning), it is possible that stimuli within the visual field exert more control than stimuli outside of it (Prinzmetal, 1981, and Wolford, 1975). If the correct path extends outside of the visual field, sections of it may not be perceived as part of the same path. This could be the case even if the subject has a cognitive map of the maze.

The global and local properties of the maze refer to the characteristics of the maze currently controlling performance. For example, if at level 2 of planning the subject responds based on directness of the goal at the choice point then its performance is controlled by the immediate or local properties. However, if the response depends on the continuity of the path, the subject would have to search the maze for the direction of each available path. The path may move away from the goal and turn before reaching the next choice point. This search of the maze would be control by the global properties. The characteristics of the maze may have different effects depending on the global or local properties that currently control performance. Moreover, the characteristics may affect the transition from local to global properties expected to occur during training. Thus, the level of planning achieved may be affected by the factors that have not been methodically manipulated in training.

If these factors do exert some behavioral control, that effect must remain constant for an appropriate species comparison of maze navigation. Otherwise, quantitative differences across species (i.e., degree or level of one process) may be interpreted as a qualitative difference (i.e., absence of a process in one of the species). This series of studies were aimed at determining the effect, if any, of various parameters inherent in the construction of the mazes used with the touch screen technology with pigeons. The studies discussed here began with two groups of pigeons receiving exclusive training with either forced or facultative choice points. In experiment 1, a test with novel mazes assessed the effect of this training on the opposite choice point type. The performance of both groups was then compared across distance discrimination and angle tasks to assess if the differential training affected other areas of maze navigation. Experiment 2 measured the effect of distance to the goal on control by the path characteristics. Experiment 3 addressed distance discrimination and Experiment 4 measured the possible effect of directional changes in performance.

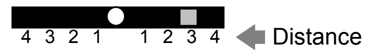
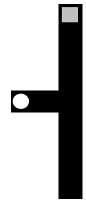
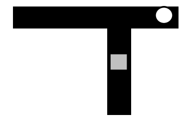
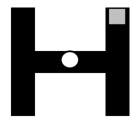
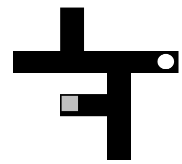
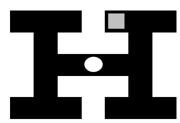
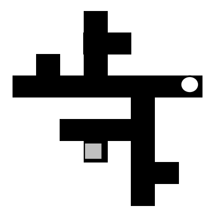
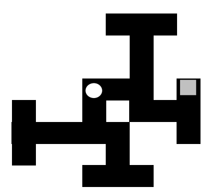
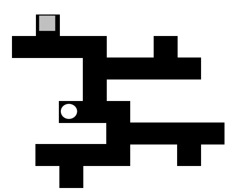
II. EXPERIMENT 1

The sub goals of a maze are the choice points leading to the goal location. Forced-choice points in a maze require a directional change in responding when the maze cues change and the previous direction is no longer available. Facultative-choice points do not offer an immediate cue when a directional change is required. Given the possible inherent cue within the forced-choice points, it is possible that training involving only forced-choice points may increase responding that consists of a series of automatic responses without any search of the maze while the wall has not been reached. Thus, responding in one direction will continue until that direction is no longer available. Because the facultative-choice points can occur anywhere in the path, without a wall in the path serving as a cue, subjects trained only with this type of choice point may learn to search after every response, thus decreasing automatic responses. Because mazes can require a series of directional changes that lead into the goal location, training with facultative-choice points may develop a different response pattern than forced-choice training. Specifically, by increasing searching, facultative training might lead to the development of higher levels of planning, faster training, or self corrections (i.e., return to the correct path after an incorrect path was used) that occur sooner in the path.

Experiment 1 focused on the effect that forced- and facultative-choice point training has on novel maze performance (see Table 1). Two groups of pigeons were trained exclusively with either forced- or facultative-choice points. After training, both groups were tested with novel mazes of both types of choice points to assess how their specific training affected their responses. Their performance on the final test with novel mazes should indicate if the training lead to item-specific learning (i.e., maze specific), learning by type (i.e., choice point specific), or full maze navigation.

Item specific learning refers to navigation where the responses required to reach the goal are learned for the trained mazes only and repeated in the presence of similar cues without searching the maze. Learning that is item specific will not transfer to novel mazes that share the same characteristics but in a different order or direction. For example, in Table 1, if the forced group is able to learn the mazes in Training C, their performance would be at chance for the novel forced-choice maze in Transfer 4 because it requires a different sequence of responses than those used in the training mazes. Testing with novel mazes of the same type as those used during training should indicate whether the pigeons learn a pattern of responses or whether they search the maze for the goal location and path characteristics on every trial. Item-specific learning would show chance performance at choice points in untrained mazes.

Table 1
Description of Training and Test Phases

Phases	Description	Forced	Facultative
Pretraining	Common Training: Vertical or horizontal maze with only two directional options. One goal at distances 1-4.		
Transfer 1	Separate Testing: Four rotations of each maze type. Each maze offered four possible goal locations. The choice point offered three directional options.		
Training A	Separate Training: Each group was trained only with the mazes belonging to the group's training type from Transfer 1.		
Transfer 2	Separate Testing: Two rotations of each maze type. Each maze offered four possible goal locations. Goal placed only at the end of the paths.		
Training B	Separate Training: Each group was trained only with the mazes belonging to the group's training type from Transfer 2.		
Transfer 3	Separate Testing: Two rotations of each maze type. Each maze offered eight possible goal locations.		
Training C	Separate Training: Each group was trained only with the mazes belonging to the group's training type from Transfer 3.		
Transfer 4	Common Testing: Both groups were tested with both novel mazes. No additional rotations of the mazes were used. Each maze offered eight possible goal locations. The first choice point of the forced maze offered two directional options. All other choice points offered three options.	 	

Note: Circles indicate the start location and squares indicate one of the possible goal locations. All possible goal locations are shown in Appendix A.

Learning by type refers to navigation where performance in novel mazes is similar to baseline as long as the type of choice point is the same (i.e., baseline is a standard protocol of steady state performance). In the case of the specific choice points trained here, if both groups learned by type, then they would be able to reach the goal on novel mazes that have the same type of choice points in Transfer 4, but they would not be able to perform above chance when tested on the opposite type of choice point.

Full maze navigation refers to navigation where performance in novel mazes with novel properties is statistically similar to the mazes used in training regardless of the properties of the maze. Reaching the goal in the opposite choice point types in Transfer 4 would be evidence of full maze navigation in pigeons.

Method

Subjects and Housing. Six White Carneaux pigeons (*Columba livia*) between the ages of 4 and 6 years participated in the experiment. The pigeons were kept at approximately 80% of their free-feeding weight. They were housed in individual home cages with unlimited access to water and grit. The colony room was maintained in a 12-hr light-dark cycle. The pigeons were tested 6 days a week.

Apparatus. The chamber was a wooden box (38-cm wide x 36.5-cm deep x 39.5-cm high) with a Dayton Electric axial fan (Model 4WT40) on the back panel that provided both ventilation and white noise. A custom-built food hopper was centered below the monitor (FlexScan T566 color monitor; 17-inch flat screen CRT; 800 x 600 pixel resolution) on the front panel. A wood frame on the front panel recessed the touch screen by 6.35 cm from the main floor area, and a thin piece of glass mounted in a 25-cm h x 17.5-cm w viewing window separated and protected the monitor from the pigeon's responses to the CarrolTouch infrared touch screen (UniTouch 17”). The houselight at the top of the chamber was lit during the 15-s intertrial intervals (ITI).

Stimuli. Four types of stimuli were used: target, goal, maze, and directional keys. All measurements presented here are approximate pixel dimensions. The target was a white circle (1.3 cm in diameter); the goal was a grey square (1.3 cm on each side); and the mazes were made of brown walls and black pathways of different dimensions. The directional keys had specific colors (i.e., left key = red, right key = blue, up key = yellow, down key = green) and were either vertical (1.3-cm h x .64-cm w) or horizontal (.64-cm h x 1.3-cm w) rectangles. An invisible square on top of each rectangle detected the responses (1.3 cm on each side), thus detecting responses slightly outside the rectangle.

Procedure

Examples from all phases in this experiment are shown in Table 1 (for all the configurations used see Appendix A). All pigeons had the same Pretraining sessions. After pretraining the Forced group was trained with forced-choice points only. The three pigeons in this group were Luke, Moe, and Pierre. The Facultative group was trained with facultative-choice points only. The three pigeons in this group were Jupiter, Nicholai, and Lev.

Pretraining. At the beginning of this phase the pigeons were trained to peck (i.e., response) at individual directional keys. A black background covered the entire screen instead of maze-defining walls. Training began with the presentation of one key per trial and after a response to the key the hopper was activated, providing access to food for three seconds. Next, each key was presented in the middle of the goal and the target. A response to the key made it disappear and the target moved into the goal, activating the hopper. The arrangement of the goal and the target was dependent on the key used in the trial. Each of the four keys moved the target in a different direction (i.e., left, right, up, down). Next, an additional response to the target inside the goal was required for the activation of the hopper. After this initial training, the distance between the target and the goal was increased on all four directions from distance 1 to distance 4. Path distance is defined as the number of responses necessary to reach the goal. After a response to the key, all keys disappeared and the target moved 1.3 cm in the direction represented by the key. For distances greater than 1 (e.g., 6), once the target stopped the keys reappeared and another response was required to move the target. Inside the goal the color of the target changed to black. Inside the mazes used in the rest of the study, keys that would move the target into the wall were not available (see Figure 5).

The training with increasing distances lasted nine sessions. Because three keys were available at most choice points in later phases, both groups received an additional training phase with two keys to train them to switch keys. By definition this is a forced-choice point task. The trials during this training were horizontal or vertical trials where either the left and right or the up and down keys were present simultaneously and one goal appeared at the end of one of the paths. This training lasted for ten sessions. Next, for an additional 10 sessions, the trials with two keys were trained with maze-defining walls surrounding the pathway areas. Each pretraining session had 80 trials, counterbalanced for distance and side.

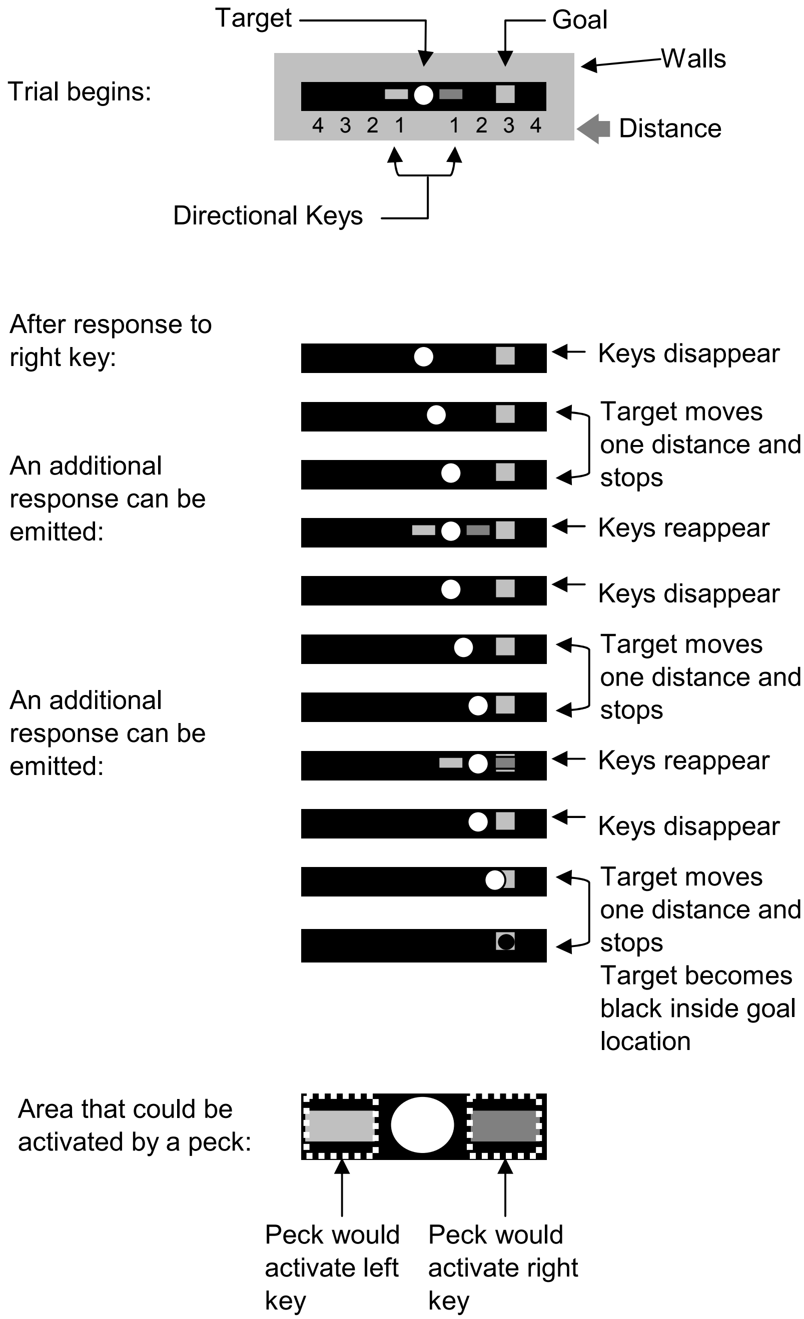


Figure 5. Movement of the target after a response to a directional key. After a response to any directional key, all available keys disappear and the target moves one distance. After the target stops the available keys reappear. To allow for differences in pecking, the area that activated the directional key was larger than the colored area.

Transfer test 1: One choice point. After the pretraining phase, pigeons received their first transfer test. Test trials consisted of mazes that offered two pathways of motion, one towards the goal location and the other a blind pathway, both of the same length. The distance to the goal was two or four from the choice point. Four rotations of the mazes shown in Table 1 offered a total of 16 trials per choice point type (see Appendix A for all the configurations used). These were presented over 2 sessions, constituting a block, and repeated over 5 blocks. A test session consisted of 80 trials, 72 trials from Pretraining and eight test mazes. The Forced group was tested with forced-choice mazes only, whereas the Facultative group was tested with facultative-choice points only.

Forced-choice points could be formed by one of two types of arrangements: 1) the trial began with the target between two paths and the first response required a response on either direction, or 2) the target was moved to an intersection first. At that location the key previously used was no longer available. Facultative choice points were formed by arranging the path so that when the target arrived at the choice point the same key for that movement was still available.

Both types of mazes offered two paths with an equal amount of choice points branching off from the initial location, thus eliminating the possibility of solving the task by moving the target towards the longest path. This is different from the mazes used by Fragaszy, et al. (2003), which could be solved by selecting the path that led into an additional choice point. In addition, each transfer test increased the number of choice points in the maze by one. Thus, each additional choice point changed the angle and distance to the goal location. Each additional test was used as an increase in task difficulty.

Pigeons had a time limit of one minute to complete each maze. After one minute had expired, the maze disappeared and the screen remained black for 6 seconds. An ITI of 15 seconds was in place between trials. Aborted trials were not repeated on the session but the responses made before the time limit expired were used in the analyses.

Training A. The pigeons were trained for a minimum of three days on the mazes presented during Test 1 for their group only. Each session consisted of 80 trials, with five repetitions of each maze (1 choice point each), for a total of 80 choice points. For all training phases, criteria were met when a pigeon performed one day at 85% correct (Equation 1) and were trained for at least three days. Percent correct is defined as the total number of correct responses from the total number of choice points within the correct path in a session. A correct response was defined as moving the target in the direction of the path that led to the goal. Only the first pass through a choice point was used in the analyses. This value assures that the pigeons reached the last choice point on most mazes before the level of difficulty was increased. This is different from Fragaszy et al. (2003), where completing 75% of the mazes within a session was the criterion before increasing difficulty. The criterion was changed for this experiment to be dependent on choice point performance assuring that the pigeons learned to move toward the goal. This criterion would not allow pigeons to change phases when they reached the goal after selecting the wrong path during their first pass at each choice point.

$$\frac{\text{Observed Correct Responses Per Session}}{\text{Total Choice Points Per Session}} \times 100 \qquad (1)$$

The second criterion was that a pigeon must complete a minimum of three sessions of training on all phases before moving to the next phase. This criterion allowed practice on all possible mazes for the current difficulty level.

Transfer test 2: Two choice points. Test trials consisted of an additional choice point. An additional 90^0 rotation of the mazes shown in Table 1 offer a total of 8 trials for each choice point type (see Appendix A for all the configurations used). All trials for a given type were presented in one session, and repeated over 5 sessions. All goals were located at distance four from the first choice point. A test session consisted of 80 trials, 72 trials from Training A and eight test facultative- or forced-choice point mazes, depending on the group.

Training B. The pigeons were trained for a minimum of three days on the mazes presented during the Test 2 for their group only. Each session consisted of 40 trials, with 5 repetitions of each maze (2 choice points each), for a total of 80 choice points. Criterion was met when the pigeon performed one day at 85% correct and was trained for at least three days.

Transfer test 3: Three choice points. Test trials consisted of an additional choice point at the location where the goal was located in Test 2. An additional rotation of the mazes shown in Table 1 offer a total of 16 trials for each choice point type (see Appendix A for all the configurations used). These were presented over 2 sessions, constituting a block, and repeated over 5 blocks. All goals were located at distance 5 from the first choice point. A test session consisted of 48 trials, 40 trials from Training B and eight test facultative or forced choice mazes, depending on the group.

Training C. The pigeons were trained for a minimum of three days on the mazes presented during the Test 3 for their group only. Each session consisted of 32 trials, with 2 repetitions of each maze (3 choice points each), for a total of 96 choice points. Criterion was met when the pigeon performed one day at 85% correct and was trained for at least three days.

Transfer test 4: Novel forced and facultative mazes. Test sessions consisted of three types of trials: baseline, novel forced-choice point transfer, and novel facultative-choice point transfer. Baseline trials consisted of the mazes used during Training C: forced-choice point mazes for the Forced group and facultative-choice point mazes for the Facultative group. Both types of transfer mazes were novel to both groups and both groups were shown both types of mazes for the first time. A test session consisted of 40 trials, 32 trials from Training C, four test facultative-choice point mazes and four test forced-choice point mazes. The mazes shown in Table 1 offer a total of 8 goals per maze type. These were presented over 2 sessions, constituting a block, and repeated over 5 blocks (see Appendix A for all the configurations used). All goals during transfer trials were located at distance 6 from the first choice point.

Results

Increments in choice points. To examine whether training had any effect on learning, the days to reach criterion, performance at the end of each training phase, and performance for each test that increased the number of choice points was compared. If performance during these phases was different for each group then the conclusions for the final test with novel mazes may be compromised. That is, if one group took longer to learn the mazes then their improved performance in the novel mazes may be due to the increased practice with the mazes and not the specific training. Days to criterion (i.e., 85% in one session, minimum of three sessions) did not differ between groups across training phases at the .05 significance level (see Table 2). This result was supported by a Two-Way repeated measures ANOVA for Phase (A, B, C) as a within subjects factor and Group (Forced, Facultative) as a between subjects factor, which found no main effect of phase, $F(2, 8) = 1.00$, $p = .41$, group, $F(1, 4) = .29$, $p = .62$, or an interaction, $F(2, 8) = 1.5$, $p = .28$. Thus, neither group received additional training in the mazes.

During the last three days to reach criterion, the two groups did not differ in the number of completed mazes, as shown by a Two-Way repeated measures ANOVA for Training Phase (A, B, C) as a within subjects factor and Group (Forced, Facultative) as a between subjects factor, which found no main effect of phase $F(2,8) = .54$, $p = .61$, or group, $F(1, 4) = .06$, $p = .81$. This analysis did show an interaction, $F(2,8) = 4.41$, $p = .05$, because the forced group began training with a higher number of completed trials but the roles were inverted in the second and third training phases (see Table 2). Overall, these results indicate that both groups were at a similar level of accuracy when they were tested with additional choice points.

Table 2
Performance Across Training A, B, and C

	A		B		C	
	Forced	Facultative	Forced	Facultative	Forced	Facultative
Days to Criterion	4 (1.73)	5.67 (1.53)	4 (1.73)	3.67 (1.15)	10 (11.27)	4 (1.73)
Mazes Completed	97.92 (3.61)	90 (7.12)	87.78 (7.92)	94.72 (1.73)	90.97 (1.59)	94.44 (6.94)

Note: SD are in ().

To examine whether either group showed better transfer to additional choice points and increased distances, and to compare their performance before the final novel test, performance across tests 1-3, which increased the number of choice points of the same type used during training, was analyzed. Both groups showed similar accuracy at each test phase (see Table 3). For test 1, a Two-Way repeated measures ANOVA of Trial Type (Baseline, Choice Point 1) as a within subjects factor and Group (Forced, Facultative) as a between subjects factor revealed a significant difference between trial types, $F(1, 4) = 30.24$, $p = .01$, but no difference between groups, $F(1, 4) = .09$, $p = .78$, and no interaction, $F(1, 4) = .04$, $p = .85$. For the second test a Two-Way repeated measures ANOVA of Trial Type (Baseline, Choice Point 1, Choice Point 2) as a within subjects factor and Group (Forced, Facultative) as a between subjects factor revealed a significant difference between trial types, $F(2, 8) = 26.25$, $p < .01$, and an interaction, $F(2, 8) = 26.23$, $p < .01$, but no group effect, $F(1, 4) = 4.08$, $p = .11$. The interaction occurred because the facultative group had a higher performance in the first choice point than the forced group but a lower performance at the second choice point. For the third test a Two-Way repeated measures ANOVA of Trial Type (Baseline, Choice Point 1, Choice Point 2, Choice Point 3) as a within subjects factor and Group (Forced, Facultative) as a between subjects factor revealed a significant difference between trial types, $F(3, 12) = 4.06$, $p = .03$, but no group effect, $F(1, 4) = .34$, $p = .59$, and no interaction, $F(3, 12) = .75$, $p = .55$.

Table 3
Performance Across Transfer Tests 1, 2 and 3*

Group	Transfer Test 1			
	Baseline	Transfer Choice Point		
		1		
Forced	92.31 (5.55)	67.92 (16.79)		
Facultative	91.20 (2.36)	65.00 (9.44)		
	Transfer Test 2			
	Baseline	Transfer Choice Point		
		1	2	
Forced	85.46 (4.22)	71.94 (6.99)	82.22 (10.01)**	
Facultative	85.00 (3.74)	76.11 (1.27)	55.00 (4.33)**	
	Transfer Test 3			
	Baseline	Transfer Choice Point		
		1	2	3
Forced	85.58 (6.32)	80.42 (9.21)	77.08 (6.29)	77.50 (8.20)
Facultative	86.46 (3.56)	82.08 (4.02)	78.33 (2.89)	84.58 (9.71)

Note: SD are in ().
* All transfer tests used choice points appropriate for the group.
**Significant difference between the forced group and the facultative group at choice point 2, $F(1, 2) = 48.26$, $p < .05$.

To examine whether there was a difference between groups at the choice point level, additional Pairwise Comparisons for choice point performance against baseline performance were performed (see Table 4). The results indicate that the facultative group performed below baseline at most choice point increments while the forced group had more transfers to new choice points that were similar to baseline.

In summary, the increments in the number of choice points had similar effects on both groups. That is, both groups learned their respective mazes at the same rate and performed with similar accuracy over the last three days of training. The initial analysis showed that both groups had similar performance during transfer, however, the more detailed Pairwise Comparisons showed that the facultative group performed below baseline on most choice points. These results suggest that transfer to novel facultative mazes is more difficult than transfer to forced mazes. However, after the initial test both mazes were learned at the same rate.

Novel mazes. To examine whether the groups could transfer to novel mazes of the trained type and choice points of the opposite type, performance on transfer test 4 (i.e., novel mazes of both types) was analyzed. Performance on novel mazes that had the same type of choice point used during training was similar to performance on baseline mazes for both groups (see Figure 6). A Two-Way repeated measures ANOVA of Maze Type (Baseline, Novel Forced) x Choice Point (1, 2, 3) for the forced group revealed no main effect of maze type, $F(1, 4) = 4.35$, $p = .17$, choice point, $F(2, 4) = .46$, $p = .66$, or an interaction, $F(2, 4) = 3.33$, $p = .14$. A Two-Way repeated measures ANOVA of Maze Type (Baseline, Novel Facultative) x Choice Point (1, 2, 3) for the facultative group revealed no main effect of maze type, $F(1, 4) = 1.98$, $p = .30$, choice point, $F(2, 4) = 2.06$,

$p = .24$, or an interaction, $F(2, 4) = 2.03$, $p = .25$. Both groups were able to complete mazes of the same training type (i.e., item-specific learning).

When the performance in the opposite choice point type was analyzed, the forced group had a lower performance in the facultative maze but the facultative group had a performance similar to baseline in the forced maze (see Figure 6). This conclusion was supported by a Three-Way repeated measures ANOVA of Maze Type (Baseline, Forced, Facultative) x Choice Point (1, 2, 3) as the within-subject factors and Group (Forced, Facultative) as the between-subjects factor. This analysis revealed only a significant effect of Maze Type, $F(2, 8) = 13.27$, $p < .01$ and a significant interaction of Maze Type x Group, $F(2, 8) = 5.63$, $p = .03$. A Two-Way repeated measures ANOVA for the Choice Points in the facultative maze (1, 2, 3) as a within-subject factor and Group (Forced, Facultative) as a between-subjects factor revealed a significant effect of group, $F(1, 4) = 13.1$, $p = .02$, but no effect of choice point, $F(2, 8) = .66$, $p = .54$, or interaction, $F(2, 8) = 3.46$, $p = .08$. A Two-Way repeated measures ANOVA for the Choice Points in the forced maze (1, 2, 3) as a within-subject factor and Group (Forced, Facultative) as a between-subjects factor did not reveal any effect of group, $F(1, 4) = 1.31$, $p = .32$, choice point, $F(2, 8) = 3.93$, $p = .07$, or an interaction, $F(2, 8) = 2.91$, $p = .11$. These results suggest that performance differed only for the novel facultative maze but not for baseline or the novel forced maze. The results also suggest that the forced group did not achieve full maze navigation because performance in the facultative maze was below baseline. The facultative group did achieve full maze navigation because performance on both novel mazes was similar to baseline.

Table 4
Pairwise Comparisons for Baseline Trials and Increments in the Number of Choice Points

Group	Test	Comparison	Mean difference	Standard error	P-value
Forced	1	Baseline - CP1	-24.4	6.68	0.07
	2	Baseline - CP1	-13.52	2.09	0.02
		Baseline - CP2	3.24	4.55	0.55
	3	Baseline - CP1	5.17	1.68	0.09
		Baseline - CP2	8.5	1.44	0.03
		Baseline - CP3	8.08	2.03	0.06
Facultative	1	Baseline - CP1	-26.2	6.32	0.05
	2	Baseline - CP1	8.89	1.43	0.03
		Baseline - CP2	30	4.62	0.02
	3	Baseline - CP1	4.38	3.84	0.37
		Baseline - CP2	8.13	0.43	0.00
		Baseline - CP3	1.88	3.76	0.67

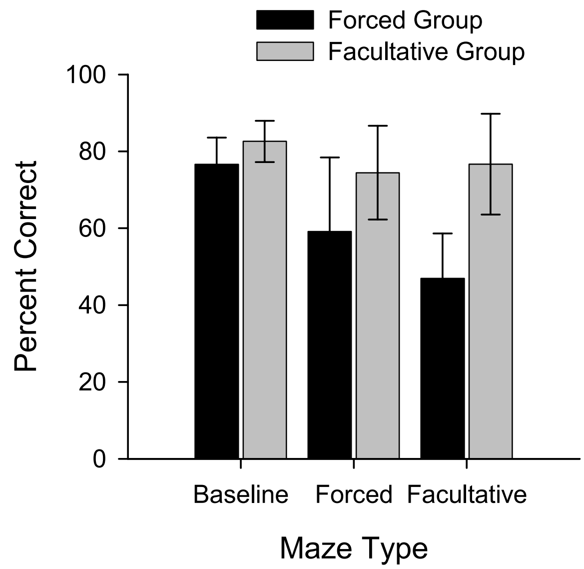


Figure 6. Percent correct in transfer 4 as a function of maze type and choice point type used during training. The baseline mazes were specific to each training type. The forced and facultative mazes were novel to both groups. The bars represent the standard deviation.

Separate t-tests suggest that the groups' performance in the facultative maze differed for choice point 3, $t(4) = 4.06$, $p = .02$, but not for choice point 1, $t(4) = 2.05$, $p = .11$, and choice point 2, $t(4) = 2.65$, $p = .06$ (see Table 5). The percent correct analysis compares the observed responses against the total number of choice points in the correct paths. Thus, the lower performance from the forced group on facultative mazes could be an effect of incorrect responses at the choice points or that the target never reached those choice points. A new set of analysis assessed access to the choice points and the type of errors observed in order to understand the difference between groups.

Responses at choice points. To examine whether the results from the previous analyses represented errors at the choice points or that certain choice points were not even reached, the number of choice points accessed by each group was compared. For the facultative maze, separate t-tests for each choice point indicated that the facultative group had more access to choice points than the forced group in choice points 2, $t(4) = 3.09$, $p = .04$, and 3, $t(4) = 3.29$, $p = .03$, but not for choice point 1, $t(4) = 1.71$, $p = .16$ (see Figure 7). For the forced maze, access to choice points was different between groups for choice point 1, $t(4) = 1.0$, $p = .02$, but not for choice point 2, $t(4) = 1.86$, $p = .16$, or for choice point 3, $t(4) = 1.52$, $p = .28$. These results indicate that both groups did not differ on the number of facultative mazes started. However, the facultative group reached the third choice point more times than the forced group in the facultative maze, and thus may have received more reinforcement than the forced group. If this was the case, then the forced group could have learned to avoid responding. Additional tests were done to assess any emerging differences between the groups.

Table 5
Type Comparison Across Novel and Trained Mazes

Group	Maze	Choice Point 1	2	3
Forced	Trained	78.44 (7.47)	76.67 (5.78)	74.79 (9.58)
	Novel Forced	60.83 (20.21)	55.00 (18.88)	61.67 (26.02)
	Novel Facultative*	54.17 (10.1)	43.33 (11.82)	43.33 (13.77)
Facultative	Trained	80.73 (4.55)	80.42 (6.59)	86.67 (3.73)
	Novel Facultative	70.00 (9.01)	74.17 (16.27)	85.83 (11.81)
	Novel Forced*	65.83 (13.77)	73.33 (7.64)	84.17 (9.46)

Note: SD are in ().
*Opposite maze type from trained mazes.

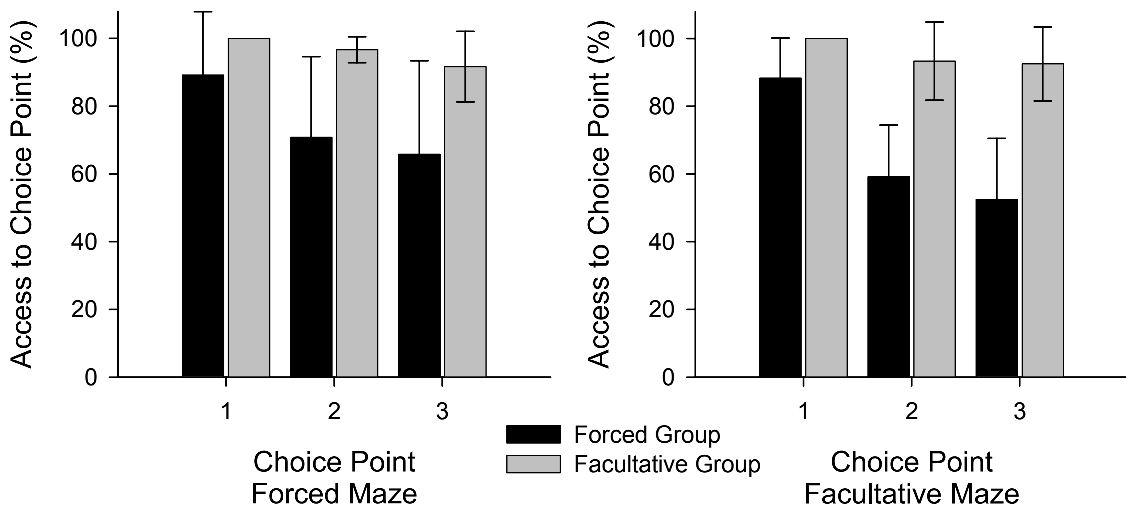


Figure 7. Access to choice point in transfer 4 as a function of the order of the choice point and the choice point type used during training for the novel forced and facultative mazes. The bars represent the standard deviation.

An analysis comparing the number of trials completed by both groups indicated that there was no difference between groups in the number of mazes completed per session. These results were supported by a Two-Way repeated measures ANOVA of Session (1-10) as a within subjects factor and Group (Forced, Facultative) as a between subjects factor, which revealed no main effect of session, $F(9, 36) = 1.32$, $p = .26$, group, $F(1, 4) = 5.36$, $p = .08$, or interaction, $F(9, 36) = 1.52$, $p = .18$. However, the groups did differ along test types. In the facultative maze, the facultative group reached the goal and completed the trial more times ($M = 92.5$, $SD = 4.73$) than the forced group ($M = 53.3$, $SD = 10.54$). For the facultative maze, a Two-Way repeated measures ANOVA of Session (1-10) as a within subjects factor x Group (Forced, Facultative) as a between subjects factor, revealed a significant difference between groups on the number of trial completions, $F(1, 4) = 9.52$, $p = .04$, but no effect of session, $F(9, 36) = 1.42$, $p = .22$, or an interaction, $F(9, 36) = .77$, $p = .65$. The groups did not show a difference in trial completion across forced mazes. In the forced maze, the facultative group reached the goal and completed the trial in a similar number of trials ($M = 89.17$, $SD = 11.15$) as the forced group (M=65.84, $SD = 19.02$). A Two-Way repeated measures ANOVA of Session (1-10) as the within subjects factor and Group (Forced, Facultative) for forced mazes only, revealed a significant interaction, $F(9, 36) = 2.38$, $p = .03$, but no main effect of session, $F(9, 36) = 1.7$, $p = .13$, or a effect of group, $F(1, 4) = 1.96$, $p = .24$. The interaction was produced because session 4 was the only session in which the forced group performed higher ($M = 100$) than the facultative group ($M = 83.33$).

Since the groups performed differently in the facultative maze, an additional analysis assessed what types of errors were committed at each choice point in those mazes to assess the differences between both groups. The errors were categorized as back (i.e., returning in the direction of the previous movement), wrong turn (i.e., changing direction), or overshoot (i.e., continuing in the current direction). Figure 8 shows the mean responses from each group for each type of error and the percent of correction after those errors. The groups did not differ in the number of responses belonging to each error type. This result was supported by a Two-Way repeated measures ANOVA of Error Type (Back, Wrong Turn, Overshoot) as a within subjects factor x Group (Forced, Facultative) as a between subjects factor, which revealed no main effect for error type, $F(2, 8) = .96$, $p = .42$, no group effect, $F(1, 4) = .01$, $p = .92$, and no interaction, $F(2, 8) = 2.66$, $p = .13$. The results suggest that the difference between both groups may be on the responses that occur after the errors. The facultative group was able to return to the correct path above 80% of the time after errors of each type. The forced group, however, only had a similar number of corrections to the facultative group after overshoots. A t-test for back errors showed a significant difference in corrections between groups, $t(4) = 3.65$, $p = .02$, and a t-test for wrong turn errors also showed a significant difference between groups, $t(4) = 4.44$, $p = .01$. A t-test for overshooting errors failed to show any difference between groups, $t(4) = .93$, $p = .40$. These results indicate that both groups could correct their responses and return to the correct path after overshooting, but the forced group remained in the wrong area of the maze after wrong turns and back errors.

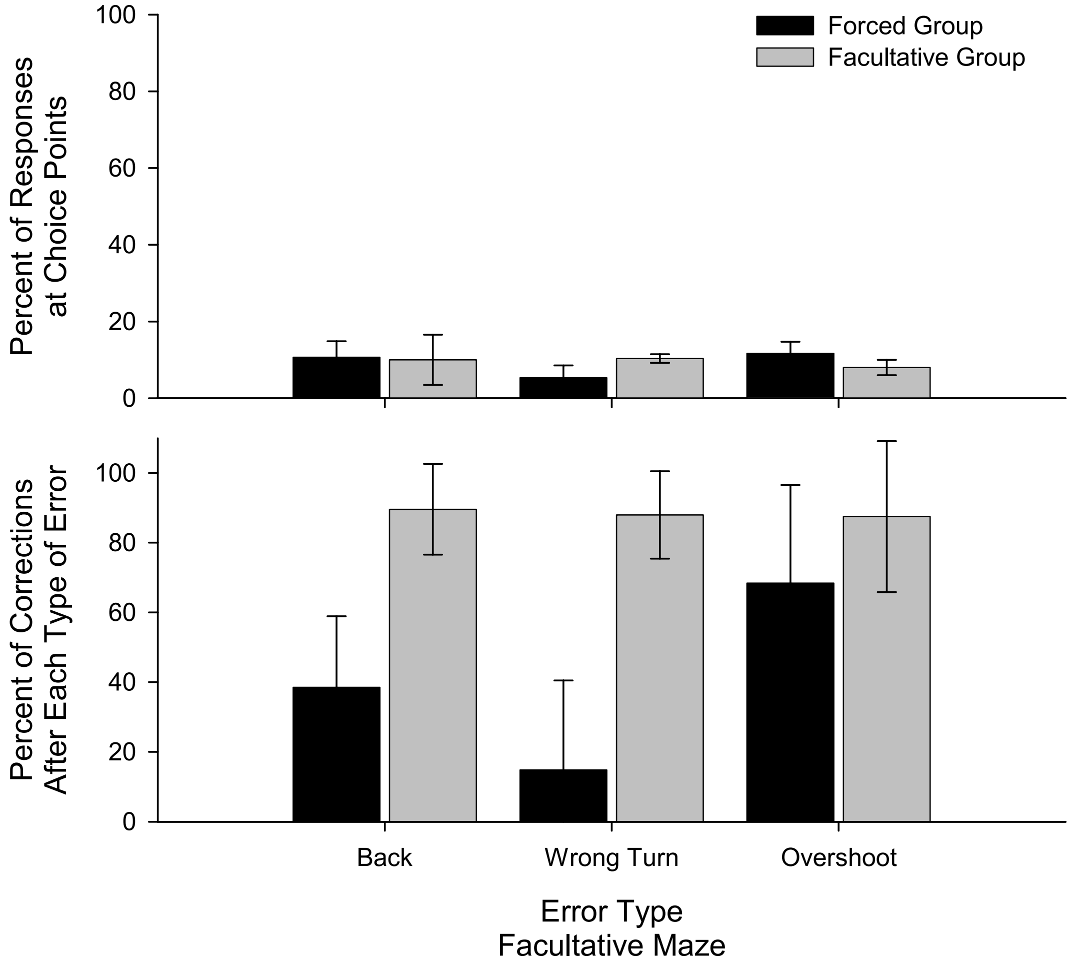


Figure 8. Type of response error in transfer 4 as a function of error type and the choice point used during training for the novel facultative maze. The mean number of correct choice point responses and choice points not accessed are included for comparison. The bars represent the standard deviation.

Separate t-tests for corrections at each choice point showed that both groups had similar number of corrections for choice point 2, $t(4) = 1.16$, $p = .31$, and choice point 3, $t(4) = 1.0$, $p = .37$. However, the groups were different for choice point 1, $t(4) = 2.83$, $p = .05$, were the facultative group ($M = 83.9$, $SD = 24.05$) had better performance than the forced group ($M = 28.07$, $SD = 24.31$). These results clarify that the difference found in the facultative maze while using Equation 1 was due to the fact that the forced group did not reach the third choice point, especially after mistakes in the first choice point.

Levels of planning. The previous results indicate that the type of training affected performance with novel mazes. The facultative group was able to correct their responses after all types of errors and reached the goal more than the forced group. It could be possible that the groups achieved different levels of path-planning depending on the type of choice point used at test time. The current task differed from Fragaszy et al. (2003) in that the available directional keys moved the target along the paths only and not into the walls. Thus, the analysis begins at level 1, bodily planning. To reach level 1 the subjects must be able to reach the choice points and perform at chance at the choice points. All novel choice points, with the exception of the forced maze, offered three paths. Performance at each choice point was compared to chance (i.e., 50% for the first choice point of the forced maze and 33% for all other choice points) in a series of One-sample t-tests (Equation 2). These analyses showed that neither group could perform above chance in the first choice point of both types (see Table 6). In the forced maze, the forced group performed above chance on choice point 2, $t(2) = 7.16$, $p = .02$, and choice point 3, $t(2) = 10.36$, $p = .01$, but not in choice point 1, $t(2) = 1.69$, $p = .23$. In the facultative maze, the forced group performed above chance on choice point 2, $t(2) = 4.86$, $p = .04$, and choice point 3, $t(2) = 24.71$, $p < .01$, but not in choice point 1, $t(2) = 3.59$, $p = .07$. In the forced maze, the facultative group performed above chance on choice point 2, $t(2) = 12.18$, $p = .01$, and choice point 3, $t(2) = 14.34$, $p = .01$, but not in choice point 1, $t(2) = 2.33$, $p = .15$. In the facultative maze, the facultative group performed above chance on choice point 2, $t(2) = 22.04$, $p < .01$, and choice point 3, $t(2) = 17.45$, $p = .00$, but not in choice point 1, $t(2) = 1.19$, $p = .36$. Thus, at choice point 1 both groups failed to reach planning level 1 but they did achieved level 1 for choice points 2 and 3.

$$\frac{\text{Observed Correct Responses Per Choice Point}}{\text{Total Choice Points Reached Per Choice Point}} \times 100 \qquad (2)$$

Levels 2 and 3, one element planning and integrated planning, were analyzed by observing the type of errors performed at specific choice points where responding controlled by directness would result in a different response than if controlled by path continuation (see Figures 9 and 10). Level 2 planning is characterized by responses controlled by directness to the goal, where the target is moved into the path that moves in the direction of the goal location. Errors at this level occur when the direction of the path leads toward the goal but ends before reaching it or changes direction. Level 3 planning is characterized by responses controlled by path continuation, where the target is moved in the direction of the path that reaches the goal, even if its initial direction is not toward the goal. In the facultative maze (Figure 9) five goal locations offered the appropriate situation at the first choice point. For these locations the first directional response was analyzed in order to assess control by directness or path continuation. The proportion of responses controlled by directness to the goal were assessed in a Two-Way repeated measures ANOVA of increasing Angle to the Correct Path (45^0, 72^0, 110^0, 135^0) as a within subjects factor x Group (Forced, Facultative) as a between subjects factor, showing a significant effect of group, $F(1, 4) = 13.68$, $p < .01$, but no effect from the increasing angles, $F(3, 12) = 1.53$, $p = .26$, or an interaction, $F(3, 12) = 1.92$, $p = .18$. For the forced group the proportion of responses controlled by the directness to the goal increased as the angle toward the correct path increased. A One-way repeated measures ANOVA of Angle to the Correct Path (45^0, 72^0, 110^0, 135^0) revealed a significant effect, $F(3, 6) = 9.21$, $p = .01$. However this effect was not present in the facultative group, $F(3, 6) = .89$, $p = .5$.

The proportion of responses controlled by continuation of the path were assessed with a Two-Way repeated measures ANOVA of increased Angle to the Correct Path (45^0, 72^0, 110^0, 135^0) as a within subjects factor x Group (Forced, Facultative) as a between subjects factor, showing a significant effect of angle, $F(3, 12) = 11.62$, $p < .01$, but no group effect, $F(1, 4) = 1.01$, $p = .37$, or an interaction, $F(3, 12) = 2.38$, $p = 12$. For both groups, as the angle toward the correct path increased, the proportion of responses towards it decreased. Thus, in the facultative maze both groups of pigeons showed path-planning behaviors of level 3 if the angle toward the correct path was at least equal to that towards the incorrect path.

Table 6
Path-Planning Level 1 Analysis

Group	Maze	Choice Point 1	2	3
Forced	Novel Forced	60.83 (20.21)	55.0 (18.87)	61.67 (26.02)
	Novel Facultative*	54.17 (10.10)	43.33 (11.81)	43.33 (13.77)
Facultative	Novel Facultative	70.0 (9.01)	74.17 (16.27)	85.83 (11.81)
	Novel Forced*	65.83 (13.77)	73.33 (7.64)	84.17 (9.46)

Note: SD are in ().
*Opposite maze type from trained mazes.

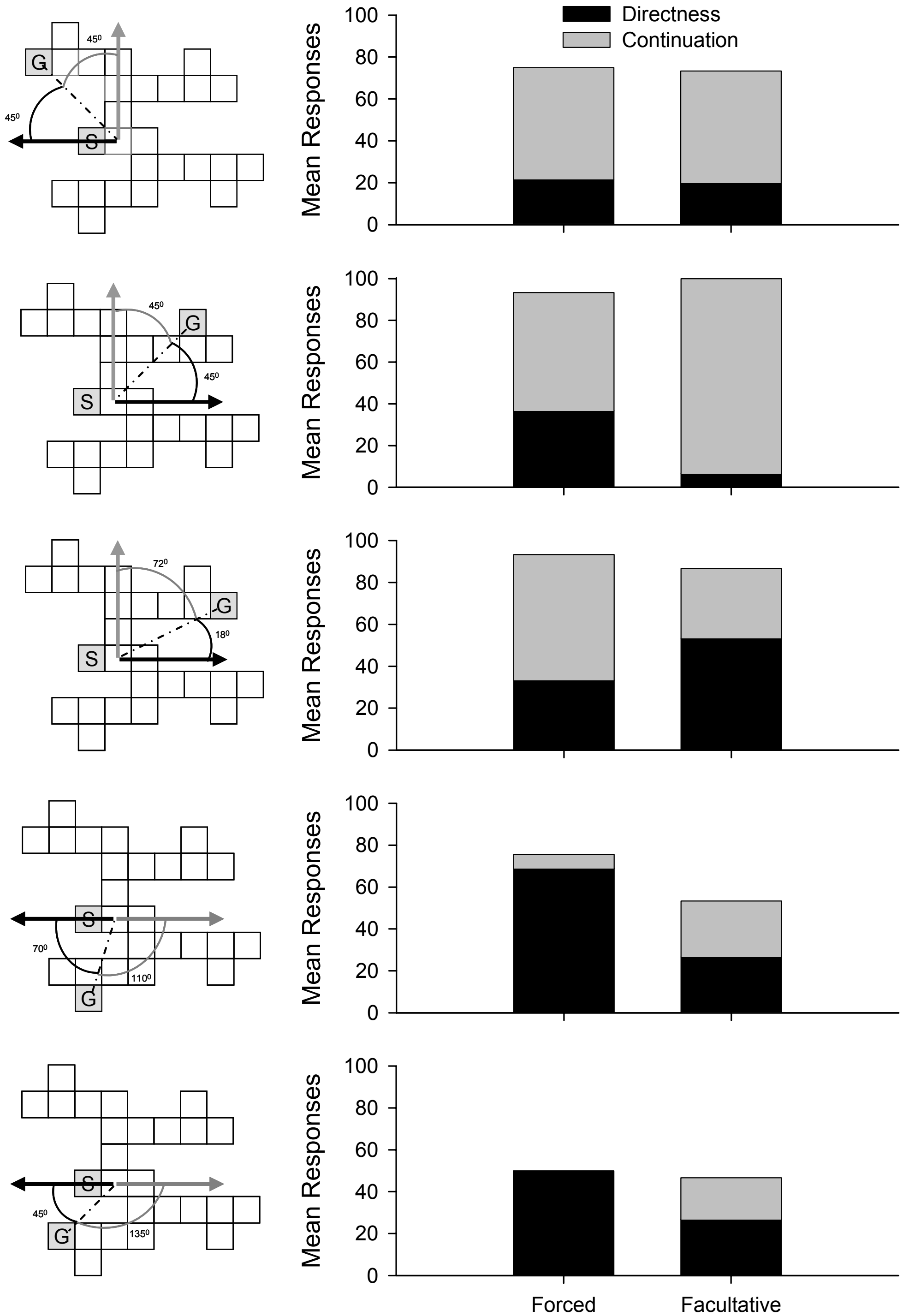


Figure 9. Configurations used to assess planning levels 2 and 3 in the facultative maze. The bars show the proportion of responses each group emitted that were controlled by the directness to the goal versus continuation of the path.

In the forced maze (Figure 10) none of the choice points within the correct path allowed for the distinction between control by directness to the goal and continuation of the path. However, if the initial response was incorrect, six of the new locations in the maze allowed for the correct conditions to be present. Again, the first response at these locations was analyzed. As shown in Figure 10, both groups had higher proportion of responses controlled by directness to the goal than continuation of the task. The proportion of responses controlled by directness were analyzed in a Two-Way repeated measures ANOVA for Angle to the Incorrect Path (Below 25^0, Above 25^0) x Group (Forced, Facultative), which failed to reveal any effect of angle, $F(1, 4) = .07$, $p = .81$, group, $F(1, 4) = .03$, $p = .87$, or an interaction, $F(1, 4) = .52$, $p = .51$. The proportion of responses controlled by continuation of the path were analyzed in a Two-Way repeated measures ANOVA for Angle to the Incorrect Path (Below 25^0, Above 25^0) x Group (Forced, Facultative), which failed to reveal any effect of angle, $F(1, 4) = .53$, $p = .51$, group, $F(1, 4) = .8$, $p = .42$, or an interaction, $F(1, 4) = .24$, $p = .65$. Thus, in the forced maze both groups showed path-planning behaviors at level 2.

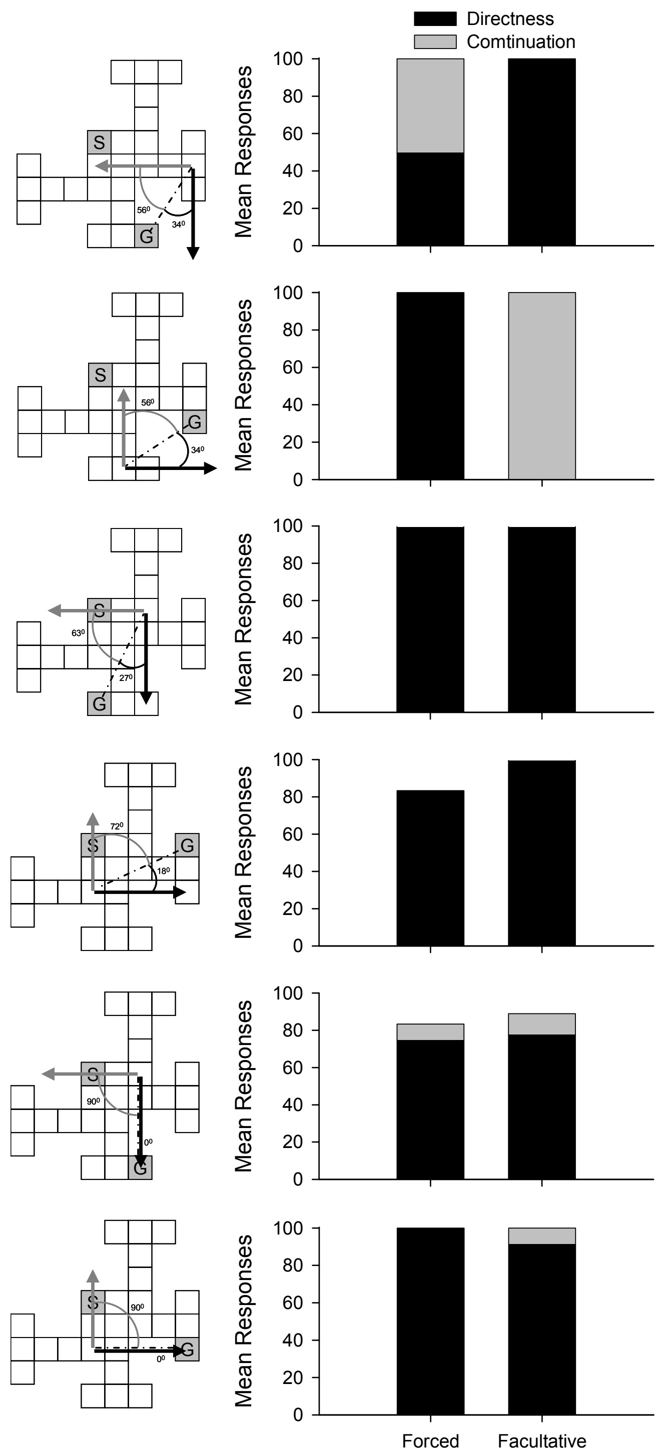


Figure 10. Configurations used to assess planning levels 2 and 3 in the forced maze. The bars show the proportion of responses each group emitted that were controlled by the directness to the goal versus continuation of the path.

Table 7 summarizes the results obtained for each planning level that could be tested within the parameters of this study. These results suggest that the level of planning is affected by the angle towards the correct path. That is, the properties of the maze affect the possible planning level achieved and depending on the angles used during testing a species could demonstrate or fail to demonstrate path-planning behaviors. The low levels of control by continuation in the forced maze could be an effect of the increased distance to the goal, since they occurred after an initial movement in the wrong direction. An alternative explanation is that the number of directional changes in the correct path was larger in the forced maze than in the facultative maze. The maximum number of changes in direction from the choice point to the goal in the facultative maze is 3 changes, while in the forced maze the minimum is 4 changes in direction.

Discussion

Both groups learned the training mazes and transferred to additional choice points at a similar rate. Their performance during the three training phases and three test phases that increased the number of choice points suggest that the differences found in transfer 4 for novel mazes can be interpreted as the effect of the type of choice point used during training on novel mazes and not to differences in accuracy between groups developed during training.

Item-specific learning cannot explain the results obtained for both groups because they performed at least similar to baseline on novel mazes of the same training type in Transfer 4. The forced group performed similarly in novel forced mazes and in trained forced mazes. This suggests that forced-choice point training can lead to learning by type (i.e., transfer to choice points of the same type). The forced group did not show full maze navigation because their performance in the facultative maze was below baseline performance. The facultative group showed full maze navigation because their performance at both novel forced mazes and novel facultative mazes was similar to baseline performance.

Contrary to expectations, the two groups did not differ on the type of response errors committed. However, the facultative group was able to reach the second and third choice points significantly more often than the forced group, suggesting that the groups differed on their self-correction responses. In addition, the analysis done with Equation 2, which compared performance across the trials were the target reached specific choice points, showed that both groups performed at chance in the first choice point and above chance on all other choice points. The facultative group did perform above the forced group on all choice points. These results suggest that maze training that is based on forced choice points will only lead to transfer to novel mazes of the same type but not to facultative choice points. However, it is not accuracy which is affected, but the corrections after errors. Training based on facultative choice points will transfer to both types of choice points.

The analysis on planning levels suggests that control by directness (level 2) and control by continuation (level 3) depends on the angles created between the available paths and the Euclidean path to the goal. The level of planning observed may also be an effect of the distance to the goal and the number of directional changes in the correct path. Training type did not seem to have an effect on the level of planning attained since both groups achieved control by continuation of the path at the same angles. The following experiments explore any additional effects of training on maze navigation.

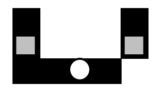
Table 7
Levels of Path-Planning by Maze Training

Level	Definition	Training	
		Forced-Choice	Facultative-Choice
0	Absence of planning The target is moved in random directions within the path and at choice points.	———	———
1	Bodily Planning Directional movement of the target within the path but random movements at choice points.	Below chance at the first choice point on both mazes. Performance above chance on choice points 2 and 3 of both mazes.	Below chance at the first choice point on both mazes. Performance above chance on choice points 2 and 3 of both mazes.
2	One element planning Movement at choice points that is controlled by one property.	Facultative Maze: Increased control by directness as the angle to the correct path increases. Forced Maze: Control by directness to the goal at all angles.	Facultative Maze: No effect of angle on responses controlled by directness. Forced Maze: Control by directness to the goal at all angles.
3	Integrated planning Movement at choice points that is controlled by two properties.	Facultative Maze: Responses controlled by continuation of the path affected by angle toward the correct path. Forced Maze: Minimal control by continuation of the path.	Facultative Maze: Responses controlled by continuation of the path affected by angle toward the correct path. Forced Maze: Minimal control by continuation of the path.
4	Sequential integrated planning Selecting a series of choice point responses before the first response in the maze.	———	———

III. EXPERIMENT 2

The construction of novel mazes is achieved by adding choice points and altering or increasing the changes in direction within a maze. A characteristic of larger mazes is that two paths may be close enough for them to be perceived as part of the same path. Experiment 2 measured if the two groups could discriminate between a path that they can move through (i.e., available) and a path that lead into a goal but ended before reaching it (i.e., unavailable). The end of the unavailable path was closer to the start location than the goal. However, control by the goal location could be stronger than control by the continuation of the path. In this experiment all test trials offered an available and an unavailable path, each with a goal at the end of it (see Table 8). The distance to both goals was manipulated to show the goal in the available path at a shorter, equal, and longer distance than the goal in the unavailable path. If performance was controlled by goal location then the direction of the first response would be towards the closest goal, regardless of path characteristics. However, if the direction of the first response was controlled by the continuation of the path, then responses would always be toward the available path regardless of goal location.

Table 8
Description of Test Types

Description	Sample
Type A Both goals at horizontal locations from the start location. No change in direction in the path.	
Type B Both goals at diagonal locations from the start location. One change in direction in each path.	
Type C The goal in the complete path is in a diagonal location from the start location while the goal in the incomplete path is at a horizontal location. One change in direction in the complete path only.	
Type D The goal in the incomplete path is in a diagonal location from the start location while the goal in the complete path is at a horizontal location. One change in direction in the incomplete path only.	

A second manipulation in this experiment compared path discrimination when one or both paths changed direction before reaching the goal. The change in direction alters the Euclidean distance to the goal and increases the number of directional keys that must be used to reach the goal. These changes may affect search of the maze and path discrimination.

It is possible that training in Experiment 1 affected path discrimination. To assess any possible effect, all baseline trials in Experiment 2 continued to use the choice point type for each group.

Method

Subjects, housing, and stimuli. The same subjects that completed Experiment 1 participated in this experiment. Baseline trials for the forced group consisted of the forced mazes used in the transfer test 1 from Experiment 1 (i.e., one choice point). Baseline trials for the facultative group consisted of the facultative mazes used in the transfer test 1 from Experiment 1 (i.e., one choice point). The stimuli and movement properties remained the same as in Experiment 1.

Mazes. An important aspect of maze navigation is to determine which paths do not lead to the goal because they are blocked or move in a different direction. An available goal location was defined as a goal location that is accessible to the target within the current path. An unavailable goal location was defined as a goal location that cannot be reached by the target within the current path. To assess which factors affect the detection of available and unavailable goals, four types of mazes were used (see Table 8). For all four types, the trial began with the target at the center of the maze and one goal on each end of a path. All mazes had one path blocked by a wall (i.e., unavailable) and one path open (i.e., available) (for all configurations used see Appendix B). Type A is a variation of the last maze used during the pretraining phase in Experiment 1, a horizontal path in which one of the paths is blocked by a wall. Both goal locations were horizontal to the target. Type B consisted of a U-shaped maze with both goal locations placed diagonally from the target. Type C placed the unavailable goal at a horizontal location and the available goal at a diagonal location. Type D placed the unavailable goal at a diagonal location and the available goal at a horizontal location.

In addition to the placement of the goals, the distance between target and goals was manipulated. The goals appeared at Manhattan distance 3 or 4 from the target. The possible locations are classified as follows: available = target closer to the available goal; equal = equal distance to both goals; and unavailable = target closer to the unavailable goal.

Scoring and analysis. Only the first directional response of the trial was used as a measure of performance. After the first response the distance and angle to both goals changed.

Procedure

Training. Both groups of pigeons were retrained with the one-choice point maze from experiment 1 on either forced- or facultative-choice points, depending on their original group. There were 32 trials per session. Both groups completed 32 sessions of training before the beginning of testing.

Test. Each of the five test sessions consisted of 32 baseline trials from training and 24 test trials (see Appendix B). Three locations (i.e., equal, available, unavailable) were used to test each maze type. Mirror images of the mazes were shown to present the correct goal both on the left and the right sides of the maze. Each of the 24 possible configurations was presented once every session.

Results

Group comparison. To assess whether training during Experiment 1 on specific type of choice points had an effect in this task, the performance from both groups was compared. The groups did not differ in their performance in this task. A Four-Way repeated measures ANOVA of Test Session (1-5) x Maze Type (A, B, C, D) x Location (Available, Equal, Unavailable) as the within-subjects factors and Group (Forced, Facultative) as a between subjects factor showed that the facultative group did not differ from the forced group across trials, $F(1, 4) = 3.68$, $p = .12$.

Availability of the path. To determine if path continuation controlled performance, the first response of the trial was assessed in terms of which goal was closer to the target at the beginning of the trial. Performance was affected by the location of the goal and continuation of the path (see Figure 11). When the closest goal was in the available path and when both goals were at equal distance from the start location both groups moved the target towards the available path (i.e., continuation of the path). This finding was supported by a One-Way repeated measures ANOVA of Location (Available, Equal, Unavailable) which showed a significant effect of location, $F(2, 238) = 22.7$, $p < .01$. A series of One-sample t-tests assessed whether performance at each possible configuration was different from chance. The analyses found that performance was above chance when the goal was in the available path, $t(119) = 8.06$, $p < .01$, and when the distance was equal to both goals, $t(119) = 6.21$, $p < .01$. However, when the goal was closer in the unavailable path, performance was at chance, $t(119) = .4$, $p = .69$. The results for the

Equal configuration suggest control by path continuation, however performance in the Unavailable configuration suggest the emergence of control by the goal location.

Maze type. To assess whether the shape of the paths affected performance, the first response was compared across maze types (see Figure 11). A One-Way repeated measures ANOVA of Maze Type (A, B, C, D) showed a significant effect of maze type, $F(3, 267) = 8.85$, $p = .00$. Performance on maze type D was not different from chance, $t(89) = 1.32$, $p = .19$. Responding was different from chance in type A, $t(89) = 2.62$, $p = .01$, type B, $t(89) = 3.3$, $p < .01$, and type C, t(89) = 9.16, $p = .00$. These results suggest that type D mazes had increased control by the goal location.

Performance on the three maze types that showed performance above chance (i.e., A, B, and C) was compared to assess any differences in control by path characteristics. The results indicated that the first response on type C mazes was significantly different from type A, $t(89) = 4.02$, $p < .01$, and type B, $t(89) = 3.5$, $p < .01$. Performance on type A was not different from performance on type B mazes, $t(89) = .45$, $p = .66$. These results suggest that the properties of the type C maze were optimal in allowing the pigeons to come under control of path continuation.

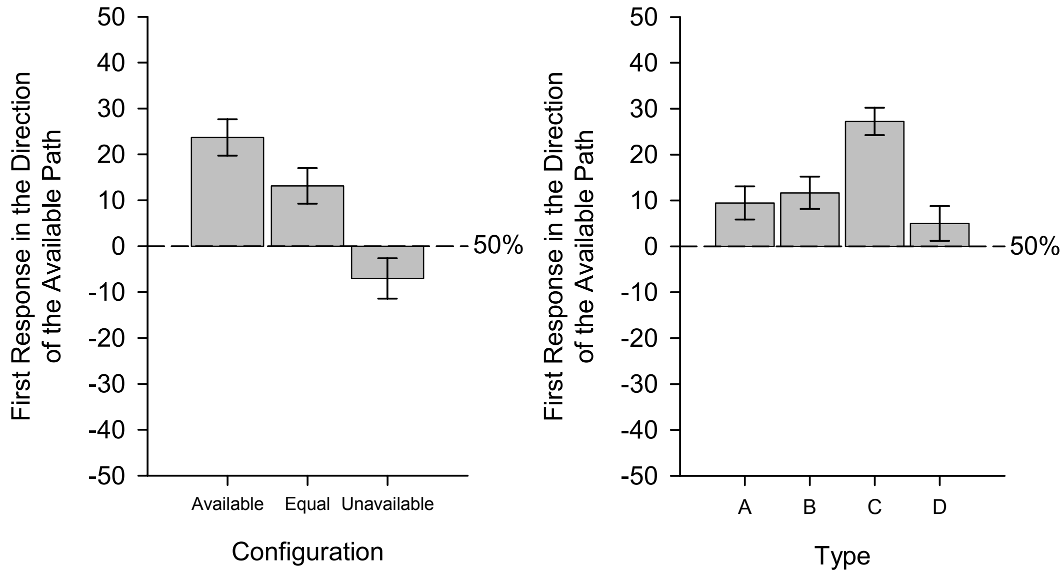


Figure 11. Performance across conditions. The left panel shows the percent of trials were the target was moved toward the available path as an effect of the distance to the nearest goal. The right panel shows the percent of trials were the target was moved toward the available path as an effect of the type of configuration. The bars represent the standard deviation.

Discussion

Both groups had similar performance in this task, and thus the previous training did not have an effect on path discrimination. The pigeons were able to discriminate between the paths; under no condition did they move more towards the unavailable path. However, distance to the goal and the shape of the paths did change control by path characteristics.

The difference between type C mazes and type D mazes, the best and worst performances, was their shape. Specifically, the mazes varied in the location of the interrupting wall. In type D the wall was at the junction between the current part of the maze and the stranded path. It is possible that the location of that wall was not detected because of control by goal location or that detection of the wall required searching two paths that moved in perpendicular directions. However, in type C mazes the location of the wall could be detected by searching one direction. Both type A and B mazes had paths with similar construction. This property of the maze may have required search of both paths before responding, thus resulting in similar performance.

In this experiment the pigeons moved the target toward the available path when the goal was closer on that side and at equal distance. They also moved toward the available goal on three out of four configuration types. These results suggest that pigeons may be affected by the distance to the goal. The following experiment assessed distance discrimination when both paths were available.

IV. EXPERIMENT 3

Distance to the goal is a factor that may affect performance. Distance for these mazes is determined by the number of responses necessary to move the target into the goal location (i.e., Manhattan distance). However, the perception of distance in this task has not been assessed. In Experiment 3 the distance from the target to two goal locations was manipulated. In addition to this distance test, on half of the trials one path required responses to one key while the second path required responses to more than one key (see Table 9). If performance is affected by the Manhattan distance alone, then they should move the target equally to both sides when the distance is equal on both mazes. But if the number of directional changes is a factor, then there should be a preference toward moving the target in the direction of the simple path even when the Manhattan distance to the other goal is shorter. If performance is influenced by Euclidean distance, then the target should be moved toward the complex path when the Euclidean distance is the shortest.

Method

Subjects, housing, and stimuli. The subjects that participated in Experiments 1 and 2 participated in the third experiment. The stimuli and movement properties remained the same as in the previous experiments.

Table 9
Description of Test Types

Description	Sample
Type A Both goals at a horizontal location from the start location. All paths were complete paths.	
Type B One goal at a horizontal location from the start location and one goal at a diagonal location. The path to the diagonaly located goal had various changes in direction.	

Mazes. Two mazes were used to assess the effect of distance on performance. Both mazes began with the target at the center of the path and a goal to both sides. The distance to either goal varied from 2 to 4 responses (for all configurations used see Appendix C). Type A mazes consisted of a horizontal path with two goals and was used to assess if pigeons could move the target towards the closest goal. Type B mazes consisted of one horizontal path (i.e., simple) and a staircase-shaped path (i.e., complex) and was used to assess if the number of directional changes, and not path distance, controlled performance.

Type B mazes allowed for 3 configurations for each of the following configurations: equal = equal Manhattan distance to both goals; simple = target closer to goal on the simple path; and complex = target closer to goal on the complex path (see Table 9). The same configurations were used for maze A, but instead the configurations were: equal = equal Manhattan distance to both goals; left = target closer to goal on the left side; and right = target closer to goal on the right side.

Scoring and analysis. Only the first directional response of the trial was used as a measure of performance. After the first response the distance and angle to both goals changed.

Procedure

Pigeons began the test sessions immediately after the completion of Experiment 2. The five test sessions consisted of 32 baseline trials and 27 test trials (9 type A mazes, 18 type B mazes). Both test mazes were inverted horizontally to present the correct goal both on the left and right side of the maze. Baseline trials consisted of the horizontal mazes used as baseline in Experiment 2.

Results

Side bias. Three pigeons developed a side bias during testing. A side bias was defined as responding below 20% towards either side (left or right). The data removed from the following analyses belong to Jupiter (Facultative group), and Moe and Luke (Forced group). The side bias may have developed because the entrance to the testing chamber was in the right side and it is possible that the pigeons learned to respond away from it. In addition, there was no contingency that required the pigeons to learn to move the target toward the closest goal. At the short distances used in this experiment there may have been no significant difference in the time taken to complete the trial and thus moving the target towards a goal located one distance farther than the other goal did not sufficiently delay the reinforcement.

Type B maze. The results are shown here as the difference between both paths and which path held the closest goal (S = simple path, C = complex path). To calculate the difference in distance between both paths, the shortest Manhattan distance was divided by the largest and then subtracted from 1. For configurations where the farthest goal was at distance 4 and the closest at distance 2, the difference was .5. For configurations where the farthest goal was at distance 3 and the closest was at distance 2, the difference was .33. And for configurations where the farthest goal was at distance 4 and the closest was at distance 3, the difference was .25.

The distance differences affected performance in the type B mazes (see Figure 12). These results were supported by a Two-way repeated measures ANOVA of Session (1-5) x Distance Differences (S.5, S.33, S.25, equal, C.25, C.33, C.5), which showed a significant effect of distance differences, $F(6, 12) = 5.93$, $p < .01$, but not for session,

$F(4, 8) = 1.58$, $p = .27$, or an interaction, $F(24, 48) = 1.64$, $p = .07$. Only the largest ratios with the closest goal on the simple side were significantly different from chance. In a series of One-Sample t-tests the only distance differences that showed performance above chance were S.5, $t(4) = 5.88$, $p < .01$, and configurations S.33, $t(4) = 4.81$, $p = .01$.When the goal was closer in the simple path the pigeons moved the target in that direction. When the goal was closer in the complex side performance was at chance. These results suggest that the distances used in this experiment were not large enough to create a noticeable difference between the goals.

Type A maze. To determine if distance also affected performance on paths that required no directional changes, similar analyzes were performed in Type A mazes. The distance differences did not affect performance in the type A maze (see Figure 13). A Two-Way repeated measures ANOVA of Session (1-5) x Ratio (.5, .33, .25) failed to reveal any significant effects. In a series of One-Sample t-tests the only distance differences that showed performance above chance were .5, $t(4) = 6.33$, $p < .01$, and .33, $t(4) = 9.0$, $p < .01$. These results are similar to those for maze B because at the largest distance differences there was distance discrimination between the goal locations.

Type A maze: equal distances. Although overall performance for these three birds was not biased, their performance in configurations with equal distances to both paths in the type A maze was biased, $t(14) = 4.01$, $p < .01$. Responses to the left accounted for 73.33 % of the trials ($SD = 22.54$). This is an interesting but unclear result because at distance difference .25 performance was at chance.

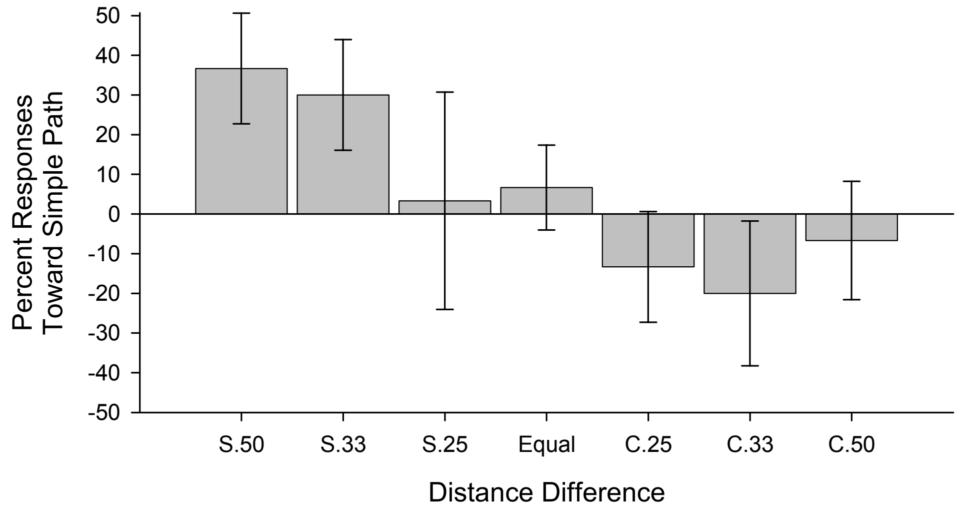


Figure 12. Performance across distance ratios toward the simple (S) and complex (C) paths in type B mazes. The bars represent the standard deviation.

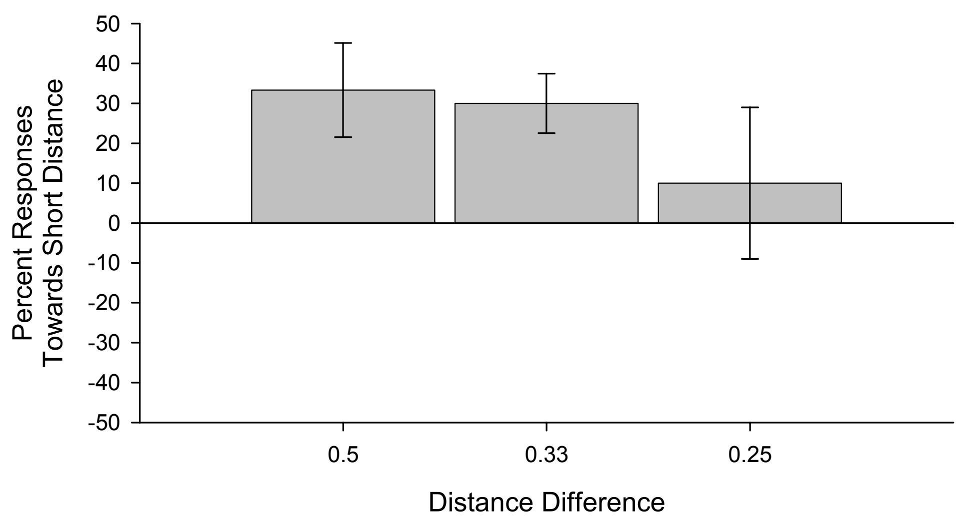


Figure 13. Performance across distance ratios in type A mazes. The bars represent the standard deviation.

Discussion

The results for type A and B mazes suggest that pigeons may be able to discriminate larger distances than the ones used here. The pigeons discriminated distances between simple paths and also when one of the paths was complex. Since they never moved the target significantly more toward the complex side, it can be concluded that within the maze properties used here they were not controlled by Euclidean distances but by Manhattan distances. However, the observable trend present in Figure 10 suggests that at larger ratios they may increase their responses toward the complex path.

The simple path used in this experiment required responding to only one directional key to reach the goal. The complex path had three changes in direction, although the different goal locations may not have required that many changes in directional keys. It is possible that most responses were towards the simple path because only one key had to be used. Experiment 4 addressed the possible effects that changes in direction could have in the responses toward two goals that were at constant Euclidean and Manhattan distances.

V. EXPERIMENT 4

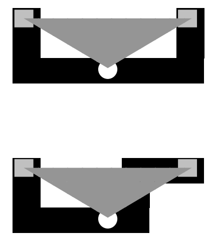
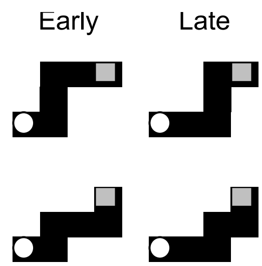
One of the maze properties changed in order to increase the novelty and complexity of the path is the number of directional changes within a path. The changes in direction may affect responding, and pigeons may explore simple paths first before moving into a complex path. Experiment 4 held the Euclidean and Manhattan distances constant for both goals while manipulating the directional changes within both paths (see Table 10). If navigation is controlled by the goal location, then the pigeons would move the target toward both paths irrespective of the number of directional changes within the path.

Mushiake et al. (2001) found that monkeys developed a preferred path to a goal location. However, this conclusion was based on the first response in the maze and the rest of the path was not analyzed. An additional manipulation in Experiment 4 showed two paths with equal number of directional changes but one of the configurations had the first change in direction close to the start location. The results from this manipulation could clarify any emerging preferences for a specific path.

Method

Subjects, housing, and stimuli. The same six subjects that participated in the previous experiments participated in Experiment 4. The stimuli and movement properties remained the same as in the previous experiments.

Table 10
Description of Test Types

Description	Sample
Type A Euclidean and Manhattan distance from the start location to both goals were held constant to both goals. The number of directional changes may be equal or different between paths.	
Type B Comparison were both paths have equal number of directional changes but the change occurs earlier or later in the path.	

Mazes. All mazes began with the target in the center of the maze and a goal at the end of each path; both goals were at distance five from the target and at the same Euclidean distance (for all configurations used see Appendix D). Type A mazes assessed the effect of the number of directional changes on performance. The paths were changed to require 1, 2, 3, or 4 directional changes to reach the goal. These manipulations allowed for 8 unique combinations of paths, for a total of 16 trials that present the simplest path to the right and the left of the target. Of these trials, 12 represent directional change ratios and 4 represent equal number of directional changes on both sides (i.e., 1, 2, 3, 4).

Type B mazes assessed the effect of the location of the first directional change on performance. The paths compared performance on two variations of the paths with two and three directional changes. Thus, each trial presented an equal number of directional changes but the first directional change occurred near the start location or near the goal location. These manipulations allowed for 2 unique combinations of paths, a total of 4 trials.

Scoring and analysis. Only the first directional response of the trial was used as a measure of performance. After the first response the distance and angle to both goals changed.

Procedure

Pigeons began the test sessions immediately after the completion of Experiment 3. The five test sessions consisted of 32 baseline trials, 16 type A trials, and 4 type B trials. Each path combination was presented once in every session. Baseline trials consisted of the horizontal mazes used as baseline in Experiments 2 and 3.

Results

The results presented here are for Lev (Facultative group) and Pierre (Forced group) because all other pigeons developed a side bias. To calculate the directional change ratios, the path with the least directional changes was divided by the largest directional changes.

Type A change ratios. To determine whether the directional changes could control responses when the Manhattan and Euclidean distances were constant, performance was compared across directional change ratios (see Figure 14). To calculate the ratios, the path with the least number of directional changes was divided by the path with the most directional changes (i.e., 1/4 = .25, 1/3 = .33, 1/2 and 2/4 = .5, 2/3 = .66, 3/4 = .75). A Two-Way repeated measures ANOVA of Change Ratio (.25, .33, .50, .66, .75) as a within subjects factor x Group (Forced, Facultative) as a between subjects factor revealed no effect of change ratio on performance, $F(4, 32) = 1.14$, $p = .36$, no effect of group, $F(1, 8) = .91$, $p = .37$, and no interaction, $F(4, 32) = .54$, $p = .71$. Thus, the number of directional changes did not control the direction of the responses. Additional One-Sample t-tests analyses showed that responding was never above chance for either path (see Table 11).

Type A: equal directional changes. To assess whether any possible side bias existed for these two pigeons, performance was compared across mazes with the same number of directional changes on each side. A Two-Way repeated measures ANOVA of Directional Change (1, 2, 3, 4) as a within subjects factor x Group (Forced, Facultative) as a between subjects factor revealed a significant interaction, $F(3, 24) = 4.51$, $p = .01$, but no main effect of directional change, $F(3,24) = .43$, $p = .73$, or a group effect, $F(1, 8)$

= 2.0, p = .2. This interaction could be the effect of Pierre's performance at three directional changes during which he never moved to the left side. Additional t-tests analyses showed that responding was never above chance (see Table 11). These results suggest that at equal directional changes in both paths, responding was at chance.

Type B mazes. To examine whether a preference toward early directional changes had emerged, performance on Type B mazes was analyzed. Performance in the Type B mazes was scored as the number of responses towards the path with the nearest directional change. The results from both birds were combined. Although performance was not different from chance at two directional changes (M = 50.0, SD = 33.33), it was different from chance at three directional changes (M = 75.0, SD = 26.35). Separate One-Sample t-test analyses corroborated these findings for two directional changes, $t(9)$ = .00, p = 1.00, and three directional changes, $t(9)$ = 3.00. p = .02. These results suggest that at the complexity of three directional changes, the pigeons moved toward the path that offered the closest change in direction.

Discussion

The number of directional changes did not affect performance. This result indicates that when the Manhattan and Euclidean distance are held constant, directional changes do not control performance. However, the findings for Type B mazes suggest that pigeons may move toward paths that offer a close change in direction. The limited number of trials and configurations do not allow for a more complete analysis of this effect.

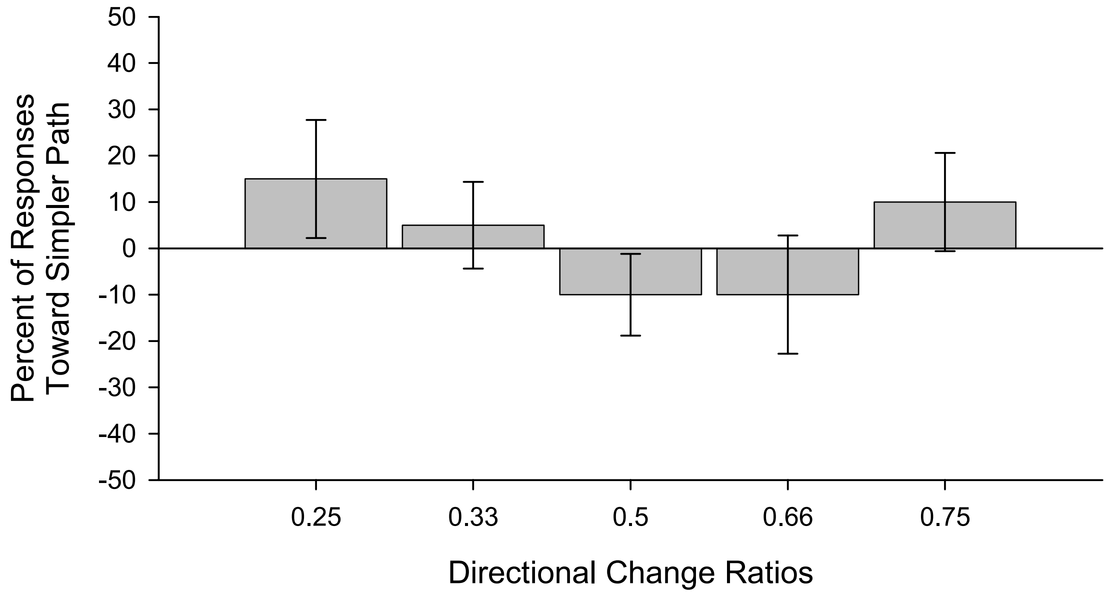


Figure 14. Performance across directional change ratios. The bars represent the standard deviation.

Table 11
One-Sample t-Tests of Individual Directional Change Rations in Comparison to Chance

Type	Configuration	Mean (SD)	df	t	P-value
A - Directional Ratios	0.25	65.0 (41.16)	9	1.15	0.28
	0.33	55.0 (28.38)	9	0.56	0.59
	0.5	40.0 (26.87)	9	1.18	0.27
	0.66	40.0 (39.44)	9	0.8	0.44
	0.75	60.0 (31.62)	9	1.0	0.34
A - Equal Directional Changes	1	70.0 (48.3)	9	1.31	0.22
	2	60.0 (51.64)	9	0.61	0.56
	3	50.0 (52.7)	9	.000	1.0
	4	70.0 (48.3)	9	1.31	0.22

VI. GENERAL DISCUSSION

Overall, the pigeons were able to navigate the various types of mazes used for testing and training. Their performance during training and testing in Experiment 1 demonstrates that they were performing above chance on most choice points. The pigeons were able to correct their path after three different types of errors, although the forced group could only reach the same level of correction after overshooting errors. The findings from Experiments 2, 3 and 4 clarify the effect that other manipulations have on responding. The location of the goal affected control by the path characteristics for both groups. Distance discrimination was possible when the difference in distance to two goals was large. And finally, changes in direction did not affect performance when no additional control by Euclidean or Manhattan distance was available. Together, the results indicate that the effect of individual factors on maze navigation for the task used for a particular species must be assessed before we can derive conclusions from their combined effects.

Maze navigation. All pigeons were able to navigate the mazes and reach the goal location as shown in the first three training and testing phases of Experiment 1. They also were able to navigate novel mazes with the same type of choice point as the one used in their respective training. However, the forced group showed deteriorated performance in the facultative maze. The differential training did not have an effect on the type of errors made, for both groups made the same proportion of moving back, wrong turn, and overshooting errors. The difference between the groups was in their responses after an error. The facultative group could return to the correct path after all types of errors, whereas the forced group had a lower number of corrections after moving back and wrong turn errors. It is possible that the training with facultative choice points increased maze search at each location for the facultative group and that this constant maze search may have allowed for detection of the incomplete path sooner for the facultative group than the forced group. If the forced group continued to move within a path until the next choice point or wall was encountered before a maze search was done, the Manhattan distance of the correct path may have had become too large in comparison to the other available paths. As Experiment 2 indicated, at shorter Euclidean distances control by path continuation decreases.

Training did not affect control by other maze characteristics. However, this effect may be due to the extensive experience both groups had with mazes at that point and that the mazes used in Experiments 2, 3, and 4 had one choice point only. In Experiment 2 both groups moved toward the available path when the alternative goal was farther than the correct goal. Both groups also performed better when the wall could be detected by searching a path with no directional changes. Similar effects of distance to the goal were observed in Experiment 3 where no walls limited access to the goals. Both groups moved towards the closest goal when the distance differences were large. This finding suggests that this study found the lower limit of the noticeable difference for distance in pigeons. Testing with larger distance differences should show more accurate distance discriminations. These results also imply that using larger distances in maze navigation tasks may increase the discrimination of the locations available in all the paths and thus improve maze navigation. Thus, species comparisons in maze navigation require testing with the appropriate distances for each species.

The results from Experiment 4 show the importance of control by Euclidean and Manhattan distances. Without those cues, performance was at chance for the available paths. Thus, the results from the planning levels in Experiment 1 were not due to only the increased directional changes necessary for self correction. The immediate angle towards the available paths may exert more control than the perceived complexity of the paths.

Path-planning behaviors. In Experiment 1, performance by both groups indicates that control by the continuation of the path (i.e., planning level 3) was dependent on the angle created by the Euclidean distance to the goal and the angle toward the correct path. Reaching level 3 on some choice points did not predict the same level of planning on other choice points. The factor predicting performance was a characteristic of the maze (angle toward the correct path).

The pigeons showed some level of control by continuation of the path in the facultative maze whereas performance was controlled by directness in the forced maze. The difference between both mazes indicates that two other possible factors affecting performance were the additional number of directional changes towards the goal and increased Manhattan distance towards the goal.

The overall results presented here suggest that pigeons can reach path-planning levels 2 and 3 provided that the appropriate maze properties are in place. Otherwise, control by directness and continuation of the path will not emerge.

Cross-species comparisons. These findings suggest various possibilities for cross-species comparisons in terms of both maze navigation and path-planning behaviors. Both groups of pigeons were able to complete the mazes in Experiment 1 and also achieved comparable planning levels as those achieved by apes and monkeys in Fragaszy et al. (2003). However, the contribution of the current analyses is that the level of planning achieved depends on the maze characteristics. Pigeons reached level 3 in the facultative maze but not in the forced maze. Thus, the results suggest that there is no qualitative difference in planning among chimpanzees, apes, and pigeons. Furthermore, it is possible that any qualitative differences found between species are the effect of the maze characteristics used for one of the species. Therefore, an appropriate species comparison across two-dimensional maze tasks should compare the choice point type used during training as well as during transfer. In addition, any species comparison must first assess the optimal manipulations for the task and the species.

Contrary to what was found with chimpanzees and apes, the pigeons did not commit one type of error more often than another (moving back errors were not reported for the primates). Both groups of pigeons committed a similar number of wrong turns, moving back, and overshooting errors. In terms of corrections, apes made more corrections after wrong turns (about 65%) than overshoots (about 32%). Monkeys made similar corrections after both types of errors (wrong turns = 45%, overshoot = 39%). The pigeons trained with facultative choice points showed correction after 85% of errors of any type. In the facultative maze the forced group showed correction after 64% of the overshooting errors, after 39% of the moving back errors, and after 16% of the wrong turn errors.

In summary, the findings in these series of studies demonstrate that the joystick analog can be used to assess maze navigation and the emergence of path-planning behaviors in pigeons. However, before any conclusion can be made as part of a species comparison, the optimal manipulations must be found for each species in their specific tasks (joystick or touch screen).

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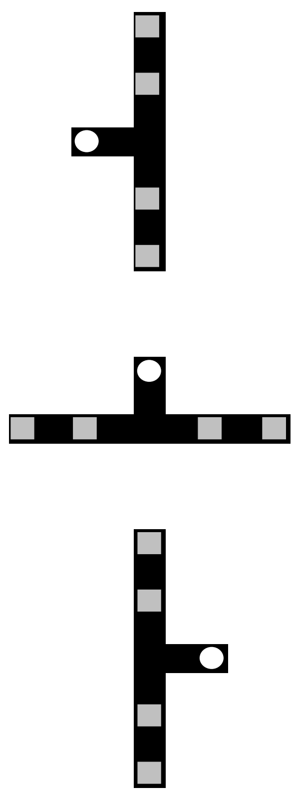
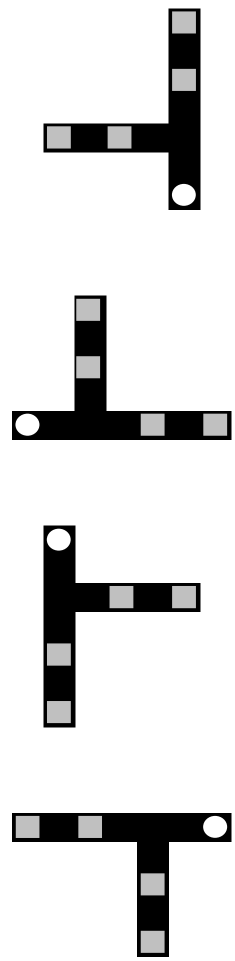
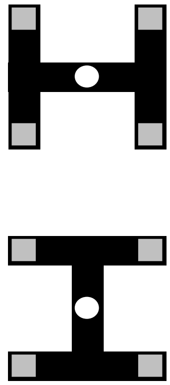
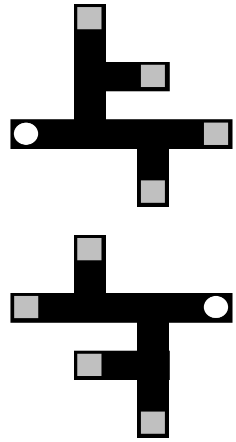
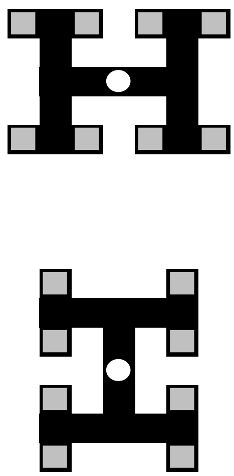
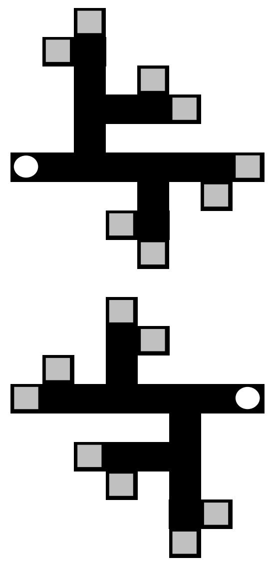
APPENDICES

Appendix A

Experiment 1 Training Configurations

The circles represent the target at the start location. The squares represent the possible goal locations of which only one was used per trial. In Experiment 2, 3, and 4 the configurations with one choice point were used as baseline trials to maintain training for the specific choice point type of each group.

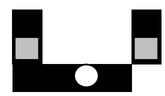
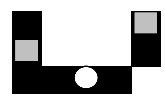
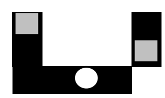
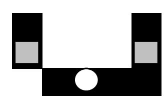
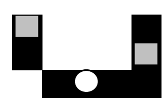
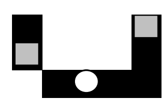
Choice Points	Forced-Choice Configurations	Facultative-Choice Configurations
1		

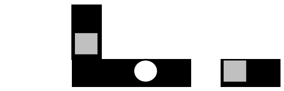
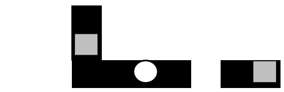
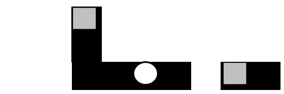
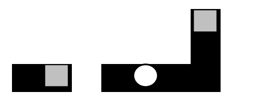
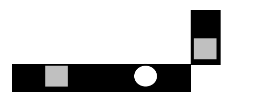
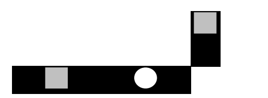
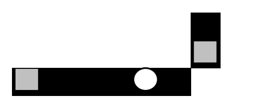
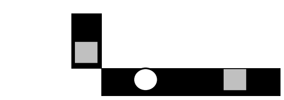
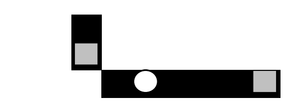
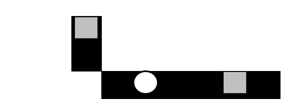
Choice Points	Forced-Choice Configurations	Facultative-Choice Configurations
2		
3		

Appendix B

Experiment 2 Test Configurations

The circles represent the target at the start location. The squares represent the goal locations of which only one could be accessed in any given trial.

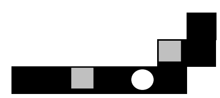
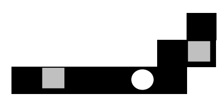
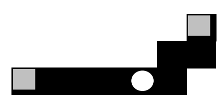
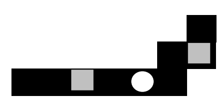
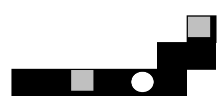
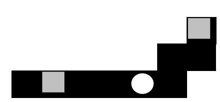
Type	Distance		Correct First Response	Location	Configurations
	Available	Unavailable			
	3	3	Left	Equal	
	3	4	Left	Available	
A	4	3	Left	Unavailable	
	3	3	Right	Equal	
	3	4	Right	Available	
	4	3	Right	Unavailable	
	3	3	Left	Equal	
	3	4	Left	Available	
B	4	3	Left	Unavailable	
	3	3	Right	Equal	
	3	4	Right	Available	
	4	3	Right	Unavailable	

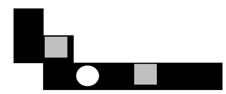
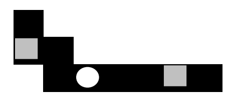
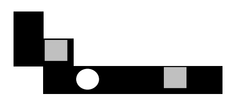
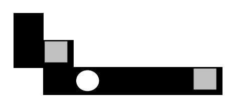
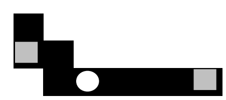
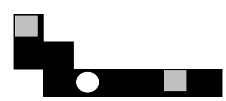
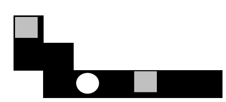
Type	Distance		Correct First Response	Location	Configurations
	Available	Unavailable			
C	3	3	Left	Equal	
	3	4	Left	Available	
	4	3	Left	Unavailable	
	3	3	Right	Equal	
	3	4	Right	Available	
	4	3	Right	Unavailable	
D	3	3	Left	Equal	
	3	4	Left	Available	
	4	3	Left	Unavailable	
	3	3	Right	Equal	
	3	4	Right	Available	
	4	3	Right	Unavailable	

Appendix C

Experiment 3 Test Configurations

The circles represent the target at the start location and the squares represent the goal locations.

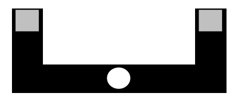
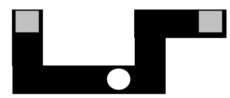
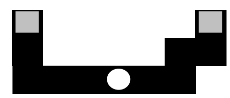
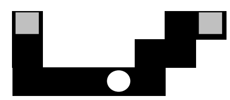
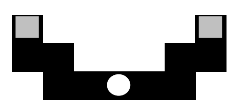
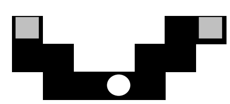
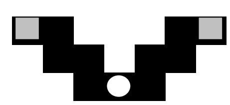
Type	Distance		Correct First Response	Distance Type	Configurations
	Left	Right			
A	2	2	-	Equal	
	3	3	-	Equal	
	4	4	-	Equal	
	2	3	Left	-	
	2	4	Left	-	
	3	4	Left	-	
	4	3	Right	-	
	4	2	Right	-	
	3	2	Right	-	
B	2	2	-	Equal	
	3	3	-	Equal	
	4	4	-	Equal	
	2	3	Left	Simple	
	2	4	Left	Simple	
	3	4	Left	Simple	

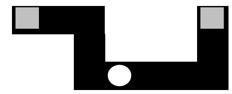
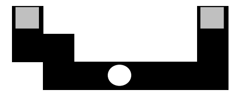
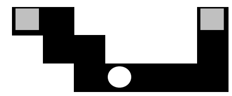
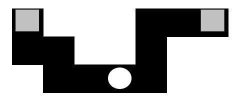
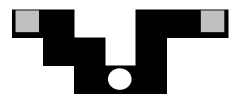
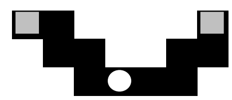
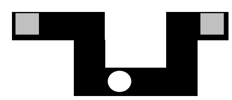
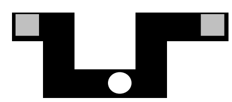
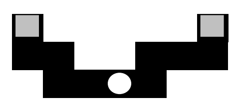
Type	Distance		Correct First Response	Distance Type	Configurations
	Left	Right			
B	4	3	Left	Complex	
	4	2	Left	Complex	
	3	2	Left	Complex	
	2	2	Right	Equal	
	3	3	Right	Equal	
	4	4	Right	Equal	
	2	3	Right	Complex	
	2	4	Right	Complex	
	3	4	Right	Complex	
	4	3	Right	Simple	
	4	2	Right	Simple	
	3	2	Right	Simple	

Appendix D

Experiment 4 Test Configurations

The circles represent the target at the start location and the squares represent the goal locations.

Type	Directional Changes: Left	Directional Changes: Right	Correct First Response	Configurations
	1	1	-	
	1	2	Left	
	1	3	Left	
	1	4	Left	
A	2	2	-	
	2	3	Left	
	2	4	Left	
	3	3	-	
	3	4	Left	
	4	4	-	

Type	Directional Changes		Correct First Response	Configurations
	Left	Right		
A	2	1	Right	
	3	1	Right	
	4	1	Right	
	3	2	Right	
	4	2	Right	
	4	3	Right	
B	2	2	-	
	2	2	-	
	2	2	-	
	2	2	-