Donald A. Riley

ANIMAL COGNITION

A Tribute to Donald A. Riley

Edited by
Thomas R. Zentall
University of Kentucky

LAWRENCE ERLBAUM ASSOCIATES, PUBLISHERS
1993 Hillsdale, New Jersey Hove and London

9 Sequential and Simultaneous Choice Processes in the Radial-Arm Maze

Michael F. Brown
Villanova University

The radial-arm maze (RAM) task, first described by Olton and Samuelson (1976), has come to be an important paradigm for the study of spatial performance in rats. The task involves sampling with replacement from a set of distinct spatial locations, with the contingencies of reinforcement encouraging a single visit to each location. Subjects must discriminate previously visited arms from those that have not yet been visited in order to perform accurately. It is clear that this discrimination involves memory for extramaze visual cues (e.g., Zoladek & Roberts, 1978; Suzuki, Augerinos, & Black, 1980). The properties of this memory have received a great deal of recent experimental and theoretical attention. The present chapter, however, is not directly concerned with the memory aspects of RAM performance. Rather, what follows examines the structure of the decision process that uses memory in order to determine which maze arm is visited during each choice.

At any particular point in the trial, a rat in the center of the RAM must choose one maze arm from among the 8 (or 12 or 17 or *n*) arms. Thus, operationally, the animal is confronted with a simultaneous-choice task. The central thesis of this chapter is that the choice process may not, in fact, be simultaneous in nature, but may be more appropriately described as sequential. That is, as the nervous system of the rat determines which arm is to be visited, multiple arms are not simultaneously considered as a possible choice. Rather, arms are considered independently and sequentially.

SIMULTANEOUS MODELS OF CHOICE AND COGNITIVE MAPS

Although a number of simultaneous models of choice in the RAM could be considered, the one that is focused on here is the theory that performance in the RAM depends on a cognitive map. A cognitive map has been variously defined as (a) a system that "provides the organism with a maplike representation which acts as a framework for organizing its sensory inputs and is perceived as remaining stationary in spite of the movements of the organism" (O'Keefe & Nadel, 1979, p. 488), (b) a "global representation of objects within some manifold or coordinate system from which their mutual spatial relationships can be derived, but that is, to some extent, independent of the objects themselves" (Leonard & McNaughton, 1990, p. 365), and (c) "a record in the central nervous system of macroscopic geometric relations among surfaces in the environment used to plan movements through the environment" (Gallistel, 1990, p. 103). Although there are differences among these various conceptions of cognitive maps, one commonality among them is the idea that the representation guiding behavior is global. When applied to the RAM this means that maze arms are simultaneously represented by the system that determines each choice. A second important defining property of a cognitive map is that it includes the spatial relations among places in the environment.

In the context of the RAM, it is possible that the visited/unvisited status of individual arms might be represented in the medium of a cognitive map and that such a representation might critically determine each arm choice. That is, by consulting a cognitive map that includes the visited/unvisited status of each arm, a rat could determine which arms are possible targets for the next choice. For the present purposes, the critical aspect of this view of choice in the RAM is that information about multiple arms is combined to determine the target of the next arm chosen. Roberts (1984) suggested that a cognitive map may include "markers" that specify the identity of the previously visited arms. According to this view, all maze arms are simultaneously considered as potential choices during at least one stage of the choice process. This view of choice processes in the RAM has been implicit in many, if not most, relevant theoretical discussions.

SEQUENTIAL VIEWS OF SIMULTANEOUS CHOICE

In contrast to the view that potential choices are considered simultaneously is the view that each observable choice is in fact composed of a number of sequential decisions about individual response alternatives. In the RAM, this means that although the rat's task is to choose from among the arms, the process by which this is accomplished involves a series of "yes/no" or "go/no-go" decisions, the

referent of each being an individual maze arm. This conception of choice processes in the RAM was first proposed by Olton (1978).

The idea that choices among simultaneous response alternatives have a microstructure involving decisions about individual response alternatives has a long history in psychological theory, including the notion of "vicarious trial-and-error" in mazes (Muenzinger, 1938; Tolman, 1938). Bower (1959) provided a model of choice in a T-maze that serves as part of the foundation and inspiration for the present analysis. Bower's model assumes that there is an observing response associated with each of the two response alternatives in a T-maze. A subject that is in the observing state associated with one alternative either chooses that alternative or rejects it and enters the observing state associated with the second response alternative. According to the model, subjects are in one of five states during the choice process: a neutral state, in which all subjects are assumed to begin each trial; the observing state associated with the first alternative; choice of the first alternative; the observing state associated with the second alternative; and choice of the second alternative. The relationships among these various states in Bower's "Model B" are illustrated in Fig. 9.1.

A critical aspect of this model for the present purposes is that each response alternative is considered independently. According to the model, choice of a response alternative occurs only when the subject is in the observing state associated with that response alternative. Bower's (1959) model also includes the idea that the choice process is Markovian in nature. This means that the transition probabilities among the states outlined earlier are fixed within each experimental trial. The importance of this is that state-to-state transition probabilities are *path independent*; that is, it does not matter how many times a subject has oriented toward each response alternative, the probability of choosing an alternative, given that orientation to that alternative occurs, is fixed.

Recently, Wright (1991, 1992; Wright & Sands, 1981) developed a model with very similar properties that describes the performance of pigeons in the matching-to-sample procedure. By using a specially constructed apparatus in which pigeons had to make an observable observing response, Wright was able

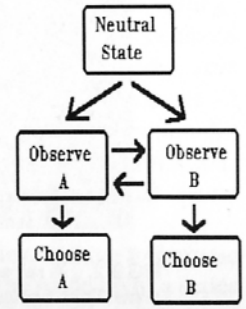

FIG. 9.1. A model of two-alternative choice presented by Bower (1959). A choice begins in a neutral state, from which subjects enter one of two observing states. Choices can be made only from the corresponding observing state. When a choice is rejected, the subject enters the observing state corresponding to the alternative choice (adapted from Bower, 1959).

to specify the frequency of test stimulus observation and the transition probabilities among observing states associated each test stimulus and choice response. Wright provided evidence that these transition probabilities were Markovian in nature. That is, as the pigeon looked back and forth at the available test stimuli, the probability of pecking a test stimulus was independent of the number and nature of previous observing responses; it depended only on the identity of the stimuli. According to this analysis, the information used to determine a choice response is limited to the stimulus currently being observed.

A similar approach to choice behavior was applied to a dolphin by Roitblat, Penner, and Nachtigall (1990). The dolphin was trained to match to sample using three-dimensional shapes as stimuli. Because the dolphin was wearing eyecups and used echolocation in performing this shape discrimination task, it was possible to directly measure the observing responses (ultrasonic emissions) of the dolphin. In contrast to the conclusions of Bower (1959) (regarding rats in a T-maze) and Wright (1991, 1992; Wright & Sands, 1981; regarding pigeons in matching-to-sample), Roitblat et al. argued that the choice behavior of their dolphin was best described by a sequential sampling model that does combine information from separate stimulus observations. This issue of whether or not previous stimulus observations affect choice behavior during an episode of stimulus sampling is returned to later.

CHOICE BEHAVIOR IN THE RAM

Brown and Cook (1986), working in Al Riley's lab, presented an "ethogram" of the behavior of rats in the RAM. In the central arena of the maze, they found the

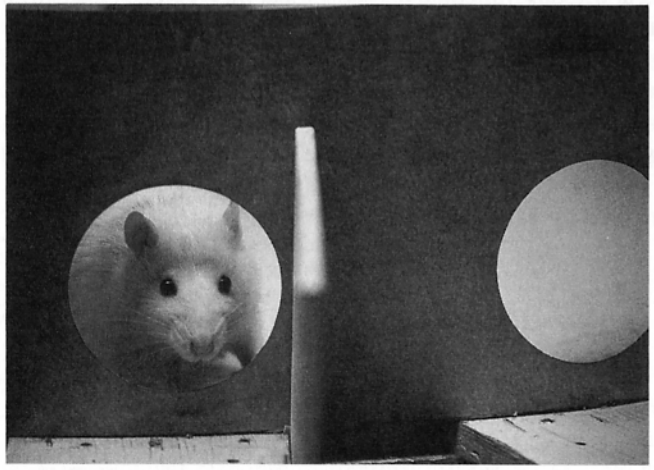

FIG 9.2. A rat engaged in visual orientation toward the end of a maze arm. This behavior is classified as a microchoice in the sequential choice model.

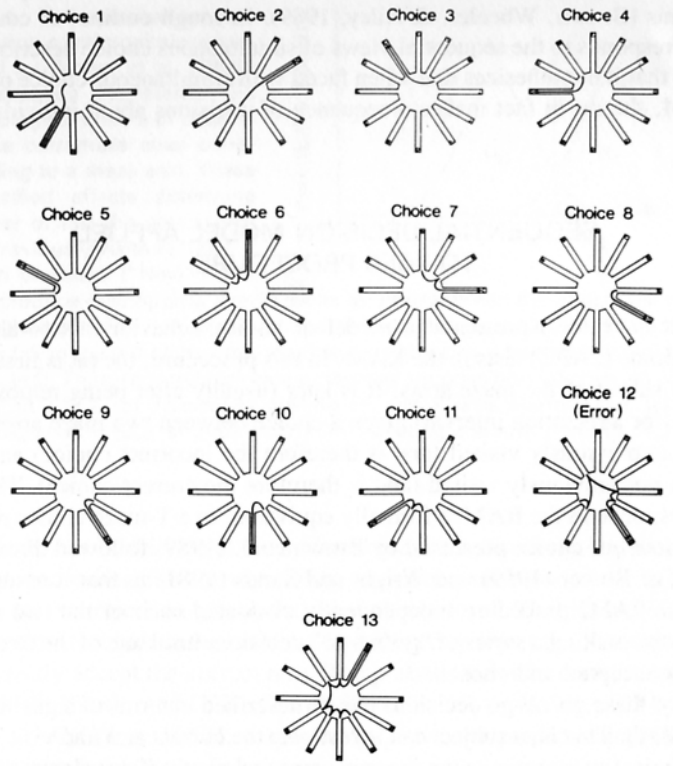

FIG 9.3. The path of a rat during a representative trial in a 12-arm radial maze. Each panel corresponds to an arm visit (macrochoice). Note that, toward the end of the choice sequence, the rat may orient toward several arms prior to visiting one. Such orientations are termed microchoices.

most predominant behavior to be "arm investigation," defined as "actively examining the entrances to the arms. . . ." Many investigators using the RAM have noticed that rats often traverse the perimeter of the central arena, "exploring" maze arms by visually orienting toward the end of the arm. This behavior increases in frequency and duration late in each trial, when most maze arms have been visited (Brown & Cook, 1986). Figure 9.2 depicts a typical instance of orientation toward a maze arm in a standard RAM in my laboratory. Figure 9.3 shows the path of a rat's snout during a representative trial in a 12-arm maze. Each panel shows the behavior leading up to a single choice. Note that the rat orients toward many arms that are not visited.

Observations like these led Evangeline Wheeler, Al Riley, and me to propose that each observable *macrochoice* in the RAM may in fact be made up of a series of *microchoices*, during which go/no-go decisions are made about individual

maze arms (Brown, Wheeler, & Riley, 1989). In rough outline, of course, this view corresponds to the sequential views of simultaneous choice described previously, in that it hypothesizes that when faced with simultaneous choice of arms in the RAM, the rat in fact makes a sequence of decisions about individual maze arms.

SEQUENTIAL DECISION MODEL APPLIED TO 2AFC PROCEDURE

Brown et al. (1989) presented a model of choice behavior in two-alternative forced-choice (2AFC) tests in the RAM. In this procedure, the rat is first allowed to visit a subset of the maze arms. It is later (usually after being removed from the maze for a retention interval) given a choice between two maze arms, one of which was previously visited (and is therefore the incorrect choice) and one of with was not previously visited (and is therefore the correct choice). The 2AFC choice response in the RAM is formally equivalent to a T-maze choice response.

The model of choice presented by Brown et al. (1989) followed directly from the work of Bower (1959) and Wright and Sands (1981) in that it assumed that rats in the 2AFC procedure independently evaluated each of the two response alternatives, making a series of "go/no-go" decisions until one of the two alternatives was accepted and chosen.

Each of these go/no-go decisions can be described in terms of signal detection theory (SDT). That is, a subject can investigate the correct arm and visit it (hit) or reject it (miss) or investigate the incorrect arm and visit it (false alarm) or reject it (correct rejection). These decision processes might be determined by processes corresponding to discriminability and criterion effects. Figure 9.4 illustrates Brown et al.'s (1989) conceptualization of microchoices in these terms. The distribution on the left represents the psychological effects of observing a previously visited maze arm. The distribution on the right represents the effects of observing an unvisited arm. The metric of this scale might be characterized as "familiarity," with values on the left end of the scale corresponding to arms that are highly familiar due to a previous visit. The dotted line represents the choice criterion, according to which the rat classifies an arm as previously visited (and therefore rejects it) or as unvisited (and therefore visits the arm).

It is important to realize that what is being described in SDT terms here are the processes that occur during each microchoice. As Wright (1991) pointed out, the ultimate choice outcome (macrochoice) is not appropriately described in SDT terms. Rather, the predicted macrochoice outcome is determined by the joint probabilities of the relevant microchoice outcomes. To illustrate, if it is assumed that the target of the first microchoice is randomly determined, and therefore is the correct arm on half of the trials and the incorrect arm on half of the trials, then the probability of a correct macrochoice occurring during the first microchoice is

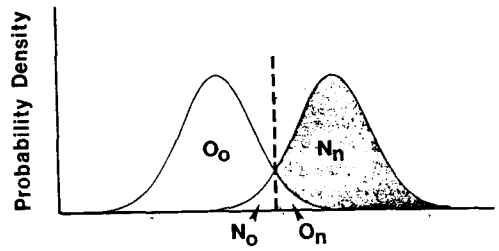

FIG. 9.4. A theoretical conceptualization of microchoices presented by Brown et al. (1989). The abscissa represents the psychological effects of observing the extramaze cues corresponding to a maze arm. These unspecified effects determine whether or not the arm is visited. Previously visited ("Old" = O) and unvisited ("New" = N) arms produce overlapping distributions of effects. When the effects fall to right of the dashed criterion line, the arm is treated as a new arm (i.e., is visited). When the effects fall to the left of the criterion line, then the arm is treated as an old arm (i.e., is rejected). Thus, four microchoice outcomes are possible: (a) correctly visiting an arm ("hit"; N_n), (b) incorrectly visiting an arm ("false alarm"; O_n), (c) correctly rejecting an arm (O_o), and (d) incorrectly rejecting and arm ("miss"; N_o).

$.5H$, where H = the hit rate at the microchoice level. Similarly, the probability of a correct macrochoice occurring during the second microchoice is $.5CH$, where C = the correct rejection rate at the microchoice level. That is, to be correct on the second microchoice, the rat must first correctly reject the incorrect arm and then correctly accept the correct arm. The probabilities of a correct macrochoice on the third, fourth, and fifth microchoices are $.5(1 - H)CH$, $.5C(1 - H)CH$, and $.5(1 - H)C(1 - H)CH$, respectively. Thus, the predicted probability of a correct macrochoice is the infinite sum,

$$.5H + \sum_{n=0}^{\infty} (.5HC^{n+1}(1 - H)^n). \quad (1)$$

Wright (1991) provides a very useful alternative way of illustrating this prediction.

One implication of the work of Brown et al. (1989) is that choice accuracy in 2AFC tests is sensitive to criterion effects, at least under certain conditions. It is commonly assumed by those applying SDT that 2AFC tests allow a pure measure of discriminability, with choice criterion effects being nullified. When stimulus presentation is under experimental control, this is probably true. Specifically, the experimenter can be sure that the subject is exposed to each stimulus for a constant period of time before the choice response occurs. However, when stimulus presentation depends on the choice behavior of the subject, and when that choice behavior is analyzed in the present terms, it can be seen that the choice criterion can have a profound effect on choice accuracy. A rat with a lax choice criterion will tend to choose the first arm (stimulus) it observes (i.e, the probability of a macrochoice during the initial microchoice is high). A rat with a

stricter criterion, on the other hand, will be more likely to observe both arms (i.e., will be likely to make more microchoices) before making a macrochoice. As a result, the rat will be more likely to visit the correct arm. In fact, Brown et al. provided evidence that just such choice criterion differences exist, and that they can, in theory, explain differences in choice accuracy. This finding and one of its implications are discussed in a different context later in this chapter.

SEQUENTIAL DECISION MODEL APPLIED TO FREE-CHOICE PROCEDURE

More recently, Brown (1992) presented a sequential decision model of performance in the standard "free-choice" RAM procedure. The model assumes that choice decisions are made about individual arms and incorporates empirically determined parameters in predicting several aspects of RAM performance. The parameters used by the model are determined by videotaping the behavior of rats in the central arena of a 12-arm RAM. Episodes of visual orientation toward maze arms are coded as microchoices. Specifically, a microchoice is defined as clear orientation toward the end of a maze arm that is either accompanied by a discernible stop in the motion of the rat's body or by a macrochoice. When a microchoice occurs, it results either in a choice of the maze arm (macrochoice) or in an arm rejection. Furthermore, the maze arm either was or was not previously visited. Thus, four classes of microchoice outcomes can be identified: hits, correct rejections, misses, and false alarms. Hit rates and correct rejection rates are determined separately for each correct macrochoice in the choice sequence (i.e., the 1st through 12th correct macrochoice). These microchoice outcomes form the first class of parameters used by the model. The second parameter used by the model has to do with the movement of the rat from microchoice to microchoice. The spatial separation between one microchoice and the next microchoice is coded in terms of the number of arms separating them. This can range from a microchoice to an arm that is adjacent to the arm that was the target of the last microchoice (separation = 1) to a microchoice to an arm that is directly across the central arena from the arm that was the target of the last microchoice (separation = 6). The distribution of these microchoice spatial separations forms the second set of parameters used by the model.

The model is implemented using a Monte Carlo simulation. Figure 9.5 illustrates the algorithm that represents the model and is used by the simulation program. A maze arm is first randomly selected as the target of the first microchoice. This arm is visited with a probability that matches the empirically determined overall hit rate. After either visiting or rejecting the maze arm (as probabilistically determined by the overall hit rate), a second maze arm is selected as the target of a microchoice. The identity of the target maze arm is determined

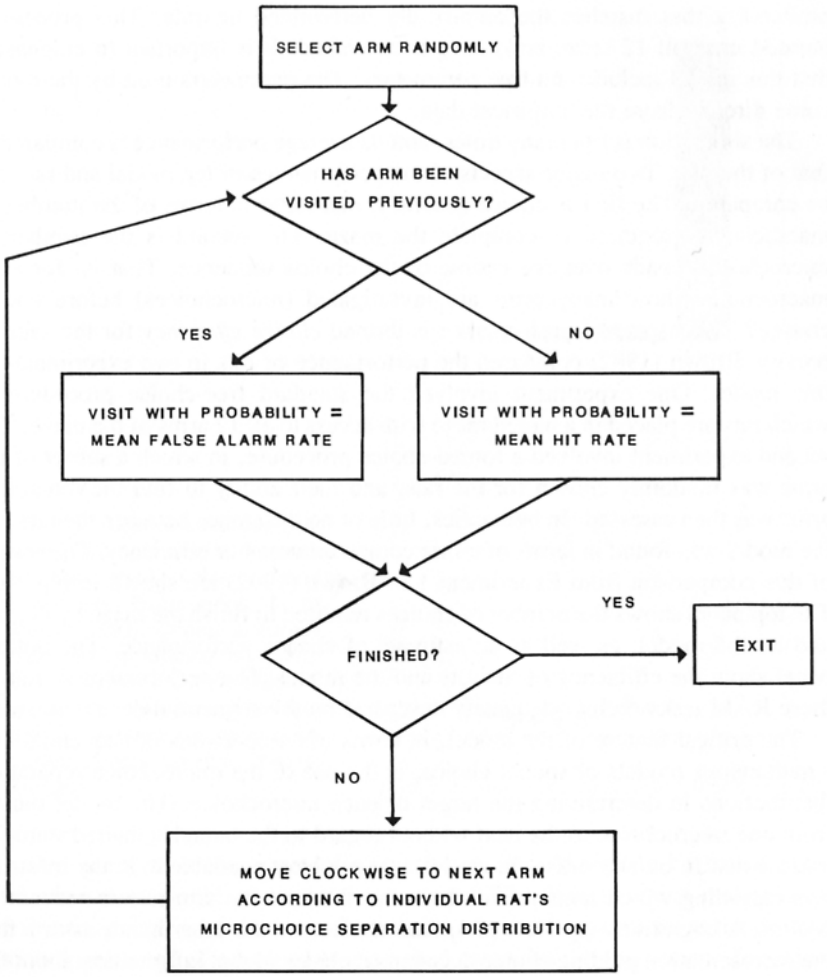

FIG. 9.5. A flow diagram of the algorithm used to implement the sequential choice model.

probabilistically according to the empirically determined microchoice separation distribution of an individual rat. For example, if the target of a microchoice by the rat is adjacent to the target of the last microchoice 75% of the time, then the computer simulation also moves from one maze arm to an adjacent arm 75% of the time as it performs microchoices. If the maze arm so selected was previously visited, then it is visited with a probability that matches the empirically determined false alarm rate. If it was not previously selected, then it is visited with a

probability that matches the empirically determined hit rate. This process is iterated until all 12 maze arms have been visited. It is important to emphasize that this model includes no free parameters. The parameters used by the model come directly from the empirical data.

The simulation is run many times, and its average performance is compared to that of the rats. Two major aspects of the performance of the model and rats can be compared. The first is choice accuracy, measured in terms of the number of macrochoices required to complete the maze. The second is the number of microchoices made over the course of the choice sequence. That is, for each macrochoice, how many arms are investigated (microchoices) before one is chosen? This aspect of performance is termed *choice efficiency* for the sake of brevity. Brown (1992) compared the performance of rats in two experiments to this model. One experiment involved the standard free-choice procedure in which rats are placed in a baited maze with access to all 12 arms of the maze. The second experiment involved a forced-choice procedure, in which a subset of the arms was randomly chosen for the rats, and their ability to find the remaining arms was then assessed. In both cases, little or no difference between the rats and the model was found in terms of either choice accuracy or efficiency. The results of this comparison from Experiment 1 of Brown (1992) are shown in Fig. 9.6. The top panel shows the number of choices required to finish the maze by the rats and by the model, as well as an estimate of chance performance. The bottom panel show the efficiency of the rats and the model. The performance of rats in these RAM tasks seems adequately described by the sequential decision model.

The critical feature of the model, in terms of comparisons of sequential and simultaneous models of spatial choice, is the use of the microchoice separation distributions in determining the target of each microchoice. The model moves from one microchoice to the next without regard to the baited/unbaited status of maze arms. In other words, the model does not have available to it any information regarding which arms remain baited at the time the arm-to-arm movement occurs. A cognitive map view of spatial choice, on the other hand, asserts that the representation guiding choice decisions includes global information about the status of multiple maze arms. If so, one straightforward way in which this information should be expressed is in guiding the rat toward arms that are baited. At the extreme, arm rejections should not occur at all because the decision process guiding behavior should not require the presence of the visual cues corresponding to maze arms. Instead, rats would be expected to travel directly from one chosen arm to the next without having to evaluate the arm and make a choice decision upon exposure to the visual cues corresponding to the arm.

Of course, it is possible that the internal spatial representation (the cognitive map) must be verified or calibrated using extramaze cues. For example, one might expect that this must occur at least once at the beginning of each trial in order to provide the cognitive map with the proper "heading" (Margules & Gallistel, 1988). However, if the cognitive map is of any use in guiding choices

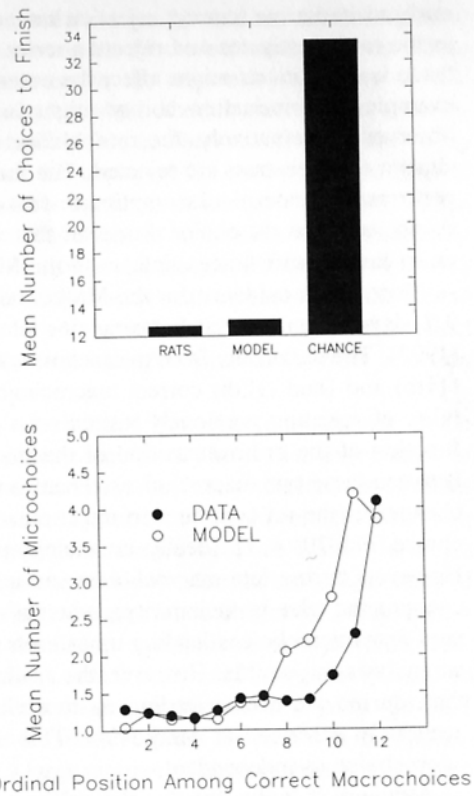

FIG. 9.6. Choice accuracy (top panel) and choice efficiency (bottom panel) of the rats and model in Experiment 1 of Brown (1992). Choice accuracy expected by chance is shown for comparison. Choice efficiency is the number of microchoices leading up to and including each correct macrochoice.

to baited arms, then the target of microchoices should tend to be baited arms more often than would otherwise be expected. The model, which moves from arm to arm according to the same distribution of spatial separations as the rats but without knowledge of which arms are baited, provides the comparison for determining whether this is the case. As indicated earlier, Brown (1992) found little or no difference between the performance of the rats and the model in standard RAM tasks. This indicates that a cognitive map is not necessary to explain accurate and efficient performance in the standard radial-arm maze task.

IS THE CHOICE PROCESS MARKOVIAN?

The sequential model of spatial choice presented by Brown (1992) assumes that the choice process is Markovian within each macrochoice, but not necessarily across macrochoices. That is, between the time that two baited arms are visited, the tendency to visit baited arms (hit rate) and the probability of rejecting previ-

ously visited arms (correct rejection rate) do not change. One might expect that as the rat investigates and rejects a series of arms, information acquired during those investigations might affect the outcome of subsequent investigations. For example, discrimination ability might improve as more extra maze cues are observed. Alternatively, the rats' choice criterion (Brown et al., 1989) might change as maze arms are rejected. The fact that the model successfully predicts performance under the assumption that no such changes occur indicates that they do not, and that the choice processes that occur during the microchoices leading up to each macrochoice conform to the Markovian assumption.

More direct evidence for the Markovian assumption is also available. Figure 9.7 shows data collected during one of the experiments reported by Brown (1992). The data come from microchoices that occurred between the penultimate (11th) and final (12th) correct macrochoice of each session. The mean probability of rejecting previously visited arms (correct rejection rate) is shown as a function of the ordinal position of the microchoice among microchoices made between these two macrochoices. There is no evidence that correct rejection rate changes as the rat continues to reject maze arms leading up to the final macrochoice [$F(5,70) < 1$]. Ideally, an analogous analysis of hit rates should be done. However, during late macrochoices, an insufficient number of baited arms are encountered (due to their rarity), whereas during early macrochoices rats make very few microchoices leading up to each macrochoice. These facts make such an analysis impossible. However, the available data are consistent with the view that, during the events leading up to each macrochoice, the choice process is accurately described as Markovian. This supports the characterization of each microchoice as independent.

Although it looks like the choice process is Markovian within each macrochoice, it is less clear whether and how choice parameters change over the course

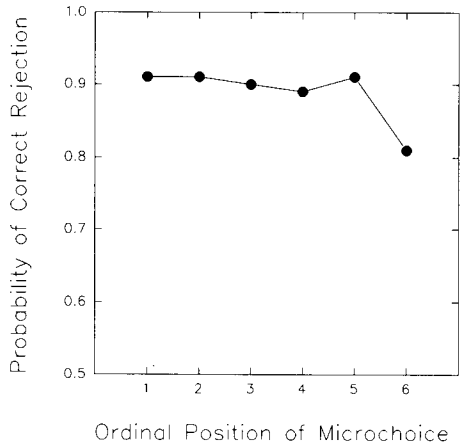

FIG. 9.7. The probability of correctly rejecting arms during microchoices that occur between the 11th and 12th correct macrochoice.

of macrochoices. Brown (1992) measured the mean hit rate and correct rejection rate as a function of ordinal position among the 12 correct macrochoices. These empirical values were used as parameters in the sequential sampling model. Thus, the model makes no assumptions regarding whether microchoice parameters change over the course of macrochoices. In Brown's Experiment 1, no evidence for a change in hit rate over the course of the macrochoice sequence was found. Analysis of correct rejection rates as a function of macrochoice number was not attempted because of the small probability of encountering previously visited arms early in the macrochoice sequence. However, in Brown's Experiment 2, some evidence was obtained that hit rate increases over the course of correct macrochoices. Unfortunately, it is difficult to interpret this effect without being able to perform the corresponding analysis on correct rejection rates.

Some additional data relevant to whether and how choice parameters might change over the course of macrochoices come from the earlier experiment of Brown et al. (1989). They allowed rats to visit a randomly selected set of either 2, 4, 6, 8, or 10 arms in a 12-arm maze, prior to a 15-min retention interval. Upon return to the maze, rats were given a choice between visiting a single available maze arm, or pressing a response manipulandum in the central arena of the maze. If the arm had been in the set of arms visited before the delay, then it was not baited but a response to the center manipulandum was reinforced. However, if the arm had not been visited, then it was baited and a manipulandum response had no effect. Thus, this procedure corresponds to a go/no-go SDT paradigm. Brown et al.'s rats were more likely to press the response manipulandum if the delay occurred following a large number of choices than if it occurred following a small number of choices. This indicated that the choice criterion shifts from a relatively lax state early in the choice sequence to a relatively strict one late in the choice sequence. Data from a more recent unpublished experiment support this conclusion. In this experiment, rats were first allowed to visit 2, 4, 6, 8, or 10 randomly selected maze arms, followed by a 15-min delay. A variety of tests followed the retention interval, but the one of interest for the present purpose was a two-alternative forced-choice (2AFC) test, in which two arms were available, one previously visited and the other not. These two arms were selected so as to be either spatially adjacent or separated by one maze arm. Analysis of videotape was used to measure microchoices to the two available arms. Figure 9.8 shows the number of microchoices that occurred as a function of the number of maze arms that had been visited before the delay. It appears that more microchoices occur when most maze arms had been visited prior to the delay than when few maze arms had been visited. Although this effect is not quite statistically reliable [$F(4, 52) = 2.25$, $.05 < p < .10$], it suggests, in agreement with the earlier data of Brown et al. that the choice criterion becomes more strict as the macrochoice sequence progresses.

Taken together, these data support the assumptions of the model that choice

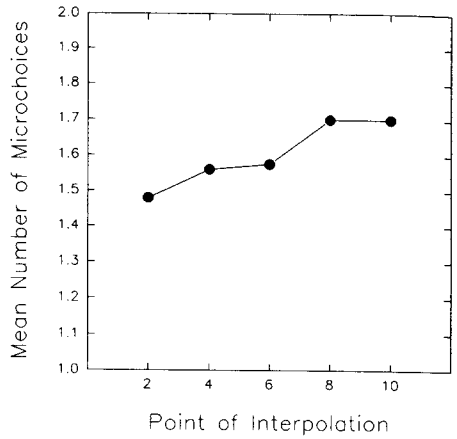

FIG. 9.8. The mean number of microchoices occurring during a two-alternative forced choice test as a function of the number of macrochoices made prior to the test (point of delay interpolation).

processes that occur during each macrochoice are Markovian. The choice parameters guiding behavior (hit rate and correct rejection rate) do not change as maze arms are observed. On the other hand, there is at least some evidence that those same parameters do change over the course of macrochoices. However, the nature of this change is not entirely clear. Data from the go/no-go and 2AFC test procedures indicate a shift in the choice criterion such that arms are less likely to be visited (lower hit rate and higher correct rejection rate) when a larger number of arms have been visited. The data of Brown (1992), however, provide no evidence that this is the case in the standard free-choice procedure. Thus, the resolution of this issue awaits further experimentation.

CONDITIONS UNDER WHICH THE SEQUENTIAL MODEL FAILS

My students and I recently completed a series of experiments similar in design to those of Brown (1992), but in which easy access to the visual cues corresponding to each maze arm is eliminated (Brown, Rish, VonCulin, & Edberg, in press). A door, blocking access to the visual cues, is positioned at the entrance of each maze arm. Furthermore, the central arena of the maze is enclosed by a tall cylinder. Thus, in order to observe the extra maze visual stimuli corresponding to a particular maze arm, the rat must perform an observing response (opening a door). The original purpose of this modification was to provide a more objectively defined microchoice. The act of opening the doors can be unambiguously coded from the videotape records. In the experiments reported by Brown, microchoices were defined by the judgement of coders. Although interrater reliabilities were high, I used the more conservative of the set of ratings obtained for each data set. This means that some microchoices may have been missed using this

measurement technique. If so, these omissions depressed the performance predicted by the model, and thus could account for the small but reliable differences between the observed performance of the rats and that predicted by the model. Thus, we hoped that the doors would provide a better measure of microchoices.

In the first experiment of this series, 10 rats were trained in a standard 12-arm RAM. During the critical test sessions, rats were first allowed to visit a randomly selected set of six maze arms. They were then removed from the maze for 15 min. Upon their return to the maze, there was a door constructed of 47 hanging stands of black hematite beads (4 mm in diameter) at the entrance to each maze arm. The strands of beads covered a circular doorway (7.5 cm in diameter) in a metal wall surrounding the central arena. Furthermore, a black fabric curtain surrounded the central arena above the metal wall. A mirror, used to videotape the behavior of the subjects in the central arena, was located above this curtain. A microchoice was defined as the rat's snout sticking through the bead door.

The data of critical importance were analyzed in the same manner as the data of Brown (1992). That is, the overall hit rate and correct rejection rate as a function of ordinal position in the sequence of correct choices was first determined using the videotape records. In addition, the distribution of spatial separations between microchoices was determined for each individual subject. These two sets of parameters are then incorporated into the model illustrated in Fig. 9.5, and the simulation was run 100 times using the microchoice separation distribution of each rat. The top panel of Fig. 9.9 shows the choice accuracy of the rats and model, as well as an estimate of chance performance for comparison. There is a significant difference between the choice accuracy of the rats and the model, although the magnitude of this difference is small when compared to chance performance. There is also a significant difference between the efficiency of the rats and model, which is illustrated in the bottom panel of Fig. 9.9.

These data appear to render the status of the sequential choice model somewhat ambiguous. The use of the bead doors was designed to improve the measurement of microchoices and possibly eliminate the small but reliable differences in the performance of the model and the rats that were found in the earlier (Brown, 1992) experiments. However, the results of the present experiment replicated the small but reliable differences between the model and the rats in terms of macrochoice accuracy and choice efficiency. One possible interpretation of these results is that, despite our intentions, some visual information might have been available through the bead doors. This possibility was encouraged by the fact that the rats appeared to orient toward bead doors without sticking their snout through the door. To the human eye, there was very little visual information available through the bead doors, although they were not completely opaque. However, given the large differences between human and rat visual ability, and especially given the importance of low spatial frequency information for rats (Birch & Jacobs, 1979), it is possible that useful information was available to the rats without performance of an operationally defined microchoice.

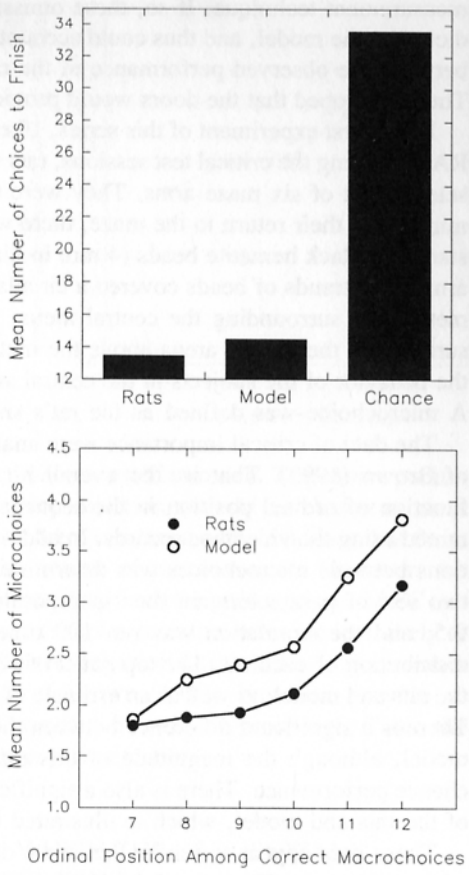

FIG. 9.9. Choice accuracy (top panel) and choice efficiency (bottom panel) of the rats and model when doors constructed of bead strands occlude visual access to the extramaze environment following the sixth macrochoice. Choice accuracy expected by chance is shown for comparison.

Because of this, we designed an improved maze-arm door. These doors were made of plywood (painted black), with a layer of black foam material on the surface facing the central arena. The doors were hinged at the top, so that the rat could push them open (microchoice) and either visit the arm (macrochoice) or reject the arm. Furthermore, to be absolutely sure that no visual information could be obtained through the cylinder that surrounded the central arena, the fabric cylinder was replaced by one made of opaque plastic. Thus, with the exception of the open end of the cylinder (88 cm above the maze surface; mostly taken up by the observation mirror), no visual information entered the central arena of the maze except when a maze door was opened by the rat. Such door openings were defined as microchoices. Figure 9.10 shows the construction of this apparatus.

A second possible explanation for the failure of the sequential choice model to explain performance in the "bead door" experiment is that, although cognitive

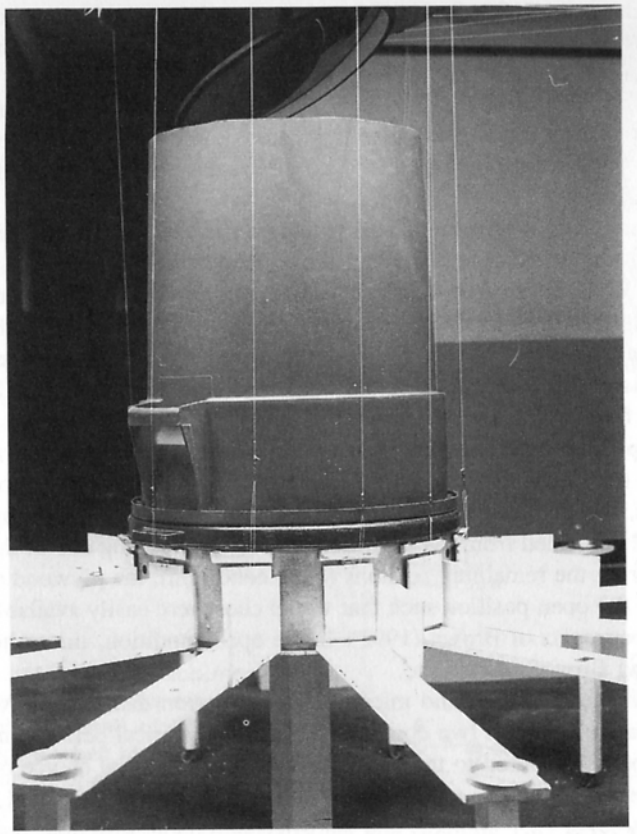

FIG. 9.10. An apparatus in which visual access to the extramaze environment requires pushing open plywood doors, hinged above the entrance to each maze arm.

maps do not to play an important role in the standard radial-arm maze task, they are invoked when easy access to visual cues is not available. In our "bead door" apparatus, rats have access to the visual cues corresponding to maze arms only when they are on the arms of the maze or when they open the door to a maze arm in the central arena. This observing response requires time and effort. Thus, it is possible that use of a cognitive map was not found in the earlier experiments of Brown (1992) even though cognitive maps are, in fact, developed during RAM training. With easy access to visual cues in a relatively undemanding task, a sequential decision process might be used despite the existence of a maplike representation. When easy access to the cues is denied, on the other hand, rats might be encouraged to make use of a cognitive map. This view that a sequential choice process might be only one of several decision processes available to rats

has precedence in Wright's (1992) recent proposal that, in the context of pigeon matching to sample, the Markov decision process should be thought of as the limit approached under most conditions, but from which animals deviate in various ways. It may be that rats in the RAM deviate from the sequential choice process by using a cognitive map to guide choice behavior when observations of the visual cues corresponding to individual maze arms require an effortful observing response.

This possibility was examined using rats that had participated in the bead door experiment described previously and the apparatus described earlier and shown in Fig. 9.10. As in the bead door experiment, the rats were first allowed to visit a randomly selected set of six maze arms and removed from the maze for 15 min. During these predelay forced choices, the cylinder was not in place, allowing free access to the extramaze visual cues from the central arena. During the postdelay free-choice test, the degree of access to the extramaze visual stimuli was manipulated over sessions. During all sessions, the cylinder was in place following the delay. During a randomly selected half of the sessions (closed condition), the plywood doors were closed so that access to extramaze visual cues could be gained from the central arena only by opening one of the plywood doors. During the remaining sessions (open condition), the plywood doors were all held in the open position such that visual cues were easily available as in the earlier experiments of Brown (1992). In the open condition, microchoices were coded using Brown's technique.

Microchoice outcomes and microchoice separation distributions were determined separately for the two conditions, and the empirical performance in each condition was compared to the predictions of the sequential choice model. The primary results are shown in Fig. 9.11. As illustrated in the top panel, there was a relatively large (2.7 choices) and statistically reliable difference between the performance of the rats and the model in the closed condition. However, in the open condition, the difference between predicted and obtained performance (1.1 choices) is not reliable. As shown in the bottom panel, neither condition produced a difference between predicted and obtained choice efficiency. These results confirm the conclusion of Brown (1992) that the sequential choice model provides an accurate description of performance in the standard (open) RAM. However, they also confirm the conclusion from the bead door experiment that the model does not accurately describe performance when access to extramaze visual cues requires an effortful observing response.

The failure of the sequential choice model indicates that, in the closed condition, information about the location of baited arms was available to rats in the central arena prior to observation of extramaze visual cues. We considered the possibility that this information was in the form of intramaze visual, olfactory, or tactile cues. However, the results of a probe test in which the maze was rotated during the delay provided strong evidence against this possibility (Brown et al., in press). Thus, we conclude that this information was in the form of a spatially

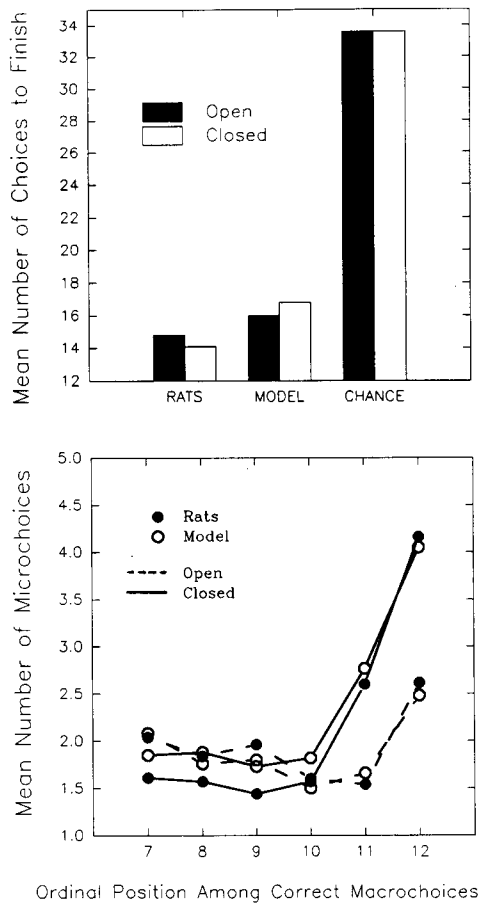

FIG. 9.11. Choice accuracy (top panel) and choice efficiency (bottom panel) of the rats and model when hinged doors constructed of plywood are either open or closed following the sixth macrochoice. Choice accuracy expected by chance is shown for comparison.

organized representation that included the baited versus unbaited status of multiple maze arms. However, this cognitive map was not involved in performance when the maze arm doors were open, allowing easy access to the visual cues corresponding to individual maze-arms. Under those conditions, rats apparently used a sequential decision process to locate baited arms.

SUMMARY AND CONCLUSIONS

Taken as a whole, the work described in this chapter indicates that, at least under the conditions typically used in the radial-arm maze, performance can be adequately described as a sequential choice process, in which each maze arm is independently evaluated and either accepted or rejected. This result may seem at

odds with a number of recent lines of evidence providing support for the existence and use of cognitive maps by rats in spatial tasks, including the radial-arm maze (e.g., Cheng, 1986; Dallal & Meck, 1990; Gallistel, 1990). However, our most recent results suggest that the critical issue may not be the existence of cognitive mapping, but rather the conditions under which cognitive maps are utilized. Under relatively undemanding conditions, such as the standard radial-arm maze task, rats apparently do not to make use of cognitive maps, but instead use a (simpler?) sequential choice process. More demanding tasks, however, may elicit the use of more sophisticated choice processes, perhaps including the use of cognitive mapping. The modeling approach outlined in the present chapter promises to help elucidate these issues.

ACKNOWLEDGMENTS

This work was supported by National Institute of Mental Health Grant MH45004. The author gratefully acknowledges the participation of Jackie Edberg, Patti Rish, and Joanna VonCulin in the unpublished work described in this chapter and thanks Ken Cheng, Bill Roberts, Tony Wright, and Tom Zentall for helpful comments on earlier versions of the manuscript or the ideas contained therein.

REFERENCES

Birch, D., & Jacobs, G. H. (1979). Spatial contrast sensitivity in albino and pigmented rats. *Vision Research, 19*, 933–937.

Bower, G. H. (1959). Choice point behavior. In R. R. Bush & W. K. Estes (Eds.), *Studies in mathematical learning theory* (pp. (pp. 109–124). Stanford, CA: Stanford University Press.

Brown, M. F. (1992). Does a cognitive map guide choices in the radial-arm maze? *Journal of Experimental Psychology: Animal Behavior Processes, 18*, 56–66.

Brown, M. F., & Cook, R. G. (1986). Within-trial dynamics of radial maze performance in rats. *Learning and Motivation, 17*, 190–205.

Brown, M. F., Rish, P. A., VonCulin, J. E., & Edberg, J. (in press). Spatial guidance of choice behavior in the radial-arm maze. *Journal of Experimental Psychology: Animal Behavior Processes.*

Brown, M. F., Wheeler, E. A., & Riley, D. A. (1989). Evidence for a shift in the choice criterion of rats in a 12-arm radial maze. *Animal Learning and Behavior, 17*, 12–20.

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23*, 149–178.

Dallal, N. L., & Meck, W. H. (1990). Hierarchical structures: Chunking by food type facilitates spatial memory. *Journal of Experimental Psychology: Animal Behavior Processes, 16*, 69–84.

Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT. Press.

Leonard, B., & McNaughton, B. L. (1990). Spatial representation in the rat: Conceptual, behavioral, and neurophysiological perspectives. In R. P. Kesner & D. S. Olton (Eds.), *Neurobiology of comparative cognition* (pp. 363–422). Hillsdale, NJ: Lawrence Erlbaum Associates.

Margules, J., & Gallistel, C. R. (1988). Heading in the rat: Determination by environmental shape. *Animal Learning and Behavior, 16*, 404–410.

Muenzinger, K. F. (1938). Vicarious trial and error at a point of choice: 1. A general survey of its relation to learning efficiency. *Journal of Genetic Psychology, 53*, 75–86.

O'Keefe, J., & Nadel, L. (1979). Precis of O'Keefe & Nadel's *The hippocampus as a cognitive map. The Behavioral and Brain Sciences, 2*, 487–533.

Olton, D. S. (1978). Characteristics of spatial memory. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Olton, D. S., & Samuelson, R. J. (1976). Remembrance of places past: Spatial memory in rats. *Journal of Experimental Psychology: Animal Behavior Processes, 2*, 97–116.

Roberts, W. A. (1984). Some issues in animal spatial memory. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), *Animal cognition* (pp. 425–443). Hillsdale, NJ: Lawrence Erlbaum Associates.

Roitblat, H. L., Penner, R. H., & Nachtigall, P. E. (1990). Matching-to-sample by an echolocating dolphin (*Tursiops truncatus*). *Journal of Experimental Psychology: Animal Behavior Processes, 16*, 85–95.

Suzuki, S., Augerinos, G., & Black, A. H. (1980). Stimulus control of spatial behavior on the eight-arm maze in rats. *Learning and Motivation, 11*, 1–18.

Tolman, E. C. (1938). The determiners of behavior at a choice point. *Psychological Review, 45*, 1–41.

Wright, A. A. (1991). A detection and decision process model of matching to sample. In M. L. Commons, J. A. Nevin, & M. C. Davison (Eds.), *Signal detection: Mechanisms, models, and applications* (pp. 191–219). Hillsdale, NJ: Lawrence Erlbaum Associates.

Wright, A. A. (1992). Learning mechanisms in matching to sample. *Journal of Experimental Psychology: Animal Behavior Processes, 18*, 67–79.

Wright, A. A., & Sands, S. F. (1981). A model of detection and decision processes during matching to sample by pigeons: Performance with 88 different wavelengths in delayed and simultaneous matching tasks. *Journal of Experimental Psychology: Animal Behavior Processes, 7*, 191–216.

Zoladek, L., & Roberts, W. A. (1978). The sensory basis of spatial memory in the rat. *Animal Learning and Behavior, 6*, 77–81.