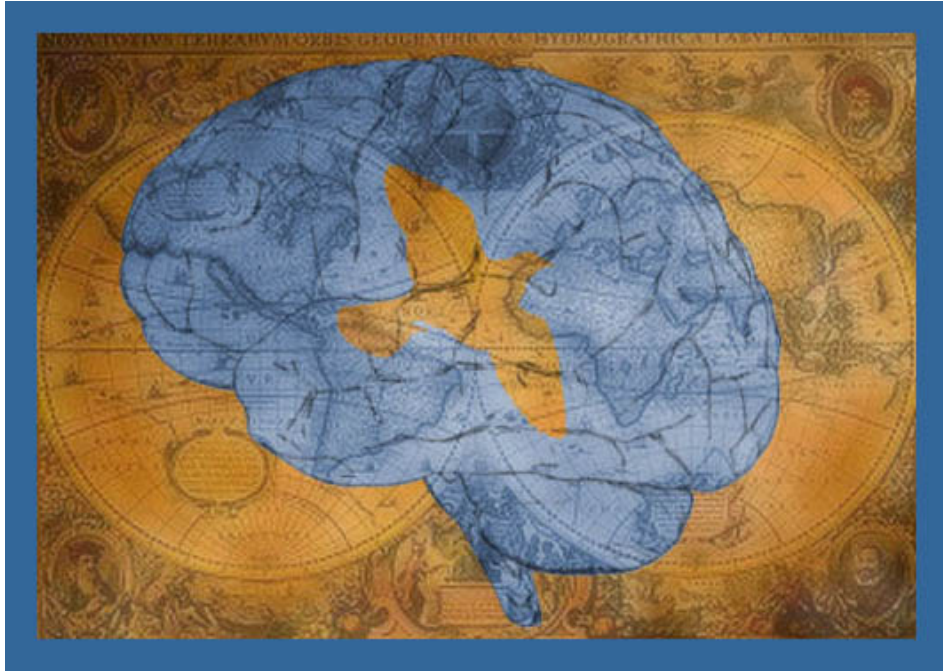


The following is a PDF copy of a chapter from this cyberbook
Not all elements of the chapter are available in PDF format
Please view the cyberbook in its online format to view all elements



Animal Spatial Cognition:

Comparative, Neural & Computational Approaches

Edited and Published by

Michael F. Brown
Department of Psychology
Villanova University

and

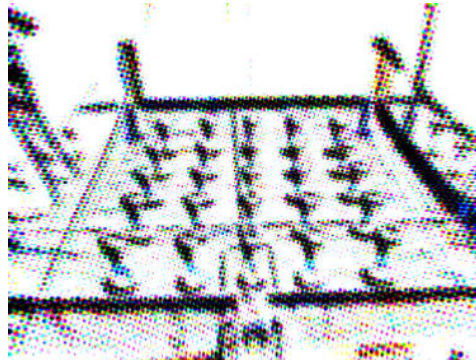
Robert G. Cook
Department of Psychology
Tufts University

In cooperation with Comparative Cognition Press
of the [Comparative Cognition Society](#)
October, 2006

This Cyberbook is Available to All at
www.comparativecognition.org
or
www.pigeon.psy.tufts.edu/asc



Abstracting Spatial Relations Among Goal Locations



[Michael Brown](#)
Villanova University

Abstract

Choices can be controlled by a spatial pattern among goal locations that does not correspond to any perceptual cues. The relationship between this form of spatial learning and other, more well understood, forms of spatial learning is described. The evidence for spatial pattern learning is reviewed and some possible mechanisms are discussed.

Chapter Outline and Navigation

- I. [Introduction](#)
- II. [Varieties of Spatial Learning](#)
- III. [Spatial Pattern Learning in the Pole Box](#)
 - [Control by a square pattern](#)
 - [Control by a linear pattern](#)
 - [Control by a checkerboard pattern](#)
- IV. [How is Spatial Pattern Learned and How is it Used?](#)
- V. [References](#)

I. Introduction

Learning can be defined and understood as the processes that allow animals to detect systematic relations among events in their world. For example, events are often correlated because of the causal relations among them. Thunder consistently follows lightning and the expectation of hearing thunder that occurs when one sees a flash of lightning is an example of classical conditioning - the well-studied and ubiquitous learning process that allows animals to detect systematic relations among the occurrence of two (or more) kinds of events. Another very well-studied kind of systematic relation among events is the fact that particular behaviors are reliably followed by particular events, usually because the behavior is the cause of the event. For example, a rat for whom food is programmed to reliably follow the pressing of a lever in a Skinner Box soon learns to press the lever. This learning about the systematic relation between one's own behavior and its outcomes, of course, is instrumental conditioning. These forms of associative learning have been described as the means by which the nervous system detects systematic patterns in the relations among event occurrences (e.g., Dickinson, 1980).

But relations among the occurrence of events is not the only sort of relations among events that exist. At least three other kinds of relations among events have been shown to support learning (Table 1). If there is a sequential relationship among events presented in a series, animals come to be controlled by that relationship. For example, if a rat is presented with a series of trials in which the number of pellets provided as reinforcement systematically increases (or decreases) over the trial series, running speed systematically increases (or decreases) over the trial series (e.g., Capaldi, Blitzer, & Molina, 1979; Hulse & Dorsky, 1980). It has been argued that this control is produced by a learning process that represents the sequential relationship among the events, in this case by representing the systematic increase (or decrease) in reward magnitude (Hulse, 1978).

Learning processes that are sensitive to temporal relations among events have received a great deal of experimental and theoretical attention. The study of animals exposed to events that are systematically separated in time by intervals on the order of seconds to minutes has led to well developed theories of learning systems specialized for learning about the temporal relations among events (see Church, 2002 for a review).

Table 1: Proposed Relational Learning Processes		
Learning Process	Type of Relation	Example
Classical Conditioning	Correlation Among Event Occurrences	One event (e.g., bell) consistently followed by a second event (e.g., food)
Instrumental Conditioning	Correlation Between Behavior and Event	Behavior (e.g., lever press) consistently followed by event (e.g., food pellet)
Serial Learning	Ordered Change in Event Property	Increase in Reinforcement Magnitude Over Trials
Interval Timing	Systematic Temporal Interval Between Events	Reinforcement Available on a Fixed Interval Schedule
Spatial Pattern Learning	Systematic Spatial Relations Among Events	Reinforcement Arranged in a Consistent Spatial Pattern

This cyber-chapter is about the means and mechanisms by which *spatial* relations are learned. The focus is on a series of experiments that attempt to isolate learning about the spatial relations among locations and the control of behavior by those relations.

Two illustrations of the Pole Box apparatus used in our spatial pattern learning experiments are shown below (Figure 1A, 1B). Poles are equally spaced, with separations in different versions of the apparatus ranging from 12 cm to 21 cm. The poles are arranged in a matrix - we have used apparatus with 4 X 4, 5 X 5, and 4 X 5 matrixes of poles. There is a well on top of each pole, in which a pellet (or other small food item) can be hidden. In the critical conditions of our experiments, the location of the baited poles varies unpredictably from trial to trial. Nevertheless, the baited poles form a consistent spatial pattern over trials. Figure 1C shows one exemplar of each of three spatial patterns for which we have evidence of behavioral control and, by inference, of spatial pattern learning. Spatial pattern learning can be contrasted with other forms of spatial learning that have been described, as outlined in [Part II: Varieties of Spatial Learning](#) of this cyberchapter. The evidence for control by the square (top panel), line (middle panel), and checkerboard (bottom panel) patterns is reviewed in [Part III: Spatial Pattern Learning in the Pole Box](#).

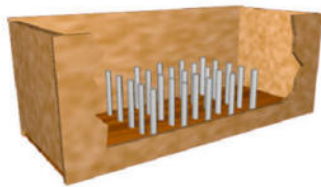


Figure 1A. Drawing of 5 X 5 Pole Box apparatus (front wall cutaway for illustration purposes). (Drawing by Morgan Terrinoni)



Figure 1B. Photograph of 5 X 5 Pole Box apparatus

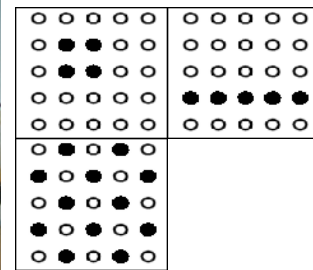


Figure 1C. Exemplars of three spatial patterns used in experiments with the poles box (Left: one of 16 possible exemplars of the square pattern; Right: one of eight possible exemplars of the line patterns; Bottom: one of two possible exemplars of the checkerboard pattern)

II. Varieties of Spatial Learning

"Of all the constraints on nature, the most far reaching are imposed by space. For space itself has a structure that influences the shape of every existing thing."
(Stevens, 1974)

Tolman's (1948) original construct of a cognitive map regained influence with the publication of O'Keefe and Nadel's (1978) *The Hippocampus as a Cognitive Map*. O'Keefe and Nadel argued that the hippocampus is the site of spatial representations and that information stored by the hippocampus includes the spatial relations among locations in familiar environments. Publication of this work marked the beginning of a wave of experimental and theoretical work aimed at understanding the physiological and cognitive mechanisms of spatial learning and memory.

Several mechanisms have since been identified that allow animals to navigate accurately in two-dimensional and three-dimensional space. A relatively simple mechanism is often referred to as **beacon homing** (Gallistel, 1990). A beacon is a perceived landmark (visual, auditory, or chemical cue). Beacon homing is simply moving toward a beacon (Figure 2A). Of course, moving toward a beacon is not a trivial problem - there must be some means of determining when one is moving toward the beacon. An increase in the apparent size of the perceived beacon, for example, has been identified as a mechanism by which some animals used visual stimuli as beacons. Detecting an increase in the concentration of a chemical is a cue that can be used to detect the source of a chemical through beacon homing; it is used by many animals to find food.

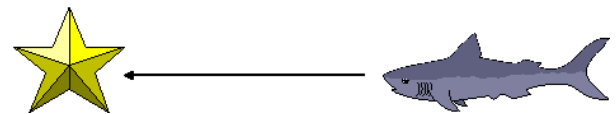


Figure 2A. Beacon homing. Animal moves toward (or away from) a perceived, localized cue.

Beacon homing allows animals to locate a place, as long as there is a perceivable cue coincident with the goal location. When cues are present, but not coincident with the goal location, many animals are able to **pilot** to a goal location using landmarks that have a consistent spatial relation to the goal location and to each other (Gallistel, 1990). In order to do so, the animal must have learned the spatial relations among the landmarks and goal location(s) (Figure 2B). Such learned spatial relations correspond closely to the cognitive mapping process that Tolman described.

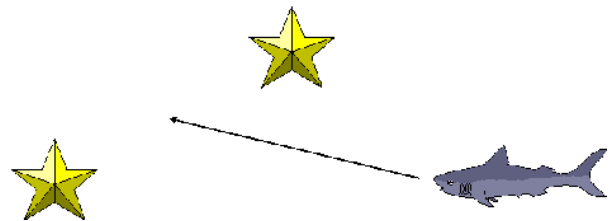


Figure 2B. Piloting. Animal moves toward (or away from) a location defined by its spatial relations to perceived, localized cue(s).

Cheng (1986) first proposed that a global spatial frame, within which the goal location(s) is consistently located, can serve as learned spatial cues. The evidence for this view is described by [Cheng and Newcombe](#) elsewhere in this book. The evidence indicates that animals acquire a representation of the spatial properties of the global space in which they search for food (e.g., a rectangular arena). The representation includes the location of the goal(s) within that spatial framework. The location of a food site or other important place is coded in terms of its spatial relation position within the represented spatial frame. Cheng argued that this process constitutes

a **geometric module** which functions somewhat independently of other forms of spatial control. In Figure 2C, an animal is navigating with a rectangular area (represented by the orange rectangle surrounding the shark). A cognitive representation of the geometric properties of the area is represented by the orange rectangle inside the animal.

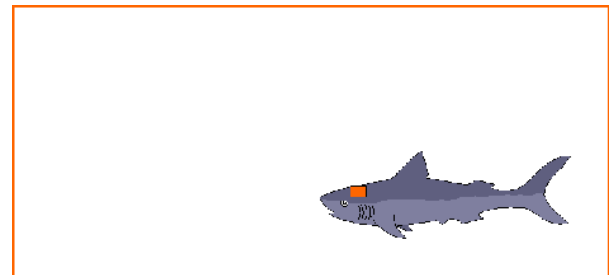


Figure 2C. Control by geometry. Animal moves with reference to the perceived shape of a space (or a perceived cue that is determined by the shape of the space (see Cheng, this volume).

Beacon homing, landmark use, and control by geometry all rely on the presence of perceived visual (or auditory or chemical) cues. In contrast, the spatial pattern learning that is the subject of the present chapter occurs in the absence of perceivable cues. Rather, the context of the spatial pattern learning that we have studied is the configuration of hidden food locations. No beacons or landmarks correspond to the correct food locations. In our experiments, rats are foraging in a rectangular arena, similar to the ones used by Cheng (1986). However, the food locations on any particular trial are not predictable in terms of location within the arena. Thus, beacons, landmarks and geometric cues can not be involved in the ability of rats to find the baited poles in the pole box task.

Another mechanism known to be involved in animal navigation is **dead reckoning** (also known as **path integration**). Internal movement cues (provided primarily by the vestibular system) allow the animal to integrate its position in space relative to a starting point (Biegler, 2000; Collett, Collett, Bisch, & Wehner, 1998; Etienne, Berlie, Georgakopoulos, & Maurer, 1998; Mittelstaedt & Mittelstaedt, 1980; Wehner & Srinivasan, 1981). Thus, when an animal moves a given distance and direction (indicated by the arrow behind the animal, Figure 2D), the vestibular system provides information about the distance and direction moved (relative to a starting location). There is abundant evidence that this information allows the animal to find its way back to the starting location. It has been argued (e.g., Gallistel, 1991) that this ability is mediated by a representation that has the form of a vector coding the distance and direction to the starting location (indicated by the arrow in the animal's head below). This vector is continuously updated as the animal moves. In the pole box task, the baited locations have consistent spatial relations with each other. Thus, it is possible that dead reckoning could be involved in the mechanism by which those relations are learned.

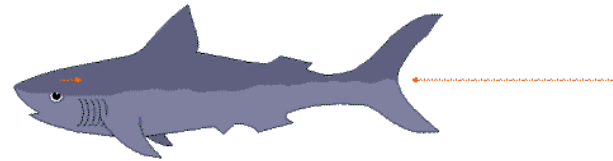


Figure 2D. Dead Reckoning. Animal moves according to internal cues that are determined by the direction and distance of its recent movement (e.g., vestibular cues).

III. Spatial Pattern Learning in the Pole Box

3.1 Control by a Square Pattern

Brown and Terroni (1996) reported the first evidence for control by a spatial pattern of baited poles. In a 4 X 4 pole box, one of nine possible 2 X 2 square arrangements of four baited poles was available on each daily trial. Figure 3A illustrates the critical fact that, over trials, the identity of the baited poles was unpredictable prior to each trial, but the baited poles were consistently arranged in the square pattern.

The video to the right (Figure 3B) shows a typical trial in the 4 X 4 pole box apparatus, after some exposure to a square pattern. The baited poles during this sample trial are indicated by the red rings (superimposed on the video for illustration purposes).

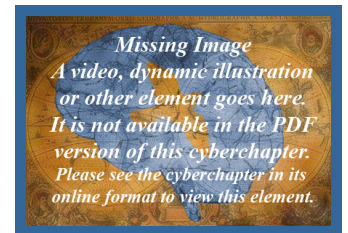


Figure 3A. The pattern exemplar changes unpredictably from trial to trial. (Animation will show a sequence of examples)

As this sample trial suggests, rats come to be controlled to some extent by the consistent spatial arrangement of the baited poles. Prior to each, the location of the baited poles is unpredictable unless, of course, the rats can perceptually detect them - using odor cues, for example. We have consistently found in all of our pole box experiment that, in fact, the rats are no more likely to choose a baited pole than would be expected on the basis of chance. Thus, the rats are not locating the baited poles using odor or any other perceptual cues.

If a rat learned that the baited poles are arranged in a 2 X 2 square pattern, then the discovery of one or more baited poles might be expected to provide information about the location of the remaining baited poles. In particular, after the discovery of one baited pole (indicated by the black circle in Figure 3C, left panel), the square pattern indicates that the remaining three baited poles must be among the eight nearby poles (indicated by the yellow circles).

After the discovery of two adjacent baited poles (Figure 3C, center panel), the square pattern indicates that the remaining two baited poles must be one of two adjacent pairs of poles (indicated by the yellow circles). And after three baited poles have been discovered (Figure 3C, right panel), the the location of the one remaining baited pole is completely determined.

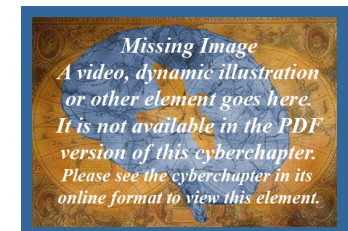


Figure 3B. Video example of pole box trial.

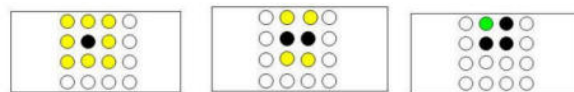


Figure 3C. Logic of control by a square pattern. Black circles represent discovered baited poles. Yellow circles represent poles that may be baited, given location of discovered baited poles. Green circles represent poles that must be baited, given location of discovered baited poles.

The clearest evidence for behavioral control by the square pattern comes from an analysis of the choices that immediately follow the discovery of the second and third baited poles. Following the second discovery of the baited pole (marked "2" in Figure 4), is the rat relatively more likely to next choose a pole that conforms to the pattern (i.e., the two poles marked "S")? An accurate assessment of such control by the pattern requires that two other factors affecting pole choices be considered. First, there is a strong tendency to choose poles that are spatially proximal to the most recently chosen pole. Thus, the analysis compares choice of poles that conform to the pattern ("S" poles in the figure) to choice of poles that are also adjacent to the most recent choice but do not conform to the pattern (the "X" pole in the figure). Also, rats may have a tendency to avoid revisits to poles chosen earlier in the trial, just as they avoid revisits to maze arms in a radial-arm maze (Olton & Samuelson, 1976). In fact, it is clear that rats are able to avoid pole revisits in the pole box task, albeit to a much lesser extent than they avoid revisits of maze arms in the radial-arm maze. To control for any possible confounding of control by the pattern with control by previous pole visits, only initial visits to poles are included in the analysis (i.e., revisits of poles are not included in the analysis).

Figure 5 shows the results of this analysis in the experiment reported by Brown and Terrinoni (1996) in which rats were exposed to a square pattern for 120 daily trials. The empirical results, shown in blue, are in terms of the proportion of choices made immediately following the discovery of a second baited pole and to a previously unvisited and spatially adjacent pole which were to a pole consistent with the square pattern (i.e., choices to poles represented by the "S" poles in Figure 4). These data can be compared to the proportion that would be expected on the basis of chance, shown in red. This proportion is given by the proportion of previously unvisited and spatially adjacent poles that were consistent with the pattern.

So, in the example trial above, the Proportion Expected is:
 $2 \text{ ("S" poles)} / 3 \text{ ("S" poles} + \text{"X" poles, assuming that none of them have been previously visited during the trial)} = .67$

Note that the expected proportion is affected by the number of adjacent poles that have been previously visited during the trial and by the location of the square exemplar on any given trial (i.e., whether the square is in the center, edge, or corner of the pole box matrix). The proportions obtained and expected were calculated for each rat during each trial block. The rats chose poles that were consistent with the square pattern more often than expected by chance, and this difference increased over the three trial blocks.

Choices following the third discovery of a baited pole were analyzed separately in a directly analogous manner. Figure 6 shows an example of the possibilities for choices included in the analysis following discovery of the third baited pole. In this case, there is always exactly one pole consistent with the pattern (i.e., the remaining baited pole) and up to two choices that would be inconsistent with the pattern.

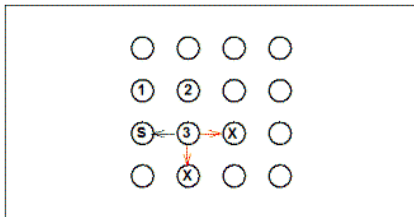


Figure 6. Logic of the Brown and Terrinoni analysis of choice conformity to the square pattern following discovery of a third baited pole. 1 = first baited pole chosen during trial; 2 = second baited pole chosen during trial; 3 = third baited pole chosen during trial; S = poles adjacent to the third baited pole chosen that conform to the square pattern; X = poles adjacent to the third baited pole that do not conform to the square pattern. Green arrows show conforming moves and red arrows show non-conforming moves. The analysis compares the proportion of moves conforming to the pattern to the proportion expected on the basis of chance, based on these values for each rat cumulated over trials.

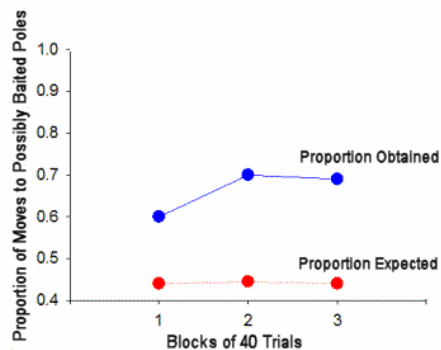


Figure 7. The proportion of choices following discovery of a third baited pole that conformed to the square pattern was greater than the proportion expected on the basis of chance. The difference between empirical and expected performance increased over trial blocks.

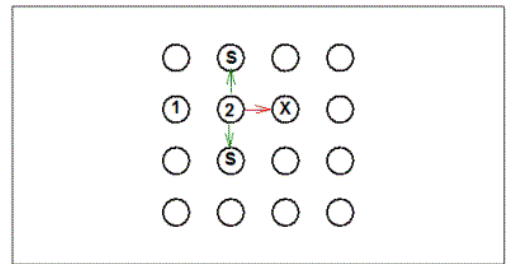


Figure 4. Logic of the Brown and Terrinoni analysis of choice conformity to the square pattern following discovery of a second baited pole. 1 = first baited pole chosen during trial; 2 = second baited pole chosen during trial; S = poles adjacent to the second baited pole chosen that conform to the square pattern; X = poles adjacent to the second baited pole that do not conform to the square pattern. Green arrows show conforming moves and red arrows show non-conforming moves. The analysis compares the proportion of moves conforming to the pattern to the proportion expected on the basis of chance, based on these values for each rat cumulated over trials.

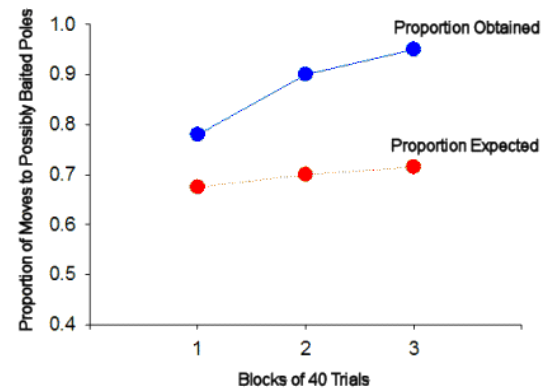


Figure 5. The proportion of choices following discovery of a second baited pole that conformed to the square pattern was greater than the proportion expected on the basis of chance. The difference between empirical and expected performance increased over trial blocks.

The obtained and expected proportions of choices made that were consistent with the pattern in Brown and Terrinoni's experiment are shown in Figure 7. Again, rats chose poles consistent with the square pattern more often than would be expected on the basis of chance and the tendency to do so increased over the course of the experiment.

We have replicated Brown and Terrinoni's evidence that choices come to be controlled by a square pattern of baited poles several times (Brown, Yang, & DiGian, 2002; DiGian, 2002; Lebowitz & Brown, 1999; Wintersteen, 2003).

One important detail in all of these experiments is that we use several methodological and analytic techniques to be sure that the choice of baited poles can not be explained by any perceivable cue. The most obvious possibility is that the rats can use odor to locate baited poles. In all of our recent experiments, we use poles that include a "sham" bait pellet. The structure of these poles is shown in Figure 8.



Figure 8. Outer sleeve of pole (being held) and inner core (to right). Sham pellet (on every pole) is placed in well at top of inner core. Baited poles have a second (accessible) pellet in the well at top of sleeve.

Each pole is constructed with an inner core of dowel. A single "sham" pellet is hidden in a well drilled in the top of the pole. The core is covered by a sleeve made of PVC (removed from the core for purposes of this illustration). The top of the sleeve includes a well in which a single pellet can be hidden when the pole is baited. The floor of the well is nylon mesh material. Thus, any odor from the 45 mg sucrose pellets is present in every pole. However, only the baited poles contain a pellet that is accessible to the rat. The second means of determining whether odor or any other perceptual cues play a role in locating the baited poles is to examine rats' ability to locate the first baited pole discovered during each trial. Because the location of the baited poles varies unpredictably from trial to trial, the ability to locate the baited poles should be no more accurate than expected on the basis of chance - unless the rats can detect the pellets perceptually.

We have examined this aspect of performance in each of the experiments we have done using the pole box apparatus. We have not found any evidence that rats locate the first baited pole any better than would be expected on the basis of chance. (See Lebowitz & Brown (1999) for a discussion of some of the complexities involved in this measure.) Thus, the ability of rats to locate additional baited poles after discovering the location of one baited pole must be based on learning the pattern.

3.2 Control by a Linear Pattern

In several experiments, we have shown that choices can also be controlled by a linear pattern of baited poles. In some of these experiments, the baited poles form *either* one row or one column of the pole matrix (Brown & Terrinoni, 1996; Brown, DiGello, Milewski, Wilson, & Kozak, 2000). In others, the baited poles form a linear pattern with the same orientation on every trial, but a different row of the matrix (DiGello, Brown, & Affuso, 2002; DiGian, 2002). This latter version of a linear pattern is illustrated in Figure 9.

The video in Figure 10 shows a trial in the experiment of DiGello, et al. (2002). One of the four rows of poles is baited on each trial. The baited poles on this sample trial are the four poles in the row adjacent to the wall of the pole box that cuts across the lower right corner of video (indicated by the green arrows superimposed on the video). Those four poles are baited on 25% of the trials, with each of the three parallel rows of poles also being baited on 25% of the trials.

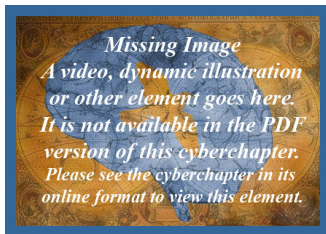


Figure 10. Video of trial in experiment using the row pattern. The poles baited on this example trial are indicated by the green arrows.

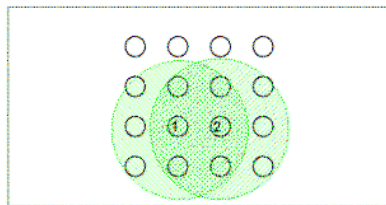


Figure 11. Explanation for control by a square pattern in terms of overlap of spatial generalization gradients around the previously discovered poles. In this case the gradients produced by two baited poles discovered earlier in the trial overlap at the location of poles that conform to the square pattern, but not at the location of poles that do not.

Two features of the linear pattern are particularly interesting for our understanding of pattern learning. First, an alternative explanation for control by the square pattern involves spatial gradients of generalized excitation surrounding baited poles that have been discovered. That is, when a rat finds a baited pole, perhaps the area surrounding the pole increases in attractiveness - a form of generalization.

Figure 11 illustrates how two overlapping gradients of excitation (represented by the green areas) centered on two previously discovered baited poles can result in more generalized excitation to poles that are consistent with the square pattern (i.e., the poles above and below the previously discovered baited poles) than to adjacent poles not consistent with the pattern (i.e., the pole to the right of the 2nd discovered pole). Thus, control by the square pattern could be explained by generalization. A line pattern, however, requires that rats make choices that are inconsistent with generalization. Thus, control by the line pattern rules out a general explanation of control by spatial patterns in terms of generalization.

The second important feature of the the row pattern is the fact that locating an unbaited pole (as well as locating a baited pole) provides potential information - if one pole in a row is not baited, then none of the poles in that row are baited. We have shown that rats' choices are controlled by this contingency (DiGello et al., 2002).

DiGello, et al. tested rats in a 4 X 4 pole box in which one of four columns of poles was baited on each trial, as in the video in Figure 10. If a rat has discovered one or more baited poles (e.g., the pole indicated in black in Figure 12A), then the remaining baited poles are determined - they are the other poles in the same column (e.g., the poles indicated in yellow).

If a rat chooses a pole and that pole is **not** baited (e.g., the pole indicated in green in Figure 12B), then none of the remaining three poles in that column are baited, and the baited poles are in one of the three remaining columns. Thus, although determining that a pole is not baited does not provide as much information as discovering a baited pole, it does narrow down the possibilities. DiGello, et al. (2002) showed that rats come to be controlled by both sources of information. They acquire both a tendency to choose poles in the same column after choosing a baited pole and a tendency to choose poles in a **different** column after choosing an unbaited pole.



Figure 12. (A) Positive information provided by choice of a baited pole when a column pattern is in force. When a baited pole is chosen (black circle), the remaining baited poles (yellow) are in the same column. (B) Negative information provided by discovery of an unbaited pole when a column pattern is in force. When an unbaited pole is chosen (green circle), the remaining poles in that column are not baited (unfilled circles) and the baited poles are in one of the three other columns (yellow, orange, or red).

3.3 Control by a Checkerboard Pattern

A third spatial pattern that we have studied is the checkerboard pattern. This pattern has only two exemplars, as illustrated in Figure 13.

Our analysis of control by the checkerboard pattern involves consideration of the relative probability of three kinds of "moves" (transitions from one choice to the next). The first is choice of a pole adjacent to the pole most recently chosen. In Figure 14, filled circles represent baited poles and the arrows indicate two examples of an adjacent move (left panel). An "adjacent" move is consistent with the checkerboard pattern following choice of an unbaited pole (i.e., an adjacent move following choice of an unbaited pole would result in choice of a baited pole). However, an adjacent move following choice of a baited pole would result in choice of an unbaited pole.

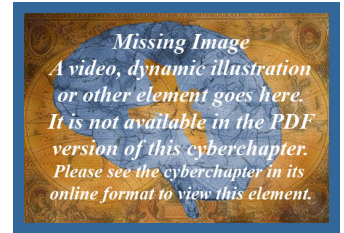


Figure 9. Several exemplars of the row pattern. (Animation will show a sequence of examples)

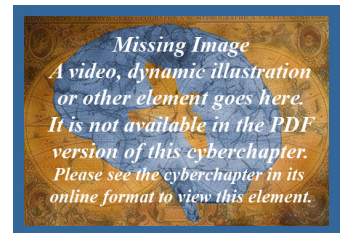


Figure 13. Animation of the two exemplars of a checkerboard pattern.

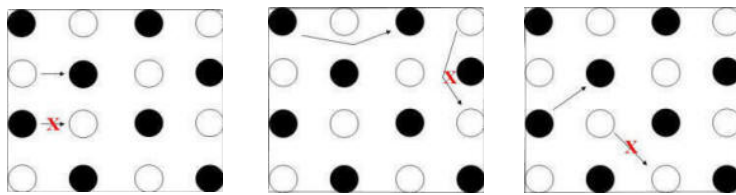


Figure 14. Transitions from one choice to the next that are diagnostic of control by the checkerboard pattern. Black circles represent poles that were baited at the beginning of the trial. Arrows show diagnostic transitions. Arrow with red "X" indicates transition contra-indicated by pattern. Left Panel: Adjacent moves correspond to choice of a baited pole only if they are made from an unbaited pole. Middle Panel: Skip moves correspond to choice of a baited pole only if they are made from a baited pole. Right Panel: Diagonal moves correspond to choice of a baited pole only if they are made from a baited pole.

A "skip" move is choice of a pole separated by one pole (in either a row or column of the pole matrix) from the most recently chosen pole. As shown in Figure 14 (middle panel), a skip move is consistent with the checkerboard pattern (i.e., would result in choice of a baited pole) following choice of a baited pole, but not following choice of an unbaited pole.

Finally, a "diagonal" move is choice of a pole that is adjacent along a diagonal axis to the most recently chosen pole. As shown in Figure 14 (right panel), a diagonal move (like a skip move) is consistent with the checkerboard pattern following choice of a baited pole, but not following choice of an unbaited pole.

Brown, Zeiler, & John (2001) found that rats acquire a tendency to make adjacent moves following choice of an unbaited pole and skip and diagonal moves following choice of a baited pole. Figure 15 shows their data in an experiment with 60 daily trials. Over the course of three blocks of 20 trials each, the relative likelihood of adjacent moves increases following choice of an unbaited pole and decreases following choice of a baited pole. The opposite chance occurs for skip moves and diagonal moves. Thus, rats acquire tendencies to make choices that conform to the checkerboard pattern in which baited poles are arranged. This evidence for control by a checkerboard pattern was replicated by Brown and Wintersteen (2004).

These results show that rats can learn a variety of spatial patterns. It should again be emphasized that these are not spatial relations among particular places defined by their location in allocentric space. The location of food varies unpredictably from trial to trial. Thus, the spatial relations among the baited locations must be abstracted from any allocentric map that is anchored by specific locations in space. We infer that an abstract representation of the spatial pattern is formed as the rat experiences the spatial relations that exist among places where food has been found within each trial. The next section explores some mechanisms that might be involved in this ability.

IV. How is a Spatial Pattern Learned and How is it Used: Motion, Memory, & Mapping

Clearly, spatial choices can be controlled by the spatial relations among goal locations despite the fact that those goal locations are not designated by any visual or other perceivable beacons, landmarks, or geometric cues. What is the mechanism of this spatial pattern learning?

One possibility is that rats acquire response tendencies that result in choice of poles with particular spatial relations to previously chosen poles, and that such acquired response tendencies constitute the mechanism of control by spatial patterns (Olthof, Sutton, Slumskie, D'Addetta, & Roberts, 1999). After being exposed to the square pattern, for example, a rat might acquire the following response tendency: *After finding two adjacent baited poles, turn left or right and choose the next pole* (Figure 16A). This rule would result in finding a third baited pole. It requires that the rat discriminate and remember the spatial relation between the first two baited poles and then respond in a manner that is contingent on that relationship.

A similar (although somewhat more complex) rule could be acquired that would increase the likelihood of choosing the fourth baited pole in a square pattern. The response rule that would produce control by a linear pattern is the converse of the one that would be acquired for a square pattern: *After finding two adjacent baited poles, move in the same orientation as those two poles and choose the next pole* (Figure 16B).

In the case of a checkerboard pattern, the description of a response tendency explanation of control by the pattern corresponds directly to the measure of control by the checkerboard pattern described in [Part III: Spatial Pattern Learning in the Pole Box](#). That is, rats develop a tendency to make adjacent moves following choice of an unbaited pole and/or a tendency to make skip & diagonal moves following choice of a baited pole.

Brown, Zeiler, and John (2001) showed that the acquisition of such response tendencies cannot explain control by spatial patterns, at least in the case of the checkerboard pattern. Brown, et al. (Experiment 2) exposed rats to a checkerboard pattern in a 5 X 5 pole box. Barriers (constructed of plastic mesh material allowing the rats to see through the barriers) prevented moves to poles in the same row or column (Figure 17). Thus, without walking around a barrier, rats could only choose poles along a diagonal axis.

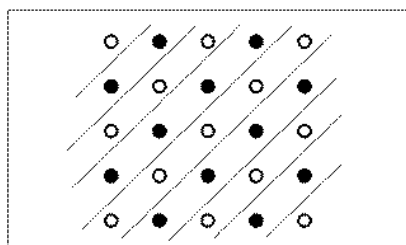


Figure 17. Exemplars of the checkerboard pattern, with clear plexiglass walls forming diagonal alleys of poles shown. This arrangement was used during the training phase of Brown, Zeiler, and John's (2001) experiment.

Therefore, during this training phase, a rat could not have acquired response tendencies that correspond to adjacent or skip moves. Nevertheless, when the barriers were removed, the rats immediately demonstrated a stronger tendency to make adjacent moves following choice of an unbaited pole and a stronger tendency to make skip moves following choice of a baited pole. This result shows that spatial relations among goal locations control behavior in the absence of specific response tendencies.

If the mechanism of control by spatial patterns is not the development of response tendencies, then what is it? We conclude that an abstract representation of the spatial relations among the goal locations is acquired. Such a representation would allow novel paths from one goal location to another to be followed. The logic of the Brown, Zeiler, and John's (2001) experiment and the conclusion that a flexible spatial representation is necessary to explain the results are analogous to Tolman, Richie, and Kalish's (1946) classic "shortcut" experiment and the resulting argument that a flexible representation (cognitive map) of familiar locations is acquired. However, there is a critical difference between the spatial relations involved in the pole box task and the spatial relations among particular locations. In the case of Tolman's experiment, as in the case of almost all more recent and current work on cognitive mapping, the locations are specific locations in allocentric space, defined by spatial cues (e.g., beacons, landmarks, geometric cues). In the pole box task, however, the goal locations vary unpredictably from trial to trial. The goal locations, therefore, must be coded in a temporary manner. The relationships among the baited locations, on the other hand, are consistent across trials and must

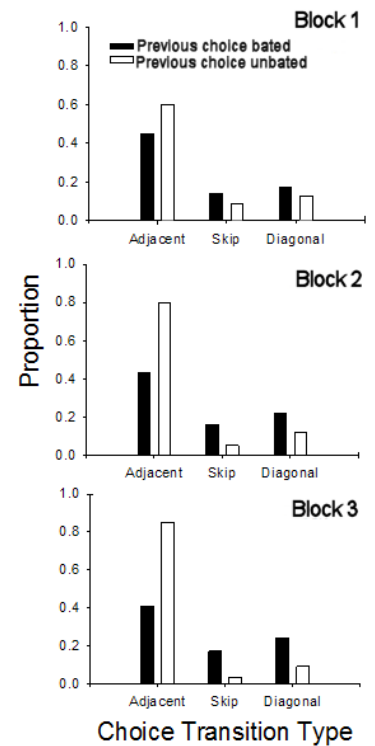


Figure 15. Results from Brown, Zeiler, & John (2001). By Trial Block 3, Adjacent moves were more likely following choices of an unbaited pole, whereas Skip and Diagonal moves were more likely following choice of a baited pole. These results provide evidence of control by the checkerboard spatial pattern.

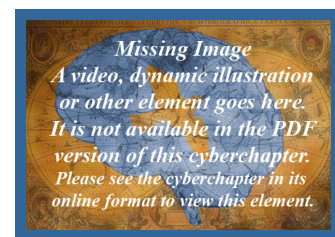


Figure 16. (A) An S-R explanation of correct responding following discovery of two baited poles when pole are baited in a square pattern. (B) An S-R explanation of correct responding following discovery of two baited poles when poles are baited in a linear pattern.

be coded in a permanent manner in order to effectively control choices in accord with the pattern. This is the sense in which the spatial pattern must be abstract: it must be abstracted from the relation of the particular locations that are baited on particular trials.

In order to abstract the spatial relations among goal locations, given that the goal locations change unpredictably in allocentric space, rats must somehow be perceiving the spatial relations among the baited poles found during individual trials. Two possible mechanisms for doing so can be distinguished. First, a *working memory* system could be used to code the allocentric location of poles previously discovered during a trial. The spatial relations among those locations could then be determined on the basis of working memories for their locations. The abstracted spatial relations among baited locations would then be coded in a more permanent memory system. According to this view, the process of spatial pattern learning is analogous to concept learning in that the spatial relations are abstracted from particular exemplars of baited pole locations experienced over trials.

Alternatively, a *dead reckoning* system could be used that integrates the distance and direction from each baited pole discovered to the next. According to this view, rats need not code the locations of particular baited poles during the trial. Instead, their spatial relationship is coded directly in terms of the vector provided by dead reckoning as the rat moves in the pole box and chooses poles. A new vector is initiated each time the rat discovers a baited pole. The resulting set of vectors specifying the relations among each pair of poles forming the pattern constitutes the learned spatial pattern.

We recently completed a series of experiments designed to investigate the possibility that working memory for the location of previously discovered baited poles is involved in pattern learning. To do so, we developed pole box apparatus that allowed us to provide visual cues corresponding to poles visited during each trial.

The video in Figure 18 shows a trial from an experiment using the first of two versions of this apparatus. As the rat visits poles, a spotlight (produced from above using a data projector) marks the location of visited poles. It was expected that such cues would allow the rats to make fewer revisits of poles. The question was whether it would also enhance control by the checkerboard pattern of baited poles. If so, that would constitute evidence that working memory is also used to keep track of where the previously discovered baited poles were, and that these temporary memories about the elements of particular exemplars of the pattern are involved in the ability to learn the abstracted pattern.

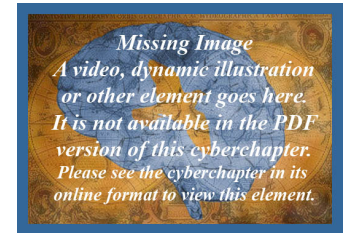


Figure 18. Video of rat in in polebox with feedback stimuli indicating chosen arms. Click image to play video.



Figure 19. (A) Apparatus used by Brown and Wintersteen. Translucent base of each pole can be illuminated from below



(B) Close-up of poles in the Brown and Wintersteen apparatus. Pole in foreground is not illuminated. Two poles in background are illuminated. Pole illumination was used as a cue indicating whether pole had been visited earlier during the trial.

Unfortunately, the visual cues had no effect on either pole revisits or control by the pattern. It is likely that this failure of the cues to affect behavior was due to the brightness of the light produced by the data projector. We suspect the rats may not have been able to discriminate the cues because they were masked by the ambient light produced by the projector.

A modification of the technique used to provide visual cues resulted in cues that did affect behavior. The base of the poles in this second version of the apparatus (shown in Figure 19A) were constructed of translucent material and mounted on top of holes cut in the floor of the arena. A data projector was used to project light up from underneath the apparatus, thereby allowing poles to be individually illuminated (as shown in Figure 19B).

Brown and Wintersteen (2004) trained rats with one of the two exemplars of the checkerboard pattern defining the location of the baited poles on each trial. During training, the base of the pole was illuminated whenever a rat choose the pole (or, for half of the rats, all the poles were illuminated at the beginning of the trial and the illumination was turned off when the rat visited a pole). During a test phase, half of the trials did not involve use of the visual cues (the illumination of the poles did not change). This allowed comparisons of performance with and without the visual cues corresponding to visited locations. The visual cues did enhance the ability of the rats to avoid revisits to poles visited earlier during the trial. However, there was no

evidence that the cues had an effect on control by checkerboard spatial pattern. Because visual cues corresponding to visited poles facilitated the ability of rats to avoid revisits of those poles but had no effect on control by the checkerboard pattern, Brown and Wintersteen argued, the working memories for pole locations used to avoid revisits must not be involved in the acquisition of pattern learning or in the use of learned patterns to locate baited poles. They suggested that two separate working memory systems may be used in the pole box task: one set of working memories reduce visits to those (previously visited) locations and a second set of working memories code the location of previously discovered baited poles.

Although the existence of two separate working memory systems can explain the dissociation of memory for previous pole visits from control by spatial patterns, another possibility is that working memory for the location of previously visited poles is not involved in the learning or use of spatial patterns at all. Instead, rats could acquire the spatial pattern of baited poles using dead reckoning. Dead reckoning could be used to detect and code the spatial relations among the poles baited in a pattern if discovery of a baited pole defines the end of integration of one dead reckoned vector and the beginning of another. Furthermore, the product (vectors) of the dead reckoning process would have to be stored across trials. Biegler (2000) has proposed an analogous function of dead reckoning in the development of allocentric cognitive maps ([see Biegler in this cyberbook](#)).

Figure 20 shows a hypothetical path of a rat as it moves from one baited pole to another. Note that the route of the rat might be quite indirect and might include visits to other (non-baited) poles. The suggestion is, however, that the discovery of a baited pole defines the end of an instance of path integration (and the beginning of a new one). Thus, each transition from one baited pole to another produces a vector (the arrow in Figure 20) that defines the spatial relationship between those two baited poles. Each transition from one baited pole to the next would produce one such vector.

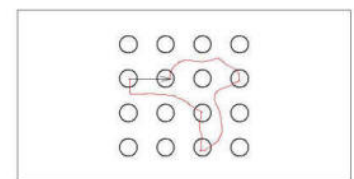


Figure 20. Illustration of path integrated spatial relation between two poles. Rat follows path indicated in red from on pole to the other, but codes the spatial relation between them as indicated by the arrow, based on information provided by path integration.

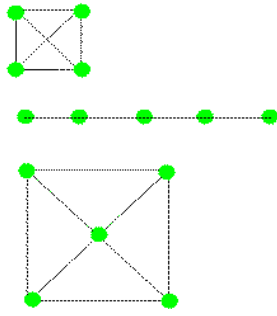


Figure 21. Hypothetical vectors representing abstracted spatial relations among locations (green dots). These could be formed as a result of moving among the locations *via* dead reckoned spatial relations.

The resulting vectors would be cumulated over discoveries of baited poles both within a trial and over trials. Over the course of trials, the square, line, and checkerboard patterns would result in a set of vectors that code the spatial relationships among the baited poles in the three patterns. In Figure 21, the vectors produced by dead reckoning are represented by the lines connecting the (green) goal locations. The goal locations are defined exclusively in terms of the vectors. That is, there is no coding of the location of the goal locations in allocentric space. Their position is learned only in relation to each other. Dead reckoning provides a mechanism for this relational spatial coding.

A weakness of this account of spatial pattern learning is that it does not explain the ability of rats to choose in accordance with the pattern after choosing an unbaited pole. This ability was clearly shown in the case of a line (row) pattern by DiGello, et al. (2002). Furthermore, the tendency to choose adjacent poles following choice of an unbaited pole in the checkerboard pattern also indicates that rats not only learn the spatial relationships among baited poles, but also learn the spatial relationships between baited poles and unbaited poles.

It is, of course, possible to extrapolate the dead reckoning view of pattern learning by proposing that the spatial relationship between all pairs of consecutively chosen poles is discriminated using dead reckoning and that the bait status of the poles is also coded along with the resulting set of vectors. An illustration of one version of this idea is shown below for the checkerboard pattern (Figure 22). The green nodes represent baited poles and the red nodes represent the unbaited poles that separate the baited poles in the rows and columns of the matrix. Learned vectors define the relations among the baited locations and between the adjacent baited and unbaited locations.

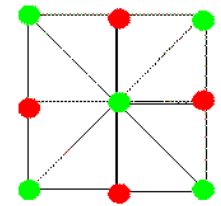


Figure 22. Hypothetical vectors representing abstracted spatial relations among two kinds of locations - baited (green dots) and unbaited (red dots)

Thus, dead reckoning provides a potential mechanism for abstracting the spatial relations that control choices in the pole box. We do not yet have any direct evidence for or against the possibility that dead reckoning is providing this information. Abstraction of the spatial relations among baited poles may be mediated either by working memories for the particular locations baited on individual trials or by dead reckoning.

V. References

- Brown, M.F., DiGello, E., Milewski, M., Wilson, M., & Kozak, M. (2000). Spatial pattern learning in rats: Conditional control by two patterns. *Animal Learning & Behavior*, *28*, 278-287.
- Brown, M.F., & Huggins, C.K. (1993). Maze-arm length affects a choice criterion in the radial-arm maze. *Animal Learning & Behavior*, *21*, 68-72.
- Brown, M.F., & Lesniak-Karpiak, K.B. (1993). Choice criterion effects in the radial-arm maze: Maze-arm incline and brightness. *Learning and Motivation*, *24*, 23-39.
- Brown, M.F., & Terronni, M. (1996). Control of choice by the spatial configuration of goals. *Journal of Experimental Psychology: Animal Behavior Processes*, *22*, 438-446.
- Brown, M.F., & Wintersteen, J. (2004). Spatial pattern learning and spatial working memory. *Learning & Behavior*, *34*, 391-400.
- Brown, M.F., Yang, S.Y., & DiGian, K.A. (2002). No evidence for overshadowing or facilitation of spatial pattern learning by visual cues. *Animal Learning & Behavior*, *30*, 363-375.
- Brown, M.F., Zeiler, C., & John, A. (2001). Spatial pattern learning in rats: Control by an iterative pattern. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*, 407-416.
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, *23*, 149-178.
- Dahl, D., & Winson, J. (1985). Action of norepinephrine in the dentate gyrus. I. Stimulation of locus coeruleus. *Experimental Brain Research*, *59*, 491-496.
- 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.
- Dickinson, A. (1980). *Contemporary animal learning theory*. Cambridge: Cambridge University Press.
- DiGello, E., Brown, M.F., & Affuso, J. (2002). Negative information: Both presence and absence of spatial pattern elements guide rats' spatial choices. *Psychonomic Bulletin & Review*, *9*, 706-713.
- Gallistel, C.R. (1990a). *The organization of learning*. Cambridge, MA: M.I.T. Press.
- Kamil, A.C., & Jones, J.E. (2000). Geometric rule learning by Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Experimental Psychology: Animal Behavior Processes*, *26*, 439-453.
- Lebowitz, B.K., & Brown, M.F. (1999). Sex differences in spatial search and pattern learning in the rat. *Psychobiology*, *27*, 364-371.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Oxford University Press.
- Olthoff, A., Sutton, J.E., Slumskie, S. V., D'Addetta, J., & Roberts, W.A. (1999). In search of the cognitive map: Can rats learn an abstract pattern of rewarded arms on the radial maze? *Journal of Experimental Psychology: Animal Behavior Processes*, *25*, 352-362.
- Olton, D.S., & Samuelson, R.J. (1976). *Journal of Experimental Psychology: Animal Behavior Processes*, *2*, 97-116.
- Pearce, J.M., Ward-Robinson, J., Good, M., Fussell, C., & Aydin, A. (2001). Influence of a beacon on spatial learning based on the shape of the test environment. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*, 329-344.
- Stevens, P.S. (1974). *Patterns in nature*. New York: Little, Brown & Co.

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

Thinus-Blanc, C. (1996). *Animal spatial cognition: Behavioral and neural approaches*. Singapore: World Scientific.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review, 55*, 189-208.

Acknowledgements

The work reviewed in this chapter was supported by grant IBN-9982244 from the National Science Foundation. I thank the many graduate and undergraduate students who have contributed to this project.



©2006 All copyrights for the individual chapters are retained by the authors. All other material in this book is copyrighted by the editor, unless noted otherwise. If there has been an error with regards to unacknowledged copyrighted material, please contact the editor immediately so that this can be corrected. Permissions for using material in this book should be sent to the editor.