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ALTERNATIVE REPRESENTATIONS**

By

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ABSTRACT

HOW DO BEES COMPUTE THE POSITION OF THE SUN? ALTERNATIVE REPRESENTATIONS

By

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To use the sun as a compass, animals must compensate for its apparent movement. This is complicated by the fact that the rate of change of the horizontal component of the sun's position, or azimuth, which provides the directional information, varies over the course of the day. Additionally, the daily pattern of change varies with season and latitude. It has long been known that bees learn the local pattern of movement, and that they can estimate the position of the sun at times of day when they have never seen it. However, the mechanism has remained a mystery. When bees are restricted to fly only in the afternoon, thereby limiting the information available for learning, they nonetheless have a relatively accurate estimate the position of the sun in the morning, indicating a position for the azimuth in the morning about 180° from the position experienced in the afternoon. These results contradicted the predictions of all previous computational models of sun-compass learning, which all assumed that the insects' neural computations rely on linear estimates of azimuthal rate. However, these results suggest that they include aspects of the nonlinearity of the natural pattern in their computations. In this dissertation, I present two new methods of modeling the sun-compass-learning process. Both classes of models incorporate the nonlinear aspects of the problem; one class of models is symbolic (it

maintains a symbolic representation of azimuth position and time) while the other is nonsymbolic (it does not maintain a symbolic representation of azimuth position and time). The nonsymbolic models are connectionist neural networks. The symbolic model attempts to take into account the varying rate of change of the azimuth over the course of the day. It is based on the geometry of an ellipse. In the nonsymbolic connectionist model, the connection weights of the network are assumed to be preconfigured in such a way that a bee is able to quickly recognize or quickly learn the course of the sun. Neural processes that roughly correspond to either of these broad classes of models could account for the bees' behavior.

To Sarah, for understanding

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None of this would have been possible without the loving support and understanding of my wife, Sarah.

TABLE OF CONTENTS

LIST OF TABLES.....	ix
LIST OF FIGURES.....	x
CHAPTER 1	
OVERVIEW.....	1
CHAPTER 2	
SUN COMPASS ORIENTATION.....	13
2.1 The Solar Reference.....	14
2.2 Discovery of the Sun Compass.....	22
2.3 Distribution in the Animal Kingdom.....	24
2.4 Directional Information from the Sun.....	36
2.4.1 The Sun as a Point Source.....	36
2.4.2 The Sun Defines a Local Direction.....	37
2.4.3 The Sun Defines a Global Direction.....	38
2.4.4 The Sun Defines Any Flexible Direction.....	39
2.5 Honey Bees as a Model System.....	39
2.5.1 Long Distance Orientation.....	40
2.5.2 Short Distance Orientation.....	41
2.5.3 The Dance Language.....	46
2.6 Other Celestial Compass Mechanisms.....	49
2.6.1 The Lunar Compass.....	49
2.6.2 The Stellar Compass.....	49
2.7 Summary.....	50
CHAPTER 3	
THE REPRESENTATION OF THE SUN'S COURSE.....	51
3.1 Previous Studies.....	52
3.2 Experimental Methods.....	63
3.2.1 Colony 1.....	63
3.2.2 Colony 2.....	64
3.2.3 Colony 3.....	64
3.2.4 Colony 4.....	65

3.3 Results and Discussion.....	67
3.3.1 Colony 1.....	67
3.3.2 Colony 2.....	75
3.3.3 Colony 3.....	79
3.3.4 Colony 4.....	83
3.4 Summary.....	86
CHAPTER 4	
NONLINEAR SYMBOLIC MODELS.....	87
4.1 A Symbolic Model of Sun Compass Learning.....	87
4.2 The Ellipse Rate Function.....	91
4.2.1 The Geometry of the Ellipse.....	92
4.2.2 The Equation of the Ellipse.....	100
4.3 The Ellipse Azimuth Function.....	102
4.4 Estimating the Parameters of the Ellipse.....	109
4.5 Fit of Ellipse Azimuth Function to Experimental Data.....	110
4.6 Fit of Ellipse Azimuth Functions to Other Data Sets.....	116
4.7 Reducing the Number of Parameters.....	118
4.8 Estimating k with Restricted Experience.....	120
4.9 The Effect of the Time Interval.....	123
4.10 Summary.....	125
CHAPTER 5	
CONNECTIONIST MODELS.....	126
5.1 Connectionist Computations.....	127
5.2 Connectionist Characteristics.....	130
5.3 Connectionist Representations of the Sun's Course.....	131
5.4 A Binary Representation.....	132
5.4.1 Pattern Matching.....	133
5.4.2 Learning Advantage.....	143
5.5 A Continuous Representation.....	155
5.6 Summary.....	162
CHAPTER 6	
CONCLUSIONS.....	163
6.1 Innate Structure.....	165
6.2 Templates.....	166
6.3 Symbolic versus Nonsymbolic.....	169
6.4 A False Dichotomy?.....	173
6.5 Caveat.....	175
6.6 Representing the Regularities of the World.....	175
REFERENCES.....	176

LIST OF TABLES

Table 2.1 Distribution of the Sun Compass in the Animal Kingdom.....	26
Table 3.1 Regression Analysis of Individual Bees' Azimuth Estimates (Colony 1)...	70
Table 3.2 Regression Analysis of Individual Bees' Azimuth Estimates (Colony 2)...	78
Table 3.3 Regression Analysis of Individual Bees' Azimuth Estimates (Colony 3)...	81
Table 4.1 Fit of Models to Experimental Data (R^2).....	115
Table 4.2 Expected and Observed Parameters of the Ellipse.....	115
Table 4.3 Fit of Ellipse Model to New & New (1962) Data (R^2).....	117
Table 4.4 Expected and Observed Parameters of the Ellipse (New & New, 1962)..	117
Table 4.5 Estimates of k from the Training Period of Colony 1.....	122
Table 5.1 Hamming Distance between Azimuth Training Patterns.....	150
Table 6.1 Comparison of New Models.....	165

LIST OF FIGURES

Figure 1.1.....	5
The Computational-Representational Approach. A. The traditional view. B. The computational-representational view.	
Figure 2.1.....	17
Pattern of solar movement for different seasons and latitudes. The figure represents a projection of the sun onto the celestial hemisphere. The center points correspond to the zenith, which is the point directly overhead of the observer. The outer circles correspond to the horizon line. The sun's hourly position is plotted by the dark circles. The distance from the horizon line to the sun corresponds to the sun's elevation in the sky. The distance from the zenith point to the sun is the zenith distance. Extending an imaginary line from the zenith through the sun's position to the horizon reveals the position of the sun's azimuth which provides the directional information for sun compass orientation. See example for 40° N equinox. The rate of change of the azimuth varies over the course of the day and with season and latitude. This can be seen in the comparison of the change in azimuth between 7:00 and 9:00 vs. 11:00 and 13:00 (drawn for 40° N).	
Figure 2.2.....	18
Seasonal and latitudinal variation of the ephemeris function. A. Ephemeris functions for 5°, 25° and 40° North latitude for the equinox. B. Ephemeris functions for 5°, 25° and 40° North latitude for the solstice. Solar azimuth is plotted against local sun time. The two panels show the considerable variation in the rate of change of the azimuth over the course of the day and with season and latitude.	
Figure 2.3.....	45
Proportion of choices to each of four directions with respect to the training direction. A. Sunny. B. Partly cloudy C. Completely overcast. D. Delay. The probabilities presented are the binomial probabilities that the	

pattern of choices occurred by chance (25% correct choice; 75% incorrect).

Figure 2.4.....48

The dance language of the honey bee. The communicative waggle dance indicates the distance and direction to the food. A. The angle indicated by the waggle run (α) with respect to vertical corresponds to the angle of the food with respect to the sun's azimuth. B. The flight path from the hive (H) to a food source (F) relative to the sun's azimuth the angle α is the same as in (A). Over the course of the day, the dance angle changes as the solar azimuth moves along the horizon. Distance is indicated by the length of the waggle run.

Figure 3.1.....56

Solar azimuths inferred from the dances of the bees in New and New's (1962) experiments. Data are from colony 1 in Trinidad ($10^{\circ}38'$) on (A) April 15, (B) April 16, (C) April 17, (D) April 18, (E) April 20, and (F) April 21. Data were obtained from New and New's (1962) Figure 3 and replotted to correspond to solar azimuths rather than dance angles.

Figure 3.2.....62

Predictions from previous computational models about how insects fill gaps in their experience with the sun's course. The shaded region corresponds to the time period of experience with the sun's course. The lines represent the predictions of the position of the azimuth at other times of day based on the various models. A. Interpolation: a constant rate of change between the end of the one training period and the beginning of the next on the subsequent day. B. Forward extrapolation: the rate of change observed at the end of the training period extended forward through the night and into the morning of the subsequent day. C. Backward extrapolation: the rate of change of the azimuth observed at the beginning of the training period and extended backward into earlier portions of the day.

Figure 3.3.....69

Solar azimuths inferred from the dances of restricted experienced bees from colony 1. The curved line corresponds to the actual path of the sun on July 22. The straight lines are the predictions from the previous computational models. A. Interpolation. B. Forward extrapolation. C. Backward extrapolation. D. 180° step function. The open symbols correspond to two bees that differed qualitatively from the rest.

Figure 3.4.....	73
-----------------	----

Solar azimuths inferred from the dances of four individual bees from colony 1 that show gradual shifts during the transition period.. A. Bee 32. B. Bee 74. C. Bee 78. D. Bee 87.

Figure 3.5.....	77
-----------------	----

Solar azimuths inferred from the dances of restricted experienced bees (A) and fully experienced bees (B) of colony 2.

Figure 3.6.....	82
-----------------	----

Solar azimuths inferred from the dances of restricted experienced bees of colony 3. Solar azimuth curve is for August 10.

Figure 3.7.....	85
-----------------	----

Solar azimuths inferred from the vanishing bearings of colony 4. The data are means $\pm$ standard error of significantly oriented groups of bees (10 of 12) at two different release sites (squares and circle). Tests occurred between August 11 and 26. The azimuths inferred for each release day are plotted. The solar azimuth shown corresponds to August 18.

Figure 4.1.....	95
-----------------	----

The ellipse approximation of the azimuth rate function. The rate of change of the azimuth varies systematically over the course of the day. A. The full 24 hour azimuth function for 40° N at the equinox. B. The 24 hour azimuth function for 10° N at the equinox. C. The azimuth rate function for the azimuth curve in A, computed over 8 minute intervals. D. The azimuth rate function for the azimuth curve in B, computed over 8 minute intervals. E. An ellipse based on the rates in C (semimajor axis = $23^\circ/\text{hr}$; semiminor axis = $10^\circ/\text{hr}$). F. An ellipse based on the rates in D (semimajor axis = $85^\circ/\text{hr}$; semiminor axis = $3^\circ/\text{hr}$).

Figure 4.2.....	99
-----------------	----

The true azimuth rate function plotted in polar coordinates. The values plotted correspond to the numerically calculated rate of change of the azimuth over 8 minute intervals. A. 40° N and 10° N for the equinox. B. 10° N for April 16 (declination $9^\circ 54'$). C. 40° N for the summer solstice. In all cases the curves are not truly elliptical. The shape varies considerably with season and latitude.

Figure 4.3.....	105
-----------------	-----

The scaled and unscaled ellipse azimuth functions for different seasons and latitudes. A. The true solar azimuth is plotted with two ellipse azimuth functions for 40° north latitude at the equinox. The squares correspond to the scaled ellipse azimuth function and the diamonds correspond to the unscaled azimuth function. The ellipse parameters for both ellipse azimuth functions are $a = 23$, $b = 10$ (as in Figure 4.1 E). The scaling function is described in the text. The true sun azimuth curve is depicted by the heavy line. B. The solar azimuth function (heavy line) and two ellipse azimuth estimates (scaled = squares; unscaled = diamonds) for 10° north latitude at the equinox. Ellipse parameters are $a = 85$, $b = 3$. C. The solar azimuth function (heavy line) and two ellipse azimuth estimates (scaled = squares; unscaled = diamonds) for 40° north latitude during the summer solstice. Ellipse parameters are $a = 48$, $b = 9$ (these values were determined from the actual azimuth rate function numerically calculated over 8 minute intervals as in Figure 4.1 C and D, and depicted in Figure 4.2 C. D. The solar azimuth function (heavy line) and two ellipse azimuth estimates (scaled = squares; unscaled = diamonds) for 10° north latitude on April 16 (declination 9°54'). Ellipse parameters are $a = 662$, $b = 1.5$. The values for the ellipse parameters a and b were determined from the actual azimuth rate function, numerically calculated over 8 minute intervals as in Figure 4.1 C and D, and depicted in Figure 4.2.

Figure 4.4.....	108
-----------------	-----

Ellipse azimuth functions for 40° N and 5° N at the northern summer solstice. The parameters of the ellipse rate function were estimated from numerical calculations of the actual azimuth rate function over 8 minute intervals (as in Figures 4.1, 4.2, and 4.3) (40° N: $a = 48$, $b = 9$; 5° N: $a = -43$, $b = -1$). The actual ephemeris functions are plotted for comparison.

Figure 4.5.....	112
-----------------	-----

A range of ellipse azimuth functions corresponding to the data from colony 1 (see Chapter 3). A. Parameters corresponding to the best fitting ellipse function ($a = 1076$, $b = 1$). B. Intermediate parameters ($a = 600$, $b = 3$). C. Intermediate parameters ($a = 300$, $b = 6$). Theoretical (expected) parameters of the ellipse (numerically calculated from the true azimuth rate function as in Figure 4.1, 4.2, and 4.3) ($a = 36$, $b = 10$). The shaded region corresponds to an ideal step function based on the data from colony one. The region corresponds to the mean (270° or 90°) $\pm$ one standard deviation ($\sim 30^\circ$) of the data.

Figure 4.6.....	119
-----------------	-----

Range of the parameters of the ellipse that generate equivalent ellipse azimuth functions (see footnote 6). All of the parameters yield azimuth curves that fit the data of colony 2 equally well ($R^2 = .94$). The linear relationship suggests that the two parameters necessary to describe the ellipse azimuth function may be reduced to a single ratio.

Figure 4.7.....	124
-----------------	-----

The effect of time interval on the ellipse azimuth estimate. For all of the curves, k is 1076 as in the best-fitting ellipse azimuth function for colony 1. Time intervals are (A) 1, (B) 2, (C) 5, (D) 10, (E) 20, and (F) 40 minute intervals. The curve that is most like a step function is the curve for 40 minute intervals.

Figure 5.1.....	128
-----------------	-----

General form of a feed-forward connectionist network. I: input units H: hidden units. O: output units. w : connection weights.

Figure 5.2.....	136
-----------------	-----

Idealized solar ephemeris functions used as the training set for the connectionist models. The patterns consist of a matrix of ones and zeros, with the ones corresponding to the black squares and the zeros corresponding to the white squares. Each point corresponds to a pairing of azimuth position and time of day. These patterns correspond roughly to the natural range of solar azimuth functions (See Figure 2.2).

Figure 5.3.....	137
-----------------	-----

Network architecture. The network has 100 input units and 100 output units that correspond to azimuth-time coordinates. There are 25 hidden units. See text for explanation of connection patterns. The connections are not shown because of the number of them. Activation is shown by the gray scale (white = zero; black = one).

Figure 5.4.....	142
-----------------	-----

Responses of preconfigured network to test patterns consisting of partial ephemeris functions. The test patterns (A) consist of inputs arranged in an array of ones and zeros as in Figure 5.2. The responses (B) for each test pattern are presented immediately to the right. The responses consist of

the activation level of each of the output units. They range from zero to one and are all on the same scale. See text for a description of the network.

Figure 5.5..... 146

Comparison of Hamming and Pythagorean distances. In this diagram, the standard linear (Pythagorean) distance from the step function to each of the others pictured varies, while the Hamming distance is constant. A. Pythagorean distance = 2, Hamming distance = 4. B. Pythagorean distance = 4, Hamming distance = 4. Hamming distance is a measure of overlap between the patterns. In each of the cases, two points have changed, which gives a Hamming distance of 4 (turning off the old point and turning on the new point for each of the two changes). The linear distance between the old points and the new points makes a difference for the Pythagorean distance but not for the Hamming distance.

Figure 5.6..... 149

Binary retraining trials for azimuth network trained on one azimuth pattern and retrained on another. Binary retraining percentage is the number retraining trials to reach an error criterion of .05 as a percentage of the training time for the original pattern. Data are the means $\pm$ standard error for 10 replicates for each of the 7 azimuth patterns retrained on the 6 other patterns. They are plotted against the Hamming distance (number of binary substitutions) between the two patterns. This is clearly the major explanatory variable.

Figure 5.7..... 153

Average hamming distance from each azimuth curve to every other curve. The curves are to the nearest ten degrees. The average Hamming distances are plotted with respect to their latitude-declination coordinates. Panel A shows the situation when the curves are restricted to the tropics (between 20° N and 20° S). Panel B shows the situation when temperate curves are included (between 40° N and 40° S).

Figure 5.8..... 154

Binary retraining trials for azimuth curves discussed in Figure 5.7. For the range of Hamming distances that exist between the azimuth curves represented in figure 5.7, a network trained on one azimuth pattern and retrained on another. The network had 324 inputs and outputs and 81 hidden units. Binary retraining is the number retraining trials to reach an error criterion of .05 as a proportion of the training time for the original

pattern. Data are the means $\pm$ standard error for 5 replicates for each Hamming distance (filled circles). They are plotted against the relative Hamming distance (number of binary substitutions)/(number of elements) between the patterns. For comparison the data from Figure 5.6 are included (open circles).

Figure 5.9..... 158

Diagram of simple connectionist network used for the interpolation network. I: input unit. H: hidden unit. O: output unit. B: bias unit. w : modifiable connection weights.

Figure 5.10..... 161

Response of interpolation network to three different training regimes for learning the same specific azimuth function. The azimuth function corresponds to 25° N on April 22 (solar declination 12°). A. Response of a network over 24 hours at half-hour intervals for a training set of hourly azimuth angles between sunrise ($\sim 06:00$) and sunset ($\sim 18:00$) (local solar time). B. 24 hour response of a network trained only on hourly positions in the late afternoon and evening (15:00 to 18:00). C. Response of a network trained on afternoon positions in B but with additional constraints ($\text{Azimuth}_{12:00} = \text{Azimuth}_{18:00} - 90^\circ$; $\text{Azimuth}_{06:00} = \text{Azimuth}_{18:00} - 180^\circ$).

Chapter 1

OVERVIEW

The natural world is full of regularities. Life itself depends on the regularities of the world, and has evolved to take advantage of them. Many of the regularities are incorporated into the genetic code. Others are learned and remembered by animals. The distribution of resources in the environment is one factor that has led organisms to adopt both of these strategies. In the short run resources may be distributed unequally through the environment, and this makes certain locations more important than others for the survival of the animal. The environment also varies over generations as conditions fluctuate and populations migrate into new areas. This requires an animal to learn the local conditions or evolve to take advantage of the new conditions. It may be advantageous to move between regular locations in the environment. This in turn may lead to the evolution of orientation mechanisms and memory for places.

Learning has evolved to help maximize the performance of an animal in a world of unpredictable predictabilities. These are events that occur with regularity and can be predicted but are not regular enough to engender a specific response. Events of this type cannot be genetically hard-wired into the behavior of an animal because the exact nature

of the events varies, yet there is a regularity that allows predictions to be made based on previous experience.

The brain is the organ of learning. Recent theories in psychology have suggested that there is a close correspondence between the regularities of the world and those of the brain (Shepard, 1987). The brain is an immensely complicated computational system (Churchland & Sejnowski, 1989) that evolved over millennia in the context of fluctuating yet regular environments. One approach to understanding the function of the brain involves understanding the environmental pressures that lead to its evolution. A fundamental view of the brain is that it consists of a number of modules with specific computational characteristics (Gallistel, 1990). These may have evolved as solutions to very specific problems presented by the environment. In order to understand the functioning of the brain as a whole it is important to understand the functioning of its parts. The properties of the brain that seem unified in experience may in fact be a haphazard conglomeration of modules that evolved to solve very specific yet different environmental problems. The human brain is particularly complex and it is quite difficult to decipher individual computational modules with the exception of the those involved in the most basic levels of sensory processing. Therefore, to understand the functioning of individual specialized modules it is fruitful to look at animals that have much smaller brains and have very specific environmental problems to solve.

Gallistel (1990) has focused considerable attention on such animals as a means of understanding the organization of learning and of the brain. Gallistel has championed a computational-representational approach to animal learning. In this framework important elements of the animal's external world are represented in the animal's internal world. Gallistel maintains that these representations are functionally isomorphic with the entities in the real world. He uses isomorphism in the formal mathematical sense, in which one set of entities can be mapped onto another, such as the relationship between geometry and algebra (Gallistel, 1990). Thus, for Gallistel, there is a one-to-one relationship maintained between the parameters of the natural world and the parameters of the representations. In Gallistel's view, computations can be performed on the representations to yield new forms of the representations needed to guide behavior. He calls these derived representations. For example, a representation of quantity can be combined with a representation of time to yield a new representation of rate. This general scheme is diagrammed in Figure 1. For comparison, the computational-representational approach contrasts with the traditional behaviorist approach (Watson, 1925), which posits that only behavior can be studied experimentally and not the internal structures that determine behavior. Although this approach is essentially dead, it has left an indelible mark on American psychology and the study of learning (e.g. Macphail, 1987). By contrast, the computational-representational approach maintains that behavioral experiments can be used to distinguish between alternative internal processing mechanisms. Thus it basically opens the black box of the behaviorist approach. In addition, black boxes remain within the former boundaries of the stimulus-response box. These new boxes contain specific neural computations. The goal

of research in this paradigm is to decipher the nature of the representations and the computations involved in specific information-processing problems. A significant part of Gallistel's motivation is to guide neurophysiological research to the right questions based on the contents of computational boxes. That is, what types of neural processes are necessary to perform these specific computations.

Gallistel (1990) highlights navigation as a subject to explore the computational solutions to specific environmental problems. The ability to remember locations in the environment and to navigate between known locations is fundamental for the competitive ability of many animals. This ability is ubiquitous in the animal kingdom. To navigate accurately the animal must be able to solve certain computational problems. Understanding the types of problems that need to be solved and the ways that animals solve them sheds considerable light on cognitive processes and the neural mechanisms that underlie them.

Navigation is one realm of learning that may have very specific information-processing requirements. By understanding the specific requirements and the particular solutions to navigational problems, we may gain insight into the range of information-processing capabilities that animals have. Additionally, we can see how those capabilities may be shaped by evolution to solve very specific problems.

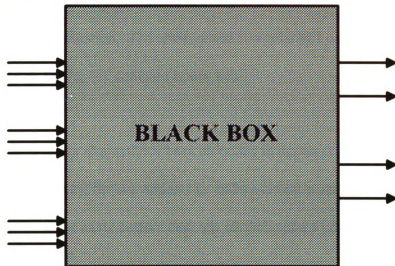
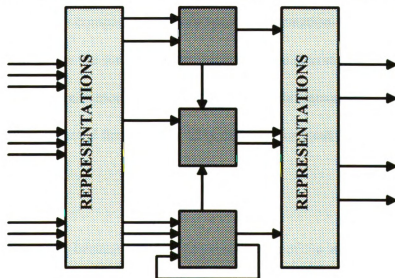
A**Stimulus****Response****B****Sensory Inputs****Computations****Behavioral Outputs**

Figure 1.1 The Computational-Representational Approach. A. The traditional view. B. The computational-representational view.

In this dissertation, I will show how an environmental regularity has been encoded in the brain of an animal to facilitate the rapid learning of a pattern that forms a critical reference point for effective navigation. The environmental regularity I consider is the sun and the animal is *Apis mellifera*, the common honey bee.

For aeons the earth has alternatively been shrouded in darkness and bathed in the light of the sun. During the day, the sun appears to make a circuit across the sky. This forms a regular pattern, yet the exact pattern depends on the vantage point on the earth and the time of the season.

The sun is a dominant reference point for orientation in many species (reviewed in Able, 1980). As a compass mechanism it is pervasive in the animal kingdom (see Table 2.1). Yet using the sun as a compass poses very specific information-processing problems that must be solved. Since the sun appears to move over the course of a day, an animal that uses it as a compass reference point must account for that movement. This is a significant problem that has attracted the attention of researchers for most of this century, but it has yet to be explained.

The problem emerges because the directional reference of the sun compass, the azimuth, changes at a varying rate over the course of the day. In addition the daily pattern of movement varies with season and with latitude, so an animal must be able to use the

correct local pattern. A wide range of animals are able to deal with the special requirements of using the sun as a compass. Throughout the dissertation, I will focus on honey bees as a model system for understanding this problem.

In Chapter 2, I discuss the nature of the sun as a directional reference. In particular, its apparent movement defines a complex pattern that has certain regular features but is not completely predictable because the pattern varies with season and with latitude. I review the distribution and use of the sun compass in the animal kingdom. I consider the information that is available from the sun, and the ways in which animals use this information.

The major portion of this dissertation is concerned with how insects learn about the course of the sun for use as a sun compass. Chapter 3 describes the previous computational models that have attempted to explain this process, and it introduces a series of experiments that were designed to distinguish among the previous models. The results were surprising and suggested that none of the previous models could account for the behavior of the bees. In particular they suggested that the bees may have some sort of innate template that is modified with experience. Specifically, their representation of the sun's course includes aspects that they could not have observed. These include nonlinearities in the natural pattern that were not incorporated into the previous computational models.

In Chapters 4 and 5, I explore alternative ways of modeling the sun compass learning problem. Chapter 4 extends the previous models to deal with the additional information that the insects appear to possess. The previous models were of a symbolic algebraic nature. The predictions that they produced emerged from the algebraic manipulation of information available to the insects in their experience: the position of the sun at particular times of day. The models assume that a neural process carries out the equivalent of the algebraic manipulation of the experienced information about the sun. In the new model, the symbolic nature of the process is retained. Information about solar position and time are used to form estimates of sun's position at new times of day. Unlike the previous models, there is additional information included in the process about the general pattern of movement of the sun. In particular, whereas previous computational models assumed that insects relied on linear estimates of the rate of change of the sun's azimuth, the new symbolic model accounts for the new evidence that insects are informed of the non-linear relationship between azimuth and time. This new model utilizes the geometry of an ellipse to express the pattern of movement of the sun.

In Chapter 5, I present an alternative method of modeling the sun compass learning problem. This is a connectionist neural network model (Feldman & Ballard, 1982). This contrasts with all of the previous computational models that were of a symbolic nature, including the new model presented in Chapter 4. A connectionist neural network is a nonsymbolic model (Rumelhart & McClelland, 1986; Smolensky, 1988). In contrast with the symbolic models, the representations in connectionist neural network models consist of

the distributed pattern of connections between neural elements. In the case of the sun compass learning problem, a connectionist representation does not encode an explicit algebraic equation describing the position of the sun at different times of day.

Connectionist neural networks are loosely inspired by the structure of real biological neural networks (McCulloch & Pitts, 1943). They consist of a large number of simple processing elements operating in parallel (Feldman & Ballard, 1982). A representation in a connectionist neural network is distributed across the connection weights between the neural elements (Hinton et al., 1986). This contrasts with the structure of a representation in a symbolic model in which the representation consists of symbols manipulated by logical operations (Feldman & Ballard, 1982). In the connectionist framework, the operations on the neural elements are numerical and can be considered subsymbolic (Smolensky, 1988) because they operate on a level below the traditional symbol. A symbol of the traditional artificial intelligence framework may be distributed across hundreds of neural elements in the connectionist framework. The elements independently perform numerical operations on their component of the higher level symbol. Thus, the computations on the symbols are not isomorphic to the higher level logical operations. For example, in a connectionist model of stereopsis, there is no unit that computes depth (Boden, 1991). Rather the computation of depth is distributed across numerous simple elements that each respond to local inputs, computing some microfeature of the overall pattern. The representation of depth emerges from the activity pattern of the network as a whole.

In the symbolic representation of the sun compass learning problem, input symbols corresponding to azimuth position and time of day are manipulated by an explicit algebraic function to yield output symbols also corresponding to azimuth position and time of day. Since there is no explicit algebraic function that computes outputs from inputs in the connectionist framework, the representation of the sun's course emerges from the activity pattern of an entire network. It is computed from the numerous independent numerical computations of the units in the network. This is a new way of looking at the sun compass learning problem.

One problem with the approach advocated by Gallistel is that it focuses extensively on the symbolic aspects of computation to the point of excluding *a priori* nonsymbolic solutions to certain computational problems. Connectionist neural networks (Feldman & Ballard, 1982) may form just such a solution to some of the computational problems that Gallistel (1990) presents. Gallistel (in press) has argued strongly that certain processes in insect navigation cannot be implemented in a nonsymbolic (connectionist) framework. He singles out the sun compass learning problem as one such process. This issue will comprise a central focus of this dissertation.

Yet Gallistel (1990) deserves credit for focusing attention on the information-processing problems of navigation. This presents clear computational problems that must be solved, even in the brains of some of the smallest animals. Connectionism has often focused on

much larger and more intractable problems such as language (e.g. Sejnowski & Rosenberg, 1986).

The content of Chapters 4 and 5 sets up a dichotomy between symbolic and nonsymbolic models. Some would argue that this is a false dichotomy (see Boden, 1991). Boden argues that the two approaches are not as different as they might seem. In fact, both can trace their heritage to the seminal work of McCulloch and Pitts (1943). The differences between the approaches may reduce to differences in focus: while the symbolic approach focuses on *what* is being computed, the connectionist approach focuses on *how* it is being computed. It may in fact be more fruitful to use Marr's (1982) framework, which divides information-processing problems into three levels: computation, algorithm, and implementation. The question of what is being computed lies at the first level. The second level consists of the specific algorithm used to perform the computation. There are potentially multiple algorithms for any given computation. Finally, there is the level of the hardware implementation. Likewise, the same algorithm may be implemented on different hardware. The traditional symbolic approach is top-down, starting with the computational level and proceeding to the algorithmic level. In contrast, the connectionist approach is essentially bottom-up, although it does not start with a specific neural implementation but a generalized one. Nevertheless, it is not easy to integrate the approaches, because they meet on uneasy ground at the level of the algorithm and do not flow smoothly together (Clark, 1990). With this in mind, I will follow the distinction that has been maintained from both sides of the issue (Smolensky, 1988; Gallistel, in press).

In Chapter 6, I present a general discussion of the issues raised in the previous five chapters. I will focus on comparing the assumptions and predictions of the models presented in Chapters 4 and 5. Although this entire project was based on behavioral experiments and modeling, it attempts to describe something about the neural computations that are occurring in the brain of the bee. From the data presented in Chapter 3, it is clear that insects account for the nonlinear pattern of the movement of the sun's azimuth in order to use it as a compass reference. It is still unclear exactly how they do this. Through the construction of models presented in Chapters 4 and 5, I have explored the domains in which this behavioral problem must be solved in the brain. There is no question that this is a computational problem that an animal with a relatively small brain can solve. There is considerable debate about the nature of representations in the brain and the types of computational process that exist (Smolensky, 1988; Gallistel, in press). The symbolic-nonsymbolic dichotomy is a major question in this debate. The sun compass problem may be able to shed some light on this issue. In Chapters 4 and 5, I show that the neural processes necessary for sun-azimuth estimation could exist in either a symbolic or a nonsymbolic form. Although there may be an infinite number of computational models that could approximate the behavior of the bees in sun compass learning, the modeling effort yields testable predictions about the behavior that may be able to guide neurophysiological research. Thus behavioral experiments combined with modeling can be a powerful tool to help decipher the nature of neural computations on a complex spatiotemporal representation.

Chapter 2

SUN COMPASS ORIENTATION

Compasses are mechanisms for determining direction. For most people, the most familiar compass measures directions relative to the earth's magnetic field. The needle on the compass points to the geomagnetic pole. Many animals have a compass sense (reviewed in Able, 1980). The most common of these are magnetic and celestial. I will focus on the latter, and I will be specifically concerned with the use of the sun as a celestial compass. A compass can be used in combination with other mechanisms to determine position, but a compass itself only provides directional information. In this dissertation, I will be concerned solely with the determination of direction. I will not be concerned about determinations of position or distance, though they are essential aspects of the navigation process. These are interesting problems in their own right, but they are independent from questions about the sun compass that I will be considering. Two animals could have entirely different representations of position or distance, including none at all, and still use the same compass mechanism for determining direction.

2.1 The Solar Reference

The sun is by far the most prominent object in the daytime sky, and it provides a useful compass reference for diurnal animals. However, unlike the geomagnetic poles, the sun is not a fixed geographic point. Rather the sun appears to move during the day because of the rotation of the earth. Any animal that uses the sun as a compass must account for this apparent movement.

The pattern of solar movement is consistent and predictable--it always rises in the eastern part of the sky and sets in the western part of the sky--but the precise pattern of movement varies with season and with latitude. During the northern summer, the sun rises in the northeast and sets in the northwest, while during the northern winter, it rises in the southeast and sets in the southwest. In the northern temperate regions, the sun always passes to the south at local noon, while in the southern temperate regions it always passes to the north at local noon. In the tropics at noon, it passes either north, south or directly overhead depending on the season.

The general features of solar movement are conveyed in Figure 2.1 which shows the pattern of solar movement for 40°, 25° and 5° north latitude at the equinox and at the northern summer solstice. The figure represents a projection of the sun onto the celestial hemisphere. The center points correspond to the zenith, which is the point directly overhead of the observer. The outer circles correspond to the horizon line. The sun's hourly position is plotted by the dark circles. The distance from the horizon line to the sun

corresponds to the sun's elevation in the sky. The distance from the zenith point to the sun is the zenith distance.

The figure illustrates an important element of solar movement that complicates its use a compass. This emerges from the fact that the directional information is given by the sun's position along the horizon. In the figure, the angle on the polar plots corresponds to direction, which is measured clockwise from north (0°). This angle is the sun's azimuth. The pattern of movement of the azimuth is more complex than the pattern of movement of the sun itself. The azimuth does not change at a constant rate throughout the day. During an hour the sun moves 15° along its arc, but the distance traveled along the horizon varies with time of day, season and latitude. Extending arcs from the zenith through the sun's hourly position to the horizon illustrates this point (see example for 40° N at the equinox in Figure 2.1). The angular change in the sun's hourly position around the horizon is relatively small during the early and late parts of the day as the sun is rising and setting, but is much larger during the middle of the day. This pattern of variation is slightly different for different seasons and latitudes. At high latitudes the variation in the rates of change of the azimuth is much less than it is in low latitudes.

Figure 2.1 Pattern of solar movement for different seasons and latitudes. The figure represents a projection of the sun onto the celestial hemisphere. The center points correspond to the zenith, which is the point directly overhead of the observer. The outer circles correspond to the horizon line. The sun's hourly position is plotted by the dark circles. The distance from the horizon line to the sun corresponds to the sun's elevation in the sky. The distance from the zenith point to the sun is the zenith distance. Extending an imaginary line from the zenith through the sun's position to the horizon reveals the position of the sun's azimuth which provides the directional information for sun compass orientation. See example for 40° N equinox. The rate of change of the azimuth varies over the course of the day and with season and latitude. This can be seen in the comparison of the change in azimuth between 7:00 and 9:00 vs. 11:00 and 13:00 (drawn for 40° N).

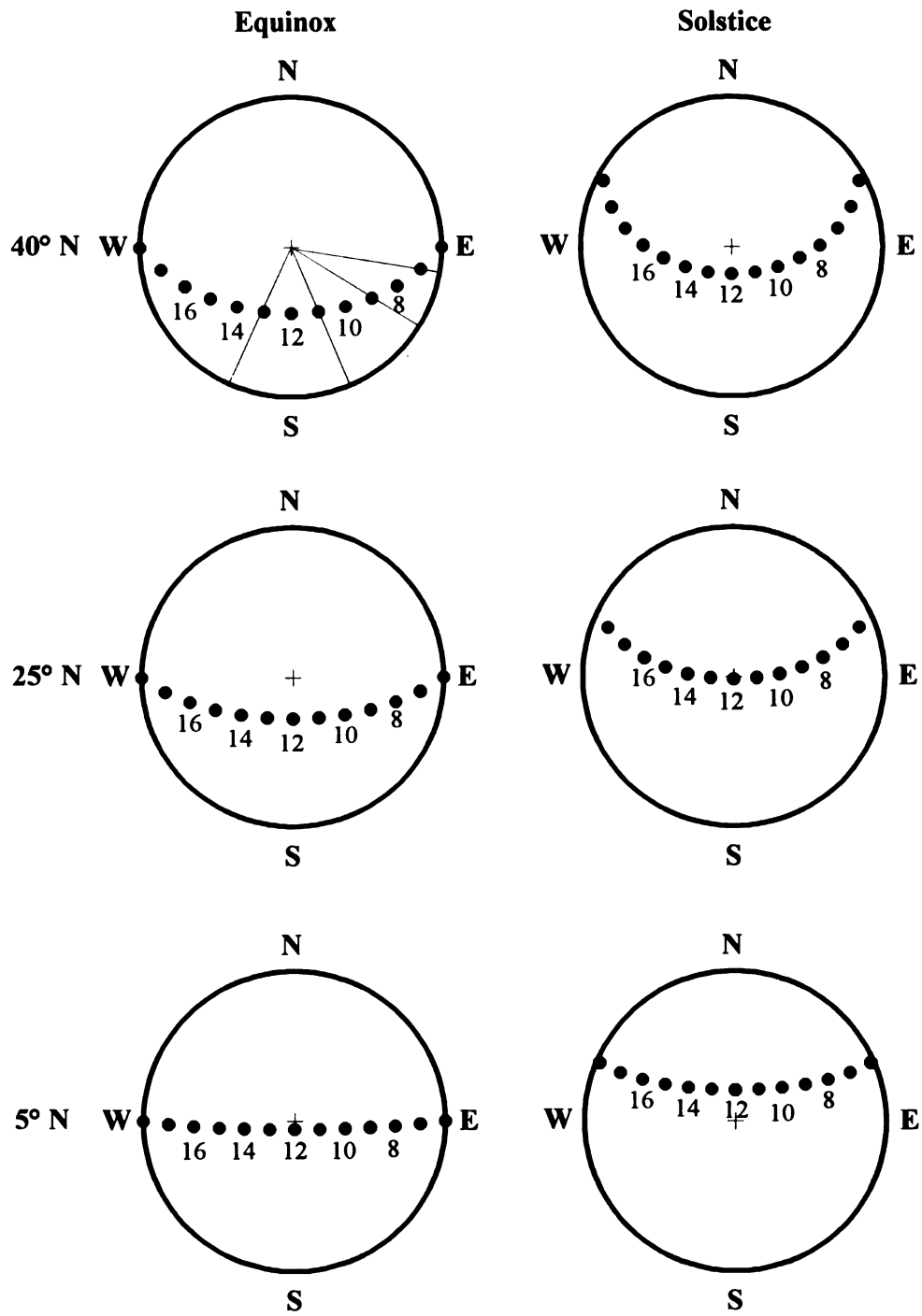


Figure 2.1

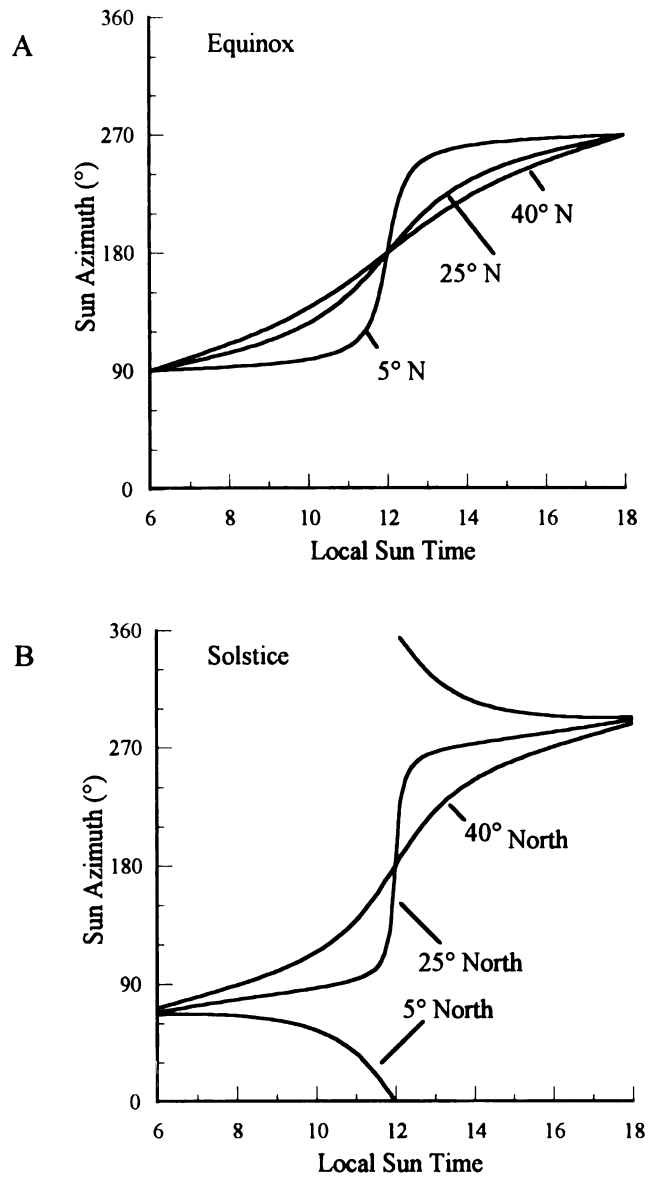


Figure 2.2 Seasonal and latitudinal variation of the ephemeris function. A. Ephemeris functions for 5°, 25° and 40° North latitude for the equinox. B. Ephemeris functions for 5°, 25° and 40° North latitude for the solstice. Solar azimuth is plotted against local sun time. The two panels show the considerable variation in the rate of change of the azimuth over the course of the day and with season and latitude.

The variation in the rate of change of the azimuth, with respect to time of day, season and latitude, is more easily analyzed when the azimuth angle is plotted against time as in Figure 4.2. Figure 4.2 presents the "azimuth curves" for the same six season-latitude combinations illustrated in Figure 4.1. In general, the graphs of azimuth position against time take the form of S-shaped curves. The curves are steepest during the middle of the day when the azimuth is changing most rapidly and flatter in the early and late portions of the day when the sun moves more slowly along the horizon. Azimuth curves from tropical regions show a more extreme variation in slope (or rate of change of the azimuth) between the middle and ends of the day than curves from temperate regions. A negative slope at lower latitudes indicates that the azimuth is moving counter-clockwise around the horizon and passing to the north of the observer at noon rather than to the south as is typical of northern latitudes.

The shapes of the azimuth curves reveal that there are considerable nonlinearities in the rate of change of the azimuth. To obtain directional information from the sun, an animal must be able to account for the nonlinear relationship between the sun's azimuth and time of day. Furthermore, since the pattern of change varies with season and latitude, the animal must be able to utilize the appropriate local pattern of change. It has long been known that animals are able to do this. Such an animal is said to have a time-compensated sun compass. There are several possible mechanisms that could accomplish time compensation.

The mechanisms can be grouped in two main categories. First, information about the position of the sun's azimuth at a particular time of day could be extracted from a look-up table (Churchland & Sejnowski, 1989) (analogous to an ephemeris table, e.g. Whiting, 1669). Such a look-up table could conceivably be genetically hard-wired. Second, the azimuth could be computed from the relevant information, which could include time of day, season and latitude. This second class of solutions corresponds to Gallistel's (1990) computational-representational framework. Both these methods could be used to obtain either the actual azimuth angle for a specific time of day or they could be used to obtain approximate or estimated azimuth angles for specific times of day.

There are three further subdivisions based on the amount of information about the movement patterns of the sun that is encoded in the animal's genes. First, the animal could have a complete innate ephemeris function. This would be a universal ephemeris that would be good any time of day and season, anywhere on the planet. To account for seasonal and geographic variability, the animal would need to have some way of using the appropriate innate ephemeris function. This is true regardless of whether the animal is using a look-up table or computing the function. In order to access the true ephemeris function, the animal would have to assess time of day, time of year (solar declination, the angle of latitude at which the sun is directly overhead at noon) and latitude. The true solar ephemeris is a function of these three variables. To compute the position of the azimuth with these parameters, the following equations are used (Brines, 1978):

$$\cos(ZS) = \sin(D)\sin(L) + \cos(D)\cos(L)\cos(T) \quad (2.1)$$

$$\sin(A) = \frac{\sin(D) - \cos(ZS)\sin(L)}{\sin(ZS)\cos(L)} \quad (2.2)$$

where A is azimuth, ZS is solar zenith distance, D is solar declination, L is the latitude of the observer, and T is time degrees from local noon. The solar zenith distance (ZS) can be determined from equation 2.1 and substituted into equation 2.2 to obtain azimuth.

The main problem for an animal using these equations to compute the azimuth angle is in obtaining information about the latitude and the declination of the sun. Both of these variables are confounded in the zenith distance of the sun (equation 2.1), so it would be difficult to assess them independently.

Second, the animal could have an innately determined ephemeris that is not universal, but is adapted to the local geographic range of the animal. This eliminates the need to assess latitude. This function could vary with season, or, if the animal is particularly short-lived, and lives at a certain time of year, a single genetically determined ephemeris function may be suitable for the animal's entire life. Again, this could be implemented with either a look-up table or an explicit function. In this case, some of the variables in equations 2.1 and 2.2 would be constants.

Third, the animal could learn the local pattern of movement with respect to local geographic features. This could be done by filling a look-up table with time-linked azimuth positions. This would be a form of associative learning. Alternatively, the animal could use observable quantities such as time of day and position of the azimuth to calculate the position of the azimuth. Such a calculation would not depend on the latitude or declination of the sun. This calculation could be an approximation of the true azimuth function. If the animal is long-lived and/or travels long distances latitudinally the animal would have to update its representation of the sun's course.

Many experimental studies have implicated this third solution to the problem of accurately compensating for the changing azimuth over the course of the day (see below for details). Different animals may use different solutions to the problem, but the main emphasis of this dissertation will be on the animals that rely on the third alternative. Of those animals, I will be primarily concerned with how insects (particularly honey bees) solve this problem.

2.2 Discovery of the Sun Compass

Suggested as early as 1911 by Santschi (Santschi, 1911, discussed by Wehner, 1990), the use of a time-compensated sun compass for orientation was first demonstrated for both birds (Kramer, 1950) and bees (Frisch, 1950) in 1950. The sun compass has subsequently been demonstrated in a wide range of vertebrates and invertebrates.

In order to conclude that an animal is using a sun compass, its effect on the homing ability of an animal must be dissociated from other possible compass mechanisms such as a magnetic compass or other cues such as landmarks. If an animal orients accurately on a sunny day, but is disoriented on a completely overcast day, that is strong evidence that the sun is necessary for orientation. Note that even if the sun is obscured by clouds, but blue sky is visible, a sun compass may be used, since the position of the sun can be determined from the polarization patterns of skylight. Many animals effectively use these cues for orientation (Adler & Phillips, 1985; Fent, 1986; Rossel & Wehner, 1986; Phillips & Moore, 1992).

Evidence that an animal orients correctly on a completely overcast day does not rule out the possibility that it can use the sun as a compass on a sunny day. Most orientation mechanisms have multiple redundant systems (Able, 1980). The animal may simply use an alternative compass mechanism or landmarks if the sky is cloudy. To distinguish between the possible roles of different orientation cues, the cues need to be put in opposition. Many animals will favor the sun compass when it is in opposition with other cues. One method of accomplishing this is to clockshift the animal (Hoffmann, 1960), by putting it on a light-dark cycle that is shifted in phase relative to the actual light-dark cycle. In these circumstances an animal will orient in a predictable wrong direction, since the actual position of the sun is different from the predicted position based on the animal's internal sense of time. Another method of dissociating the direction indicated by the sun compass from alternative compass mechanisms is to transport the study animal to a new longitude

where the animal's internal clock is out of phase with the local time (Papi, 1955; Renner, 1959). Again, if the animal is relying on the sun compass it will orient in a predictable wrong direction. Longitudinal translocations also prove that the temporal information is endogenous and independent from the position of the sun itself.

2.3 Distribution in the Animal Kingdom

A wide range of animals can use the sun for orientation. Table 2.1 provides a compendium of the animals in which a sun compass has been strongly implicated. Time compensation is suggested (though not definitively proved) in all of the cases in the table. Historical precedence has been implemented throughout the table. In many cases, later studies provided additional (sometimes critical) evidence, but they have not been included. The list of references for each species is not exhaustive.

Much of the work on the sun compass in animals has focused on birds and arthropods. Nevertheless, the assortment of work in other groups reveals the widespread use of the sun compass. One is present for example in nearly all groups of extant vertebrates. Intriguingly, our own group, the mammals, may be the least likely to use this mechanism. This probably stems from the nocturnal activity patterns of most mammals (Bovet, 1992). But there are nevertheless several examples of sun compass orientation in mammals.

Among the invertebrates, numerous arthropods have been shown to use the sun as a compass. Other groups have been investigated much less, but the sun compass has been

implicated in mollusks (Warburton, 1973; Hamilton & Russel, 1982) and even in a cnidarian (Scyphozoa) (Hamner et al., 1994). This latter fact is particularly intriguing since jellyfish do not have a centralized nervous system.

The variety of animals that exhibit sun compass orientation is impressive, and one could potentially draw some conclusions regarding the evolution of the trait. But when considering the evolutionary implications of this list, it is important to distinguish between species that have not been tested and those that have been tested, and no evidence of sun-compass orientation was found. It is much harder to isolate examples of this latter type from those in which the sun compass has been verified. It is less clear which groups specifically do not have the ability to use the sun as a navigational compass. This problem could stem in part from non-publication of negative results, or even more significantly, from the lack of study of groups assumed not to have complex orientation mechanisms. The context in which definitive negative results are likely to be published are in comparative studies among groups of species, some of which use the sun as a compass and some of which do not. Unfortunately, there are very few comparative studies of this type. In the cases where this has been studied, some interesting patterns of the presence and absence of a sun compass emerge. This is particularly true in the Coleoptera, where some families have sun-compass orientation (e.g. Frantsevish, 1977) and others do not (Scapini et al., 1993). A similar pattern appears to exist within the isopod genus *Tylos* (Hamner et al., 1968; Ugolini et al., 1995). Further investigation of cases of this type would be of considerable interest in an evolutionary analysis of the sun compass.

Table 2.1 Distribution of the Sun Compass in the Animal Kingdom

Phylum	Class	Genus species (Order: Family)	Reference
Cnidaria	Scyphozoa	<i>Aurelia aurita</i> (Semaeostomae) (jellyfish)	Hamner et al., 1994
Mollusca	Gastropoda	<i>Nerita plicata</i> (Prosobranchia: Neritidae) (snail)	Warburton, 1973
		<i>Aplysia brasiliana</i> (Opisthobranchia: Anaspidea) (sea hare)	Hamilton & Russel, 1982
Arthropoda	Chelicerata	<i>Arctosa perita</i> (Araneae: Lycosidae) (wolf spider)	Papi, 1955a
		<i>Lycosa fluviatilis</i> (Araneae: Lycosidae) (wolf spider)	Papi & Syrjämäki, 1963
	(Crustacea) Malacostraca		
	Amphipoda	<i>Talitrus saltator</i> (Amphipoda: Talitridae) (sandhopper)	Pardi & Papi, 1952
		<i>Talorchestia</i> spp. (Amphipoda: Talitridae) (sandhopper)	Pardi & Grassi, 1955

Table 2.1 (cont'd)

	<i>Orchestia mediterranea</i> (Amphipoda: Talitridae) (sandhopper)	Pardi, 1960
	<i>Orchestoidea</i> spp. (Amphipoda: Talitridae) (sandhopper)	cited in Herrnkind, 1972
Decapoda		
	<i>Goniopsis cruentata</i> (Decapoda: Grapsidae) (mangrove crab)	Schöne, 1963
	<i>Ocypode ceratophthalma</i> (Decapoda: Ocypodidae) (ghost crab)	Daumer et al., 1963
	<i>Uca tangeri</i> (Decapoda: Ocypodidae) (fiddler crab)	Altevogt & von Hagen, 1964
	<i>Pagurus longicarpus</i> (Decapoda: Paguridae) (hermit crab)	Rebach, 1978
	<i>Callinectes sapidus</i> (Decapoda: Portunidae) (blue crab)	Nishimoto & Herrnkind, 1982
	<i>Palaemonetes antennarius</i> (Decapoda: Palaemonidae) (freshwater shrimp)	Ugolini et al., 1989

Table 2.1 (cont'd)

Isopoda		
	<i>Tylos latreilli</i> (Isopoda: Tylidae) (littoral isopod)	Pardi, 1954
	<i>Idotea baltica</i> (Isopoda: Idoteidae) (marine isopod)	Ugolini & Messana, 1988
Insecta		
Collembola		
	<i>Hypogastrura socialis</i> (Collembola: Hypogastruridae) (springtail)	Hågvar, 1992
Orthoptera		
	<i>Nemobius sylvestris</i> (Orthoptera: Gryllidae) (wood cricket)	Beugnon, 1983
	<i>Pteronemobius lineolatus</i> (Orthoptera: Gryllidae) (swimming cricket)	Beugnon, 1987
	<i>Gryllotalpa gryllotalpa</i> (Orthoptera: Gryllotalpidae) (mole cricket)	Ugolini & Felicioni, 1991
Dermaptera		
	<i>Labidura riparia</i> (Dermaptera: Labiduridae) (earwig)	Ugolini & Chiussi, 1996
Hemiptera		
	<i>Velia currens</i> (Hemiptera: Veliidae) (waterstrider)	Birukow, 1956 (but cf. Heran (1962) and Schmidt-Koenig (1975))

Table 2.1 (cont'd)

Coleoptera		
<i>Scarites terricola</i>	Papi, 1955b	
(Coleoptera: Carabidae) (ground beetle)		
<i>Omophron limbatum</i>	Papi, 1955b	
(Coleoptera: Carabidae) (ground beetle)		
<i>Dyschirus numidicus</i>	Papi, 1955b	
(Coleoptera: Carabidae) (ground beetle)		
<i>Phaleria provincialis</i>	Pardi, 1956	
(Coleoptera: Tenebrionidae) (darkling beetle)		
<i>Paederus rubrothoracicus</i>	Ercolini & Badino, 1961	
(Coleoptera: Staphylinidae) (rove beetle)		
<i>Stenus bipunctatus</i>	Ercolini & Scapini, 1976	
(Coleoptera: Staphylinidae) (rove beetle)		
<i>Lethrus</i> spp.	Frantsevish et al., 1977	
(Coleoptera: Scarabaeidae)		
<i>Eurynebria complanata</i>	Colombini et al., 1994	
(Coleoptera: Carabidae) (ground beetle)		

Table 2.1 (cont'd)

Hymenoptera		
	<i>Apis mellifera</i> (Hymenoptera: Apidae) (honey bee)	Frisch, 1950
	<i>Formica rufa</i> (Hymenoptera: Formicidae) (wood ant)	Jander, 1957
	<i>Lasius niger</i> (Hymenoptera: Formicidae)	Jander, 1957
	<i>Cataglyphis</i> spp. (Hymenoptera: Formicidae) (desert ant)	Wehner, 1972
Diptera		
	<i>Diamesa</i> spp. (Diptera: Chironomidae) (wingless glacier midge)	Kohshima, 1985
Chordata		
(Pisces)		
Osteichthyes		
	<i>Lepomis</i> spp. (Perciformes: Centrarchidae) (sunfish)	Hasler et al., 1958
	<i>Roccus (Morone)</i> <i>chrysops</i> (Perciformes: Centrarchidae) (white bass)	Hasler et al., 1958
	<i>Aequidens</i> <i>portalegrensis</i> (Perciformes: Cichlidae) (port-cichlid)	Braemer, 1959

Table 2.1 (cont'd)

<i>Cichla</i> <i>severus</i> (Perciformes: Cichlidae) (South American cichlid)	Schwassmann & Hasler, 1964
<i>Uru</i> <i>amphiacanthoides</i> (Perciformes: Cichlidae) (South American cichlid)	Schwassmann & Hasler, 1964
<i>Scarus</i> spp. (Perciformes: Scaridae) (parrot fish)	Winn et al. 1964
<i>Oncorhynchus nerka</i> (Salmoniformes: Salmonidae) (sockeye salmon)	Groot, 1965
<i>Anableps</i> spp. (Cyprinodontiformes: Anablepidae) (four-eyed fish)	Schwassmann, 1967
<i>Anguilla rostrata</i> (Anguilliformes: Anguillidae) (American eel)	Miles, 1968
<i>Gambusia affinis</i> (Cyprinodontiformes: Poeciliidae) (mosquito fish)	Goodyear & Ferguson, 1969
<i>Fundulus notti</i> (Cyprinodontiformes: Poeciliidae) (starhead topminnow)	Goodyear, 1970
<i>Zenarchopterus dispar</i> (Cyprinodontiformes: Hemiramphidae) (halfbeak)	Forward, et al., 1972

Table 2.1 (cont'd)

	<i>Micropterus salmoides</i>	Loyacano et al., 1977
	(Perciformes: Centrarchidae) (largemouth bass)	
	<i>Cheirodon pulcher</i>	Levin et al., 1992
	(Characiformes: Microcharacidae) (tetra)	
Amphibia		
	<i>Acris</i> spp.	Ferguson 1963
	(Anura: Hylidae) (cricket frog)	
	<i>Bufo fowleri</i>	Ferguson & Landreth, 1966
	(Anura: Bufonidae) (Fowler's toad)	
	<i>Pseudacris triseriata</i>	Landreth & Ferguson, 1966
	(Anura: Hylidae) (chorus frog)	
	<i>Ascaphus truei</i>	Landreth & Ferguson, 1967a
	(Anura: Ascaphidae) (tailed frog)	
	<i>Taricha granulosa</i>	Landreth & Ferguson, 1967b
	(Caudata: Salamandridae) (rough-skinned newt)	
	<i>Rana catesbeiana</i>	Ferguson et al., 1968
	(Anura: Ranidae) (bullfrog)	
	<i>Rana pipiens</i>	Jordan et al., 1968
	(Anura: Ranidae) (southern leopard frog)	
	<i>Bufo boreas</i>	Gorman & Ferguson, 1970
	(Anura: Bufonidae) (western toad)	
	<i>Ambystoma tigrinum</i>	Taylor, 1972
	(Caudata: Ambystomatidae) (tiger salamander)	

Table 2.1 (cont'd)

Reptilia		
<i>Terrapene c. carolina</i>	Gould, 1957	
(Testudinata: Testudinidae) (box turtle)		
<i>Chrysemys picta</i>	Gould, 1959	
(Testudinata: Testudinidae) (painted turtle)		
<i>Lacerta viridis</i>	Fisher & Birukow, 1960	
(Squamata: Lacertidae) (emerald lizard)		
<i>Crotalus atrox</i>	Landreth, 1973	
(Squamata: Viperidae) (rattlesnake)		
<i>Natrix sipedon</i>	Newcomer et al., 1974	
(water snake) (Squamata: Colubridae)		
<i>Regina septemvittata</i>	Newcomer et al., 1974	
(water snake) (Squamata: Colubridae)		
<i>Trionyx spinifer</i>	DeRosa & Taylor, 1980	
(Testudinata: Trionychidae) (softshell turtle)		
<i>Alligator mississippiensis</i>	Murphy, 1981	
(Crocodylia: Alligatoridae) (American alligator)		
<i>Uma notata</i>	Adler & Phillips, 1985	
(Squamata: Iguanidae) (fringe-toed lizard)		

Table 2.1 (cont'd)

	<i>Sceloporus jarrovi</i> (Squamata: Iguanidae) (desert lizard)	Ellis-Quinn & Simon, 1991
	<i>Thamnophis</i> spp. (Squamata: Colubridae) (garter snake)	Lawson, 1994
Aves		
	<i>Sturnus vulgaris</i> (Passeriformes: Sturnidae) (starling)	Kramer, 1950
	<i>Columba livia</i> (Columbiformes: Columbidae) (pigeon)	Matthews, 1953
	<i>Lanius collurio</i> (Passeriformes: Laniidae) (red-backed shrike)	von St. Paul, 1953
	<i>Sylvia nisoria</i> (Passeriformes: Sylviidae) (three barred warbler)	von St. Paul, 1953
	<i>Sturnella neglecta</i> (Passeriformes: Icteridae) (western meadowlark)	von St. Paul, 1956
	<i>Anas platyrhynchos</i> (Anseriformes: Anatidae) (mallard)	Matthews, 1963
	<i>Pygoscelis adeliae</i> (Sphenisciformes: Spheniscidae) (Adelie penguin)	Emlen & Penney, 1964

Table 2.1 (cont'd)

	<i>Zonotrichia albicollis</i> (Passeriformes: Emberizidae) (white-throated sparrow)	Able & Dillon, 1977
	<i>Aphelocoma coerulescens</i> (Passeriformes: Corvidae) (scrub jay)	Wiltschko & Balda, 1989
	<i>Erithacus rubecula</i> (Passeriformes: Turdidae) (European robin)	Helbig, 1991
Mammalia		
	<i>Apodemus agrarius</i> (field mouse) (Rodentia: Muridae)	Lüters & Birukow, 1963
	<i>Delphinus delphis</i> (Cetacea: Delphinidae) (common dolphin)	Pilleri & Knuckey, 1969
	<i>Microtus pennsylvanicus</i> (Rodentia: Cricetidae) (meadow vole)	Fluharty et al., 1976
	<i>Spermophilus tridecemlineatus</i> (Rodentia: Sciuridae) (thirteen-lined ground squirrel)	Haigh, 1979
	<i>Eptesicus fuscus</i> (Chiroptera) (big brown bat)	Buchler & Childs, 1982

2.4 Directional Information from the Sun

The sun can provide a directional reference for many different types of oriented activity. These range from relatively simple directional movements to true navigation over long distances. In this section, these categories are introduced. The next section provides a detailed account of sun compass orientation in a particular animal.

2.4.1 The Sun as a Point Source

The simplest form of directional orientation takes the form of a taxis in which the organism makes directed movements toward or away from a particular cue (see Schöne, 1984). Phototaxis is a common type of this movement. Since the sun is the strongest point source of light on the planet, many organisms make directed movements toward it. This would not be classified as sun compass orientation, even though it can lead to oriented behavior. Organisms that exhibit merely a phototactic response rather than time-compensated sun compass orientation are not included in Table 2.1.

When an animal moves at a fixed angle relative to a directional point source, it exhibits a form of orientation termed *menotaxis* (see Schöne, 1984). This mechanism can be relative to the sun or other celestial bodies and involve time compensation: *chronometric astromenotaxis*. For many animals that use this orientation mechanism, the sun defines a locally important direction.

2.4.2 The Sun Defines a Local Direction

Many animals live in environments with important directions defined only in one dimension. This occurs for species that live along an ecotone, such as the shore of a ocean, lake or river. Many of the species that live in such areas have orientation mechanisms that allow them to determine the local direction perpendicular to the ecotone. This form of orientation has been termed y-axis orientation (Ferguson, 1967) to distinguish it from orientation along the x-axis: the shore or ecotone. This mechanism has also been called zonal orientation (Jander, 1975) and it has received considerable attention (see Herrnkind, 1983; Pardi & Ercolini, 1986). The sun compass is a dominant orientation reference that is used in these circumstances, although it is one of many possible mechanisms (Hartwick, 1976). In these cases, the sun defines a locally important direction for species that move efficiently to safety zones that are in one particular direction. The directed movements occur irrespective of time of day, so this compass mechanism is time compensated. An example of this type of movement is between the edge and the middle of a lake. This mechanism is used by many fishes (Goodyear, 1970; Goodyear & Bennett, 1979) and amphibians (Ferguson & Landreth, 1966; Ferguson, 1967; Landreth & Ferguson, 1967; Ferguson et al., 1968; Jordan et al., 1968) in addition to some insects and crustaceans. An analogous situation occurs on beaches where the y-axis direction is perpendicular to the beach. Many littoral zone animals use this mechanism as an escape response (reviewed in Herrnkind, 1972, 1983). This orientation system has been extensively studied in the amphipod crustacean *Talitrus saltator*, which has revealed

genetic and learned components of the behavior (Pardi & Papi, 1952; Pardi, 1960; Pardi & Scapini, 1983; Ugolini & Macchi, 1988; Scapini & Fasinella, 1990).

2.4.3 The Sun Defines a Global Direction

Y-axis orientation can be thought of as a mechanism of local direction-finding.

Specifically, the local direction is the direction toward or away from a shoreline. The sun can also define a global direction. Thus the local environment can be linked with a global geocentric reference frame. This is particularly important for long distance migrants.

Migrating birds for example must fly in a particular geocentric direction (e.g. north).

Many birds use the sun or the pattern of skylight polarization to determine their migrational direction and/or calibrate their magnetic compass (reviewed in Wiltschko, & Wiltschko, 1991). In some cases there is no evidence of time compensation (or it has not been examined) (Moore, 1980) while in others there is (Helbig, 1991). Thus the sun or skylight polarization patterns can be used to define a geocentric coordinate without necessarily being used as a time-compensated compass. Since the sun always sets in the western half of the sky if restricted to a particular time of year, the sunset defines a static direction. Sunset calibration could thus occur without a true time-compensating sun compass. In Table 2.1 I have attempted to restrict the cases to species in which time compensation is likely.

2.4.4 The Sun Defines Any Flexible Direction

In many cases, the sun compass can be used to obtain directional information about any flexible local direction. An example of this type of orientation is seen in the decapod crustacean *Ocypode ceratophthalma* (Daumer et al., 1963). This crab provides a contrast to the many beach-dwelling crustaceans and insects that merely exhibit y-axis orientation. The crab maintains a burrow in the sand, the entrance of which is not demarcated by landmarks. After moving about the beach in search of food, if this crab encounters a potential predator it will run directly to its burrow instead of adopting a stereotyped response direction toward or away from the water. The escape run is oriented by the sun and the skylight polarization patterns and its use of the sun compass is time-compensated. This suggests a flexible system that is capable of learning any direction with respect to the sun. Such a system is constantly updated as the position of the animal and the position of the sun change. This system, known as path integration, has been extensively studied in desert ants (Wehner & Wehner, 1986; Müller & Wehner, 1988) and it appears to exist in beetles (Frantsevish et al., 1977) and bees (Frisch, 1950, 1967) among other arthropods. Many vertebrates have the ability to use the sun to define flexible directions. It has been particularly well studied in homing pigeons (e.g. Matthews, 1953; Keeton, 1969; Wiltschko, et al., 1976, 1984; Wiltschko, & Wiltschko, 1981).

2.5 Honey Bees as a Model System

It is clear that numerous animals may use the sun as a compass. In this dissertation, I am mainly concerned with how the sun compass is learned and how animals are able to

estimate the position of the sun at times of day when they have never seen it. (I will describe this phenomenon in detail in the next chapter). The data that I rely most heavily on come from insects, particularly honey bees. This section examines the role of the sun compass in the life of the bee.

2.5.1 Long Distance Orientation

The sun compass provides directional information for orientation over long distances. It is by no means the only source of such information. Other potential compass mechanisms such as a magnetic compass could play a role, and landmarks play a prominent role in orientation. It is unclear exactly what mechanisms freely flying bees use most often to navigate, but it is safe to assume that the sun compass and landmarks play the dominant roles (Dyer, 1996). This information has been gained through displacement experiments. In the most common type, bees are trained to obtain a sucrose solution from an artificial feeding station a particular distance and direction from the hive in one landscape. Subsequently, overnight, the hive is moved to a new landscape and when the hive is opened during the day, the landings of bees are recorded at identical feeders placed at various directions from the hive (Frisch, 1967). Alternatively, bees are captured at the feeding station and subsequently released in a novel location. The new environment in either of these cases may have landmarks that resemble the site from which they originally experienced, or the site may have no prominent landmarks or landmarks that do not resemble the ones from the original feeding site. Hives can also be moved over much

greater distances longitudinally (Renner, 1959) or latitudinally (Lindauer, 1957) to distinguish the role of the celestial compass from a magnetic compass.

It is clear that when there are no landmarks present, the bees use the sun to navigate (Frisch, 1967). When landmarks are present that mimic the landmarks from the training site, the bees generally use the landmarks (Frisch & Lindauer, 1954). However, the landmarks must be very prominent to overrule the sun compass. In some cases, bees will ignore even very large landmarks and follow the direction indicated by the sun (Menzel et al., 1990).

2.5.2 Short Distance Orientation

In addition to determining a directional heading for long distance orientation, the sun compass can play a role in short-distance orientation. In this context, the sun compass can be used to resolve ambiguous landmarks (Dickinson, 1994).

It has long been known that insects use landmarks to guide their approach to a goal (Tinbergen, 1938). Recent studies have suggested that the insects move to a position to match a stored retinal image of the landmarks (Wehner, 1972; Collett & Land, 1975; Wehner & Räber, 1979; Cartwright & Collett, 1983; Dill et al., 1993). This poses a problem for a free flying insect that might encounter a landmark from any number of angles. Many potential landmarks such as trees and shrubs have radial symmetry which would render them directionally ambiguous. Because they look the same from all

directions, an insect trying to match a retinal image would search in an annulus. To resolve this ambiguity an external direction reference is required.

Lindauer (1960) first suggested that the sun might provide such a reference. He trained bees to obtain food from one corner of a symmetrical table. The rewarded corner was consistently in a particular compass direction. Subsequently, he moved the hive to a new location and placed the feeding table in a new direction. Nonetheless the bees predominantly visited the original position on the feeder. Lindauer concluded that the bees were using a time-compensated celestial compass mechanism in this task. However, other potential directional references could not be ruled out, such as the earth's magnetic field.

To determine if bees were using the sun compass to resolve ambiguous landmarks on this small of a scale, I trained bees to obtain food in an arena at one of four identical feeders placed in the cardinal compass directions from a prominent cylindrical landmark (Dickinson, 1994). Walls around the arena excluded panoramic landmarks and the cylinder was symmetrical so any directional information the bees used would have to come from an external reference. Bees were trained individually to find food at one of the feeders. In the test, there was no food present, and the number of landings on each feeder (out of the first 10) were scored. Bees learn this task very rapidly; on a sunny day they search in the appropriate direction after only two visits to the correct feeder. Figure 2.3

(A) shows the proportion of visits to the correct feeder on their fifth return to the arena. Clearly they are able to resolve the ambiguous landmark.

To determine what directional reference the bees were using, I tested them under three additional conditions. Figure 2.3 (B) shows the responses under partly cloudy sky with the sun obscured but with polarization cues available; Figure 2.3 (C) shows the responses of the bees on completely overcast days; and Figure 2.3 (D) shows the responses of bees that were subjected to a delay of three to four hours (90° of azimuthal arc) between the last training trial and the test trial. The bees were significantly oriented under all conditions except those of complete overcast. This suggests that they were using a time-compensated celestial compass to resolve the ambiguity of the landmarks as Lindauer (1960) originally suggested.

These results are somewhat puzzling in light of some recent results obtained by Collett and Baron (1994). In a similar study to the one described above, they found that bees adopt a stereotypic viewing angle of the landmarks near a goal. The viewing angle is maintained with respect to the earth's magnetic field. Adopting such a consistent viewing angle is an alternative means of resolving the ambiguity of landmarks (Collett, 1992).

In additional studies using a large screen to exclude polarization patterns, I replicated my original findings and found no evidence that the bees could use a magnetic compass to choose the appropriate direction (Dickinson, unpublished data). However, it appears that

the bees may simply take much longer to learn to rely on magnetic cues in these circumstances. In Collett and Baron's (1994) experiments, the bees had a much longer training period, amounting to more than a day. This contrasts considerably with the five visits that the bees had in my experiments.

Nevertheless, whether or not the bees are capable of using a magnetic compass under certain circumstances, it is clear that bees are able to use the sun as a directional reference for orientation over short distances.

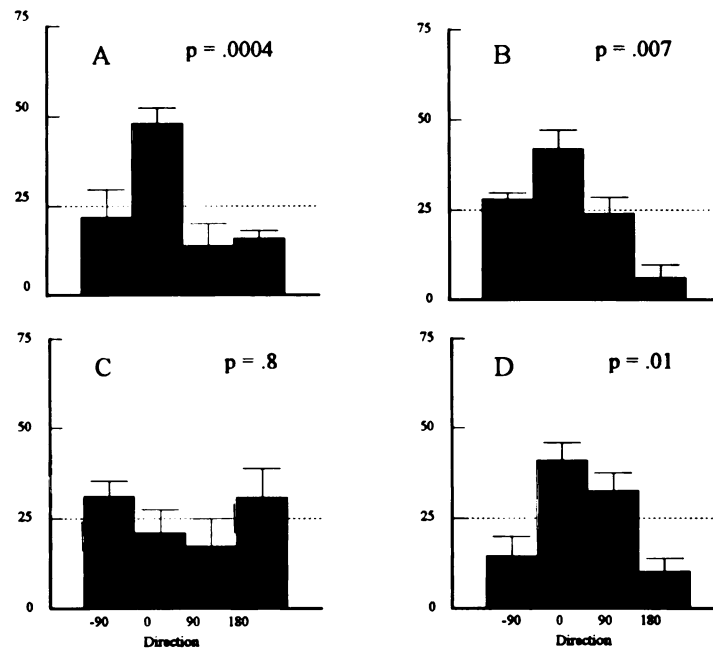


Figure 2.3 Proportion of choices to each of four directions with respect to the training direction. A. Sunny. B. Partly cloudy C. Completely overcast. D. Delay. The probabilities presented are the binomial probabilities that the pattern of choices occurred by chance (25% correct choice; 75% incorrect).

2.5.3 The Dance Language

In addition to using the sun as a navigational compass, the sun's azimuth plays a prominent role in the communicative dance language of honey bees (Frisch, 1967). Honey bees direct colony mates to profitable food sources by means of a symbolic waggle dance. The dance is so named because the prominent feature of the dance involves the bee vigorously shaking her abdomen. In the process, she completes a number of circuits in which she waggles in a straight line at a particular angle on the vertical comb. Between waggle runs, the bee turns alternatively to the left or right and returns to the starting position where she commences another waggle run.

The dance communicates the distance and direction to a food source. Distance is determined by the duration of the waggle run. Direction is determined by the angle of the waggle run with respect to vertical. The angle of deviation from vertical corresponds to the angle of deviation of the direction of the food from the sun's azimuth. For example, a bee dancing 75° to the left of vertical is indicating direction 75° to the left of the sun's azimuth (see Figure 2.4).

Over the course of a day, a bee visiting the same food source will change her angle of dance as the sun's azimuth changes position. On a cloudy day, when the bee cannot see the sun, she orients her dance to a memory of the sun with respect to landmarks (Dyer & Gould, 1981). Over an entire day, her dances changes orientation to reflect the changing

position of the sun (Dyer, 1987). This provides an essential tool for studying the bee's representation of the sun's course (Lindauer, 1957; New & New, 1962; Wehner, 1972; Wehner & Räber, 1979; Dyer, 1985, 1987; Dyer & Dickinson, 1994).

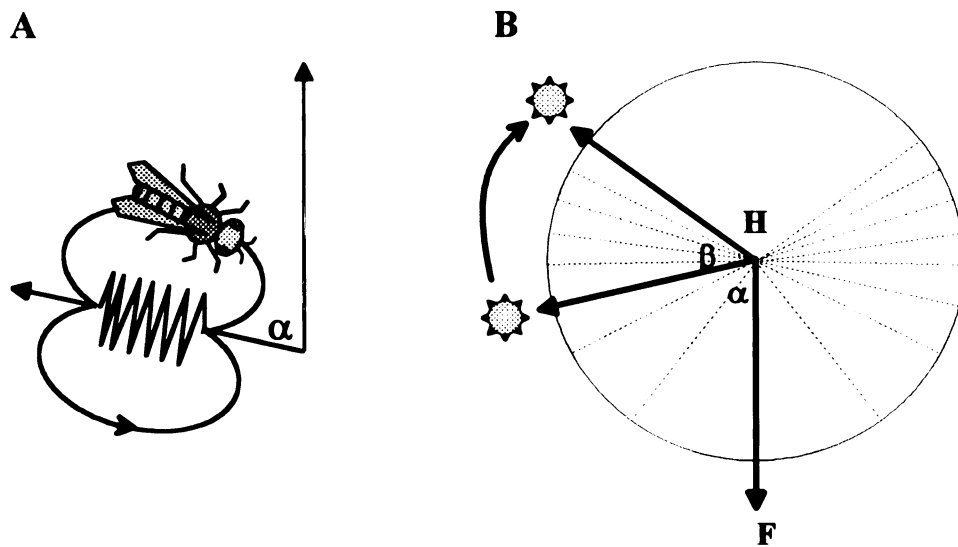


Figure 2.4 The dance language of the honey bee. The communicative waggle dance indicates the distance and direction to the food. A. The angle indicated by the waggle run (α) with respect to vertical corresponds to the angle of the food with respect to the sun's azimuth. B. The flight path from the hive (H) to a food source (F) relative to the sun's azimuth the angle α is the same as in (A). Over the course of the day, the dance angle changes as the solar azimuth moves along the horizon. Distance is indicated by the length of the waggle run.

2.6 Other Celestial Compass Mechanisms

Besides the sun, there are other celestial bodies that can contribute to orientation. In principle they have similar requirements to the sun compass, and they may reveal similar learning mechanisms.

2.6.1 The Lunar Compass

The lunar compass has been implicated in at least two species of amphipod crustaceans:

Talitrus saltator (Papi, 1960) and *Orchestoidea corniculata* (Enright, 1961).

Compensating for the change in lunar azimuth is considerably more difficult than compensating for the change in solar azimuth, because the pattern of lunar azimuthal change differs nightly.

The Asian honey bee *Apis dorsata* flies by the light of the moon at night (Dyer, 1985), but it does not use the moon in place of the sun to orient its dances at night. Instead, it continues to use the sun as a reference in the communicative waggle dance. It appears to extrapolate the position of the sun after sunset (see Chapter 3). Diurnal insects may orient to the moon if they are forced to be active at night, but they appear to use it as the sun (Jander, 1957; Wehner, 1982).

2.6.2 The Stellar Compass

Just as ancient sailors did, animals that are active during the night have the opportunity to use the stars as a navigational guide. For some birds that migrate at night, this seems to

be the case (Sauer & Sauer, 1960). In the case that has been most thoroughly studied, the birds obtain global directional information from the stars. This information comes from the overall pattern of rotation (Emlen, 1967a, b). The center point of the rotation defines true geographic north (or south). This orientation mechanism is not affected by clock shifting the birds (Emlen, 1967b), so with respect to time compensation the system is distinct from the sun compass.

2.7 Summary

Numerous animals use the sun compass for orientation in many different circumstances. Animals that use a time-compensated sun compass for orientation must account for a nonlinear change in direction indicated by the sun's azimuth with respect to time of day. Further complicating the matter is the fact that the nonlinear pattern of change varies with season and latitude. Yet the animals that use the sun compass for orientation are able to solve these problems. The mechanisms that could account for this ability are considered in the subsequent chapters.

Chapter 3

THE REPRESENTATION OF THE SUN'S COURSE

The complex pattern of movement of the sun's azimuth (described and illustrated in the previous chapter) presents a problem to all animals that use the sun as a compass. Since the pattern of movement of the azimuth varies with time of day, season and latitude, the animal must somehow be informed of the correct local pattern of movement. As discussed in the previous chapter, there are several possible types of solutions to this problem, which vary in the degree of learned versus innate information about the sun's course included in the model. In this chapter I will discuss recent experiments with honey bees that suggest that the sun compass is neither exclusively innate nor learned.

These studies suggest that honey bees employ a computational solution to the problem of compensating for the sun's apparent movement. First I will describe the previous studies that set the stage for a thorough investigation into the nature of the computations and representations involved. In the main body of this chapter, I will present the data from recent experiments by Dyer and Dickinson (1994) that provided critical new insights into the nature of the computations and representations. In addition to presenting the original data from Dyer and Dickinson (1994), I present two other data sets, and I provide new

analyses of all of the data to further illuminate the nature of the computations involved. In Chapters 4 and 5, I present new models of the computational processes of sun compass learning that may shed light on the underlying mechanisms.

3.1 Previous Studies

For honey bees it has long been known not only that bees learn the course of the sun, but that they can estimate the position of the sun at times of day when they had never seen it (Lindauer, 1957, 1959). Behavioral experiments over the nearly 40 intervening years have elucidated to a considerable degree the nature of the honey bee's representation of the sun's course.

Some of the earliest evidence about the nature of the bee's representation came from the observation of bees dancing within a colony during the night (Lindauer, 1954). These "marathon" dances occur for considerable lengths of time without the dancing bee leaving the colony. Over time the dance angles change in correspondence with the change in the sun's azimuth. While "marathon" dances can occur during the day or the night, the nocturnal dances are particularly striking because the bees would have never had an opportunity to observe the position of the sun during the night.

The use of the sun compass during an animal's physiological night has been reported for several other species including sandhoppers (Pardi, 1958b) spiders (Tongiorgi, 1959; Papi & Syrjämäki, 1963), beetles (Pardi, 1958a), water striders (Birukow, 1956; Birukow &

Busch, 1957) (but cf. Heran (1962) and Schmidt-Koenig (1975)), ants (Wehner, 1982), fish (Braemer, 1959) and birds (Hoffmann, 1959; Schmidt-Koenig, 1961, 1963). These studies have relied on three types of methods: shifting the phase of the animal's internal clock (Birukow & Busch, 1957; Pardi, 1958b; Braemer, 1959; Tongiorgi, 1959; Schmidt-Koenig, 1961; Papi & Syrjämäki, 1963), presenting an artificial light source (Birukow, 1956; Pardi, 1958a; Braemer, 1959), and transporting the animal north of the Arctic Circle to expose it to the midnight sun (Hoffmann, 1959; Papi & Syrjämäki, 1963; Schmidt-Koenig, 1963).

Bees can also estimate the position of the sun during the day at times when they have never seen it (Lindauer, 1959). When honey bees are restricted to view the path of the sun during a portion of the whole day, they nonetheless can estimate the position of the sun during other times of the day. In Lindauer's (1959) experiments, he restricted the experience of bees by raising brood in an incubator and establishing a colony of which he could completely control the experience. He only opened the colony and allowed the bees to acquire information about the sun during a limited portion of the day.

Lindauer (1957) trained the bees in the afternoon to find food in the south. Subsequently, the hive was moved to a new location (so the bees could not rely on landmarks), and the bees were allowed to fly for the first time in the morning. Four feeding stations were set up in the cardinal compass directions and the number of bees arriving were recorded. The bees flew predominantly to the south in search of food if they had seen the afternoon sun

for five days. With only three days of experience, the bees failed to choose the correct feeding station.

This was the first indication that the course of the sun was learned by the bees. Indeed, it also showed that bees do not simply remember observed positions of the sun at various times of the day, but that they can compute the position of the sun at times of day when they had never seen it. The nocturnal dances and the behavior of Lindauer's (1959) bees in the morning support the conclusion that bees can generalize their experience to other times of day. In other words, the bees appear to form a representation of the sun's course that consists of a complete function, even though they may have experience with only a portion of the function.

Unfortunately, Lindauer's (1959) data were not accurate enough to determine the computational methods the bees used to fill in the gaps in their experience with the sun. This is because in the experiments in which he restricted the bees' experience, he only measured their response to the nearest 90° (since the feeders were placed in four directions). However, subsequent studies have provided potential answers to this question and have revealed more of the details of the insect's representation of the sun's course.

Some of the most illuminating data come from studies conducted in the tropics. As illustrated in the previous chapter, the pattern of change in the solar azimuth is most variable in the tropics. The most extreme variation in the pattern of solar movement in the

tropics occurs when the azimuth abruptly switches from passing to the south at noon to passing to the north (or vice versa). New and New (1962) studied this transition period in colonies of bees in the tropics. They used the honey bees' dance language (Frisch, 1967) (see section 2.5.3) to investigate the bees' representation of the sun's course during the transition time. They trained bees to an artificial food source and recorded the dance angles of the bees visiting the food source as they changed from indicating the position of the food relative to an eastern azimuth and indicating the position of the food relative to a western azimuth. They found that the bees had consistently oriented dances even when the sun passed very close to the zenith. However, the bees' representation of the sun differed from the actual sun's course in systematic ways (see Figure 3.1). During the transition phase, the rate of change of the sun's azimuth indicated in the bees' dances was less rapid than the actual change in the sun's azimuth. Perhaps more striking is the fact that the bees anticipated the transition from a southern to a northern noon position before it actually occurred. Some individual bees (not shown in Figure 3.1) differed from each other in the pattern of azimuthal movement they indicated. New and New (1962) concluded that the bees were interpolating between known positions of the sun. That is, the bees behaved as if they were shifting their dance angles at a constant rate between memorized positions of the sun. New and New suggested that the interpolation occurred during the noon transition because the actual changes in the azimuth were below the visual acuity threshold of the bees. A similar mechanism could be used to fill other gaps in experience, such as during the night or during long periods of time during the day that the bees do not experience the pattern of azimuthal movement.

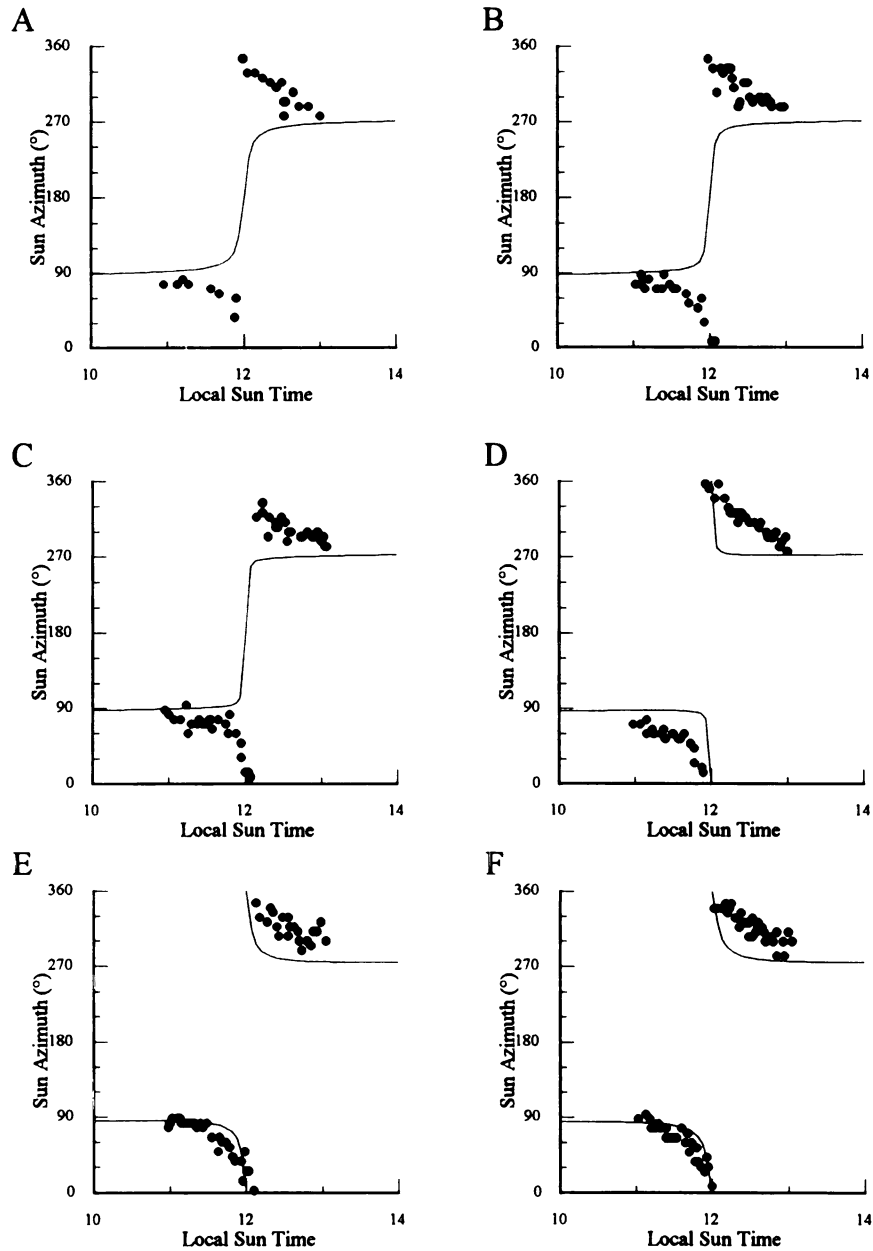


Figure 3.1 Solar azimuths inferred from the dances of the bees in New and New's (1962) experiments. Data are from colony 1 in Trinidad ($10^{\circ}38'$) on (A) April 15, (B) April 16, (C) April 17, (D) April 18, (E) April 20, and (F) April 21. Data were obtained from New and New's (1962) Figure 3 and replotted to correspond to solar azimuths rather than dance angles.

The interpolation hypothesis of New and New (1962) is one of four distinct computational strategies that have been proposed to explain how insects can fill in the gaps of their experience with the sun's course. Three of the mechanisms assume that observed positions of the sun at specific times of day are used to calculate the position of the sun at other times of the day. The fourth mechanism assumes that the insects rely on the average rate of movement of the sun (15° per hour). Once a rate is obtained, all of the models assume that the position of the sun's azimuth could be determined by a neural implementation of an equation equivalent to the following:

$$A_{\tau+t} = A_{\tau} + rt \quad (3.1)$$

where $A_{\tau+t}$ is the unknown azimuth; A_{τ} is the observed azimuth; τ is the time of observation; t is the time interval between the observed and estimated azimuths; and r is the rate of change of the azimuth. The computational models differ in how the rate of change of the azimuth (r) is determined.

First, in the average rate hypothesis, r is simply 15° per hour. This is distinct from the other three methods which imply that the bees measure or calculate a rate of compensation but that they differ in the method of calculation.

Second, in the interpolation hypothesis, r is determined by computing the rate of change of the azimuth between two observed positions of the sun. This assumes a neural implementation of the standard rate equation:

$$r = \frac{A_2 - A_1}{\tau_2 - \tau_1} \quad (3.2)$$

where A_1 and A_2 are two observations of azimuth position at two specific times of day (τ_1 and τ_2).

Third, an alternative mechanism of computing r for use in equation 3.1 that has been proposed relies on the extrapolation of a single observed rate of change of the azimuth (Gould, 1980). This single value of r could be used to determine the position of the sun's azimuth later in the day (forward extrapolation).

Fourth, in a variation of the extrapolation hypothesis, a single value of r could be used to determine the position of the sun's azimuth earlier in the day (backward extrapolation) (Dyer, 1985).

Until recently, the experimental results were ambiguous regarding which method of computing the rate of change of the azimuth was used to fill in the gaps of an insect's experience with the pattern of change of the sun's azimuth. None of the data supports the conclusion that the average rate of movement is used. Several studies with honey bees (New & New, 1962; Dyer, 1987) and desert ants (Wehner & Lanfranconi, 1981; Wehner, 1982) support the interpolation hypothesis. On the other hand other studies with bees have been more consistent with the forward (Gould, 1980; Dyer, 1985) or backward

(Dyer, 1985) extrapolation hypotheses. Lindauer's (1959) data are consistent with all of these mechanisms because of the 90° separation between the test feeding stations.

Recent data (Wehner & Müller, 1993; Dyer & Dickinson, 1994) have suggested a new way of thinking about how insects fill the gaps in their experience. When bees and ants were confronted with large gaps in their experience of solar movement they nevertheless form a representation of the sun's course that approximated its actual course during the entire day. None of the previous computational mechanisms could account for this performance. The results of these experiments suggest that the insects have a certain amount of innate structure in their representation about the sun's course. Presumably the innate structure could be modified with experience. The previously hypothesized computational mechanisms may still play some role in the process (Dyer, 1987), but they are not used to estimate the position of the sun's azimuth during large gaps in experience.

In the subsequent sections of this chapter I will describe the experiments of Dyer and Dickinson (1994) in further detail. In addition, data from two additional colonies are presented, and new analysis are presented for all of the data. In the subsequent chapters, new computational models are presented which may shed further illumination on the process leading to the patterns observed by Dyer and Dickinson (1994) and Wehner and Müller (1993).

In the experiments with Fred Dyer, I utilized the technique developed by Lindauer (1959) of establishing colony of bees naive to a portion of the sun's course in an attempt to distinguish between the previous computational hypotheses. Instead of relying on feeding stations, I utilized the communicative waggle dance of the honey bee (Frisch, 1967) (see section 2.5.3), which can provide a readout of the position of the sun. This occurs because in the symbolic system, the distance and direction to the food is indicated with respect to the sun. The angle of the dance on the vertical comb in the hive corresponds to the angular deviation between the solar azimuth and the food source. This system is used even on completely overcast days when bees do not have a view of the sun (Dyer & Gould, 1981). During these times, bees rely on a memory of the sun's position with respect to landmarks.

In these experiments, bees were allowed to fly only in the late afternoon, hence they had experience only with a small portion of the sun's course (~20%). How the bees estimated the position of the sun in the morning was determined by their dances on a completely overcast day. Figure 3.2 shows the predictions for this experiment based on the previous computational models. With the large size of the gaps in the experience in the bees in these experiments, the predictions for the previous computational models of interpolation, and forward and backward extrapolation were very different. For interpolation (line A), a linear rate of time compensation is expected between the last view of the sun in the evening and the first view of the sun in the afternoon of the following day. This prediction overestimates the movement of the sun in the morning. For forward extrapolation (line

B), a linear rate of compensation based on the observed rate during the training period is expected. This rate is used to extrapolate the position of the sun's azimuth forward, through the night and into the morning of the following day. This prediction considerably underestimates the movement of the sun in the intervening time period. For backward extrapolation (line C), the same linear rate of compensation is used as in forward extrapolation, only it is extended backward into an earlier portion of the day. This prediction overestimates the position of the sun in the morning by a considerable margin. It was our hope with this experiment that we would be able to decide among the three hypothesized mechanisms.

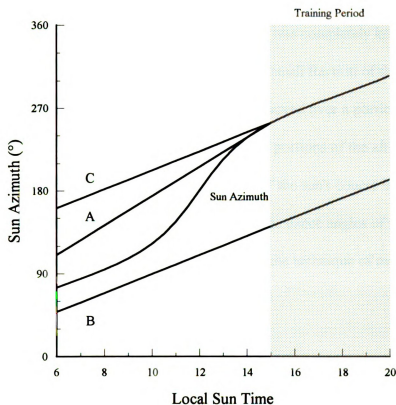


Figure 3.2 Predictions from previous computational models about how insects fill gaps in their experience with the sun's course. The shaded region corresponds to the time period of experience with the sun's course. The lines represent the predictions of the position of the azimuth at other times of day based on the various models. A. Interpolation: a constant rate of change between the end of the one training period and the beginning of the next on the subsequent day. B. Forward extrapolation: the rate of change observed at the end of the training period extended forward through the night and into the morning of the subsequent day. C. Backward extrapolation: the rate of change of the azimuth observed at the beginning of the training period and extended backward into earlier portions of the day.

3.2 Experimental Methods

Combs of the European honey bee (*Apis mellifera*) were hatched out in an incubator and used to establish colonies of bees whose experience was completely known. In the four colonies, the bees were allowed to fly only during a small fraction of the day. During this time, the bees gained experience with the sun as it moved over a portion of its diurnal course. Three of the four colonies were exposed to portions of the afternoon course of the sun. The fourth colony experienced a portion of the sun's course in the morning. For the first three colonies the technique of measuring the dance angles of the bees on a cloudy day was used (Dyer, 1987). For the fourth colony, the technique of measuring flight bearings on a sunny day was used (Meder, 1958).

3.2.1 Colony 1

The first colony was established from incubator-reared bees in a two-frame observation colony adjacent to an alfalfa field on the farms of Michigan State University, East Lansing, Michigan (43° 45' N). Bees were trained to find food at an artificial feeder containing sucrose solution 350 m to the south along a prominent line of trees. Bees were individually labeled with numbered tags. The colony was open from 15:00 until dark (~19:00) (local sun time). Each night after dark the colony was closed and removed from the field. Bees in the hive were exposed to diffuse light during daylight hours in an attempt to maintain the colony's circadian cycle.

On a cloudy day when bees cannot see the sun, the colony was opened in the morning. The dances were recorded to the nearest 5° with a protractor referenced to gravity. The inferred solar azimuths were calculated from the dance angles (azimuth = 180° - dance angle). This colony corresponds to colony 1 in Dyer and Dickinson (1994).

3.2.2 Colony 2

The experiment was repeated with similar conditions for the second colony. The colony was established in the same location and the bees received similar regime of training. Again, the colony experienced the sun for about the last four hours of daylight. In contrast to colony 1, the hive contained two groups of bees that received different treatments. One group was allowed to fly only during the late afternoon. The second group, however, was able to fly during the entire day. To accomplish this, the restricted-experience bees had small pieces of plastic glued to their thoraxes (G. E. Robinson, personal communication). A grating over the entrance of the hive precluded these bees from leaving the colony during certain times. The other bees were able to crawl through the small openings of the grating. This colony corresponds to colony 2 in Dyer and Dickinson (1994).

3.2.3 Colony 3

Colony 3 received a different amount of experience with the sun's course than colony 1 and colony 2. Colony 3 was established in the same location as colonies 1 and 2.

This colony was open from noon (local sun time) onward, so they experienced a considerably larger portion of the sun's course than either colony 1 or colony 2. This amounted to 50% of the diurnal course of the sun. The bees were trained as in colonies 1 and 2, but they were only trained 150 m south along the treeline. (To separate the potential ambiguity between an accurate representation of the sun's course and the ability of the bees to see the sun or polarized light through the clouds, these bees were originally intended to be tested in an alternative location, but no bees reached the feeder in several attempts).

3.2.4 Colony 4

For this manipulation, the flight bearings of bees captured at the feeder and released in a novel environment after a holding period were used to determine the bees' estimates of the sun's course. This technique has been successfully used in the past as a measure of the honey bee's representation of the sun's course (Meder, 1958). Under these circumstances, bees orient their flights with respect to the sun compass, compensating for the change during captivity.

Colony 4 was established in a ten-frame hive at the Inland Lakes Research Center on the Michigan State University campus. This colony experienced the sun only during the morning hours from dawn until 10:00 local sun time. The colony was closed at that time by simulating rain with a garden sprinkler (G. E. Robinson, personal communication). This stops the majority of bees from leaving the colony. After a steady "rain" of about 30

minutes, the colony was sealed with a screen and the entrances shaded from a view of the sky.

The bees were trained to an artificial sucrose source 400 m west through an open field of grass and wild flowers. A small lake was located 30 m north of the flight route and a few scattered trees and an interstate highway was located 30 m south of the flight route.

Bees leaving the colony were automatically dusted with a bright fluorescent pigment (Day-Glo Color, Cleveland, Ohio). This allowed bees visiting the feeder from other colonies to be identified (by their lack of pigment), so that only restricted-experience bees were used in the releases. Additionally, bees were painted at the feeder and were given a unique color for each day they were at the feeder. After several days of foraging at the feeder, the bees were captured individually in vials and held in a dark place before their release time.

Subsequently, the bees were released at a new location 3.2 km from the training location. The bees were released between an alfalfa field and an abandoned field on the Michigan State University Farms.

3.3 Results and Discussion

3.3.1 Colony 1

An unexpected pattern was revealed in the bees' estimates of the position of the solar azimuth in the morning. Figure 3.3 shows the solar azimuths inferred from the dances of the bees in the first experiment. In the morning, the bees danced as if they estimated the sun to be approximately 180° from the position in the middle of the afternoon training period ($M = 89.5^\circ$, $SD = 29.0^\circ$, $n = 133$). The colony shifted from indicating a morning direction to indicating an afternoon position around noon. For this colony the shift appears to occur at 10:50 rather than noon. The descriptive statistics presented here employ the assumption that time of day distinguishes the morning and afternoon groups. The means and standard deviations were computed using the appropriate methods for the analysis of circularly distributed data (Batschelet, 1981).

Over the entire morning the bee's estimation of the sun's position did not change. A linear regression of the morning data was not significant, (T (two-tailed) = 1.77, $df = 134$, $p > .025$) meaning that during the morning they were not compensating for a changing solar azimuth (i.e. the slope of the regression line was not different from zero) (see Table 3.1). For all of the regression analyses reported, the groups were split by angle rather than time (i.e. morning is less than 180° and afternoon is greater than 180°). I did this because I wanted to examine the behavior of individual bees, and I assumed that individual bees would have slightly different circadian rhythms. The individual would nonetheless shift

from a morning angle ($< 180^\circ$) to an afternoon angle ($> 180^\circ$) at her individual representation of noon.

Around noon the bees abruptly shifted as a group to indicate solar positions consistent with the middle of the training period ($M = 276.77^\circ$, $SD = 24.0^\circ$, $n = 404$). By contrast, the afternoon group did have a significant regression slope, but it was very small ($1.4^\circ/\text{hr}$, $R^2 = .02$, $T = 2.94$, $df = 399$, $p < .005$) (see also Table 3.1). The actual rate of change in the azimuth during the middle of the training period was $9.5^\circ/\text{hr}$.

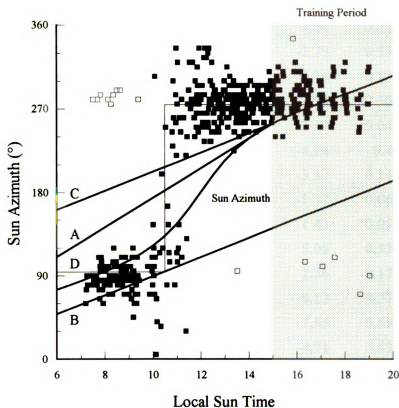


Figure 3.3 Solar azimuths inferred from the dances of restricted experienced bees from colony 1. The curved line corresponds to the actual path of the sun on July 22. The straight lines are the predictions from the previous computational models. A. Interpolation. B. Forward extrapolation. C. Backward extrapolation. D. 180° step function. The open symbols correspond to two bees that differed qualitatively from the rest.

Table 3.1 Regression Analysis of Individual Bees' Azimuth Estimates (Colony 1)

Bee	Morning				Afternoon			
	Slope	R²	prob.	n	Slope	R²	prob.	n
11					3.64	0.22	0.06	12
20	7.3	0.09	0.17	12	-2.79	0.53	0.03	7
22					2.76	0.12	0.15	11
23					7.23	0.56	0.04	6
32					2.19	0.04	0.18	25
48	2.46	0.06	0.29	8	-4.24	0.4	0.01	13
49	2.44	0.12	0.17	12	-3.37	0.14	0.06	12
51					-1.37	0.06	0.28	8
52	3.18	0.04	0.24	16	1.43	0.05	0.18	18
55					5.08	0.33	0.02	14
61					2.36	0.17	0.02	25
64					6.13	0.77	< 0.005	8
74	15.99	0.6	< 0.005	10	7.86	0.69	< 0.001	25
77					-4.71	0.63	0.02	7
78					-8.16	0.63	< 0.001	16
85					-1.83	0.16	0.13	10
87	13.4	0.46	< 0.01	12	3.3	0.17	0.04	19
88					-3.46	0.23	0.11	8
90	4.23	0.16	0.08	14	1.06	0.06	0.2	14
93	6.36	0.35	0.02	12				
98	-0.85	0	0.43	14	-1.53	0.04	0.2	21
104					0.9	0.01	0.37	15
106					-14.06	0.86	< 0.005	6
108					-4.98	0.25	0.02	19
114					3.79	0.34	0.02	13
115					4.93	0.54	< 0.005	15
191					-0.06	< 0.001	0.49	19
Total	3.3	0.02	0.04	136	1.41	0.02	< 0.005	401

The bees' estimate of the position of the sun in the morning is almost exactly 180° from the sun's mean position in the afternoon during the training period and the mean azimuth indicated in the afternoon by the bees. Two bees indicated positions of the sun throughout the day that were qualitatively different from the rest of the bees. These bees are indicated by the open symbols in Figure 3.3 and they are not included in the calculation of the statistics. These two bees estimate a pattern of solar movement during the day that differs from the remainder of the bees in a systematic way. These bees indicate an abrupt transition the position of the azimuth around noon as well, but indicate a transition from approximately 270° to 90° instead of from 90° to 270° .

Overall, the behavior of the bees is well described by a 180° step function. This model assumes that the morning angle is exactly 180° from the azimuth experienced at the middle of the training period (270°). At midday (10:50 for this colony), the afternoon angle abruptly replaces the angle assumed in the morning. This model explains a high proportion of the variance in the data ($R^2 = .85$) and the fit of the data to the 180° step function is significantly better than the fit of the data to the actual ephemeris function ($R^2 = .59$) ($F_s = 2.01$, $df = 536, 536$, $p < 0.001$). We tested this by comparing the variances described by each model function. It is used throughout, as a means of comparing the fit of data to nonlinear curves. This is of course a *post hoc* test, but it describes the data well, and forms a standard and a prediction for future comparisons.

The 180° step function raises questions about the mechanisms underlying the sun compass. It is clear from previous data (Dyer, 1987), that the estimates of the sun's position throughout the day appear to be based on a continuous function for bees with complete experience with the sun. It is difficult to imagine what type of mechanism would lead to a transition from a discrete function to a continuous function (this will be explored extensively in the subsequent chapters). Preliminary evidence suggests, however, that individual bees from colony 1 may indeed represent the sun's course as a continuous function. Although the group of bees shifts abruptly at noon, bees that performed dances during the transition period seemed to change their dance angles gradually. Figure 3.4 shows the solar azimuths inferred from the dances of four individual bees that danced during the transition period. Several of the bees appear to indicate solar transitions that are considerably less abrupt than the 180° function would suggest. One of the bees indicates a solar transition to the north at noon rather than the south. This is particularly striking since the sun never passes to the north at noon in the temperate zone. This behavior bears a striking resemblance to the data that New and New (1962) obtained (see Figure 3.1).

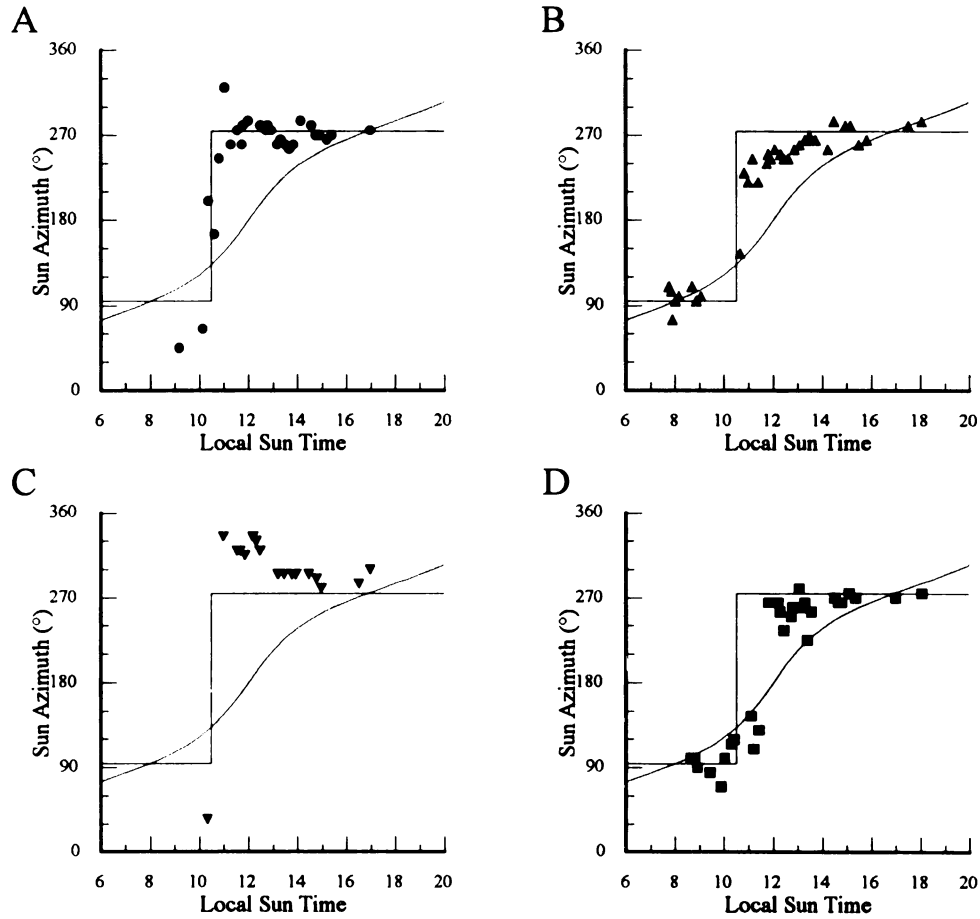


Figure 3.4 Solar azimuths inferred from the dances of four individual bees from colony 1 that show gradual shifts during the transition period. A. Bee 32. B. Bee 74. C. Bee 78. D. Bee 87.

An alternative and more quantitative way of analyzing the nature of the representation of individual bees is by a linear regression analysis of the solar azimuths indicated in the morning and afternoon. Although a linear model clearly cannot explain the underlying mechanism for the entire day, by examining portions of the overall curve, it may be possible to discern whether the underlying function is truly a 180° step function, or a more gradual function.

The results of this analysis for colony 1 are presented in Table 3.1. Data were analyzed for bees that had more than five dances in either the morning or the afternoon. Whether solar azimuths were grouped with the morning data or the afternoon data depended on the azimuth angle rather than the time. Two-tailed T tests were used to assess whether the slopes of the regressions were significantly different from zero. Data with significant slopes are presented in bold typeface.

In the afternoon, there were 11 significant regression slopes out of 26 tested. Six of the significant slopes were positive while five were negative. Some of the slopes are relatively large compared to the colony as a whole. In the morning, there were fewer bees to compare; three of nine had significant slopes. All three of the significant regressions had positive slopes. The fact that there are a variety of slopes present in the data sorted by individual bees suggest that there is more to the overall pattern than a simple step function. This is one of the primary concerns of the subsequent chapters.

The clearest conclusion from the data of colony 1 is that none of the previous computational models are supported by the results. For all of the previous computational models, a single constant rate of time compensation was expected. This is clearly not what occurred. By indicating the position of the sun in the morning to be approximately 180° from the afternoon position, the bees incorporated some of the nonlinearities of the rate of change of the azimuth into their estimates.

3.3.2 Colony 2

The data from colony 2 support and extend the main conclusions from colony 1. Figure 3.5 shows the inferred estimates of the sun from the dances of the restricted-experience and the fully experienced bees of colony 2. Although not as extreme of a pattern is produced, the restricted-experience bees of colony 2 estimated positions of the sun in the morning ($M = 97.8^\circ$, $SD = 19.4^\circ$, $n = 95$) that were approximately 180° from the position indicated in the afternoon ($M = 257.6^\circ$, $SD = 20.3$, $n = 85$).

The step function provides a significantly better fit than the actual ephemeris function ($R^2 = .91$, $F_s = 2.76$, $df = 179, 179$, $p < .001$). The experienced bees, by contrast, tracked the sun's course more accurately. For these bees, the actual ephemeris function provides a better fit than the step function ($R^2 = .85$, $F_s = 2.64$, $df = 59, 59$, $p < .001$).

Unlike colony 1, the solar azimuths indicated in the morning and the afternoon appear to change over time at a rate that roughly matches the rate of change of azimuth that the bees

experienced in the afternoon. Both the morning data and the afternoon data have significant regression slopes. In the morning the slope is 6.9° per hour ($R^2 = .24$, $T = 5.31$, $df = 91$, $p < .001$) while in the afternoon, the slope is 12.2° per hour ($R^2 = .47$, $T = 8.63$, $df = 85$, $p < .001$). These are both quite close to the actual pattern of movement of the azimuth in the middle of the afternoon training pattern, which was $10.8^\circ/\text{hr}$. The regression slopes for the morning and the afternoon are significantly different from each other ($T = -2.74$, $df = 176$, $p < .005$); however, for the two bees that had significant regression slopes for both the morning and the afternoon, the slopes did not differ significantly from each other. All of the individual bees in colony 2 that had significant linear regressions had positive slopes (see Table 3.2).

These results from restricted-experience bees in colony 2 contrast markedly with those from colony 1. In particular, the representation formed by the bees in colony 2, though still approximate, more closely matched the local ephemeris function than did the representation formed by bees in colony 1. The bees in colony 2 had a more accurate representation of the rate of change of the azimuth in the morning and the afternoon. From the positive slopes of the regression lines, one could infer that the bees also have a more accurate representation of the midday transition (the fact that the sun passes to the south at noon at this latitude) than colony 1. Unfortunately, because of a period of heavy rain, there are too few dances during the transition to test this conclusion.

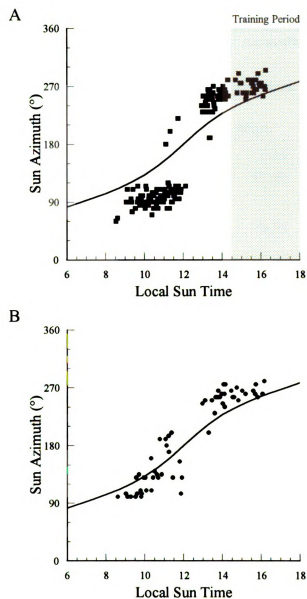


Figure 3.5 Solar azimuths inferred from the dances of restricted experienced bees (A) and fully experienced bees (B) of colony 2.

Table 3.2 Regression Analysis of Individual Bees' Azimuth Estimates (Colony 2)

Bee	Morning				Afternoon			
	Slope	R²	prob.	n	Slope	R²	prob.	n
210	1.79	0.03	0.28	16	8.18	0.81	< 0.001	12
233	8.97	0.59	< 0.005	11	17.84	0.87	< 0.005	6
235	5.57	0.33	< 0.01	18				
265					31.04	0.96	< 0.001	6
270	11.34	0.74	< 0.001	11				
291	5.33	0.45	0.02	9	13.86	0.78	< 0.005	7
311					10.68	0.32	0.07	8
316	6.68	0.19	0.2	6				
373	7.2	0.59	0.01	8	14.33	0.33	0.07	8
Total	6.94	0.24	< 0.001	93	12.22	0.47	< 0.001	87

3.3.3 Colony 3

Since colony 3 had three additional hours of experience with the sun's course in the early afternoon, the results were expected to differ qualitatively from those of colony 1 and colony 2. This is because they had experience with a much larger portion of the sun's course, including portions with relatively fast and relatively slow rates of change of the azimuth. However, the data presented in figure 3.6 suggest that this is not the case. The data for both the afternoon ($M = 223.7^\circ$, $SD = 14.0^\circ$, $n = 67$) and the morning ($M = 65.5^\circ$, $SD = 16.6^\circ$, $n = 25$) are consistently below the expectations from the actual ephemeris function. The afternoon data are puzzling because in both colony 1 and colony 2 the solar azimuths indicated in the afternoon initially fell above the curve of the true solar azimuth for the early portion of the afternoon. Like colony 1, however, the rate of change of the azimuth in the afternoon is lower than the expected rate of change (slope = $3.7^\circ/\text{hr}$, $R^2 = .16$, $T = 3.49$, $df = 65$, $p < .001$). The afternoon slope is considerably less than the morning slope ($20.6^\circ/\text{hr}$, $T = 3.35$, $df = 23$, $p = .001$) (see Table 3.3). The two slopes are significantly different ($T = 2.71$, $df = 88$, $p < .005$).

A 180° step function through the middle of the training time (azimuth = 255°) explains a high proportion of the variance ($R^2 = .82$) but the fit is not significantly better than the fit with the true ephemeris function ($R^2 = .76$) ($F_s = 1.11$, $df = 91, 91$, $p > .05$). This result is somewhat troublesome in light of the results from colonies 1 and 2. Colony 3 had a different training regime than the two other colonies. The bees of this colony experienced

a much larger proportion of the sun's daily course. The original prediction for the emphemeris function estimated by the bees of this colony was not a step function. With the increased experience, one of the predictions was that the bees would have a more accurate representation of the sun's course for the entire day. In fact, the prediction corresponded to actual emphemeris function. This presented a potential problem of interpretation because if the bees indicated the accurate azimuth function, it would be impossible to distinguish between whether they were relying on an accurate representation of the sun's course or a view of the sun through the clouds. Because of this, the experimental plan included transporting this colony to a nearby location with a similar array of landmarks in a different orientation (this technique had been successfully used in the past (Dyer, 1987)). Several attempts were made to complete this manipulation, but the bees failed to visit the feeder. After an unsuccessful attempt to get the bees to fly in the test location in the morning, the colony was opened in the training location in the afternoon and the bees immediately began to visit the feeder and dance in the hive. These data were subsequently recorded knowing the potential ambiguities that could result. The overcast consisted of a dense fog at times, so it seems unlikely that the bees could directly detect the sun. Systematic errors of the type evident in the data of colony 3 are not uncommon in the sun compass literature (e.g. Wehner and Lanfranconi (1981)). It is this type of systematic error, and the error evident in the step function of colonies 1 and 2 that will allow different potential mechanisms to be distinguished. The following chapters will explore the nature of the potential mechanisms.

Table 3.3 Regression Analysis of Individual Bees' Azimuth Estimates (Colony 3)

Bee	Morning				Afternoon			
	Slope	R²	prob.	n	Slope	R²	prob.	n
41					-1.99	0.16	0.22	6
59	6.29	0.37	0.07	7	5.11	0.71	< 0.001	22
Total	20.58	0.33	< 0.001	25	3.66	0.16	< 0.001	67

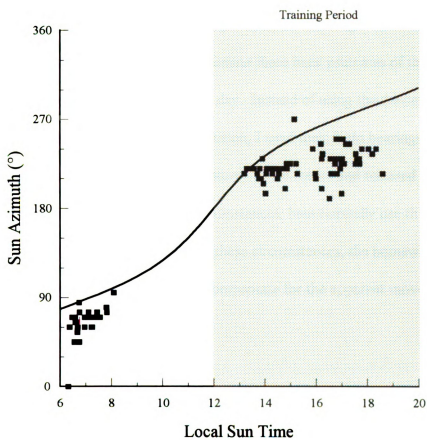


Figure 3.6 Solar azimuths inferred from the dances of restricted experienced bees of colony 3. Solar azimuth curve is for August 10.

3.3.4 Colony 4

The procedures used for colony 4 differed from the other three colonies in several respects. This colony was restricted to fly only in the morning instead of the afternoon, and I used an alternative method to determine these bees' estimates of the solar positions during the unexperienced portion of the day. Instead of using the dances of the bees to infer their representation of the sun's position, I used their flight bearings in unfamiliar territory on a sunny day. Bees were captured at the feeder and released in a novel location after a holding period. Under these circumstances, bees normally use the sun compass to set a homeward course (even though in these circumstances, the homeward direction takes them in the wrong direction) and they compensate for the apparent movement of the sun during their captivity (Meder, 1958).

Results of these manipulations are presented in Figure 3.7. The results show considerably more variance than method of using the dance language. Therefore, I have plotted the means $\pm$ standard errors for the 10 significantly oriented groups of bees (out of 12) in Figure 3.7. Nine of these were from a single release site and one was from another release site. Most of the data corresponds roughly to the true ephemeris function. With the high error variance, the fit to the azimuth function was low ($R^2 = .25$), but the fit to a step function was considerably worse ($R^2 = -.61$).

Several factors could have contributed to these results. First, the colony was set up in an area with numerous other large hives, so it is possible that experienced bees could have drifted to the restricted experience colony. Second, the bees could have used landmarks for orientation. Both the training site and the test site had a row of trees that bore some resemblance. They were of different densities and of different distances, but they may have contributed to the orientation. This conclusion is supported (albeit weakly) by the fact that one set of releases from an alternative site has a mean that falls a considerable distance from the sun azimuth curve (see the circle in Figure 3.7). The mean for these data is almost exactly 270° , and it is further from the sun azimuth curves than any of the other sets. Unfortunately, there was not time to make further releases from this site before the colony was compromised by an insufficient closing.

Although the data from flight bearings is considerably more variable than the data from dance angles, it is somewhat easier to collect because of the required weather conditions. This suggests that although colony 4 does not contribute much to the results presented here, it may nonetheless serve as a useful guide to future investigations.

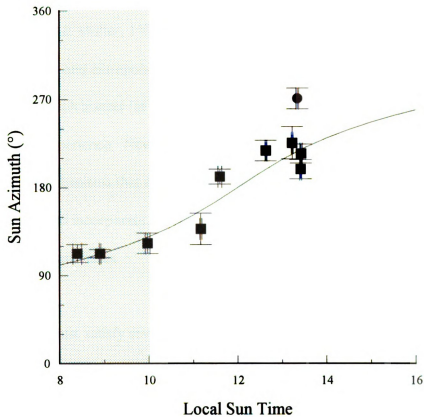


Figure 3.7 Solar azimuths inferred from the vanishing bearings of colony 4. The data are means $\pm$ standard error of significantly oriented groups of bees (10 of 12) at two different release sites (squares and circle). Tests occurred between August 11 and 26. The azimuths inferred for each release day are plotted. The solar azimuth shown corresponds to August 18.

3.4 Summary

The data presented here for honey bees and the data obtained from similar experiments with ants (Wehner & Müller, 1993) suggest that the previous computational models of linear interpolation and extrapolation are inadequate in their explanation of the mechanisms by which insects (at least hymenopterans) compute the position of the sun to fill gaps in their experience. New models are required to understand the underlying computational mechanisms that results in the ability of ants and bees to fill large gaps in their experience and incorporate aspects of the nonlinear pattern of the movement of the azimuth into their estimates.

The new models must satisfy several conditions that the experiments with experience-restricted bees revealed. First, the bees indicate a position for the morning sun that is 180° from the position of the sun in the afternoon. Second, the transition between these positions occurs at about noon. Third, the bees seem to rely on a continuous function to estimate the position of the sun. Fourth, the representation of the sun's course is more accurate with more experience.

Dyer and Dickinson (1994) suggested that the bees may have something analogous to a template as described for bird song (Marler, 1976, 1984) that would account for their behavior. It may be fruitful to think about the models in the subsequent chapters as templates for learning about the sun's course.

Chapter 4

NONLINEAR SYMBOLIC MODELS

It is clear from the data presented in Chapter 3 that the previous computational models of sun compass learning cannot adequately account for the behavior of the insects in the most recent experiments. New models are needed to fill these gaps. In this chapter and in the subsequent chapter, several new models will be presented. The models are based on contrasting approaches to modeling cognition and they differ considerably in their underlying representational structure (i.e. how they represent the sun's course). In this chapter I will consider a nonlinear symbolic model, while in the next chapter I will consider a nonlinear nonsymbolic (or connectionist neural network) model. My goal will be to examine how each of these approaches might be applied to the sun compass learning problem.

4.1 A Symbolic Model of Sun Compass Learning

In the previous models of sun compass learning, measurements of the rate of change of the azimuth at an observed time were used to compute the position of the sun at a new time. The symbolic quantities of azimuth position and time are maintained throughout the computation. The input symbols are manipulated mathematically to yield output symbols.

The neural implementation of this computation would involve neural symbols that represent azimuth position and time. Gallistel has specifically argued that the sun compass learning problem can only be solved symbolically (Gallistel, in press). This conclusion will be critically examined in the following chapter with the development of a nonsymbolic model, but the first priority is to determine if there is a symbolic process that the insects could use to fill gaps in their experience with the sun.

The equations of the true solar azimuth function are symbolic (equations 2.1 and 2.2). These equations have three input variables (latitude, solar declination, and time of day) that could be used to calculate the output variable of azimuth position. As indicated in Chapter 2, two of the input variables (latitude and declination) would be difficult for an animal to assess. Both of these variables are confounded in the zenith distance of the sun. In order to use the zenith distance as a means of determining the azimuth function, the animal would have to have an independent measure of either declination or latitude. This is not out of the range of possibility. Latitude for instance could be determined from the inclination of the earth's magnetic field (Wiltschko & Wiltschko, 1995). However, it does not appear necessary to postulate a mechanism for the independent assessment of latitude and declination. Experiments suggest that the zenith distance of the sun does not play a role in the sun compass of many animals. Recall that longitudinal translocations indicate that the animals respond to the sun's azimuth and their internal sense of time without regard for the sun's zenith distance (Papi, 1955; Renner, 1959). The equivalent effect has been shown in animals with a phase-shifted circadian clock (Hoffmann, 1960). In

addition, experiments with artificial suns have shown that the zenith distance does not play a role in the determination of direction (St. Paul, 1953; Brines & Gould, 1979).

Instead of attempting to disentangle the potential inputs of zenith distance and latitude, I will focus on the directly observable quantities. This is what the previous computational models have done. The variables of azimuth angle and time are directly measurable by the animal. Specific instances of these variables could be used to estimate a parameter that describes the relationship between the variables. In the case of the previous computational models, the parameter is the rate of change of the azimuth. The parameter is a constant that can be used to compute specific values for the output variables of azimuth position and time, given specific input values. The data suggest that more is needed. None of the previous models were supported by the experimental results of Wehner and Müller (1993) and Dyer and Dickinson (1994). They found that insects somehow account for the varying rate of change of the azimuth over the day. Thus the rate of change of the azimuth (r) is not a constant, but is itself a variable. The goal of the present model is to determine a function that could describe the varying rate of change of the azimuth over the course of the day.

The pattern of the curves in Figure 2.2 indicates that the rate of change of the azimuth systematically varies over the course of the day. Thus r is also a function of time. It is the azimuth rate function. But what form does this function take? In nature this equation is the first derivative of the azimuth function (equations 2.1 and 2.2) with respect to time.

But if it is reasonable to assume that the animals do not have access to the true azimuth function (since they would need to independently assess latitude and declination), it is reasonable to assume that they do not have access to its first derivative. These two suppositions are further substantiated by the fact that bees that have restricted experience do not have completely accurate representations of the sun's course (Dyer & Dickinson, 1994). Therefore, the azimuth rate function that the bees used is assumed to be an approximation of the true azimuth rate function. Furthermore, this approximation should be based on the readily observable quantities of azimuth angle and time of day. These quantities would allow the parameters of the function to be estimated.

One function that meets these qualifications is based on the geometry of an ellipse. This model was originally suggested in qualitative terms by Rudolf Jander (personal communication). I have formalized this model and will show that it describes the experimental data well. This model allows the generation of complete azimuth functions from experience with very small portions of the actual azimuth function. The azimuth functions generated from the model are approximations of the true azimuth function, but they are approximations that would allow a high degree of accuracy with a relatively small investment in time to learn the pattern. The fit of the model functions to previous data sets is very good.

4.2 The Ellipse Rate Function

In this new symbolic model, the true azimuth rate function is assumed to be approximated by an ellipse plotted in polar coordinates. In this form, the angle of the plot corresponds to time, which cycles over 24 hours, and the length of the radius vector corresponds to the rate of change of the azimuth. Ellipses of different shapes would correspond to azimuth functions for different seasons and latitudes. Specifically, rounded ellipses correspond to temperate latitudes and squashed ellipses correspond to tropical latitudes. This provides a means of visualizing the relationship between the rate of change of the azimuth and the time of day.

The geometry of an ellipse intuitively seems to provide a good description of the variations in the rate of change of the azimuth over the course of the day. The rate (radius) varies systematically with time of day (angle). As the radius sweeps around the ellipse (like the hands of a distorted clock) it increases to a maximum at the semimajor axis and decreases to a minimum at the semiminor axis. Thus the equation of the ellipse in polar coordinates may be a function that closely approximates the rate function of the actual azimuth.

In the following sections, I will first bolster the case that the geometry of the ellipse provides a good approximation for the true rate function. I will subsequently introduce the equation of the ellipse in polar coordinates as an approximation for the true rate function. The first part of my argument is purely geometrical.

4.2.1 The Geometry of the Ellipse

From Figure 2.2 (see also Figure 4.1 below), it is clear that the rate of change of the azimuth varies systematically over the course of the day. It reaches a maximum at midday and symmetrically increases prior to midday and decreases after midday. The true rate function and its hypothesized relationship with an ellipse function is portrayed in Figure 4.1. The first panel of Figure 4.1 (A and B) shows the full 24 hr azimuth function for a temperate latitude (40° N) and a tropical latitude (10° N) for the equinox. In both azimuth functions, the rate of change of the azimuth varies systematically over the course of the day. The rate of change of the azimuth for a given time of day corresponds to the slope of the azimuth curve at that point. In both curves the slope starts out high and decreases. It subsequently increases to a maximum at noon before decreasing again. The systematic variation in the slope is what needs to be explained by a rate function. The pattern of the variation of the slope over the course of the day defines the azimuth rate function.

In the second set of graphs (Figure 4.1 C and D), the rate of change of the azimuth is plotted against time. This plot shows the systematic variation in the rate of change of the azimuth with time of day that was described in reference to the curves in Figure 4.1 A and B. The rates plotted in the second panel were calculated numerically over intervals of 8 minutes. The plots for both latitudes reveal a similar pattern, although the range between the maximal and minimal rates is more extreme in the tropical curve. If the x-axis were stretched out to include several days, the pattern of change in the rate would repeat itself;

therefore, the true rate function is a cyclic function with alternating increasing and decreasing rates of change of the azimuth. Polar coordinates are well suited to the representation of cyclical functions. The idea of the ellipse function is that the pattern of increasing and decreasing rates of change of the azimuth would correspond to an ellipse if they were plotted in polar coordinates. Thus, the equation of the ellipse would form an approximation of the true rate function. In the third pair of graphs in Figure 4.1 (E and F), a hypothetical pair of ellipses are plotted. Time is plotted in degrees with the following relationships: $00:00 = 0^\circ$; $06:00 = 90^\circ$; $12:00 = 180^\circ$; $18:00 = 270^\circ$. The lengths of the semimajor and semiminor axes of the ellipses correspond to the maximal and minimal rates of change in the azimuth plotted in C and D of the figure. The resulting pattern is clear. An ellipse has the potential to describe a wide variety of ephemeris functions. Relatively rounded ellipses correspond to the ephemeris functions of temperate latitudes, while relatively squashed ellipses correspond to the ephemeris functions of tropical latitudes.

Figure 4.1 The ellipse approximation of the azimuth rate function. The rate of change of the azimuth varies systematically over the course of the day. A. The full 24 hour azimuth function for 40° N at the equinox. B. The 24 hour azimuth function for 10° N at the equinox. C. The azimuth rate function for the azimuth curve in A, computed over 8 minute intervals. D. The azimuth rate function for the azimuth curve in B, computed over 8 minute intervals. E. An ellipse based on the rates in C (semimajor axis = $23^\circ/\text{hr}$; semiminor axis = $10^\circ/\text{hr}$). F. An ellipse based on the rates in D (semimajor axis = $85^\circ/\text{hr}$; semiminor axis = $3^\circ/\text{hr}$).

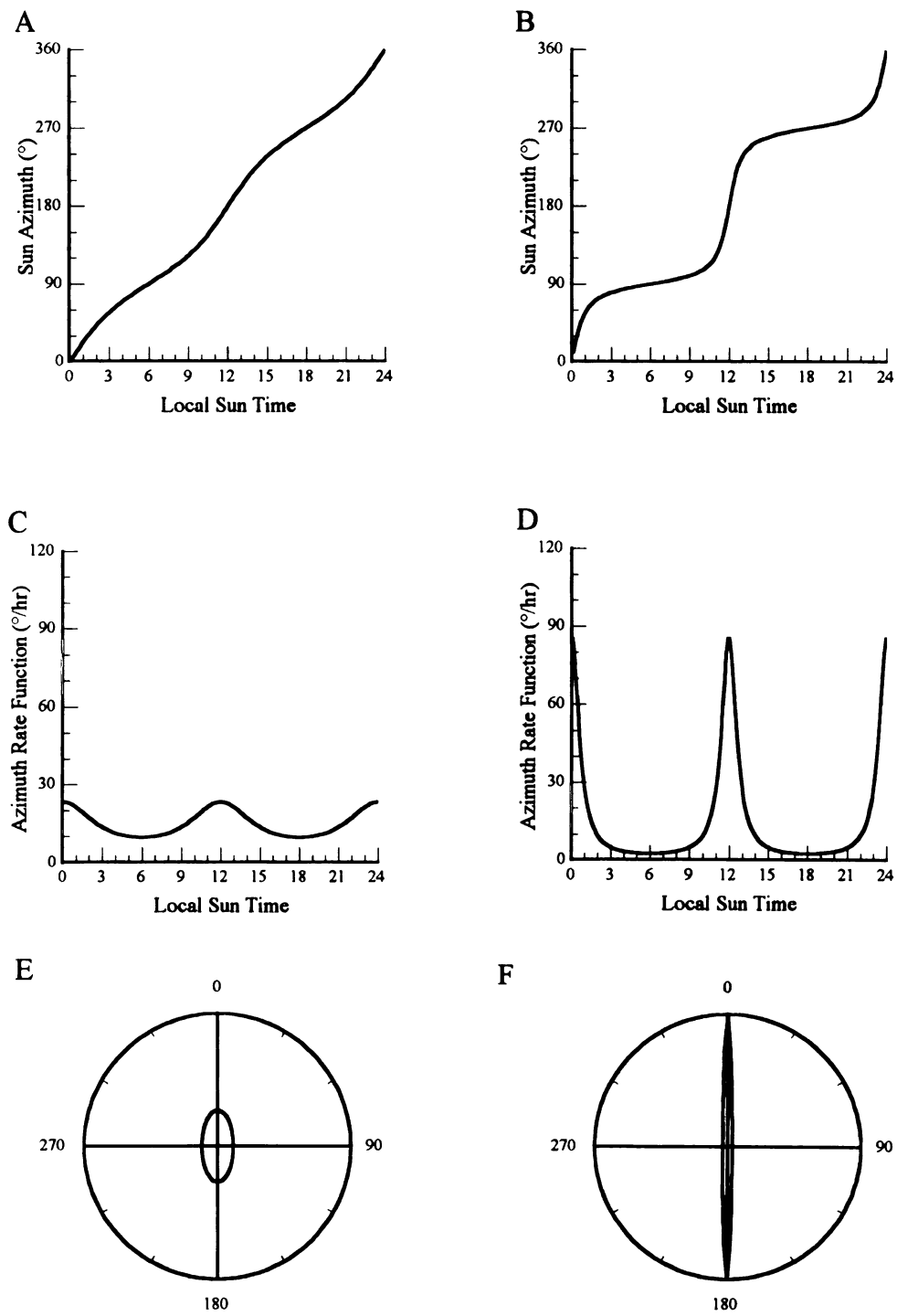


Figure 4.1

The hypothetical correspondence between the shape of an ellipse and the latitude of an azimuth function is intuitively satisfying. Whether it actually approximates the true rate function is another question. The actual values of the rate of change of the azimuth plotted in Figure 4.1 C and D can be plotted in polar coordinates to check their correspondence of the ellipse functions plotted in E and F of Figure 4.1. Figure 4.2 (A) provides a comparison of the true rate functions plotted in polar coordinates with the ellipses generated in Figure 4.1 E and F. In this case, the curves for the different latitudes are plotted in the same figure (the scale is the same as Figure 4.1 E and F). The ellipse is a very good description of the azimuth rate curve for 40° north latitude. The azimuth rate curve is nearly identical to the ellipse when plotted in polar coordinates. In contrast, the azimuth rate curve varies slightly from the form of the ellipse for the 10° N curve. However, the ellipse may still provide a good approximation to this 10° N rate function.

Figure 4.2 (A) still shows the special case of the equinox. As the declination of the sun changes, the pattern of the polar plot of the true rate function changes considerably, and the shape diverges significantly from that of a true ellipse. Panels B and C of Figure 4.2 show this effect. In panel B, the true rate function is plotted for 10° N on April 16 (declination 9°54') when the sun passes nearly directly overhead at noon. The scale of the plot has been changed 100 fold to reveal the change in the pattern. Since the azimuth is shifting abruptly from east to west, there is a spike in the rate around noon. Note that the pattern is now asymmetrical, since there is no corresponding spike at midnight. The

pattern is more clearly evident in panel C of Figure 4.2 which shows the true rate function for 40° north latitude at the equinox.

Although the pattern of the true rate function plotted in polar coordinates is clearly asymmetrical and not elliptical, the ellipse may nonetheless provide a good approximation of the true rate function, particularly during the day. The pattern of the function between 06:00 (90°) and 18:00 (270°) is symmetrical around noon and well approximated by half an ellipse. This corresponds to the majority of the hours of daylight, particularly in the tropics. The fact that the nocturnal values would not be well approximated by the daytime ellipse is not a serious problem. This would in fact be an interesting prediction of the ellipse model. This would suggest that the solar positions estimated at night by animals relying on a representation of the sun's movement based on an ellipse would correspond to the pattern of movement of the sun during the day, even if the true nocturnal pattern differed considerably. For temperate latitudes, the nocturnal values that would be observed do not deviate considerably from an ellipse estimated from the daytime values.

Figure 4.2 The true azimuth rate function plotted in polar coordinates. The values plotted correspond to the numerically calculated rate of change of the azimuth over 8 minute intervals. A. 40° N and 10° N for the equinox. B. 10° N for April 16 (declination $9^{\circ}54'$). C. 40° N for the summer solstice. In all cases the curves are not truly elliptical. The shape varies considerably with season and latitude.

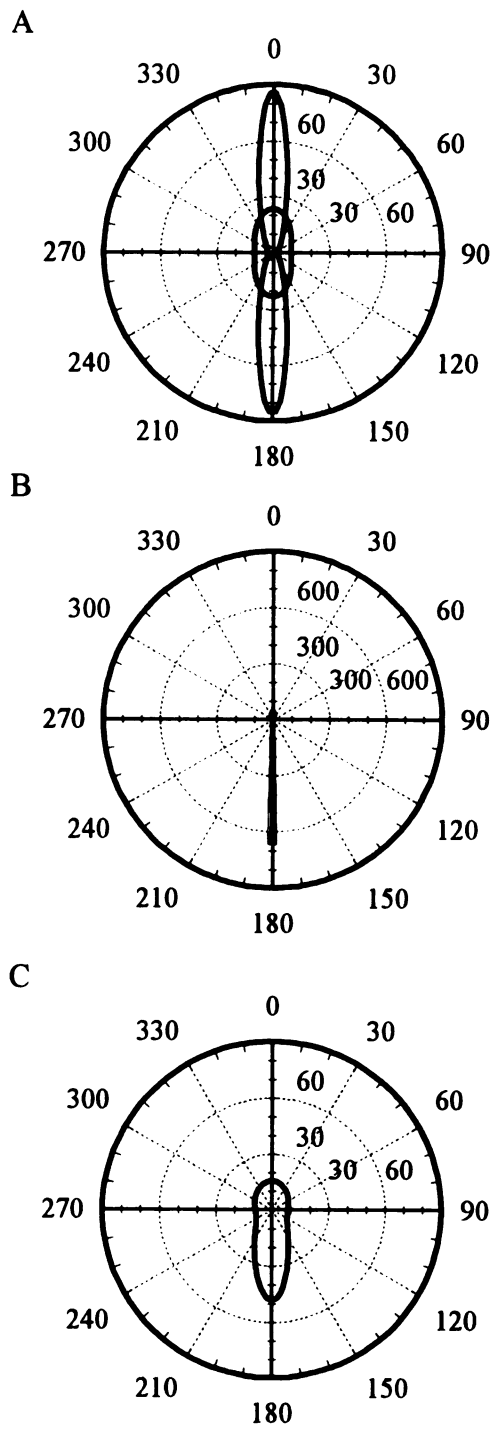


Figure 4.2

4.2.2 The Equation of the Ellipse

Since the ellipse function appears to be a relatively good candidate as an approximation to the true rate function, the equation of the ellipse in polar coordinates can be used to describe the functional relationship between time of day (τ) and the rate of change of the azimuth (r). Thus:

$$r = \frac{ab}{\sqrt{a^2 \sin^2(\tau) + b^2 \cos^2(\tau)}} \quad (4.1)$$

where r is the rate of change of the azimuth; τ is the time angle (with 15° per hour); and a and b are the parameters of the ellipse. These parameters are equivalent to the parameters a and b in the familiar Cartesian equation of the ellipse which correspond to length of the semimajor axis and the semiminor axis respectively:

$$\frac{x^2}{a^2} + \frac{y^2}{b^2} = 1 \quad (4.2)$$

The values of the parameters a and b determine the shape of the ellipse. When a and b are roughly equal, the ellipse is nearly circular. When a is very large with respect to b , the ellipse has a much more squashed shape. In terms of the rate of change of the azimuth, the greater the variation between the maximal and minimal rates, the more tropical the azimuth function is (see Figure 4.1).

Equation 4.1 can be used in combination with equation 3.1 to determine the position of the azimuth for a particular time of day. Equation 4.1 yields a series of values for the rate

of change of the azimuth (r) for different times of day. These values can substituted into equation 3.1 at the appropriate times of day in the calculation of the azimuth.

Using these two equations to calculate azimuth, one of which is a discrete difference equation, bypasses an obvious alternative approach. Since the rate of change of the azimuth (r) is a function of time, and it is theoretically the first derivative of the azimuth function, if the antiderivative of the rate function can be found, an explicit function of the azimuth in terms of time would exist and could be used to directly calculate azimuth positions by time of day. However, no such explicit function appears to exist for equation 4.1. In addition, using the difference equation (3.1) with the ellipse rate function (4.1) provides a direct parallel between the previous linear models of sun compass learning and this nonlinear model, since all of the previous models can be expressed in terms of equation 3.1 (see Chapter 3).

One byproduct of using a difference equation is that shape of the resulting function varies with the number of time steps used, as in any difference equation. This technically adds another parameter to the azimuth estimation function, although it is not a parameter that the bees would have to estimate. However, this effect of the time steps may help describe some of the results of previous experiments (Dyer & Dickinson, 1994), because it turns out that using a function with fewer time intervals increases the likelihood of generating an azimuth estimate that corresponds to a step function (see section 4.9 below).

In the next section, I will consider the range of functions that result from a use of a combination of the ellipse rate function (equation 4.1) and the azimuth difference equation (3.1). The values of the ellipse parameters a and b required to produce these curves will be generated, but I will leave it to the following section to discuss how the parameters can be estimated by the insects.

4.3 The Ellipse Azimuth Function

Figure 4.3 shows the azimuth functions generated using equations 3.1 and 4.1 for the same seasons and latitudes as discussed in the previous section (and Figures 4.1 and 4.2). Panel A of Figure 4.3 shows the true azimuth function for 10° north latitude at the equinox and two azimuth functions generated from the model equations. Clearly, the model does a very good job of approximating the true azimuth function, since one of the lines completely overlaps the true function. The azimuth functions produced from the ellipse rate function in Figure 4.3 (A) both used an ellipse with the same parameters ($a = 23$, $b = 10$). These are the same parameters that were derived from the true rate function in Figure 4.1. The two curves differ slightly because one has been scaled to 360° (squares) and the other has not (diamonds). Looking at Figure 4.3 (B) it is apparent that scaling is necessary to accurately approximate the true azimuth function. This shows the actual azimuth function and two ellipse azimuth estimates for 10° north latitude at the equinox. The ellipse parameters for this ellipse azimuth function were again taken from the true rate function for 10° north latitude as in Figure 4.1 (D) ($a = 85$, $b = 3$). The scaled ellipse azimuth function again provides an extremely close correspondence to the actual

azimuth function. In this case, however, the unscaled ellipse azimuth function provides an extremely poor approximation. This probably results from the fact that the true rate function does not correspond to an ellipse in this case (see Figure 4.2 A). Scaling the ellipse azimuth function forces equation 3.1 to sum to the appropriate level (360°). Without scaling, the accumulation of errors can lead to results that deviate substantially from the true pattern.

The third and fourth panels of Figure 4.3 (C and D) show the effects of seasonal variation on the approximation of the ellipse azimuth function to the actual azimuth function. Again the curves are for 10° and 40° north latitude. The declinations of the sun correspond to those considered in Figure 4.2. The summer solstice curve is plotted for the 10° latitude line and the April 16 curve is plotted for the 10° north latitude. The scaled and unscaled ellipse azimuth functions are plotted as in A and B above. Again, the need for scaling the resulting functions is apparent, particularly in D. Additionally, even the approximation of the scaled ellipse azimuth function is not as good as in the functions plotted for the equinox. Because of the symmetry of the ellipse, the ellipse azimuth functions are constrained to pass through 90° at 06:00 solar time and 270° at 18:00 solar time. Thus the correspondence to the actual azimuth functions is not as good, since the true azimuth functions do not have this constraint. This is one of the most important predictions of the ellipse model.

The necessity of scaling the output is probably not a serious problem for this model. Since it is a neural model (the symbolic calculations are assumed to be implemented in isomorphic neural processes) the outputs would not be scaled identically to the numerical values presented here. The output could easily be a ratio based on another value in the calculation. The scaling function I used relies on this simple manipulation:

$$A_t^* = \frac{A_t}{A_N} 360 \quad (4.3)$$

where the scaled azimuth at time t (A_t^*) is equal to the ratio of the unscaled azimuth at time t (A_t) and the unscaled azimuth for the last time interval (A_N) multiplied by 360° . This implies that the azimuth at midnight is 360° . The ellipse azimuth function could just as easily be scaled to 180° at noon. Both of these alternatives force the ellipse function to take on values that may not necessarily exist for a given latitude and season (i.e. if the sun actually passes to the north at noon). However, the ellipse azimuth function could also be scaled to pass through 90° at 06:00 or 270° at 18:00. All actual azimuth functions pass close to these values and all scaled ellipse azimuth functions pass through them.

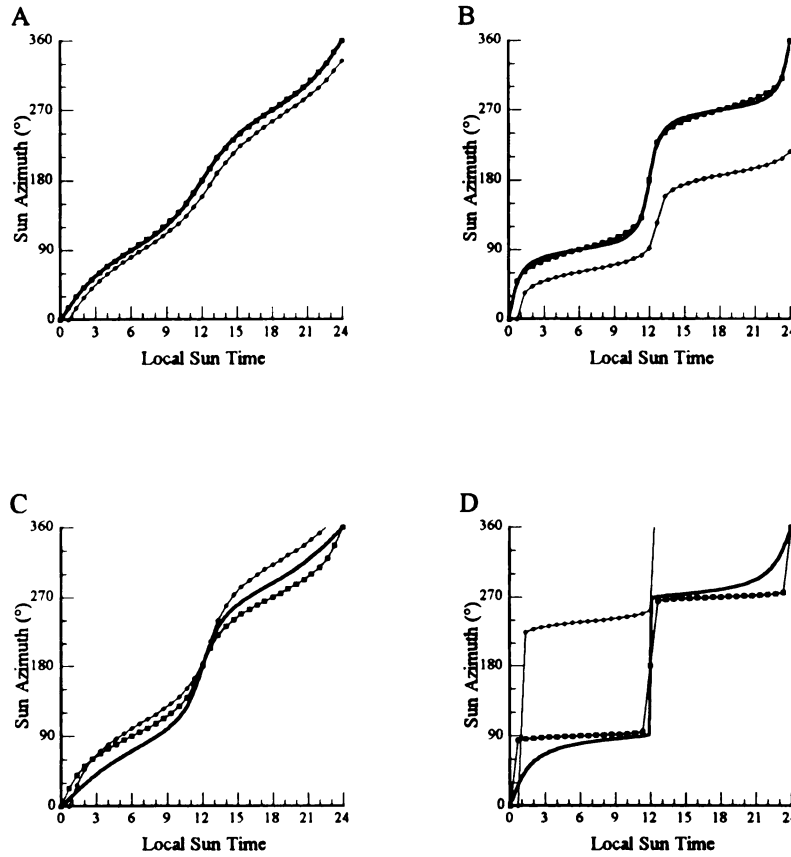


Figure 4.3 The scaled and unscaled ellipse azimuth functions for different seasons and latitudes. **A.** The true solar azimuth is plotted with two ellipse azimuth functions for 40° north latitude at the equinox. The squares correspond to the scaled ellipse azimuth function and the diamonds correspond to the unscaled azimuth function. The ellipse parameters for both ellipse azimuth functions are $a = 23$, $b = 10$ (as in Figure 4.1 E). The scaling function is described in the text. The true sun azimuth curve is depicted by the heavy line. **B.** The solar azimuth function (heavy line) and two ellipse azimuth estimates (scaled = squares; unscaled = diamonds) for 10° north latitude at the equinox. Ellipse parameters are $a = 85$, $b = 3$. **C.** The solar azimuth function (heavy line) and two ellipse azimuth estimates (scaled = squares; unscaled = diamonds) for 40° north latitude during the summer solstice. Ellipse parameters are $a = 48$, $b = 9$ (these values were determined from the actual azimuth rate function numerically calculated over 8 minute intervals as in Figure 4.1 C and D, and depicted in Figure 4.2 C). **D.** The solar azimuth function (heavy line) and two ellipse azimuth estimates (scaled = squares; unscaled = diamonds) for 10° north latitude on April 16 (declination 9°54'). Ellipse parameters are $a = 662$, $b = 1.5$. The values for the ellipse parameters a and b were determined from the actual azimuth rate function, numerically calculated over 8 minute intervals as in Figure 4.1 C and D, and depicted in Figure 4.2.

All of the ellipse azimuth functions presented up to this point concern azimuth functions that pass to the south at noon: those typically viewed from the northern latitudes. But during the northern summer, from most vantage points on the earth, the sun passes to the north at noon. At the northern summer solstice this occurs from viewing positions from the tropic of Cancer ($23^{\circ}26' \text{ N}$) southward. In these cases, the sun appears to move counterclockwise around the northern horizon. By convention, the rate of change of the azimuth in these cases would be negative. The rate of change is still maximal around noon. The functional relationship between the rates of different times of day is maintained; therefore, it would seem that they too can be described by an ellipse function. However, by inspection of equations 4.1 and 4.2 (the equations of the ellipse), it is clear that the ellipse will have a positive radius (r , the rate of change of the azimuth) even if the parameters a and b are negative. The easiest way around this problem is to assume that information about direction of movement is maintained in a separate channel of information flow in the nervous system. This information can be implemented by changing the sign in equation 3.1 and subtracting changes in azimuth from previous values throughout the day.

Figure 4.4 shows the results of a case of counterclockwise movement. In this figure, the azimuth functions for 5° N and 40° N on the summer solstice are plotted with the corresponding scaled ellipse functions (40° N : $a = 48$, $b = 9$; 5° N : $a = -43$, $b = -1$).

Although it is technically inaccurate, for simplicity, I have conveyed the information about the direction of movement in the signs of the parameters a and b . I will use this

convention henceforth. The values for a and b are theoretical estimates, derived from a numerical calculation of the true azimuth rate functions for the two ephemeris functions (as in Figures 4.1, 4.2, and 4.3). Additionally, the actual theoretical value for b is 1, instead of -1. This occurs because in the tropics the azimuth's movement along the horizon can reverse directions. But for the model, I will assume that b has the same sign as a .

From Figures 4.3 and 4.4 it is apparent that the combined use of equations 4.1 and 3.1 (the ellipse azimuth function) with appropriate scaling functions, can yield sun azimuth positions that closely approximate the true sun azimuth function for any particular season and latitude.

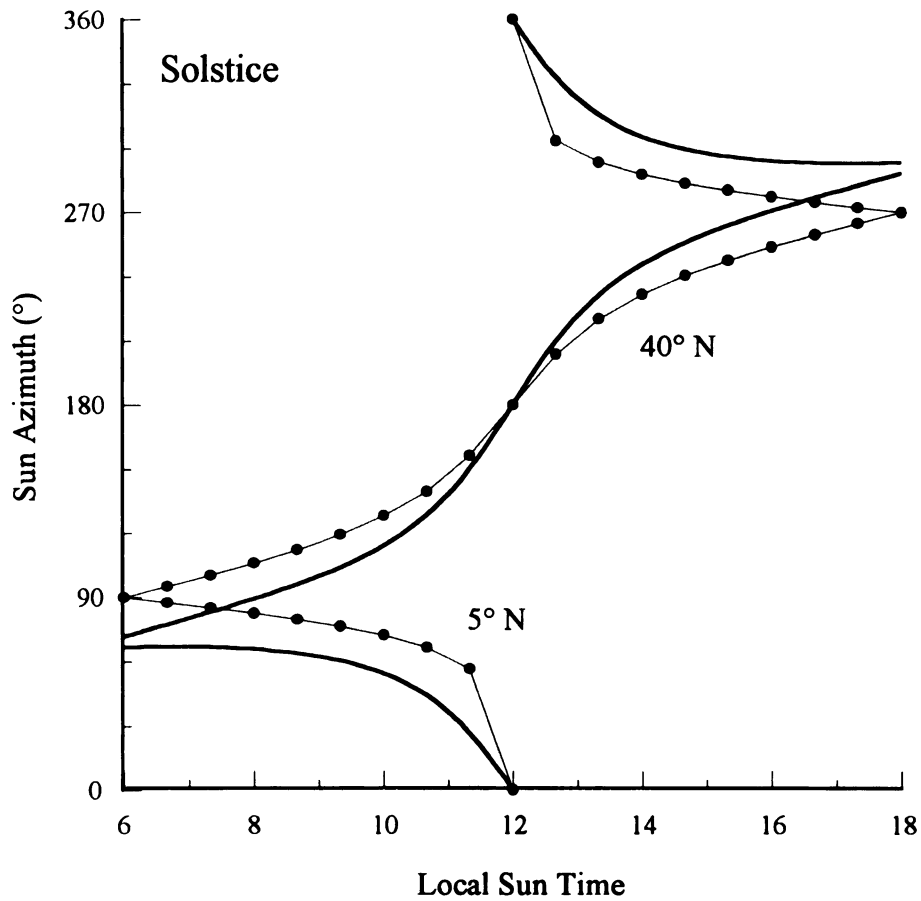


Figure 4.4 Ellipse azimuth functions for 40° N and 5° N at the northern summer solstice. The parameters of the ellipse rate function were estimated from numerical calculations of the actual azimuth rate function over 8 minute intervals (as in Figures 4.1, 4.2, and 4.3) (40° N: $a = 48$, $b = 9$; 5° N: $a = -43$, $b = -1$). The actual ephemeris functions are plotted for comparison.

4.4 Estimating the Parameters of the Ellipse

The ellipse rate function (equation 4.1) has two parameters that determine its shape (a and b). These parameters can be estimated from the readily observable quantities that have been used in the previous symbolic models of this process: azimuth position and time of day. For a bee to estimate the position of the sun using computations equivalent to equations 3.1 and 4.1, she would have to estimate the parameters of the ellipse at a time of day when the rate of azimuthal movement has been observed. With two observations of the rate of change of the azimuth and time (this could involve four observations of azimuth position and time, see equation 3.2), the parameters a and b can be estimated with the following two equations:

$$a = r_1 r_2 \sqrt{\frac{|\sin^2 \tau_1 - \sin^2 \tau_2|}{|r_1^2 \sin^2 \tau_1 - r_2^2 \sin^2 \tau_2|}} \quad (4.4)$$

$$b = r_1 r_2 \sqrt{\frac{|\sin^2 \tau_1 - \sin^2 \tau_2|}{|r_1^2 \cos^2 \tau_1 - r_2^2 \cos^2 \tau_2|}} \quad (4.5)$$

in which a and b are the estimated parameters of the ellipse and r_1 , r_2 , τ_1 , and τ_2 are specific observations of the rate of change of the azimuth at specific times of day.

Equations 4.3 and 4.4 were generated by solving equation 4.1 for a and b and substituting each equation into the other. I have added the absolute value operators to prevent imaginary numbers from resulting. They have no effect on the magnitude of a or b , only whether they are real or imaginary. This manipulation is required because not all rates

and times that could be observed by a bee necessarily fall on a true ellipse since the ellipse is an approximation of the true function. If equations 4.4 and 4.5 were not constrained in this way, the resulting function would not necessarily be an ellipse.

Note that once again the effects of observed negative rates (counterclockwise movement of the azimuth) are eliminated in equations 4.4 and 4.5 (assuming the two observations of rate have the same sign). This occurs because the rates are multiplied together and squared in equations 4.4 and 4.5, eliminating negative sign of the rates. This substantiates the need for an independent channel to carry information about the direction of movement.

4.5 Fit of Ellipse Azimuth Function to Experimental Data

The ellipse azimuth function is flexible enough to represent a wide range of azimuth functions. By determining the values of a few parameters, an animal can have a representation of a full 24-hour function which closely approximates the course of the sun. In the data presented in Chapter 3, it was established that honey bees can relatively accurately estimate the position of the sun in the morning, even if they have previously seen it only during the late afternoon. However, the bees' representation of the sun's course was not completely accurate. Instead, the data suggested that a 180° step function describes the mechanism they were using. Figure 4.5 shows that the ellipse azimuth function can produce curves that range from 180° step functions to relatively flat curves that correspond more closely to a sun azimuth curve from a temperate region. The parameters (a and b) for the ellipse azimuth functions range from the theoretically

expected values (given the actual maximum and minimum rates of change of the azimuth for those dates) to the values that best fit the experimental data. The set of parameters of the ellipse function that produced the best fitting azimuth curves to the data was actually one set of out of many sets of parameters that fit the data equally well. Because of the discrete nature of one of the equations (3.1) used to generate the ellipse azimuth function, the best-fitting parameters had to be determined iteratively rather than analytically. I used a hill climbing algorithm to make small adjustments to a and b in order to find the values of the parameters that maximized R^2 . The algorithm stopped repeatedly at local maximum that produced R^2 values very close to each other, often differing only in the fifth decimal place. A systematic exploration of the space revealed a long ridge of roughly equal height. For the values of the parameters reported, I used the values closest to the theoretically predicted values that resulted from 50 runs from different randomly chosen starting points.

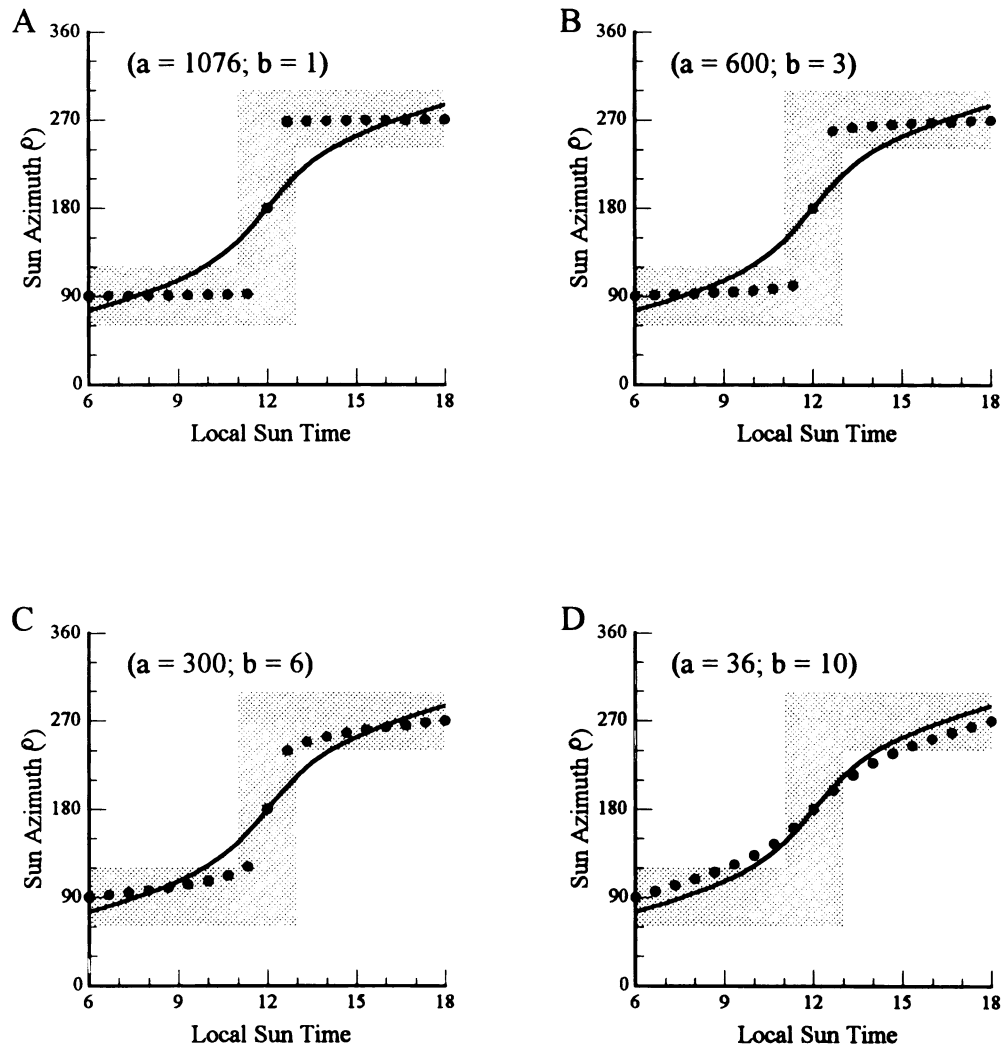


Figure 4.5 A range of ellipse azimuth functions corresponding to the data from colony 1 (see Chapter 3). A. Parameters corresponding to the best fitting ellipse function ($a = 1076$, $b = 1$). B. Intermediate parameters ($a = 600$, $b = 3$). C. Intermediate parameters ($a = 300$, $b = 6$). Theoretical (expected) parameters of the ellipse (numerically calculated from the true azimuth rate function as in Figure 4.1, 4.2, and 4.3) ($a = 36$, $b = 10$). The shaded region corresponds to an ideal step function based on the data from colony one. The region corresponds to the mean (270° or 90°) $\pm$ one standard deviation ($\sim 30^\circ$) of the data.

An azimuth function generated with a combination of equations 3.1 and 4.1 fits the data from colony 1 well ($R^2 = .87$; $a = 1076$, $b = 1$). This is 2% better than the fit of the 180° step function, but it is a statistically significant difference ($F_s = 1.16$, $df = 536,536$, $p < .05$). This difference probably results from the fact that the ellipse function explains the variance of the bees' estimates during the midday transition period better than a step function. See Table 4.1 for a comparison of goodness-of-fit with the actual azimuth function and the 180° step function. The parameters of the ellipse function that produce the azimuth curve that best fits the data are considerably different from the theoretically expected parameters (see Figure 4.5 and Table 4.2). The theoretically expected parameters were derived from numerical calculations of the true rate function. The value of a in the best-fitting ellipse was 1,076° per hour which was nearly 30 times the 36° per hour expected maximal rate around midday. It would seem that if the bees are using this type of mechanism to estimate the unknown azimuth, they are using an ellipse that is considerably more squashed than the most appropriate ellipse for this season and latitude. This could be a default mechanism.

For colony 2 an azimuth function generated from the ellipse rate model explains a considerable proportion of the data ($R^2 = .94$; $a = 421$, $b = 3$) of the experience-restricted bees. The fit of the data to the ellipse model is significantly better than the fit of the data to the actual ephemeris function ($F_s = 4.23$, $df = 179,179$, $p < .001$), and to the 180° step function ($F_s = 1.53$, $df = 179,179$, $p < .005$). Again, the observed parameters of the ellipse

that produced the best fitting azimuth curve were different from the theoretically expected values (see Table 4.2).

The ellipse model, with different parameters of shape, also explains a considerable fraction of the data for the fully experienced bees ($R^2 = .87$; $a = 36$, $b = 3$). This is significantly better than the 180° step function ($F_s = 2.85$, $df = 59, 59$, $p < .001$). The ellipse function appears to explain slightly more of the data than the actual azimuth function, but the difference is not statistically significant ($F_s = 1.29$, $df = 59, 59$, $p = .17$). Thus the fully experienced bees appear to be using an ellipse azimuth function based on a more accurate estimate of a and b .

For colony 3, the ellipse azimuth function fits the data as well as the 180° step function ($R^2 = .82$; $a = 13$; $b = 9$); there is no statistical difference between them.

For colony 4, the ellipse azimuth function fits the data about as well as the true azimuth function ($R^2 = .27$; $a = 31$; $b = 16$). The fit of the data to the ellipse azimuth was not statistically different from the fit to the true sun azimuth, although both were substantially better than the step function. There is considerably more error variance for this colony, which relied on flight bearings rather than dance angles to determine their estimates of the solar azimuth.

Table 4.1 Fit of Models to Experimental Data (R^2)

<u>Data Set</u>	<u>Azimuth</u>	<u>Step-Function</u>	<u>Ellipse</u>
Colony 1	0.59	0.85	0.87
Colony 2 (RE)	0.73	0.91	0.94
Colony 2 (FE)	0.85	0.65	0.87
Colony 3	0.76	0.82	0.82
Colony 4	0.25	-0.61	0.27

RE: restricted experience; FE: full experience

Table 4.2 Expected and Observed Parameters of the Ellipse

<u>Data Set</u>	<u>Expected</u>		<u>Observed</u>	
	<u><i>a</i></u>	<u><i>b</i></u>	<u><i>a</i></u>	<u><i>b</i></u>
Colony 1	36	10	1,076	1
Colony 2 (RE)	27	10	421	3
Colony 2 (FE)	27	10	36	3
Colony 3	32	10	13	9
Colony 4	30	10	31	16

RE: restricted experience; FE: full experience

4.6 Fit of Ellipse Azimuth Functions to Other Data Sets

In addition to fitting the experimental data from Chapter 3 well, the ellipse model may be applied to other data sets with similar success. The data from New and New (1962) provide an example of the generality of this model as a description of sun compensation. Recall that New and New (1962) observed the dance of bees in the tropics as the sun passed very close to the zenith at noon. They found that bees compensated during midday at a very rapid rate over the approximately 180° separating the morning and afternoon azimuths of the sun. The data (see Figure 3.3) have long been interpreted as evidence that bees interpolated linearly between the morning and afternoon positions of the sun. The alternative explored here is that the bees were using a continuous function based on an ellipse. With suitable parameters, the ellipse azimuth function describes the data very well (see Table 4.3). In this case, the observed parameters of the best fitting ellipse azimuth functions are quite close to the expected parameters (see Table 4.4).

One striking result of New and New (1962) was the fact that the bees anticipated the sun passing to the north at noon several days before this occurred. With the ellipse model, this would suggest that the bees were using the parameters of a single ellipse throughout the days during the transition period. The pooled data (for colony 1) from New and New (1962) for April 15 to 21 are well described by a single ellipse azimuth function ($R^2 = .91$, $a = -251$, $b = -2$).

Table 4.3 Fit of Ellipse Model to New & New (1962) Data (R^2)

Data Set	Azimuth	180° Step-Function	Ellipse
April 15	-0.42	0.51	0.92
April 16	0.14	0.5	0.92
April 17	0.48	0.63	0.9
April 18	0.36	0.19	0.97
April 20	0.72	0.33	0.89
April 21	0.74	0.31	0.91

Data from New & New (1962): Colony 1, Trinidad (10°38' N)

Table 4.4 Expected and Observed Parameters of the Ellipse (New & New, 1962)

Data Set	Expected		Observed		R^2
	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>	
April 15	240	3	-229	-1	0.92
April 16	254	3	-359	-2	0.92
April 17	263	3	-415	-2	0.9
April 18	-262	-3	-166	-2	0.97
April 20	-238	-3	-218	-2	0.89
April 21	-227	-3	-192	-2	0.91

Data from New & New (1962): Colony 1, Trinidad (10°38' N)

4.7 Reducing the Number of Parameters

As I indicated above, in the search for the parameters that yielded the ellipse azimuth functions that best fit the data, I encountered multiple pairs of parameters that produced curves that fit the data equally well. In retrospect, this is to be expected since the effect of the scaling function is to render the particular values assumed by the parameters a and b somewhat irrelevant. This is because it is only the shape of the ellipse that is important in determining the values that the ellipse azimuth function assumes. This suggests that it is the relative magnitude of the parameters a and b that is important. Figure 4.6 further substantiates this inference. Figure 4.6 shows the range of values of the parameters of the ellipse (a and b) that yield ellipse azimuth functions that fit the data equally well (or very close to it). These data are for the restricted experienced bees of colony 2. The linear relationship between the values of a and b indicates that it is the relative magnitude that is important. This same pattern appears for almost all of the other data sets examined. The data for colony 1 provide an apparent exception to this rule, which is probably a special case where the slope of the line is zero. This probably results from the fact that all parameters for the best-fitting ellipses for colony 1 yield ellipse azimuth functions that approximate step functions. Thus, all of these functions explain the variance in colony 1 equally well. In other words, once the step-function threshold is surpassed, there is a wider range of parameters that yield equivalent azimuth curves.

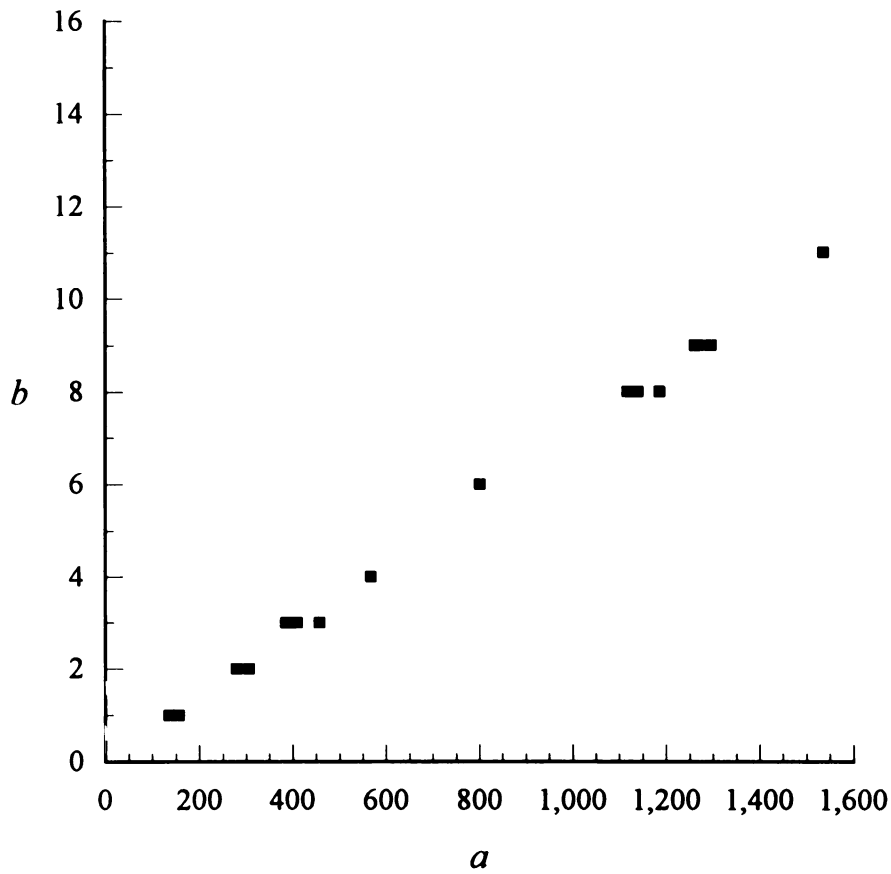


Figure 4.6 Range of the parameters of the ellipse that generate equivalent ellipse azimuth functions (see footnote 6). All of the parameters yield azimuth curves that fit the data of colony 2 equally well ($R^2 = .94$). The linear relationship suggests that the two parameters necessary to describe the ellipse azimuth function may be reduced to a single ratio.

This relationship between the parameters a and b suggests that the number of parameters that need to be estimated to generate an ellipse azimuth function may be reduced to one. A single parameter would be powerful enough to generate approximations to all of the azimuth functions on the planet. I will define this parameter as k which is simply the ratio of a to b . From equations 4.4 and 4.5, a means of estimating k directly can be generated:

$$k = \sqrt{\frac{|r_1^2 \cos^2 \tau_1 - r_2^2 \cos^2 \tau_2|}{|r_1^2 \sin^2 \tau_1 - r_2^2 \sin^2 \tau_2|}} \quad (4.6)$$

This parameter can be used with the following equation to produce an ellipse of standardized size:

$$r = \frac{k}{\sqrt{k^2 \sin^2 \tau + \cos^2 \tau}} \quad (4.7)$$

The semiminor axis of this ellipse is always one and the semimajor axis is k which corresponds to the ratio of a and b . This ellipse requires the use of a scaling function to produce the correct range of values.

4.8 Estimating k with Restricted Experience

So far I have shown that ellipses can be used to generate a range of azimuth functions and that with the right parameters, these ellipse azimuth functions provide a good fit to the experimental data. With equations 4.4, 4.5 and 4.6, I have shown how the bees could

theoretically estimate the parameters of the ellipse. There is a considerable gap, however, between this theory and the practice of actually estimating the parameters given the restricted experience of the bees. I conducted numerical simulations to see if this is at least possible. I randomly picked four times of day falling within the training period of colony 1. These defined two time periods over which I estimated the rate of change of the azimuth, using the azimuth for the last day of training. For 1000 simulation runs, the results suggest that accurate estimates of k could be obtained with the restricted experience (see Table 4.5). The mean k was 4.1 which is very closed to the predicted 3.6, but very far from the observed 1,076 of the best fitting ellipse azimuth function. The maximum k from this run was only 160.7.

This result raises the question of how the ellipse model can account for the data. This question can be allayed somewhat by introducing error into the bee's ability to estimate the position of the azimuth. New and New (1962) first suggested this as one of the potential reasons behind the data they observed. Introducing error, or limits on visual acuity into the estimate greatly increases the range of parameters estimated from the restricted experience period. Even small errors of 1° can have large effects. New and New (1962) suggested that a 3° acuity level best described their data. Table 4.5 shows the estimates of k from 1° , 3° and 5° limits on acuity.

Table 4.5 Estimates of k from the Training Period of Colony 1

<u>Acuity Threshold</u>	<u>Mean k</u>	<u>Maximum k</u>	<u>Median k</u>	<u>Standard Deviation of k</u>
0°	4.1	106.7	1.9	10.4
1°	41.3	16,700	2.1	602.1
3°	51	13,000	2.2	561
5°	32.3	2,698	2.3	160.1

4.9 The Effect of the Time Interval

Since a discrete difference equation (3.1) is used in the generation of the ellipse azimuth function, the length of the time interval over which it is summed has an effect on the resulting function. I suggested above that this essentially added a parameter to the equations. Presumably the bees (or other animals) have a specific time interval or average interval that they would use in this process. It makes sense that it is a finite interval, since the predicted change in azimuth should be above the perceptual threshold of the animal. In the determination of the best fitting ellipse parameters, a single time interval was used for all of the data sets: 40 minutes. Initially, I did not hold this parameter constant. The result of numerous runs suggested that the best-fitting parameter was between 20 and 60 minutes. I assumed that the interval size should not vary considerably between individuals or colonies. The 40 minute size is also corresponds to some empirical data that suggests that bees update their information about the sun's position about every 40 minutes (Gould, 1984).

One of the effects of using this relatively large time interval (with respect to instantaneous updates) is that error gets incorporated into the function that is generated. This is equivalent to sloppy integration. It appears that this error increases the range of functions that can be produced, particularly those resembling step functions, which correspond to the experimental findings (Dyer & Dickinson, 1994). Figure 4.7 shows this effect.

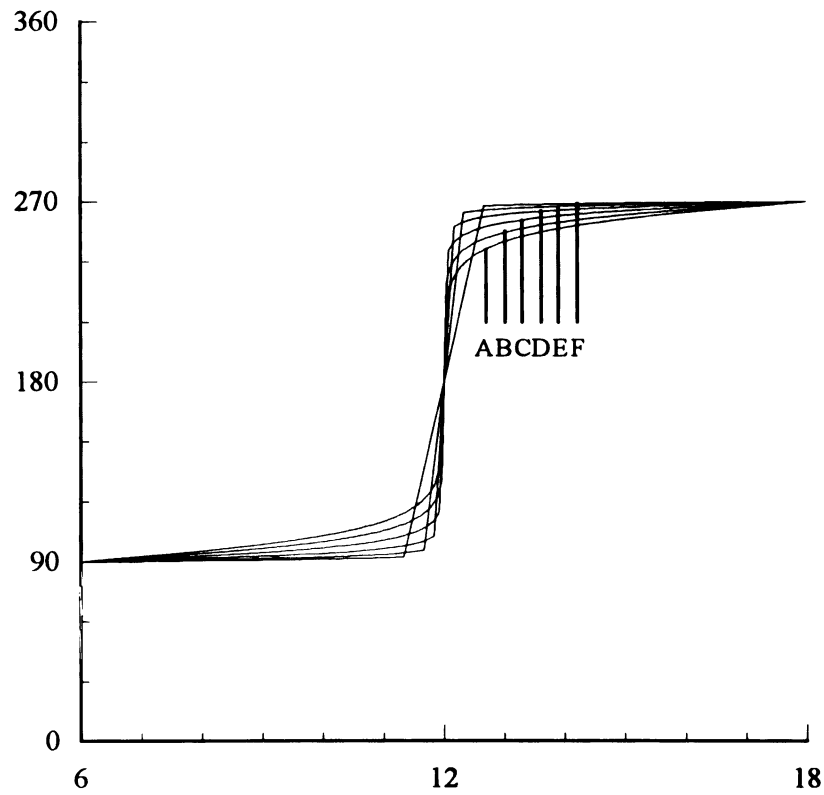


Figure 4.7. The effect of time interval on the ellipse azimuth estimate. For all of the curves, k is 1076 as in the best-fitting ellipse azimuth function for colony 1. Time intervals are (A) 1, (B) 2, (C) 5, (D) 10, (E) 20, and (F) 40 minute intervals. The curve that is most like a step function is the curve for 40 minute intervals.

4.10 Summary

In this chapter, I have shown that it is possible to derive a symbolic model that could account for the recent experimental results regarding the sun-azimuth functions used by ants (Müller & Wehner, 1993) and bees (Dyer & Dickinson, 1994). The critical departure from previous models of sun compass learning is in the fact that this new model incorporates the variation of the rate of change of the azimuth throughout the day. Although other functions may perform as well, this model relied on the intuitively satisfying model of a rate function based on the geometry of an ellipse.

Chapter 5

CONNECTIONIST MODELS

In this chapter I present a set of models that provides a contrast to the symbolic model described in Chapter 4. In all of the models of sun compass learning presented in Chapters 3 and 4 the assumption was that insects rely on an explicit function to calculate azimuth position using the time of day. Regardless of whether the models relied on linear or nonlinear rates of change of the azimuth in their calculations, the processes involved the manipulation of symbols that corresponded to the observable quantities of azimuth position and time.

In this chapter, I will present a set of connectionist models (Feldman & Ballard, 1982) that contrast with all of the previous models of sun compass learning, including the model presented in Chapter 4. In these models there is no explicit function computing azimuth angle from inputs of time of day. There is no mechanism manipulating symbols that correspond to azimuth position and time of day. These models will include nonlinearities (Grossberg, 1988) that may allow them to account for the nonlinearities of the pattern of solar movement that appear to be incorporated into the bees' (Dyer & Dickinson, 1994) and ants' (Wehner & Müller, 1993) estimates of the sun's position at times of day they

have never seen it. These models could therefore be considered nonlinear nonsymbolic models in contrast with the nonlinear symbolic model of Chapter 4.

These connectionist models of sun compass learning illustrate the types of behavior that could result from a network of interconnected simple computing units (i.e. neurons) in which there no explicit coding of an azimuth function. Such a network could form the basis of an innate template that is modified with experience. This connectionist template may allow insects to quickly recognize the local ephemeris function or quickly learn the local ephemeris function or both.

5.1 Connectionist Computations

Connectionist neural networks generally consist of a large number of interconnected processing units (Feldman & Ballard, 1982; Rumelhart et al., 1986a). For the networks I will consider, the neural elements are arranged in layers with connections between the elements of each layer, but not within the layer. The information flows in one direction from the input layer (sensory) to the output layer, making them feed-forward networks or perceptrons (Rosenblatt, 1958; Rumelhart et al., 1986b). The power of a network to learn a complex representation comes from the number of layers in the network and the number of units in the layers. Figure 5.1 shows a diagram of a simple feedforward network.

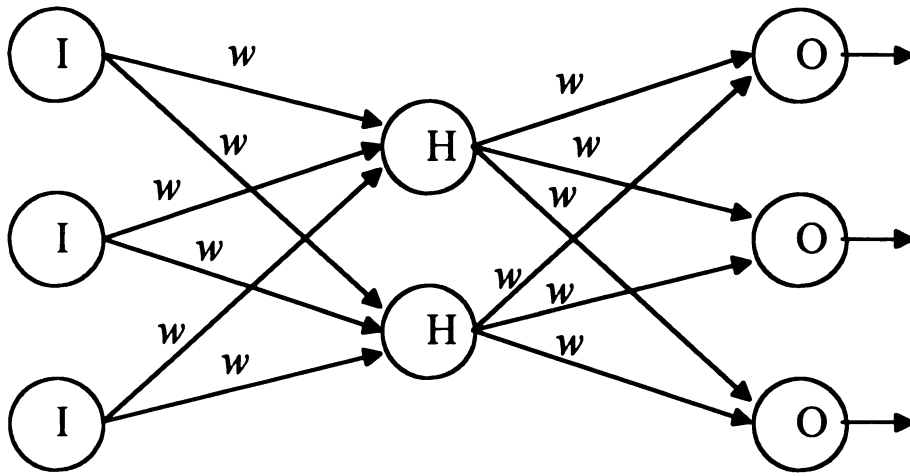


Figure 5.1 General form of a feed-forward connectionist network. I: input units H: hidden units. O: output units. w : connection weights.

Each individual unit essentially computes a weighted sum of its inputs to determine its output. The sum is weighted by the connection strengths (or weights) between the units. This weighted sum is described by the following equation:

$$x_j = \sum y_i w_{ji} \quad (5.1)$$

in which the total input (x_j) of the j th neuron is the sum of the outputs (y_i) of the i th layer and the connection weights between the layers (w_{ji}) (Rumelhart et al., 1986c). The output of the unit is a nonlinear function of the weighted sum of the inputs. Generally, this function is a sigmoid:

$$y_j = \frac{1}{1 + e^{-x_j}} \quad (5.2)$$

where y_j is the output of the j th and x_j is the weighted sum of the inputs to the j th neuron as in equation 5.1 (Rumelhart et al., 1986c).

Networks composed of these simple units that are arranged in at least three layers (Rumelhart et al., 1986c) can learn a wide range of arbitrary mappings between inputs and outputs. In fact, they are universal approximators (Hornik et al., 1989). This means that given the appropriate network size and training time, they can learn to approximate any functional relationship between a set of inputs and a set of desired outputs. Simple perceptrons (Rosenblatt, 1958) are limited in their learning abilities (Minsky & Papert, 1969), but the inclusion of the internal layer of "hidden units" greatly increases their capacity to form a wide range of representations (Rumelhart et al., 1986c).

For a network to learn a complex representation it must have a mechanism for adjusting the connection weights (w_{ji}) between the layers of neural elements. Connection weights could be set by hand, but the complexity of such networks usually requires a learning algorithm that adjusts the connection weights progressively to reduce the error between the outputs of a network and the desired outputs. One of the most common and most powerful algorithms is the method of backpropagation of error (Rumelhart et al., 1986c). This is a method for finding the global error minimum in multidimensional weight space. The backpropagation algorithm adjusts each weight such that it achieves the steepest descent in error. Thus errors in the output of the network as a whole can be used to modify the connection weights within the network.

This learning method lacks biological realism in the exact mechanism of learning, the modification of the connection weights. Nonetheless, the major advantage of backpropagation is that it allows the behavior of large networks of simple units to be investigated. These are good models for the behavior of distributed representations that can provide insights into brain mechanisms (McClelland et al., 1995).

5.2 Connectionist Characteristics

Aside from their flexible learning abilities, perhaps the property of connectionist networks that has attracted the most attention is their ability to generalize the learned relationship between the input and output sets. This allows networks to classify novel inputs and to

complete partial patterns. The ability of connectionist networks to recognize and complete patterns has long been recognized (Rosenblatt, 1958; Minsky & Papert, 1969), but the widespread application to this area awaited a sufficient learning algorithm (Rumelhart et al., 1986b).

An example of this is seen in the face-recognition network of Cottrell and Metcalfe (1991). This network, which had an architecture analogous to that in Figure 5.1 but with different numbers of units, was trained on a set of images to classify human faces by name and gender. Subsequently, the network could recognize different images of the same faces in the training set and it could classify novel faces by gender. Additionally, when presented with partial views of the faces, it could reconstruct the entire face. This was done without any explicit coding of the geometrical properties of faces. The same network would undoubtedly have been able to learn to recognize images of different bird species, or the leaves of different tree species, and to classify partial images of these natural shapes.

5.3 Connectionist Representations of the Sun's Course

The ability of connectionist networks to complete partial patterns seems to parallel the ability of insects to fill gaps in their experience with the sun's course. In this construction, the sun compass learning problem is a pattern completion problem or a perceptual recognition problem. This is based on the assumption that completing the pattern of solar

movement is analogous to the other types of patterns that connectionist neural networks are able to complete.

I will consider both the learning capabilities and the pattern completion capabilities of connectionist networks as I examine their relevance to the sun compass problem.

Additionally, I will consider two alternative ways of representing the sun's course in a connectionist framework. The first is a binary mapping and the second is a continuous mapping.

5.4 A Binary Representation

It is clear from the experimental data presented in Chapter 3 that bees and ants are able to fill gaps in their experience with the sun to such an extent that they relatively accurately infer the position of the sun during large portions of the day or night. To model this with a connectionist architecture, we must consider that the network that the bees bring to the problem must be innately configured so that it can estimate unknown solar positions.

Thus, the training of this network could not have involved the experience with these portions of the sun's course. We are therefore dealing with a network trained during evolutionary history. In principle, however, standard connectionist training principles might apply. In this case, the errors generated by the network would be minimized through the action of natural selection.

A preconfigured network could have several forms, each with different potential advantages to a small-brained, short-lived animal. Such a network may allow an animal to quickly access the appropriate solar ephemeris function for its foraging lifetime. Honey bees forage outside the colony for only about 10 days before they die, and they make relatively few flights before they start foraging. A preconfigured network may allow them either to quickly recognize the correct local ephemeris pattern or to quickly learn the correct local ephemeris pattern or both. I will consider these alternatives in turn.

5.4.1 Pattern Matching

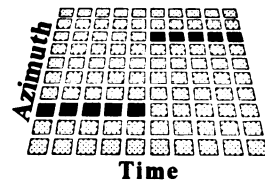
Like the face recognition problem outlined above, a network configured to recognize a solar ephemeris function would be trained (over evolutionary time) on a range of azimuth functions. The strategy employed in this model was to train a network on a range of azimuth functions and subsequently test the network with partial azimuth functions. This is analogous to bees with an innately-configured network receiving restricted experience with the sun's course (Dyer & Dickinson, 1994).

The training patterns for this network (Figure 5.2) were idealizations of a range of solar ephemeris functions that would normally occur at different seasons and latitudes (see Figure 2.2 for a range of real azimuth functions). A binary mapping was used to represent the ephemeris functions (in Figure 5.1, black = one, white = zero). The pattern of ones and zeros indicates the presence or absence of a particular combination of azimuth angle and time of day. Some preprocessing would be required to get observations of azimuth

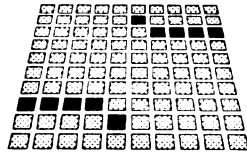
angles at times of day into this format. Each 10 by 10 array corresponds to a coarse-grained depiction of a particular solar azimuth function. The specific size of the array was originally constrained by the maximum size of the input array in the computer simulation package that I initially used (Caudill & Butler, 1992). Seven patterns were generated to correspond to a range of ephemeris functions: from a 180° step function approximating a tropical azimuth curve to gradual curves approximating the typical ephemeris functions of the northern and southern temperate regions. Given the coarseness of the binary mapping, seven patterns provided the complete range between a step function and a gradual function.

Figure 5.2 Idealized solar ephemeris functions used as the training set for the connectionist models. The patterns consist of a matrix of ones and zeros, with the ones corresponding to the black squares and the zeros corresponding to the white squares. Each point corresponds to a pairing of azimuth position and time of day. These patterns correspond roughly to the natural range of solar azimuth functions (See Figure 2.2).

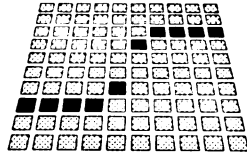
A



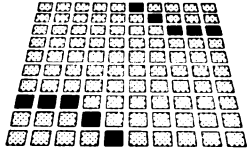
B



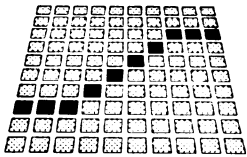
C



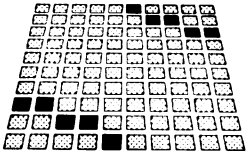
D



E



F



G

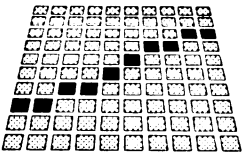


Figure 5.2

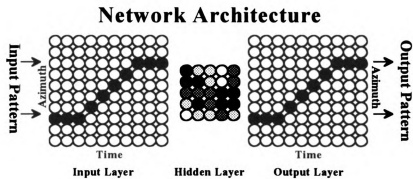


Figure 5.3 Network architecture. The network has 100 input units and 100 output units that correspond to azimuth-time coordinates. There are 25 hidden units. See text for explanation of connection patterns. The connections are not shown because of the number of them. Activation is shown by the gray scale (white = zero; black = one).

The network was trained to recognize each of the seven training patterns. The network had 100 input units and 100 output units. Between the input and output layers was a single hidden layer of 25 units. Each of the input units was fully connected with each of the hidden units and each of the hidden units was fully connected with each of the output units. The original findings were obtained with a commercially available simulation package (Caudill & Butler, 1992), but they have been replicated and extended with models run on *Mathematica*® and *Mathcad*®. The initial connection weights were pseudorandom numbers ranging from -0.3 to 0.3. The learning constant (η) was set at 0.5. (This determines the size of the weight changes). The networks were trained through repeated exposure of the network to the patterns until the mean squared error between the desired and the actual outputs of the network was reduced to 5%. The backpropagation algorithm was used to adjust the connection weights during training (Rumelhart et al., 1986c).

After the networks reached the criterion, they were presented with test patterns consisting of fragments of ephemeris functions (see Figure 5.4 A). These test patterns were analogous to the partial ephemeris functions experienced by the bees in the experiments presented in Chapter 3. The responses of a trained network to each of the test patterns are presented in Figure 5.4 B. These responses consist of the activity levels (the result of equations 5.1 and 5.2) for each of the output units. The values range from zero to one because of the effect of the sigmoid activation function (equation 5.2) of each of the units, which asymptotically approaches zero and one. Although the patterns presented in Figure

5.4 (B) correspond to a single network configuration produced through training, the results of other replicates were consistent. The results are presented in this way to show the subtleties that exist in the representation of the pattern in a single network. The results presented in Figure 5.4 correspond to a network with 25 hidden units; nearly identical effects are seen in networks with only 10 hidden units.

In response to the test patterns, the network filled the gaps in the partial azimuth curves. When the test pattern consisted only of solar positions in the late afternoon (analogous to what afternoon-experienced honey bees faced (Dyer & Dickinson, 1994) or in the early morning (analogous to what morning-experienced desert ants faced (Wehner & Müller, 1993)), the network produced a pattern of activation resembling the 180° step function that the experience-restricted bees and ants develop. For several of the test patterns with late afternoon azimuth fragments, the network produced a step-function that also exhibited variability during the midday transition. This mimics the behavior of some of the bees from colony 1 (Figure 3.3 and 3.4) and of the bees in New and New's (1962) study.

In contrast with the patterns that produce a step function, several of the test patterns, corresponding to midday time-azimuth positions, resulted in gradual functions. This suggests that experience at different times of day might lead to different representations of the sun's course.

One of the test patterns was unnatural and indicated time-azimuth positions that would never occur on the earth (e.g., bottom panel of Figure 5.4). The preconfigured network ignores this type of spurious information.

These results demonstrate that certain aspects of the sun compass learning problem in insects can be mimicked by a neural network that does not explicitly encode a mathematical expression corresponding to the relationship between azimuth angle and time. With experience over the entire day, the network may be able to recognize the appropriate local ephemeris function. But with partial experience, the overlap among the possibilities causes the network to partially activate several of the alternatives, leading to the highest activation of the intermediate function: the 180° step function.

Figure 5.4 Responses of preconfigured network to test patterns consisting of partial ephemeris functions. The test patterns (A) consist of inputs arranged in an array of ones and zeros as in Figure 5.2. The responses (B) for each test pattern are presented immediately to the right. The responses consist of the activation level of each of the output units. They range from zero to one and are all on the same scale. See text for a description of the network.

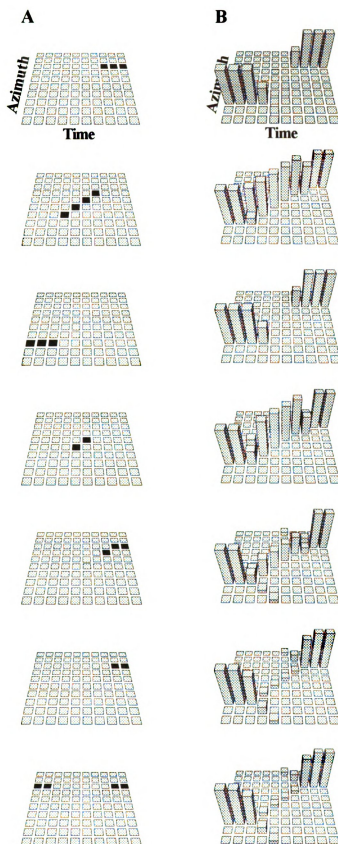


Figure 5.4

5.4.2 Learning Advantage

An alternative potential advantage of a preconfigured neural network may be that it allows the insect to rapidly learn the appropriate local pattern. The question in this case is whether a network that has learned one representation of the sun's course can quickly replace that representation with one that corresponds to the actual pattern of movement observed.

The 180° degree step function provides a logical starting place for this question. An insect using a 180° step function during any season or at any latitude would experience the least average error in its estimation of the sun's position than one using any other azimuth function. This is because the 180° step function is the average of all of the solar ephemeris functions encountered on the earth (i.e. all ephemeris functions at all latitudes for all days of the year) (Dyer & Dickinson, 1996). This suggests that a step function would be a good template. By using the 180° step function as a template, an insect would on average make fewer errors before the current local pattern is learned. This is not a learning advantage *per se* but it is an advantage during the learning process. In addition, a step function might also allow a more rapid learning of the local pattern than an unconfigured network would. There are several reasons this might be true.

First, it may simply be easier to learn a pattern corresponding to an ephemeris function once any other ephemeris function has been learned. If this were the case, all ephemeris

functions would work equally well, although the step function would still have the advantage of making fewer errors while learning.

Second, since the 180° step function is the average of all ephemeris functions encountered on the earth, it may be a good starting place for learning the other curves. This may occur because the step function is intermediate between all of the other possible curves. Thus the average amount the curve would have to change would be minimized (Dyer & Dickinson, 1996).

Third, the step function may share more points in common with other ephemeris curves than any of the other curves would. Because of this overlap, fewer substitutions (of time-azimuth coordinates) would have to occur on average to move from a starting point of a step function to any other curve than from any other starting curve to another curve. The number of substitutions between the patterns can be measured by the Hamming distance (Hamming, 1986). Hamming distance is an information-theoretic concept that describes the amount of overlap between binary strings. It is expressed as the number positions in two strings that do not overlap, therefore, the Hamming distance between $\{1,1,1\}$ and $\{1,1,0\}$ is one, and the distance between $\{1,1,1\}$ and $\{0,1,0\}$ is two.

This third alternative uses a different metric for measuring distance than the second alternative does. The third alternative measures distance between points in the azimuth patterns in Hamming distance rather than conventional linear distance, which is implied in

the second hypothesis above. Standard linear distance, or Pythagorean distance is calculated with the following formula:

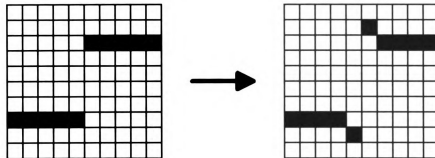
$$d^2 = \sum (x - y)^2 \quad (5.3)$$

while Hamming distance is calculated:

$$d = \sum |x - y| \quad (5.4)$$

(see Hamming, 1986). Figure 5.5 illustrates these distance metrics with two time-azimuth patterns. The figure depicts the transitions between a step function and two other azimuth curves. The Hamming distance between the step function and each of the other curves is the same (4), but the Pythagorean distance is different (2 and 4).

A



B

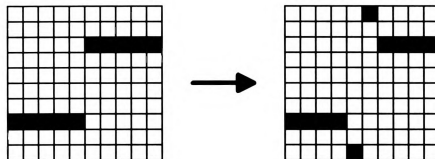


Figure 5.5 Comparison of Hamming and Pythagorean distances. In this diagram, the standard linear (Pythagorean) distance from the step function to each of the others pictured varies, while the Hamming distance is constant. A. Pythagorean distance = 2, Hamming distance = 4. B. Pythagorean distance = 4, Hamming distance = 4. Hamming distance is a measure of overlap between the patterns. In each of the cases, two points have changed, which gives a Hamming distance of 4 (turning off the old point and turning on the new point for each of the two changes). The linear distance between the old points and the new points makes a difference for the Pythagorean distance but not for the Hamming distance.

I investigated these alternative advantages of a preconfigured network with a series of retraining experiments. In each case a network was trained to learn one of the ephemeris functions depicted in Figure 5.2 and was subsequently retrained on each of the other curves (the ending weights for the first training were used as the starting weights for each of the retrainings). The network characteristics (e.g. layer size, learning constant, criterion) were the same as described above.

Figure 5.6 shows the results of these experiments. In all of the cases, the retraining time was considerably less than the initial training time. The retraining times are represented as a percentage of the original training time, and they are all well under 100 percent. This suggests that there is an advantage to starting with a preconfigured network no matter what its form. It would be advantageous to start with a step function since the fewest errors would occur during the learning process, but are there any further advantages of a step function, corresponding to the second or third possibilities listed above? This too is apparent from the results of the retraining experiment (Figure 5.6). The results are extremely consistent and fall into a clear pattern. There are three distinct groups of points. The overlapping points in each group all are the same Hamming distance (Hamming, 1986) from the original training pattern. This corresponds to the third of the alternatives listed above. The retraining time appears to be a function of the Hamming distance between the patterns and not the linear distance (as implied by the second hypothesis listed above). This makes sense in light of the fact that the networks considered are fully

interconnected; this means there is actually no geometry to the grids depicted in Figure 5.2. Each of the points in the grid is equally close to each of the other points.

The Hamming distance between each of the azimuth curves is shown in Table 5.1 (The letters correspond to the letters in Figure 5.2). The step function (A) is among the curves with equally short average Hamming distances to each of the other curves. In this case, however, the step function is only one of five curves that is closest to all of the other curves in the number of binary substitutions that would have to occur during retraining. This does not alone give it an advantage over the other curves as starting configurations for an innate template of the sun compass. This may not be true for binary representations of ephemeris curves that have greater detail. It is possible that with a smaller grid size the step function would share more overlapping regions with more of the other curves. But it is also the case that with greater detail will come a greater average Hamming distance between the curves.

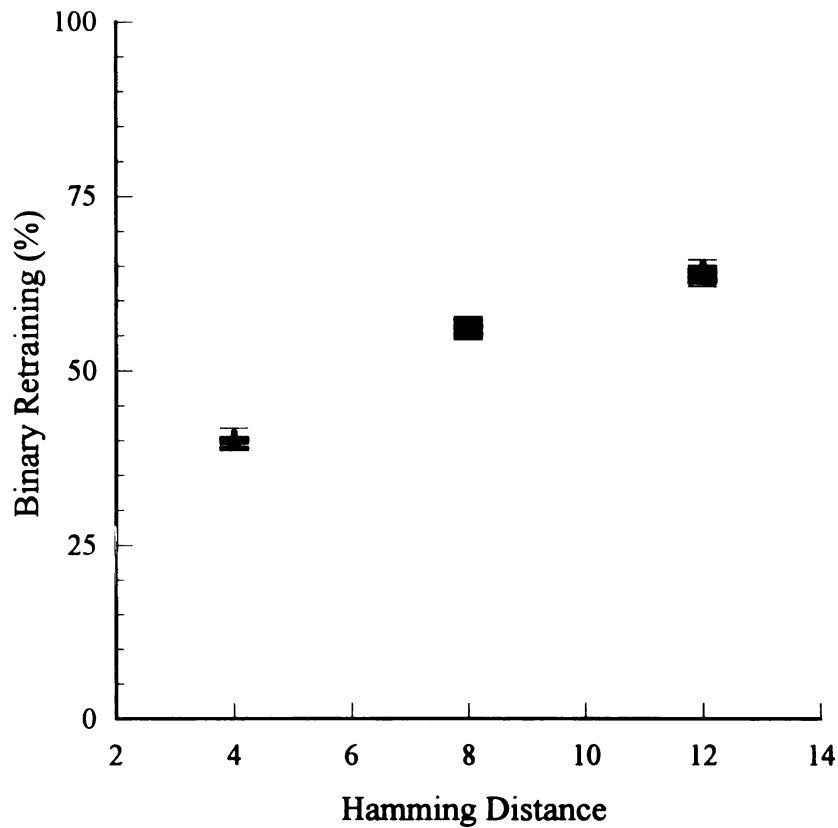


Figure 5.6 Binary retraining trials for azimuth network trained on one azimuth pattern and retrained on another. Binary retraining percentage is the number retraining trials to reach an error criterion of .05 as a percentage of the training time for the original pattern. Data are the means $\pm$ standard error for 10 replicates for each of the 7 azimuth patterns retrained on the 6 other patterns. They are plotted against the Hamming distance (number of binary substitutions) between the two patterns. This is clearly the major explanatory variable.

Table 5.1 Hamming Distance between Azimuth Training Patterns

	A (Step)	B	C	D	E	F	G
A (Step)	0	4	4	8	8	12	12
B	4	0	4	8	8	12	12
C	4	4	0	8	8	12	12
D	8	8	8	0	8	4	12
E	8	8	8	8	0	12	4
F	12	12	12	4	12	0	12
G	12	12	12	12	4	12	0
Mean	8	8	8	8	8	10.67	10.67

To examine the effect of grid size on the Hamming distance between the curves, I produced a set of azimuth curves to the nearest ten degrees. Like the curves in Figure 5.2, these azimuth curves were restricted to the daytime and consequently consisted of 18 by 18 grids. I subsequently looked at the average Hamming distance from each curve to every other curve. If the search is confined to the tropics, the step function indeed has the lowest average Hamming distance to every other curve (see Figure 5.7 A). However, when the temperate latitudes are included, this changes (see Figure 5.7 B). Figure 5.7 A shows the average Hamming distance between azimuth curves corresponding to each set of latitude-declination coordinates to each of the others. Curves were produced for ten degree increments of latitude and of declination from 20° N latitude and declination to 20° S latitude and declination. The pit in the center of Figure 5.7 A shows that the lowest average Hamming distance to all other curves corresponds to the azimuth curve for 0°

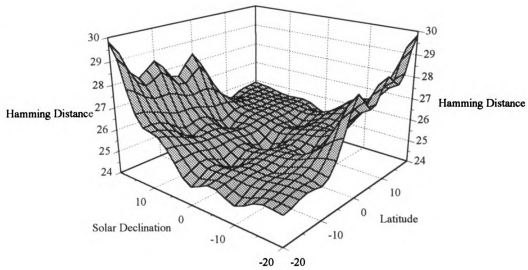
latitude and 0° declination, which is a 180° step function. However, when the temperate latitudes are included, the picture changes, as Figure 5.7 B indicates. Figure 5.7 B shows the average Hamming distance between all curves from 40° N latitude and 20° N declination to 40° S latitude and 20° S declination. In this case, the curve with the lowest average Hamming distance is a more temperate curve. The step function no longer has the lowest average Hamming distance to all other curves. This effect is somewhat surprising, although in retrospect it is understandable. With higher latitudes come flatter azimuth curves; therefore, the more curves from high latitudes that are considered, the more flat curves there are. These curves subsequently have a high degree of overlap with each other, and hence they have a lower average Hamming distance.

There is still a considerable retraining advantage, however, for the curves discussed in Figure 5.7 B, even for the curves that are farthest apart. Figure 5.8 shows the results of a retraining experiment involving these azimuth curves. Since Hamming distance is the relevant factor, I restricted the experiment to a sampling of each of the Hamming distances between the curves in Figure 5.7 B, instead of looking at all of the pairwise comparisons. The Hamming distances range from 0 to 36. Each of the points in Figure 5.8 represents a set of five replicates for each Hamming distance. Although the Hamming distances are larger than those represented in the previous retraining experiment (Figure 5.6), the retraining times are similar. This suggests that it is not Hamming distance *per se* that is important. Since all of the azimuth curves have the same proportion of ones and zeros, it might be reasonable to assume that it is the relative Hamming distance that is important.

For this reason, I plotted the results in terms of relative Hamming distance and have included the results from the previous experiment for comparison. I have defined relative Hamming distance as the Hamming distance divided by the number of elements in the pattern.

In summary, a preconfigured network would seem to confer a learning advantage. Once a network has been trained on one curve, it can more quickly learn another curve. If the preconfigured curve were in the form of a step function, further advantages would accrue. A preconfigured network that resulted in a step function would give the insect an advantage in the early stages of learning, because a step function leads to the smallest average error for all possible ephemeris functions observable on Earth. This is the reduction of errors during the learning process that is mentioned above. Additionally, the step function would be among the curves with the lowest average Hamming distance to all other curves, particularly in the tropics. These three factors could lead to the evolution of this mechanism. For a temperate animal it would make sense to have a preconfigured network in the form of a flat curve rather than a step function; however, this is only the case if the animal is confined to either the northern or the southern temperate regions.

A



B

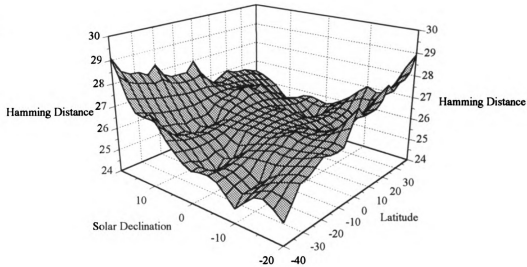


Figure 5.7 Average hamming distance from each azimuth curve to every other curve. The curves are to the nearest ten degrees. The average Hamming distances are plotted with respect to their latitude-declination coordinates. Panel A shows the situation when the curves are restricted to the tropics (between 20° N and 20° S). Panel B shows the situation when temperate curves are included (between 40° N and 40° S).

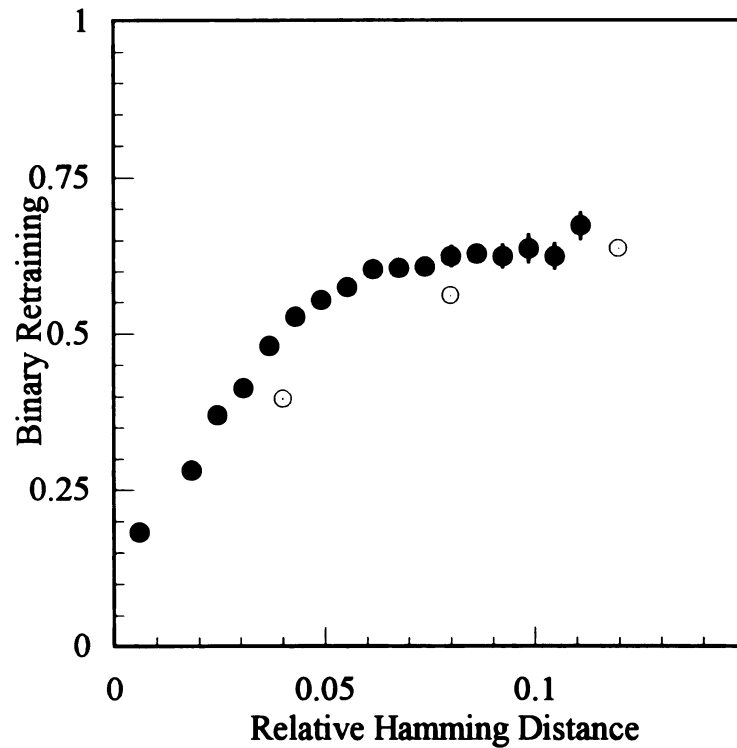


Figure 5.8 Binary retraining trials for azimuth curves discussed in Figure 5.7. For the range of Hamming distances that exist between the azimuth curves represented in figure 5.7, a network trained on one azimuth pattern and retrained on another. The network had 324 inputs and outputs and 81 hidden units. Binary retraining is the number retraining trials to reach an error criterion of .05 as a proportion of the training time for the original pattern. Data are the means $\pm$ standard error for 5 replicates for each Hamming distance (filled circles). They are plotted against the relative Hamming distance (number of binary substitutions)/(number of elements) between the patterns. For comparison the data from Figure 5.6 are included (open circles).

5.5 A Continuous Representation

The models described in the previous section have a drawback that could limit their applicability. Real insects can estimate the position of the sun at night. However, this part of the sun's course falls outside of the range of the time-azimuth combinations in the training patterns for the preconfigured networks. Since the networks are assumed to be trained over evolutionary time, the responses of the ancestors of the bees to these times would have to be incorporated into the training sets, yet no ancestor could have seen the solar position at night. Additionally, in the binary mapping, not only can points outside the range of the training pattern not be estimated, but also points within the range and below the resolution of the network cannot be estimated, because of the discrete nature of the binary mapping. For example, if the time dimension were coded at a resolution of one point per hour, it would be impossible to estimate azimuth angles at intermediate points on the half hour. This problem, and the problem of the range of the training set, may be eliminated with an alternative mapping. Such an alternative representation would be to use a continuous mapping rather than binary mapping.

To explore the effect of a continuous mapping, I turned to simple network with only three neural elements and an input unit (see Figure 5.9). This network has one input unit and one output unit. In addition there is one hidden unit and one bias unit. A bias unit is a unit that whose activation is always one. It is connected to the other units via connections with variable weights (See Figure 5.9). Bias units can increase the range of functions a

network can learn and decrease the convergence time (Rumelhart et al., 1986c). The bias unit appears to be necessary for convergence in this case. The input corresponds to time of day and the output corresponds to azimuth angle. Because of the sigmoid activation function used, these numbers for both time and azimuth angle ranged from zero to one. This network can be trained to learn particular time-azimuth correspondences. Because of the continuous mappings of the inputs and outputs, there is no constraint on the values that the test inputs can assume. A network trained on time-azimuth correspondences can be tested with time inputs from the night. It can also be tested with inputs that are intermediate to the training values. Both of these were impossible in the preconfigured networks with binary mappings.

Figure 5.10 shows the responses of several networks with different training regimes. The networks can be trained on a set of time-azimuth input/outputs and tested on a novel set of time inputs.

In Figure 5.10 (A), the network has been trained on the azimuth angles at two hour intervals between sunrise and sunset. The curve shows the responses of the network when tested at half hour intervals throughout the 24-hour period. During the day, at values intermediate to the training set, the network does a very good job of filling the gaps. However, outside the range of the training set, the network performs much more poorly. This is expected from the general behavior of neural networks, and it has been

demonstrated elsewhere (Johnson & Picton, 1996). The nocturnal azimuth estimates of this network vary considerably from the true azimuth patterns.

The architecture and the mapping of this network allow it to interpolate between points in the training set and to extrapolate forward and backward to points outside the range of the points in the training set. This is a very important feature of the network that is parallel to the mechanisms implicated in the sun compass learning problem (New & New, 1962; Gould, 1980; Wehner & Lanfranconi, 1981; Wehner, 1982; Dyer, 1985, 1987) (and see Chapter 3). Because of these distinctive features of this network, I will call it the *interpolation network*.

The architecture of this network also allows it to be trained on a small portion of the sun's daily course and to be tested on another part of it. This is analogous to the experiments presented in Chapter 3 (Wehner & Müller, 1993; Dyer & Dickinson, 1994). In this case (see Figure 5.10 B), the network does a very poor job of estimating the position of the azimuth in the unexperienced portion of the day.

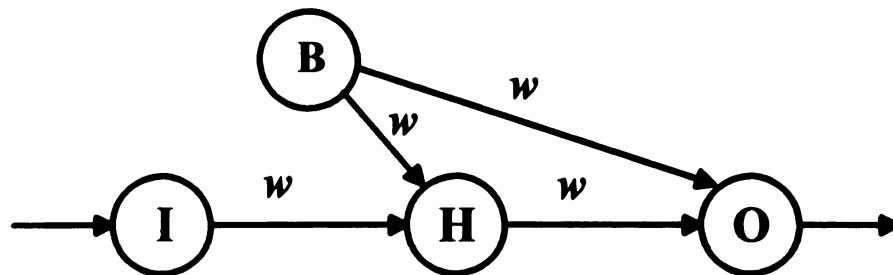


Figure 5.9. Diagram of simple connectionist network used for the interpolation network. I: input unit. H: hidden unit. O: output unit. B: bias unit. w : modifiable connection weights.

Although this network does a good job generalizing to azimuth positions temporally close to those they have experienced, it does not estimate azimuths as well as insects at times several hours from the training period. However, this model could be rescued if there were a way to incorporate some structure in the model that is analogous to the type of innate structure that appears to be present in bees (Dyer & Dickinson, 1994).

There are several mechanisms that could be used. Like the preconfigured networks in sections 5.3 and 5.4, this network could have preconfigured connection weights.

Alternatively, there may be a different way of imposing structure on the learning process. This could be achieved by incorporating some of the universal features of solar movement into the training set. The 180° step function (Dyer & Dickinson, 1994) observed in the behavior of experience-restricted bees can be used to accomplish this goal.

To do this, I trained a network with the same training set as in Figure 5.10 (B), but I also included two additional points in the training set. These points were for time inputs of 06:00 and 12:00 (solar time). The azimuth angles for these times were derived from the azimuth angle observed at 18:00. For the azimuth angle for 06:00, 180° is subtracted from the azimuth angle at 18:00. Likewise for the angle at noon, it is obtained by subtracting 90° from the azimuth angle at 18:00.

By including these additional angles in the training set, the network produces a much closer approximation to the true position of the sun when tested during the new time of

the day (see Figure 5.10 (C)). This suggests that this simple connectionist network is capable of broadly simulating the behavior revealed in experiments. This seriously challenges Gallistel's assertions about the ability of nonsymbolic models to solve the sun compass learning problem. This last model might verge on symbolic elements, such as deriving the additional training patterns through subtraction; but the essential computations of the network are subsymbolic and they are not isomorphic to any logical mechanism of computing azimuth angle from time.

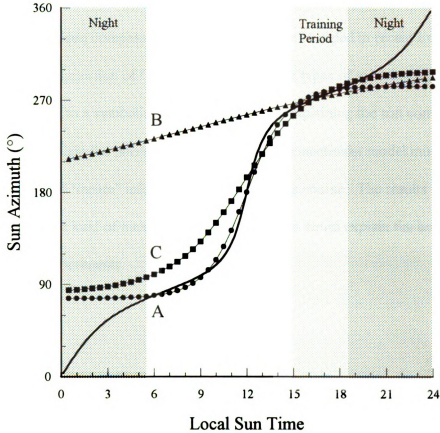


Figure 5.10 Response of interpolation network to three different training regimes for learning the same specific azimuth function. The azimuth function corresponds to 25° N on April 22 (solar declination 12°). A. Response of a network over 24 hours at half-hour intervals for a training set of hourly azimuth angles between sunrise (~06:00) and sunset (~18:00) (local solar time). B. 24 hour response of a network trained only on hourly positions in the late afternoon and evening (15:00 to 18:00). C. Response of a network trained on afternoon positions in B but with additional constraints ($\text{Azimuth}_{12:00} = \text{Azimuth}_{18:00} - 90^\circ$; $\text{Azimuth}_{06:00} = \text{Azimuth}_{18:00} - 180^\circ$).

5.6 Summary

In this chapter I have shown that connectionist models could account for several of the characteristics of sun compass learning that have been revealed in recent experiments. In contrast to the suggestion of Gallistel (in press), these types of models may provide a viable alternative to a symbolic model as a means of explaining the sun compass learning problem. To explain the phenomenon, however, a connectionist model must include a certain amount of "innate" information about the sun's course. The results presented here suggest that some kind of innately configured network could explain the behavior of the animals in the experiments.

Chapter 6

CONCLUSIONS

The sun compass has proved to be an excellent avenue into gaining a more complete understanding of the nature of a representation in the brain of an animal. Behavioral experiments alone have gone a long way towards delineating computational mechanisms by which the sun compass learning problem must be solved. The problem consists of the ability of small-brained animals such as bees and ants to estimate positions of the sun at times of day (and night) when they have never seen it. The actual solution is still a mystery, but new experiments have shown that the problem may be solved by an innate template that is modified with experience (Chapter 3), and I have shown how two broad classes of computational mechanisms could solve the problem (Chapters 4 and 5).

I have focused on the dichotomy of symbolic and nonsymbolic processing that has emerged out of the field of cognitive science (see Smolensky, 1988; Boden, 1991) and has intersected with the problem of animal orientation (Gallistel, in press). Taking up Gallistel's challenge that symbolic computations provide the best explanation for the sun compass learning problem, I have established several models of how subsymbolic

connectionist models could underlie the sun compass learning problem. In addition, I have formalized a conceptual model of how the problem can be solved in the symbolic domain.

Both classes of models account for some of the aspects of the observed behavior that were not present in the previous models. This suggests that the actual neural computations that underlie the estimation of the sun's course may involve equivalent mechanisms. The computational mechanisms hypothesized by these models may contribute to the elucidation of the neural mechanisms that insects use to compute the position of the sun and indeed how brains represent information about the environment. The symbolic and connectionist frameworks posit fundamentally different views of how the brain processes information. The symbolic framework lacks a correspondence with neuroscience: the fundamental elements of a symbol-processing mechanism have yet to be identified (Gallistel, in press). On the other hand, the connectionist framework lacks a correspondence with major areas of psychological theory: processes that appear to be characterized by the logical manipulation of symbols (Boden, 1991; Gallistel, in press). By examining how the sun-azimuth estimation process can be accomplished by these two broad classes of models, I have shown what types of symbol-manipulating mechanisms are necessary to solve the problem, and how connectionist models can solve this apparently symbolic process. In Table 6.1, I present a synopsis of the features of the four main models that have emerged from this endeavor. Included in the table are the main distinguishing features of the models. I will consider each of these aspects in greater detail in the text.

Table 6.1 Comparison of New Models

Model	Representation	Modification with Experience	Symmetry Assumptions	Nocturnal Compensation
Ellipse	Continuous	Yes (Averaging)	Yes	Yes
Pattern Matching Network	Binary	No (Matching)	No	No
Learning Advantage Network	Binary	Yes (Learning)	Implicit	No
Interpolation Network	Continuous	Yes (Learning)	Some	Yes

6.1 Innate Structure

All of the models are consistent with the conclusion (Wehner & Müller, 1993; Dyer & Dickinson, 1994) that there is innate structure to the mechanism employed by the bees and ants to estimate the position of the sun at new times of day. This statement is based on the observation that all of the models require global information about the task to come close to simulating the behavior of the bees and ants in the experiments. That is, the local information (the observed positions of the sun's azimuth at certain times of day) appears to be insufficient to determine the position of the sun at vastly different times of day. Instead, either more information or some means of interpreting the available information is needed. In the symbolic framework, the additional information is embodied in the functional relationship between time and azimuth position. This even applies somewhat to the linear models (New & New, 1962; Gould, 1980; Wehner & Lanfranconi, 1981; Dyer, 1985, 1987) of compensation, but it is more clearly evident in the nonlinear (ellipse-based)

model. The global information is that the azimuth changes at a varying rate that approximates an elliptic function of time. In the connectionist models, the global information resides in the connection weights of the preconfigured networks or in the constraints imposed upon the learning process (interpolation network).

6.2 Templates

Dyer and Dickinson (1994) suggested that the implied innate structure might be analogous to a sensory template after Marler (1976, 1984). Marler invoked the sensory template concept as a heuristic model to describe the development of species-specific song in birds, and he suggested that it may apply to other types of behavior in other organisms, though he focused on vocal behavior. The template is a genetic constraint on learning that makes the organism particularly sensitive to particular types of stimuli at particular times. Marler (1976, p. 328) states:

Sensory templates provide a structural framework for the perceptual analysis of arrays of stimuli that is both plastic and yet constrained. After more or less extensive modification by experience, with their number added to or subjected to attrition, and changed in specification so that their properties may now be both species-specific and also population-, group-, or even individual-specific, they then guide motor development by a process of sensory feedback. Phases of this multistage process may interdigitate in time or they may be temporally separated, proceeding most readily at particular developmental stages or "sensitive periods."

In the sun compass learning problem, there are clearly specific classes of stimuli that are important. These correspond to azimuth position and time of day. In honey bees, the learning occurs rapidly and during a specific period of the individual's life (Lindauer,

1959), though it is not clear that it cannot occur at other times. There are physiological changes in the brain that correspond with this period in the bee's life, which are hypothesized to be related to the many things she has to learn as she begins to forage (Withers et al., 1993).

Perhaps the most critical correspondence between Marler's (1976) sensory template concept and the sun compass learning problem is the feature of the template model that suggests that the response to certain stimuli is both plastic and constrained. I would argue that this is true for all four of the specific models I have considered. In general terms there are specific stimuli (azimuth angle and time) that must be represented in a flexible enough framework to correspond to the range of azimuth functions encountered on the earth, but they may also be constrained to fall into a particular range.

This is most evident in the pattern matching network. Encoded in the connection weights of this network are a range of patterns of azimuth movement that correspond to the range of natural patterns. If a spurious combination of azimuth position and time is entered into the network, it has no effect on the response of the network. From the noisy information is generated a complete pattern of azimuth-time mappings. This is seen in the response of simulated network to one of the test patterns that included a spurious time-azimuth coordinate not included in any of the training patterns.

With the learning advantage network, this may not be as much of an issue. Spurious azimuth-time coordinates will be included in the learning process. If they are consistent the network will relearn the new pattern. It is conceivable that the network would learn the new pattern faster than it would have without the preconfigured connection weights. This would occur even if the spurious coordinates were beyond the range of the natural patterns of azimuth-time coordinates, since by the Hamming distance rule, only the amount of overlap matters and not the Pythagorean distance between the points. However, the network would nonetheless be biased toward the step-function response in the early stages of retraining. Since the step function is encoded in the initial connection weights, the initial responses of the network would be biased toward a step function, but as new inputs are encountered, the connection weights would shift to represent the new pattern.

The interpolation network provides an excellent example of the need for global information in the sun compass learning problem. A network trained on a subset of time-azimuth coordinates can estimate the azimuth angle for new times of day. If the training set is restricted to a portion of the day, the estimates in the other part of the day would vary considerably from their actual values. In order to solve the problem a global constraint is needed. One such constraint that reduces this problem is to include in the learning set some universal relationships, such as that at 6:00 it is 180° from its position at 18:00 and vice versa.

In the symbolic model, the observable quantities of azimuth position and time are flexible, but the functional relationship is strictly constrained. The values must fit an ellipse.

Spurious values may lead to ellipses that are considerably different in shape from the true seasonal and latitudinal azimuth rate function. This may underlie the behavior of the bees in the experiments presented in Chapter 3 (Dyer & Dickinson, 1994). In these experiments the bees' representation of the sun's course corresponds to a curve approximating a 180° step function. If something akin to the ellipse azimuth function were the underlying mechanism, the ellipse being used to approximate the rate of change of the azimuth would be a much more squashed ellipse than the ellipse corresponding to the true azimuth rate function of the season and latitude of the experiments.

6.3 Symbolic versus Nonsymbolic

I have maintained throughout that the models differed in their underlying representational structure. The major distinction I have used is between symbolic and nonsymbolic processes. At the level of behavior, it is very hard to distinguish between these alternatives. The indeterminacy of behavioral data certainly has contributed to much of the debate among cognitive scientists regarding this distinction (Smolensky, 1988; Boden, 1991; Gallistel, in press). Table 6.1 suggests some of the distinctions between the models that may be amenable to behavioral test. Two of these features make very specific predictions about the positions of the sun estimated during the night. The fact that many animals are able to estimate the position of the sun at night enforces a major constraint on the types of processes that may underlie the behavior. In their current state, this fact

appears to eliminate the possibility of the two preconfigured networks with the binary mapping. With the binary mapping there can be no interpolation for points not in the training set. This seems to limit models of this sort. However, there may be several ways around this problem. For the preconfigured pattern matching network, it is assumed that responses of the ancestors of the bees and ants responded appropriately to observed positions of the sun at different seasons and latitudes. Through natural selection an appropriately configured network could conceivably emerge. But since, the ancestors could not see a range of values for azimuth functions during the night, they would not evolve a preconfigured network to deal with a nocturnal position of the sun. However, there are seasons and latitudes in which the sun is visible at night. Moreover, there are populations of arthropods that live in such areas and that orient by the sun throughout the night (Papi & Syrjämäki, 1963), e.g., Finnish populations of wolf spiders (*Arctosa cinerea*). It is true, however, that there is not a range of azimuth functions visible at night. But one of the results from many studies of the nocturnal compensation is that a gradual constant rate of compensation is observed rather than a varying rate like during the day (Pardi & Ercolini, 1986).

There are two problems with the hypothesis the Arctic sun could determine the nocturnal patterns in an preconfigured network, however. First, Italian populations of *Arctosa cinerea* do not compensate during the night, suggesting that the Finnish populations are learning the nocturnal course. Second, some arthropods, including, other spiders,

compensate for the nocturnal period by reversing the apparent movement of the azimuth, and this is not how the Arctic sun moves (Tongiorgi, 1959; Papi & Syrjämäki, 1963).

For the learning advantage network, it is not clear that ancestors of an animal using this mechanism would actually have to see the position of the sun at night for the network to have it encoded in its connections. Since one of the advantages of this type of network is decreased learning time, having some representation of the nocturnal sun's course may be better than having none. The representation could be arbitrary, it could be a step function extended through the night, or it could be an observed gradual function extended through the night.

Both the nonsymbolic interpolation network and the symbolic ellipse model could achieve nocturnal compensation, but they differ significantly in their predictions, and both differ somewhat from reality. In the ellipse model, the nocturnal movement of the sun is assumed to be in the same direction as its movement during the day, and the pattern of change in rate would be symmetrical with the daytime pattern. This is not necessarily true of actual sun azimuth functions. In many cases the azimuth reverses directions during the night. This pattern appears throughout the tropics. In addition, the pattern of movement during the night (the azimuth's rate of change) is not necessarily symmetrical with the pattern during the day. In fact, only during the equinox is it truly symmetrical.

There are also specific predictions for the pattern of nocturnal compensation if the underlying mechanism resembles the connectionist interpolation network. The predictions in this case depend on the constraints placed on the learning. If no constraints are placed on the position of the sun at night, the network will extrapolate nonlinearly into the night. At midnight, there will be an abrupt shift to a pattern that resembles backward extrapolation (Dyer, 1985) although it too is nonlinear (see Figure 5.10 A).

The diverse predictions of the models with respect to nocturnal compensation suggest that these models can be distinguished experimentally. The models also differ in predictions and assumptions about the symmetry of the pattern of solar movement. In most of the models there is some symmetry imposed that is not seen in the natural pattern of movement of the sun's azimuth. In the ellipse model, this symmetry comes from the pattern of movement assumed for the night, as discussed above. This is one of the most substantial predictions of the ellipse model, and it is one that can be addressed experimentally. There is evidence suggesting that this might be the case. The explanatory power of the 180° step function (Dyer & Dickinson, 1994) rests on this symmetry. The behavior of many systematic errors made in sun compensation also support this conclusion (Wehner & Lanfranconi, 1981).

The symmetry assumptions in the other models may not be as substantial. Symmetry assumptions are encoded in the preconfigured networks, although symmetry may not be necessary. Some kind of symmetry assumption is required to impose the necessary

constraints on the interpolation network. In the current model, an assumption of 180° symmetry is necessary for the network to accurately estimate the position of the sun in the morning with only afternoon experience with azimuth-time pairings.

6.4 A False Dichotomy?

Throughout this dissertation I have maintained a dichotomy between symbolic and nonsymbolic solutions to the problem of estimating the position of the sun during unexperienced times of day. This dichotomy has a tradition in the literature (Smolensky, 1988; Gallistel, in press), but there are also those who suggest that the approaches are not as different as they have been portrayed (Boden, 1991; Oden, 1994). The distinction may be more an issue of what is computed versus how it is computed (Boden, 1991).

Symbolic models provide an hypothesis about what is computed while connectionist models provide an hypothesis about how distributed networks of simple elements compute. Attempts to integrate these levels of explanation are emerging (Smolensky et al., 1994). I favor Marr's (1982) three levels of explanation (computation, algorithm, and implementation). Resolving the symbolic-nonsymbolic dichotomy into Marr's trichotomy would be a worthwhile challenge.

For the sun compass learning problem, traditional symbolic models have provided a framework for investigating the problem (New & New, 1962; Gould, 1980; Wehner & Lanfranconi, 1981; Dyer, 1985, 1987), after all, they made specific predictions that could be falsified by behavioral experiments (Dyer & Dickinson, 1994). It could be argued that

to a certain extent, they are phenomenological models that are meant to describe the behavior rather than the neural implementation of the behavior. Yet they have been interpreted as the latter (Gallistel, 1990, in press). Even New and New (1962) suggested this in the following statement: "in fact they appear to have an innate mechanism that can divide angles by time" (p. 287).

At a fundamental level there may be no difference between these approaches. The interpolation network looks very much like a symbolic model. The equations that describe it are indeed quite simple because of the limited number of neural elements. Equations 5.1 and 5.2 can be combined in a relatively simple form to describe the output of this network. In this sense, the connection weights (w), become the parameters of the functional relationship between inputs and outputs, and in this case there are only four of them, which is in the range of the parameters required for the symbolic model based on the equation of the ellipse. Since connectionist networks are universal approximators (Hornick et al., 1989), a network not fundamentally different from the interpolation network could approximate any functional relationship the variables in this case (azimuth position and time). Thus over a given range, the nonsymbolic model would have exactly the same characteristics as a symbolic model. The network would then be functionally isomorphic with the symbolic model in a very real sense. Clever experimental manipulations may be able to distinguish whether the animal's representation is truly isomorphic with the true parameters of the problem or whether it is functionally isomorphic over the range in which the problem is normally solved.

6.5 Caveat

The modeling effort cannot stand alone. It must be thoroughly based in data, and it must be amenable to experimental falsification. The models presented here conform to these requirements. It is clear that there may be multiple ways to model the sun compass learning problem, but without models of the possible mechanisms it is unclear exactly what questions to ask with experiments.

6.6 Representing the Regularities of the World

I began with a very broad statement about the regularities of the world. Throughout this dissertation, I have focused on a very narrow aspect of one environmental regularity, the sun's course, and how it could be represented in the brain of an insect. In this case it is clear that the regularities of solar movement are encoded in the brain of the insect. This regularity is not completely genetically hard wired in the insect's brain, but aspects of the regularity are encoded in the insect's brain. This allows an insect with very little experience with the sun's course to have a relatively accurate representation of the sun's course. But it is flexible enough to allow a more accurate representation develop with more experience. I have attempted to show in very broad terms how this could be accomplished with models of two general classes. The nature-nurture debate has been raging for centuries, but far too infrequently are problems at the cusp addressed systematically.

REFERENCES

REFERENCES

- Able, K. P. 1980. Mechanisms of orientation, navigation, and homing. In *Animal Migration, Orientation and Navigation*, ed. S. A. Gauthereaux. New York: Academic Press.
- Able, K. P., and P. M. Dillon. 1977. Sun compass orientation in a nocturnal migrant, the white-throated sparrow. *Condor* 79:393-395.
- Adler, K., and J. B. Phillips. 1985. Orientation in a desert lizard (*Uma notata*): Time-compensated compass movement and polarotaxis. *J. Comp. Physiol., A* 156:547-552.
- Altevogt, R., and H. O. von Hagen. 1964. Über die Orientierung von *Uca tangeri* Eydoux im Freiland. *Z. Morph. Ökol. Tiere* 53:636-656.
- Batschelet, E. 1981. *Circular statistics in biology*. London: Academic Press.
- Beugnon, G. 1983. Terrestrial and celestial cues in visual orientation of the wood-cricket *Nemobius sylvestris* (Bosc). *Biol. Behav.* 8:159-169.
- Beugnon, G. 1987. Time-compensated celestial orientation in the cricket *Pteronemobius lineolatus*. *Behav. Proc.* 15:109-115.
- Birukow, G. 1956. Lichtkompassorientierung beim Wasserläufer *Velia currens* F. (Heteroptera) am Tage und zur Nachtzeit. I: Herbst- und Winterversuche. *Z. Tierpsychol.* 13:463-492.
- Birukow, G., and E. Busch. 1957. Lichtkompassorientierung beim Wasserläufer *Velia currens* F. (Heteroptera) am Tage und zur Nachtzeit. II: Orientierungsrhythmik in verschiedenen Lichtbedingungen. *Z. Tierpsychol.* 14:184-203.
- Boden, M. A. 1991. Horses of a different color? In *Philosophy and connectionist theory*, ed. W. Ramsey, D. E. Rumelhart, and S. P. Stich. Hillsdale, NJ: Erlbaum Press.
- Bovet, J. 1992. Mammals. In *Animal homing*, ed. F. Papi. London: Chapman & Hall.
- Braemer, W. 1959. Versuche zu der im Richtungsfinden der Fische enthaltenen

Zeitschätzung. *Verh. deutsch. zool. Ges. Zool. Anz. Suppl.* 23:429-441.

- Brines, M. L. 1978. Skylight polarization patterns as cues for honey bee orientation: Physical measurements and behavioral experiments. Ph.D. Dissertation. Rockefeller University, New York.
- Brines, M. L., and J. L. Gould. 1979. Bees have rules. *Science* 206:571-573.
- Buchler, E. R., and S. B. Childs. 1982. Use of the post-sunset glow as an orientation cue by big brown bats (*Eptesicus fuscus*). *J. Mammal.* 63:243-247.
- Cartwright, B. A., and T. S. Collett. 1983. Landmark learning in bees. *J. Comp. Physiol., A* 151:521-543.
- Caudill, M., and C. Butler. 1992. *Understanding neural networks: Computer explorations*. Cambridge, MA: MIT Press.
- Churchland, P. S., and T. J. Sejnowski. 1989. *The Computational Brain*. Cambridge, Mass.: MIT Press.
- Clark, A. J. 1990. Connectionism, competence, and explanation. In *The philosophy of artificial intelligence*, ed. M. A. Boden. Oxford: Oxford University Press.
- Collett, T. S. 1992. Landmark learning and guidance in insects. *Phil. Trans. R. Soc. Lond., B* 337:295-303.
- Collett, T. S., and J. Baron. 1994. Biological compasses and the coordinate frame of landmark memories in honeybees. *Nature* 368:137-140.
- Collett, T. S., and M. F. Land. 1975. Visual spatial memory in a hoverfly. *J. Comp. Physiol.* 100:59-84.
- Colombini, I., L. Chelazzi, and F. Scapini. 1994. solar and landscape cues as orientation mechanisms in the beach-dwelling beetle. *Marine Biology* 118:425-432.
- Cottrell, G. W., and J. Metcalfe. 1991. EMPATH: Face, emotion, and gender recognition using holons. In *Advances in neural information processing systems* 3, ed. R. P. Lippmann, J. E. Moody, and D. S. Touretzky. San Mateo, CA: Morgan Kaufmann.
- Daumer, K., R. Jander, and T. H. Waterman. 1963. Orientation of the ghost-crab *Ocypode* in polarized light. *Zeit. vergl. Physiol.* 47:56-76.
- DeRosa, C. T., and D. H. Taylor. 1980. Homeward orientation mechanisms in three species of turtles (*Trionyx spinifer*, *Chrysemys picta*, and *Terrapene carolina*). *Behav. Ecol. Sociobiol.* 7:15-23.

- Dickinson, J. A. 1994. Bees link landmarks with celestial compass cues. *Naturwissenschaften* 81:465-467.
- Dill, M., R. Wolf, and M. Heisenberg. 1993. Visual pattern recognition in *Drosophila* involves retinotopic matching. *Nature* 365:751-753.
- Dyer, F. C. 1985. Nocturnal orientation by the Asian honey bee, *Apis dorsata*. *Anim. Behav.* 33:769-774.
- Dyer, F. C. 1987. Memory and sun compensation by honey bees. *J. Comp. Physiol., A* 160:621-633.
- Dyer, F. C. 1996. Spatial memory and navigation by honeybees on the scale of the foraging range. *J. exp. Biol.* 199:147-154.
- Dyer, F. C., and J. A. Dickinson. 1994. Development of sun compensation by honey bees: How partially experienced bees estimate the sun's course. *Proc. Natl. Acad. Sci. USA* 91:4471-4474.
- Dyer, F. C., and J. A. Dickinson. 1996. Sun-compass learning in insects: Representation in a simple mind. *Curr. Dir. Psychol. Sci.* 5:67-71.
- Dyer, F. C., and J. L. Gould. 1981. Honey bee orientation: A backup system for cloudy days. *Science* 214:1041-1042.
- Ellis-Quinn, B. A., and C. A. Simon. 1991. Lizard homing behavior: The role of the parietal eye during displacement and radio-tracking, and time-compensated celestial orientation in the lizard *Sceloporus jarrovi*. *Behav. Ecol. Sociobiol.* 28:397-407.
- Emlen, J. T., and R. L. Penney. 1964. Distance navigation in the Adelie Penguin. *Ibis* 106:417-431.
- Emlen, S. T. 1967. Migratory orientation in the indigo bunting, *Passerina cyanea* part I: Evidence for the use of celestial cues. *Auk* 84:309-342.
- Emlen, S. T. 1967. Migratory orientation in the indigo bunting, *Passerina cyanea* part II: Mechanisms of celestial orientation. *Auk* 84:463-489.
- Ercolini, A., and G. Badino. 1961. L'orientamento astronomico di *Paederus rubrothoracicus* Goeze. *Boll. Zool.* 28:421-431.
- Ercolini, A., and F. Scapini. 1976. Fototassia negativa e orientamento astronomico solare in due specie di Stafilinidi ripari (*Paederus rubrothoracicus* Goeze e *Stenus bipunctatus* Edrichson). *Redia* 59:135-153.

- Feldman, J. A., and D. H. Ballard. 1982. Connectionist models and their properties. *Cog. Sci.* 6:205-254.
- Fent, K. 1986. Polarized skylight orientation in the desert ant *Cataglyphis*. *J. Comp. Physiol., A* 158:145-150.
- Ferguson, D. E. 1963. Orientation in three species of anuran amphibians. *Ergebn. Biol.* 26:128-134.
- Ferguson, D. 1967. Sun-compass orientation in anurans. In *Animal orientation and navigation*, ed. R. Storm. Corvallis, OR: Oregon State University Press.
- Ferguson, D. E., and H. F. Landreth. 1966. Celestial orientation of Fowler's toad *Bufo fowleri*. *Behaviour* 26:105-123.
- Ferguson, D. E., J. P. McKeown, O. S. Bosarge, and H. F. Landreth. 1968. Sun-compass orientation of bullfrogs. *Copeia* 1968:230-235.
- Fisher, K., and G. Birukow. 1960. Dressur von Smaragdeidechsen auf Kompassrichtungen. *Naturwissenschaften* 47:93-94.
- Fluharty, S. L., D. H. Taylor, and G. W. Barrett. 1976. Sun-compass orientation in the meadow vole, *Microtus pennsylvanicus*. *J. Mammal.* 57:1-9.
- Forward, R. B., K. W. Horch, and T. H. Waterman. 1972. Visual orientation at the water surface by the teleost *Zenarchopterus*. *Biol. Bull.* 143:112-126.
- Frantsevish, L., V. Govardovski, F. Gribakin, G. Nikolajev, V. Pichka, A. Polanovsky, V. Shevchenko, and V. Zolotov. 1977. Astroorientation in *Lethrus* (Coleoptera, Scarabaeidae). *J. Comp. Physiol., A* 121:253-271.
- Frisch, K. von. 1950. Die Sonne als Kompass im Leben der bienen. *Experientia* 6:210-221.
- Frisch, K. von. 1967. *The dance language and orientation of bees*. Cambridge, MA: Belknap Press.
- Frisch, K. von, and M. Lindauer. 1954. Himmel und Erde in Konkurrenz bei der Orientierung der Bienen. *Naturwissenschaften* 41:245-253.
- Gallistel, C. R. 1990. *The Organization of Learning*. Cambridge, Mass.: MIT Press.
- Gallistel, C. R. in press. Symbolic processes of the brain: the case of insect navigation. In *An invitation to cognitive science*, vol. 4, ed. S. Sternberg, and D. Scarborough. Cambridge, MA: MIT Press.

- Goodyear, C. P. 1970. Terrestrial and aquatic orientation in the starhead topminnow, *Fundulus notti*. *Science* 168:603-605.
- Goodyear, C. P., and D. H. Bennett. 1979. Sun compass orientation of immature bluegill. *Trans. Am. Fish. Soc.* 108:555-559.
- Goodyear, C. P., and D. E. Ferguson. 1969. Sun-compass orientation in the mosquitofish, *Gambusia affinis*. *Anim. Behav.* 17:636-640.
- Gorman, R. R., and J. H. Fergeson. 1970. Sun-compass orientation in the western toad, *Bufo boreas*. *Herpetologica* 26:34-45.
- Gould, E. 1957. Orientation in box turtles, *Terrapene c. carolina* (Linnaeus). *Biol. Bull.* 112:336-348.
- Gould, E. 1959. Studies on the orientation of turtles. *Copeia* 1959:174-176.
- Gould, J. L. 1980. Sun compensation by bees. *Science* 207:545-547.
- Gould, J. L. 1984. Processing of sun-azimuth information. *Anim. Behav.* 32:149-152.
- Groot, C. 1965. On the orientation of young sockeye salmon (*Oncorhynchus nerka*) during their seaward migration out of the lakes. *Behaviour* Suppl 14.
- Grossberg, S. 1988. Nonlinear neural networks: Principles, mechanisms, and architectures. *Neural Networks* 1:17-61.
- Hågvar, S. 1992. Long distance, directional migration on snow in a forest collembolan, *Hypogastrura socialis* (Uzel). *Acta Zool. Fennica* 196:200-205.
- Haigh, G. R. 1979. Sun-compass orientation in the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus*. *J. Mammal.* 60:629-632.
- Hamilton, P. V., and B. J. Russel. 1982. Celestial orientation by surface-swimming *Aplysia brasiliana* Rang (Mollusca: Gastropoda). *J. Exp. Mar. Biol. Ecol.* 56:145-152.
- Hamming, R. W. 1986. *Coding and information theory*. Englewood Cliffs, NJ: Prentice-Hall.
- Hamner, W. M., P. P. Hamner, and S. W. Strand. 1994. Sun-compass migration by *Aurelia aurita* (Scyphozoa): Population retention and reproduction in Saanich Inlet, British Columbia. *Marine Biology* 119:347-356.

- Hamner, W. M., M. Smyth, and E. D. Mulford. 1968. Orientation of the sand-beach isopod *Tylos punctatus*. *Anim. Behav.* 16:405-409.
- Hartwick, R. F. 1976. Beach orientation in talitrid amphipods: Capacities and strategies. *Behav. Ecol. Sociobiol.* 1:447-458.
- Hasler, A. D., R. M. Horrall, W. J. Wisby, and W. Braemer. 1958. Sun-orientation and homing in fishes. *Limnol. Oceanog.* 3:353-361.
- Helbig, A. J. 1991. Dusk orientation of migratory European robins, *Erithacus rubecula*: The role of sun-related directional information. *Anim. Behav.* 41:313-322.
- Heran, H. 1962. Anemotaxis und Fluchtorientierung des Bachläufers *Velia caprai* Ta, (= *Velia currens* F). *Zeit. vergl. Physiol.* 46:129-149.
- Herrnkind, W. F. 1972. Orientation in shore-living Arthropods, especially the sand fiddler crab. In *Behavior of marine animals*, vol. 1, ed. H. E. Winn, and B. L. Olla. New York: Plenum Press.
- Herrnkind, W. F. 1983. Movement patterns and orientation. In *The biology of Crustacea*, vol. 7, ed. F. J. Vernberg, and W. B. Vernberg. New York: Academic Press.
- Hertz, J., A. Krogh, and R. G. Palmer. 1991. *Introduction to the theory of neural computation*. Reading, MA: Addison-Wesley.
- Hinton, G. E., J. L. McClelland, and D. E. Rumelhart. 1986. Distributed representations. In *Parallel distributed processing: Explorations in the microstructure of cognition*, vol. 1, ed. D. E. Rumelhart, and J. L. McClelland. Cambridge, MA: MIT Press.
- Hoffmann, K. 1959. Die Richtungsorientierung von Staren unter der Mitternachtssonne. *Zeit. vergl. Physiol.* 41:471-480.
- Hoffmann, K. 1960. Experimental manipulation of the orientational clock in birds. *Cold Spring Harbor Symp. Quant. Biol.* 25:379-387.
- Hornik, K., M. Stinchcombe, and H. White. 1989. Multilayer feedforward networks are universal approximators. *Neural Networks* 2:359-366.
- Jander, R. 1957. Die optische Richtungsorientierung der roten Waldameise (*Formica rufa* L.). *Zeit. vergl. Physiol.* 40:162-238.
- Jander, R. 1975. Ecological aspects of spatial orientation. *Ann. Rev. Ecol. Syst.* 6:171-188.
- Johnson, J. H., and P. D. Picton. 1996. How to train a neural network. *Complexity*

1(6):13-28.

- Jordan, O. R., W. W. Byrd, and D. E. Ferguson. 1968. Sun-compass orientation in *Rana pipiens*. *Herpetologica* 24:335-336.
- Keeton, W. T. 1969. Orientation by pigeons: Is the sun necessary? *Science* 165:922-928.
- Kohshima, S. 1985. Migration of the Himalayan wingless glacier midge (*Diamesa* sp.): Slope direction assessment by sun-compassed straight walk. *J. Ethol.* 3:93-104.
- Kramer, G. 1950. Weitere Analyse der Faktoren, welche die Zugaktivität des gekäfigten Vögels orientieren. *Naturwissenschaften* 37:377-378.
- Landreth, H. F. 1973. Orientation and behavior of the rattlesnake, *Crotalus atrox*. *Copeia* 1973:26-31.
- Landreth, H. F., and D. E. Ferguson. 1966. Evidence of sun-compass orientation in the chorus frog, *Pseudacris triseriata*. *Herpetologica* 22:106-112.
- Landreth, H. F., and D. E. Ferguson. 1967. Movements and orientation of the tailed frog, *Ascaphus truei*. *Herpetologica* 23:81-93.
- Landreth, H. F., and D. E. Ferguson. 1967. Newts: Sun-compass orientation. *Science* 158:1459-1461.
- Lawson, P. A. 1994. Orientation abilities and mechanisms in nonmigratory populations of garter snakes (*Thamnophis sirtalis* and *T. ordinoides*). *Copeia* 1994:263-274.
- Leggett, W. C. 1977. The ecology of fish migrations. *Ann. Rev. Ecol. Syst.* 8:285-308.
- Levin, L. E., P. Belmonte, and O. González. 1992. Sun-compass orientation in the characid *Cheirodon pulcher*. *Env. Biol. Fish.* 35:321-325.
- Lindauer, M. 1954. Dauertänze und ihre Beziehung zur Sonnenbahn. *Naturwissenschaften* 41:506-507.
- Lindauer, M. 1957. Sonnenorientierung der Bienen unter der Äquatorsonne und zur Nachtzeit. *Naturwissenschaften* 44:1-6.
- Lindauer, M. 1959. Angeborene und erlernte Komponenten in der Sonnenorientierung der Bienen. *Zeit. vergl. Physiol.* 42:43-62.
- Lindauer, M. 1960. Time-compensated sun orientation in bees. *Cold Spring Harbor Symp. Quant. Biol.* 25:371-377.

- Loyacano, H. A., J. A. Chappell, and S. A. Gauthreux. 1977. Sun-compass orientation in juvenile largemouth bass, *Micropterus salmoides*. *Trans. Am. Fish. Soc.* 106:77-79.
- Lüters, W., and G. Birukow. 1963. Sonnenkompassorientierung der Brandmaus (*Apodemus agrarius* Pall.). *Naturwissenschaften* 50:737-738.
- Macphail, E. M. 1987. The comparative psychology of intelligence. *Behav. Brain Sci.* 10:645-695.
- Marler, P. 1976. Sensory templates in species-specific behavior. In *Simpler networks and behavior*, ed. J. C. Fentress. Sunderland, MA: Sinauer.
- Marler, P. 1984. Song learning: Innate species differences in the learning process. In *The biology of learning*, ed. P. Marler, and H. S. Terrace. Berlin: Springer.
- Marr, D. 1982. *Vision*. San Francisco: W.H. Freeman.
- Matthews, G. V. T. 1953. The experimental investigation of navigation in homing pigeons. *J. exp. Biol.* 28:508-536.
- Matthews, G. V. T. 1963. The astronomical bases of "nonsense" orientation. *Proc. Intern. Ornithol. Congr.* XIII:415-429.
- McClelland, J. L., B. L. McNaughton, and R. C. O'Reilly. 1995. Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psych. Rev.* 102:419-457.
- McCulloch, W. S., and W. Pitts. 1943. A logical calculus of the ideas immanent in nervous activity. *Bull. Math. Biophys.* 5:115-133.
- Meder, E. 1958. Über die Einberechnung der Sonnenwanderung bei der Orientierung der Honigbiene. *Zeit. vergl. Physiol.* 40:610-641.
- Menzel, R., L. Chittka, S. Eichmüller, K. Geiger, D. Peitsch, and P. Knoll. 1990. Dominance of celestial cues over landmarks disproves map-like orientation in honey bees. *Z. Naturforsch.* 45:723-726.
- Miles, S. G. 1968. Laboratory experiments on the orientation of the adult American eel, *Anguilla rostrata*. *J. Fish. Res. Bd. Canada* 25:2143-2155.
- Minsky, M., and S. Papert. 1969. *Perceptrons*. Cambridge, MA: MIT Press.
- Moore, F. R. 1980. Solar cues in the migratory orientation of the savannah sparrow, *Passerculus sandwichensis*. *Anim. Behav.* 28:684-704.

- Müller, M., and W. Wehner. 1988. Path integration in desert ants, *Cataglyphis fortis*. *Proc. Natl. Acad. Sci. USA* 85:5287-5290.
- Murphy, P. A. 1981. Celestial compass orientation in juvenile American alligators (*Alligator mississippiensis*). *Copeia* 1981:638-645.
- New, D. A. T., and J. K. New. 1962. The dances of honeybees at small zenith distances of the sun. *J. exp. Biol.* 39:271-291.
- Newcomer, R. T., D. H. Taylor, and S. I. Guttman. 1974. Celestial orientation in two species of water snakes (*Natrix sipedon* and *Regina septemvittata*). *Herpetologica* 30:194-200.
- Nishimoto, R. T., and W. F. Herrnkind. 1982. Orientation of the blue crab *Callinectes sapidus* Rathbun: Role of celestial cues. *Mar. Behav. Physiol.* 9:1-11.
- Oden, G. C. 1994. Why the difference between connectionism and anything else is more than you might think but less than you might hope. In *Artificial intelligence and neural networks: Steps toward principled integration*, ed. V. Honavar, and L. Uhr. Boston: Academic Press.
- Papi, F. 1955. Astronomische Orientierung bei der Wolfspinne *Arctosa perita*. *Zeit. vergl. Physiol.* 37:230-233.
- Papi, F. 1955. Experiments on the sense of time in *Talitrus saltator* (Montagu) (Crustacea-Amphipoda). *Experientia* 11:201-202.
- Papi, F. 1955. Orientamento astronomico in alcuni Carabidi. *Atti. Soci. Tosc. Sci. Nat. Pisa Mem. Ser. B* 62:83-97.
- Papi, F. 1960. Orientation by night: The moon. *Cold Spring Harbor Symp. Quant. Biol.* 25:475-480.
- Papi, F., and J. Syrjämäki. 1963. The sun-orientation rhythm of wolf spiders at different latitudes. *Arch. ital. Biol.* 101:59-77.
- Pardi, L. 1954. Über die Orientierung von *Tylos latreillii* Aud. & Sav. (Isopoda terrestria). *Z. Tierpsychol.* 11:175-181.
- Pardi, L. 1956. Orientamento solare in un Tenebrionidae alofilo: *Phaleria provincialis* Fauv. (Coleopt.). *Boll. Ist. Mus. Zool. Univ. Torino* 5:1-39.
- Pardi, L. 1958. Esperienze sull'orientamento solare di *Phaleria provincialis* Fauv. (Coleopt.): Il comportamento a luce artificiale durante l'intero ciclo di 24 ore. *Atti.*

- Accad. Sci. Torino* 92:1-8.
- Pardi, L. 1958. Modificazione sperimentale della direzione di fuga negli anfipodi ad orientamento solare. *Z. Tierpsychol.* 14:261-274.
- Pardi, L. 1960. Innate components in the solar orientation of littoral amphipods. *Cold Spring Harbor Symp. Quant. Biol.* 25:395-400.
- Pardi, L., and A. Ercolini. 1986. Zonal recovery mechanisms in talitrid crustaceans. *Boll. Zool.* 53:139-160.
- Pardi, L., and M. Grassi. 1955. Experimental modification of direction-finding in *Talitrus saltator* (Montagu) and *Talorchestia deshayesi* (Aud.) (Crustacea-Amphipoda). *Experientia* 11:202-205.
- Pardi, L., and F. Papi. 1952. Die Sonne als Kompass bei *Talitrus saltator* (Montagu), (Amphipoda, Talitridae). *Naturwissenschaften* 39:262-263.
- Pardi, L., and F. Scapini. 1983. Inheritance of solar direction finding in sandhoppers: Mass crossing experiments. *J. Comp. Physiol., A* 151:729-735.
- Phillips, J. B., and F. R. Moore. 1992. Calibration of the sun compass by sunset polarized light patterns in a migratory bird. *Behav. Ecol. Sociobiol.* 31:189-193.
- Pilleri, G., and J. Knuckey. 1969. Behaviour patterns of some Delphinidae observed in the western Mediterranean. *Z. Tierpsychol.* 26:3-72.
- Rebach, S. 1978. The role of celestial cues in short range migrations of the hermit crab, *Pagurus longicarpus*. *Anim. Behav.* 26:835-842.
- Renner, M. 1959. Über ein weiteres Versetzungsexperiment zur Analyse des Zeitsinnes und der Sonnenorientierung der Honigbiene. *Zeit. vergl. Physiol.* 42:449-483.
- Rosenblatt, F. 1958. The perceptron: a probabilistic model for information storage and organization in the brain. *Psych. Rev.* 65:386-408.
- Rossel, S., and R. Wehner. 1986. Polarization vision in bees. *Nature* 323:128-131.
- Rumelhart, D. E., G. E. Hinton, and J. L. McClelland. 1986. A general framework for parallel distributed processing. In *Parallel distributed processing: Explorations in the microstructure of cognition*, vol. 1, ed. D. E. Rumelhart, and J. L. McClelland. Cambridge, MA: MIT Press.
- Rumelhart, D. E., G. E. Hinton, and R. J. Williams. 1986. Learning internal representations by error propagation. In *Parallel distributed processing:*

Explorations in the microstructures of cognition, vol. 1, ed. D. E. Rumelhart, and J. L. McClelland. Cambridge, MA: MIT Press.

Rumelhart, D. E., G. E. Hinton, and R. J. Williams. 1986. Learning representations by back-propagating errors. *Nature* 323:533-536.

Rumelhart, D. E., and J. L. McClelland. 1986. *Parallel distributed processing*, vol. 1. Cambridge, MA: MIT Press.

St. Paul, U. von. 1953. Nachweis der Sonnenorientierung bei nächtlich ziehenden Vögeln. *Behaviour* 6:1-7.

St. Paul, U. von. 1956. Compass directional training of western meadowlarks (*Sturnella neglecta*). *Auk* 73:203-210.

Santschi, F. 1911. Observations et remarques critiques sur le mécanisme de l'orientation chez les fourmis. *Rev. Suisse Zool.* 19:305-338.

Sauer, E. G. F., and E. Sauer. 1960. Star navigation of nocturnal migrating birds. The 1958 planetarium experiments. *Cold Spring Harbor Symp. Quant. Biol.* 25:463-473.

Scapini, F., and D. Fasina. 1990. Genetic determination and plasticity in the sun orientation of natural populations of *Talitrus saltator*. *Marine Biology* 107:141-145.

Scapini, F., A. Mascagni, and A. Sforzi. 1993. Zonal recovery and orientation in respect to various stimuli of *Heterocerus fenestratus* Thunberg, 1784 (Coleoptera, Heteroceridae). *J. Insect Physiol.* 39:665-675.

Schmidt-Koenig, K. 1961. Die Sonnenorientierung tichtungsdressierter Tauben in ihrer physiologischen Nacht. *Naturwissenschaften* 48:110.

Schmidt-Koenig, K. 1963. Sun compass orientation of pigeons upon displacement north of the arctic circle. *Biol. Bull.* 127:154-158.

Schmidt-Koenig, K. 1975. *Migration and homing in animals*. Berlin: Springer-Verlag.

Schöne, H. 1963. Menotaktische Orientierung nach polarisiertem und unpolarisiertem Licht bei der Mangrovekrabbe *Goniposis*. *Zeit. vergl. Physiol.* 46:496-514.

Schöne, H. 1984. *Spatial orientation*. Princeton, NJ: Princeton University Press.

Schwassmann, H. O. 1967. Orientation of Amazonian fishes to the equatorial sun. *Atas. Simp. Biota Amaz.* 3:201-219.

Schwassmann, H. O., and A. D. Hasler. 1964. The role of the sun's altitude in sun

orientation of fish. *Physiol. Zool.* 37:163-178.

Sejnowski, T. J., and C. R. Rosenberg. 1986. NETtalk: A parallel network that learns to read aloud. In *Neurocomputing: Foundations of research*, ed. J. A. Anderson, and E. Rosenfeld. Cambridge, MA: MIT Press.

Shepard, R. N. 1987. Evolution of a mesh between principles of the mind and regularities of the world. In *The latest on the best*, ed. J. Dupre. Cambridge, MA: MIT Press.

Smolensky, P. 1988. On the proper treatment of connectionism. *Behav. Brain Sci.* 11:1-74.

Smolensky, P., G. Legendre, and Y. Miyata. 1994. Integrating connectionist and symbolic computation for the theory of language. In *Artificial intelligence and neural networks: Steps toward principled integration*, ed. V. Honavar, and L. Uhr. Boston: Academic Press.

Taylor, D. H. 1972. Extra-optic photoreception and compass orientation in larval and adult salamanders (*Ambystoma tigrinum*). *Anim. Behav.* 20:233-236.

Tinbergen, N. 1938. Über die Orientierung des Bienenwolfes. III. Die Bevorzugung bestimmter Wegmarken. *Zeit. vergl. Physiol.* 25:292-334.

Tongiorgi, P. 1959. Effects of the reversal of the rhythm of nycthemeral illumination on astronomical orientation and diurnal activity in *Arctosa variana* C. L. Koch (Araneae-Lycosidae). *Arch. ital. Biol.* 97:251-265.

Ugolini, A., and R. Chiussi. 1996. Astronomical orientation and learning in the earwig *Labidura riparia*. *Behav. Proc.* 36:151-161.

Ugolini, A., and S. Felicioni. 1991. Celestial orientation in *Gryllotalpa gryllotalpa*. *Physiol. Entomol.* 16:355-360.

Ugolini, A., and T. Macchi. 1988. Learned component in the solar orientation of *Talitrus saltator* Montagu (Amphipoda: Talitridae). *J. Exp. Mar. Biol. Ecol.* 121:79-87.

Ugolini, A., and G. Messina. 1988. Sun compass in the orientation of *Idotea baltica* (Pallas) (Isopoda, Idoteidae). *Mar. Behav. Physiol.* 13:333-340.

Ugolini, A., F. Morabito, and S. Taiti. 1995. Innate landward orientation in the littoral isopod *Tylos europaeus*. *Ethol. Ecol. Evol.* 7:387-391.

Ugolini, A., P. Talluri, and M. Vannini. 1989. Astronomical orientation and learning in the shrimp *Palaemonetes antennarius*. *Marine Biology* 103:489-493.

- Warburton, K. 1973. Solar orientation in the snail *Nerita plicata* (Prosobranchia: Neritacea). *Marine Biology* 23:93-100.
- Watson, J. B. 1925. *Behaviorism*. New York: Norton.
- Wehner, R. 1972. Dorsoventral asymmetry in the visual field of the bee, *Apis mellifica*. *J. Comp. Physiol.* 77:256-277.
- Wehner, R. 1972. Visual orientation performances of desert ants (*Cataglyphis bicolor*) toward astromenotactic directions and horizon landmarks. In *Animal orientation and navigation*, ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, and R. E. Belleville. Washington, DC: NASA.
- Wehner, R. 1982. Himmelsnavigation bei Insekten Neurophysiologie und Verhalten. *Vierteljahrsschr. Naturforsch. Ges. Zürich* 5:1-132.
- Wehner, R. 1990. On the brink of introducing sensory ecology: Felix Santschi (1872-1940) -- Tabib-en-Neml. *Behav. Ecol. Sociobiol.* 27:295-306.
- Wehner, R., and B. Lanfranconi. 1981. What do the ants know about the rotation of the sky? *Nature* 293:731-733.
- Wehner, R., and M. Müller. 1993. How do ants acquire their celestial ephemeris. *Naturwissenschaften* 80:331-333.
- Wehner, R., and F. Räber. 1979. Visual spatial memory in desert ants, *Cataglyphis bicolor* (Hymenoptera: Formicidae). *Experientia* 35:1569-1571.
- Wehner, R., and S. Wehner. 1986. Path integration in desert ants. Approaching a long-standing puzzle in insect navigation. *Monitore Zool. Ital.* 20:309-331.
- Whiting, J. 1669. *An ephemeris for the year of our redemption 1669. And from the worlds creation 5618. Being the first from bissextile or leapyear. Wherein is contained the state of the whole year the lunations, conjunctions, aspects of the planets, with the sun and moons place every day at noon, the suns rising and setting every day in the year, with a table of moons age every day in the year; likewise a tide table with tables of board and timber measure, and many other things pleasant for all sorts of men.* Cambridge, England: John Field.
- Wiltschko, R., and W. Wiltschko. 1981. The development of the sun compass orientation in young homing pigeons. *Behav. Ecol. Sociobiol.* 9:135-141.
- Wiltschko, R., and W. Wiltschko. 1995. *Magnetic orientation in animals*. Berlin: Springer-Verlag.

- Wiltschko, W., and R. P. Balda. 1989. Sun compass orientation in seed-caching scrub jays (*Aphelocoma coerulescens*). *J. Comp. Physiol., A* 164:717-721.
- Wiltschko, W., and R. Wiltschko. 1991. Magnetic orientation and celestial cues in migratory orientation. In *Orientation in birds*, ed. P. Berthold. Basel: Birkhäuser Verlag.
- Wiltschko, W., R. Wiltschko, and W. T. Keeton. 1976. The effect of a "permanent" clock-shift on the orientation of young homing pigeons. *Behav. Ecol. Sociobiol.* 1:229-243.
- Wiltschko, W., R. Wiltschko, and W. T. Keeton. 1984. The effect of a "permanent" clock-shift on the orientation of experienced homing pigeons. *Behav. Ecol. Sociobiol.* 15:263-272.
- Winn, H. E. 1964. Sun-compass orientation by parrot fishes. *Z. Tierpsychol.* 21:798-812.
- Withers, G. S., S. E. Fahrback, and G. E. Robinson. 1993. Selective neuroanatomical plasticity and division of labour in the honeybee. *Nature* 364:238-240.

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