CURRENT DIRECTIONS IN PSYCHOLOGICAL SCIENCE

Sun-Compass Learning in Insects: Representation in a Simple Mind

Fred C. Dyer and Jeffrey A. Dickinson

Although most research in cognitive psychology focuses primarily on human beings—or on vertebrate animals used as models for studying human behavior—insects and other invertebrates potentially have an important role to play in the study of cognition. The behavioral capacities of such organisms present a rich array of phenomena that can test the generality of theories of information processing by biological systems. Invertebrates have long served as models for elucidating basic sensory and neural mechanisms. More recently, some cognitive scientists,[1,2] defying conventional wisdom, have suggested that insects may also offer insights into how nervous systems are organized to acquire and use complex internal representations of events or relationships in the outside world.

This article examines a phenomenon of learning in honeybees that at least partially vindicates this generous view of insect cognition. The phenomenon in question is the ability, which is widely shared by other animals, to memorize the sun's pattern of movement over the day and to use this stored pattern for navigation. We review evidence that this ability constitutes a truly representational form of learning, and then discuss recent studies that provide new insights into processes that underlie the development of the bee's internal representation of the sun's course. We then point out some general insights that could emerge from further studies of this system in insects.

Fred C. Dyer is Associate Professor in the Department of Zoology at Michigan State University. **Jeffrey A. Dickinson** is a graduate student in zoology and in the Program in Ecology and Evolutionary Biology at Michigan State. Address correspondence to Fred Dyer, Department of Zoology, Michigan State University, East Lansing, MI 48824; e-mail: fcdyer@msu.edu.

ORIENTATION USING A CELESTIAL COMPASS

A wide variety of vertebrate and invertebrate species can use the azimuth of the sun (its compass direction) to steer paths between fixed points on the earth's surface. Honeybees also refer to the sun (and sun-linked patterns of polarized light in blue sky) to communicate the compass direction of food in their dance language.[3] Using the sun as a compass requires an ability to compensate for its movement during the day. This ability implies in turn a mechanism that integrates information about the sun's changing direction (which in bees and many other species is measured relative to landmarks) with information about time of day (which in most animals is provided by an internal clock synchronized to the light-dark cycle).

Although many animals use landmarks to measure changes in the sun's direction, most species can navigate using the sun in unfamiliar terrain. Such an ability implies that the pattern of solar movement, once learned, provides a directional reference independent of the reference used to learn it.

An additional challenge is that the azimuth changes at a variable rate over the day, shifting relatively slowly in the early morning and late afternoon and relatively quickly near midday (Fig. 1). Furthermore, the daily pattern of change, which astronomers call the solar ephemeris, changes with season and with latitude (Fig. 1b). Animals that are physiologically equipped to be active over a range of seasons and latitudes would do well to learn the current local ephemeris and use it as the basis of their celestial compass.

THE HONEYBEE'S CELESTIAL COMPASS

Since the 1950s, scientists have known that honeybees use a celestial compass that has all of these properties[3] and that the bees' knowledge of the current local ephemeris develops through learning.[4] The frame of reference by which bees detect and memorize the sun's pattern of movement is provided by landmarks surrounding the nest. Experienced bees draw upon this memory to determine the solar azimuth on completely overcast days, when clouds obscure both the sun and patterns of skylight polarization.[5] Their memory allows them to perform dances communicating the direction of food relative to the solar azimuth even when they have not seen celestial cues during the flight to the food. Bees perform dances in the nest on the vertical sheets of comb, encoding flight direction in the orientation of the body relative to gravity (where the upward direction represents the current direction of the sun; see

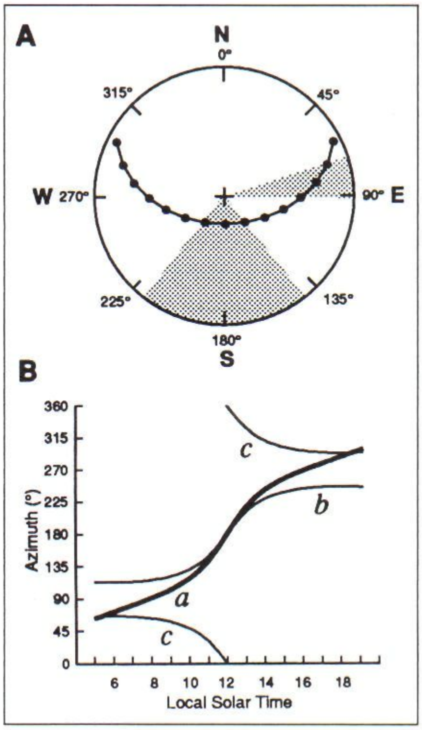

Fig. 1. The solar ephemeris. The sun's course on the summer solstice in East Lansing, Michigan (≈43°N) is shown in (a). The circles show the hourly positions of the sun from 0500 hr to 1900 hr as it makes its transit across the sky. The sun moves at a constant rate (15°/hr) along its arc, but the rate of change of the azimuth (its compass direction) varies over the day as the sun rises toward the zenith (cross) and then descends again. Shaded sectors show the change in azimuth over two equal (2-hr) time periods. The rate of change in the morning period, when the sun is low in the sky, is 9.5°/hr; the rate of change at midday, when the sun is high in the sky, is 37.5°/hr. An alternative method for displaying change in solar azimuth over the day (the solar ephemeris) is shown in (b). The heavy line (*a*) plots the sun's course shown in (a). The other curves represent the ephemerides at the equator on the December solstice (*b*), when the azimuth shifts clockwise (left to right) across the southern horizon, and on the June solstice (*c*), when the azimuth shifts counterclockwise (right to left) across the northern horizon.

Fig. 2). A bee that has returned from a flight under a cloudy sky bases her dance on the solar azimuth encoded in memory for that time of day. Honeybees' dances incidentally provide human observers a window on the contents of the bees' memory of the sun's course. For example, over several hours of cloudy weather, bees' dances to a fixed feeding site change in accordance with the change in the azimuth of the sun, indicating that the bees can store the details of the current solar ephemeris in memory.

How could a bee form an internal representation of the solar ephemeris as a result of her experience seeing the sun moving relative to the terrain? In pioneering studies of sun-compass learning, Lindauer[4] excluded the obvious possibility that bees simply memorize a list of time-linked solar positions, thus compiling a sort of lookup table recording their experience. He found instead that bees can estimate the sun's position at times of day when they have never seen it. In his experiments, he trained incubator-reared bees to fly to a feeding place in the south from noon onward for several days, but otherwise deprived the bees of an opportunity to leave the nest. When Lindauer tested the bees' ability to find the compass direction of the food (in a new landscape, so that they could not use familiar landmarks), he did so in the morning. The bees searched predominantly in the trained compass direction. This finding implied that they knew something about the course of the sun in the morning (as the azimuth moves from east to south), although they had previously seen it only in the afternoon (as the azimuth shifts from south to west). Other studies have strengthened this conclusion by showing that insects can estimate the sun's position at night.[6]

PREVIOUS MODELS

Thus, whatever learning mechanism underlies the development of the sun compass in insects, it must perform some sort of computation that fills gaps in an animal's experience of the sun's course, and hence derives from incomplete sensory information a representation that encodes, at least roughly, the sun's entire course. This is the sort of phenomenon that gave rise to the cognitive revolution in psychology: a behavior that can be understood only by considering the internal processes that organize sensory information and encode representations of external events.

Several studies have examined how an insect could fill a gap in its experience of the sun's course. The general assumption has been

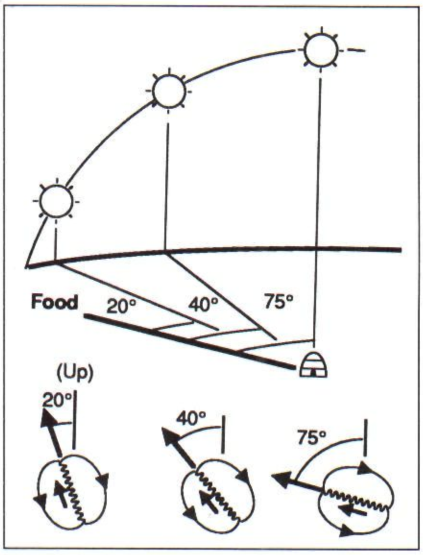

Fig. 2. Communication of flight direction in honeybee dances. The top of the figure shows the sun at three successive positions along its course, and the resulting change in the angle between the solar azimuth and the flight direction from a bee hive to a fixed feeding site. At the bottom of the figure are three dances corresponding to these three positions of the azimuth. In the dance, a bee repeatedly turns a figure-eight pattern. The central element in this pattern is the "waggling run," in which the bee runs in a straight line while waggling her body vigorously from side to side. The dancer's orientation relative to gravity during the waggling run encodes the direction of the food relative to the current solar azimuth.

that the insect records a set of time-linked solar azimuth positions at times of day when she sees the sun, and then derives from this information a single rate of compensation for estimating solar movement at other times of day. Three distinct computational mechanisms have been proposed, each with experimental or observational support. First, insects might estimate unknown positions of the sun by interpolating at a uniform rate between temporally adjacent known positions of the solar azimuth.[7] Second, they might extrapolate forward from the most recent known position of the sun, using the rate of azimuthal shift observed at that time.[6,8] Third, they might extrapolate backward, using the sun's azimuth and rate of movement observed at a later time of day.[6] Most previous evidence favored the interpolation hypothesis, but the extrapolation mechanisms could not be excluded as explanations for certain observations. All three hypotheses could account for Lindauer's original results.

A NEW APPROACH

We developed a new experimental approach[9] in the hope of deciding which of these hypotheses best accounts for bees' ability to estimate unknown positions of the sun. To our surprise, our results led us to reject all three previous models of sun learning in honeybees. Instead, our data were consistent with a completely different model that resembles one proposed independently to account for sun learning by ants.[10]

Following Lindauer,[4] we used incubator-reared bees and allowed them to see only a small portion of the sun's daily course for at least 7 days. During their daily flight time, in the 4 hr before sunset, we trained bees to find a dish of scented sugar water in a particular compass direction, and labeled them individually so that we could keep track of their experience. Then we examined how these afternoon-experienced bees estimated the course of the sun when they flew for the first time in the morning and middle of the day. To do this, we allowed the bees to leave the hive only when the sky was overcast, and then observed their dances when they returned from the food. As mentioned, the orientation of a dancer relative to gravity signals the angle that she has flown relative to the sun (Fig. 2). Because we observers knew the direction the bees had flown, we could infer from each bee's dance where she had determined the sun to be relative to the line of flight. By observing bees on cloudy days (when they could not see the sun's position during the flight) at times of day when they had never flown before (so they could not rely on a remembered position of the sun), we hoped that the dances would tell us how the bees filled the large gap in their experience of the sun's course.

We performed this experiment with two colonies of incubator-reared bees and obtained similar results for both colonies.[9] Figure 3 shows the data from one colony. Each data point is the solar azimuth inferred from a single dance by a bee visiting the hive between trips to the food. We observed 554 dances by 46 different bees in this colony. The data fall into a striking

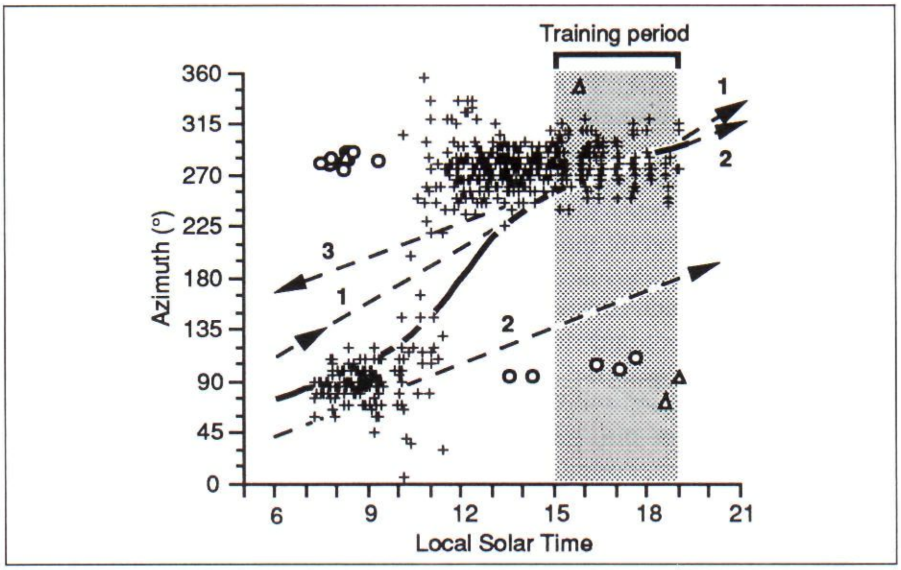

Fig. 3. Solar positions estimated by 46 partially experienced (incubator-reared) bees during an entire cloudy day, as inferred from 554 dances performed in the hive between visits to a feeder.[9] The bees had previously been exposed to a small portion of the sun's course during the late afternoon (shaded area). The cloud cover obscured celestial cues, and hence required bees to remember (or estimate) the sun's position. Each symbol is the solar azimuth inferred for a single dance. The open symbols (circles and triangles) show data from 2 bees that departed qualitatively from the pattern exhibited by the rest. The curved line shows the solar ephemeris at the time of this experiment. The dashed lines show the predictions of three different computational mechanisms that had been proposed to underlie the ability of bees to estimate unknown positions of the sun (see the text): 1, linear interpolation at a uniform rate between the solar azimuth at the end of one daily training period and the azimuth at the beginning of the next; 2, forward extrapolation from the position and rate of movement of the azimuth at the end of the daily training period; 3, backward extrapolation from the position and rate of movement of the azimuth at the beginning of the daily training period (as observed by the bees on days prior to the test).

pattern that was highly consistent among bees (with only two qualitative exceptions, discussed in the next section), and among different dances by individual bees. In the morning, the bees used a solar azimuth that was almost exactly 180° from the average solar azimuth experienced during the daily training period. They continued to use this angle until a short interval near midday (well before the normal starting time of the training period), when they changed their dances by 180° and began using the evening azimuth of the sun. The linear interpolation and extrapolation mechanisms proposed in previous studies do a very poor job of describing this pattern. In particular, because these hypotheses assume that bees derive a single linear rate of compensation to estimate unknown portions of the sun's course, none predicts the bees' abrupt midday transition from the morning angle to the afternoon angle. If anything, the bees' estimate of the sun's course most closely resembles the actual course of the sun, but the thickness of the cloud cover, as well as other evidence, precluded the possibility that the bees had detected the (approximate) position of the sun during the flight.[9]

We suggest that our partially experienced bees based their dances on an internal representation that approximated the actual pattern of solar movement over the day, even at times when the bees had never seen the sun. In both the internal ephemeris and the real ephemeris, the sun rises opposite where it sets (as measured relative to features of the local landscape), with the azimuth changing relatively slowly during the morning and during the afternoon, and moving from one side of the local meridian to the other at midday. In the conditions of our experiment, the bees' approximate ephemeris was well described by a step function that switched instantaneously by 180° at midday, but bees that did several successive dances during the midday transition actually changed their orientation progressively (if rapidly), implying that the underlying representation would be better described by a continuous function. We also found, as in previous studies,[5] that bees whose flight experience spanned a larger portion of the day developed an internal ephemeris that more closely tracked the current solar ephemeris.

AN INNATE MODEL OF THE SUN'S COURSE

Our experiments imply that bees are innately informed of the approximate dynamics of solar movement over the day. As bees begin to acquire flight experience, this innate information allows them to develop an internal representation that reflects portions of the sun's course previously seen and approximates the pattern of solar movement at other times of day. With further experience, this innate template is modified to conform more closely to the actual course of the sun.[5,9]

As mentioned, 2 bees deviated qualitatively from the pattern that led us to this interpretation, and yet these exceptions conform to our general hypothesis. These bees, whose dances are indicated by open symbols in Figure 3, used the afternoon azimuth early in the day and the morning azimuth late in the day. One bee switched at midday (when all the other bees switched from using the morning azimuth to using the afternoon azimuth). The other switched late in the afternoon. These 2 bees resemble the 44 others that we observed in using internal representations encoding (approximately) the entire pattern of solar movement, but their ephemerides appear to have been out of phase (either spatially or temporally) with the one used by the other bees.

The hypothesis that insects are equipped with an innate template encoding the sun's approximate course not only explains our results[9] and recent data from ants[10] better than do the linear interpolation and extrapolation hypotheses, it is also consistent with much of the data that was considered to support these earlier hypotheses[6,7] and thus may lead to a more general account of the development of the sun compass, at least in insects.[9]

The mechanism implied by our hypothesis would offer certain advantages to a small-brained, short-lived organism. The bee's task is to "discover" the current local solar ephemeris, and presumably to do so as quickly as possible: Honeybee foragers have only about 10 days in which to collect food for the colony before they die, and they make only a few flights from the nest prior to beginning foraging. The bees' default knowledge of the sun's general pattern of movement could simplify (and speed up) the process of discovering the actual ephemeris. Our results suggest, for example, that the "initialized" state of the neural network that encodes the ephemeris approximates the state attained after an actual ephemeris has been learned. Intriguingly, the average solar ephemeris experienced by organisms on Earth (i.e., the ephemeris averaged over all latitudes and all days of the year) is a 180° step function (Fig. 4). A neural network that by default encodes an ephemeris of this shape (as appears to be the case in our bees) would presumably have to change less on average to conform to any given actual ephemeris than one that by default estimates the

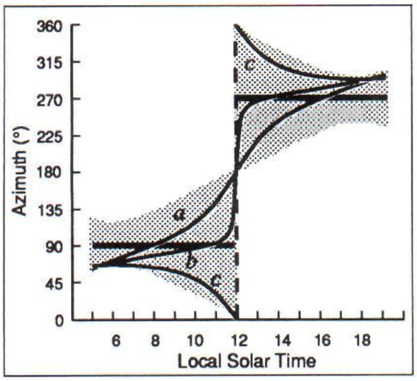

Fig. 4. Actual patterns of solar movement on Earth. The shaded area covers all possible solar ephemeris functions that could be observed on the Earth's surface (i.e., all latitudes and all days of the year). The mean of all these functions is the step function shown by the heavy line (the dashed vertical line at noon indicates that the mean azimuth at noon is indeterminate). The mean ephemeris essentially matches the approximate ephemeris developed by our partially experienced bees (see Fig. 3). Shown for comparison are the actual solar ephemeris functions for three latitudes on the summer solstice: *a*, 43°N (East Lansing, Michigan); *b*, 25°N; *c*, 15° N.

solar azimuth at random at different times of day.

Furthermore, an approximate ephemeris in the shape of a 180° step function would allow a bee to begin to use her sun compass with relatively little error throughout the day even if she had sampled only a small portion of the sun's course (Fig. 4). This is especially true during much of the year at low latitudes, where the actual solar ephemeris resembles the step-shaped representation developed by our afternoon-experienced bees: The azimuth changes little throughout the morning, shifts by about 180° at local noon, then changes little throughout the afternoon. By contrast, the interpolation and extrapolation mechanisms hypothesized previously could achieve similar accuracy only after a bee pieced together an internal ephemeris through extensive sampling of the sun's course at different times of day.

BEYOND INSECTS

Sun-compass learning in insects appears to rely upon a purpose-built learning mechanism appropriate for a small-brained animal, but we believe that further studies of this mechanism may illuminate broader questions about learning and cognition. For one thing, a critical property of the bee's mechanism is that general features of the pattern to be learned are innately encoded. As ethologists have long known, learning processes in many animals, including vertebrates, have this property. A relatively simple example is song learning in birds: Certain species seem predisposed to learn sounds that are patterned like their species-specific song.[11] A more complex example is language learning in children, which appears to be guided by innate rules for recognizing speech sounds and organizing them into words and grammatical sentences.[12] Sun-compass learning in insects may provide an opportunity to identify neurobiological mechanisms by which innately specified information mediates the integration of newly acquired information by the nervous system.

Another issue that might be illuminated by further studies of sun-compass learning is the role of time as a variable in the neural code by which the brain represents certain environmental patterns. Many species share with bees and ants the ability to learn the pattern of solar movement relative to time of day. Also, many animals, including bees, can learn the occurrence of events such as the availability of food in relation to time of day, as read from their internal clocks.[1] Although molecular neurobiologists are closing in on the mechanisms underlying biological timekeeping, scientists have virtually no idea how the clock provides input about time of day to neural circuits involved in learning. Conceivably, the bees' sun-learning mechanism could serve as a model system for exploring this question.

Finally, further studies of sun-compass orientation may provide insights into the evolutionary design of learning mechanisms. The correspondence between the bee's default knowledge and the sun's actual pattern of movement bespeaks an important role for natural selection in shaping the underlying mechanisms. The key evolutionary questions concern how these mechanisms arose, how they differ from mechanisms underlying other learning phenomena (including those in other species), and why (in terms of survival value) they have the specific properties that they do. Exploring the adaptive specialization of learning mechanisms, an area of intense theoretical interest,[1,2,13] requires combining a broad comparative perspective with focused study of specific mechanisms. Many animals orient using the sun as a compass, and yet must solve very different specific tasks in learning the sun's course. Consider, for example, that a long-lived and wide-ranging animal such as a bird needs to recalibrate its internal ephemeris throughout its life to track the varying patterns of solar movement that it experiences,[14] whereas a short-lived and sedentary animal may need to learn only the solar ephemeris experienced early in its life. Conceivably, such comparisons could provide insights into how natural selection has adapted the learning mechanism underlying sun-compass orientation to fulfill different navigational demands.

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Visual Perception of Location and Distance

Jack M. Loomis, José A. Da Silva, John W. Philbeck, and Sergio S. Fukusima

Visual perception of three-dimensional space is one of the classic problems in philosophy and experimental psychology. It is important for two reasons. First, explaining the phenomenology of visual experience, of which space perception is central, is one of the major concerns of research on consciousness, mental events, and human cognition. Second, visual space perception plays an essential role in the control of much of human spatial behavior.

Jack M. Loomis and **John W. Philbeck** are, respectively, Professor and graduate student in the Department of Psychology at the University of California, Santa Barbara. **José A. Da Silva** and **Sergio S. Fukusima** are Professors in the Department of Psychology at the University of São Paulo, Ribeirão Preto, São Paulo, Brazil. Address correspondence to Jack M. Loomis, Department of Psychology, University of California, Santa Barbara, CA 93106-9660, or José A. Da Silva, Department of Psychology, FFCLRP, University of São Paulo, Ribeirão Preto, SP, Brazil, CEP 14050-901.

WHAT NEEDS TO BE EXPLAINED?

Research on the topic has addressed two quite distinct empirical domains: the psychophysics of visual space and the visual control of action. Researchers concerned with the former have been interested in such issues as the mapping between physical and visual space; the intrinsic geometry of visual space; the stimulus cues and internal constraints that determine visual space; the interrelationship of perceived direction, distance, size, and motion; and the sensory mechanisms and neural computations involved in perceiving space.[1] Researchers concerned with the latter have focused largely on how visual information is used by the observer in the control of spatial behavior, such as reaching, ball catching, running, or driving.[2]

It is unfortunate that the programs of research on visual space and on the control of action have been conducted so independently of one another. The majority of visual perception researchers probably believe they are justified in investigating the psychophysics of visual space in isolation because the process of visual perception acts as a module functionally distinct from other modules involved in controlling action (e.g., the module that specifies the commands to the extraskeletal muscles). Furthermore, the output of the perception module—visual space—exists independently of any of the actions to be controlled. In this view, once the process of visual perception and the structure of visual space have been worked out, this knowledge can be readily applied to the problem of controlling action.

Taking issue with this view, however, are those researchers working on the control of action within the ecological framework. Their opposing view is that action

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