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ANIMAL COGNITION: The Representation of Space, Time and Number

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INTRODUCTION

Experimental investigations of animal behavior suggest that many animal brains routinely deal with the basic abstractions underlying scientific and lay discourse—space, time, and number.

Space. When a foraging ant leaves the nest, it winds this way and that in a tortuous search for fodder, but when it finds something, it turns and runs more or less directly back toward its nest (Harkness & Maroudas 1985; Wehner &

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Wehner 1986), a 1-mm hole in the ground as much as 200 m away (Wehner 1985a). It does not retrace its outward path. If the ant is displaced at the start of its homeward run, it nonetheless runs straight in the predisplacement direction of the nest for a distance approximately equal to the predisplacement distance to the nest, then breaks into a search pattern (Wehner & Srinivasan 1981). It is hard to resist the inference that the foraging ant possesses a continually updated representation of its spatial position relative to its starting point—a moment-to-moment representation of the direction in which the nest lies and how far away it is.

When one displaces the landmarks that immediately surround either a bee's feeding source or the nest hole of a digger wasp, the position to which the animal flies is systematically displaced (Tinbergen & Kruyt 1938; Cartwright & Collett 1983). It is hard to resist the inference that the animal represents something about the spatial relationship between the landmarks and its goal and uses this representation to direct its flight toward the goal.

Time. When rats are fed once or twice per day at a fixed time, they develop anticipatory running behavior: A few hours before each feeding, they begin to run, and their running activity reaches a peak just when food is due. If food fails to appear on schedule, the running and other anticipatory activities subside, only to resume again a few hours before the next scheduled feeding (Bolles & Moot 1973). If the rats are returned to ad libitum feeding, the anticipatory activity ceases immediately, but it reappears whenever their food is again removed. The anticipatory peaks reappear at the correct times on the first day of renewed deprivation, before renewed experience of the scheduled feeding.

If the rats are kept under constant light conditions in the intervening period of ad libitum feeding, the endogenous approximately 24-hr rhythm in their daily activity is no longer synchronized to the local day-night cycle and they "free-run." Their internal circadian clock runs systematically faster (or slower) than the correct time; hence subjective dusk, when activity abruptly begins, occurs progressively sooner (or later) every day. Under these conditions, renewed food deprivation also leads immediately to peaks of anticipatory activity, but these peaks do not occur at the correct local time (the time of day of the earlier regular feedings); rather, they occur at the correct phase of the animal's activity cycle, that is, at the correct time on the animal's internal clock (Coleman et al 1982; Honmah et al 1983; Rosenwasser et al 1984). It is difficult to resist the inference that animals represent the time of day (circadian phase) at which events occur and use this representation to adapt their behavior to the daily regularities in their environment.

Temporal intervals. Rats may be taught to press a lever when the appearance of a stimulus (such as a steady light or noise) signals that pressing may be rewarded by the delivery of food (typically, on 50% of the trials, pressing

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is eventually rewarded). If there is a fixed latency between the onset of the signal and the (probabilistic) arming of the feeder, then the rat's rate of pressing the lever reaches a peak at a latency that approximately coincides with the arming latency (Church & Gibbon 1982; Roberts 1981). This simple result suggests that the brain of the rat also represents elapsed temporal intervals and can compare the magnitude of the currently elapsed interval to a standard stored in memory.

Number. Rats may be taught to press a lever a certain number of times in order to produce the unsignalled arming of a photocell-activated food delivery system (Platt & Johnson 1971). When the delivery system is armed, interrupting the light beam in front of the food hopper triggers the delivery of food. When the delivery system is not armed and the rat interrupts the beam prematurely, there is a penalty: the lights go out and everything shuts down for 10 seconds and/or the response counter is reset to 0, requiring the rat to start over again. The number of presses the rat has to make to arm the delivery system is varied from 4 to 24 in blocked training sessions. For each value of N, the required number of presses, the experimenter plots the frequency at which an animal breaks off pressing and tries the feeder, as a function of n, the number of presses the rat has made since the last resetting of the response counter. Under the right penalty conditions, the value at which this function peaks—the count at which the rat is maximally likely to break off and try the feeder—exactly corresponds to N, the required number of presses. These results are invariant under motivational manipulations that alter the rate of pressing and hence the time it takes to make the requisite number of presses (Mechner & Guevrekian 1962). This suggests that the brain of the rat can keep a running estimate (count) of the number of presses the rat has made and compare this to a standard stored in memory.

Rate. Rate is number divided by time. It is well established that the relative distribution of foraging time among various foraging sites (or "foraging keys") accurately reflects the relative rates of food occurrence at those sites or during those activities—over a wide range of relative and absolute rates [Baum & Rachlin 1969 (pigeon); Godin & Keenleyside 1984 (cichlid fish); Harper 1982 (ducks); Herrnstein 1961; Herrnstein & Loveland 1975 (pigeon); Milinski 1979 (stickleback fish)]. The assumption that animals like rats, pigeons, ducks, and fish can represent both number and temporal intervals and perform with these representations operations that are formally analogous to division would explain the fine tuning of their behavior to the observed rate of prey occurrence. It has proved difficult to account for the apportionment of behavior on the basis of relative rate using models that assume an animal cannot really represent rate per se but behaves as though it did by virtue of the dynamics of an associative process (Lea & Dow 1984). On the other hand, the behavior is elegantly accounted for by a simple model, a central postulate of

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which is that an animal's rate of switching to any given "patch" (or response key) is a Poisson process whose rate parameter is proportionate to the rate at which food has been observed to occur in or at that "patch" (Myerson & Miezin 1980). An implication of this postulate would seem to be that the animal has a representation of the rate.

In this review, I examine some of the experimental evidence that animals represent space, time, and number. I consider computational models of the processes by which a brain might arrive at these representations.

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THE DEFINITION OF REPRESENTATION

A brain is said to represent an aspect of the animal's environment when there is a *functioning isomorphism* between that aspect of the environment and some of the brain processes that adapt the animal's behavior to that aspect of the environment. The term isomorphism is employed in the mathematical sense of a utilizable formal correspondence between systems. The best known isomorphism is the one discovered by Descartes and Fermat between geometry and algebra. The use of Cartesian coordinates maps the entities studied by geometers—points, lines, curves, and surfaces—into the entities of algebra—vectors (strings of numbers) and equations. The discovery of a formal correspondence between, for example, a straight line and a "linear" equation enabled mathematicians to represent geometric problems algebraically and thereby bring algebraic methods of proof to bear on geometric problems (and vice versa). It is the *use* of the formal correspondence that makes isomorphisms powerful engines of mathematical development rather than analytic curiosities. Similarly, it is the exploitation of formal correspondences between its internal processes and external reality that makes brain-world isomorphisms into *functioning* isomorphisms. The functional importance of these isomorphisms makes their identification a key to understanding higher brain function.

An isomorphism exists if there is a procedure or process that maps entities, relations, and operations in the represented system into entities, relations, and operations in the representing system *in such a way that* a given relation holds within the represented system if and only if (written *iff*) it holds among the corresponding entities, operations, and relations within the representing system. For example, under the Cartesian procedure for mapping points on a plane into number pairs (2-dimensional vectors), two lines intersect (geometric relation) *iff* there is a common solution to their corresponding equations (algebraic relation).

In a neuroscientific context, an isomorphism exists when there is a sensory-perceptual process that maps aspects of the environment (entities in the represented system) into neural activities (entities in the representing system)

in such a way that brain processes formally isomorphic to corresponding environmental processes may operate on these neural activities to produce behavioral outputs that correctly anticipate *implicit* relations among the perceived entities—relations not directly given in the original sensory input. The homeward-bound ant's turning in the direction of the nest and running approximately the right distance before starting its search pattern is an example of a behavioral output that anticipates or corresponds to a spatial relationship not directly given in sensory input. The spatial relationship between the ant and its nest must be computed from sensory inputs received over the course of the ant's tortuous outward journey.

The concept of a functioning isomorphism between arithmetic and selected aspects of reality plays a central role in the modern theory of measurement (Krantz et al 1971). Measurement is the art of devising procedures that map nonnumerical entities into numbers in such a way that some arithmetic relations and operations may be validly employed with the resulting numbers (employed to draw correct conclusions about relations among the measured entities). The theory of measurement makes clear the important point that representations come in varying degrees of richness, depending on how many operations and relations within the representing system may be employed to draw valid conclusions about the represented system.

Representation is commonly used in psychology and neuroscience in the sense of a mental or neural entity (for example, the activity of a feature detector) that is imagined simply to "stand for" some nonneural entity (such as a horizontal line). This is a maximally impoverished use of the term (or else it confuses the notion of a representative with the notion of a representation). Such a representation is nominal in both senses of the word. It functions only as a unique naming device. There is only one relation in the representing system that may validly be employed, the identity or equals relation. The standard example is the representation of athletes by the numbers on their jerseys. If it is only in this limited sense that the brain "represents" the world, then the skeptics of representational approaches to brain function (e.g. Freeman & Skarda 1988) are justified in their skepticism.

There is substance to the claim that the brain represents reality only if combinatorial processes in the brain operate on the results of sensory/perceptual mappings in ways that mirror processes and relations in the mapped system. If the only sense in which the brain represents number is that there is a sensory/perceptual mapping from numerosity to brain states (the activities of detectors for specific numerosities), which make possible simple numerical discriminations, then the brain's representation of number is a representation in name only. Only if the brain brings combinatorial processes to bear on the neural entities that represent numerosities may we say that the brain represents number in an interesting sense of the term representation.

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Thus, I will be particularly attentive to evidence that suggests the operation of such processes.

The computation of a signal representating a rate by a process in which a signal representating a numerosity is divided by a signal representating a temporal interval would be an instance of the sought-for kind of combinatorial process. At the neurophysiological level of analysis, this would require finding a neural process in which a signal that was a scalar function of the numerosity of some set of rewards combined with a signal that was a scalar function of the temporal interval over which those rewards were experienced to generate a signal that was a scalar function of the ratio between the two input signals (thus a scalar function of the rate of reward occurrence). One would then need to show that the animal's rate-dependent behavior was appropriately influenced by experimental manipulation of the output signal (the signal that represents rate). The day when such experiments are done will not come until the community of experimentalists is convinced that processes like this are to be found in the brains of animals, even quite lowly animals.

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THE REPRESENTATION OF SPACE IN ANIMAL NAVIGATION

Navigation is the process of (*a*) *determining* and (*b*) *maintaining* a course or trajectory from place to place. It is a fundamental behavioral process for any animal that departs from and returns to fixed points in its environment, such as nutrient sources, mating spots, and nests or resting places. The range of animals whose behavior patterns include returning to fixed points is large, including many if not most insects and other arthropods, as well as most if not all vertebrates.

In the absence of a beacon emanating from the destination, determining or setting a course requires a spatial representation, a representation of geometric relationships between the animal's position in space and the position of the points to which it directs its movements. Maintaining a course, on the other hand, requires a directional stimulus or directional signal. The distal stimuli used in determining one's position and orientation during the process of setting a course are often not important in the process of maintaining the course, and vice versa, as for example, when one takes a positional fix from star sightings in order to determine what course to steer, then steers by the magnetic compass (a directional stimulus).

Setting a course requires positional information. There are two quite distinct processes for obtaining the requisite information. One, *dead reckoning*, is carried on more or less continuously; while the other, *taking a positional fix*, is episodic.

Dead reckoning is the process of determining the change in position (from a

known starting point) by integrating velocity with respect to time. It gives a continuous representation of one's position in the world, but it is inherently subject to a cumulative error; the indication of position becomes more and more inaccurate the longer the interval of integration.

To correct the cumulative error in the "reckoning," one must occasionally obtain a fix of one's position by means of *sightings* on points that have a known position, that is, points whose positions relative to one's goal are represented on a *map* (or on an *ephemeris,* in the case of a celestial object, whose position relative to the goal is a function of time). A map, in the most general sense, is a representation of some or all of the geometric relations among points, lines, and surfaces. A sighting is the determination by some means (not necessarily visual) of the direction (bearing) of a charted point—a point whose position is represented on the map. More rarely—because it is more difficult—a sighting may also involve the determination of one's distance from the sighted point. The taking of a positional fix by sightings on charted points corrects the value of the integral that represents one's position in the "known" (charted) world.

The processes of animal navigation appear analogous to formalized marine navigation in that (*a*) Many mobile animals maintain a representation of their position in the world by means of a process analogous to dead reckoning. In the literature on animal navigation, this process is called path integration. (*b*) They also make a map of the terrain surrounding points of interest like nests and food sources and they use this map and sightings of charted points to correct the errors in their path integration. (*c*) The taking of fixes appears to be episodic; most of the time the animal's representation of its position in the world is based on its map and its reckoning, not on moment-to-moment fix-taking. The result is sometimes comically inappropriate behavior, when the spatial reality to which the animal is "reacting" no longer corresponds to the map upon which its "reactions" are based. (*d*) In maintaining a course, animals often use the sun or the wind, or inertial or kinesthetic input as sources of directional information, none of which is used in taking fixes. Thus, the process of taking a fix is quite distinct from the process of holding a course, even though both processes depend upon directional inputs. Animals look to the terrain to tell where they are, but they steer by the sun, the stars, and the wind. (*e*) The sun is a principal source of directional input in the holding of a course, which is remarkable because the sun's direction is a function of the time of day and the season of the year. To use the sun as a source of directional information requires an *ephemeris,* a representation of its position as a function of time.

In reviewing the literature relevant to these conclusions, I consider most extensively a few well-designed experiments with ants and bees for two reasons: (*a*) Some of the most elegant and compelling experiments have been

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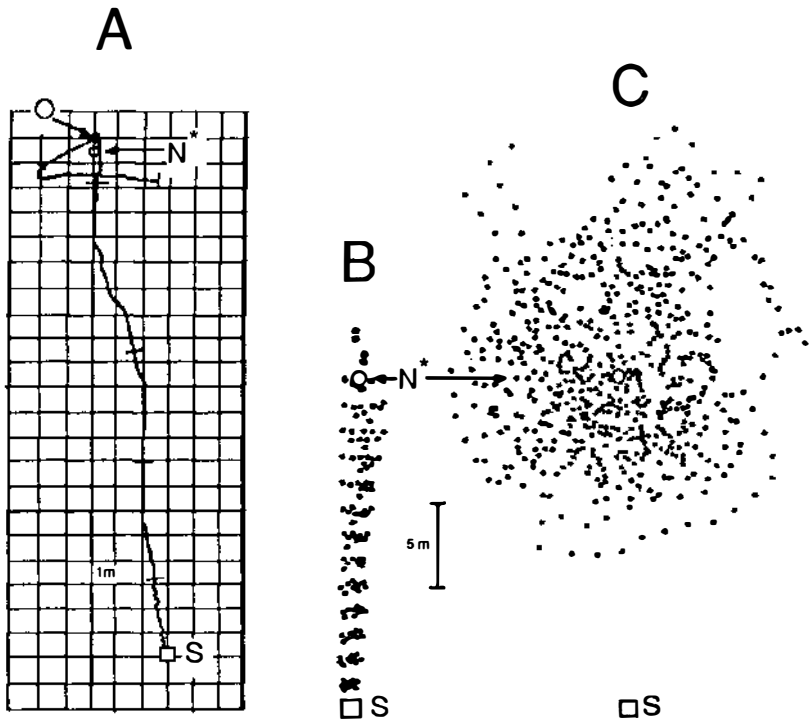

Figure 1 Course holding by dead-reckoning in the ant. *A. (above)* Tracing of an ant's course from its release point (S) to the sharp turn (O) that marks the onset of its search for the (fictive) nest (N*). Crossbars on tracing mark 10-sec intervals. *B. (above)* Superimposed plots of the positions of 10 ants at 10-sec intervals from their release to the onset of their search patterns. The larger dots surrounding the fictive nest mark the onsets of searching. *C. (above)* Superimposed plots of the positions of the 10 ants at 10-sec intervals during the first 15 min of their search. (Redrawn from Figure 2, p. 318 of Wehner & Srinivasan 1981, by permission of the authors and the publisher.) *D. (opposite)* Tracing of an ant's course during minutes 22–60 of its search. The fictive nest was between the open circle with which the trace commences and the filled circle with which it concludes. (Reproduced from Figure 3b, p. 320, of Wehner & Srinivasan 1981, by permission of the authors and the publisher.)

done with these animals. Because they make many journeys every day between their nest or hive and one or more food sources and because they are relatively unperturbed by quite drastic experimental manipulations—for example, displacement in mid-trip into completely unfamiliar territory—they make excellent subjects. (*b*) If we are persuaded that these conclusions are true for insects, then we are more likely to find explanations of vertebrate behavior in these terms plausible. In the realm of higher brain function, we are reluctant to deny to the rat and the pigeon what we concede to the bee and the ant.

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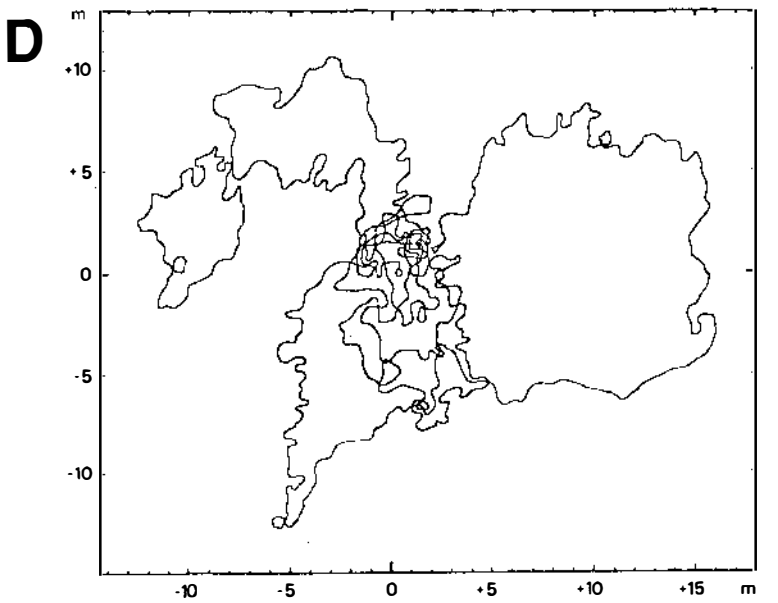

Dead Reckoning (Path Integration)

Wehner & Srinivasan (1981) set up feeding stations 20–40 m away from the nest of a colony of large fast-moving desert ants *(Cataglyphis bicolor)*. On the desert 600 m away (well beyond the foraging range of this species), they painted a gridwork of lines at 1-m intervals. They captured foragers as they left the feeding station, released them at a fictive feeding station in the area with the gridwork, and traced their subsequent movements on a data sheet with a 100:1 reduction of the grid, marking the tracing of the course with crossmarks on the beep of a timer that signalled 10-sec intervals. Figure 1A shows a typical run, from the release site to a point within a few meters of the fictive nest, where the ant broke off its straight homeward run to begin a systematic search for the entrance. Figure 1B is a superimposed display of the positions of each of 10 ants every 10 sec from release to commencement of the search pattern. Figure 1C is a superimposed display of the positions of the 10 ants every 10 sec after the start of the search pattern. Figure 1D is the tracing of a representative search pattern from minutes 22 through 60 of the (necessarily futile) search for the (fictive) nest.

When released in unfamiliar territory, where there was no nest to be found, ants homeward bound at capture followed a straight course within a degree or two of the correct homeward course from the capture point to the real nest for a distance within 10% of the correct distance. This implies: (*a*) There were in the nervous system of the ant at the time of its capture neural activities

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representative of the bearing of its nest from the site of its capture and of the linear distance between the capture site and the nest. Similar neural activities find behavioral expression in the well-known dance by which the successful honeybee forager indicates to other foragers the direction and distance of the food source (von Frisch 1967). (*b*) In moving along its homeward course, the ant updated its position— for example, by decrementing the activity representative of its linear distance from the nest. (*c*) The ant has a directional reference accurate and steady enough to permit it to hold a straight course for 40 m (more than 4000 body lengths). It has long been known that the sun is the preferred source of this directional input in the ant (Jander 1957; Santchi 1913) and most other diurnally active animals (Emlen 1975; Mittelstaedt 1962; Wehner 1985b), including the free-swimming Brazilian *Aplysia* (Hamilton & Russell 1982).

The focus of Wehner & Srinivasan's analysis was not the homeward run but the search pattern. The searching ant follows an extraordinarily tortuous course, full of twists and turns, big loops and small (Figure 1D), but the spatial probability density function for its position at any moment after the commencement of the search pattern approximates the bivariate Gaussian distribution (Figure 1C). The distribution remains centered on the starting point of the search no matter what postsearch interval is chosen for its determination. What changes is the standard deviation of the distribution; the more time has elapsed since the start of the search, the greater the standard deviation. What this means is that the ant ranges farther and farther from its starting point, making ever bigger loops, but it returns time and again to that starting point, so that the most densely searched area remains the area immediately around the starting point, no matter how long it has searched. This makes sense if the starting point is taken to be the best estimate of where the nest is and if there is some probability of having missed the nest in a given area no matter how densely the area has been searched.

What is most remarkable is that the search is conducted by dead reckoning. The ant does not take a fix on the terrain around its starting point and return to the starting point by reference to the terrain; rather, it keeps track of its position relative to the starting position of the search by path integration. The path integration system is sufficiently accurate that after an hour's search following the kind of course portrayed in Figure 1D, the ant's representation of its position relative to the starting position of the search is accurate to within a meter or two. Further displacement experiments showed that the repeated returns to the starting position are effected by path integration: Midway in the search, the ant was recaptured and released on the periphery of the area it had so far searched, a displacement of about 10 m. In continuing its search, the ant now often traversed portions of the territory it had already traversed, but the center of the search, the point to which it returned most

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often, was displaced by a vector equal to the midsearch experimental displacement. One might explain this by supposing that the ants started over "from scratch" after the second displacement, taking a new fix, and so on. However, the size of the loops they made after the second displacement were characteristic of the later stages of a search, not the early stages.

Computational models of the path-integration process have been elaborated (Gallistel 1989; Mittelstaedt 1978, 1985; Mittelstaedt & Mittelstaedt 1982; Müller & Wehner 1988), but space does not permit a critical review of them. What they have in common is what any model of path integration would seem to require—the additive combination of successive angular and linear displacement signals. Müller & Wehner propose stride-by-stride summation of linear and angular changes; whereas Mittelstaedt and Gallistel favor continuous models—that is, the integration of velocity signals. The integration of a velocity signal with respect to time is the limiting case of adding successive small displacement signals, so the models are alike in assuming the additive combination of displacement/velocity signals. Path integration, then, is our first example of a combinatorial process in the nervous system that mirrors a process external to the nervous system in a functional manner—a functioning isomorphism.

Homing by path integration has been experimentally investigated in the spider (Mittelstaedt 1985), in the gerbil (Mittelstaedt & Mittelstaedt 1980), and in passively transported geese (von Saint Paul 1982). It appears to be ubiquitous in vertebrate and arthropod behavior.

The Ephemeris Function

In marine navigation, an ephemeris table gives the data and equations necessary to compute the geographical position of the sun and commonly used stellar references as a function of year, day, and time. Animals that steer by the sun must construct their own ephemeris function. The ephemeris function enables the nervous system to compute the current azimuthal position of the sun from the time indicated by the internal clock. The azimuthal position of the sun is the angular deviation from due south (or from some other geostable reference direction) of the perpendicular from the sun to the horizon. Moment-to-moment knowledge of this ever-changing position is a prerequisite for using the sun to hold a straight course.

One of the more engaging of the many experimental demonstrations that the sun-compass mechanism depends on an internal timekeeping mechanism was done by Renner (1960). He trained honeybees to find artificial nectar at a certain time of day on a table located to the northwest of their hive in a nondescript field on Long Island, New York. One night, he packed up the hive and flew to California, where he opened the hive the next day in a nondescript field near Davis. He had arrayed tables at 45° intervals in a circle

around the reopened hive, with observers at each table to tally the bees that came and when they came. The time difference between Davis and Long Island is slightly more than 3 hr, so the azimuthal position of the sun for an observer at Davis is on average 45° counterclockwise from its contemporaneous position for an observer on Long Island. When a bee from Long Island uses an internal clock synchronized to Long Island solar time to compute from its Long Island ephemeris function the azimuthal position of the sun, in order to steer a northwesterly course, it will fly a westerly course if it happens to be in California, which is what Renner's bees did. [They also came to the tables 3 hr early—see the section below on *Time of Occurrence (Circadian Phase)*.]

An ephemeris function is a representation of the position of a celestial body like the sun *with respect to the terrain surrounding the point of observation,* as a function of the time of day. Since the azimuthal position and velocity of the sun at a given time of day change with the seasons, an animal that steers by the sun must have a process that permits the continual recalibration of its ephemeris function. Gould (1980, 1984) has shown that the recalibration process involves combining the records from several successive determinations of the azimuthal position of the sun. The combining of the results of several successive sightings of the sun's azimuthal position to obtain a representation of its time-dependent azimuthal velocity is another instance of a combinatorial process in the nervous system that mirrors an external process in a functionally useful manner—another functioning isomorphism.

The sightings from which a bee calibrates its ephemeris function are separated by intervals during which the bee is in the hive out of sight of the sun. A sighting of the sun is a measurement of its azimuthal angle with respect to a direction defined by the local terrain or a geostable directional signal like the signal from a magnetic compass. To combine the results from separate sightings, the bee must be able to orient itself reproducibly with respect to the earth, which implies that it has a terrain map, a magnetic compass, and/or some other process for determining a geostable direction (Dyer & Gould 1983).

Dyer & Gould (1981) showed that the bee's ephemeris function gives the azimuthal position of the sun with respect to a map of the local terrain by displacing beehives on heavily overcast days to fields with terrain similar to the terrain in the home field, but with the salient features running in a different compass direction (say, an east-to-west treeline in the new field in place of the south-to-north treeline in the home field). Before displacement, the bees had been trained to forage at a source, say, to the west of the hive. When the bees emerged from the displaced hive under complete overcast, they flew to the south (the direction that was correct if one took the treeline in the new field to be the treeline in the old field). When they returned to the hive, their dance

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had the orientation with respect to the current position of the (invisible) sun that one would follow to reach a source to the west of the hive—the solar heading they "thought" they had just flown rather than the solar heading they had in fact just flown. The bees that responded to this dance, however, flew to the south, which was the direction from which the dancing bees had in fact returned. What these results show is that neither the dancing bees nor the responding bees could see the sun through the heavy overcast. The dancing bees signalled the solar bearings of the food by indicating the direction of the food relative to an ephemeris representation of the sun's current position, a representation rendered erroneous by the displacement; and the responding bees interpreted the dance in terms of a similar representation of where the sun supposedly was in relation to the local terrain. Evidently, this representation of the sun's current azimuthal position—the ephemeris function—uses prominent directional features of the terrain (e.g. the treeline) as the geostable directional reference.

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The Cognitive Map

A cognitive map is a representation of the relative positions of points in the environment. The map makes it possible for an animal to orient toward or approach a point that has no currently perceived distinguishing characteristics by reference to (*a*) currently perceivable points that can be identified with points on its map (currently recognizable charted points) and (*b*) geometric relationships between the currently recognizable charted points and the goal (geometric relationships recoverable from the map). In navigational terminology, *piloting* is orienting toward or away from various points (for example, hidden shoals) by adopting an appropriate orientation with respect to recognizable features of the terrain with a known (charted) spatial relationship to the goal.

It is widely assumed that animals orient toward points primarily on the basis of distinctive sensory cues emanating from those points (beacon homing), rather than orienting toward a position in a larger spatial framework. However, evidence is accumulating that orienting toward a point by virtue of the position it occupies in the larger environmental framework is the rule rather than the exception. Hence, cognitive maps, which make possible this kind of orientation, may play a ubiquitous role in animal behavior, coming into play whenever the animal moves toward or away from any goal.

Map-based orientation is most convincingly demonstrated when the point to which the animal moves has no distinctive features of its own, when "there is no there there" (to quote Gertrude Stein's *mot* about Oakland, California). The hoverfly's station, for example, is a position in mid-air, where it hovers for minutes at a time, darting away now and then to chase passing flies, but resuming its station when the foray is over. Collett & Land (1975) showed

that the hoverfly's return to its station is guided by the geometric relationship between the station and surrounding landmarks. When the landmark is an isolated, experimentally provided, patterned board, displacement of the board displaces the station. Their studies of station finding and holding in the hoverfly reveal a number of properties of map use that appear to be quite general in the animal kingdom.

Hoverflies approach their station from any angle, and their orientation with respect to the landmark upon arrival varies greatly from occasion to occasion. Thus, the hoverfly recognizes a landmark from different distances and angles, regardless of the portion of its retina upon which the image of the landmark falls. The hoverfly's fix-taking—that is, its computation of its position relative to the landmark—is episodic. The fly takes a fix on the landmark when it resumes its station after a foray, but it does not continue to monitor its position relative to the landmark while on station; rather it relies on global image motion to hold its position (an optomotor position-holding mechanism). The fix-taking mechanism does not rely on image motion, but upon static properties of the image—its size and shape relative to a presumed memory image. The optomotor position-holding mechanism does not assign a special significance to any segment of the environmental image, whereas the fix-taking mechanism assigns special significance to the segment or segments of the environmental image that correspond to the objects or terrain on which the fix is taken.

A paradigm that has been used to demonstrate that rats can find points solely on the basis of their position relative to the larger environmental framework is the Morris water maze (Morris 1981; Rudy et al 1987; Whishaw & Mittleman 1986), which is a circular or rectangular pool filled with opacified water, with a submerged platform located somewhere in it. Once they have found the submerged platform, rats dropped into any point in the pool set a course more or less directly toward the platform.

Even when the goal has distinctive remotely perceivable sensory features, animals seem to prefer to find it by means of its geometric relationship to the larger environment rather than by beacon homing. *Amphiprion* are a genus of fish that live within the tentacles of sea anemone, venturing out for distances of only a meter or so. In aquarium experiments, when an amphiprion's home anemone is displaced (either while the fish is within its tentacles or when the fish is away on a foray), the fish returns to the position in the tank previously occupied by the anemone, even though the fish is a highly visual animal and "its" anemone is among the more salient objects in the tank (Mariscal 1972).

THE LOCAL MAP OF THE HONEYBEE The use of surrounding landmarks to localize a nectar source has been extensively studied by Collett and his collaborators (Cartwright & Collett 1983; Cheng et al 1987). They used

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cylindrical landmarks within an otherwise featureless room. They trained the bees to find a nectar source by reference to these landmarks, then examined the pattern of the bee's search flight on trials when the nectar source was absent. When the nectar had been at a fixed distance from a single cylinder, the bee's search was rather imprecise but clearly centered at the correct distance and direction from the cylinder. This result implies that the bee learns the compass bearing of the landmarks from the nectar source,[1] rather than simply the appearance of the landmark. A cylindrical landmark appears the same from every direction; if finding the nectar source by reference to the cylinder were based solely on the cylinder's appearance, the bee would search in an annulus around the cylinder.

Increasing the size of the cylinder increased the distance at which the bee's search was centered, which implies that the bee takes up the appropriate distance from the landmark by means of triangulation, rather than by, for example, "flying it off." In other words, the bee finds the distance at which the apparent (proximal) size of the landmark matches its remembered apparent size. It should not be concluded from this that the bee does not represent the distance between the landmark and the source or the true (distal) size of the landmark. Triangulation is the principal means of determining position in most navigational schemes and positioning by apparent size is a form of triangulation. Under natural circumstances, the use of apparent size is a *means of determining distance* and is taught as such in manuals on navigation. This method, of course, presumes that the true size of the landmark being used is fixed!

Adding landmarks (additional cylinders at other compass points) greatly narrowed the focus of the bee's search. When there was more than one cylinder, increasing their size had no effect on the locus of search, which is to be expected, since triangulation is much more accurate when it is based on sighted contours with wide angular separations (the different cylinders) rather than on sighted contours with narrow angular separations (the contours of a single cylinder). When the bee was confronted with two configurations of cylinders on test trials, which varied in how closely they conformed to the training configuration, the bee preferred the configuration that conformed more closely. Thus, the bee's triangulation process is an error-minimizing one, not an all-or-nothing match-or-mismatch process.

Even with configurations of three or more cylinders, which were rich enough to define a unique search point without reference to compass bearings,

[1]The compass bearing of Point B from a Point A is the angle measured at A between the point B and a line passing through A with a known direction on the surface of the earth, e.g., the direction of the sun's culmination (maximum elevation). There is no necessary connection between the determination of a compass bearing and the use of a magnetic indicator of geophysical direction.

the bees nonetheless required that the landmarks have approximately the correct compass bearings. This means that the coordinate framework within which the bee utilizes the landmarks is anchored to the room (a geocentric system of coordinates) rather than to the landmark configuration.[2] This surprising and important conclusion derives from experiments in which Cartwright and Collett rotated the landmark configuration, pitting coordinate frameworks anchored to the landmarks against geocentric frameworks. When the bee was at the correct point within a coordinate framework anchored to the landmarks, then the compass bearings of the landmarks were wrong; the landmarks lay in the wrong direction in a geocentric framework. When the landmark configuration was rotated by 90° or more, the bees rejected the landmark identifications and searched at random in the room. The parallel to marine practice is striking. A mariner generally knows at least approximately where he is, by dead reckoning from his last known position, and which way is north. Hence, the mariner knows the approximate compass bearing a sought-for landmark must have. A headland that resembles what the mariner is looking for will not be accepted as such if its compass bearing is too far out.

The use of a map to find a position in the world requires establishing a correspondence between what is currently perceived and what is preserved on the map (the "memory image"). An obvious question is the level of abstraction at which this comparison operation is carried out. Put another way, how much image processing precedes the comparison stage? The lowest level of abstraction would involve storing retinal "snapshots" of the landmarks and comparing the current image of the landmarks with the memory image point for point. Replacing opaque square landmarks with frame outlines would defeat a mechanism based on point-by-point matching, a mechanism in which there was negligible image processing prior to the matching of current input with remembered input. It does not, however, defeat the bee. Cartwright and Collett (1983) showed that the bee would accept a frame outline in lieu of the solid landmark it was trained with, suggesting that the matching operation occurs after a contour extraction process (or high-pass filtering of the retinal image, an operation that produces an image in which contours predominate). Beusekom (1948) showed that the digger wasp would tolerate replacement of a triangular array of pine cones with an open plastic triangle, which suggests that the matching operation may also follow a stage of low-pass image filtering. (The images of the pine cone array and of the plastic triangle would resemble each other more and more strongly as one blurred the focus of an imaging lense, which is a low-pass filtering operation.)

[2]A coordinate system is said to be anchored to a point if the coordinates of the point are always the same within that coordinate system.

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Gould (1987) confronted honeybees with choices between landmarks that matched the training configuration in shape and area versus ones that matched it only in area and found that they strongly preferred the configuration with the correct shape. In elegantly designed parametric experiments, he measured the angular resolution of the memory images used in fixing a food source, revealing a horizontal resolution of about 3° and a vertical resolution of 5–6°. This resolution is poorer than the 1° visual resolution established for the honeybee using optomotor tests (Wehner 1981), indicating that the remembered "sketch" of the environment does not include all the detail that the bee's visual system is capable of resolving. On the other hand, this resolution is better than the 8–10° limit of resolution that Gould (1986b) has demonstrated in the bee's memory for the optical pattern of the source itself. The bee would appear to make a higher-resolution map of the terrain surrounding the source than it does of the source itself. Incidentally, it has also been found that the bee learns the pattern of the source itself primarily while hovering over the source prior to landing on it (Gould 1988a), while it learns the relation between the source and the surrounding landmarks while hovering over it prior to departure (Gould 1988b).

At the opposite extreme from the matching of unprocessed retinal images is the matching of a representation of the currently perceived 3-dimensional shape of the environment with a record of its previously perceived 3-dimensional shape (the map). Matching carried out at this level of abstraction requires that the images and other relevant sensory inputs (e.g. velocity signals) received over time have been processed to the point of extracting from them a coding of the macroscopic shape of the environment. Thus, it implies that the bee has a map in the ordinary sense of the term, since the lay meaning of map is a representation of the macroscopic shape of the environment.

Whether the bee has a map in the ordinary sense of the term depends in part on the extent to which metric geometric relationships are incorporated into its record of the terrain (its map) and used in navigation, since metric relationships are fundamental determinants of shape as we ordinarily conceive it. Metric relationships are geometric relationships involving distances and angles. We have already seen that the compass bearings of the landmarks from the food source are incorporated into the bee's representation of the geometric relationship between the source and the landmarks and are used in relocating the source. Compass bearings are metric relationships. Cheng et al (1987) have shown that in triangulating the location of the food source, the bee relies on nearby landmarks more than remote landmarks, even when the remote landmarks have been made larger than the nearby landmarks so that the two pairs of landmarks produce matching retinal images. This result implies that the bee incorporates into its map of the food locale a representation of both the

compass bearings of, and the distances to, surrounding terrain contours and uses this information in positioning itself relative to those contours. This conclusion is equivalent to the conclusion that the bee's record of the terrain contains all the information required to construct a map in the ordinary sense of the term, an explicit representation of the shape of the environment.

One formally elegant way to demonstrate that the spatial representation an animal uses in finding a position contains metric information is to subject the local environment to an affine transformation (Cheng & Gallistel 1984). Nonmetric geometric relationships are invariant under affine transformation; hence, any navigational scheme based on nonmetric spatial relations will perform equally well in an affinely transformed environment and will, in fact, not recognize the difference between the transformed and untransformed environments. Cartwright & Collett (1983) trained bees to find nectar in the center of a square configuration of cylinders, then offered them choices between the square configuration and rectangular configurations produced by compressing the square along an axis parallel to one of its sides. A rectangle is an affine transformation of a square. A navigation system like the "qualitative" system proposed by Levitt et al (1987), which relies only on records of paired landmarks, would have no basis for choosing a rectangle over a square. [This also applies to other nonmetric models of animal cognitive maps—e.g. Deutsch (1960); Lieblich & Arbib (1982).] Cartwright & Collett found, however, that the greater the compression of the rectangle, the more the bees preferred the square array. Thus, the bee's local map preserves metric relationships among the sought-for point and the surrounding terrain.

Either the bee's nervous system contains a map of the terrain in the ordinary sense of the term or it contains the equivalent of a surveyor's field notes—the contour sketches, bearings, and distances from which a cartographer constructs a map. Cartwright & Collett (1987; see also Collett 1987) favor a model along the latter lines. In their model, the bee navigates from the equivalent of the surveyor's field notes, not from the cartographic reworking of those notes. Since the information content of the surveyor's notes and a cartographic product based on those notes are the same, it is going to be difficult to decide unequivocally from behavioral work alone what actually occurs inside the bee's nervous system. Cartwright & Collett's preference for a noncartographic model seems to rest on intuitions to the effect that such models are computationally simpler than models based on a cartographic representation of environmental shape, which, it has been argued, is why Portolan charts with rhumb-line sailing instructions antedate projective maps in the history of marine chart making (Wehner & Wehner 1986). Those whose intuitions about what is neurobiologically plausible are influenced more by mathematical considerations of elegance, simplicity, and ease of computational implementation may prefer cartographic models.

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THE GLOBAL MAP OF THE HONEYBEE Rhumb-line sailing maps (and modern piloting manuals) give course and distance directions linking one port to another and, sometimes, sketches of headlands near each port. Thus, they closely resemble a surveyor's field notes. They are easy to use in navigation, provided that all one wants to do is follow one of the courses given. Since they contain the information required to construct a cartographic representation of the spatial relations among the ports, they may also, in principle, be used to steer from any port to any other, but they are not easily used for this more general purpose, which explains the universal marine preference for true maps, representations that give the relative positions of all the represented points in a manner that permits easy computation of the compass bearing and distance of any charted point from any other. Experiments in which animals are captured, transported to arbitrary release points within a familiar territory, and induced to home to different destinations are relevant to judging the plausibility of the "cartographic" model of the bee's Euclidean representation of the terrain versus the "surveyor's-notes" model favored by Cartwright & Collett (1987) and Wehner & Wehner (1986).

It has long been known that wasps and honeybees released at arbitrary points within their foraging range set "bee-line" courses back toward the hive or nest (Fabre 1919; Romanes 1885), and there are numerous similar results with birds (Papi & Wallraff 1982) and bats (Mueller 1966; Gunier & Elder 1971). An elegant series of experiments of this kind with the honeybee has recently been reported by Gould (1986a). He trained bees to fly from their hive at the bottom of a field to a feeding station in a small opening in the woods that bordered the field (Site A in Figure 2A). While the bees could be expected to be familiar with all of the terrain shown in Figure 2A, they were trained in such a way that it was unlikely that any bee ever flew from the hive to the feeding station at A by way of the Site B. Gould then captured marked foragers known to be regularly shuttling between the hive and the station at A, as they emerged from the hive en route to A, carried them around for a while in a dark box, then released them either at B or at H. He also captured unmarked foragers, shuttling between the hive and some feeding source other than A. These he captured either as they emerged from the hive en route to their diverse destinations or as they returned to the hive from diverse directions. Both groups were released at B. Site B was downhill from the woods that surrounded A. The tree-top horizon in the direction of Site A was 24–28 m above the elevation of B, preventing any view of A from B.

Gould recorded the departure bearings of each released bee. These are plotted as filled circles, open triangles, and open squares on the unit circle in Figure 2B. The thin lines without arrowheads indicate the bearing of the various destinations from the various release sites. The lines with arrowheads give the mean departure vectors for the four different categories of released

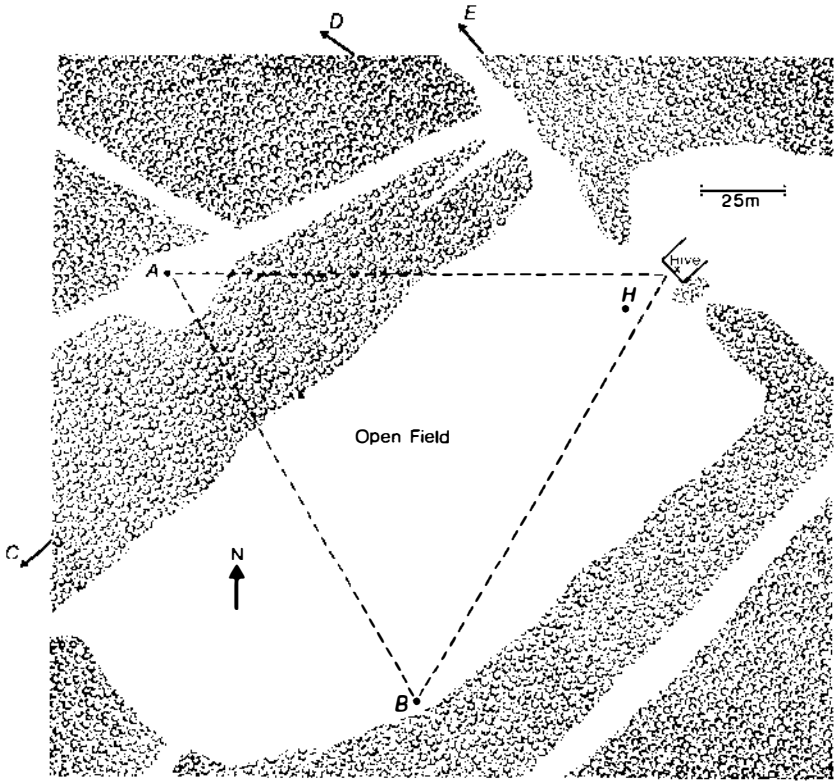

Figure 2 *A. (above)* Plan of Gould's test area. X=hive; A= feeding station; B=out of the way release site; H=release site near hive. *B. (opposite)* Departure bearings. Each symbol is the departure bearing of one released bee. Open triangles = bees destined for A, captured at the hive and released at H (Mean Vector 2). Filled circles = bees destined for A, captured at the hive and released at B (Mean Vector 1). Open squares = unmarked bees returning from diverse and unknown sources, captured on arrival at the hive and released at B (Mean Vector 3). The thin lines give the correct bearings of the destinations (hive or A) from the release sites (B or H). The heavy arrows give the mean vectors for the three groups whose symbols are plotted, plus a fourth group of unmarked bees with diverse and unknown destinations captured as they left the hive and released at B (Mean Vector 4, symbols not plotted). [Adapted from Gould (1986a,) by permission of the author and the publisher.]

bees: (*a*) those released at B and bound for A; (*b*) those released at H bound for A; (*c*) those released at B bound for the hive; (*d*) those released at B bound for diverse and unknown feeding sources. For the first three groups, the mean departure vectors have highly significant lengths (the r's in Figure 2B), which means that there is a statistically significant clustering of departure bearings. The directions (θ's) of the statistically significant mean departure vectors do not deviate significantly from the correct bearing of the bees' destinations

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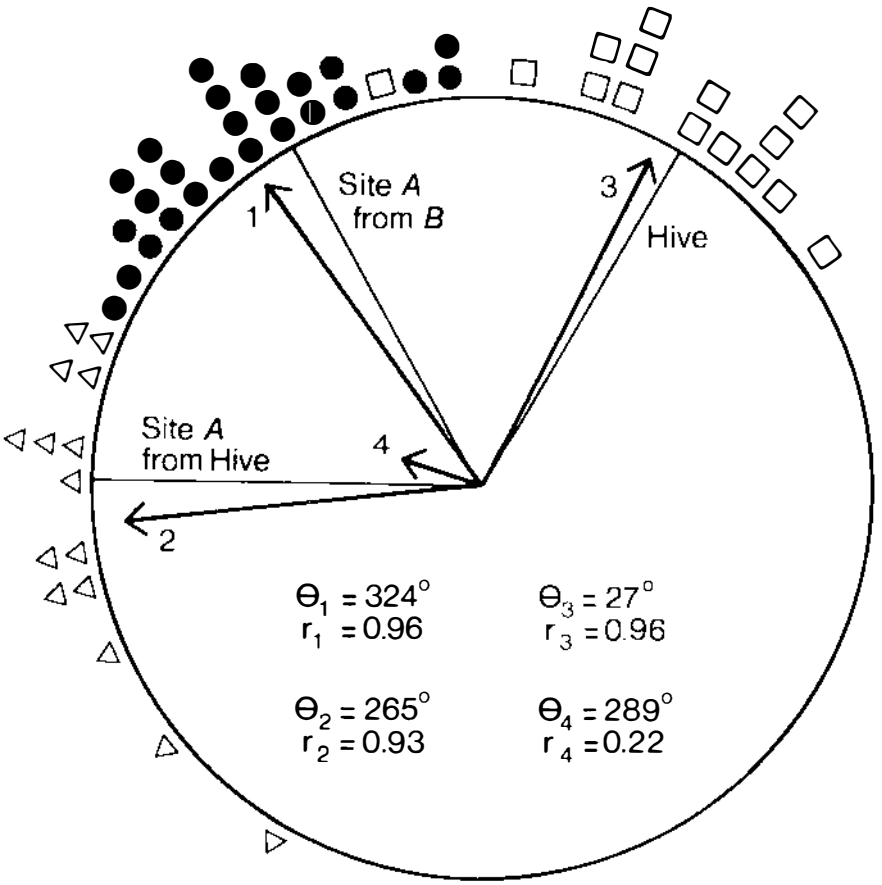

from their release sites. For the fourth group, those with diverse destinations, there is no significant clustering of departure bearings; they flew off in all directions.

Gould ran a number of interesting variations and further controls, but space does not permit a full account of this important series of experiments. What the experiments establish is the important conclusion that one and the same honeybee can quickly set approximately correct courses to different destinations from arbitrary release points within familiar terrain (when released in unfamiliar terrain, the bees never return to the hive). This is what one might expect if bees process the metric spatial information they demonstrably acquire into a unified coding of the macroscopic shape of their environment and use this unified metric representation of the shape of their environment in setting courses, plotting their ephemeris function, finding local feeding

sources, and interpreting the dances of returning foragers (see below). This kind of performance is not what one might expect from an animal that kept its knowledge of the spatial relations in its environment in the disjointed form of surveyor's field notes, although it is probably possible to account for this kind of behavior with such a model (Cartwright & Collett 1987).

The integrated-map, or cartographic, model of the bee's cognitive map would also appear more consistent with the results of an experiment reported by Gould & Gould (1988). By setting up feeding stations on rowboats, they trained some marked bees from a hive to fly to a feeding station in the middle of a lake. By keeping the quality of the artificial nectar low, they induced these marked foragers not to dance during the training period when the rowboat was moved by small steps to the middle of the lake. (Returning foragers do not signal the location of their source to other foragers when the sugar content of the nectar is low.) When the marked foragers were regularly shuttling between the rowboat in the middle of the lake and the hive, the Goulds increased the sweetness, so that the returning foragers now danced vigorously. However, the other foragers generally refused to heed their dance, even though the other foragers would heed a dance signalling a source on the far side of the lake or at any point along the shore of the lake. This result suggests that a bee's reaction to the dance of a returning forager is mediated by its map of the terrain. If the position of the source on the map, as indicated by the dance, falls where there cannot ordinarily be food, the dance is ignored. This result seems to favor the hypothesis that an integrated metric map of the shape of the environment is linked to other environmental characteristics and forms a foundation for the bee's behavior, entering into every aspect of the behavior that involves moving from place to place.

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Dead Reckoning and the Map

Animals possess sophisticated sensory/perceptual processes for determining the distances and directions of distal stimuli—that is, for forming an egocentric representation of the spatial positions of distal stimuli (Brownell 1984; Collett 1978; Collett & Harkness 1982; Ellard et al 1984; Lock & Collett 1979; Simmons & Kick 1984; Wallace 1959). Gallistel (1989) sketches the computations by which the representations of the animal's geocentric position (provided by the dead-reckoning module) may be integrated with the egocentric representations of the terrain surrounding a given viewpoint to yield a geocentric representation of the terrain, a representation built up from observations made at different places and different times.

Gallistel goes on to suggest that the dead-reckoning system is linked to the map in such a way that the animal has a moment-to-moment representation of its position on the map, which it uses to govern its movements. The hypothesis is that the course of an animal's movements through its environment is

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governed by a continuously updated representation of its position on its map, not by its immediate perceptions of the environment. The velocity components of its immediate percepts are used in the updating process (path integration). Static components of the percepts are used episodically to confirm and correct the representation of position on the map by taking a fix. Simply put, the hypothesis is that routine animal movements are governed by a navigational process closely analogous to everyday marine practice. This practice rests on an extensive isomorphism between the geometry of motion and position and the computational processes that underlie navigation. At the neurophysiological level of analysis, the hypothesis implies that the mathematical description of the processes in the animal brain that function during animal navigation parallels the mathematical description of the computations a human or computerized navigation system makes.

One attraction of the hypothesis is that it explains the many instances of "stupid" behavior in the face of a transformed environment, as when bats continue to avoid wires that are no longer there (Neuweiler & Möhres 1967), rats run into the walls of shortened segments of familiar corridors, turn into nonexistent branches of lengthened corridors (Carr & Watson 1908), run off the end of shortened planks in elevated mazes (Dennis 1932), and run right over large piles of food placed in the middle of an alley they have learned to run for a food reward at the end (Stoltz & Lott 1964). It also explains why clock-shifted homing pigeons released within sight of their home loft initially depart on an erroneous compass bearing, which is predictable from the extent of the clock shifting (Foa & Albonetti 1980; Graue 1963; Matthews 1968; Schmidt-Koenig 1972). They steer by their sun compass even when they are within sight of their destination.

Is Position-Fixing a Purely Geometric Congruence-Finding Process?

Cheng (1986; see also Gallistel 1989) ran rats in a variety of tasks in a rectangular environment where they had to find hidden food after being shown its location. The rats were kept in the dark between trials and carried to and from the experimental box in the dark, in an effort (not entirely successful) to disorient them with respect to the world at large, so that they would get their orientation while in the box entirely from the box itself, rather than carrying with them by dead reckoning during passive transport an orientation obtained outside the experimental environment (Carr 1917; Carr & Watson 1908; von Saint Paul 1982). Cheng provided very prominent and distinctive landmarks in each of the four corners of his boxes: panels that looked, felt, and smelled distinctively different from each other. He even made one wall of the enclosure of white Styrofoam, which contrasted strongly with the matte black plywood of the other three walls. Nonetheless, his rats persistently

made rotational confusions; half the time they looked for the food at the spot that was the rotational equivalent of the correct location. They behaved as if they took their orientation within the box from its shape alone, ignoring the distinctive properties of the surfaces that composed that shape. Since the shape was axially symmetric, orientations based solely on the finding of a congruence between the remembered shape of the environment (the map) and the currently perceived shape would be erroneous by 180° half the time.

Margules & Gallistel (1988) showed that when the rats were trained in a lit room where they could easily assess their orientation to the extramaze environment, one did not see these rotational confusions, but when these same rats were then run under Cheng's conditions (disoriented with respect to the extramaze environment), they made rotational confusions on 50% of the trials, despite the presence of salient corner landmarks, which were present and fixed in their given corners during all phases of training, both initially when the rats were oriented to the extramaze environment and later when they were not.

Cheng (1986; see also Gallistel 1989) suggests that there is a module that encodes the shape and only the shape of the environment. Properties of environmental surfaces other than their relative positions—the smells, reflectance characteristics, textures, etc of a surface—are stored in other memory modules and linked to the representation of environmental shape (the map proper) by means of addresses, the equivalent of the latitude and longitude or number and letter addresses that link the cities or streets in a map index to positions on the map. Gallistel (1989) suggests that in taking a fix the animal brain computes shape parameters for the currently perceived locale (for example, the centroid and principal axes of an enclosed space like the rectangular box) and matches these to the corresponding shape parameters for regions on its map. Because shape parameters are a function solely of the relative positions of the surfaces that define a shape, such a process would be impenetrable to the distinctive properties of surfaces—their smells, reflectance characteristics, and so on.

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THE REPRESENTATION OF TIME

Time of Occurrence (Circadian Phase)

Living systems contain self-sustaining biochemical and biophysical oscillations, whose periods range from fractions of a second to a year and perhaps more (for reviews, see Aschoff 1981; Connor 1985; Farner 1985; Jacklet 1985; Turek 1985). These endogenous oscillations play a ubiquitous role in behavior and physiology, because they provide the foundation for timekeeping and time-utilizing processes in the nervous system. We have already seen the role the internal time sense plays in the sun-compass mechanism. In this

section, we review some of the experimental evidence that in storing information about events, part of what gets stored is the time of occurrence or circadian phase of the event—that is, a time-stamp derived from a reading of the internal clock.

Naturalistic and experimental observations early in this century established that bees learn the time of day at which food is to be found at a given source and time their visits accordingly (von Stein Beling 1923; von Buttel-Reepen 1915; Forel 1910; Kleber 1935). After a few days' experience with a food source where artificial nectar is only available during the same 2-hr period each day, there is a sharp increase in the visits of marked foragers an hour to a half-hour *before* the beginning of the feeding period (Wahl 1932, 1933). One and the same bee learns to visit different feeding stations at different times of the day (Wahl 1932). If there is a distinctive color or odor present at certain times and a different color or odor at other times, the bee's learned preference between the colors and odors becomes a function of the time of day: It prefers one odor or color at one time of day and the other odor or color at the other time of day (Kolterman 1971). These learned behavioral dependencies on the time of day are cued by the bee's internal clock, not by external cues (Renner 1959; Wahl 1932)—that is, they are based on the momentary phase of an endogenous circadian oscillation, not on some time-varying environmental variable, such as the elevation of the sun.

In the course of a single day, a foraging honeybee may learn to distinguish 19 different times of day (19 different momentary phases of an endogenous oscillation). Kolterman (1971) did a painstaking experiment, working with only one bee at a time to avoid the complications that might arise from communication in the hive among bees simultaneously trained. His individual foragers shuttled between the hive and the station every 5 min. On the training day, each forager experienced a geraniol odor at the food source for three visits from a quarter past to a half past each hour between 09:00 and 18:00. The next day, the test day, Kolterman repeatedly probed the bee's response to two empty beakers, only one of which smelled of geraniol. On this day, the bee found a single odorless beaker filled with sugar water, except on the probes, which were made on single visits at 20-after and 10-to each hour. The probes at 20-after coincided with the times at which the bee had smelled geraniol at this source the previous day, while the probes at 10-to coincided with times when it had not. On a probe visit, the bee was confronted with two beakers, both empty, one smelling of geraniol, the other of thyme. (Untrained bees had no preference between the geraniol and thyme odors.) The beakers were so constructed that the bee had to enter them to discover they were empty. In the course of a single visit to an empty beaker, the bee landed on and entered it repeatedly ("double-checking" that the beaker was empty). The number of such landings before the bee gave up provided a measure of search

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intensity. Kolterman found that a trained bee always overwhelmingly preferred the beaker smelling of geraniol to the beaker smelling of thyme. Thus, its memory for which odor had been associated with nectar in that locale was active at all times of day. However, the intensity of its searching in the beaker smelling of geraniol was significantly higher on every probe run at 20 min after the hour and significantly lower on every probe run at 10 before the hour. There were 19 different probes, alternating between 20-after and 10-to the hour, and the search intensity on each probe differed very significantly from the probe preceding and the probe following it.

The rat, like the bee, learns the time at which it finds food (Bolles & Moot 1973). It, too, can learn more than one feeding time per day (Bolles & Moot 1973; Edmonds & Adler 1977), and for it, too, the temporal cue comes from an internal endogenous circadian oscillator (Aschoff et al 1983; Boulos et al 1980; Coleman et al 1982; Edmonds & Adler 1977; Gibbs 1979; Honmah et al 1983; Rosenwasser et al 1984). Other experiences are also stamped with the time of day: In the one-trial passive avoidance paradigm, there is a strong dependence of avoidance performance upon the time of training; the rat's hesitancy to enter the chamber where it has once been shocked, while strong regardless of the time of testing, is strongest when the time of testing coincides with the time of day at which it had the one training trial (Holloway & Wansley 1973a,b). A similar effect is seen in a one-trial appetitive learning task (Wansley & Holloway 1975). When a rat is given conflicting aversive and appetitive reinforcements for entering a compartment, the extent to which the appetitive reinforcement counteracts the effect of the aversive reinforcement depends upon the relative times of day at which it has had the conflicting experiences; it is greatest when the appetitive experience is given at the same time of day as the aversive experience (Hunsicker & Melgren 1977). In an escape task, extinction is slowest when the extinction trials occur at the same time of day as the training trials (Holloway & Sturgis 1976).

While many animals are known to have an internal clock with a period of about a year (Farner 1985), there is, surprisingly, almost no literature addressed to the question whether animals can learn temporal intervals or periods measured in days. When bees are fed at the same time every other day, they show no sign of learning the 48-hr feeding schedule (Wahl 1932). In birds, however, Gallistel (1989) gives an account of an unpublished experiment by M. Denise Caubisens and Susan Edmonds. In January and February, they went out every day to a bird feeder in a wooded area in Purchase, New York. They carried a sack of seed with them to the feeder every day, but they only used it to stock the feeder every other day. After a while, the mixed flock of chickadees, titmice, and nuthatches that frequented the feeder was there waiting for them only every other day, suggesting that birds can learn an every-other-day schedule.

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Whether animals can distinguish one day from the next remains to be determined, but it is now well established that many of the records that animals keep of their experiences are stamped with, at least, the time of day at which the experience occurred. Gallistel (1989) suggests that the time stamp and the address stamp (record of where the experience occurred) play a unique role as index variables in memory, variables that permit one record to be linked to another.

Temporal Intervals

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The capacity of rats and pigeons to remember the duration of stimuli and the latencies from the onset of a stimulus to the (probabilistic) occurrence of a reward have been extensively studied by Church, Gibbon, Meck, and Roberts. Their work has been reviewed in Gibbon & Allan (1984). For more recent work, see Holder & Roberts (1985), Meck (1988), Meck & Church (1984, 1987), Meck et al (1984, 1987), and Olton (1987).

This work demonstrates a rich representation of time in that the animals respond to the *ratio* between a currently elapsed interval and the remembered latency at which reward occurs [in the peak procedure (Gibbon et al 1984)]. Or, still more complexly, in the time-left procedure, they respond to the *ratio* of the *difference* between a currently elapsed interval and a remembered comparison interval (the numerator) and yet another comparison interval (the denominator). In timing the duration of a stimulus that is interrupted by gaps, the animals do not normally time the gap; they respond to the first segment of the stimulus plus the second segment. However, they may be taught to respond to the first segment, plus the gap, plus the second segment (Roberts & Church 1978). These results may indicate either variable use of the switch that gates pulses to an accumulator (Church 1984), or they may indicate the addition of temporal intervals computed by subtracting times of onset and times of offset (Gallistel 1989). Rats can also process two elapsing intervals simultaneously, making a ratio comparison of each elapsing interval to a different remembered standard (Meck & Church 1984). In short, there exist in the brains of birds and rodents (at least) time-measuring processes that enable them to store variables that represent temporal intervals. These variables enter into combinatorial response-determining processes isomorphic to arithmetic addition, subtraction, and division.

THE REPRESENTATION OF NUMBER

Many vertebrates can be taught a discrimination based on the number of items or stimuli in a set, whether the set is presented simultaneously [Davis 1984 (raccoon); Davis & Bradford 1986 (rat); Matsuzawa 1985; Rumbaugh et al 1987 (chimpanzee); Pepperberg 1987 (parrot)] or sequentially (Capaldi &

Miller 1988; Davis & Albert 1986; Davis & Memmott 1983; Fernandes & Church 1982—all with rats). For a review of earlier number-discrimination work see Davis & Memmott (1982).

While most work has used small numerosities, rats and pigeons discriminate the numbers of responses they have made in the range 16–50 (Mechner 1958; Mechner & Guevrekian 1962; Platt & Johnson 1971; Rilling 1967; Rilling & McDiarmid 1965). The upper limit on the numerosities common lab animals can discriminate has yet to be established. The accuracy with which animals discriminate numerosity (the extent to which they generalize to neighboring numerosities) is a function of the magnitude of the numerosity. As with other scalar dimensions of experience, the generalization function gets wider as the number gets bigger (Mechner 1958; Platt & Johnson 1971). Even when the numbers are large, however, the discriminative capacity is reasonably good: The pigeon discriminates 45 pecks from 50 pecks with about 70% accuracy and 40 from 50 with close to 90% accuracy (Rilling & McDiarmid 1965).

When, as is commonly the case, the duration of a sequence covaries with its numerosity during discriminative training, rats learn both the numerical cue and the temporal cue and use either dimension alone to discriminate when the other is held constant (Meck & Church 1983). Pigeons are more disposed to use the numerosity of the responses they have made in tasks that require a discrimination based on temporal interval than they are to use the temporal interval as a discriminative cue in tasks requiring a discrimination based on number (Rilling 1967), when the numbers of responses being counted are in the 30–50 range and the intervals being timed are in the 30–45 sec range. Thus, the pigeon's capacity to represent large numerosities and use these representations as a basis for discriminative responding would appear to be on a par with, or superior to, its capacity to utilize its representations of temporal intervals measured in tens of seconds.

The results of number-discrimination experiments imply that there is a systematic mapping from the numerosities of simultaneously and sequentially presented sets to states of the nervous system. It seems likely that this mapping process is a counting process of some kind. Gelman & Gallistel (1978) give a formal analysis of counting. Meck & Church (1983) show that a modification of the switch control mechanism in their timing model yields a counting mechanism [whose formal properties conform to the analysis of Gelman & Gallistel; see Gallistel (1989)]. In several ingenious experiments, they have obtained extensive experimental evidence that the counting and timing mechanisms are closely related (Church & Meck 1984; Meck et al 1985). Capaldi & Miller (1988) have applied the Gelman & Gallistel analysis of counting in systematic tests of the hypothesis that rats count rewarded and unrewarded trials in runway experiments.

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However, it continues to be argued that the mapping process in the discrimination of small numbers by animals must be a nonserial perceptual process called subitizing (Davis & Pérusse 1988; Rumbaugh et al 1987). In this view, twoness is discriminated from threeness by perceptual processes analogous to those by which we discriminate cowness from treeness. The persistence of this view is puzzling given the experimental evidence that "there is no such thing as 'the immediate cognition of number' " in adult human subjects (Mandler & Shebo 1982, p. 2; Kaufman et al 1949, p. 525): In humans, the reaction-time function for the estimation of the numerosity of visual arrays has a significant positive slope over its entire range, including from one to two (Mandler & Shebo 1982).

Given the existence of a mapping from numerosities to neural representatives of numerosities, the question whether animals have a concept of number would appear to turn on the answers to the following two questions: (*a*) Do they represent numerosity as a distinct property of a set, separable from the properties of the items that compose the set? (*b*) Do they perform with the representatives of numerosity combinatorial operations isomorphic to the arithmetic operations that define the number system ($=, <, +, -, \times, \div$)? The answer to both questions appears to be "yes."

If the numerosity of a set is represented as a property that is separable from the properties of the items that compose the set, then an animal taught a numerical discrimination with one set should respond appropriately and without further training when the same numerosities are instantiated with sets composed of items with properties different from the properties of the items in the training sets. The immediate generalization of numerical discriminations from the training sets to other sets composed of different types of items, or stimuli in other modalities, has been demonstrated in the chimpanzee (Matsuzawa 1985) and the rat (Capaldi & Miller 1988; Church & Meck 1984).

The chimpanzee presented with a choice between two trays, each having two wells, with various numbers of chocolate bits in each well, reliably chooses the tray with the greater total (Rumbaugh et al 1987). This may mean that the chimpanzee is adding separate estimates of number (one for each well of a tray). On the other hand, it may mean only that the chimpanzee continues its count as it shifts its attention from one well to the next. In any event, the chimpanzee's systematic preference for the greater number implies a relational decision process isomorphic to the "$>$" operator in arithmetic. The best evidence for a combinatorial process isomorphic to subtraction comes from experiments in which the rat must press a lever a certain number of times prior to trying the food-delivery system, with a penalty for premature attempts. The value of n, the number of responses made, at which the rat is maximally likely to break off pressing and try the feeder, is greater than N, the required number of presses, by a fixed amount (a fixed difference), and the magnitude of this

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difference is a function of the penalty: the greater the penalty, the bigger the difference (Mechner 1958; Platt & Johnson 1971). This result would seem to imply a decision process based on the size of the *difference* between the animal's current count and a learned comparison value. On the other hand, when a rat is trained to discriminate 2 from 8 and then presented with intermediate numerosities, it makes a *ratio* comparison of the intermediate numerosities to the learned discriminant values: The intermediate numerosity at which the rat is equally likely to choose either of the alternatives is the logarithmic (equiratio) midpoint not the arithmetic (equidifference) midpoint (Meck & Church 1983).

Given the evidence that animal brains perform operations isomorphic to addition, subtraction, and division with the representatives of temporal intervals and the evidence that they have a closely related system for representing numerosity, it may reasonably be conjectured that their well-documented ability to match the allocation of their foraging behavior to the relative rates of prey occurrence (see Introduction) depends upon a representation of rate obtained by dividing representatives of numerosities by representatives of temporal intervals. It is not clear how else they obtain their representation of rate, since models based on temporally decaying "running averages" do not work at all well (Lea & Dow 1984; Gallistel 1989). If rate estimates are obtained in the suggested manner, then the animal representation of number is a rich one.

CONCLUSIONS

The empiricist view of mind has been the dominant view in behavioral and neural science since their inceptions as experimental disciplines. Very roughly, this is Locke's view that "there is nothing in the mind that was not first in the senses." From this perspective, the primitives in the brain's representation of the world are simple sensory signals, which are functions of first-, second-, or third-order properties of proximal stimuli (wavelength, intensity, position on the sensory surface, the spatio-temporal intensity distribution, and so on). Representations of such abstract properties of the world as space, time, and number are arrived at, if at all, by some poorly understood process of inference from regular patterns observed in the simple sense data. And, it has often been argued, such abstract representations play no role in the behavior of the many animals that we imagine to be in some sense substantially simpler creatures than ourselves.

An alternative view is again very roughly captured by Leibnitz's rejoinder that "there is nothing in the mind that was not first in the senses, except the mind itself." By "mind itself," a modern behavioral or neuroscientist might understand brain circuits that are tuned to the location of objects in egocentric

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space (Knudsen 1982; Sparks & Nelson 1987; Suga 1982), or to the animal's position and orientation in geocentric space (Muller et al 1987; Ranck 1984), and endogenous rhythmic processes that indicate the time (Connor 1985; Farner 1985; Jacklet 1985). The experimental data just reviewed are consistent with the view that natural selection has shaped brains in such a way that there exists the kind of brain-world parallelism of formal structure that Leibnitz seems to have envisaged. The formal (mathematical) descriptions of many brain processes appear to mirror the formal descriptions of the external realities to which those processes adapt the animal's behavior. Because space, time, and number are such fundamental aspects of an animal's environment, their formal characteristics are mirrored in the formal characteristics of basic brain processes. The formal similarity between these aspects of the environment and the brain processes that adapt the animal's behavior to them is what justifies a computational-representational approach to the behavioral and neurobiological analysis of higher brain function.

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