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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

6 Can Honey Bees Create Cognitive Maps?

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Honey bees (*Apis mellifera*) have attracted the attention of scientists, philosophers, and the world at large for several reasons (Crane 1983; Gould and Gould 1988). For centuries, they were the only source of a sweetener available year-round in much of the world. Beeswax, too, contributed to the economic importance of honey bees; candles of beeswax burn cleaner than tallow candles and do not sag in warm climates. (Indeed, in some parts of Europe taxes were levied as quantities of beeswax.) The economic importance of honey and beeswax led to practical attempts to understand the behavior and social organization of honey bees, with the very tangible goal of improving the ease and efficiency of harvesting these valuable resources.

Another source of interest was the peaceful and apparently efficient social organization of honey bees, as well as their seemingly selfless work ethic. Countless sermons and philosophical essays took inspiration from this paragon of insect socialism.

Finally, and most important, the techniques developed to study honey bees made the details of their behavior and sensory abilities relatively easy to discover. Thus it was that color vision, ultraviolet vision, polarized-light sensitivity, an internal time sense, sun compensation, polarized-light navigation, the use of backup systems in behavior, and a host of other abilities were uncovered first in honey bees (von Frisch 1967; Gould and Gould 1988). Perhaps the most remarkable of the (then) novel abilities of bees was their dance-language system of communication.

Cognition?

Prior to about 1980, honey bees provided perhaps the best example of intricate innate programming to be seen in nature (Gould and Gould 1982). Their dance language—second only to human language in its ability to communicate information—was one example; their remarkable navigational abilities provided another; and the elaborate innate organization of their flower-learning programming was the most complex instance of species-specific learning known (Gould and Gould 1988). In addition, bee learning displayed many apparent similarities to the learning behavior of vertebrates (Bitterman 1996), inviting comparisons with the seemingly mindless conditioning so extensively studied by Behaviorists (Schwartz 1984).

Yet there were hints that innate wiring might not entirely account for honey bee behavior (Lindauer 1961; von Frisch 1967; Griffin 1976, 1984). The decision-making process in swarming, eerie anomalies during training to a food station, and a too-quick ability to grasp learning tasks combined to sow seeds of doubt. However, asking intelligently whether honey bees might have abilities beyond the basics of instinct and conditioning requires criteria for cognition.

Technically, cognition is knowing or knowledge; by this rather generous standard, innate information provides animals with one level of cognition. To most minds, however, cognition implies an ability to step outside the bounds of the innate, including the innate wiring that permits animals to learn through classical and operant conditioning. It means, instead, a capacity to perform mental operations or transformations and thus to plan or make decisions.

This definition may still be too broad, since some mental operations (such as the ability to infer the sun's position from the polarization of a patch of blue sky, or to compensate for the sun's movement) are hardwired in honey bees (Gould and Gould 1988). There is a real danger of a double standard in such criteria. For instance, one common component of certain sorts of human intelligence tests is the ability to recognize a

rotated object. It now transpires that both honey bees and bumble bees can do the same (Gould and Gould 1988; Plowright et al. 2001); so can pigeons (Holland and Delius 1983). Because pigeons are faster and more reliable at this task than humans, the usual interpretation is that the ability must be hardwired in them, and thus it is not a cognitive ability (for pigeons). (The experimental conditions necessary to test bees making visual choices do not allow researchers to measure short response times; thus we do not know whether, like pigeons, bees can judge any rotation with equal speed. Humans, in contrast, take longer to analyze larger rotations, leading to the suggestion that rotation matching is a cognitive rather than a native ability in humans.)

Route Planning

Perhaps the least controversial criteria for cognition are (1) planning of a novel response—often a route to a goal—and (2) concept formation. Both abilities, if they exist in bees, qualify as "cognitive maps" (Tolman 1948). As Tolman, who coined the term, envisioned a cognitive map, it was any mental transformation that enabled an animal to formulate a plan or make a cognitive decision. Later workers have sometimes supposed that some sort of literal map needs to be involved, but the original definition is the one used here.

The route-planning issue is slightly problematic with bees in that they are hard to see when flying. One can judge departure bearings and arrival locations and times, and generally infer that if the departure directions and arrival locations are consistent, and the transit time short, then the animals probably flew directly from the release location to the arrival spot. Another potential problem with this experimental strategy is the poor visual resolution of honey bees: about 1–2° real-time vision (roughly equivalent to 20/2000 human vision, a value that exceeds the threshold for legal blindness), and 3–4° for the

landmark memory that presumably is used in solving displacement tasks (Gould 1987). Thus testing must take into account the possibility that the bees may not be able to infer their location unless large and unambiguous landmarks are clearly visible at the release site.

The first test aimed at discovering whether honey bees could plan novel routes involved training foragers to go a feeding station in a forest clearing 150 m from the hive, and then after several days of regular visitation to this station, capturing these foragers on their departure from the hive (Gould 1986). The foragers were then carried in the dark to a site at the edge of an open field 150 m and 60° from both the hive and the training station; the training station, hive, and release point thus formed an equilateral triangle. The release site was near a large tree that stood alone in the field, away from the forest that lined the field. The kidnapped bees were released one at a time and their release bearings recorded. The mean vector of the release bearings was significantly oriented toward the unseen feeding station.

Initial attempts to repeat this experiment met with mixed results. Tests at undescribed sites failed, except for some bees under overcast conditions (Wehner and Menzel 1990). [Under overcast skies, bees depend heavily on landmarks (Dyer and Gould 1981).] It is possible that these disappointing results were a consequence of failing to provide the bees with large and unambiguous landmarks (Gould 1990, 1991). A second set of tests also provided mixed results. At a site along forest edges, where unambiguous landmarks (as seen by honey bees) would be absent, the foragers were disoriented; at a site at the corner of a woodlot, where their position would be unambiguous to bees familiar with the area, the foragers were well oriented (Dyer 1991). The researcher explained the difference in results in terms of the presumed ability of the bees to see the foraging station from the corner release site; given the visual resolution of bees, this explana-

tion seems unlikely (Gould 1991; Gould and Gould 1995).

The most recent pair of tests have provided clear proof for the ability of honey bees to use novel routes (Menzel et al. 1998, 2000). In both sets of experiments, the researchers performed their tests quite near a prominent landmark (a steep, isolated hill). They used a slightly different technique in which the foragers were kidnapped at the training station and moved to the release site. In the first test, the bees were well oriented upon release from a novel location midway between two familiar training stations. The second test sought to see if this result might be an artifact of the intermediate position of the release site. In this experiment, release sites were chosen from around the compass, up to 180° from the hive. The release bearings were nevertheless well oriented toward the hive. As in the original tests (Gould 1986), bees released from much greater distances were not well oriented.

There are two lessons from these tests. The first is the importance of techniques (in this case, the use of proper landmarks) and an understanding of the sensory limitations of the animal being tested. The second is that bees, like many animals, have redundancy in their navigational systems and thus may use one strategy when it works best and another when the primary strategy cannot be used. Thus the researchers performing the last test described here believe (quite reasonably) that route memorization takes precedence over use of a maplike representation of familiar landmarks in guiding flights. In short, animals have backup systems and an ability to choose the one likely to yield the best results under a given set of circumstances.

What we do not know is how the map of nearby landmarks is first created, stored, and used. The inability to track the complete movements of individual honey bees over the many days during which mapping and testing must occur limits our potential knowledge. So too does the poor visual resolution of bees, which makes

experimentation (for instance, adding, moving, or removing large landmarks) difficult. [This sort of manipulation can be done on a local scale near food sources or the hive (Gould 1987), but it is not at all obvious whether the behavior observed in these contexts is relevant to route planning.]

Concept Formation

Concepts are abstractions that make it possible for animals to solve novel choice problems without prior experience of the specific exemplars offered. For instance, pigeons can learn such concepts as tree, fish, or human (Herrnstein 1984). Alex the parrot can identify the color, material, number, and other characteristics of an object or object set without having seen the object(s) before (Pepperberg 1990). The animals in these tests depend instead on an abstract property or (in the case of pigeons, a set of properties of probabilistic value) that is independent of the exemplar.

Preliminary tests showed that honey bees could learn to recognize and distinguish human letters independent of size, color, position, or font (Gould and Gould 1988). Recent work has focused on more specific concept-related questions. In one set of tests, foragers were taught that symmetrical targets offered food while asymmetrical ones did not (Giurfa et al. 1996); in another set they were taught the opposite lesson. By the seventh visit, the bees could chose the correct novel stimulus over the incorrect one.

The learning curve is different from that of more standard tests in which bees are taught that a particular odor, color, or shape is always rewarded. During concept learning there is no evident improvement over chance performance until about the fifth or sixth test, whereas in normal learning there is incremental improvement beginning with the first test. This delay is characteristic of what has been called "learning how to

learn," which is interpreted as a kind of "ah-ha" point at which the animal figures out the task (Schwartz 1984).

The main difference is that honey bees are much quicker at deciphering what the experimenter wants than are pigeons and other standard laboratory animals. Another difference is that the researchers testing honey bees chose to interpret their results as indicating an innate sense of symmetry in bees, and thus imply a noncognitive basis for their results (Giurfa et al. 1996). Of course, on the one hand there is good evidence that human infants prefer symmetrical visual stimuli (Grammer and Thornhill 1994) (which would argue that symmetry is not entirely a learned concept for humans either), while on the other we are still left to wonder what sort of mental leap allowed these bees to understand that this particular concept was the one that the experimenters wanted them to key in on.

Another kind of concept formation and use has been demonstrated in honey bees. In this case, the concepts are "same" and "different." The technique, which is well known from conventional laboratory tests, is delayed match-to-sample (Schwartz 1984). The animal is shown a pattern or color and then is later offered a choice between the same pattern or color and a different pattern or color. If the animal learns the concept, it can be shown a novel initial stimulus and then choose the correct same or different stimulus (depending on which concept is being taught) when presented with the choice. After 30–40 training trials, honey bees began to respond to the "same" or "different" stimulus at levels above chance (Giurfa et al. 2001).

Clearly the time has come to try honey bees with more conventional concept-learning tasks. Such experiments must keep in mind their low visual resolution and their many innate biases in approach; for instance, a preference for "busy" targets—figures with high spatial frequency (Gould and Gould 1988). Perhaps the simplest and most objective tests would focus on number: three petals during training, say, of varying color, shape, and position, followed by a choice between a target with a novel combination of three petals versus two- and four-petaled targets. Extension of the training for letter recognition also seems like a powerful way to probe the potential for abstract concept formation in honey bees.

Conclusion

The evidence that honey bees can perform tasks that are considered to require cognitive powers when they are performed by higher vertebrates suggests at least three possibilities. One is that cognition is a capacity that has evolved as needed among animals, independent of size, number of legs, or whether the creature has an external or internal skeleton. As such, cognitive differences among phyla would be quantitative rather than qualitative (Gould and Gould 1994).

Another (not mutually exclusive) possibility suggested by these observations is that behaviors that require cognition in humans may be innate in "lower" species. Thus it could be that map formation and use by bees is hardwired, using the kind of fill-in-the-blanks strategy so evident in their learning (Gould and Towne 1987). In rodents and primates, on the other hand, the ability is genuinely cognitive; that is, it is not a consequence of innate skills.

A third alternative is that the human capacities we commonly label as cognitive have, at least in part, an unappreciated innate basis (Gould and Gould 1994). The animal kingdom is filled with examples of innately directed learning, including no less an achievement than human language (Gould and Marler 1984). This possibility, for which there is considerable suggestive evidence in the form of species-specific "cognitive" abilities (Shettleworth 1998), brings us back to the basic definition of cognition; by the strictest standards, perhaps there is no genuine cognition in any species, our own included. To the extent that cognition is a product of evolution, we should not be surprised if natural selection has provided

a rich set of adaptive biases that help shape cognitive performance.

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