Honeybees use a 'Speedometer' to Navigate Successfully

Moushumi Sen Sarma

We move around, find our bearings in an unfamiliar place, quickly learn the way home, or school, without even being aware of the processes which enable us to do so. The skills required to navigate in a complex world like ours is not easy: We must be able to have a measure of distance and direction, recognize landmarks and use a host of other cues to successfully find our way around. Every animal that moves around, needs to be able to navigate successfully and thus needs similar skills. To appreciate how important it is to navigate successfully, consider an animal that leaves behind the helpless young in a nest and must come back with food: the cost of making mistakes could be extremely high.

There are a few species of wasps, which make a tiny inconspicuous nest to lay eggs and then make a few trips to provide the nest with enough food for the larvae. The individual learns to precisely distinguish its nest from surrounding stones, mounds of soil and other confusing details. This ability is called homing, which was studied for the first time in digger wasps by the pioneering Dutch ethologist, Nikolaas Tinbergen (1907-1988). Tinbergen, along with Konrad Lorenz (1903-1989) and Karl von Frisch (1886-1982) shared the Nobel Prize in 1973, for revolutionizing the field of animal behavior with their path-breaking studies on wasps, honeybees, fishes and birds.

The social insects like ants and honeybees build nests, housing hundreds of individuals and brood, which thrive and reproduce over a period of several months. Everyday, individuals go out in search of food and come back to share it with nest mates and recruit helpers to the site of food. Each of these individuals make hundreds of trips in their lifetime to and fro between the nest, which is fixed in space and the food, which can be found distributed over a radius of up to several kilometres.

Most ants and some bees lay scent trails to mark routes to enable themselves to return home or even lead others to the food. In contrast, honeybees and some species of ants don't lay scent trails to recognize routes. They use cues provided by the environment to tell them where they are going and how to get back home. To be able to navigate successfully, such an animal should have the ability to measure the direction of the food source with reference to the nest, and the distance.

It is now well-known that many animals including honeybees have internal compasses. In the case of honeybees the compass used most often is one, which is calibrated with reference to the sun, first described by Karl von Frisch. Bees that fly out for the first few times from the hive learn the position of the sun in the sky. Using this information, honeybees can extrapolate the trajectory that the sun takes in the course of the day. They use this information to calculate direction with reference to the sun at any time of the day.

After following a complicated route with many twists and turns to the food, ants and bees are able to figure out the shortest route back to the nest. Work carried out on desert ants by Wehner and co-workers, have shown that this is done by a process of computation employed by the ant, called path integration. Essentially the animal computes the resultant vector of all the vectors, which comprise the route it is taking to the food, and this vector points to the direction of the nest, hence called the 'home-vector'. This home-vector is computed and updated constantly so that if at any point in its journey to the food, the ant is interrupted and offered a tasty tit-bit, it immediately returns to its nest following the home-vector. Experiments carried out on honeybees indicate that they too navigate by path integration.

When honeybees discover a new patch of flowers, they recruit helpers who harvest the nectar as fast as possible before competitors arrive. These helpers (referred to as recruits) are informed by the bee, which discovered the floral patch (referred to as the scout), about how far is the patch and in which direction from the nest. Karl von Frisch discovered that bees communicate this by the dance language [1]. He did this by training bees to come to a feeder offering sugar solution and watching the bees' behavior once they returned with the food to the hive. By changing the distance of the feeder from the hive, he found that the dance language comprises two kinds of dances: the round dance and the waggle dance (see *Figure* 1). The waggle dance comprises two key compo-

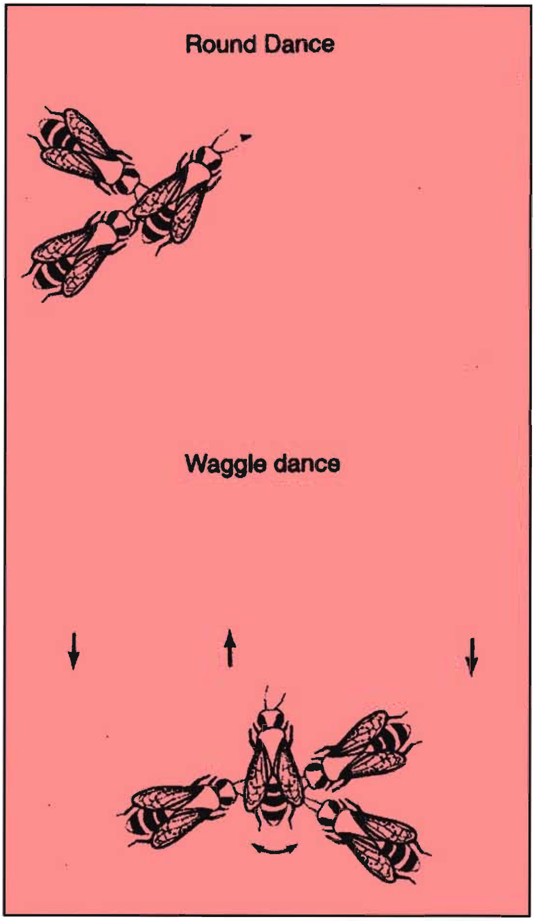


Figure 1. The dance language of the honeybee: In the round dance the honeybee runs in clockwise and anti-clockwise circles on the comb surface, this indicates availability of food within 80m. In the waggle dance the honeybee runs in a figure of '8', the central portion of the 8 is the waggle run of the dance where the animal waggles its abdomen, the frequency is an indication of the distance.

nents: a waggle run, which indicates the direction to the food, and the waggle duration or number of waggles per minute which indicates the distance. For distances less than 50m the waggle dance looks like what is best described as a round dance.

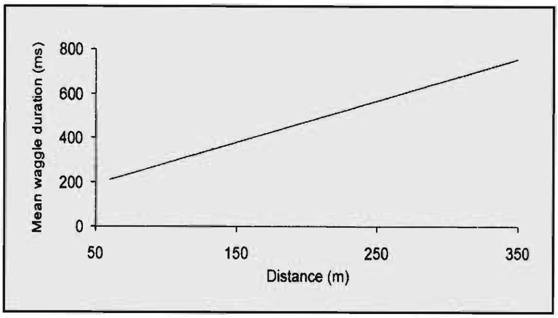
This ability of bees to measure and communicate distances lead scientists to wonder how do the honeybees measure distance? Karl von Frisch proposed that honeybees measure distance between two points as a function of the energy that they have spent in flying between these two points, hence called the energy hypothesis. However this theory did not hold ground after a number of experiments showed that bees could estimate distance correctly even when they were actually spending extra energy. For example, experiments by Esch and co-workers showed that bees that had to fly up to a balloon floating at different heights above the ground to get to a feeder did not take the height into account at all, when estimating distance. In fact with greater heights the bees actually underestimated the horizontal distance!

Honeybees can be induced to fly through a small tunnel to collect a reward in the form of sugar syrup from a feeder inside. Once they come regularly to the feeder, one can remove the feeder and demonstrate that the bees had learnt where the feeder was, because they search for the feeder at the correct position where the feeder was originally kept. It can also be demonstrated that this learning is not dependent on scents that might be left behind by the bees or the length of the tunnel or other cues. In fact the pattern on the walls of the tunnel was discovered to have an important bearing on this learning. The learning of position was most accurate when the pattern was in the form of vertical stripes or random patterns. But this estimation of position broke down when the pattern consisted of stripes that ran parallel to the long axis of the tunnel. Esch and Burns [2] hypothesized that bees were estimating distance by measuring the extent to which objects in their field of vision moved across the retina, this was called the optic flow hypothesis. Experiments carried out to test this hypothesis showed that bees measure the angular speed of the objects that flash past their eye and integrate this image motion to get an estimate of distance [3]. Srinivasan and co-workers have proposed that an odometer helps the bees measure angular speed (an odometer is an instrument for measuring distance travelled, also used by an automobile (*Amer.* var. of hodometer – Greek hodó(s) way + meter). It was further confirmed that this speed is measured independently of the structure of the image, thus making the stripes denser or sparser did not affect the bees' estimation of distance. However, this estimation depends on the distance separating the animal from the image. Thus making the bee fly through narrower or broader tunnels make them overestimate or underestimate the distance they have flown, respectively.

Through a set of simple but stringent experiments, Srinivasan and others [4] have not only confirmed that the optic flow hypothesis is the correct explanation for what the bees do, but have also shown how the odometer is calibrated to translate image motion into the language of the waggle dance. By making individually marked bees fly through tunnels of known width and a known distance, and analyzing the waggle dances of these bees on the hive, the authors have shown that flight through a narrow tunnel carrying a random pattern on the walls makes the bees overestimate the distance they have flown. By how much do they overestimate this distance? It turns out that flying 6 m in this tunnel was perceived as equivalent to a flight of 186 m outdoors. Apparently the distance flown is not perceived directly as distance units but in terms of the amount of image motion experienced by the eye. The authors have calculated that moving forward by a distance of 1 cm in the centre of the 11 cms wide tunnel (bees are known to centre themselves when flying through narrow tunnels), would cause the image of the wall to move backward by an angle of 10.3°. Therefore, a flight of 6 m in the tunnel would result in a total image motion of 6180°. Now using the graph represented in *Figure* 2 one can calculate that 186 m of outdoor flight results in a waggle duration of 350 ms (see *Box* 1). Therefore, an image motion of 17.7° on the eye results in a waggle duration of 1 ms.

Even though the image motion generated on the eye would depend strongly on the average distance of surrounding foliage and the ground, and is therefore environment-de-

Figure 2. There is a linear relationship between the distance flown by a bee and the waggle duration of its dance. By training bees to feeders at various distances outdoors, and watching their dances, Srinivasan and others were able to generate a distance calibration curve as shown above. Using this curve, they read off the corresponding distances for the waggle durations elicited by flight through the experimental tunnel (graph adapted from Srinivasan and others, 2000).



The Translation of Linear Motion to Angular Motion, which is Encoded in the Waggle Run.

1. 1cm of forward motion causes the image of the wall to move by $\tan^{-1}(1/5.5)$ which is equal to 10.3°.

2. 6 m of forward motion equals (600*10.3°) of angular motion = 6180°.

3) Experimental result: 6 m of flight inside tunnel is equivalent to 186 m of flight in outdoor environment.

4) From the slope of the regression line (waggle duration = 95.91 + 1.88*distance) in *Figure* 2, it can be calculated that 186 m of outdoor flight is encoded by 350 ms of waggle duration (1.88*186 ~ 350 ms).

5) Therefore, the image motion which is encoded by 1 ms of waggle dance is (6180/350) = 17.7°. Or in other words, 17.7° of image motion elicit 1 ms of waggle duration.

6) It can also be shown mathematically that the total angular motion that a bee experiences in a flight is independent of the flight speed.

pendent, this system would be expected to work quite well, since the new recruit bees tend to take the same route as the experienced scout bee. What do the ants do when they cover similarly several kilometres on foot to look for food? Preliminary evidence indicates that they don't use an odometer but instead might count steps!

Suggested Reading

[1] Karl von Frisch, *The dance language and orientation of bees*, Harvard Univ. Press, Cambridge, MA, USA, 1993.
[2] H E Esch and J E Burns. Distance estimation by foraging honeybees, *The Journal of Experimental Biology*, Vol.199, pp. 155-162, 1996.
[3] M V Srinivasan, S W Zhang, M Lehrer, and T S Collett, Honeybee Navigation en route to the goal: Visual flight control and odometry, *The Journal of Experimental Biology*, Vol. 199, pp. 237-244, 1996.
[4] M V Srinivasan, S W Zhang, M Altwein, and J Tautz, Honeybee Navigation: Nature and Calibration of the Odometer, *Science*, Vol. 287, pp. 851-853, 1996.

Moushumi Sen Sarma, Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India. Email: moushumi@ces.iisc.ernet.in

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Learning from a Sea Snail: Eric Kandel

Rohini Balakrishnan

In the year 2000, Eric Kandel shared the Nobel Prize in Physiology and Medicine[1] with two other neurobiologists: Arvid Carlsson and Paul Greengard. Whereas Carlsson and Greengard were awarded for their work on dopamine, an important neurotransmitter in the brain, changes in the level of which result in Parkinson's disease, Eric Kandel was honoured for his extensive and invaluable contribution to our understanding of the cellular and molecular mechanisms of learning and memory.

If learning may be defined as the acquisition of information during the lifetime of an individual, which may be used to direct and modify future behaviour, then memory is the form in which this information is stored. Together, they represent one of the most valuable and powerful adaptations ever to have evolved in nervous systems, for they allow the future to access the past, conferring flexibility to behaviour and improving the chances of survival in unpredictable, rapidly changing environments.

The scientific study of learning began only at the end of the nineteenth century. Before that, learning and behaviour in general, were attributed to vital forces rather than to materialistic processes. The latter half of the nineteenth century saw an increasing interest in animal psychology, due in large part to Darwin's views: "The difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind" (Charles Darwin, 1871).

Resonance readers can look forward to another article on the same subject in a forthcoming issue.