Path integration in insects
Thomas S Collett* and Matthew Collett†

The most notable advance in our knowledge of path integration in insects is a new understanding of how the honeybee measures the distance that it travels during its foraging trips. Data from two groups show that the bee’s odometer records distance in terms of the net amount of image motion over the retina that is accumulated during a flight. Progress has also been made in clarifying the relation between path integration and other navigational strategies. On unfamiliar ground, path integration is the only available means of navigation. In familiar surroundings, however, guidance by landmarks may override guidance by path integration. Path integration then becomes a back-up strategy that is used primarily when landmarks fail.

Addresses
*Sussex Centre for Neuroscience, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK; e-mail: T.S.Collett@sussex.ac.uk
†Department of Zoology, Michigan State University, East Lansing, MI 48824, USA; e-mail: collettmm@msu.edu

Current Opinion in Neurobiology 2000, 10:757–762

Abbreviation
PI path integration

Introduction
A remarkably wide range of animals, from insects to man, has discovered how to navigate using path integration (PI). On leaving some significant starting point, such as a nest, an animal updates an accumulator that keeps a running tally of its current direction and distance from the origin so that it can always take a direct path back to its starting point. The study of PI in insects began in the early 1900s: Piéron [1] displaced a foraging ant that was returning home. The ant continued in the same compass direction and then, at the appropriate point, stopped and searched for its nest as though the displacement had not occurred. A little later, Santschi [2] proved that the sun provides ants with a compass for directional control. The next milestone was von Frisch’s discovery that the waggle dance of honeybees encodes the distance and direction between feeding sites and the hive [3]. Bees are recruited by this dance and extract from it the necessary information to navigate to the site guided by PI. One of the problems von Frisch raised, but did not fully solve, was how bees might measure the distance they fly. The first half of our review surveys new work on this question. In the second part, we discuss navigation using PI and its relationship to other navigational strategies.

Odometry
The retinal image movement experienced by insects flying through their surroundings provides ‘optic flow’ that...
serves to controls many aspects of flight. Three recent studies show that flying honeybees measure and control the distance that they travel by integrating such optic flow during the flight. Experimental proof is possible because the system monitoring optic flow is ignorant of the distance of features in the world that generate it: flying a short distance close to a surface produces the same integrated optic flow as flying a longer distance further from the surface. Esch and Burns [4] trained bees to collect sucrose from a balloon, the height of which could be varied. The higher the feeder, the less the optic flow and the shorter the distance signalled by the waggle dance, although the longer the actual distance flown. Srinivasan et al. [5,6] trained bees to collect sucrose from a feeder within a 22 cm-wide channel. When the channel was narrowed, giving more image motion per unit distance, bees searched for the feeder closer to the entrance. They searched further along the channel when it was wider. In the third experiment, Srinivasan et al. [7•] compared the distance signalled by waggle runs from bees flying over open ground with those after flight through an 11 cm-wide channel. Perceived distance in this narrow channel is greatly exaggerated: each meter of flight along it increased the distance signalled by an amount that was equivalent to 30 m flight over open ground.

Bees fly faster in wider channels or at higher altitudes [5,8•]. Thus, like flies [9], they adjust their flight speed to keep the speed of optic flow constant. A constant image speed means that in the experiments described above [5,6,7•], flight time and the amount of optic flow are both proportional to perceived distance. The relative importance of time and of optic flow in estimating distance can, however, be disentangled because speed compensation is imperfect in windy weather. Ground speed is slower in head-winds than in tail-winds, and optic flow turns out to be a better predictor of distance flown in the channel than is flight time [6]. It is possible that the PI system has become optimised to a particular image speed, with the accumulator performing most accurately with that input, but producing errors in strong winds.

Keeping their optic flow speed fixed makes bees automatically decelerate as they lose height [5]. It has recently been shown that a bee’s rate of descent when landing on a horizontal surface is linked to its forward speed, so enabling it to achieve a smooth landing without explicit knowledge of height or of velocity [8•]. Because flying a short distance close to the ground or close to objects in the lateral visual field is perceived as equivalent to flying a longer distance high above the ground or further from a lateral surface.
[4,7•], a controlled height is needed for accurate PI. Height control is not yet well understood, but it probably relies on information from a textured ground. When the texture is fine, as over a lake, bees descend until they detect surface features [10]. More generally, bees fly at approximately 2–3 m above open ground, with small up and down movements (F Dyer, personal communication) that generate parallax cues with which height could be set.

Because bees can be subject to unpredictable winds during flight, ground speed and distance are most reliably controlled and measured through image motion. Insects that walk on the ground, and are not subject to passive transport by wind, need not rely on optic flow to monitor their progress. Optic flow has no detectable influence on the walking speed of various beetles [11] and only a small effect on the walking speed of fruit flies [12] and honeybees [13]. In desert ants, the control of distance is slightly altered by the optic flow that is generated by a moving belt beneath a transparent floor [14]. The ant’s odometer, however, can function independently of ventral or lateral optic flow [15•], implying that the ant assesses distance through some proprioceptive or internal monitor of motor performance.

Navigation using PI

PI is not only used on homeward journeys. Desert ants, like bees, can navigate by PI to a food site. To demonstrate this use of PI, the possibility of landmark guidance must be excluded. Such proof was obtained in ants [16•] by allowing them to learn feeder co-ordinates within a channel that excluded sight of the surrounding landscape. The ants’ paths were then recorded over open ground with the channel shortened and the feeder removed. When the channel was rotated to force ants along a detour, ants leaving the channel immediately re-directed their path towards the approximate site of the feeder (Figure 1). Desert ants have several search strategies to cope with the inaccuracies of PI. A newly discovered example is the use of scent to locate food. If a food source is first discovered by its smell, then subsequent trips are not directed to the food itself, but to a position slightly downwind of it. The final approach to the food can then be guided by the ‘odour plume’ [17•].

To navigate towards a goal using PI, an individual requires both an accumulator to provide instantaneous position, and a memory of the goal’s position. The two positions must then be compared in order to determine the direction of subsequent movement (for example, at the end of the channel in Figure 1). This process appears to be calibrated throughout the lifetime of a forager [16•]. If desert ants experience consistent errors in PI on reaching a goal, they adjust their computational process. Re-calibration is observed when ants are carried repeatedly over part of their journey, so that PI on the outward and return journeys does not agree (Figure 2). The form of the re-calibration suggests that the accumulator of the PI navigation system is not updated continuously over a whole
Von Frisch’s decipherment of the waggle dance raised the question of how potential recruits can obtain the PI coordinates of the food site that are encoded in the dance. The direction of the food source relative to the sun is given by the direction of the waggle run with respect to gravity. Followers must determine this direction among a jostling crowd in the dark (for a review, see [19]). Only followers positioned behind the dancer seem to do so successfully [20]. Followers gradually attain this position during a waggle run, but that it is reset to a zero value at both the nest and the turning point (e.g. a food site) [18*].

Second, does the use of landmarks increase the accuracy of navigation? The uncertainty of a bee’s measurement of distance within a channel increases with the distance that it travels (Figure 3) [6,32*]. Precision is greater if the bee passes a familiar landmark positioned partway along the channel [6], because the shorter vector from the landmark to the feeder determines where the bee searches (Figure 3; see also [33]). Accuracy is thus improved by breaking the journey into segments that are defined by landmarks [6].

Third, what happens when there is conflict between the information supplied by PI and landmarks? In a situation in which PI and landmarks signal different directions of travel, a desert ant takes the direction normally linked to the landmark [30]: walking flies approaching a jet of air produced by the wings of the dancer (J Storm, A Michelsen, K Rohrseitz, personal communication). Whereas potential recruits face the problem of accurately determining the direction of waggle runs, dancers seem to build scatter into their waggle runs so as to spread recruits evenly over patches of flowers [22]. The scatter in the directions of the waggle runs of bees trained to forage at a feeder decreases with increasing distance of the feeder from the hive [3,23*]. In contrast, dances signalling a potential nest site have less directional scatter, and the scatter is independent of distance [23*].

**PI and landmark navigation**

On familiar terrain, ants, bees and wasps tend to follow fixed paths guided by visual landmarks (for reviews, see [3,24,25]). A desert ant returning from a food site will follow precisely the same route whether it homes normally, or whether it is first allowed to reach the vicinity of the nest before being carried back and replaced near to the food [24], suggesting, perhaps, that routes can be run independently of PI. How do PI and landmark guidance interact in such situations? We consider three questions of current interest.

First, do insects associate some kind of local vector with landmarks so that, on passing a landmark, they take the correct course for the next segment of their route? In small-scale laboratory environments, honeybees associate a vector of a given direction [26] and distance [6,26] with the sight of a particular scene or landmark and reproduce that vector on encountering the landmark. The same process probably occurs in large-scale natural environments as well [27,28]. Although ants have been shown to link a particular direction of travel to the passing of a familiar landmark [29], there is as yet no evidence that such local vectors have a length that corresponds to the distance to the goal or to the next landmark. Instead, landmarks initiate an inertial effect, possibly related to a new behaviour described in *Drosophila* [30]: walking flies approaching a landmark will temporarily keep to the same direction should the landmark suddenly disappear, as happens when walking over irregular ground. The direction of local vectors can be determined by celestial compass cues [29]. The direction of responses cued by landmarks can also be egocentric. Honeybees flying through mazes can, for instance, be trained to turn left or right on seeing a particular colour irrespective of compass direction [31].
cues, the ant reverts to the path given by PI. Information from the landmark briefly overrides that from PI. A similar effect is seen in honeybees flying through a channel, past a landmark, to a feeder [6]. When the landmark is shifted towards the entrance of the channel, the distance that the bees fly before searching for the feeder is shortened by the same amount (Figure 3).

Drawing together the answers to our questions, we see that on familiar landmarked terrain, directional guidance from PI can be suppressed, and that landmark cues lead the insect with greater certainty to its goal. The PI accumulator is probably updated all the while, so that, in the absence of landmark cues, PI information is available as a backup [29].

Conclusions and future directions
This review has emphasised the progress that can be made by applying an old and technologically demanding method to new problems. Channels provide a controlled visual environment and their use has improved our understanding of the odometer and the way in which information from familiar landmarks and PI combine to guide an animal's path. New technologies should expand our horizons further. So far, the use of virtual reality to simulate the optic flow experienced by moving insects has been limited to flies [34]. Work on PI using such techniques holds promise, but is still uncommon [35]. To date, only the sensory inputs to PI have been studied neurophysiologically, most notably the sky compass [36,37*–39*]. The combination of tethered animals and virtual reality may make it possible to study the neural mechanisms of more-central components of PI navigation. Genetic techniques may help in working out which neural structures mediate different navigational strategies. Strauss [40*] gives an example of this approach in *Drosophila*. On a larger scale, radar tracking enables the path of individual bees to be followed during foraging [41*,42*] and may help to clarify how different navigational strategies are deployed in complex, natural environments.

The study of a wider array of animals may also allow new insights into the mechanisms of PI. Fiddler crabs [43,44*] are unusually informative in displaying a continuous readout of the state of their PI system. The crab leaves its burrow to forage on the open beach. If startled, it scuttles sideways straight home. Escape time is reduced by turning continuously so that one side always points at the burrow entrance, even if the entrance hole is masked (Figure 4). This behaviour makes it possible to examine the precision of path integration while the accumulator is being updated, rather than waiting for the results to be expressed in the performance of a homing vector. Artificial animals have also made a contribution. Robots enable the performance of different models to be compared under natural conditions. Thus, work with robot ‘desert ants’ has sharpened the discussion of how information from polarised light might be used to maintain an ant’s direction [45]. A robot honeybee mimicking the waggle dance has been able to inform foragers of the direction, although not the distance, of a food source [46].

Acknowledgements
We are very grateful to Fred Dyer, Tom Labhart, Axel Michelsen, Mandym Srinivasan, Harald Wolf and Jochen Zeil for information, and to Mandym Srinivasan and Jochen Zeil for illustrations. Few papers on PI have been published within the annual period of review and we have marked and annotated all the papers that we have seen.

References and recommended reading
Papers of particular interest, published within the annual period of review, have been highlighted as:
• of special interest
•• of outstanding interest


8. Esch and Burns [4] established that the duration of the waggle component of the bee dance depends on perceived optic flow. To calibrate the relation between waggle duration and flow more precisely, waggle dances were observed after bees had flown through a channel. Waggle duration after flying 1 m through an 11 cm-wide channel is equivalent to that performed after flying 30 m over open ground.


10. Bees achieve smooth landings by keeping image speed constant so that they decelerate as they lose height, and by linking their speed of descent to their forward velocity.


18. Walking speed and distance measurement are unaffected either by the ant’s distance from lateral optic stimuli, or by painting over the ventral area of retina. Ants do not need optic flow for measuring distance.


Training ants to follow a one-way circuit can cause their trajectories to be transformed. A fuller explanation of this recalibration is found in [18*].


25. Collett TS, Zeil J: Bees signal the direction of a potential nest site more accurately than they can follow the plume upwind. Desert ants use odour plumes to help locate a food source. They aim slightly downwind of the source so that they can follow the plume upwind.


37. Labhart T: How polarization-sensitive interneurones of crickets see the polarization pattern of the sky: a field study with an optoelectronic model neurone. J Exp Biol 1999, 202:757-770. Many insects obtain directional information from the polarisation pattern in the sky, even when the pattern is partially obscured by cloud cover or by pol- lutants. The ability of insects to detect weak polarisation patterns was analysed using an optoelectronic model of the insect polarisation system, which was tested under a natural autumn sky in different weather conditions.


