

DISTANCE ESTIMATION BY FORAGING HONEYBEES

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Summary

Honeybees are widely believed to assess feeder distances by the energy spent on foraging flights. However, a critical review of this ‘energy hypothesis’ reveals many inconsistencies in the experiments from which it was derived. In fact, new evidence shows that the energy hypothesis cannot be correct. Foragers loaded with weights do not overestimate distance, as indicated by their waggle dances performed upon return to the hive. Bees that climb to a feeder on top of a high building (50 m) signal the same distance as hive mates that visit an equidistant feeder at ground level. Foragers visiting a feeder suspended from a balloon at 70 m from their hive underestimate the distance flown dramatically when the balloon lifts the feeder from ground level to 90 m, even though the energy required to reach the feeder *increases* considerably. Foragers from a

hive situated on a high building (50 m) that fly to a feeder on the roof of another high building (34 m) signal a much shorter distance than the actual distance flown. We propose instead an ‘optical flow hypothesis’: bees use the speed of retinal image motion perceived from the ground to estimate the distance flown. Flight altitude is important for distance estimation by retinal image flow, because objects move faster and farther across the retina when the bee flies closer to the ground. When the forager’s flight behavior is considered, the optical flow hypothesis does not conflict with previous findings.

Key words: distance estimation, energy hypothesis, optical flow, foraging, dances, honeybee, *Apis mellifera*.

Introduction

Foraging honeybees find their way using an egocentric system of references (Wehner, 1992). They must measure the distances and directions of all of their moves in order to be continually informed about their home vector. Upon return to the hive, important components of a foraging trip can be ‘replayed’ time and again in dances. This dancing behavior provides the experimenter with the tools for investigating the mechanisms used during acquisition of flight information.

The dance performed in the hive by successful foragers recruits hive mates to a profitable food source. It contains information on both the direction and the distance of the food source. In extensive work conducted over several decades (reviewed by von Frisch, 1967a), Karl von Frisch and his students showed that the angle between the direction to the food source and the sun’s azimuth is represented by the direction of the waggle run with respect to gravity, and its distance is encoded in the tempo of the dance, i.e. in the number of waggle runs per unit time or, equivalently, the number of waggle movements performed on a waggle run. The duration of a dance cycle and the number of waggle movements increase with the feeder’s distance. Indeed, a human observer can determine the feeder’s location simply by observing the dances of bees returning from there (von Frisch, 1967a).

The role of the dance language in providing information about the feeder location to hive mates was subject to a long-lasting controversy (Wenner and Johnson, 1967; von Frisch, 1967b; Gould, 1975a,b, 1976; Wenner and Wells, 1990),

which has not been settled up to the present day. The role of the dance language in providing distance information to a human observer, in contrast, has never been challenged. Our present review focuses on the latter.

How do bees acquire the information transferred in the dance? The possible mechanisms underlying acquisition of directional information are rather well understood. The direction of the feeder can be determined by using a number of cues, such as sun position, the polarization pattern of skylight (von Frisch, 1967a), landmarks (Dyer, 1987, 1991) and possibly even magnetic fields (Schmitt and Esch, 1993). Depending upon the experimental conditions, bees may prefer one reference system over another.

The mechanism(s) by which foragers determine distance is less clear. von Frisch first observed that distance information – as reflected in the foragers’ dance tempo – does not always agree with the actual distance to the food source. He found that bees flying against wind on their way out signal in their dances a larger distance than bees collecting food on windless days. In addition, bees that had a tailwind on their way to the food source indicated shorter distances. ‘Errors’ are manifested at all wind speeds higher than 1 m s^{-1} . These results (reviewed by von Frisch, 1967a), obtained in experiments conducted during 1945–1947, led to the so-called ‘energy hypothesis’, which proposed that distance estimation is based on energy expenditure. This hypothesis has influenced further thinking for several decades.

On the basis of the energy hypothesis, it seemed reasonable to assume that overcoming a gradient would have a similar effect on the dance tempo as flying against wind. Several further studies, some of which are reviewed in the next section, were conducted to investigate this assumption.

Observations between 1952 and 1988

The energy hypothesis and Heran's mountain slope experiments

A series of experiments involving foraging routes uphill or downhill were conducted by Heran and Wanke (1952) and by Heran (1956) on Mount Treuchtling at Tragöss in Styria and on the Schöckl near Graz. These experiments were performed to test the hypothesis that it is the energy required to reach a feeder, not the energy spent on an entire foraging trip, that is used as a measure for feeder distance.

An observation hive was placed half way up a steep mountain slope (inclination 15–37°) (Heran and Wanke, 1952). Foragers collected sugar water uphill and downhill from the hive. Only two out of seven experiments gave the expected results: bees collecting food uphill reported greater distances than individuals foraging downhill. The other five experiments showed no significant differences between dances of uphill and downhill foragers. Heran explained these negative results by invoking interference from wind. For Heran (1956) and von Frisch (1967a), two successful experiments provided enough evidence to prove the energy hypothesis. Most members of the von Frisch school shared this view. Heran concluded from the results of the two experiments that, of all the energy consumed during a foraging flight, only the amount used on the way out to the feeder is considered for distance estimation. Bees foraging uphill need less energy on the whole foraging trip than bees foraging downhill. They climb unloaded against gravity on the way to the feeder, but they can drop to the altitude of the hive when loaded with sugar water. Bees foraging downhill have to carry their nectar load back uphill. The assumption that only the energy needed on the outward journey is used as the measure for distance is very important. It should be confirmed in independent experiments.

Is the energy used for the outward flight the critical measure?

Experiments by Otto (1959) suggested that foragers use the whole flight as the basis for distance estimation. Otto carried foragers to a greater distance from the hive after they had settled on a feeder and then allowed them to return to the hive. According to von Frisch, Otto's results are 'unambiguous' (von Frisch, 1967a). von Frisch proposed an interpretation that brings Otto's results in line with the energy hypothesis: bees that were moved from the feeder to a greater or smaller distance during feeding were disturbed. They took the backward flight as an 'outward flight, but one now toward the hive' (quote from von Frisch, 1967a) and then averaged the two flights. We have no experimental evidence for the correctness of this suggestion. It is based on two unproven

assumptions, namely that foragers take both parts of their trip as an outward flight and that they average both trips to signal the result.

Other support for the energy hypothesis

Loading foragers with lead weights or attaching tinfoil to them both caused them to signal larger feeder distances (Scholze *et al.* 1964; von Frisch, 1967a). No discrimination between the importance of the outward and homeward flights was possible in such experiments. The energy required on both flights was increased. However, these observations could not be confirmed later (Neese, 1988).

von Frisch derived a strong argument for the 'energy hypothesis' from Bisetzky's 'runway experiments': foragers walked to a feeder through a narrow runway (they could not fly). Waggle dances were observed when they walked more than 3 m (Bisetzky, 1957). Bees from the same colony also performed waggle dances after they had flown to feeders at distances between 50 and 100 m. Scholze *et al.* (1964) determined indirectly that walking 3 m requires as much energy as flying 55–100 m. The runway observations apparently supported the notion that the same amount of energy used in the approach to a feeder leads to the same distance message for that feeder.

The energy hypothesis was discussed one more time: Neese (1988) attempted to dissect the energy-measuring mechanism. He hypothesized that a change in the tension of the honey sac wall is used for distance estimation. Neese assumed that a forager empties part of the honey sac content into the intestine during flight and that this amount is proportional to the distance flown. He had no direct evidence for the correctness of his assumptions. More interestingly, he could not confirm that foragers loaded with additional weights signal larger feeder distances. Thus, Neese did not provide new support for the energy hypothesis.

While reading the original papers, one gains the impression that evidence supporting the energy hypothesis was favored over arguments against it.

An early optical flow hypothesis

The discussion of whether feeder distance might be determined by 'optical flow' was introduced by von Frisch with the sentence 'That the bee's estimation of distance is not determined through optical examination of the surface beneath her is confirmed by another observation...' (von Frisch, 1967a). He refers to foragers who flew to a feeder at a distance of 363 m by crossing a calm lake. He assumed that the lake surface provided no optical input. These bees signalled that their feeder was 80 m closer than an equidistant feeder reached over land. von Frisch notes that the lake foragers had a slightly faster dance tempo (signalled a shorter distance). A repetition of these experiments during the following year produced very similar results. A shorter distance (60 m shorter) was reported when bees had flown 340 m over calm water. However, another experiment was disturbed by strong headwinds (2–3 m s⁻¹). Lake bees

signalled a greater distance than their comrades that had flown over land and were carried by wind. This result certainly did not contradict an optical flow hypothesis. However, von Frisch averaged data from the 'disturbed' and the 'undisturbed' experiments, and the combined results showed that flight over water had no apparent effect.

von Frisch and others (Heran and Lindauer, 1963) noticed that foragers flew very low over calm water. Many foragers flew so low that they drowned. Flying so low was probably due to the bees' (unsuccessful) attempt to find some visual cues below them (see also Heran, 1956). Foragers that did not drown must have seen the water surface below them, i.e. optical input was present. The optical flow hypothesis could not be rejected on the basis of von Frisch's lake experiments. On the contrary, von Frisch's experiments provided evidence that it might be a valid alternative to the energy hypothesis.

Indeed, von Frisch concluded the discussion with the statement 'For the present one may not with certainty exclude the possibility that perception of the structured surface beneath plays a modest part in estimation of the distance' (von Frisch, 1967a).

Observations between 1988 and 1995

A repetition of the 'mountain slope' experiments

Heran was not satisfied with the results of the 'mountain slope' experiments. Too many experiments had failed and the energy calculations (Heran, 1956) were not satisfactory (H. Heran, personal communication). In the early 1960s, Heran and one of us (H.E.E.) planned to repeat the experiments under better controlled conditions (specifically excluding wind as a potential disturbance). We never found the opportunity.

A few years ago, one of us (H.E.E.) repeated the basic 'mountain slope' experiment under much more favorable conditions (Goller and Esch, 1990). We trained two groups of bees to fly to feeders 158 m north of a hive, one on top of a large building (height 50 m), the other at ground level, almost in the same direction (15° to the east) (Fig. 1). Experiments were conducted only on days with wind speeds lower than 1 m s^{-1} . Dancers from both groups were video-taped at the same time. We found no differences in distance signalled between dances of the two groups (Table 1), even though calculations indicated that significantly more energy was required to reach the high feeder (1.522 J) than the ground feeding site (1.032 J) (Goller and Esch, 1990).

Table 1. Mean dance cycle time and calculated energy requirements for bees that flew to ground or roof feeders

	Dance cycle time	N	Calculated energy requirement (J)
Ground feeder	1.73±0.27	1313	1.032
Roof feeder	1.76±0.20	1206	1.522

N, number of cycles evaluated.

Values are means ± S.E.M.

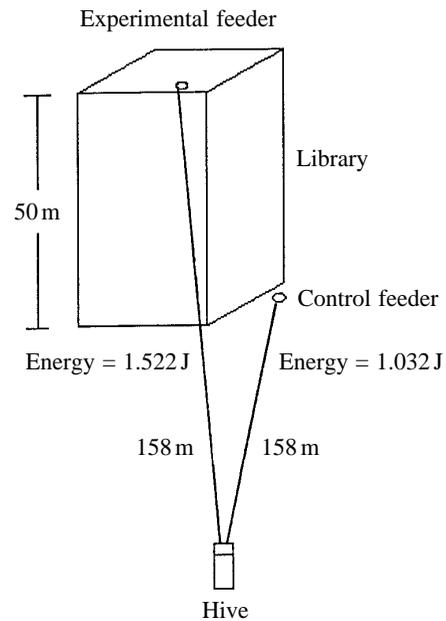


Fig. 1. Diagram shows feeding site locations and energy requirements.

A repetition of the runway experiments

The outcome of our 'mountain slope' experiments suggested a repetition of Bisetzky's (1957) runway experiments. Bees were made to walk 3 m as part of their foraging trip. During the 3 m walk, the oxygen uptake of individuals was measured. We could thus correctly calculate the energy required during walking (Fig. 2) (Esch *et al.* 1994). Our bees did not signal greater distances corresponding to their oxygen consumption after walking 3 m to a food source. The energy consumed during walking depended on ambient temperature. Walkers attempted to regulate their thorax temperatures to 40 °C (Fig. 3). Less than 1% of the energy needed for heating at an ambient temperature of 20 °C was used for actual locomotion. Oxygen uptake during the 3 m march varied greatly from $45 \mu\text{l min}^{-1} \text{ bee}^{-1}$ at 20 °C ambient temperature to $<1 \mu\text{l min}^{-1} \text{ bee}^{-1}$ near 40 °C (Fig. 4). One would have expected that distance messages would depend strongly on ambient temperature under these conditions, but they did not. We measured how walking 3 m after flying 65 m affects the distance signal. Energy consumed during a 3 m march (at 25 °C ambient temperature) is sufficient to fly 128 m. The distance signal, however, is not affected by walking (Table 2) (Esch *et al.* 1994).

A new approach: the balloon experiment

In a series of recent experiments, we approached the question by using a feeder attached to a helium-filled weather balloon (Esch and Burns, 1995). We first established a distance curve by training bees from an observation hive to feeders at various distances and recording their dances on video tape (30 frames s^{-1}). Number of waggles per waggle run, as well as dance shape (round dance, sickle dance, waggle dance), were measured during slow-motion replay and related to distance

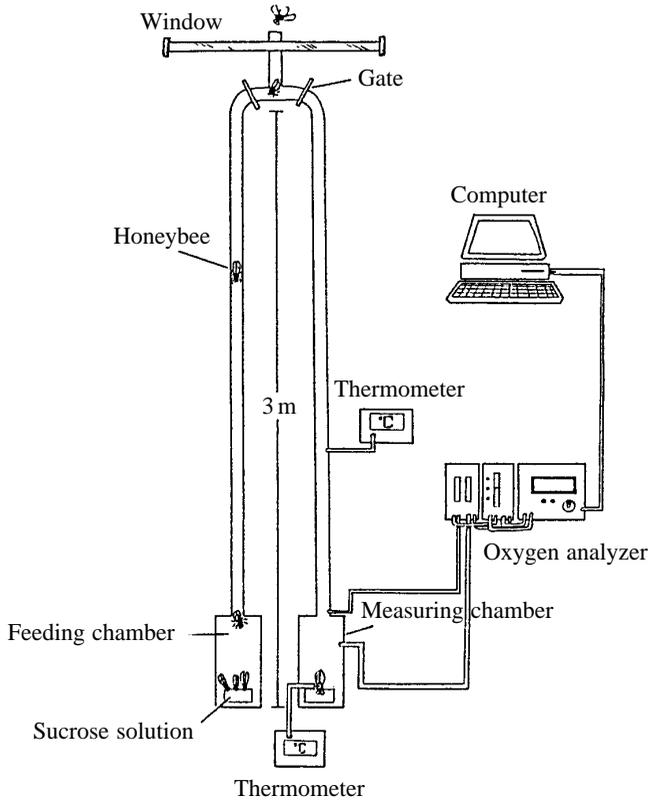


Fig. 2. Diagram of the experimental arrangement. The tube system is seen from above. After entering the tube outside the laboratory window, individuals can be gated either to the feeding or to the measuring chamber (after Esch *et al.* 1994).

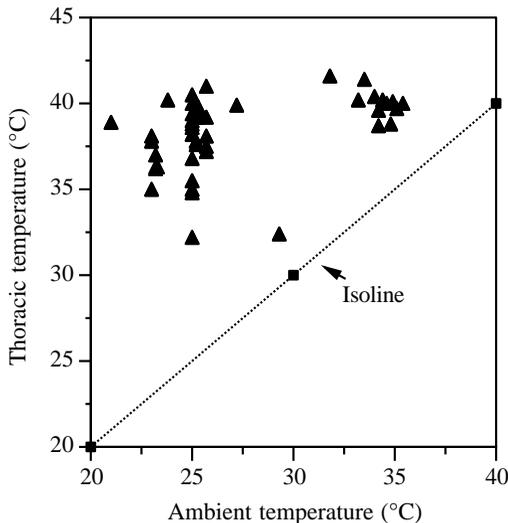


Fig. 3. Thoracic temperatures (triangles) of foragers in the measuring chamber at various ambient temperatures (based on eight individuals) (after Esch *et al.* 1994).

(Fig. 5). Waggle per waggle run is a very convenient measure of distance. It can be determined reliably from video tapes and can be used at close distances where cycle time or other

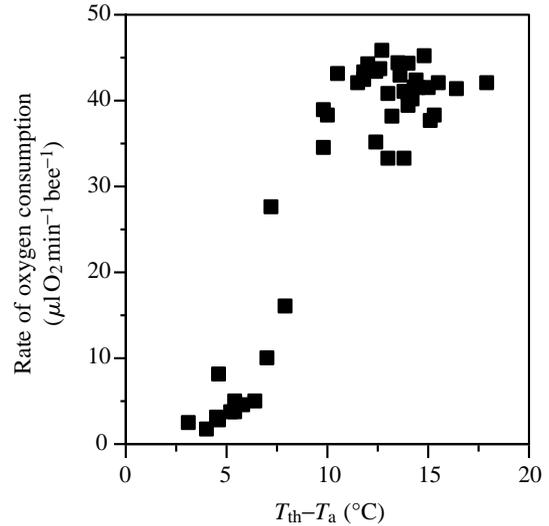


Fig. 4. Rate of oxygen consumption plotted against temperature difference between thorax (T_{th}) and environment (T_{a}) in the measuring chamber (based on eight individuals) (after Esch *et al.* 1994).

Table 2. Comparison of observed and predicted distance signalled by waggles

	Number of waggles per waggle run	<i>N</i>
Observed values		
Feeder at tube entrance (65 m)	2.98±0.03	1173
Feeder at end of tube (65 m + 3 m)	3.49±0.03	1279
Predicted values		
Value for foragers that walked 3 m and flew 65 m		
From Scholze <i>et al.</i> (1964)	5.50	
From O ₂ uptake measurements this study	7.40	
<i>N</i> , number of waggle runs evaluated.		
Measured values are means ± S.E.M.		
Observations at $T_{\text{a}} = 25^\circ\text{C}$.		

distance-related behaviors become very unreliable. Because round dances indicate short distances, whereas waggle dances indicate larger distances (the sickle dance being an intermediate case), the shape of the dance is another reliable cue to the dancer's estimate of feeder distance.

We then allowed marked individuals from the same hive to visit a feeder containing 2 mol l^{-1} sucrose solution in a large, dry meadow. The feeder was attached to a helium-filled weather balloon (diameter 1.2 m) 70 m from the hive as measured at ground level. Balloon and feeder were slowly raised to a height of 90 m (within 2 h). They were held at 30 and 60 m on the way up to record several hundred dances by all individuals at each altitude.

Experienced foragers headed straight for the balloon, as far as we could see. Their vigorous dancing indicated that they had no problem finding the feeder in the sky (no other food sources

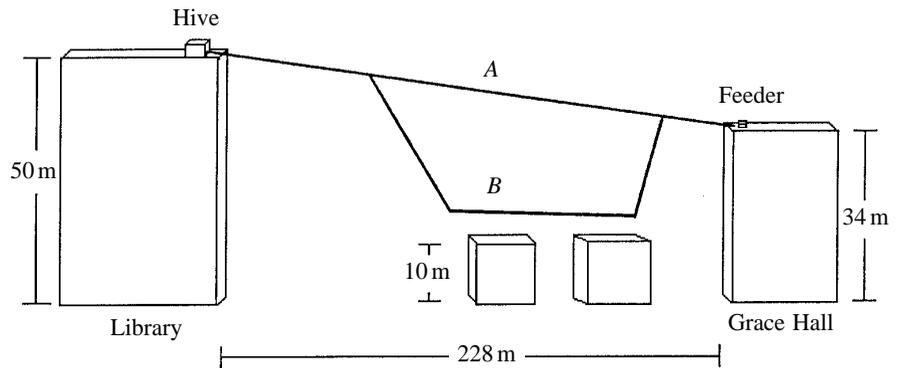


Fig. 6. Bees were trained to fly from the Library to the roof of Grace Hall (228 m away). A direct flight path is indicated by A. Path B was chosen if foragers flew lower to receive optical input from two buildings between the hive and the feeding site.

altitude: foragers use the retinal image flow of ground motion to gauge feeder distance. The optical input of foragers changes drastically on the way to the balloon. During locomotion, contours of near objects move faster and farther on the animal's eye than do contours of more distant objects. Bees lack stereoscopic vision or other means for depth perception (reviewed by Collet and Harkness, 1982). They use, instead, the speed of image motion to infer the range of objects (reviewed by Lehrer, 1991). Although the bees flying to the balloon might 'know' that they are ascending, they cannot communicate this information. The dance language has no words for altitude (von Frisch, 1967a).

The high building experiment

Under the optic flow hypothesis, bees from a hive placed on the roof of a high building visiting a feeder placed on another high building are expected to indicate shorter distances than bees flying the very same distance from a ground hive to a ground feeder. To examine this expectation, we placed an observation hive on top of the library (50 m) at the University of Notre Dame and trained foragers to collect food from a feeder on top of Grace Hall (34 m) 228 m away (Fig. 6). Foragers left their hive in level flight towards the feeding station and disappeared after 30–50 m. They also approached the feeding station in level flight. Even if they descended after the initial flight, they travelled a large part of the trip at high altitude. Their optical input was different from that of bees foraging at ground level. Dances of high-building foragers indicated a mean distance of 125 m (2.974 ± 0.042 waggles; mean \pm S.E.M., $N=891$), significantly different from 200 m (3.739 ± 0.055 waggles; mean \pm S.E.M., $N=460$) at ground level. These results support the optical flow hypothesis (J. E. Burns and H. E. Esch, in preparation).

Optical flow as a measure of distance

The optical flow hypothesis assumes that the signal for feeder distance is derived from the optic flow. The most probable parameter is the speed (and not the temporal frequency) of image motion perceived during locomotion. It has been shown several times that bees measure the speed of image motion and use it in a variety of visual tasks (reviewed by Lehrer, 1994). If a forager measures the time she has spent on the route, she can infer the distance flown from the speed

of the image motion (distance = speed \times time). We have reasons to believe that bees can measure time. Even von Frisch considered flight time as a possible candidate for distance estimation, but he discarded the idea because the energy hypothesis seemed to provide a better explanation for many of his observations (von Frisch, 1967a). Our results combined with the evidence provided by von Frisch and his students make it most likely that the speed of image flow on the way to the feeder is used to estimate feeder distance.

Wind compensation and flying over different surfaces

Heran (1956) determined flight velocities of foragers at various wind speeds and directions. Bees attempted to keep a constant ground speed and changed their flight efforts to compensate for wind drifts. The drift was not completely compensated by flight velocity. This type of wind compensation is only possible with the help of optical input. Heran showed in laboratory experiments that bees alter flight velocity in response to changing optical inputs (Heran, 1956).

Heran and Lindauer (1963) compared foragers traveling 248 m to a feeder over a lake with bees flying 248 m over land. All bees needed optical ground patterns to achieve 'normal' flight altitude and velocity: over a mirror-smooth lake surface, many bees lost height and crashed head first into the water. This did not happen when wind rippled the water surface or when the experimenters provided artificial optical landmarks.

A rippled water surface does not provide the same optical clues as land. Foragers flew *slow* and *low* (6.34 m s^{-1} , 0.5 m) over water as compared with bees flying over land (8 m s^{-1} , 2.5 m). Flying bees tried to maintain constant velocity of image flow over the retina. To achieve a constant image speed, they altered either flight speed or flight altitude, i.e. they flew fast at high altitudes and slow near the ground (Heran and Lindauer, 1963; see also Srinivasan *et al.* 1996).

Heran and Lindauer provided equations that allow prediction of flight altitude from flight velocity. These equations are mainly based on studies of optomotor responses of tethered flying bees (Kunze, 1961). We used these equations to calculate the relationship between flight altitude and flight velocity, controlled by ommatidia looking 10° ahead (from vertical) for a pattern speed of 40 ms (optimum from Heran, 1956) (Fig. 7). Some important consequences result from the attempt to keep optical flow speed constant.

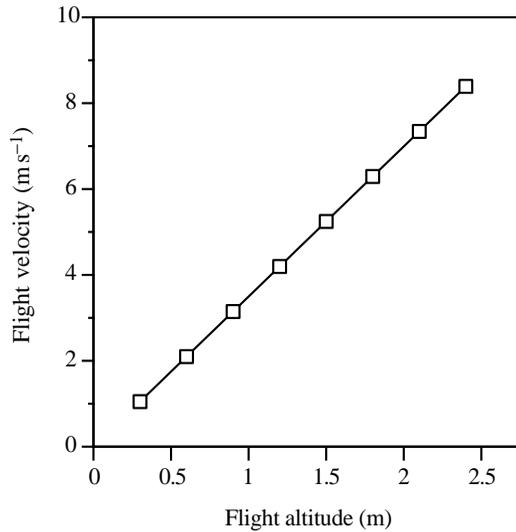


Fig. 7. Flight velocity of foragers at various flight altitudes above the ground, calculated from equations published by Heran and Lindauer (1963). Refer to text for parameters used.

(1) Flight velocity increases with flight altitude. (2) The range of flight velocities reported in the literature (up to 11 m s^{-1}) (von Frisch, 1967a) suggests that most foraging flights occur at an altitude of a few meters above the 'optical plane' (optical landmarks above ground increase flight altitude). An individual forced to fly at an altitude different from 'optimal' (owing to poor landmarks, additional load, flying up- or downhill) should select a different flight velocity. A bee whose flight velocity is changed by external interference (wind drift, decreased velocity caused by increased drag) should choose a different altitude. Foragers have the ability to monitor their flight velocity with respect to the surrounding air (Heran, 1959; Neese, 1965) and they could take this into consideration. (3) Distance estimation based on optical flow parameters might not work well when individuals are forced to fly considerably higher than a few meters above ground. This could mean that the 'balloon bees' measured only the first part of the journey, i.e. the part that was flown at low altitude. This might also explain the behavior of bees visiting the balloon feeder at 650 m. Foragers could fly to near 500 m, begin to ascend and lose the ability to measure additional distances. Thus, they indicate feeders at all altitudes larger than 30 m as being equidistant.

The role of flight altitude in energy hypothesis experiments

Flight altitude could be crucial in the interpretation of Heran's mountain slope experiments. Foragers flew to an uphill feeder under ideal conditions (no wind, no thermal updraft) at a velocity of 4.7 m s^{-1} and to a downhill feeder at a velocity of 8.6 m s^{-1} (Heran, 1956). In this case, a longer flight time could explain the larger distance signalled by uphill foragers. von Frisch, however, did not mention these results in his discussion of the mountain experiments. Most of the foragers flew under non-optimal conditions. They needed the

same time to fly uphill as downhill (von Frisch, 1967a). Bees flying uphill are forced to fly closer to the ground when they attempt to maintain level flight. The perceived speed of image motion thus becomes faster (the opposite is true for bees foraging downhill). Since, under the optical flow hypothesis, distance is calculated as the product of flow speed and time, uphill feeders should be signalled as being further away than equidistant downhill feeders which is, indeed, the case.

Bees that fly against the wind strive to keep retinal image speed similar to that encountered on windless days by flying faster. However, they only compensate for maximally 33% of speed loss (reviewed in von Frisch, 1967a), so they alter their flight altitude to make up for the difference in optic flow speed (see Bräuninger, 1964). Flights into the wind last longer than similar flights on windless days. Since distance is the product of optic flow speed (same as on windless days) and flight time (longer than on windless days), the distance flown is overestimated when bees fly to the feeder against wind.

The shape of the distance curve

The shape of the distance curve reveals a striking consistency in all of the experiments described so far in the literature (reviewed by von Frisch, 1967a): it is not linear. At small feeder distances, the slope of the curve is large, i.e. the signal representing estimated distance changes rapidly with feeder distance. At larger feeder distances, the curve levels to an almost linear portion with a small slope. von Frisch (1967a) tried to explain this phenomenon with differential 'forgetting'. In the light of our suggestion (see above) that bees strive to maintain a constant speed of image motion during flight (see also Srinivasan *et al.* 1996), there is a simpler explanation. Foragers that visit feeders in the vicinity of a hive fly lower than bees going to feeders further away (Bräuninger, 1964). To obtain the same image speed as during higher flight, low-flying individuals fly more slowly. Flights covering a given distance at low altitude thus last longer than flights for the same distance at higher altitude. Because distance is estimated as the product of image flow speed and flight time, flights at low altitude result in overestimation of the distance flown (large slope) when compared with similar flights at higher altitude (smaller slope). The distance curve becomes linear at larger distances because feeders at large distances are usually approached at a constant flight altitude.

A look at other hymenopterans

The possible mechanisms for estimating the distance that must be travelled have also been investigated in homing *Cataglyphis* ants. The energy hypothesis has to be dismissed, because these ants assess feeder distance accurately, irrespective of the load they have to carry (Wehner, 1992). Their potential use of optical distance estimation was tested with moving floor patterns. Moving patterns affect the ants' distance estimation. Speed of image motion is more important than contrast frequency, because floor patterns of different spatial wavelength do not affect distance perception.

Experiments with structureless floors or with ants wearing eye covers revealed, however, that optical flow parameters are not the only cues for assessing distance in ants (Ronacher *et al.* 1994).

Preliminary experiments with walking honeybees in our laboratory indicate that changes in spatial wavelength of ground patterns affect the perceived distance, as indicated by dancing. However, recent experiments with flying foragers have clearly shown that estimation of the distance flown is independent of spatial frequency (Srinivasan *et al.* 1996). It is possible that the mechanism for measuring distance during flight differs from the one that is used during walking. Further experiments are needed to test this possibility.

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