The influences of landmarks on distance estimation of honey bees

LARS CHITTKA*, KARL GEIGER & JAN KUNZE

Institut fuer Neurobiologie, Freie Universitaet Berlin, Koenigin-Luise-Str. 28–30, 14195 Berlin, Germany

Abstract. Honey bees, *Apis mellifera*, were trained to fly from their hive to a feeding site along a flight path marked by visually discriminable landmarks 3·46 m high. The landmarks were placed at regular intervals of 90 m. During training, the feeder was located directly in front of the third (target) landmark. In the tests, bees were given the choice of landing at the trained distance or at the target landmark which had been displaced to a different distance. Bees preferred to land at the target landmark when the discrepancy between the two indicated distances was small, but landed mostly at the trained distance if the discrepancy was large. Furthermore, distance estimation depended on landmarks encountered during flight. When the target landmark was placed at a distance from the hive closer than the trained distance, the bees' readiness to respond to this landmark could be increased only if bees had already passed the landmark that preceded the target landmark during training. Thus, a given flight goal is defined in the bees' memory by its distance from the hive, landmarks that mark the goal, and landmarks that precede the goal during flight. At the same time, the bees, as a group, exhibited considerable flexibility to land in places that were defined by only one or two of these cues.

© 1995 The Association for the Study of Animal Behaviour

A familiar food source is specified in the bee's memory by a vector encoding distance and direction from the hive (von Frisch 1967; Cartwright & Collett 1983; Collett 1993). The directional component is defined by the sun compass (Wolf 1927) and the distance component may be estimated by means of energy investment during flight (Heran 1956, but see also Esch et al. 1994). It is unlikely, however, that these mechanisms alone will reliably guide an insect during long-distance orientation in natural conditions.

The estimation of distance and direction may be disrupted by external influences such as wind or thick cloud cover impairing sun compass application (von Frisch & Lindauer 1954; von Frisch 1967; Dyer & Gould 1981; Chittka & Geiger 1995a) as well as internal errors inherent in the mechanisms employed by the animals for the respective assessments (Wehner & Srinivasan 1981; Mueller & Wehner 1988; Wehner & Wehner 1990). To cope with such disruptions, landmarks must be integrated into the sequence of instruc-

tions to follow a fixed route (Collett 1992, 1993; Chittka & Geiger 1995a, b). Theoretically, a sequentially stored set of instructions that links consecutive landmarks would suffice for navigation towards a goal even if vector information were not available, given that the respective next landmark is detectable and recognizable from the respective last landmark.

Two easily conceivable problems might compromise such a strategy under natural conditions. First, consider a long-distance foraging trail through an environment rich in detail, such as a forest. The insect would have to memorize practically an infinity of landmarks or panoramas to guide itself reliably along a given route. A strategy to save memory space would be to store only conspicuous landmarks and link these in memory by flight vector instructions. Second, different constellations of natural landmarks, such as bushes, trees or rocks, may often look similar (Collet & Kelber 1988; Collett 1992). To avoid mistakes, a given landmark should be defined in memory not only by its own visual appearance, but also by, for example, the direction and distance in which it lies from other targets, for example the last one passed en route.

*Present address: Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, U.S.A.

Consequently, bees must integrate landmarks into their vector estimation, and vice versa: they must use vector instructions to bring them close enough to a familiar landmark or panorama, so that this landmark or panorama can be recognized and used for the final approach to the target (Collett 1993; Chittka & Geiger 1995a, b). Indeed, Collett et al. (1993, also Collett & Kelber 1988) have recently shown that bees are able to memorize not only that (1) a given mark is supposed to follow a given other mark and (2) a given flight vector has to follow after another vector, but also (3) the instruction to fly a given distance in a certain direction can be triggered by a visual stimulus. These observations, however, were made in set-ups that marked only the immediate surroundings of a food source, and bees might theoretically employ other mechanisms when navigating over longer distances.

To understand how flight vector information and landmark information are weighted during long-distance orientation, we trained bees along rows of large artificial landmarks (coloured tents). In subsequent tests, the landmark sequence was altered, and bees were given the choice of landing either at the trained distance or at another location indicated by the new set-up of landmarks. We show that landmarks, even if encountered at unfamiliar locations, strongly influence the bees' choice of goal distance. This is true both for landmarks marking the immediate surroundings of the food source and for those that mark the flight path from the hive to this food source.

MATERIAL AND METHODS

Honey bees, *Apis mellifera*, were trained to collect sucrose solution at a feeder located directly in front of a 'target landmark' 270 m from the hive. The flight path was marked by two further landmarks (at 90 and 180 m) which differed in colour and shape from the target landmark. Landmarks were coloured tents (3·46 m high) with the shape of a regular tetrahedron (Chittka & Geiger 1995a, b). Some of the landmarks were formed by two or three such tents directly adjacent to each other, touching each other at one of the corners. The experimental site was chosen so that it provided a minimum of orientation cues in the surrounding landscape. The array of landmarks was set up on a large, even meadow with a very homogeneous horizon profile (Chittka & Geiger 1995a). Approximately 100 bees shuttled continuously back and forth between the hive and the feeder.

In the tests, the landmark set-up was altered, and bees were given the choice between feeders at the trained distance and one or more alternative locations indicated by various landmarks or landmark arrays (see below). To make sure that all bees participating in the tests had come from the hive, we prepared the tests as follows. (1) The hive entrance was closed. (2) The bees on the feeder were blown off and eventually flew back to the hive. They gathered at the location of the entrance until the hive was reopened. A small number of bees sometimes continued searching at the location of the feeder. These were caught before the tests were started. A feeder was briefly set up and all the bees that landed were captured by means of forceps and kept until the end of the test. (3) Meanwhile, the landmark set-up was changed and test feeders were placed in various locations (see below).

Subsequently, the tests were started by opening the hive entrance. Those bees that had been waiting inside the closed hive usually arrived very quickly after removal of the hive entrance barrier, whereas those that had been sitting outside typically first went into the hive, then flew out and made their choices at the test feeders a few minutes later. Bees arriving at the test feeders were captured with forceps by experimenters placed at each feeder. They were counted and kept in a box until the end of the test. Bees were never rewarded at any of the feeders during tests. Experiments were stopped when no further bees arrived at the feeders (after about 30 min). The training landmark set-up (including the feeder) was then restored and bees were allowed to forage freely for at least 30 min.

Bees were trained along two different sequences of landmarks. Since the two experiments were performed in 2 consecutive years and thus with entirely different individuals, the choice behaviour in one experiment could not be influenced by what any bees had experienced in the respective other set-up. Preliminary experiments had shown that bees discriminate very well between all the colours and shapes of landmarks to be described in the following sections (L. Chittka, unpublished data).

Chi-squared goodness-of-fit tests were used to evaluate the data.

Landmark Set-up I

Yellow tents were positioned at 90, 180, 270 and 360 m. The tent at 270 m was flanked by two blue tents, so that the feeder was marked by a 'three-peak' landmark (the target landmark) coloured blue–yellow–blue. The sequence on the way to the feeder was thus AAB (different letters indicate landmarks that differ in shape and colour). The feeder was located immediately before B, the target landmark. To see whether bees would land at B even if it was encountered at distances that differed from 270 m, we moved the blue tents so that they flanked the yellow tent at either 360 m (Fig. 1, test 1a), 180 m (Fig. 1, test 1b) or 90 m (Fig. 1, test 1c). Test feeders were then set up in front of all of these landmarks and at the trained distance of 270 m. Control tests were performed with the original landmark set-up and test feeders at the same locations (Fig. 1, controls 1a and 1b).

Sample sizes and choice values for all experiments are given in the figures.

Landmark Set-up II

Bees were trained along a sequence of landmarks XYZ. Landmark X (90 m from hive) consisted of three yellow tents, Y was a green tent (180 m from hive) and Z (the target landmark, 270 m) was composed of two blue tents. Before the experiments with altered landmarks were started, a control test (Fig. 2, control 2a) was performed in order to confirm that bees had learned to land at the correct location. For this purpose, test feeders were placed in front of all three landmarks.

In a second control test, the landmarks X and Y were removed, and Y was replaced by another Z (henceforth Z_1, because it is the first one encountered on the way from the hive). Bees were then given the choice between Z at the correct distance of 270 m (henceforth Z_2) and Z_1 at the shortened distance of 180 m (Fig. 2, control 2b). In all the following tests, bees had to choose between these two locations, and in all tests these were marked by identical landmarks Z. The tests differed in terms of the landmarks that were placed between the hive and Z_1. The question asked was: would

different parts of the trained landmark sequence, inserted before Z_1, change the ratio between the numbers of bees landing at Z_1 (the one at the incorrect distance) and Z_2 (the one at the trained distance)?

The following combinations were tested (Fig. 2): XZ_1Z_2 (test 2a); YZ_1Z_2 (test 2b); XYZ_1Z_2 (test 2c); YXZ_1Z_2 (test 2d); UUZ_1Z_2 (test 2e). If there was only one landmark inserted between the hive and Z_1, it was placed at 90 m; if there were two, these were placed at 60 and 120 m. UU were two landmarks with which the bees had had no previous experience, namely single white tents.

RESULTS

Landmark Set-up I

In the training situation, the feeder was marked by a landmark that differed in shape and coloration from all others in the array. At the same time, the feeder's location was also defined by its distance from the hive. The question asked in this section is: if the test set-up produces a contradiction between the trained distance and the distance at which the target landmark is encountered, which distance will be chosen by the bees? Does this choice depend on the magnitude of discrepancy between the two indicated distances?

In the control test with the unchanged training landmark set-up and test feeders placed in front of the landmarks at 180, 270 and 360 m, the vast majority of the bees (88%) arrived at the training site (Fig. 1, control 1a). When the target landmark B was moved either to 360 m (test 1a) or to 180 m (test 1b), the majority of the bees chose the feeder marked by this landmark (76% at 360 m, 61% at 180 m; Fig. 1). The second highest percentage in both tests arrived at the original training site at 270 m (23% in test 1a and 38% in test 1b). The distribution of choices in both tests is significantly different from control 1a (test 1a versus control 1a: $\chi^2 = 134$, $df = 2$, $P < 0.0001$; test 1b versus control 1a: $\chi^2 = 102$, $df = 2$, $P < 0.0001$).

Even though most bees chose to alight at B (even when B was not at the trained position), the percentage of bees that arrived at B in test 1a and b was reduced relative to control 1a (where B was at the training position): 76% (test 1a) or 61% (test 1b) versus 88% (control 1a). This difference is significant in both cases (test 1a versus control 1a: $\chi^2 = 24.6$, $df = 1$, $P < 0.0001$; test 1b against control

Animal Behaviour, 50, 1
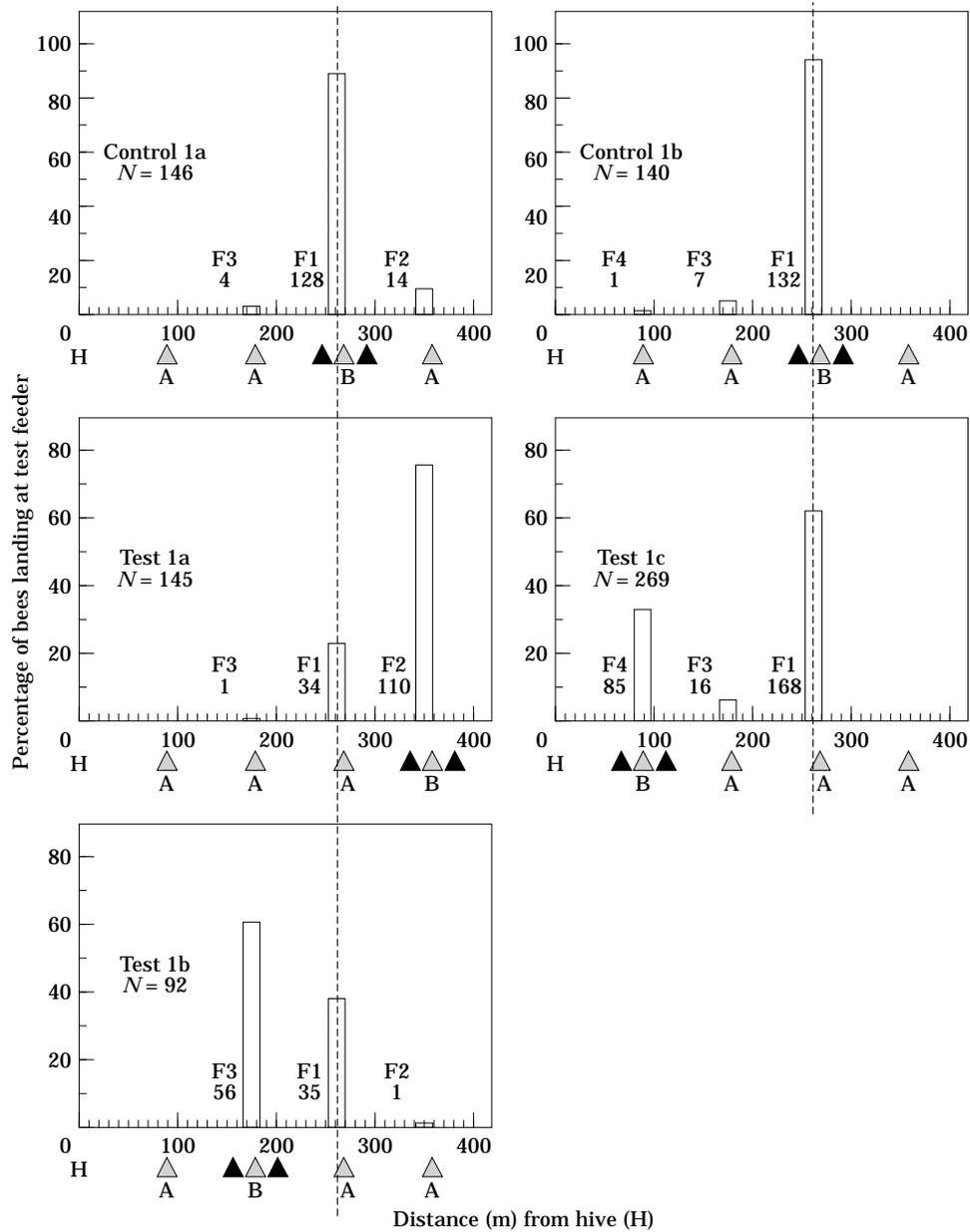
Figure 1. The percentage of bees that landed at the test feeders in test 1. Test feeders were placed directly in front of landmarks if marked F; F_1 was always at the trained position. Numbers below F1, F2, etc., indicate absolute choice values, N denotes the sample size. Landmarks are denoted by triangles under the abscissa; they are also given 'one letter labels' according to the text. The dashed line marks the distance of the feeder during training. The training landmark sequence is shown in control 1a and control 1b, with feeders only at the F1 position. During training, bees passed two identical landmarks (yellow tents, grey triangles) before they encountered a third 'three-peak-landmark'. This landmark (the target landmark) consisted of one central yellow tent and two adjacent blue tents (black triangles) and was placed directly behind the feeder (at 270 m, see landmark symbols in control 1a, b). It was arranged perpendicular to the flight path. In the tests, the target landmark was placed at either 360 m (test 1a), 180 m (test 1b) or 90 m (test 1c) from the hive. Control experiments (controls 1a and 1b) were performed with the original (training) array and test feeders comparable to the ones in the tests described above.

1a: $\chi^2 = 7.73$, $df = 1$, $P < 0.005$; number of bees that landed at B relative to all other bees in the respective test). Interestingly, significantly more bees landed at B in test 1a (where B was further than the trained distance) than in test 1b (where B was encountered before the training distance; $\chi^2 = 5.21$, $df = 1$, $P < 0.05$).

When the target landmark B was placed at 90 m, and test feeders were set up at 90, 180 and 270 m, only 32% of the bees alighted at the target landmark (Fig. 1, test 1c). The proportion of bees landing at the target landmark relative to those landing at other locations is significantly lower than in the tests described above (test 1c versus test 1a: $\chi^2 = 73$, $df = 1$, $P < 0.0001$; test 1c versus test 1b: $\chi^2 = 24$, $df = 1$, $P < 0.0001$). A control test with the original landmark array and feeders at the same positions (control 1b) yielded choices highly significantly different from test 1c ($\chi^2 = 55$, $df = 2$, $P < 0.0001$).

Landmark Set-up II

The control test with an unaltered landmark sequence showed that bees had indeed very accurately learned to alight at the correct location (Fig. 2, control 2a, 99% at Z). In control 2b, where bees had to choose between two identical landmarks Z at 180 and 270 m (with no landmarks preceding Z_1), the majority of bees (73%) still landed at the trained position, but the remaining 27% landed at Z_1 at 180 m. Since this and all the following tests are dual choice tests ($df = 1$), we give only percentages for Z_1 (at 180 m); the percentage of bees landing at Z_2 (at 270 m) is obviously 100% minus the percentage at Z_1.

The question underlying all the subsequent tests is: to what extent can the decision to land at Z_1 be influenced by which parts of the trained sequence the bee has already passed? Could the bees be 'made to believe' that they have already flown far enough at 180 m if they have passed X and Y, or parts of this sequence, before Z_1?

In comparison with control 2b, the number of bees landing at Z_1 was not significantly increased when unfamiliar landmarks were inserted before Z_1 (test 2e, sequence UUZ_1Z_2, 36%; $\chi^2 = 2.09$, $df = 1$, $P > 0.1$) or when only the landmark that was closest to the hive during training (X) was present (test 2a, sequence XZ_1Z_2, 29%; $\chi^2 = 0.09$, $df = 1$, $P > 0.5$). However, significantly more bees alighted at Z_1 in all tests that contained the landmark Y which preceded the target landmark during training (test 2b, sequence YZ_1Z_2, 41%; $\chi^2 = 7.04$, $df = 1$, $P < 0.01$; test 2c, sequence XYZ_1Z_2, 51%; $\chi^2 = 19$, $df = 1$, $P < 0.0001$; test 2d, sequence YXZ_1Z_2, 48%; $\chi^2 = 11.1$, $df = 1$, $P < 0.001$). There are no significant differences between pairs of these last three tests, indicating that bees did not care about where along the flight path they had encountered Y, nor whether it was preceded or followed by X (test 2b versus test 2c: $\chi^2 = 2.91$, $df = 1$, $P > 0.1$; test 2c versus test 2d: $\chi^2 = 0.25$, $df = 1$, $P > 0.5$; test 2b versus test 2d: $\chi^2 = 0.98$, $df = 1$, $P > 0.5$). Thus, the encounter of Y triggered a specific expectation that Z was to follow, and this expectation was sustained even if X occurred first after Y (test 2d). Landmark X played a minor role in the distance judgment: its presence was responded to in terms of slight increases of the number of bees landing at Z_1 in all the tests where it occurred versus comparable tests that lacked this landmark; however, none of these increases was significant (i.e. test 2a versus control 2b: $\chi^2 = 0.09$, $df = 1$, $P > 0.5$ as well as test 2c and 2d versus 2b; statistics see above).

Comparison between Landmark Set-ups I and II

If there is a target landmark at 180 m, is the decision to land at this landmark made when it is first encountered along the flight path, or do bees first look for a target landmark at the training distance of 270 m? To answer this question, a comparison between test 1b and the experiments of test 2 is useful. In all these tests there was a target landmark at 180 m, and test feeders at both 180 and 270 m. The experiments differ in that in test 1b, there was a 'non-feeder' landmark at the training site at 270 m, whereas in test 2, there was always a second target landmark at 270 m. If the decision to land at 180 m was made when the target landmark at this distance was first encountered, the percentage of bees landing at this site should be independent of whether the landmark at 270 m was a target landmark or not. However, this is clearly not the case. In test 1b, 61% of the bees landed at 180 m, whereas in test 2, the highest percentage ever reached in any of the numerous experiments was 51%. Test 1b and test 2b are particularly comparable because in both experiments the target landmark at 180 m was preceded only by the landmark that was also encountered before the target landmark during training. The

difference between the choice values in the two tests is significant ($\chi^2=9\cdot4$, $df=1$, $P<0\cdot005$; only the choice values at 180 and 270 m are compared). It thus appears that many bees in test 1b chose to land at 180 m only after discovering that there was an 'incorrect' landmark at the trained location of 270 m.

DISCUSSION

The experiments reported here address the following questions: do bees respond to a familiar landmark in the same way as during training if this landmark is placed out of sequence and away from the trained distance? In other words, does the landmark's own visual appearance suffice to trigger the behavioural responses (in this case, the 'landing response') associated with this landmark during training? Or is the readiness to respond to such a landmark also dependent on the context under which it is encountered? By context we mean events that precede the encounter: (1) landmarks seen in flight and their sequential arrangement compared with that during training; and (2) the bees' flight trajectory, relative to that in the training situation. We have shown that bees memorize a given goal together with its distance from the hive, landmarks marking this goal, and landmarks preceding this goal in flight. Bees, as a group, however, exhibit considerable flexibility in handling these cues in an isolated fashion.
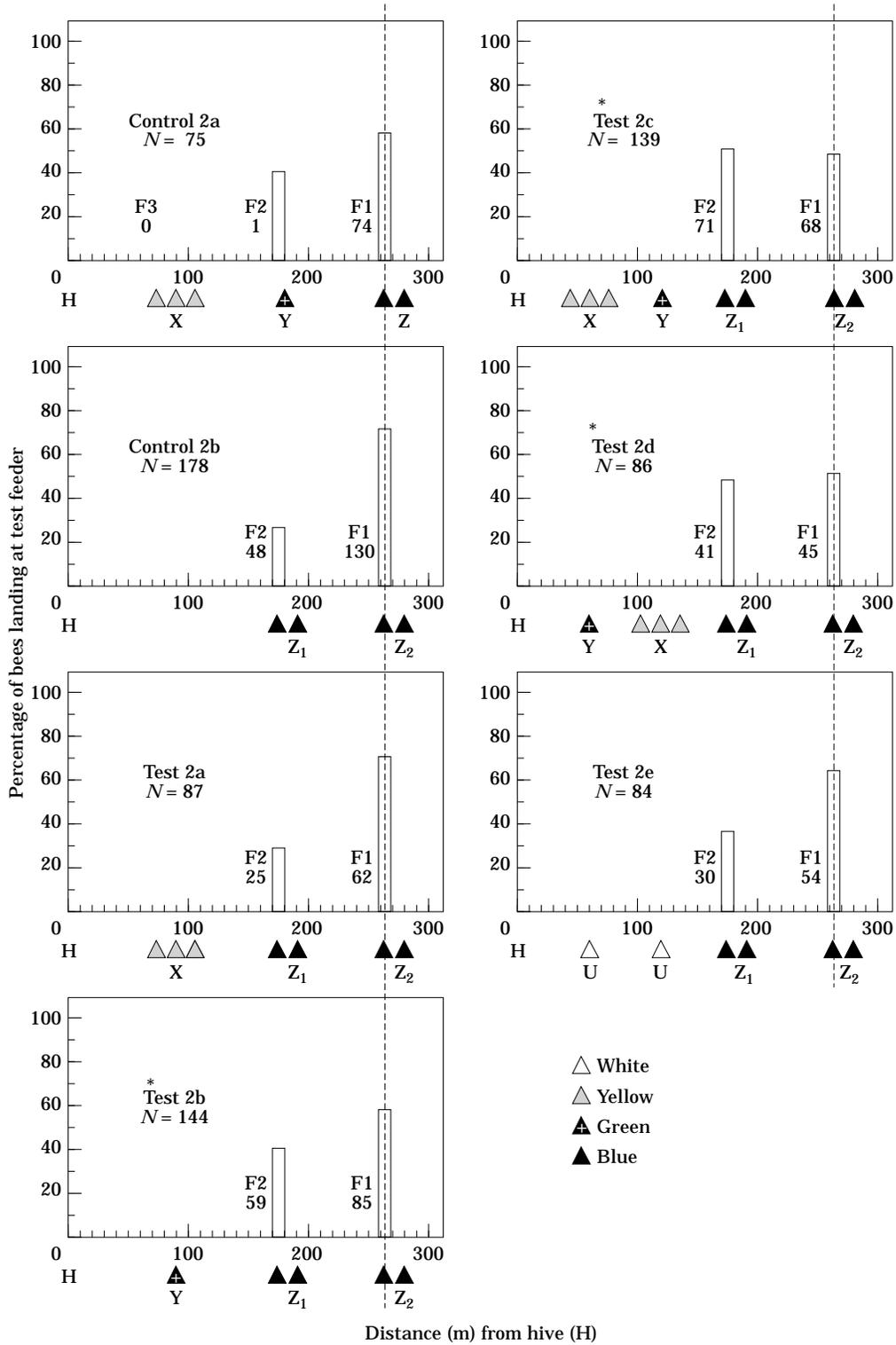
Bees responded appropriately to a landmark when it was encountered away from the trained distance and out of sequence (test 1). In fact, the behavioural reactions of bees to a given landmark set in a training situation can often be elicited whenever this landmark set is encountered in a test (Collett & Kelber 1988; Dyer 1991; Dyer et al. 1993). In a biological sense, this ability may be particularly valuable if a bee gets lost, which is probably not infrequent. Humans often temporarily lose their way in a novel or even partially familiar environment, and there is no reason to assume that bees, with their fundamentally poorer visual acuity, should perform any better. In such situations, the bee's ability to get back on track depends on the recognition of any familiar landmark, and to use it for redirection of its course (Collett 1992). If a series of landmarks could be addressed only in the correct sequence, a single landmark encountered out of sequence would be meaningless. Consequently, a lost bee would remain lost until it found the respective next landmark in the sequence after the one last seen on the familiar path, which may be unlikely.

The probability that bees landed at a landmark that was out of place was, nevertheless, not independent of where it occurred in our tests. The further away this landmark was placed away from the trained distance, the more bees preferred the trained distance over the trained target landmark. This is similar to what one observes in the use of landmarks for direction estimation by bees (Chittka & Geiger 1995a). Thus, the readiness to respond to the target landmark increases as the bee gets closer to the end of the flight vector from the hive towards the feeder. Additional support for this idea comes from the observation that, when the target landmark was encountered at a location too close to the hive (test 1b), it is apparently first bypassed by many bees, and only reapproached after the bees had flown the entire training distance of 270 m, and discovered that the target landmark was missing at that location. These bees must have followed their flight vector instruction before activating the search for the target landmark. Furthermore, more bees arrived at the target landmark if it was placed behind the trained distance (test 1a) than when it was located an equal distance before the trained distance (test 1b). This also indicates that the expected distance is flown by many bees before the memory for the target landmark is retrieved. Bees are simply more likely to look for this landmark straight ahead than to turn around when they discover that this landmark is missing at the expected distance.

Figure 2. The percentage of bees that landed at the test feeders in test 2. Control 2a shows the array of landmarks XYZ during training. In the training situation, food was offered only at the F1 position. In control 2b, X was removed, and Y was replaced by another Z. All further tests differ with regard to the landmarks inserted before this Z. All landmarks that consisted of more than one tent were arranged perpendicular to the flight path. Asterisks indicate tests in which the choices were significantly different from control 2b. For further information see Fig.1 and text.

Control 2a
N = 75
F3 0   F2 1   F1 74

*
Test 2c
N = 139
F2 71   F1 68

Control 2b
N = 178
F2 48   F1 130

*
Test 2d
N = 86
F2 41   F1 45

Test 2a
N = 87
F2 25   F1 62

Test 2e
N = 84
F2 30   F1 54

*
Test 2b
N = 144
F2 59   F1 85

△ White
△ Yellow
▲ Green
▲ Blue

Percentage of bees landing at test feeder

Distance (m) from hive (H)

That the search for familiar landmarks is activated only after a learned trajectory has been completed was previously reported for desert ants, *Cataglyphis bicolor* (Burkhalter 1972), but there is ample evidence that bees frequently exhibit similar strategies. For example, bees displaced from the hive entrance when starting towards a destination known to the experimenter will often follow the sun compass direction they would have flown from the hive to this destination had they not been displaced, and irrespective of whether they are familiar with landmarks surrounding the release site or not (Menzel et al. 1990). On the other hand, if one displaces bees that have just completed a given learnt trajectory (such as bees that arrive at the hive from a known food source) they will correctly use landmark information to redirect their course to the hive if released at a familiar site, or head off in random directions if displaced to an unknown location (Wehner et al. 1990; Chittka et al. 1992).

Nevertheless, the relative weighting of training distance and the target landmark can only explain the differences of choice behaviour within the various test 1 experiments, and the general difference between test 1b and all test 2 experiments. The flight vector instruction is not followed 'blindly' without taking into account features of the landscape through which the bee passes in flight. In the second series of experiments, two target landmarks were offered at fixed distances. The degree to which bees chose to land at either the one or the other depended exclusively on whether they had already flown past landmark Y. Thus, bees had obviously memorized that Y preceded the target landmark during training, and passing this landmark during a test increased their readiness to respond to the target landmark, even though the latter was encountered at a location too close to the hive. Interestingly, this was the case independently of where along the flight path Y was positioned, and independently of where X, the landmark that was closest to the hive during training, was placed. The expectation that Z was going to follow after the encounter of Y (as expressed in terms of a higher percentage of bees landing at Z_1 in all experiments where Y was present) was not disrupted if X was encountered after Y. Generally, the influences of X on distance judgment were weak; we observed only slight (but non-significant) increases of bees landing at Z_1 in all tests in which it was present versus those in

which it was not. This may seem contradictory to the results of a previous investigation (Chittka & Geiger 1995b) in which we found that several previously passed landmarks influenced the bees' distance estimation; however, that experiment differed in that the feeder was not immediately marked by a landmark (it was placed halfway between two landmarks) and all the landmarks used were identical. In such a situation, bees have to take particular care that they have passed the complete set of landmarks that mark the way during training in order to retrieve the goal. In the present experiment the strong influence of the target landmark may well override such an effect.

These results indicate that the retrieval of the memory for a given landmark (in this case the target landmark) is not only triggered by the encounter of that target itself, but is also dependent on the context of that encounter. First, the readiness to respond to this landmark is dependent on the bees' own recent activities; it is highest when positioned at the end of the bees' trained flight vector, and decreases as the landmark is moved further away from this position (test 1). Second, the readiness to retrieve the memory for the target landmark is dependent on the encounter of familiar cues of the landmark array prior to first hitting the target landmark (test 2). It thus appears that the target landmark is further defined in memory not only by an expected distance from the hive (Cartwright & Collett 1983), but also by landscape features that immediately precede the flight target during training.

REFERENCES

Burkhalter, A. 1972. Distance measuring as influenced by terrestrial clues in *Cataglyphis bicolor*. In: *Information Processing in the Visual System of Arthropods* (Ed. by R. Wehner), pp. 303–308. Berlin: Springer-Verlag.

Cartwright, B. A. & Collett, T. S. 1983. Landmark learning in bees. *J. comp. Physiol.*, **151,** 521–543.

Chittka, L., Bonn, A., Geiger, K., Hellstern, F., Klein, J., Knoll, P., Koch, G., Meuser, S. & Menzel, R. 1992. Do bees navigate by means of snapshot memory

pictures? In: *Rhythmogenesis in Neurons and Networks: Proceedings of the 20th Goettingen Neurobiology Conference* (Ed. by N. Elsner & D. W. Richter), pp. 1–695. Stuttgart: Georg Thieme Verlag.

Chittka, L. & Geiger, K. 1995a. Honeybee orientation in a controlled environment. *Ethology*, **99**, 117–126.

Chittka, L. & Geiger, K. 1995b. Can honey bees count landmarks? *Anim. Behav.*, **49,** 159–164.

Collett, T. S. 1992. Landmark learning and guidance in insects. *Phil. Trans. R. Soc. Lond. B*, **337,** 295–303.

Collett, T. S. 1993. Route following and the retrieval of memories in insects. *Comp. Biochem. Physiol. A*, **104,** 709–716.

Collett, T. S., Fry, S. N. & Wehner, R. 1993. Sequence learning by honeybees. *J. comp. Physiol. A*, **172,** 693–706.

Collett, T. S. & Kelber, A. 1988. The retrieval of visuo-spatial memories by honeybees. *J. comp. Physiol. A*, **163,** 145–150.

Dyer, F. C. 1991. Bees acquire route-based memories but not cognitive maps in a familiar landscape. *Anim. Behav.*, **41,** 239–246.

Dyer, F. C., Berry, N. A. & Richard, A. S. 1993. Honeybee spatial memory: use of route based memories after displacement. *Anim. Behav.*, **45,** 1028–1030.

Dyer, F. C & Gould, J. L. 1981. A backup system for cloudy days. *Science*, **214,** 1041–1042.

Esch, H., Goller, F. & Burns, J. E. 1994. Honeybee waggle dances: the 'energy hypothesis' and the thermoregulatory behavior of foragers. *J. comp. Physiol. B*, **163,** 621–625.

von Frisch, K. 1967. *The Dance Language and Orientation of Bees*. Cambridge, Massachusetts: Harvard University Press.

von Frisch, K. & Lindauer, M. 1954. Himmel und Erde in Konkurrenz bei der Orientierung der Bienen. *Naturwissenschaften*, **41,** 245–253.

Heran, H. 1956. Ein Beitrag zur Frage nach der Wahrnehmungsgrundlage der Entfernungsweisung der Bienen. *Z. vergl. Physiol.*, **38,** 168–218.

Menzel, R., Chittka, L., Eichmueller, S., Geiger, K., Peitsch, D. & Knoll, P. 1990. Dominance of celestial cues over landmarks disproves map-like orientation in honeybees. *Z. Naturf.*, **45,** 723–726.

Mueller, M. & Wehner, R. 1988. Path integration in desert ants, *Cataglyphis fortis. Proc. natn. Acad. Sci. U.S.A.*, **85,** 5287–5290.

Wehner, R., Bleuler, S., Nievergelt, C. & Shah, D. 1990. Bees navigate by using vectors and routes rather than maps. *Naturwissenschaften*, **77,** 479–482.

Wehner, R. & Srinivasan, M.V. 1981. Searching behaviour of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J. comp. Physiol.*, **142,** 315–338.

Wehner, R. & Wehner, S. 1990. Insect navigation: use of maps or Ariadne's thread? *Ethol. Ecol. Evol.*, **2,** 27–48.

Wolf, E. 1927. Ueber das Heimkehrvermogen der Bienen II. *Z. vergl. Physiol.*, **6,** 221–254.