Bumblebee Ocelli and Navigation at Dusk

Abstract. *Western bumblebees fly straight while homing by polarized light, but zigzag when they use landmarks. That flight difference was used to determine the roles of the dorsal ocelli and parts of the compound eyes in homing. Polarized light and ocelli can prolong foraging at twilight, when landmarks are no longer visible.*

Honeybees with their dorsal ocelli covered begin to fly later and stop foraging earlier than normal bees (*1*). The shortened day of the treated bees has been taken to indicate that dorsal ocelli are used to record either the absolute level of brightness or its rate of change at twilight. When the terrain is too dimly lit for their compound eyes to distinguish the contrasts or colors of familiar landmarks, however, deocellated bees may be having greater difficulties with homing procedures near the ground than with brightness levels overhead (*2*). Thus, the briefer flight period of the treated bees is equally consistent with another hypothesis; that is, the dorsal ocelli may be used to steer by polarized light from the zenith (*3*) when the ground is too dimly lit for homing by landmarks.

The method of testing this hypothesis exploited two kinds of homing flights displayed by workers of the western bumblebee, *Bombus terricola occidentalis* Grne. (*4, 5*). When there was polarized light overhead, homing workers spiraled steeply after takeoff, then flew straight to their nest 180 m distant. They flew straight over intervening trees, not around them. Whenever polarization in the zenith failed (*6*), however, the bees flew low, zigzagging from one shrub or flower bed to another.

Caught and tested on the ground beneath a sheet of Polaroid, marked individuals displayed behavioral differences related to the two types of flight. Grounded bees did not respond to the polarizer whenever flying bees were zigzagging from one landmark to another. But when all homing bees were flying straight, bees on the ground reacted to each abrupt turn of the polarizer by immediately changing direction through a comparable angle (*7*).

As the flight patterns of normal bees were so consistently related to the state of the sky, they could be used to schedule tests of treated bees (*8*). The latter were prepared by covering parts of their eyes with quick-drying red plastic paint. Five different treatments produced the results described here.

1) *Ocelli covered.* During the day, deocellated bees flew straight or zigzagged whenever normal bees did so. On the ground, they also responded like intact bees under the polarizer. But whenever normal workers would not turn with the polarizer, some deocellated bees stopped crawling altogether.

At dusk, the treated bees stopped flying and crawling at higher light intensities than the normal bees [1 to 2 compared with 0.2 to 0.5 lux (*9*)], a result comparable with that reported for honeybees (*1*). But after deocellated bees stopped flying, no intact bee zigzagged between landmarks. The remaining flights homeward were all straight, with the bees relying completely on the sky above.

2) *Compound eyes covered.* One-third of the bees with their compound eyes completely covered lost so much tonus in the metathoracic legs (*10*) that they could not be tested on the ground or in the air. The remainder could be induced to crawl or to fly only when normal bees were responding to the polarizer on the ground or were beelining homeward.

At such times, treated bees on the ground took 1 to 3 seconds to complete turns under the polarizer that normal bees made instantaneously. And in flight they spiraled upward through five or six turns instead of the normal one or two, often towering 16 to 18 m before beelining. But they ultimately flew straight, on courses within $\pm 3°$ of the 165° heading that the normal bees followed to their nest. As bees with only ocelli functioning had no ground reference by which they could maintain altitude, however, they either climbed slowly out of sight, or plummeted suddenly after traveling 30 to 50 m.

At twilight, these treated bees responded to the polarizer on the ground or flew on the proper heading as long as normal bees were flying (0.2 to 0.5 lux). All the treated workers were lost, however, because they could not maintain level flight.

3) *Bottom halves of compound eyes covered.* Unlike those in group 2, some members of ~~this~~ group could maintain level flight, although they occasionally had difficulty landing. But having the tops of their compound eyes as well as their ocelli free gave them no better view of landmarks than their counterparts in group 2 had. Consequently, while normal bees used landmarks in cloudy weather, these treated individuals rested quietly at the foraging place, trapped in daylight or twilight until the zenith cleared [see (*1*)]. When the sky was clear at dusk, members of group 3 responded like those of group 2 on the ground and in flight.

4) *Ocelli and top halves of compound eyes covered.* During daylight or dusk, bees that could not see upward never responded to the polarizer on the ground (*11*). Unless they were in direct sunlight, they sat quietly or wandered aimlessly. They were able to orientate by radiant heat in direct sunlight, traveling toward the sun when cool and away from it when overheated (*7*).

Aerial tests compared members of the nearest colony (used in tests 1 to 3) with individuals from a more distant nest. Intact workers from the distant colony visited the site only when they could navigate by polarized light, because the route to their colony had no landmark. Consequently, when overhead polarization failed, the bees already at the site had to stay there, resting quietly until the zenith cleared and they could fly home. Thus, their behavior was in direct contrast to that of the nearby workers, which changed from beelining to zigzagging and back again as clouds entered and left the zenith.

Without a view of the daytime sky, and with no landmark to guide them, workers from the distant colony were trapped at the foraging site when only the bottoms of their compound eyes were left uncovered. They could not fly home even when normal workers from both colonies were steering by polarized light. In contrast, their counterparts from the nearby colony were able to zigzag home by landmarks, whether or not the normal individuals were beelining [see (*11*)].

Because of that difference in homing ability, only the workers from the nearby colony could be tested at dusk. With no view of the overhead sky, they stopped zigzagging homeward when lateral light readings decreased to 3 to 4 lux, a higher range than the intensities at which the bees of groups 1, 2, and 3 stopped flying.

5) *Top halves of compound eyes covered.* Bees with their ocelli and the bottoms of their compound eyes functioning were flight-tested in daylight and at dusk. All could maintain level flight during both periods, and treated members of both colonies were able to spiral and beeline whenever normal bees were doing so, until intensities fell to 0.3 to 0.5 lux. Treated bees from the nearby colony also were able to zigzag homeward by landmarks whenever their normal counterparts did so.

The results show that the western bumblebee can use its dorsal ocelli alone or in conjunction with the tops of its compound eyes to steer by polarized light. The compound eyes are necessary for maintaining altitude, steering by landmarks, and alighting: that is, for any task requiring perception of form or color. But the larger-apertured ocelli appear to function longer than the small-faceted compound eyes at dusk. With ocelli, the bees can prolong their foraging by continuing to use the directional pattern overhead when the surroundings are too dimly lit for their compound eyes to distinguish landmarks.

Perception of polarized light is not restricted to the ocelli, even in the bumblebee. There are many anocellate species which can perceive polarized light, whether or not they utilize it. An extreme example, the European earwig, *Forficula auricularia* L., is anocellate, photonegative, and highly nocturnal, yet it responds weakly by day and more strongly at dusk to rotation of the Polaroid (*5*). And many other kinds of anocellate insects have enlarged facets in the upper parts of their compound eyes, in effect combining ocellar and ommatidial functions. So dorsal ocelli are no better correlated with polarized-light navigation than they are with the presence of wings or the diurnal habit (*12*).

There are, in fact, so many types of dorsal ocelli that it would be unrealistic to expect only one function (*13*). But conflicting roles have been ascribed to them (*14*), even though most texts still list them with other "stimulatory organs," a group for which no satisfactory explanation exists. There might be less confusion if insects were observed more often in their natural surroundings, where an ocellar linkage with behavior should be easier to discern than it has been indoors (*6, 7*). When the habits of an insect in its natural setting include directed travel by daylight or twilight, steering by zenith polarization patterns becomes one ocellar function worth considering.

W. G. WELLINGTON
Department of Plant Science and
Institute of Animal Resource Ecology, University of British Columbia, Vancouver, Canada, V6T 1W5

References and Notes

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2. M. Lindauer, *Annu. Rev. Entomol.* **12**, 439 (1967). Some greens appear gray to the honeybee eye even in daylight. At dusk, large parts of that gray scale would be virtually indistinguishable.
3. K. von Frisch, *Bees: Their Vision, Chemical Senses, and Language* (Cornell Univ. Press, Ithaca, N.Y., 1971), pp. 113–136. As the greatest percentage of polarized light lies midway between the solar and antisolar points, the band of most intense polarization near sunrise and sunset runs north-south through the zenith.
4. Hymenoptera: Apidae. H. E. Milliron, *Mem. Entomol. Soc. Can. 82* (1971), pp. 58–67.
5. This is part of a study of diurnal changes in the ability of several kinds of flying insects to steer by plane-polarized light (W. G. Wellington, in preparation).
6. Overhead polarization failed regularly around midday near summer solstice, when unpolarized glare near the high sun invaded the zenith, and more sporadically whenever sufficiently heavy clouds, smoke, or haze obscured the zenith. The increasingly smoggy atmosphere near major industrial areas is making outdoor tests more difficult.
7. W. G. Wellington, *Nature (Lond.)* **172**, 1177 (1953); *Ann. Entomol. Soc. Am.* **48**, 67 (1955).
8. Each ground test involved a pair of treated and normal bees. As flight tests were synchronized with types of normal flight or particular states of the sky, each treated bee could be compared with four to eight normal workers flying simultaneously. The following data refer only to bees treated. Group 1, 20 on the ground, 30 in the air; all made multiple flights. Group 2, 26 of 40 on the ground crawled, 50 of 72 in the air flew, none returned. Group 3, 30 flew, none were recovered. Group 4, 30 on the ground; 50 from the nearby colony in the air, all flew, all recovered; 40 from the distant colony could not leave feeding site. Group 5, 50 tested from each of the two colonies; 5 were recovered from that nearby, none from the distant colony.
9. A Kahlsico light meter, model 268WA620, was read in the center of a lawn 24 m in diameter with a sensor 1 m above the ground, facing northward, not skyward.
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15. I thank the Polaroid Corporation for the sheet of Polaroid. Supported by grant A 6239 from the National Research Council of Canada.

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Testing of Computer-Assisted Methods for Classification of Pharmacological Activity

Recently Ting, Lee, Milne, Shapiro, and Guarino (*1*) have investigated the relationship between the pharmacological activity of a set of 66 sedatives and tranquilizers and their mass spectra. They applied several distance criteria for judging mass spectra as similar or different. With the aid of a computer they could transform the mass-spectral data so that drugs with similar pharmacological activity would be "close," and those with different pharmacological activity would be "distant." They then found that they could distinguish sedatives from tranquilizers and thus classify test compounds on the basis of their "neighbors."

It seemed to me quite likely that the authors' set of drugs is not suitable for testing the relationship between pharmacological activity and mass spectrum. The sample population lacks independence, inasmuch as some drugs are obviously related to others. More than half the sedatives are barbiturates and more than half the tranquilizers are phenothiazines. Thus it is not surprising that Ting *et al.* (*1*) could classify cyclobarbital with the other barbiturates. With some of their other successes dependence is not so obvious, and some may be nontrivial. Yet it is possible that a large portion of the set of sedatives (or of tranquilizers) is made up of several families of compounds with similar structures and mass spectra. If so, it is trivial that the mass-spectral data can be transformed so that similar drugs cluster. And the ability to classify a drug would merely reflect the fact that it is a member of a family of sedatives (or tranquilizers). Thus it is not clear to what extent the authors' success is due merely to this lack of independence in the sample population.

To assess the independence, I have applied the authors' simplest nearest-neighbor method just to the *names* of the drugs. To the extent that the drugs are clustered into families, there will be drugs of similar pharmacological activity with similar names. And a test drug may be classified according to the pharmacological activity of drugs with