predominate over passive transport in determining ion movement. Sodium chloride produces higher values of I_{sc} than either sodium acetate or tetramethylammonium chloride (Fig. 3). However, at concentrations above $0.05M$ the sum of I_{sc} for tetramethylammonium chloride and sodium acetate approximates I_{sc} for NaCl at the same concentration. This is shown in Fig. 4, which is based on pooled data from four tongues where each salt was investigated. This near-identity suggests a current composed of an inward Na^+ and a smaller outward Cl^- component.

A NaCl concentration of $0.035M$ produces a null potential. This is about the Na^+ concentration in saliva secreted at basal flow rates (*10*). It is also approximately the recognition threshold for salt taste in humans adapted to saliva (*11*). It is conceivable that normal salivary secretions maintain a transepithelial potential close to zero and that the salt taste response coincides with positive potential changes. Such changes may be produced either by increasing salt concentration or by passing anodal current through a concentration that would be subthreshold as a tastant. In this manner positive potentials might elicit "electric taste" (*12*) as a consequence of externally driven Na^+ and Cl^- currents.

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6. The quantity I_{sc} is defined as the current required to maintain the potential difference at zero with or without a concentration difference across the tissue. We measured the contribution of the series solution resistance to the total in the chambers by substituting filter paper for the tissue. For symmetrical Krebs-Henseleit conditions, this is 44 ohm-cm^2, a correction of 7 percent at most. With 1 mM NaCl in the mucosal bath, the resistance is 7 ohm-cm^2, a correction of 5 percent at most. Under hypertonic conditions the correction amounts to about 7 percent.
7. A detailed account of these effects will appear elsewhere (J. A. DeSimone, G. L. Heck, S. K. DeSimone, in preparation).
8. The ΔV_{oc} and I_{sc} values analyzed herein are steady-state values. Their time course with changes in concentration is, however, an important matter from the standpoint of taste reception. In one experiment in which the mucosal bath was changed from Krebs-Henseleit buffer to $1M$ NaCl, I_{sc} approached its asymptotic value of -137 μA/cm^2 exponentially with a time constant of 74 seconds and an initial rate of increase of 1.4 μA/cm^2 per second. Restoration of the system to symmetrical conditions is slower, requiring about 20 minutes to reach steady state. A complete analysis of transients will be presented elsewhere (*7*).
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Honey Bee Orientation: A Backup System for Cloudy Days

Abstract. *On cloudy days, honey bees are known to navigate to familiar food sources and orient their dances accurately. This capacity could be based on a magnetic compass sense, an ability to perceive the sun or patterns of polarized light through the clouds, or on the bees' memory of the diurnal course of the sun with respect to local landmarks. Experiments pitting these alternatives against one another demonstrate that the navigational backup system of bees is based on memory.*

Forager honey bees use the sun as the primary reference in both navigation and their dance language. The dance communicates the direction of the food to bees in the hive by means of a waggling run performed at an angle with respect to vertical which represents the angle between the azimuths of the sun and food (*1*). A bee must know the sun's position to execute the dance. Under a partial cloud cover, the sun-linked patterns of polarized light in blue sky can replace the sun as an orientation cue (*2*), but even under complete overcast bees continue to orient their dances correctly (*1*), apparently having a second backup system for such sky conditions. Von Frisch *et al.* (*3*) originally proposed that bees might see the sun directly through the clouds in the ultraviolet, but recent sky measurements (*4*) and our preliminary behavioral observations cast doubt on this hypothesis. A second possible explanation is that bees might employ a magnetic compass such as homing pigeons use under overcast (*5*); a third is that bees might be able to remember from previous days the sun's position at each time of day relative to the flight direction or landmarks.

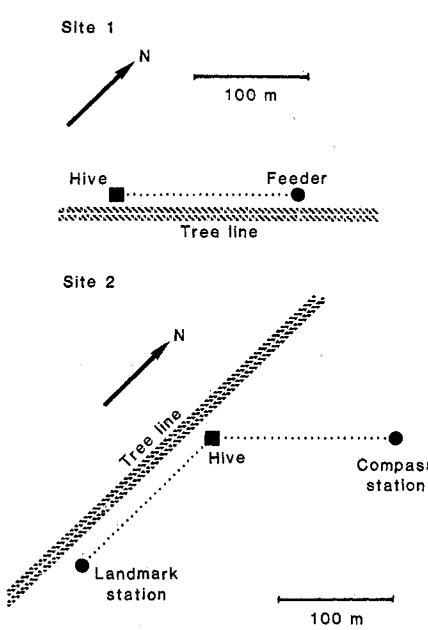

Fig. 1. Tree lines used in experiments. Bees were trained at site 1 under sunny skies, and the hive remained there at all times except on test days, when it was moved to site 2. Both sites are located on sod farms in Lawrence Township, New Jersey.

The third possibility was tested against the first two by exploiting the tendency of experienced bees to rely on landmarks for their flight navigation (*6*). When their hive is moved overnight to a site lacking conspicuous landmarks, bees trained to a food source ordinarily use the sun as a compass and search for food in the direction in which they have been flying previously (*7*). If landmarks are available along the line of flight, however, most experienced bees at a new site ignore the sun, even when it is clearly visible, and search for the food by using similar landmarks (*6*). In the present experiment foragers from an observation hive were individually marked and trained to a feeder containing a scented sucrose solution. The feeder was moved along a line of trees (site 1 in Fig. 1) to a distance of 160 m, and the trained bees were allowed to forage for several days under sunny skies. On test days, the hive was closed and moved to a similar line of trees (site 2 in Fig. 1), which differed in compass bearing from the first by 130°. Two feeders identical to the training feeder were placed 160 m from the hive, one in the original compass direction of training (compass station) and the other along the tree line (landmark station). By moving the hive to the test site on both sunny and cloudy days and monitoring the dances of the bees which used the tree line to fly to the landmark station, we could observe the bees' ability to correct their dance orientations for the 130° change in their flight direction under different sky conditions (*8*).

For each test at site 2, there were two dance directions the foragers returning from the landmark station might adopt:

1) *L prediction*. If the bees can use the sun or the earth's magnetic field correctly as a dance reference despite having used landmarks to fly a new direction to the feeder, they should indicate the true direction of the landmark station. For instance, a dance at noon (when the sun is due south) by a bee which had flown to the landmark station and had seen the sun would be nearly straight up (0°) on the comb.

2) *C prediction*. If bees cannot determine the correct solar azimuth at site 2 (because they are ignoring the sun or simply cannot see it), they should dance as if they were still at site 1. For instance, at noon the direction of the flight to the training feeder (site 1) was 130° to the left of the sun's azimuth. A bee which had treated the tree line in site 2 as the tree line in the training site would dance approximately 130° counterclockwise from vertical at noon.

When the observation hive was moved and opened at site 2 on sunny days, nearly all the trained bees followed the tree line to the landmark station, as expected, and all used the sun's position correctly in their dances (Fig. 2a). All bees flying to the landmark station danced close to the L prediction, and those which found the compass station danced close to the C prediction. The dancers to the L prediction serve as a control to show that even if bees rely exclusively on landmarks to find a food source, they use the correct solar azimuth as a dance reference when they can see the sun.

When the hive was moved and opened at site 2 on an overcast morning (Fig. 2b), orientation behavior was radically different. All the trained bees successfully found the landmark station along the tree line, yet all danced close to the C prediction. Their dances were parallel to the dances of bees which had found the compass station on sunny days (Fig. 2a), even though the flight directions of the two groups differed by 130°. It is clear that the bees flying to the landmark station beneath overcast were not determining the sun's correct position directly from the cloudy sky or by using a magnetic compass; if either had been the case, their dances should have been indistinguishable from the dances of bees flying to the landmark station on sunny days. In fact, when the sun and blue sky began to appear through the clouds in the afternoon, bees which had been dancing near the C prediction all day corrected their mistake and danced exclusively toward the L prediction.

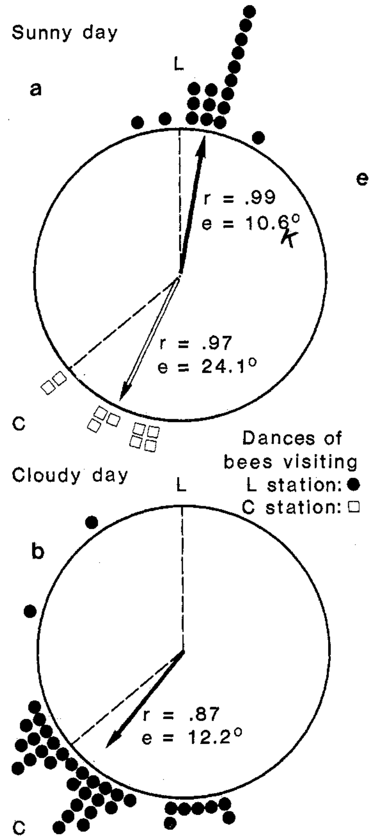

Fig. 2. Dances on the vertical comb at site 2 on both sunny and cloudy days. Each dance angle was plotted relative to the predictions at the time of the dance (see text). In this way dance angles which differed because the sun's azimuth had changed during the day were compared directly. The two predictions, like the compass orientations of the two tree lines, differ by 130°. Symbols: (●) dance by bee foraging at the L feeder; (□) dance by bee foraging at the C feeder. (a) Data compiled on 23 September 1980 [9:50 to 10:20 a.m. eastern daylight time (EDT)] and 30 September 1980 (10:30 to 11:10 a.m. EDT), both sunny days. L distribution: a total of eight bees performed the 18 dances. The mean vector was nonrandom ($P << .001$) according to the Rayleigh z test and corresponded to the L prediction ($P << .0001$) by the V test. C distribution: a total of two bees performed the nine dances. The mean vector was nonrandom ($P << .001$; z test) and oriented in the expected direction (C prediction; $P << .0001$; V test). The L distribution and C distribution are significantly different ($P << .001$; Watson U^2 test). (b) Data of 11 October 1980 (9:30 a.m. to 2:45 p.m. EDT), a cloudy day. All bees flew to the L feeder. The mean vector of 36 dances by 11 bees was nonrandom ($P << .001$; z test) in the direction of the C prediction ($P << .0001$; V test). Statistics are described in Batschelet (*9*).

Thus, experienced bees are able to forage and communicate on cloudy days by determining the solar azimuth through a memory of the sun's course with respect to local landmarks. Considering the necessity for wild honey bees to maximize their foraging efficiency or face winter starvation, it is no surprise that a backup system has evolved to permit recruitment to food under overcast. What is surprising is the sophistication of the backup system that these experiments reveal, since the bees' memory must both keep track of time and account for the movement of the sun during the day. Although most animals must orient on cloudy days, the sun compensation aspect of this landmark-based orientation system may be unique to honey bees because of the peculiar requirements of their dance language. The implication of these results for insects (and animals in general) is that, contrary to a long-established belief derived from von Frisch's original conclusions about bees (*1*, *3*), celestial orientation cues are probably not available on most overcast days.

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