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Polarized-Light Navigation
by Insects

*Experiments demonstrate that bees and ants find their way home
by the polarization of the light of the sky. The detection system
insects have evolved for the purpose is remarkably sophisticated*

by Rüdiger Wehner

The eyes of insects are sensitive to a natural phenomenon that man is blind to: the polarized light of the daytime sky. It is this capacity that underlies the remarkable navigational ability of many insect species. Exactly how can an insect navigate by polarized light? To ask this question is really to raise three separate questions: What makes the visual cell of an insect sensitive to polarized light? How do some minimum number of visual cells cooperate to determine the direction of polarization at one point in the sky? How much information from how many points in the sky does the insect need for unambiguous navigation?

The light radiated by the sun is unpolarized, that is, its waves vibrate in all directions at right angles to the line of sight. In traveling through the earth's atmosphere, however, it is scattered by molecules and other particles that are small with respect to the wavelength of light, so that at each point in the sky its waves tend to vibrate in a specific direction. This atmospheric polarization was first described by Lord Rayleigh in 1871, but it was not until 1950 that it was given a full theoretical analysis by S. Chandrasekhar of the University of Chicago. More recently a computer analysis has been developed by Zdenek Sekera and his colleagues at the University of California at Los Angeles. Their program makes it possible to specify both the directions and the degrees of polarization for all points in the sky, for different atmospheric conditions and for spectral wavelengths ranging from the infrared to the ultraviolet.

The pattern of polarization in the sky varies with the position of the sun or, more exactly, with the orientation of the plane of a triangle formed by the sun, the observer and the point observed [*see top illustration on page 109*]. At any point on the celestial sphere the direction of polarization is always perpendicular to the plane of such a triangle. By disregarding a few exceptions and applying this general rule to all points in the sky one can determine the entire pattern of polarization for any given position of the sun.

The general rule for the polarization of light by the atmosphere is easily demonstrated by making photographs of the sky with a 180-degree "fish-eye" lens fitted with a polarizing filter. Consider a pair of photographs that are taken just as the sun reaches the horizon [*see upper illustration on page 108*]. When the polarizing axis of the filter is parallel to the solar meridian (the arc connecting the sun and the zenith), a broad dark stripe runs across the celestial hemisphere at right angles to the solar meridian; the center of the stripe is 90 degrees away from the sun. When instead the polarizing axis of the filter is perpendicular to the solar meridian, no such stripe is evident. The presence of the stripe in the first instance is a function of the direction of skylight polarization at sunrise and sunset; the maximum polarization is found 90 degrees away from the sun. The pattern of polarization shifts around the celestial hemisphere as the sun moves across the sky; this too can be documented by successive fish-eye-lens photographs.

The ability of honeybees to navigate by the polarized light of the sky was first described some 25 years ago by Karl von Frisch. His finding came as a surprise; even though the polarization of skylight had been known since the 19th century, no one had really considered the possibility that the phenomenon could serve any navigational purpose. It has recently been learned, however, that about the year 1000 the Vikings were taking advantage of the polarization of skylight in their voyages west from

LONG-LEGGED ANT (*Cataglyphis bicolor*) of the North African desert was used by the author and his students in their studies of polarized-light navigation by insects. The ant forages until it finds food and then runs straight back to its nest. It can be trained for experimental purposes by rewarding it with a small piece of cheese. This ant holds cheese in its mandibles.

Iceland and Greenland to Newfoundland. The Danish archaeologist Thorkild Ramskou has pointed out that the "sunstones" described in the old sagas were nothing other than birefringent and dichroic crystals that could serve as polarization analyzers.

As I write this article I have on my table a small crystal of cordierite. When I look through it at any point in the sky, I can determine the direction of polarization by observing the changes of color and brightness as I rotate the crystal around the line of sight. Some years ago an airplane was steered with fair precision from Norway to Sondre Storm Fjord airfield in Greenland with a cordierite crystal as the only navigational aid. These crystals can be found as pebbles on the coast of Norway. Although it is unlikely that the Vikings knew anything about polarized light, they apparently perceived the relation between what they saw through a sunstone and the position of the sun (which was often hidden by clouds in those northern latitudes).

There are no polarizing crystals in the eye of insects. The eye of the members of another major group of arthropods—the now extinct marine trilobites—did have hundreds of lenses consisting of the highly birefringent crystal calcite, but the crystals were arranged in such a way that they could not have acted as polarization analyzers. Of course, that does not exclude the possibility that the trilobites were able to use the polarization of skylight for orientation in their marine habitat; Talbot H. Waterman of
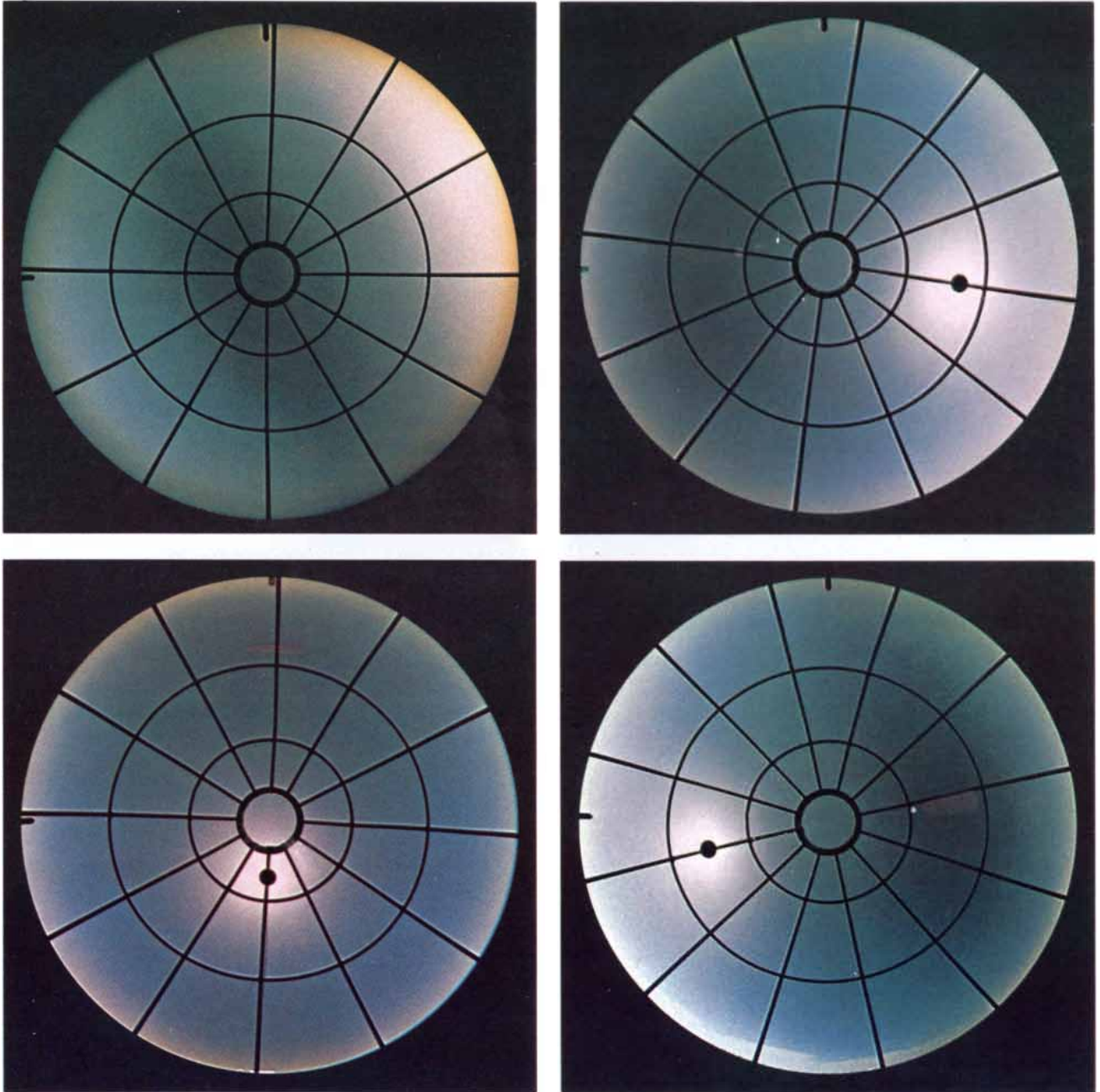
CHANGE IN THE POLARIZATION of the light of the sky at different times of the day is shown in this sequence of photographs made with a 180-degree "fish-eye" lens and a polarizing filter. The photographs, made on May 17, 1975, near Kairouan in Tunisia, were exposed at 5:15 A.M. (top left), 9:05 A.M. (top right), 12:30 P.M. (bottom left) and 3:40 P.M. (bottom right). A small black screen masks the sun in all the photographs but the first one; the screen also identifies the solar meridian. The axis of the polarizing filter was parallel to the solar meridian in all four photographs. At dawn maximum polarization (dark region), located 90 degrees from the sun, is centered in the sky. After sunrise the dark area shifts to the west. At the sun's maximum elevation in the southern sky the dark area shifts to the north; as the sun descends the dark area shifts around to the east. The two marks that appear on the horizon in the photograph indicate north and west.

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Yale University has shown that the skylight visible to underwater organisms, like that visible to organisms that live above the water or on land, is polarized. It only means that the lenses were not analyzers located in front of the visual cells. The same is true of insects. Where, then, are the structures in insects that are sensitive to polarized light?

It is now generally agreed that the structures are located within the visual cells themselves. The ability of the visual cells to analyze the axial orientation of the polarized light is the result of a molecular oddity. In all animals, invertebrates and vertebrates alike, the visual pigment rhodopsin is pres-
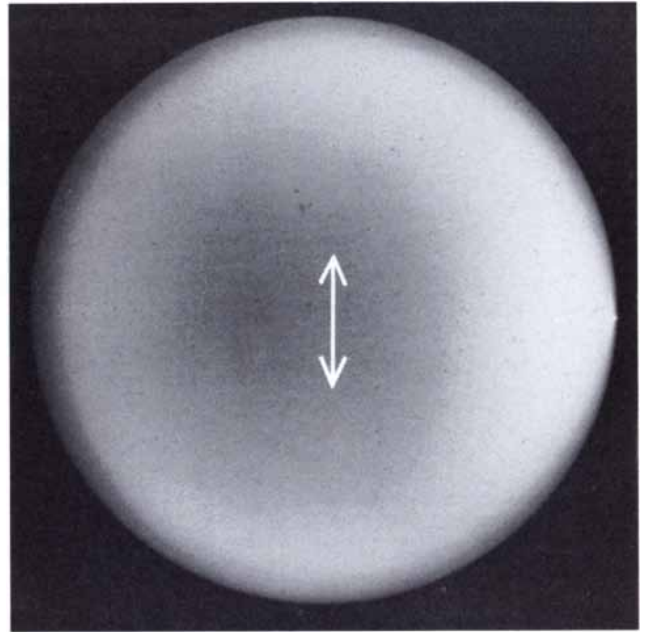
ent in the photoreceptor membrane of the visual cells in the form of dipolar molecules, that is, molecules with a distinct axis. As a result the pigment absorbs a maximum of the incoming polarized-light energy when the direction of polarization is parallel to the dipole axis of the molecule.

In insects the photoreceptor membranes are bent into arrays of narrow tubes, the microvilli [see illustration on page 110]. Timothy H. Goldsmith of Yale and I have come to the conclusion, based on spectroscopic studies we conducted together at the Marine Biological Laboratory in Woods Hole, Mass., that the rhodopsin molecules

in the microvillar membrane are preferentially aligned parallel to the axis of the microvilli. Such an orientation would of course result in the maximum absorption of polarized light when, and only when, the axis of polarization coincided with the microvillar axis. (This, incidentally, is part of the reason the human eye is blind to polarized skylight. Among vertebrates, man included, the rhodopsin molecules are free to rotate in the photoreceptor membrane, so that their axial orientation is random. There is an equal chance that any pigment molecule will maximally absorb light with any direction of polarization, and so there is
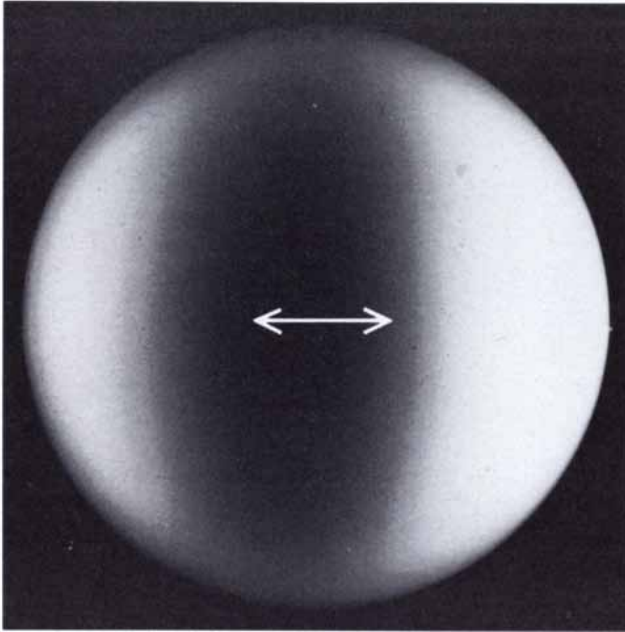
MAXIMUM POLARIZATION, demonstrated (*left*) with a fish-eye photograph of the dawn sky, is evident when the transmission axis of the polarizing filter is parallel to the solar meridian. When the axis is perpendicular (*right*), however, variation in intensity disappears.
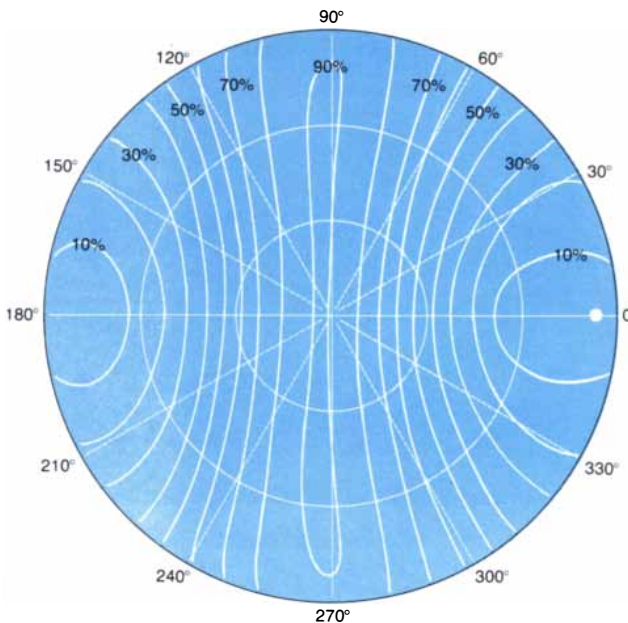
DEGREE OF POLARIZATION (*left*) and direction of polarization (*right*) at dawn are shown in these graphs of the celestial hemisphere. At the left contours connect points with an equal degree of polarization. At right arrows on contours indicate direction of polarization.
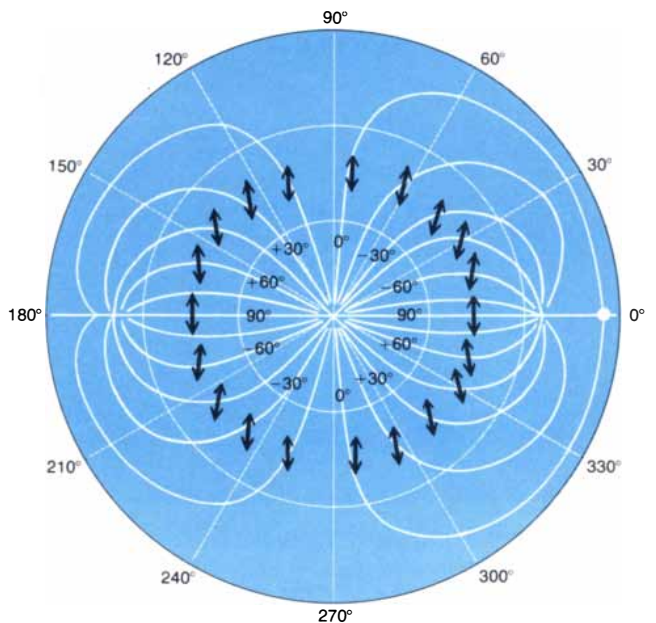
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no particular sensitivity to the polarization of skylight.)

The common orientation of the rhodopsin molecules in the insect's photoreceptor membrane is not in itself enough to allow the analysis of skylight polarization, just as one kind of color receptor is not enough to allow color vision. Different kinds of receptors, each maximally sensitive to a different direction of polarization, must work together in order to enable the detecting system to provide unambiguous results for any direction of polarization. For example, the system must be proof against confusion arising from fluctuations in mean light intensity, degree of polarization and hue of color. But how many receptors are enough? Here we suspected that the principle of parsimony might apply. The number of receptors could be held to a minimum if only one type of color receptor was involved: the ultraviolet receptor, the blue receptor or the green receptor. If two of these types of receptor or all three contributed to polarized-light analysis, more receptors would have to cooperate and more neural circuitry would be needed. Hence natural selection should strongly favor a system that receives its input from only one type of color receptor. What, then, are the spectral wavelengths involved in the perception of polarized light? This question could be most conclusively answered by behavioral experiments.

Bees are only one of many kinds of insects that have been shown to navigate by the polarization of skylight. Ants also do so, and my students and I at the University of Zurich have used both bees and ants as experimental animals in our studies. In most of our experiments a desert ant native to North Africa, the species *Cataglyphis bicolor,* has been the preferred animal for several reasons. First of all, it is difficult enough to follow a flying bee over any great distance, but to keep a polarizer or any other optical equipment in place above a bee as it flies is impossible. The desert ant is a running forager, but it rarely runs faster than 20 meters a minute, which is less than a mile an hour. This enables the experimenter to record the ant's navigational courses in full detail and at the same time to continuously interpose between the animal and the sky almost any kind of optical equipment.

In addition the desert ant is a solitary hunter; it never forages en masse along a scout's scent trail as so many other ant species do. Its desert habitat is notably lacking in conspicuous landmarks, so that the ant must rely almost exclusively on skylight cues to guide it on its forays. A typical *Cataglyphis* excursion of the kind we have often recorded begins when the ant leaves its underground nest. The ant then meanders, covering a distance that may be equivalent to the length of a football field, until it captures prey. After that it runs straight back to the nest.

When I first observed these long-legged ants eight years ago, I was fascinated both by the extraordinary precision of their orientation and by their remarkable learning
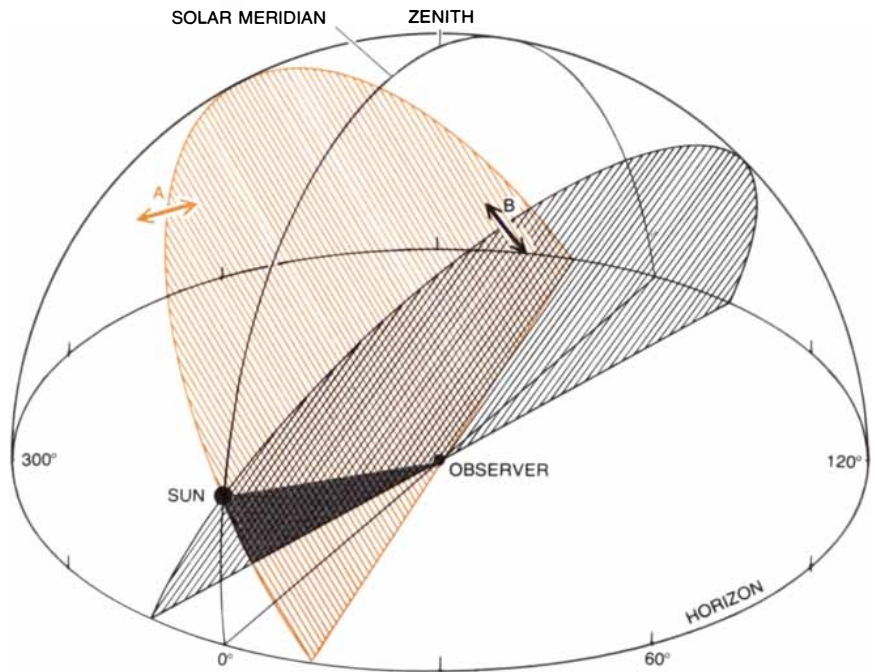

AXIS OF POLARIZATION (*short two-headed arrows*) of the light of the sky is always perpendicular to the plane of a triangle connecting the observer (*center*), the sun and the point in the sky being observed. The examples shown are for the points *A* and *B* on the celestial hemisphere. The planes of the great circles passing through the sun and each of the two points are hatched. Also shown is the solar meridian: the great circle passing through sun and the zenith.

capacity. Individual ants were easily trained to travel in a given direction for a given distance by rewarding them with a tiny piece of cheese. For experimental purposes we would transport the trained ants to a remote testing area, carrying them in individual lightproof flasks. The testing area, a hard sandy plain, was painted with a grid of fine white lines, a coordinate system that enabled us to record the ants' running courses on a reduced scale for later statistical analysis.

When each trained ant was released, it would set off in the home direction. It
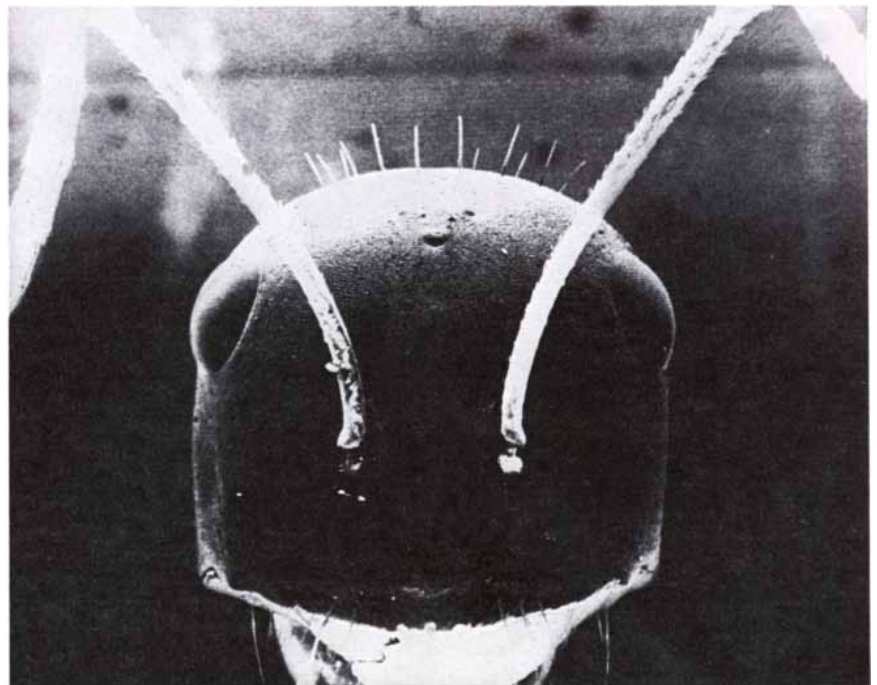
HEAD OF THE DESERT ANT is seen from the front in this scanning electron micrograph. Projecting upward from the front of the head are the antennae. At the left and right side of the head are the eyes. The fine pattern visible on the surface of the eyes is the ommatidia: the subunits into which the insect eye is divided. Each eye of desert ant is made up of 1,200 ommatidia.

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RETINAL ROD

AREA ENLARGED

25 NANOMETERS

2,000 NANOMETERS

OMMATIDIUM

AREA ENLARGED

50 NANOMETERS

1,000 NANOMETERS
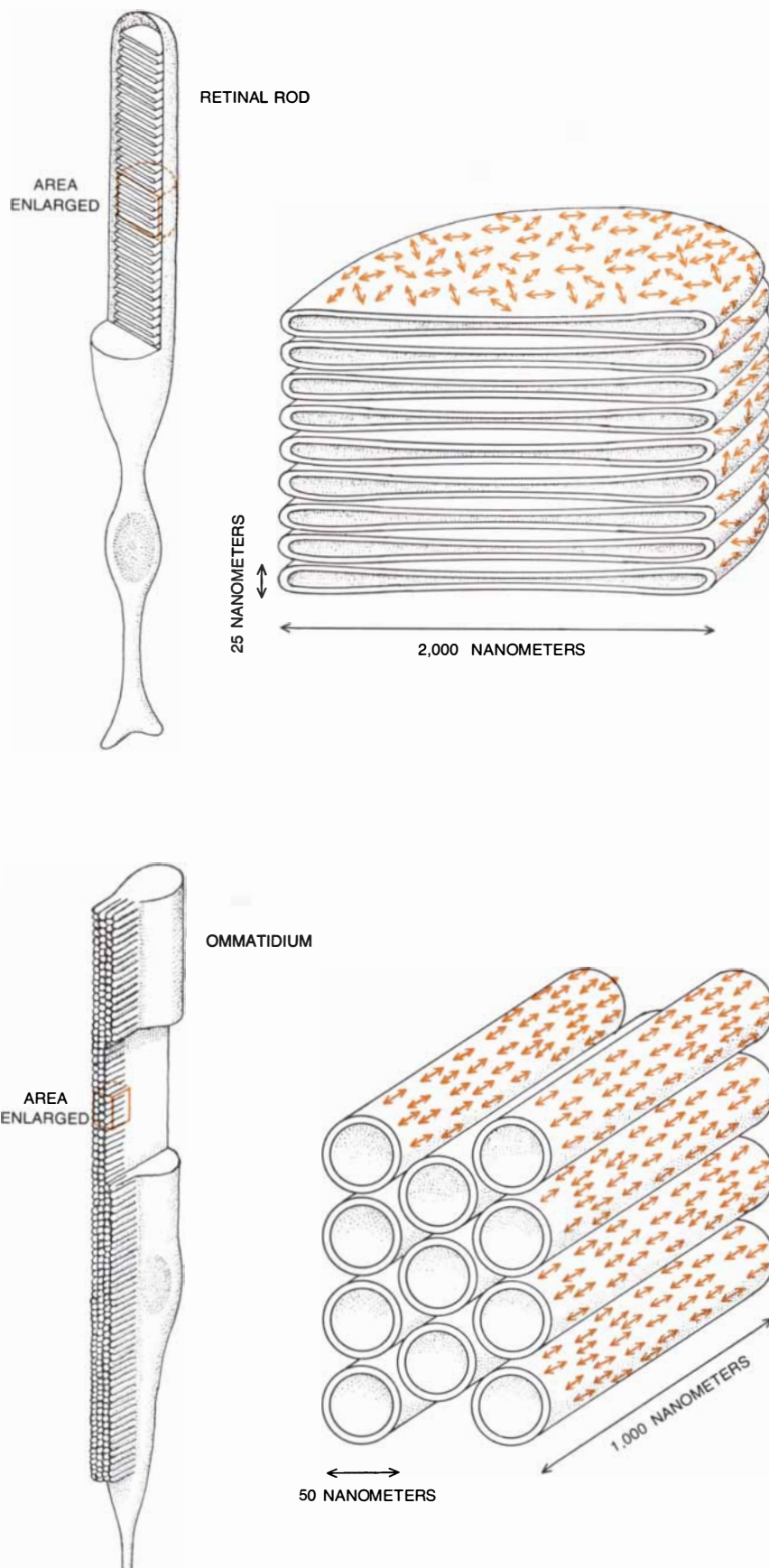
VISUAL CELLS of vertebrates (*top*) and invertebrates (*bottom*) differ in arrangement of photoreceptor membrane and orientation of molecules of visual pigment rhodopsin within membrane. In vertebrates axes of rhodopsin molecules (*color*) are randomly oriented; in insects they are parallel to long axis of tubelike microvilli. This maximizes absorption of polarized light.

would travel the distance to which it had been trained and then start to circle at the place where the nest was supposed to be. (The actual nest might have been more than a mile away, where the ant had been trained.) On its journey back from the releasing point the ant was accompanied by a small vehicle loaded with optical equipment: neutral-density filters, spectral-cutoff filters, polarizers, depolarizers, retardation plates and so on. These and many similar open-field experiments could not have been accomplished without the enthusiastic cooperation of my graduate students. I am particularly indebted to Peter Duelli (who constructed the vehicle and developed considerable skill in piloting it), Immanuel Flatt, Res Burkhalter (who is now working at the Brain Research Institute in Zurich) and Reto Weiler of the University of Munich.

In order to discover what spectral wavelengths were utilized in skylight navigation we forced the running ants to view the sky through filters of various colors. We were surprised to find that their ability to detect polarized light disappeared completely at wavelengths greater than 410 nanometers; those wavelengths include the entire range of wavelengths visible to man. In light of that spectral range the ants ran in random directions. When we extended the spectral range only a little way into the ultraviolet, however, the ants' navigational accuracy was completely restored.

We concluded from this finding that only those visual cells in the ant's eye that are responsive to ultraviolet wavelengths are involved in the perception of polarized light. This can readily be confirmed by comparing the spectral-transmission functions of the filters with the spectral-sensitivity function of the ultraviolet receptor as measured electrophysiologically. Recently Otto von Helversen and Wolfgang Edrich of the University of Freiburg have shown that in bees too the ultraviolet receptors are the only ones involved in the detection of polarized light.

It is easy to understand why natural selection has made the ultraviolet receptors the input channel for an orientation signal. The use of only one type of receptor conforms with the principle of parsimony by holding the input channels down to three, which, as we shall see, is the minimum number. That the type of receptor selected was sensitive to ultraviolet instead of, say, green or blue can be regarded as an adaptation to a purely physical fact: it is in the ultraviolet range of wavelengths that the polarization of skylight is least affected by atmospheric disturbances and is therefore the most stable.

Let us now turn to the second question and consider the insect eye in somewhat more detail. How do the ultraviolet receptors cooperate in detecting polarized light? As is well known, insects have compound, multifaceted eyes. Each eye is composed of hundreds or thousands of the subunits known as ommatidia. Our desert ant's eye

has 1,200 ommatidia; a worker bee's eye has 5,500. Each subunit has its own lens system, and underneath the lens are elongated visual cells that contain the densely packed tubular microvilli where the rhodopsin molecules are located. The microvilli are arranged so as to meet and form a central structure, the rhabdom, which functions as a light guide [see illustration below].
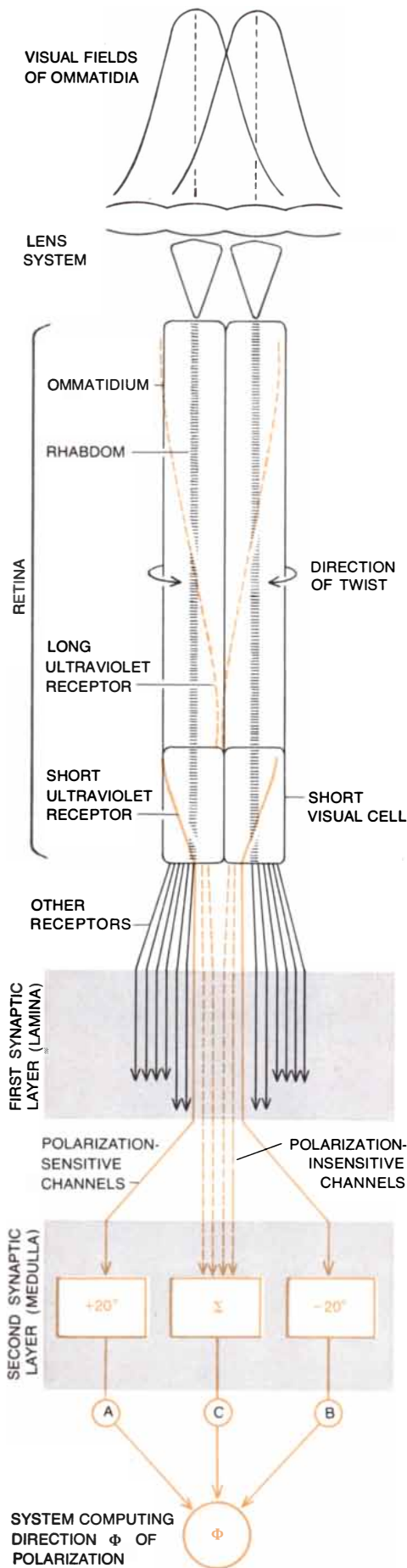
There are nine visual cells in each ommatidium. Eight of them are elongated and the ninth is foreshortened. Thus whereas the microvilli of the eight long cells contribute to the rhabdom along its total length, the contribution of the short ninth cell is confined to the lower end of the structure. From a number of independent electrophysiological and neuroanatomical studies one can draw the conclusion that in bees and ants three of the nine cells in each ommatidium are ultraviolet receptors: the
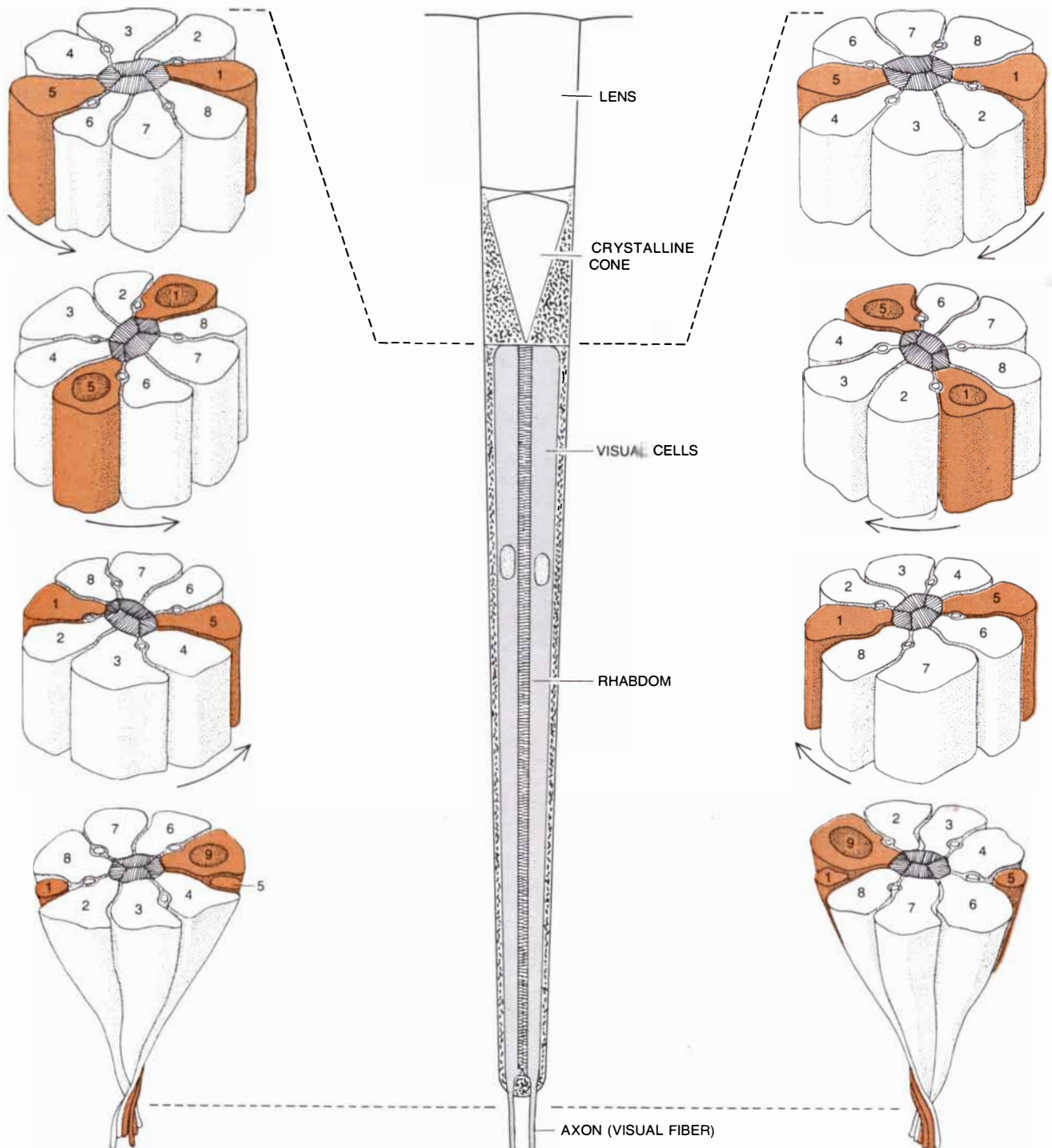
EYE OF THE HONEYBEE is made up of some 5,500 ommatidia, each consisting of nine visual cells and an overlying optical apparatus: a lens and a crystalline cone (center). Eight of the visual cells are elongated; the ninth is short and is confined to the base of the ommatidium. All nine of the cells are twisted. Half of the ommatidia in the bee's eye are twisted clockwise and half are twisted counterclockwise (left and right); the two kinds of ommatidium are randomly distributed. The microvilli, which are distributed along the inner edge of each cell, jointly form a central structure, the rhabdom; its membranes incorporate the rhodopsin molecules. Because two of the three visual cells that are sensitive to ultraviolet radiation (color) are twisted 180 degrees their preferential sensitivity to polarized light has been lost. The third cell, however, is the short cell; since it is twisted only about 40 degrees, it has retained sensitivity to polarized light.

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VISUAL FIELDS
OF OMMATIDIA

LENS
SYSTEM

OMMATIDIUM

RHABDOM

RETINA

DIRECTION
OF TWIST

LONG
ULTRAVIOLET
RECEPTOR

SHORT
ULTRAVIOLET
RECEPTOR

SHORT
VISUAL CELL

OTHER
RECEPTORS

FIRST SYNAPTIC
LAYER (LAMINA)

POLARIZATION-
SENSITIVE
CHANNELS

POLARIZATION-
INSENSITIVE
CHANNELS

SECOND SYNAPTIC
LAYER (MEDULLA)

+20°   Σ   −20°

A   C   B

SYSTEM COMPUTING
DIRECTION Φ OF
POLARIZATION

Φ

short receptor and two of the long ones. Among the workers who contributed to this conclusion are F. G. Gribakin of the U.S.S.R. Academy of Sciences, Randolf Menzel and Allan W. Snyder of the Australian National University, Hansjochem Autrum and Gertrud Kolb of the University of Munich and ourselves at the University of Zurich. Of particular note was Menzel's demonstration by intracellular recordings that the short visual cell of bees is an ultraviolet receptor.

We had started with the assumption that the most elegant system for the perception of polarized light would involve only one type of color receptor, most efficiently the ultraviolet receptor. It was satisfying to have this assumption confirmed. We were nonetheless startled by its implications, because we knew that at any given cross section of the ommatidium the microvillar orientation of the three ultraviolet receptors coincided. This meant that they could provide the analyzing system with only one input channel. Since more than one channel is needed for detecting polarization, more than one ommatidium must be involved. The question was: How many are involved?

At that time Kuno Kirschfeld of the Max Planck Institute for Biological Cybernetics in Tübingen had just proposed a theoretical model according to which three receptors with three different microvillar directions had to cooperate. When my student Esther Geiger and I looked at cross sections over fairly extensive areas of the bee's retina, however, we could not find the three necessary sets of ultraviolet receptors, which should be characterized by different microvillar directions. Furthermore, it had never

been proved beyond any doubt that the microvilli of one visual cell were really aligned parallel to one another along the entire length of the cell. The sensitivity of the cell to polarized light should nonetheless depend critically on such an alignment.

As we were working on a three-dimensional reconstruction of the ommatidia in the eye of the bee, a striking feature caught our attention and turned it in a new direction. It turns out that all rhabdoms are twisted. The twist extends the full length of the structure and amounts to about one degree per micrometer. In an elongated cell the twist totals 180 degrees from top to bottom. The twist is either clockwise or counterclockwise. Twists in each direction occur with equal frequency, and ommatidia enclosing rhabdoms twisted each way are randomly distributed in the insect's eye.

Recently Gary D. Bernard of the Yale Medical School and I conducted an optical analysis of the twisted rhabdoms. We discovered that the 180-degree twist deprives the two long ultraviolet-receptive visual cells of any sensitivity to polarized light. The short cell, however, is twisted only some 40 degrees, and so it is not severely deprived of its sensitivity to polarized light. Moreover, half of the short cells are twisted 40 degrees to the right and the other half 40 degrees to the left, so that their directions for maximum sensitivity do not coincide but are at an angle of 35 to 40 degrees. This means that any two short cells of opposite twist are perfectly designed to act as two independent polarization analyzers.

On the basis of these data we have constructed a simple theoretical model explaining how the eye of the insect analyzes the direction of skylight polarization. In brief, the model indicates that if two polarization

RESPONSE OF VISUAL CELL →

40°

A   B   C

0°   90°   180°   270°

ANGLE OF SKYLIGHT POLARIZATION (Φ)
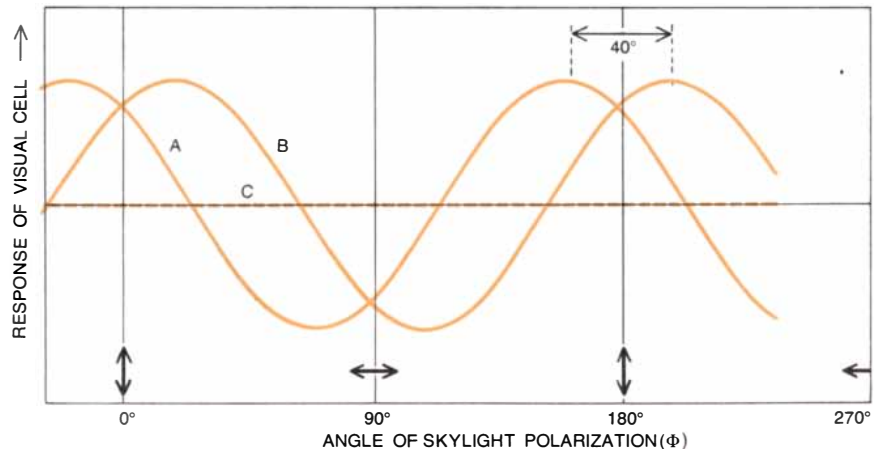
POLARIZATION-DETECTING SYSTEM of the honeybee is depicted schematically. The ultraviolet receptors of two adjacent ommatidia, one twisting clockwise and the other counterclockwise, are sufficient for the detection of any direction of polarization. Both ommatidia scan nearly the same small patch of the sky, less than five degrees in diameter. In the two ommatidia three types of ultraviolet receptors have to cooperate: polarization-insensitive cells (signal C) and two independent polarization-sensitive cells (signals A and B). This set of cells can unambiguously detect any direction of polarization (Φ). The directions of maximum sensitivity of the two polarization-sensitive cells differ by about 40 degrees, as is shown by the curves at the right. The nerve fibers extending from the ultraviolet receptors extend through the first of the insect's two visual ganglia (the lamina) to the second (the medulla). The nerve fibers extending from the receptors sensitive to green and blue light rather than to ultraviolet end in lamina.

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analyzers of opposite twist work together with at least one long ultraviolet-sensitive cell that is insensitive to the polarization of skylight, then the orientation of the skylight polarization anywhere overhead can be determined unambiguously. Hence any two adjacent ommatidia of opposite twist are equipped with all three of the necessary cells and will provide the analyzing system with all three of the necessary signals: two independent signals that are modulated by polarized skylight and one signal that is not. The unmodulated signal is identical for all the long ultraviolet receptors of the two ommatidia.

The twist of the rhabdoms was surprising at first. After all, a straight alignment of the microvilli had always been considered a prerequisite for the analysis of polarized light. We have come to realize not only that analysis is possible in spite of the twist but also that the twist is exploited in the analytical process. On the one hand the twist ensures that the one long cell of the three is an input channel free of sensitivity to skylight polarization. On the other it ensures that the axes of the microvilli in the two polarization-sensitive input channels point in two different directions.

A skilled engineer could hardly design a simpler and more elegant system. Menzel and his colleague Margaret Blakers, working at the Technische Hochschule in Darmstadt, have found that the eye of a large hunting ant, the bulldog ant of Australia, has the same two kinds of oppositely twisted rhabdoms. Thus it appears that the eyes of ants as well as those of bees have a set of ultraviolet-receptive visual cells that are specially adapted to the strategy of detecting the polarization of skylight.

To recapitulate, any system that is capable of unambiguously analyzing polarized light with only one type of color receptor has to be fed by three independent receptors. That is because any state of partially polarized light as it is analyzed by an insect can be completely described by three independent numbers: direction of polarization, degree of polarization and mean intensity. If all three receptors are sensitive to polarized light, they have to show maximum sensitivity in different directions. In an insect's eye this would mean that three ultraviolet receptors with different microvillar directions would have to cooperate. In the bee, however, only two of these polarization-sensitive receptors function. Since their directions of maximum sensitivity are neither parallel nor crossed, they have only to cooperate with a polarization-insensitive receptor, a long twisted ultraviolet receptor cell, to get all the information on a given state of polarization. There are several reasons why the system with two polarization-sensitive receptors is more advantageous than the system with three. One reason, to which I shall return, is that the long twisted ultraviolet receptor can also contribute to color vision without introducing a polarization-sensitive signal into that system.
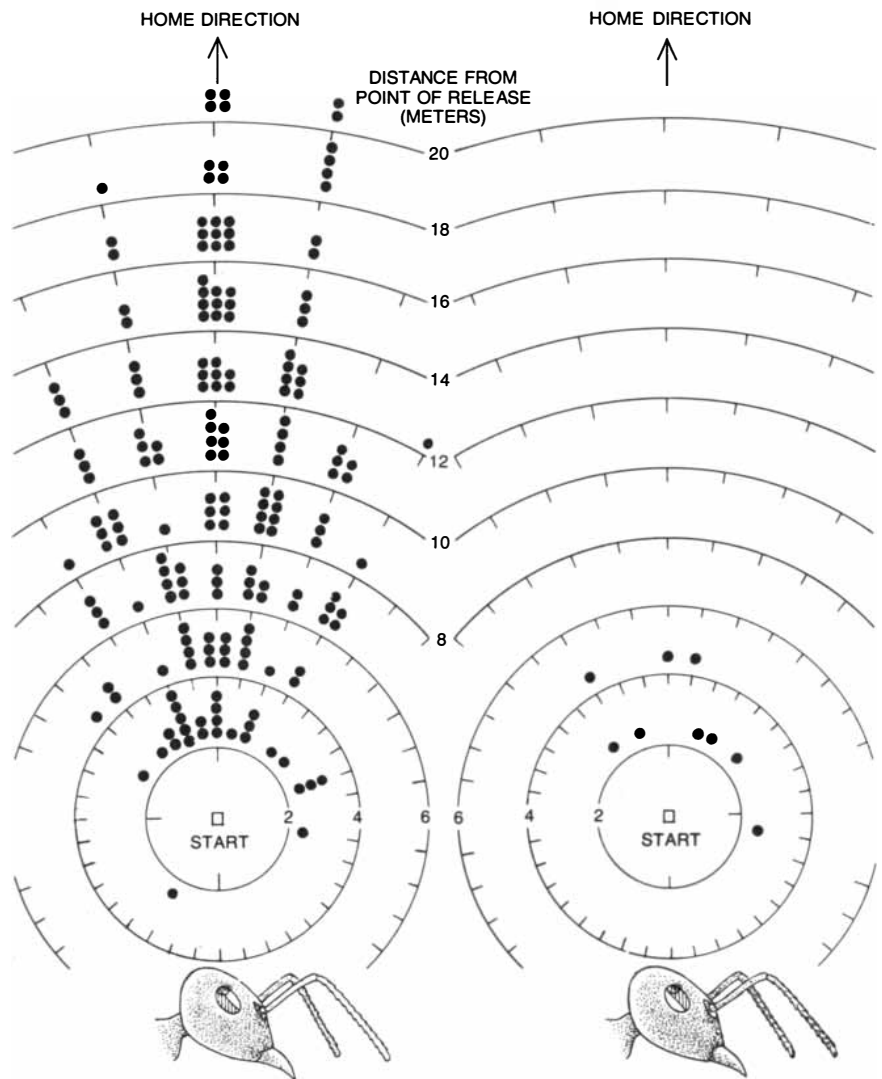
LOCATION OF OMMATIDIA in the desert ant's eye that perceive polarized ultraviolet radiation was confirmed experimentally by covering parts of ants' eyes with opaque paint. At the bottom are the heads of two experimental ants. The ommatidia that are sensitive to polarized ultraviolet radiation are at the upper front part of the eye (*small spot of color*). When the rear third of the eye was covered with paint (*hatching*), the ants' navigational ability was scarcely affected (*diagram at left*). Ants released at the starting point were found at various distances (*black dots*) along the way home. When the front third of the eye was covered, however, only a few of the ants went beyond the circle two meters from starting point, and none passed six-meter circle (*diagram at right*). Ants that remained within two-meter circle were not recorded.

The eyes of ants and bees, with their large number of ommatidia, simultaneously scan many different parts of the celestial hemisphere. And as we have seen, the light from the celestial hemisphere is differently polarized at different points in the sky. Neither insect, however, seems to have a nervous system complex enough to process signals from thousands of points in the sky. How many of these ultraviolet receptors are actually used for navigation, and which ones are they? We sought answers to these questions in two different ways. One was to cover specific regions of an ant's eyes with opaque paint and then observe its behavior. The other was to add a device to our tracking vehicle that enabled us to restrict the ant's view of the sky to one part or another of its normal visual field. Both approaches soon

demonstrated to our satisfaction that the part of the compound eye utilized by our desert ants for the detection of polarization is a small region near the upper edge of the eye. This specialized area is physically apparent from above the ant's eye as a small depression in the array of ommatidium lenses. Moreover, my former graduate student Paul L. Herrling has examined the structure of the visual cells of the ant and has found a completely different type of rhabdom near the upper edge of the eye.

The ant's dependence on the signals from this specialized area is dramatic. Insects can move their eyes only by moving their heads. When we blacked out the lower part of an ant's visual field (by inserting a screen in the device on our tracking vehicle), its behavior was unaffected until the blackout reached

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the lower edge of the area specialized for polarized-light perception. Then each upward shift of the screen was matched by a compensating upward tilt of the ant's head. As the screen was moved upward toward the zenith, a point was reached where the ant could not lift its head any higher; it would then turn a backward somersault, ending the experiment. By motion-picture analysis of the head positions we were able to plot the dimensions of that part of the eye which is concerned with the detection of polarized light.

In mapping the areas of the eye that play a role in skylight navigation we arrived at a further conclusion: In both ants and bees fewer than 10 ommatidia in the upper part of the eye are enough for the detection of polarization. So far our results do not allow us to judge whether the theoretical minimum predicted by our model—two adjacent ommatidia of opposite twist—might suffice or whether several pairs of ommatidia must cooperate to provide the precision necessary for navigation.

Here the last of the three questions arises. If an insect can unambiguously determine the direction of polarization at any point in the sky, does this ability in itself guarantee that the insect can navigate unambiguously? The answer is no. The one would unerringly lead to the other only if every point in the sky had its own exclusive direction of polarization. Such is not the case; any given direction of polarization is found at many different points in the sky.

How does the insect cope with this complicated and potentially ambiguous situation? It is hard to believe that the information about all the directions of polarization varying between different positions in the sky and different times of day are stored in an insect's brain. Most likely the insect applies a general rule. What is that rule?

Let us consider some possibilities. There is one point in the sky the insect can always view regardless of whether it is moving north, south, east or west. That point is the zenith. According to the general rule of skylight polarization outlined above, the solar meridian (the arc through the sun and the zenith) extends at right angles to the direction of polarization in the zenith. Therefore, knowing that direction, the insect knows the position of the solar meridian in the sky. What it needs for an unambiguous decision is merely some means of deciding between both arcs of the solar meridian. Any additional cue that differs between both arcs of the solar meridian could suffice: the degree of polarization, the hue of color or the intensity of ultraviolet radiation in the sky.

Our desert ant, however, does not view the zenith with the region of the eye specialized for skylight navigation, so that a more general possibility has to be considered. If the degree of polarization is sufficiently high, the direction of polarization is parallel to the horizon at every point on the solar meridian. If one proceeds along a circle of given elevation from one arc of the solar meridian to the opposite arc, the direction of polarization first deviates increasingly from the horizontal and then approaches the horizontal again. Does the insect "know" this relation?

In collaboration with Martin Lindauer of the University of Würzburg and my student Samuel Rossel I have tested the hypothesis, using bees as the experimental animal. From a practical point of view it might appear more difficult to perform the appropriate experiments with bees than it is with our desert ants. This would be true if it were not for a behavioral characteristic of bees: the

workers communicate with their fellows, translating the course to be flown to a source of food into the direction of their "waggle dance" inside the hive. The direction of the bee's waggle dance on a horizontal honeycomb coincides with the direction of its foraging flight, provided that the bee can see the sky as it dances. Hence one can confine the bee's vision to certain parts of the sky and observe the effect of this limitation on its capacity to navigate, that is, to dance correctly.

For our experiments we placed a horizontal comb inside a planetarium dome where we could keep the bees from seeing any areas of the outside sky other than the selected ones. The bees had previously been trained to fly in a certain direction and to forage at a distant food source. Each bee was individually marked with a color code. In each test the patch of sky visible to the bee was so small—10 degrees in diameter—that only skylight with a single direction of polarization entered the planetarium.

Under such conditions the bees alternately danced in two directions: in the correct direction and in another direction they had never flown. This is exactly the result one would expect, because in general each direction of polarization is found twice in a circle of given elevation. Since in our experiment the bee was allowed to view only one point in the circle of given elevation, it could not decide between the two different navigational courses indicated by an identical direction of polarization.

Surprisingly, however, the wrong direction as danced by the bee did not coincide with the wrong direction as calculated by the actual distribution of polarization angles in the sky. The mismatch between the expected dance angle and the real dance angle was not accidental but consistent. Even more surprising, we were able to mislead the bees. With the aid of a polarizer we could change the direction of polarization in the point of the sky viewed by the dancing bee. When we changed it to those directions that did not occur in the natural sky at that elevation, the bees nonetheless showed a consistent orientation. What we had expected, of course, was a random orientation. This finding is exciting and may well lead to an overall solution of the insect-navigation problem. We do not yet have all the pieces needed to complete the jigsaw puzzle. All our evidence points, however, to the fact that the bee's brain incorporates a rather generalized and simple representation of the distribution of polarized light in the sky.

Recently Kirschfeld has proposed an elegant means by which the bee could navigate using the direction of polarization in any point of the sky and the elevation of the sun. So far, however, the bee's brain has turned out to be complex enough not to reveal its strategies to the human brain. The fact remains that both bees and ants do navigate successfully. Whereas our experiment demonstrated that ambiguity will disrupt a worker bee's navigation, the disruption
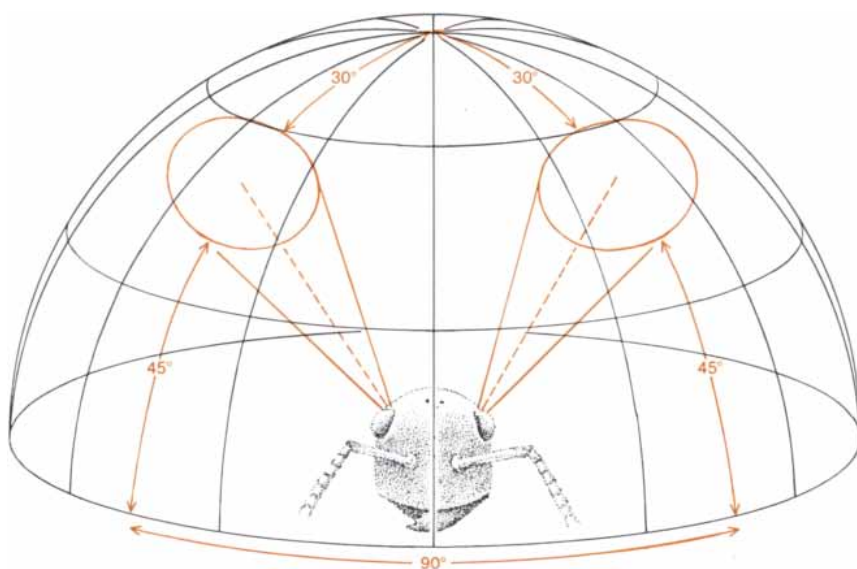

SPECIALIZED EYE REGIONS, consisting of only a few score of the 2,400 ommatidia in the desert ant's two eyes, scan a region of the sky from 45 to 60 degrees above the horizon when the ant is in a normal running position. Each of the specialized regions points in a different direction horizontally; the angle separating the two points of view is approximately 90 degrees.

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took place only when the bee's access to skylight was confined to light with a single direction of polarization. This is a highly artificial situation a worker bee is unlikely to encounter with any frequency during its short life. As soon as a bee is able to detect polarized light from more than one point in the sky the situation becomes unambiguous. The bee dances in a single direction only: the correct one.

There is one point in the sky that by itself leads to unambiguity in navigation: the position occupied by the sun. This point lacks polarized light. It is also the brightest point in the sky. When we followed our desert ants after adapting the tracking vehicle so that the entire sky was depolarized, the navigational ability of the ants became very erratic. This happened in spite of the fact that the position occupied by the sun still remained the brightest part of the depolarized sky. One might conclude that whatever the ant's internal representation of the sky may be, the sun may be predominantly recognized as the point of least polarization.

In bees that point has become particularly meaningful. Because bees have developed the abstract language of the dance as a means of telling one another about navigation angles, each individual worker bee must be able to make use of a reference point that is common to all its fellow workers. Moreover, such a common reference point must be uniquely recognizable within the overall pattern of sky polarization. Therefore the position of the sun—the point of zero polarization—is the only point bees could select for unambiguous communication. The importance of the sun as a cue in bee navigation may well have resulted from its lack of polarization rather than from its relative brightness.

W hat choices, so to speak, had to be made in the evolution of the compound eyes of ants and bees for the ability for celestial orientation to develop? I cannot refrain from speculating on the potentialities and constraints inherent in this process. As an initial assumption, let us accept that the three visual cells of each ommatidium that are ultraviolet receptors evolved specifically to allow a navigational capability based on the polarization of skylight. How about the other six visual cells? In running or flying insects an optomotor, or motion-detecting, system monitors the movement of the environment across the entire visual field and serves to stabilize the animal's course. A number of investigators have demonstrated that in bees these systems that keep the insect on a straight course are almost exclusively triggered by the green receptors. Both in bees and in our desert ants the nerve fibers of the green receptors are relatively short, so that they terminate in the first of the insect's two visual ganglia, the lamina. The three ultraviolet receptors, however, have long nerve fibers; they project through the lamina to the second visual ganglion, the medulla. It seems to me most likely that these two separate subsystems,
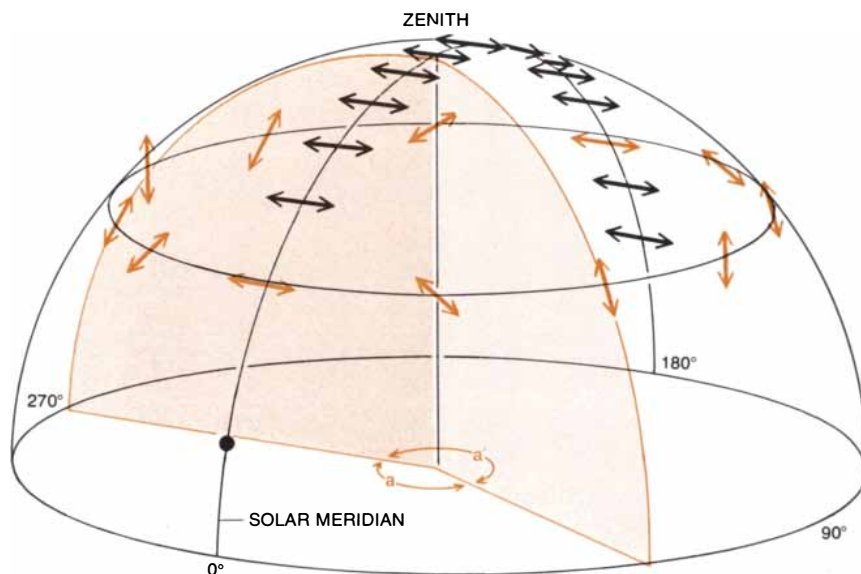
GENERAL PRINCIPLES OF THE POLARIZATION of the light of the sky are outlined. The arrows indicate the directions of polarization as they would be seen by an observer in the center of the hemisphere. Along the solar meridian (the arc through the sun and the zenith) the direction of polarization is parallel to the horizon. Along most circles of a given elevation the direction of polarization varies through all possible angles. Here the angles are plotted for the circle lying roughly halfway between the horizon and the zenith. In general each direction of polarization is found twice at each circle of elevation. (The angles a and a' denote the angular difference between the positions of identical polarization.) For this reason there is ambiguity in polarized-light navigational cues unless the insect can view more than one part of the sky.

each of which is incapable of detecting colors alone, are the ones that appeared earliest in the evolution of the insect eye. The ultraviolet system, dealing with celestial cues, has been designed to determine the direction of course in long-range orientation. The green system, on the other hand, became involved in the maintenance of course by exploiting the apparent movement of the floating environmental surround.

The green system also has to serve another function: the detection of visual objects in short-range orientation. It is likely that mechanisms for object detection have become increasingly important during the insects' evolutionary history. Whereas there is no need for color vision in celestial navigation and optomotor course control, color vision remarkably improves any mechanism that mediates the detection of objects. For bees the selective advantage of such an advance would probably have expressed itself from mid-Cretaceous times, some 100 million years ago, because it was then that the angiosperm plants, with their conspicuously colored flowers, first appeared. We can postulate an interactive evolutionary process that led on the one hand to the diversification of colors in flowers and on the other to the development of color vision in insects. For color vision to be possible, communication between the green and the ultraviolet channel had to be established. Indeed, the lamina of ants and bees is the site of synaptic connections between the two. In addition visual cells sensitive to light at blue wavelengths evolved, making the bee's color perception trichromatic. The

two blue receptors are most likely derived from two of the original six green receptors. Like the green receptors, the blue receptors have short nerve fibers that terminate in the lamina.

Different selection pressures have acted on the different visual subsystems. Sensitivity to polarized light, the sine qua non of navigation by skylight, is an entirely undesirable property when terrestrial cues need to be analyzed. That is because the polarization that results when light is reflected from terrestrial objects actually blurs the images of the objects, thereby decreasing visual acuity. As we have seen, the twisting of the rhabdom disposes of this disturbing effect for the long ultraviolet receptors; it does the same for the green and blue receptors, which are equally long. It is hard to imagine how evolution could have solved the problem of using a limited number of receptors for quite different sensory performances more efficiently. Color vision is insensitive to polarized light because the rhabdoms are twisted, and polarization vision is insensitive to the hue of color because it is confined to the ultraviolet receptors.

The insect's principal task in navigation is the retention of consecutive dead-reckoning summaries. For example, during an ant's foraging run its brain has to compute all the angles the animal has turned and all the distances it has traversed and to integrate all these vectors continuously. It is on the basis of such continuous integration that the brain is able to calculate the heading enabling the ant to return to its nest on a straight line from any point on its foraging course.

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