Visual Orientation Performances of Desert Ants (*Cataglyphis bicolor*) Toward Astromenotactic Directions and Horizon Landmarks

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IN MANY ORGANISMS different systems of direction finding and position measuring are simultaneously involved in maintaining a particular orientation course. Using a whole set of direction-indicating stimuli of the physical environment, these organisms may first increase the accuracy of their orientation performances and may also be able to measure their position in space even when one part of their navigation system no longer receives information about the external directional stimuli. This presentation gives some experimental data on the visual orientation of desert ants toward astromenotactic courses and horizon landmarks involving the co-operation of different direction-finding systems.

Cataglyphis bicolor, an ant widely distributed in desert areas of northern Africa (refs. 1 and 2) and southwest Asia, is most suitable for investigations on optical orientation mechanisms, in comparison with most of the central European species:

(1) *Cataglyphis bicolor* is a predatory and solitary hunter (fig. 1), never performing mass foraging along scent trails but mainly orienting by means of visual cues.

(2) These hunting ants can be successfully trained to feeding places and will return regularly for many days when rewarded after each predatory run.

(3) The optically uniform natural environment of the desert ant enables us to present visual patterns which can be exactly defined in their stimulus properties and may not be thought to interfere with other terrestrial cues left uncontrolled.
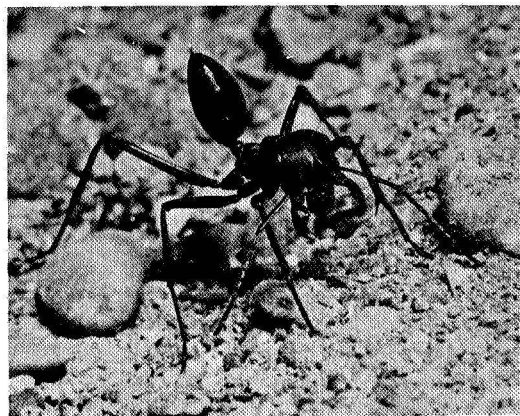

FIGURE 1. *Cataglyphis bicolor* foraging with gaster placed upright in its typical position.

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Therefore, the two main demands for studying navigation systems in animals are fulfilled by training *Cataglyphis bicolor* under natural conditions: a precise presentation and measurement of the physical cues and a well established method for recording the animal's response to the orienting stimuli.

Here, I would like to deal with three aspects of the ant's visual orientation. First, it must be determined whether the ants choose a compromise direction between an astromenotactic angle and the direction toward a horizon landmark when both angles compete with each other or whether they decide alternatively between the two courses. Second this presentation refers to adaptations of the visual system to the special demands of direction finding by astromenotactic orientation or pattern recognition. Finally some data on the parameters of visual learning behavior will be presented since all the results dealt with here were obtained by using training experiments with well-defined learning parameters.

ASTROMENOTACTIC VERSUS LANDMARK ANGLES

Until recently the most extensive work on competition between an astromenotactic angle and the azimuth of a horizon landmark has been done with bees (ref. 3), followed by some preliminary experiments with ants (refs. 4 to 6). However, in all these studies performed with natural landmarks, neither the physical stimulus properties of the terrestrial cues nor the different stages of learning processes were taken into account. Up to now, the temporal aspects of spatial orientation have been ignored, as no regard has been given to the succceeding stages of one orientation course. To consider these temporal parameters, the foraging runs of the individually trained ants were exactly recorded by means of a grid of thin threads which ex-

tended over the whole experimental area (fig. 2A). To receive directional data from these graphs, a set of concentrically arranged circles was drawn around the point marking the start of the ant's orientation course. Using this procedure, one obtains a frequency distribution in angular intervals of 5°. According to statistical methods of circularly distributed data (ref. 7), a mean vector can be calculated for every distance from the start (figs. 2B and C). This vector represents the mean direction of orientation as well as, by its length, the dispersion about the mean direction.

Before we can test orientation towards celestial and terrestrial cues by means of competition experiments, we first must prove the accuracy and time compensation of the Sun-compass courses. In contrast to the circumstantial work with bees (refs. 8 to 10) and some other insects (*Orthoptera, Hemiptera, Coleoptera*), there exists only little evidence for a time-compensated Sun-compass orientation in ants (*Formica rufa, Lasius niger*: ref. 4, see also Brun (ref. 11) who failed to prove time compensation in these two species). Therefore, *Cataglyphis bicolor* was trained for 20 m to a special azimuth and then displaced in a testing grid far away from the training grid and completely unknown to the ants. There they were released and their runs recorded (fig. 3). The mean directions of the returning ants, graphed for a distance of 5 m, respectively, 10 m from the releasing point, did not show any statistically significant difference from the home direction, irrespective of whether the ants were released at once or captured in the dark for 3.5 hr before being displaced. If there was no compensation of the Sun's course during the time of capture, one would expect a deviation of 52.5°. By a special experimental procedure (which cannot be described here in detail) it was excluded that these results were influenced by
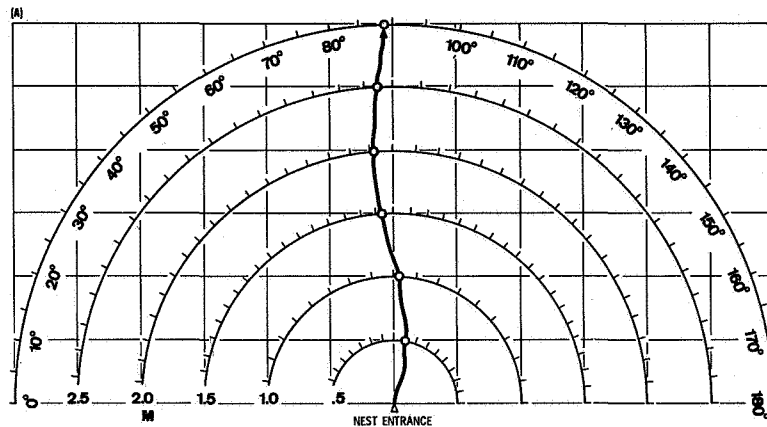
FIGURE 2. Method of recording directional data. (A) Recording of a single course by means of a rectangular grid. Concentrically arranged circles give directional information for varying distances from start of run (nest entrance).
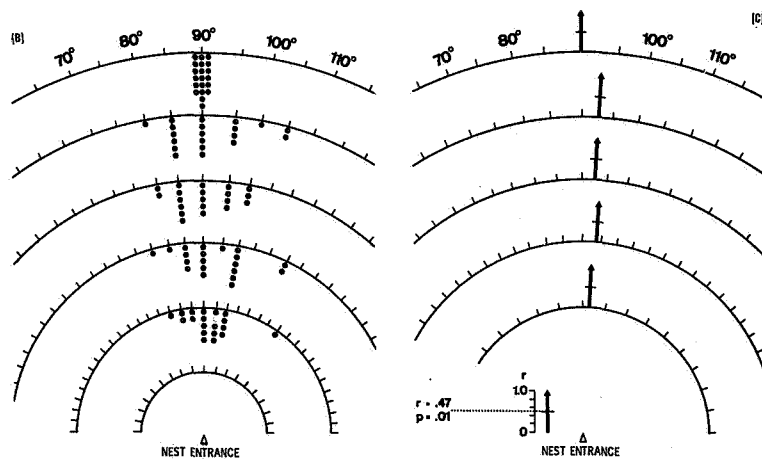

FIGURE 2 (Concluded). (B) Frequency distribution in angular intervals of 5° ($n = 20$ ants, training angle $\alpha = 90°$, three rewards). (C) Mean vectors of frequency distributions graphed in (B). $r =$ length of mean vector; $r > 0.47$: Preferred direction is statistically significant with $p < 0.01$.

the anemomenotactic orientation of *Cataglyphis bicolor.*

It must be added that the term "Sun-compass" orientation also includes the orientation toward the pattern of polarized light in the sky. This orientation performance can be proved before sunrise or after sunset when the ants show a bimodal distribution of directions according to the symmetrical pattern of polarized light at that time.[1] That ants are

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[1] WEHNER, R.: Die Konkurrenz von Sonnen-kompass- und Horizontmarken-Orientierung bei der Wüstenameise *Cataglyphis bicolor* (Hymenoptera, Formicidae). Zool. Anz. Suppl. (in press).
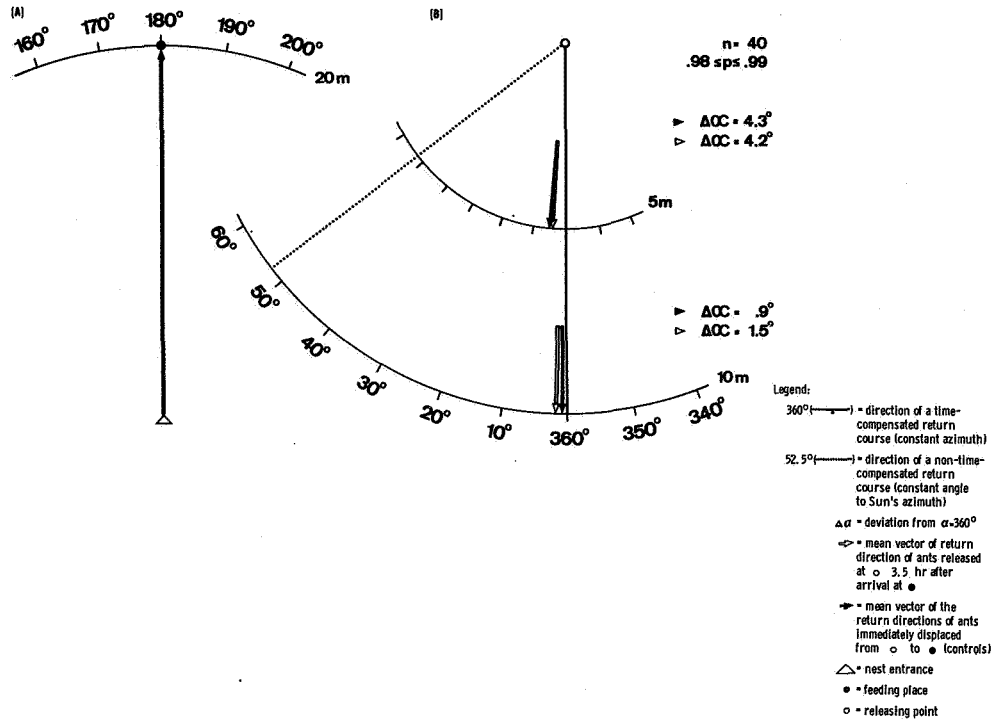
(A) 160° 170° 180° 190° 200°

20m

80°

70°

60°

50°

40°

30°

20°

10° 360° 350° 340°

(B)

n= 40
.98 sps .99

ΔΟC = 4.3°
ΔΟC = 4.2°

5m

ΔΟC = .9°
ΔΟC = 1.5°

10m

Legend:

360° (————) = direction of a time-
compensated return
course (constant azimuth)

52.5° (————) = direction of a non-time-
compensated return
course (constant angle
to Sun's azimuth)

Δα = deviation from α=360°

= mean vector of return
direction of ants released
at o 3.5 hr after
arrival at ●

= mean vector of the
return directions of ants
immediately displaced
from o to ● (controls)

△= nest entrance

● = feeding place

o = releasing point

FIGURE 3. Proof of a time-compensated Sun-compass orientation. (A) Directions of foraging runs (all shifted to 180°). (B) Directions of return runs recorded in a test grid.

able to use polarized light for their orientation performances is already known for *Lasius niger* (ref. 12), *Myrmica ruginodis* (refs. 13 and 14) and *Formica rufa* (ref. 4).

In the basic competition experiment, the ants were trained to a particular Sun-compass direction, which was marked by an artificial horizon landmark consisting of a black screen having an angle size of 10° × 10°. This procedure is called "simultaneous training." After a varying number of simultaneous training runs, the position of the black screen was relocated from the trained direction by a specific amount of degrees (60° in fig. 4). The directions of the following foraging runs, indicated by the filled circles in fig. 4A, prove a clear orientation toward the astromenotactic

angle. However, the ants were not rewarded until they had reached the black screen. In the following runs called "competition training" runs, the position of the black screen varied alternatively between the 0°- and 60°-direction so that the ants were always confronted with the competition situation between the direction to the horizon landmark and the Sun-compass direction of the preceding foraging run. As figures 4A and B demonstrate, the fifth run (indicated by the open squares and dotted lines) is mainly oriented towards the black screen. Furthermore, figure 4B qualitatively shows that changing from one orientation course to another does not consist of a continuous shift of a compromise direction but consists of an alternative
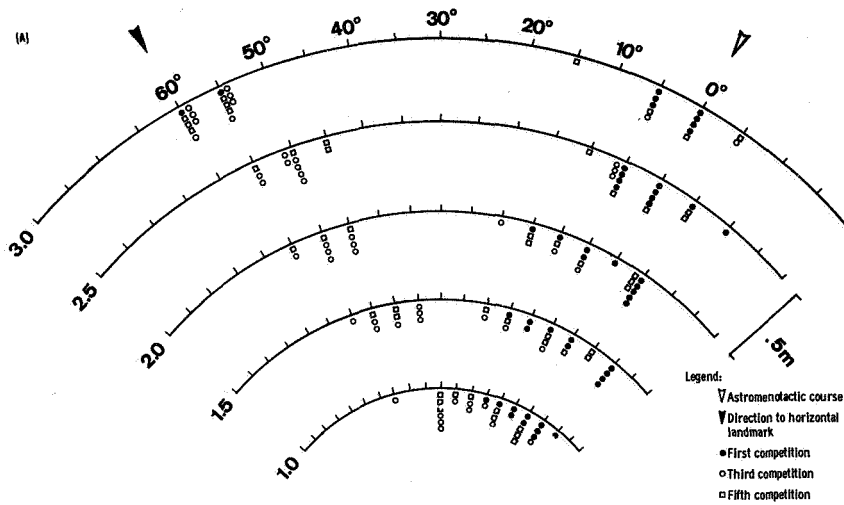
FIGURE 4. Competition between an astromenotactic course and the direction to a horizon landmark. The ants have been trained to both ($\alpha = 0°$, simultaneous training, 3 reinforcements), before the landmark is offered at 60°. See text for explanation. (A) Frequency distribution of recorded angles.
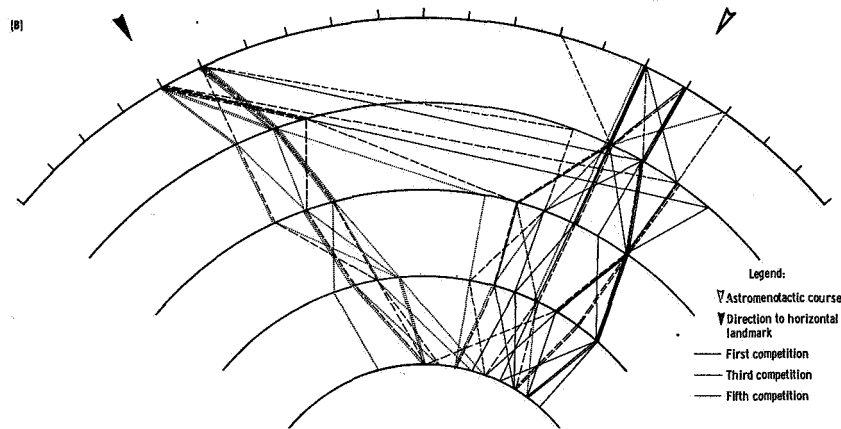
FIGURE 4 (Continued). (B) Courses of 10 individuals graphed in a generalized way.

switching over from the Sun-compass course to the terrestrial cue. The theoretically determined compromise directions, graphed in figure 4C, do not coincide with the experimental curves in figure 4B. With an increasing number of competition experiments, the point of switching over is successively relo-cated until it reaches the nest entrance where the foraging runs begin. This statement is proved in greater detail by figure 5. Hence, a mean vector cannot be calculated because of the bimodality of the angle distributions; angles α and β and their relations are determined for the succeeding stages of the courses:
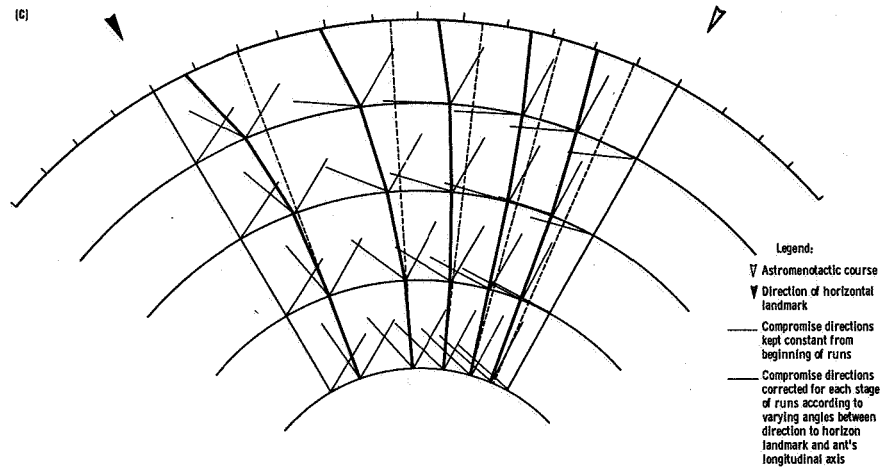
FIGURE 4 (Concluded). (C) Theoretically determined compromise directions, which do not correspond to the experimental curves in figure 4(B).

α means the deviation from the direction to the horizon landmark and β the angle included by the astromenotactic direction and the direction marked by the black screen. The relations α/β fall into two distinct groups: one about the quotient $\alpha/\beta = 1$, characterizing pure Sun-compass orientation; and the other about the quotient $\alpha/\beta = 0$, meaning orientation toward the terrestrial cue. As the lower graph (fig. 5B) shows, the proportion of the latter group relative to the first group is the larger as the distance from the nest entrance increases and as more competitive training runs are performed by the ants. Therefore, we can summarize that in the competition experiments the ants first follow the Sun-compass direction, but they can switch over to a horizon landmark by alternative decisions and not by shifting a compromise direction.

Alternative decisions are also found when the astromenotactic orientation competes: (1) with horizon landmarks in bees (*Apis mellifica*, ref. 3), where, however, the orientation courses of the flying bees could not be recorded exactly; (2) with kinaesthetic angles in spiders (*Agelena labyrinthica*, ref. 15) ; (3) with anemomenotactic angles in beetles (*Geotrupes sylvaticus*, ref. 16) and desert scorpions (*Androctonus spec.*, ref. 17). *Agelena* can also start in a compromise direction (refs. 15 and 18). Jander (ref. 4) also describes intermediate angles in the competition situation of terrestrial and celestial cues in *Formica rufa*. It must be noted, however, that compromise directions can be proved only when more than one of the animal's positions are recorded during one course. Otherwise an uncritically determined intermediate angle can mask succeeding alternative decisions. The hypothesis that compromise directions are built up by means of preceding alternative adjustments needs further analysis that may give more detailed information on the cooperation of the two mechanisms competing with each other.

At this points I wish to insert an additional remark on another cooperation of two direction-indicating systems in *Cataglyphis bicolor*—the cooperation of astromentactic
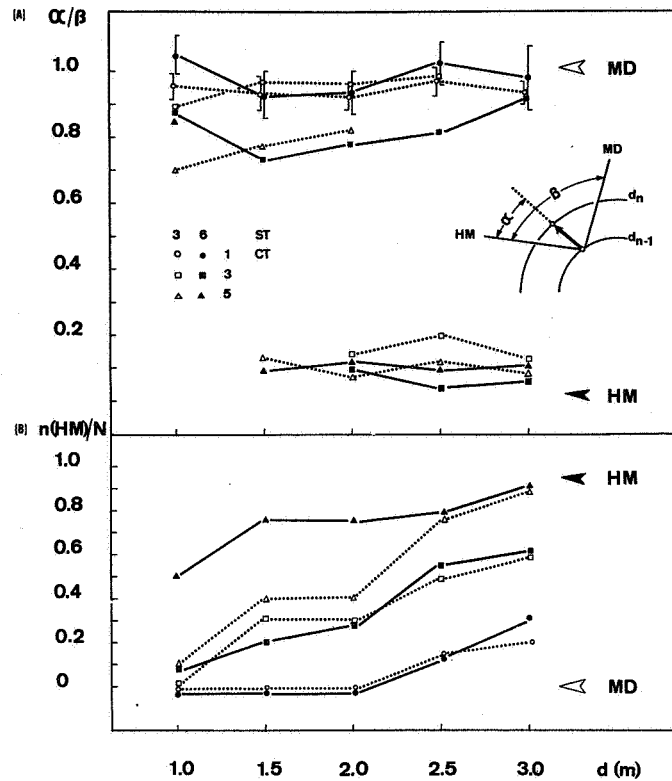
FIGURE 5. Orientation of *Cataglyphis bicolor* in competition situation between astromenotactic direction (MD) and direction to horizon landmark (HM). For explanation see figure 4 and text. Mean values are only graphed when based on at least five single values. (A) Ratio α/β in relation to different numbers of reinforcements (ST and CT) and different stages (d) of the orientation courses. $\alpha =$ deviation of the course from the direction to the horizon landmark (HM); $\beta =$ angle between astromenotactic direction (MD) and direction to horizon landmark; ST $=$ simultaneous training preceding competition experiments; CT $=$ competition training to HM during competition experiments; d $=$ distance from nest entrance. (B) Percentage of the runs directed toward horizon landmark n(HM, $\alpha/\beta \sim 0$) in relation to the total number N of runs.

and anemomenotactic orientation. Since our experiments on this subject are not yet finished, I am able to present only the main qualitative results instead of the whole quantitative data. As mentioned above, before sunrise and after sunset *Cataglyphis bicolor* orients toward the pattern of polarized light in a bimodal way by preferring the home and its counter direction. The ants were trained the previous day to an area far away from the testing grid in order to exclude all known terrestrial cues. The bimodal distribution, however, only holds for the situation when the wind is absolutely absent. When it is present and its direction coincides or—this is now important—only nearly coincides with the one during the training situation, a unimodal distribution in the right direction is obtained. However, when the wind has shifted to the counter direction, a mean vector not

statistically different from the direction 180° (home direction 0°) is due for that situation, again irrespective of the precise direction of the wind. But as soon as the Sun rises, in every case *Cataglyphis bicolor* will perform the right home direction.

From these results three main conclusions may be drawn:

(1) There exists a time-compensated Sun-compass orientation toward the pattern of polarized light because the home direction is always the counter direction of the previous training direction, notwithstanding the varying training times during the day.

(2) There does not exist a time-compensated anemomenotactic orientation although the shifts in wind direction correspond with certain hours of the day.

(3) Between the different orientation mechanisms a hierarchy can be stated as follows: The Sun-compass orientation dominates the orientation toward the pattern of polarized light, and the latter dominates the anemomenotactic orientation because varying wind directions do not result in proportionally varying home directions. The wind direc-

tion only decides which of the two courses according to the pattern of polarized light is to be taken.

Now the question may be answered: Are astromenotactic angles still recorded in an ant orienting by means of horizon landmarks, or is the mechanism of Sun-compass orientation switched off in that situation? The experiment described in figure 6 proved the former to be true. After having been trained to the two places, P_1 and P_2 which is marked by a black screen, the ants are not rewarded at the actual place of the screen (for example, P_1) but must search for the other place (for example, P_2) by means of Sun-compass orientation. If the astromenotactic mechanism had been switched off during the orientation toward the horizon landmark, the ants would follow the direction leading to P_2 as seen from the nest entrance. But, they start from P_1 in the correct direction to P_2. Therefore, an ant orienting to horizon landmarks still records the astromenotactic angle and applies that information to further navigation tasks that must be solved without the aid of landmarks. That an astromenotactic
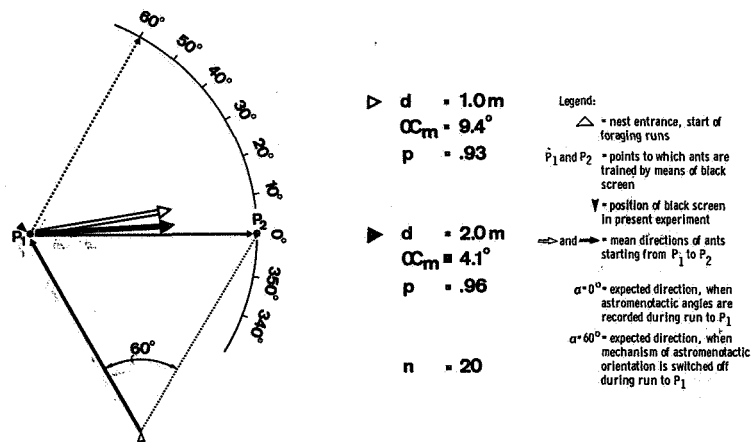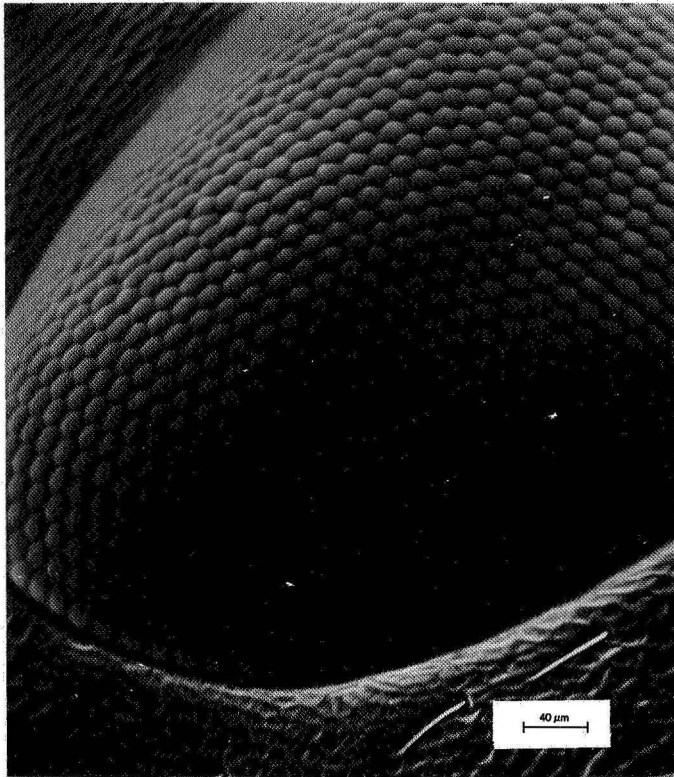

FIGURE 6. Mechanism of astromenotactic orientation is not switched off during orientation toward horizon landmarks.

FIGURE 7. Stereoscan electron micrograph of compound eye of *Cataglyphis bicolor*. View from inside-ventral. Eye was coated by a 300 Å gold layer. Prepared and photographed by R. Wessicken, Institute of Electron Microscopy, ETH, Zurich.

course can be determined by means of other physical cues than horizon landmarks (geomenotactic angles, ref. 19; anemomenotactic angles, ref. 17) is known from *Arctosa* and *Androctonus* (Arachnida).

VISUAL CUE ADAPTATIONS

Adaptations of the visual system on astromenotactic orientation and pattern recognition are now discussed. Since we have now proven two mechanisms of visual orientation which are not linked together by building up a compromise direction, one may ask whether the visual system has developed special adaptations supporting one or the other mechanism. Let us first look at some topological relations within the visual field. By scanning

electron microscopy (figs. 7 and 8) one can study receptor properties of the ant's compound eye, for example, radius of curvature and diameter of the corneal facets. When these and other parameters are measured for different size classes of the ants and different regions of the compound eye, highly significant differences can be found (fig. 9). Proceeding from the ventral to the dorsal parts of the eye, the diameter of the corneal facets decreases whereas the radius of curvature increases. Both parameters are shown for three size classes of ants with proportionally varying numbers of ommatidia.[2] They prove

[2] MENZEL, R.; AND WEHNER, R.: Augenstrukturen bei verschieden grossen Arbeiterinnen von *Cataglyphis bicolor* (Formicidae, Hymenoptera). Z. vergl. Physiol. (in press).
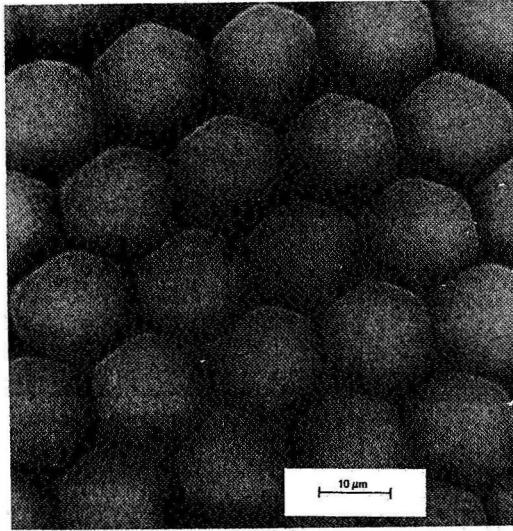
FIGURE 8. Corneal facets from ventral-external region in compound eye of *Cataglyphis bicolor*. Stereoscan electron micrograph by R. Wessicken, Institute of Electron Microscopy, ETH, Zurich.

that the interommatidial inclinations become the smaller, the more dorsal the ommatidia are situated (for bees see ref. 20). The smallest values are obtained in the internal quarter of the dorsal half of the eye where, even morphologically, a small depression can be seen looking straight upward to the sky.

Until now we have not proved whether, in desert ants, there are also adaptations of the visual system to the orientation by terrestrial cues. But our work dealing with the mechanism of pattern recognition in bees gives clear evidence that this is the case. By means of an apparatus (ref. 21) we are able to train bees to screens with black and white areas in different positions of the visual field. When the bees are trained to disks—the upper and lower halves of which are black and white, respectively (fig. 10)—the disks are chosen to a lesser degree when contrasting areas are inserted into the lower rather than into the upper part of the visual field. The reaction

frequencies of the bees to the four test patterns are related to the reaction frequency 1 of the actual training pattern. The smaller the reaction frequencies are, the more effective is the insertion of the contrasting area into the training pattern. These results lead to the conclusion that distributions of black and white areas are most precisely analyzed in the lower part of the frontal visual field upon which horizon landmarks are normally projected. As known from electrophysiological recordings, single units in the optic lobes of crustaceans (ref. 22) and flies (ref. 23) have their receptive fields in special parts of the whole visual field of the eye.

That special parts within the visual fields of arthropods are due to certain orientation performances is also known for optomotor responses (*Uca pugnax*, ref. 24), telotactic orientation toward single light sources (several insect species, ref. 25), and prey catching (*Stagmatoptera biocellata*, refs. 26 to 28). Color receptors are also disproportionally distributed over the compound eye (*Periplaneta americana*, ref. 29; *Libellula quadrimaculata*, ref. 30; *Notonecta glauca*, refs. 31 and 32; *Ascalaphus macaronius*, ref. 33; *Apis mellifica*, ref. 34). Therefore, the visual system of insects may be topologically subdivided according to the demands of the different optical orientation mechanisms.

LEARNING PARAMETERS

Finally we must consider some central processes involved in the two mechanisms of visual orientation. However, only a few remarks can be made in this presentation concerning the visual learning capacities of *Cataglyphis bicolor*. First the question arises, whether the Sun-compass direction to a special feeding place is learned during the preceding return or foraging runs. Figure 11 shows the latter is true. In this experimental
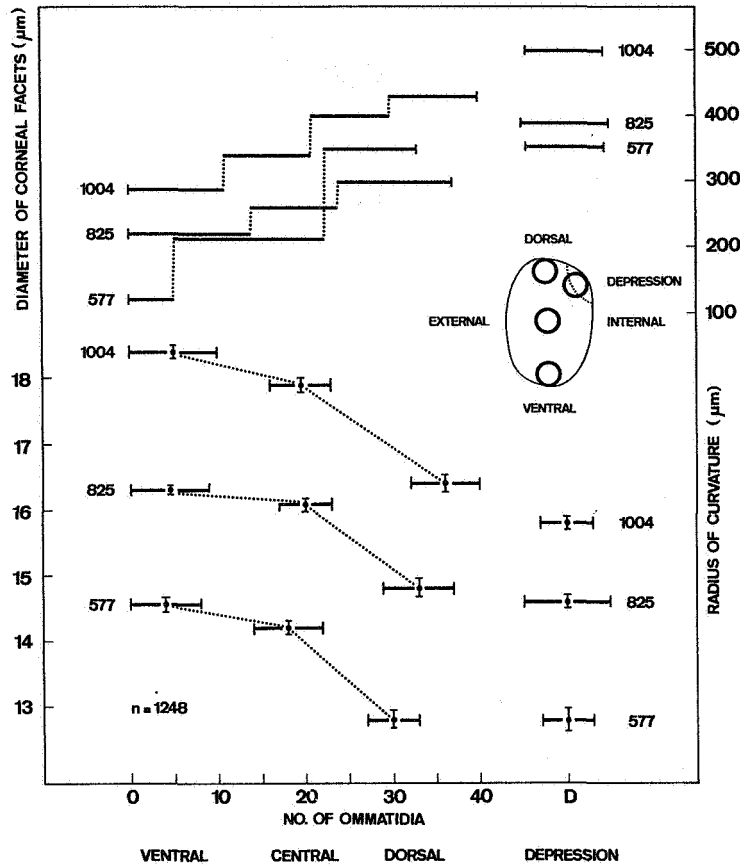
FIGURE 9. Radius of curvature (upper graph) and diameter of corneal facets (lower graph) of compound eye of *Cataglyphis bicolor* as taken from stereoscan electronic micrographs. Values are determined for small, medium and large individuum and for four regions of the eye (see inset figure). Body size (lateral length of head 1.0, 1.5 and 2.0 mm) and number of ommatidia (577, 825 and 1004) are positively correlated. In lower part, mean errors of mean values are graphed. Number beside each set of data represents total number of ommatidia in the eye.

setup the ants were trained to a feeding place and displaced to a nearby releasing point. The mean vectors of the first stages of the return runs are indicated by the black arrows. Afterward, the ants returned to the nest entrance. When measuring the directions of the following foraging runs (marked by the white arrows), one finds these directions to coincide with the Sun-compass course of the preceding foraging runs but not with the mean direction of the preceding return runs. Therefore, no learning of a new compass direction occurs when the ants return to the nest after being rewarded (refs. 10 and 35).

This conclusion is confirmed by another more direct experiment in which an astro-menotactic course competes with the direction toward a horizon landmark during the return run. In order to obtain that test situation, *Cataglyphis bicolor* was trained in a
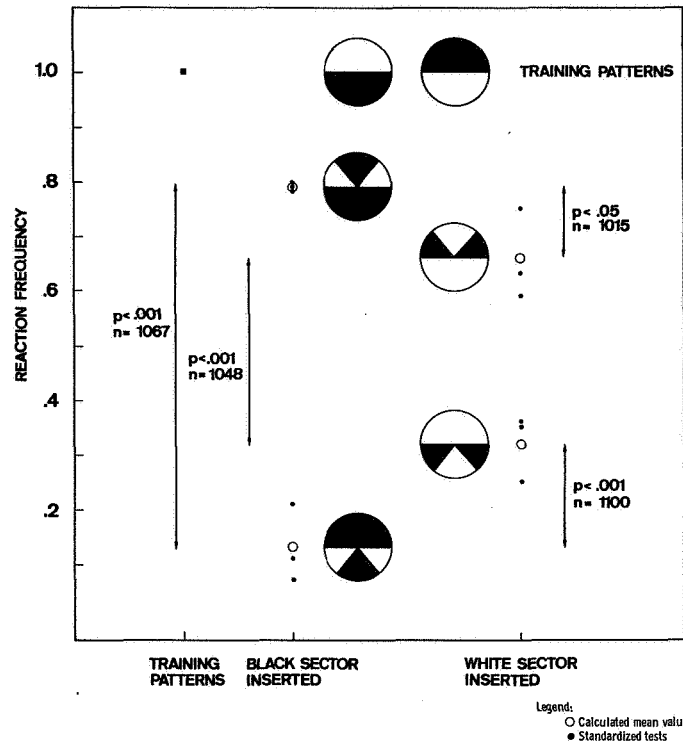
FIGURE 10. Dorsoventral asymmetry in visual field of honey bee (*Apis mellifica*). Reaction frequencies of trained bees to four test patterns (diameter 130°) are related to reaction frequency 1 to actual training pattern. Smaller reaction frequencies are more effective in insertion of contrasting area in training pattern. Each mean value is calculated from reaction frequencies of three standardized tests.

particular Sun-compass direction by means of a set of black screens. After rewarding the ants, the terrestrial cues were simultaneously displaced in such a way that the ants, when released, had to choose between the Sun-compass direction and the direction toward the black screens including an angle of 90°. They first followed the former direction but switched to the horizon landmarks with proceeding competition situations, as is true for the foraging runs. Even during the return runs no compromise directions were performed, furnishing further proof for our previous statement. While foraging, however, the ants learn the direct astromenotactic direc-

tion to a special point after reaching it in a roundabout way, but this does not hold for the return runs. When the horizon landmarks are removed, even after more than 20 competition experiments, the ants never follow the direct astromenotactic return course but choose the counter-direction of the immediately preceding foraging course. In contrast to the foraging situation, no integration and learning of astromenotactic angles seen at the return runs can be proved.

As the astromenotactic angle of the return run is determined by the counter direction of the foraging run, one may now ask whether a special constellation of horizon
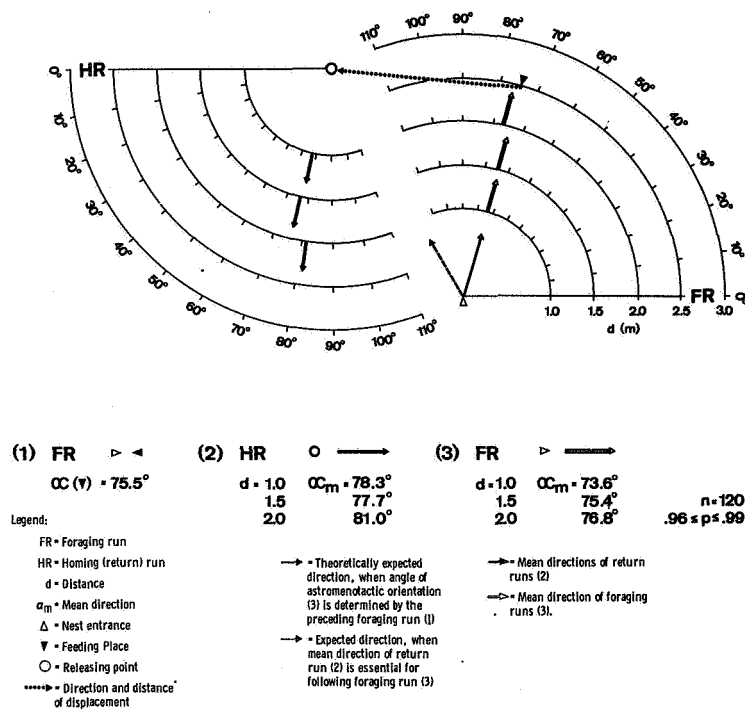
FIGURE 11. Competition between the astromenotactic angles of the preceding foraging run and the preceding homing run.

landmarks seen during the foraging run is also reversed for direction finding on the return run—more generally, whether terrestrial cues learned while foraging are also used during the return runs. Our experiments show that ants returning to the nest can only orient toward those horizon landmarks which they have seen during the preceding return runs, irrespective of whether or not these landmarks were presented during the foraging runs. From these and other experiments we may conclude that the direction of the return run is determined as the astromeno-tactic counter direction of the foraging run but not by the reversed constellation of horizon landmarks seen while foraging. The terrestrial cues used in the return situation must be separately learned during the preceding

return runs. Similar results can be taken from experiments on maze learning in bees, wasps, and ants (*Apis mellifica*, *Vespa germanica*, ref. 36; *Formica schaufussi*, ref. 37). Other learning parameters (e.g., acquisition, retention, and reversal learning) cannot be discussed here in detail.[3]

What I wanted to show is that separate orientation mechanisms are responsible for the orientation of the desert ant (*Cataglyphis bicolor*) toward astromenotactic angles and horizon landmarks. If both sets of visual stimuli compete with each other, the ants switch over from one to the other orientation

[3] WEHNER, R.: Die Konkurrenz von Sonnen-kompass- und Horizontmarken-Orientierung bei der Wüstenameise *Cataglyphis bicolor* (Hymenoptera, Formicidae). Zool. Anz. Suppl. (in press).

mechanism and do not perform a compromise direction. Depending on the physiological demands of the two mechanisms, the visual system may be topologically subdivided. Finally the storage of information presented by both sets of visual stimuli is restricted to special stages of the orientation runs.

DISCUSSION

QUESTION: What is the natural food of the ants and how do they forage?

WEHNER: In the regions where our experiments were performed (southern Tunesia), the natural food of *Cataglyphis bicolor* consists of desert beetles (e.g., *Tenebrionidae*) and other desert insects as well as amphipod crustaceans in areas near the coast. The ants reach their feeding places, which may be 100 to 200 m from the nest entrance, first in a straight course and then by searching around at random. The development of the well established learning capacities in these ants may have been supported by the necessity of foraging a freely moving prey, for a special feeding place can be kept constant only for a few foraging runs.

KLEERKOPER: Has the locomotor pattern of foraging ants been studied to any extent? Is there any indication that the moves are either random or programmed?

WEHNER: We have studied random movements by releasing ants from a point not known to them. They search at random in irregular, increasing circles. After searching around, they return to the point of original release. Therefore, no dislocation of the searching ant occurs in spite of the vast excursions performed by them.

WILLIAMS: What would happen if you deprive the ant of its Sun vision by a piece of cardboard?

WEHNER: The ant would orient quite exactly according to the pattern of polarized light in the sky. A comparable situation is established before sunrise and after sunset when the ants show a bimodal distribution of their orientation angles induced by the symmetrical pattern of polarized light at that time. This distribution suddenly switches over to an unimodal one when the Sun is visible above the horizon.

BULLOCK: What is the difference between ant and wasp behavior?

WEHNER: The solitary wasps (*Ammophila, Bembix, Philanthus*) studied by the Dutch school (ref. 38) react more precisely to natural landmarks as do *Cataglyphis bicolor* in the desert regions of southern Tunisia when confronted with artificial terrestrial cues. If *Cataglyphis bicolor* is displaced to a strange place, the ant will accurately run in the correct home direction and will search at random looking for the nest entrance after having performed a definite percentage of the real homeward course distance. Therefore, Sun-compass orientation mechanisms can be more precisely studied in these desert ants. Furthermore, that advantage is supported by the possibility of training the ants to special places and recording the orientation courses of the running ants (in contrast to the flying wasps). Additionally horizon landmarks can be presented in a definite way. Therefore, in *Cataglyphis* many orientation problems may be analyzed that are difficult to study with other insects such as wasps and bees.

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