

(1.5 by 20 cm) and eluted in 2 ml fractions with H₂O at a flow rate of 0.5 ml per minute. The data (Table 3) show the glycoprotein nature of the radioactive product, and also indicate that the leucine and glucose are being incorporated into proteins which behave similarly in the solubilization procedure.

To determine the submitochondrial localization of the incorporated leucine-¹⁴C and monosaccharide-¹⁴C, inner and outer mitochondrial membranes were prepared by the Ficoll discontinuous gradient method (24). The majority of the radioactivity in each instance was found in the mitochondrial inner membranes. The counts per minute per milligram of protein in the inner membrane and the outer membrane were as follows: leucine-¹⁴C, 1008 and 43; GDP-fucose-¹⁴C, 317 and 0; GDP-mannose-¹⁴C, 1180 and 289; UDP-glucose-¹⁴C, 1900 and 159; and UDP-galactose, 1720 and 0, respectively. The differential localization of leucine-¹⁴C in inner membranes confirms previous observations (6, 7); the preferential incorporation of the monosaccharides-¹⁴C into inner mitochondrial membranes indicates that the proteins to which the glycosyl residues are independently transferred by the isolated mitochondria are most likely the proteins which are independently synthesized by the isolated mitochondria. Although these results do not definitely rule out the possibility of smooth membrane contamination in the mitochondrial preparation, it seems unlikely that glycoprotein synthesized by smooth membrane fragments would be incorporated into mitochondrial inner membranes in this system in which cellular structural integrity is not preserved.

The results demonstrate that intact isolated mitochondria transfer monosaccharides from nucleotide diphosphate monosaccharide precursors into protein, thus creating glycoproteins. Most of the monosaccharide-¹⁴C activity was found in the inner membranes, an indication either that the glycosylations occur in these membranes or that after glycosylation the glycoproteins are incorporated into these membranes. Thus, not only can the mitochondria synthesize a portion of their own proteins, but also the isolated mitochondria can synthesize their own glycoproteins independently of other cellular structures. These conclusions do not contradict those (25, 26) in which the smooth internal and plasma membranes of the cell were implicated as sites of cellular

glycoprotein biosynthesis; rather they illustrate the ability of mitochondria to carry out some glycoprotein biosynthesis.

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28. 30 November 1968; revised 17 January 1969

Homing in the Ant *Cataglyphis bicolor*

Abstract. *Cataglyphis bicolor*, an ant widely distributed in North Africa and the Near East, orient to the sun as well as to visual patterns of the environment. These two mechanisms can be separated. Foraging ants (hunters) orient to terrestrial cues as long as possible, and only after these have become ineffective do they switch over to the menotactical sun orientation. In the digging individuals, however, the visual knowledge of locality is significantly inferior to that of the hunters. Diggers vary considerably in size, but hunters belong to the largest size group. In addition, the largest and smallest individuals orient differently toward black and white areas and stripe patterns.

Since the studies of Santschi (1), Cornetz (2), and Brun (3) there have been few investigations of optical orientation in ants (4). Their studies prove that at least some species of ants can use a time-compensated orientation to the sun's position or to the pattern of polarized light of the sky. However, an ant is unable to return to the nest menotactically after being displaced in any direction from its normal course. In such situations, visual landmarks must act as cues for optical orientation.

In our experiments on the optical orientation of ants during March and April 1968 in Israel, we studied *Cataglyphis bicolor* (var. *nigra*), a common ant of desert areas of northern Africa and southwest Asia. This species inhabits underground nests, which are indicated on the surface only by small holes surrounded by sand dikes and aggregated in little colonies. As a predatory and solitary hunter, the ant depends exclusively upon visual orientation. We demonstrated that after

the ants are displaced, neither chemical nor vibrational stimuli are decisive as orientation parameters.

Displacements were first devised to put the already learned menotactical course in competition with that to known landmarks (5). Only hunters foraging from one definite direction (zero direction) were used. This zero direction (0° in all figures) coincides with that from which most hunters returned from their feeding places, at least 40 m away. One day before the test, all hunters used were individually color-marked. On their return from the foraging grounds (0°, west), they were intercepted 0.5 to 1.5 m from the nest entrance and captured in small plastic tubes; the ants were then shifted by 180° in the opposite direction (east) and released at various distances from the nest. With the use of a grid of fine thread (mesh width, 1 m) which extended over the whole experimental area, we recorded and timed the runs of the ants.

The percentage of positive runs (runs

leading to the nest within 15 minutes) is shown in Table 1. The remaining ants reach the nest, if at all, after searching around for hours. To determine the mean direction of orientation for various distances from the point of release, we used the following procedure. With concentrically arranged circles around the releasing point, we determined the deviations of the running ants from the zero direction (direction to the nest) for all distances (DR) from the releasing point (DR = 1, 2, ... 7 m); these deviations were charted on circular diagrams (Fig. 1). According to statistical methods of circularly distributed data (6), a mean vector can be calculated for every distance (DR) from the releasing point. The angle of that vector gives the mean direction of orientation (α_m), whereas its length a ($0 < a < 1$) can be considered a measure of the dispersion about the mean direction. With increasing dispersion, the absolute value a of the mean vector decreases. These two values, α_m and a , were determined for all distances of the displacement (DD), as well as for all distances of the displaced ants from the releasing point (DR) (Fig. 1).

The courses of the ants approach the zero direction with increasing distances DR from the releasing point. But this holds only for distances of displacement (DD) up to 10 m (Fig. 2, a, c, and d). For the circular distribution obtained for DD equal to 15 and 20 m (Fig. 2b), a mean direction is found which deviates by nearly 180° from the zero direction; it coincides with the direction commonly taken by the ants returning from their feeding places. We find the same result (Fig. 2e) when we refer to the negative runs which already occur in displacement experiments within the range of $8 < DD < 10$ m (see Table 1).

From these experiments we conclude that, under natural conditions, the forays of *Cataglyphis bicolor* are fixed according to the azimuth of the sun, as well as to terrestrial cues. If both mechanisms compete with each other, the orientation to visual patterns of the environment dominates over orientation to the sun, characterized by a menotactical course. This principle of orientation is important because only the azimuth of the sun or the polarization pattern of the sky give information about direction, so that homing is impossible when the ant is displaced from its actual course. If, however, *Cataglyphis* does not possess any sun

Table 1. Results of the displacement experiments performed with the hunters. The hunters used for these experiments returned from their feeding places situated to the west (0°) of the nest. They were displaced to the east and, as a control, also to the west. Abbreviations are: DD, distance of displacement; pos., positive runs leading to the nest within 15 minutes; neg., negative runs; t_m , mean time needed by the ants to return to the nest (\pm standard deviation); α_m , mean direction; and a , length of the vector characterizing the mean direction of the displaced ants 4 m from the releasing point; values of a are significant ($P < .01$), except where noted.

| DD (m) | Direction | Ants (No.) | Pos. (%) | t_m (10^{-2} min/m) | α_m pos. | $a_{pos.}$ | α_m neg. | $a_{neg.}$ |
|--------|-----------|------------|----------|--------------------------|-----------------|------------|-----------------|------------|
| 40 | West | 17 | 100 | 35 ± 5 | 172° | .91 | | |
| 20 | West | 20 | 100 | 32 ± 3 | 176° | .97 | | |
| 5 | East | 33 | 100 | 38 ± 4 | 358° | .99 | | |
| 7 | East | 15 | 100 | 30 ± 7 | 1° | .99 | | |
| 8 | East | 17 | 83 | 48 ± 10 | 347° | .73 | | |
| 10 | East | 22 | 39 | 40 ± 8 | 348° | .95 | 182° | .66* |
| 15 | East | 15 | 20 | 73 ± 13 | | | 203° | .70 |
| 20 | East | 15 | 20 | | | | | |

* $P < .05$.

orientation mechanism, pattern recognition and learning abilities ought to be highly developed in order to enable this extraordinarily vagrant species to perform its high orientation achievements.

Our results suggest two questions, the first especially referring to the

problems of form perception and the second dealing with the cooperation of these two mechanisms of visual orientation within the central nervous system: (i) which visual parameters are necessary to rule out the sun orientation? and (ii) does the significance of

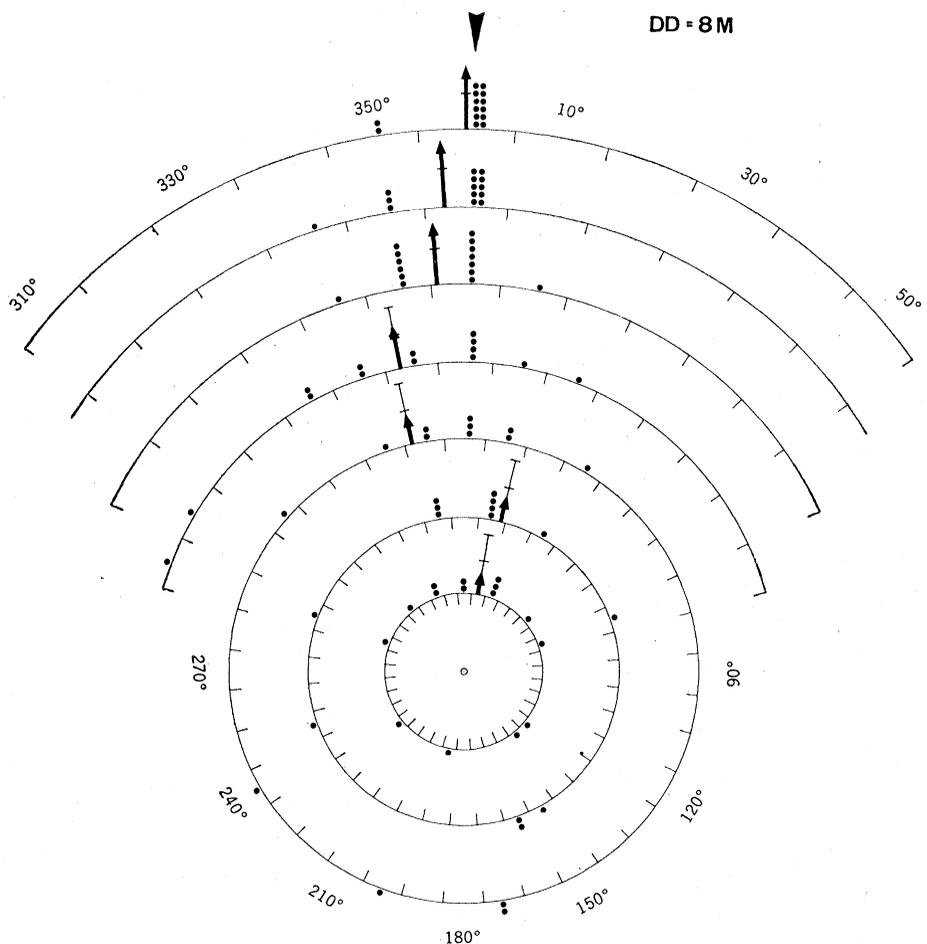


Fig. 1. The directions of return from the releasing point 8 m from the nest entrance. The mean vectors are graphed for distances of $1 \leq DR \leq 7$ m from the releasing point. The length of the thin line represents a equal to 1. If the vector (thick arrow) exceeds the little mark on that line, the mean direction is statistically significant ($P < .01$). Distance of displacement (DD) is the distance between the nest entrance (arrow at top) and the releasing point (O); DR, distance between the releasing point and the actual position of the displaced ant.

these visual parameters decrease when the distance from the nest increases? If the latter holds true, the same visual pattern offered experimentally must be effective as an orientation cue in the nest area, whereas it is eliminated by the sun orientation at a larger distance from the nest.

The differences in the optical orientation performances of hunters and diggers were examined. Although diggers and hunters vary considerably in size, the hunters always belong to the largest size group. On the other hand the sizes of the diggers differ extra-

Table 2. The results of the displacement experiments performed with the diggers. For explanation see Table 1.

| DD (m) | Ants (No.) | Pos. (%) | t_m (10^{-2} min/m) |
|--------|------------|----------|--------------------------|
| 2 | 34 | 71 | 220 ± 39 |
| 5 | 13 | 31 | 181 ± 29 |

ordinarily. But in *Cataglyphis bicolor* we do not yet know whether these are genetically fixed castes or only groups, the individuals of which are of the same age and perform the same social

functions (9). When the diggers are displaced from 2 to 5 m, the percentage of the returning individuals is much lower, and the times of return are higher than they are among hunters (Table 2). Hence the visual knowledge of the environment is by far inferior in the diggers.

A difference between the visual orientation of the smallest individuals, who often have the function of digging, and that of the largest, mainly represented by the hunters, is evident in laboratory experiments. The largest ants frequent only the white-colored half of a circular cylinder, whereas the smallest prefer the black half and, above all, the contours between the black and white areas (all three results are statistically significant, $P < .001$). Even when vertically arranged stripes are confronted with horizontal ones, the largest ants prefer none but the white areas and remain in the cylinder between the stripe patterns. In the smallest ants, however, a maximum of the distribution can be found in the vertically striped part of the cylinder ($P < .001$ in both cases). Therefore the question arises: how does basic orientation to simple distributions of black and white areas participate in building up the exact knowledge of the ant's visual environment?

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26 September 1968; revised 13 January 1969

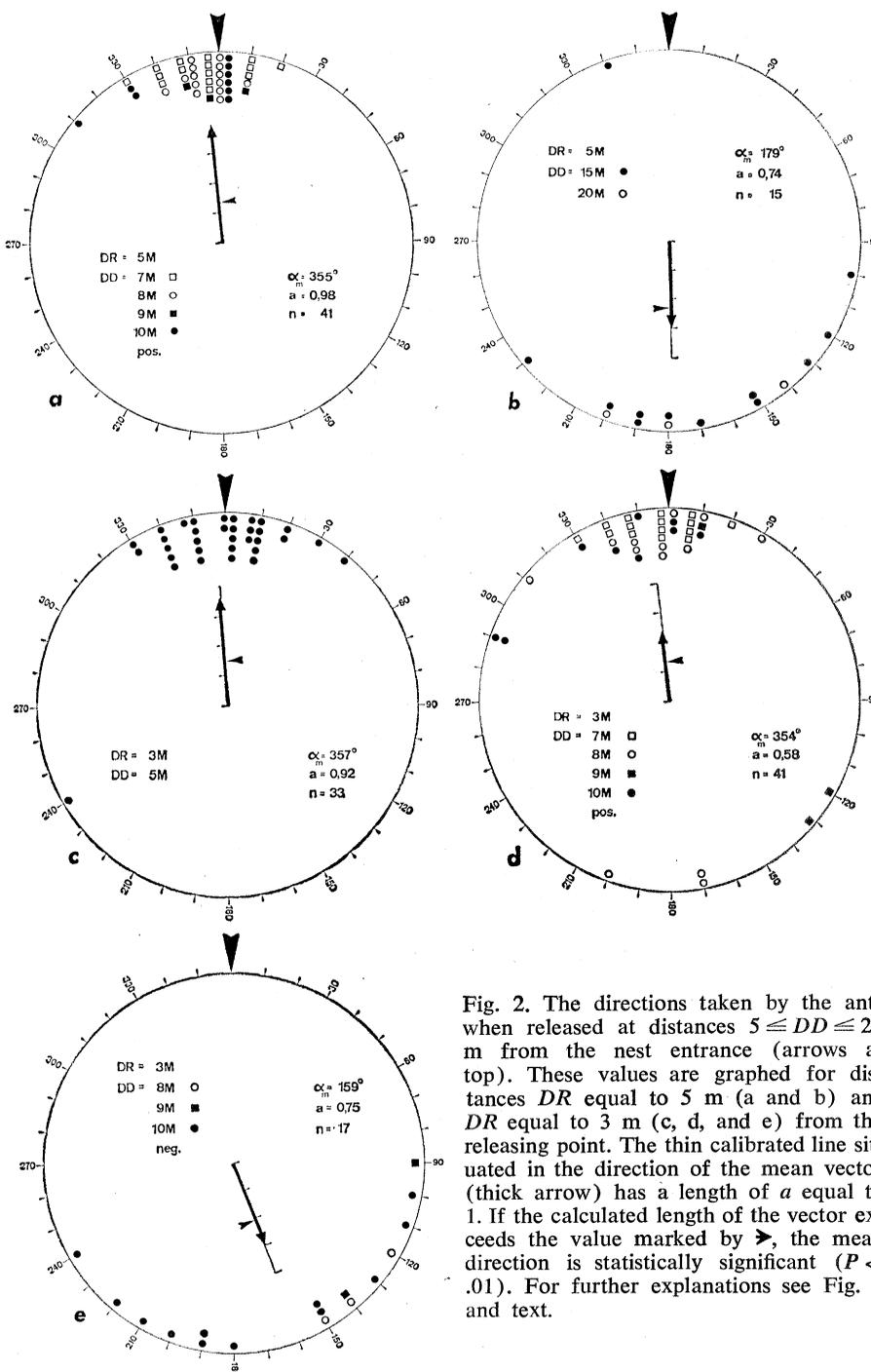


Fig. 2. The directions taken by the ants when released at distances $5 \leq DD \leq 20$ m from the nest entrance (arrows at top). These values are graphed for distances DR equal to 5 m (a and b) and DR equal to 3 m (c, d, and e) from the releasing point. The thin calibrated line situated in the direction of the mean vector (thick arrow) has a length of a equal to 1. If the calculated length of the vector exceeds the value marked by \blacktriangleright , the mean direction is statistically significant ($P < .01$). For further explanations see Fig. 1 and text.