15. G. L. Townsend and D. T. R. Cody, *Ann. Otol. Rhinol. Laryngol.* **80**, 121 (1971).
16. J. M. Frederickson, H. H. Kornhuber, D. W. F. Schwarz, in *Handbook of Sensory Physiology*, H. H. Kornhuber, Ed. (Springer-Verlag, Berlin, 1974), vol. 6, part 1, pp. 565–582.
17. S. D. G. Stephens and H. M. Ballam, *J. Laryngol. Otol.* **88**, 1049 (1974).
18. I. Hunter-Duvar, M. Hawke, D. Armstrong, *J. Otolaryngol.* **5**, 497 (1976).
19. C. A. Prosen, M. R. Petersen, D. B. Moody, W. C. Stebbins, *J. Acoust. Soc. Am.* **63**, 559 (1978).
20. Supported by grant 8-ASR-6 from the Institut National de la Santé et de la Recherche Médicale. We thank J. E. Hawkins, Jr., and D. J. Anderson for checking the English and for helpful comments.

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Canopy Orientation: A New Kind of Orientation in Ants

Abstract. *Celestial cues, such as the sun or patterns of polarized sky light, appear to have no detectable effect in the precise homing orientation of foragers of* Paltothyreus tarsatus. *Field and laboratory experiments reveal that canopy patterns are a major influence in the home range orientation of this ponerine ant, a common species in African forests. Canopy orientation appears to be well suited to the restrictive lighting conditions of tropical forests.*

Worker ants have one or more orientation mechanisms at their disposal during foraging and homing. Those of most species seem capable of a time-compensated sun orientation (sun compass orientation) (*1, 2*) and of orientation with respect to visual landmarks and to chemical cues (*1, 3*). However, the various orientation mechanisms are usually not in operation simultaneously, but alternatively, with the sequence being dependent on spatial situations (*2*) or on a hierarchical order of the orientation cues available (*4*). Most of our knowledge concerning orientation in ants stems from studies of the phylogenetically more advanced species. Very little is known about such behavior in the phylogenetically primitive ant species. A recent investigation of the African stink ant (*Paltothyreus tarsatus*) has revealed a new kind of visual orientation.

A member of the primitive subfamily Ponerinae, *P. tarsatus* is a scavenger and termite hunter, is widely distributed throughout Africa south of the Sahara, and lives primarily in forested areas (*5*). Its nest occupies a relatively large surface area (~ 10 to 25 m^2) and has multiple entrances. Individual ant workers depart from most of these exits for short foraging excursions on the ground (1 to 5 m). When homing, each returns precisely to the same exit from which it departed.

Celestial cues (sun or patterns of polarized sky light) have no significance in this precise response by *P. tarsatus* foragers. In the African forest (*6*) the view of the sun is restricted by trees most of the time, and even the sky is often completely covered with thick clouds. Despite these conditions, the ants achieve all but perfect orientation. Our experiments indicate that *P. tarsatus* workers are quite unable to use any sort of celestial orientation. When homing foragers were displaced about 20 m from their homing route, with the sun or blue sky (or both) visible above, they did not maintain the correct menotactical course, but rather moved randomly in searching loops. However, when they were placed back on their original path they immediately continued to home correctly. Possible chemical trail orientation was excluded by scraping off an approximately 0.5-cm layer of soil along the homing path before the ants started their return journey (*7*). These results suggest that visual landmarks may be the most important cues by which *P. tarsatus* workers are guided during foraging and homing.

The foraging area was subdivided by a grid (grid squares, 20 by 20 cm), so that it was possible to record the individual courses on a map with a similar grid system ten times reduced. The length of each course was then determined with a planimeter. When the length of an individual course exceeded approximately twice the distance between food source and nest entrance, the test was stopped before the ant reached the nest. As a food source, a portion of a termite nest with many termites exposed was offered at a distance of 200 cm from the nest. When a *P. tarsatus* forager discovered these insects it first killed all it could catch. Next it stacked three to five termites between its mandibles and returned directly to the nest entrance from which it had departed. Seconds after the forager had entered the nest it emerged again, returning directly to the food source. After the ant had traveled three to five times between food source and nest, I destroyed possible chemical orientation trails by scraping the soil along its line of travel.

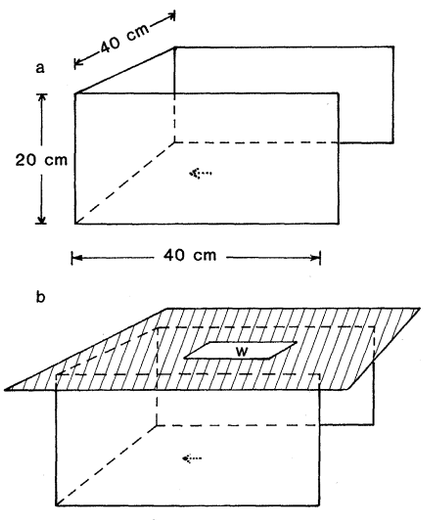

Fig. 1. (a) Blind which restricts the view of the ant (dotted arrow) to the front and to the sides. (b) The blind is covered by a cardboard, so that the ant's overhead view is blocked; *W*, red plexiglass window through which the ant can be observed.

Selected sections of the visual surroundings of the ant were then concealed in order to test their significance as homing cues. The homing ant was first surrounded by a horseshoe-shaped blind, which restricted the view of the ant to the front and to the sides (Fig. 1a). The blind was moved along the ants' course. Surprisingly, the ants still oriented toward home with great accuracy [length of course on map; experimental: $\bar{X}$ = 23.9 cm, standard deviation (S.D.) = 2.2, N = 20; control: $\bar{X}$ = 21.9 cm; S.D. = 1.5; N = 14]. Only when they were about 10 to 25 cm from the nest entrance did they experience difficulty in locating the entrance. When the overhead view was also blocked (Fig. 1b), the ants were unable to orient homeward and meandered randomly. The length of the course always exceeded twice the distance between food source and nest. When, however, only the overhead view was blocked by a piece of cardboard (40 by 40 cm) kept centered about 15 cm above the moving ant, the ant again oriented toward the nest entrance (length of course on map: $\bar{X}$ = 30.0 cm, S.D. = 6.4, N = 21), although its course was less straight than when homing with an unobstructed overhead view (t-test, $P < .001$).

These results suggested that the canopy pattern plays a major role in the home range orientation of *P. tarsatus*. Later, I was able to test this hypothesis in the laboratory under more rigorously controlled conditions. Fragments of a *P. tarsatus* colony consisting of approximately 100 workers were housed in a glass nest (14 by 14 by 1.5 cm) located at one end of a large foraging arena (75 by 150 cm). The ants had access to the arena through a small nest exit which could be closed

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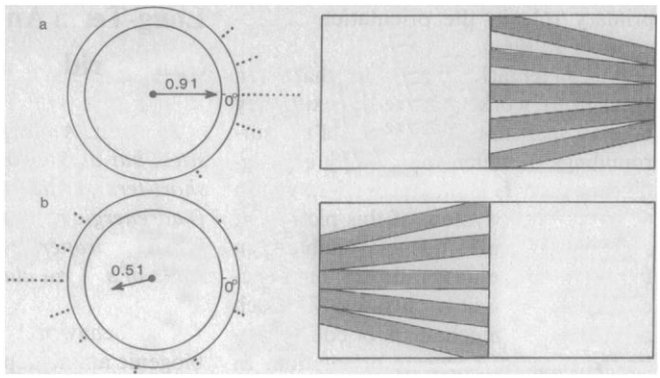

Fig. 2. (a) (Right) Half of the artificial sky of the foraging arena is patterned by five black cardboard stripes, while the other half of the sky is kept uniformly translucent white. (Left) Direction of homing movements during the control experiment. Each dot indicates where individual foragers crossed a circle (r = 25 cm), drawn around the food source. The correct homing direction is through 0°. A mean vector is shown and its length ($0 < r < 1$) is a measure of the dispersion around the mean direction (9). (b) The two halves of the artificial sky were exchanged (right) and the subsequent homing behavior of the foragers was recorded (left).

by a sliding door. A similar but unoccupied nest was placed at the opposite end of the arena. The arena was completely surrounded by walls (120 cm high) consisting of a white, densely meshed screen that obscured possible visual orientation cues to the sides, front, and back of the arena. The top of the arena was covered with translucent plexiglass plates on which a variety of black-white visual patterns were affixed. The arena and its cover were diffusely illuminated from above by neon lights.

In the first series of experiments, the half of the artificial sky under which the nest was located was patterned by five black cardboard stripes (12 by 80 cm) (Fig. 2). The other half of the sky was kept uniformly translucent white. Termites were offered on the floor in the middle of the arena, and for each test not more than two foragers were allowed to leave the nest to search for food in the arena. When they discovered the termites they exhibited the killing and stacking behavior described earlier. During this period the two halves of the artificial sky were exchanged (Fig. 2). The subsequent homing behavior of the foragers was observed through the screened walls of the arena and their course recorded as they crossed a circle (radius, 25 cm) drawn around the food source on the papered floor. Most of the ants homed approximately 180° away from their nest, orienting to visual cues overhead in preference to any olfactory cues that might have been present. Ants tested in control experiments beneath an unaltered sky returned straight to their true nest (Fig. 2a).

I then replaced the abstract patterns of the arena sky with black and white transparencies of photographs of canopies taken with a wide-angle lens (28 mm) in the foraging area of *P. tarsatus* in Kenya. The transparencies, which measured 75 by 150 cm, covered the whole arena. The experimental procedure was the same as described above; before the foragers were ready for homing, the canopy photograph was rotated 180°, and the ants' subsequent course was recorded (Figs. 3 and 4). The results demonstrate that canopy patterns can serve as an orientation cue for *P. tarsatus* foragers. In experiments with what, to human eyes, seems a far less memorable canopy pattern (Fig. 4b) only a few ants were affected in their homing orientation by a rotation of the transparency (Fig. 3, c and d). In this case, the canopy apparently was only a weak orientation cue, and other cues in and around the arena or else kinesthetic (endokinetic) orientation mechanisms were used by the ants in homing. Thus the effectiveness of a canopy as orientation cue seems to depend on the conspicuousness of the visual pattern. These laboratory experiments confirm the results obtained in the field indicating that canopy patterns play a

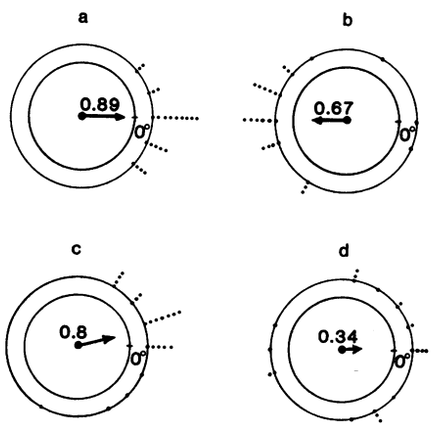

Fig. 3 (left). (a) Direction of homing movements during control experiments, carried out with the canopy pattern illustrated in Fig. 4a. (b) Direction of homing movements, after the canopy transparency (Fig. 4a) was rotated for 180°. (c) Direction of homing movements during control experiments, carried out with the canopy pattern illustrated in Fig. 4b. (d) Direction of homing movements, after the canopy transparency was rotated 180°. (For further explanations see Fig. 2.)

Fig. 4 (right). Canopy patterns photographed with a wide-angle lens in the foraging area of *P. tarsatus* in Kenya. Pattern (a) strongly affected the orientation whereas pattern (b) had only slight effect on the homing behavior of *P. tarsatus* foragers.

primary role in the orientation of foragers of *P. tarsatus*.

We can tentatively conclude that when *P. tarsatus* workers leave the exits they take a "snapshot picture" (*8*) of the surroundings of which the canopy is a significant part. The ants then orient within the coordinate system of this picture. If sufficient information is unavailable from this picture, the ants fall back on a second system, possibly chemical (*7*). Such an orientation mechanism of course limits the range of accurate orientation. In fact, the home range of *P. tarsatus* foragers above ground is not greater than about 5 m and is usually considerably smaller ($\bar{X}$ = 1.9 m, S.D. = 1.4, N = 25). Marking and recapture tests indicate that individual ants show a high fidelity in the use of specific exits. The ants travel along subterranean tunnels to these exits. What was originally considered to be nest entrances are actually exits of foraging tunnels that lead from the central nest area well into the foraging grounds. Only after the ants have left the tunnels do they conduct the individual foraging excursions during which they are guided by visual orientation cues.

Canopy orientation, which appears to have escaped attention previously, is well suited to the peculiarly restrictive lighting conditions of tropical forests. It seems likely to occur in other forest-dwelling insects and perhaps even in some vertebrates.

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References and Notes

1. R. Jander, *Z. Vergl. Physiol.* **40**, 162 (1957); B. Hölldobler, *Behav. Ecol. Sociobiol.* **1**, 3 (1976).
2. R. Wehner and R. Menzel, *Science* **164**, 192 (1969).
3. R. Wehner, Ed., *Information Processing in the Visual System of Arthropods* (Springer-Verlag, New York, 1972); R. Rosengren, *Acta Zool. Fenn.* **133c**, 1 (1971).
4. B. Hölldobler, *Science* **171**, 1149 (1971).
5. W. M. Wheeler, *Bull. Am. Mus. Nat. Hist.* **45**, 61 (1922).
6. The fieldwork was carried out in the Shimba Hills Wild Life Reserve, Kenya, during June, July, and August 1978.
7. Foragers of *P. tarsatus* can lay chemical recruitment and orientation trails with sternal gland secretions [B. Hölldobler and H. Engel, *Psyche* **85**, 285 (1979)].
8. The mechanism might be similar to that originally suggested by K. V. Frisch for the honey bees' ability to use polarized light to locate the sun. Recent data, obtained by J. L. Gould and his collaborators (personal communication), tend to support the photograph hypothesis.
9. E. Batschelet, *Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms* (American Institute of Biological Sciences, Washington D.C., 1965).
10. Supported by grants from the National Science Foundation (BNS 77-03884) and the National Geographic Society. I thank K. Horton for collecting *Paltothyreus* in the field and G. Maloiy, T. Odhiambo, R. Subra, and R. Seculik and her family for making this study in Kenya possible. H. Markl and E. O. Wilson read and commented on the manuscript.

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Long-Term Antidepressant Treatment Decreases Spiroperidol-Labeled Serotonin Receptor Binding

Abstract. *Antidepressants compete at several neurotransmitter receptor binding sites, but drug affinities do not correlate with clinical efficacy. Long-term, but not short-term, antidepressant treatment decreases the numbers of both serotonin and β-adrenergic receptors. The decrease in the number of receptor sites is most marked for [^{3}H]spiroperidol-labeled serotonin receptors and is characteristic for antidepressants of several classes.*

The behavioral depression following biogenic amine depletion by reserpine in animals and man and the potentiation of amine action by antidepressants suggest a functional deficiency of biogenic amines in depressive disorders (*1*). Although the actions of norepinephrine and serotonin are potentiated by tricyclic antidepressants and monoamine oxidase (MAO) inhibitors, these effects occur immediately, whereas there is a 1- to 3-week lag before therapeutic response (*2*). Moreover, drugs such as cocaine block the uptake of amines but are not clinically effective antidepressants (*3*), and drugs such as iprindole relieve depression but do not inhibit amine uptake (*4*). Antidepressant agents are also fairly potent blockers of muscarinic cholinergic (*5*), α-adrenergic (*6*), histamine (*7*), and serotonin (*8*) receptors. However, receptor blockade also occurs immediately and thus does not correlate with the time course of therapeutic responses. In contrast, long-term, but not short-term, treatment with antidepressants reduces the activity of a norepinephrine-stimulated adenylate cyclase in brain tissue (*9*) and reduces the number of β-adrenergic receptor sites in brain membranes (*10–12*). We now report that long-term treatment with tricyclic antidepressants, the atypical antidepressant iprindole, and the MAO inhibitor pargyline decreases the number of serotonin receptors labeled by [^{3}H]spiroperidol.

Male Sprague-Dawley rats (6 weeks old, weighing 150 to 175 g) were given daily 0.5-ml intraperitoneal injections of various drugs or saline for 21 days. Doses of all drugs were 10 mg/kg, except for pargyline (25 mg/kg). Twenty-four hours after the final injection, rats were decapitated; the brains were removed, dissected over ice, and stored at −70°C until assay. For studies of drug competiton, the fresh brains of rats that had not been given injections were used immediately for assay. The frontal cerebral cortex was used for all of the binding studies except the binding of [^{3}H]-spiroperidol to dopamine receptors, for which the corpus striatum was used. The tissues were homogenized in 10 volumes of 0.32M sucrose and centrifuged at 700g for 10 minutes. The P_1 fraction was discarded and the supernatant was centrifuged at 20,000g for 10 minutes; the sediment was suspended in tris-HCl buffer (pH 7.7 at 25°C) and centrifuged again at 20,000g for 10 minutes. The sediment was then suspended in 80 volumes of tris-HCl buffer, and the tissue was immediately used in binding assays. Briefly, 0.1 ml of ^{3}H-labeled ligand, 0.1 ml of displacing drug, and 0.8 ml of tissue suspension were incubated for varying periods (*13, 14*). The reaction was terminated by rapid filtration under vacuum through Whatman GF/B filters, which were washed three times with 5 ml of tris-HCl buffer. The labeled material retained on the filters was counted by liquid scintillation spectrometry.

The antidepressants examined compete for several receptor binding sites (Table 1). In general, the greatest potencies occur at histamine H_1 receptors labeled by [^{3}H]mepyramine. However, relative potencies of drugs at these binding sites do not correlate with clinical potencies; amitriptyline is used clinically at dosages similar to those of desipramine, but at histamine H_1 receptors, it is 75 times more potent. The antidepressants are fairly potent at muscarinic cholinergic receptors labeled by [^{3}H]quinuclidinylbenzilate ([^{3}H-]QNB), which correlates well with clinical anticholinergic side effects (*5*). Relative potencies of tricyclic antidepressants at α-adrenergic receptors labeled by [^{3}H]WB-4101 (2-([2,6-dimethoxy]phenoxyethylamino)-methylbenzodioxan) are similar to effects at muscarinic receptors and correlate with sedation and relief of psychomotor agitation (*6*). Two distinct populations of serotonin receptors are labeled, one with [^{3}H]serotonin and the other with [^{3}H]spiroperidol; [^{3}H]lysergic acid diethylamide ([^{3}H]LSD) labels both sites to the same extent (*14*). Antidepressants are much more potent at the [^{3}H]spiroperidol-labeled receptors (serotonin-2) than at the [^{3}H]serotonin-labeled receptors (serotonin-1), effects on [^{3}H]LSD binding being intermediate. The antidepressants are substantially less potent at dopamine receptors labeled by [^{3}H]spiroperidol in the corpus

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