nates, including EHDP, inhibit calcification in bone and pathologic mineral deposits by binding to hydroxyapatite deposits and preventing further crystal growth (*16–18*). In an earlier study in which bioprosthetic cusp calcification was inhibited through the use of systemic EHDP, severe adverse effects on somatic growth and bone development occurred (*19*). However, we have now performed preliminary experiments in which short-term (2 weeks) administration of EHDP with an osmotic pump (ALZET 2001, Alza, Stanford, Calif.) inhibited the calcification during the implant period, with no adverse effects on bone development or somatic growth (data not shown). Technical constraints would prohibit the use of this type of osmotic device for long-term local therapy. The long-term (84 days) controlled-release system we have developed to inhibit cuspal calcification delivered EHDP at an approximate total body dosage of 6 μg/kg. Ethylene-vinyl acetate–EHDP matrices could potentially be incorporated into clinical valve prostheses during fabrication. In addition, ethylene-vinyl acetate–EHDP may be useful in controlling calcification in other types of prosthetic implants (*20, 21*).

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References and Notes

1. A. Carpentier, G. Lemaigre, L. Robert, S. Carpentier, C. DuBost, *J. Thorac. Cardiovasc. Surg.* **58**, 467 (1969).
2. L. H. Cohn, G. H. Mudge, F. Pratter, J. J. Collins, Jr., *N. Engl. J. Med.* **304**, 258 (1981).
3. W. W. Angell, J. D. Angell, J. C. Kosek, *J. Thorac. Cardiovasc. Surg.* **83**, 493 (1982).
4. T. L. Spray and W. C. Roberts, *Am. J. Cardiol.* **40**, 319 (1977).
5. S. P. Sanders, R. J. Levy, M. D. Freed, W. I. Norwood, A. R. Castaneda, *ibid.* **46**, 429 (1980).
6. F. J. Schoen and C. E. Hobson, *Hum. Pathol.*, in press.
7. F. J. Schoen and R. J. Levy, *Cardiol. Clin.* **2**, 717 (1984).
8. Eidbo, R. J. Carroll, V. J. Ferrans, *Am. J. Cardiol.* **53**, 1388 (1984).
9. R. J. Levy, J. A. Zenker, W. F. Bernhard, *Ann. Thorac. Surg.* **36**, 187 (1983).
10. M. Fishbein *et al.*, *J. Thorac. Cardiovasc. Surg.* **83**, 602 (1982).
11. R. J. Levy, F. J. Schoen, and S. L. Howard, *Am. J. Cardiol.* **52**, 629 (1983).
12. R. J. Levy, F. J. Schoen, J. T. Levy, A. C. Nelson, S. L. Howard, L. J. Oshry, *Am. J. Pathol.* **113**, 143 (1983). Analytic-grade glutaraldehyde was obtained from Eastman-Kodak, Rochester, N.Y.
13. R. Langer, *Methods Enzymol.* **73**, 57 (1981).
14. D. S. T. Hsieh, W. D. Rhine, R. Langer, *J. Pharm. Sci.* **72**, 17 (1983).
15. P. S. Chen, T. Y. Toribara, H. Warner, *Anal. Chem.* **28**, 1756 (1956).
16. A. B. Gasser, D. B. Morgan, H. A. Fleisch, L. J. Richelle, *Clin. Sci.* **43**, 31 (1972).
17. R. Schenk, W. A. Merz, R. Muhlbauer, R. G. G. Russell, H. Fleisch, *Calcif. Tissue Res.* **11**, 196 (1973).
18. J. L. Meyer and G. H. Nancollas, *ibid.* **13**, 295 (1973).
19. R. J. Levy *et al.*, *Circulation* **68** (Suppl. 3), 395 (1983).
20. W. S. Pierce, J. H. Donachy, G. Rosenberg, *Science* **208**, 601 (1980).
21. J. B. Lian, R. J. Levy, W. F. Bernhard, M. Szycher, *Trans. Am. Soc. Artif. Intern. Organs* **46**, 429 (1981).
22. M. J. Karnovksy, *J. Cell Biol.* **27**, 137A (1965).
23. We thank E. Flynn for preparing the illustrations and L. D. Helstowski, L. Brown, and J. Kost for their assistance. This work was supported by NIH grants HL24463, HL20764, and GM26698.
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Ocelli: A Celestial Compass in the Desert Ant *Cataglyphis*

Abstract. *In addition to multifaceted lateral compound eyes, most insects possess three frontal eyes called ocelli. Each ocellus has a single lens, as does the vertebrate eye. The ocelli of some flying insects, locusts and dragonflies, have been shown to function as horizon detectors involved in the visual stabilization of course. In a walking insect, the desert ant* Cataglyphis, *it is now shown that the ocelli can read compass information from the blue sky. When the ant's compound eyes are occluded and both sun and landmarks are obscured, the ocelli, using the pattern of polarized light in the sky as a compass cue, help in guiding the ant back home.*

Insect physiologists have been reflecting for a remarkably long time on what use insects make of their ocelli (*1*). Although a lot is now known about the anatomical and physiological organization of the ocellar visual system (*2*), it is still a matter of dispute what function or functions insect ocelli serve (*3*). Recently, the old hypothesis (*4*) that flying insects (*5*) use their ocelli as horizon detectors, and thus as some means of visually stabilizing their body positions against movements about the roll and pitch axes, has been revived (*6*). We report that in a fast-running insect, the Saharan desert ant *Cataglyphis bicolor*, the ocelli can be used as a celestial compass and thus serve a function that has usually been attributed exclusively to the compound eyes (*7*).

The ants were trained to an artificial food source located 15 m from the nest. Upon arrival they were divided into three groups: COMP animals (compound eyes left open and ocelli occluded), OC animals (ocelli left open and compound eyes occluded), and blind animals (both types of eye occluded). Thereafter all ants were individually placed in unfamiliar territory, and their homing paths were recorded with the use of a grid of white lines painted on the hard desert ground. A specially designed trolley was moved along with the homing ant to restrict the ant's field of view to small parts of blue sky and to control the skylight factors displayed to the ant (for example, radiance, spectral composition, and orientation of the E vector). The trolley prevented the ants from seeing either landmarks or sun and from detecting wind direction (*8*).

In a first set of experiments the ants could view an annulus-shaped celestial window centered about the zenith (width 30°, mean elevation 40°, elevation of sun > 65°). The COMP animals were oriented in the homeward direction as precisely as controls, in which compound eyes and ocelli had been left open (Figs. 1A and 2A). We observed that even the OC animals were able to determine homeward courses, but their behavior differed strikingly from the behavior of both COMP animals and controls. First, the OC animals moved extremely slowly along tortuous paths, continuously swinging their body axes to the left and right and thus giving the impression of scanning the sky (Fig. 1B). Second, the scatter in the ant's bearings was significantly larger in the OC animals (Fig. 2B) than in ants that could use their compound eyes (Fig. 2A) (for example, 6-m distance, F-test, two-sided, d.f. = 17 and 23, $P < 0.002$). Any orientation was completely abolished when compound eyes as well as ocelli were painted out (blind animals, Figs. 1D and 2D).

This first set of experiments showed that ants that could use only their ocelli did not behave as though blind but were able to derive compass information from the sky even when the sun was not visible. However, because the ants could see a rather large part of the natural blue

sky covering all points of the compass, we could not decide on the basis of this experiment whether the ant's ocelli were really able to exploit the celestial pattern of polarization. Because of the large part of the sky displayed to the ants, the OC animals could have derived compass information from intensity or spectral gradients as well (*9*).

In a second set of experiments, the ants were presented with a single spot of artificially polarized light (diameter 40° and elevation of central point 45°) in which the orientation of the E vector could be varied. The ants in which the compound eyes had been painted out (OC animals) were able to select the proper compass course (Figs. 1C and 2C). They took the patch of artificially polarized light for neither the sun nor some point along the antisolar meridian, nor did they move phototactically toward the patch of light. They apparently selected their homeward course on the basis of the E vector orientation displayed (*10*). To control for other (visual and nonvisual) directional cues that the ants might have been able to use, the E vector was presented not where it actually occurred in the sky, but at an azimuthal distance from its natural position. The ants deviated by that distance from their true homeward direction, indicating that those ants with ocelli alone were able to read compass information from an isolated patch of polarized light in the sky.

Certainly, the ocelli are not necessary for this orientation, since painting them out has no detectable effect on the accuracy by which the ants find their way back home (Fig. 2A). Furthermore, one only has to compare the walking behavior of the OC animals (Fig. 1, B and C) with that of the COMP animals (Fig. 1A) and the controls in order to learn that the extensive body movements performed by the OC animals do not occur in ants that can use their compound eyes as a celestial compass. We do not know, however, in what respects the celestial compasses provided by ocelli and compound eyes differ from each other and whether one compass exploits specific celestial information (for example, radiant intensity, color, and E vector information) more readily or reliably than the other (*11*).

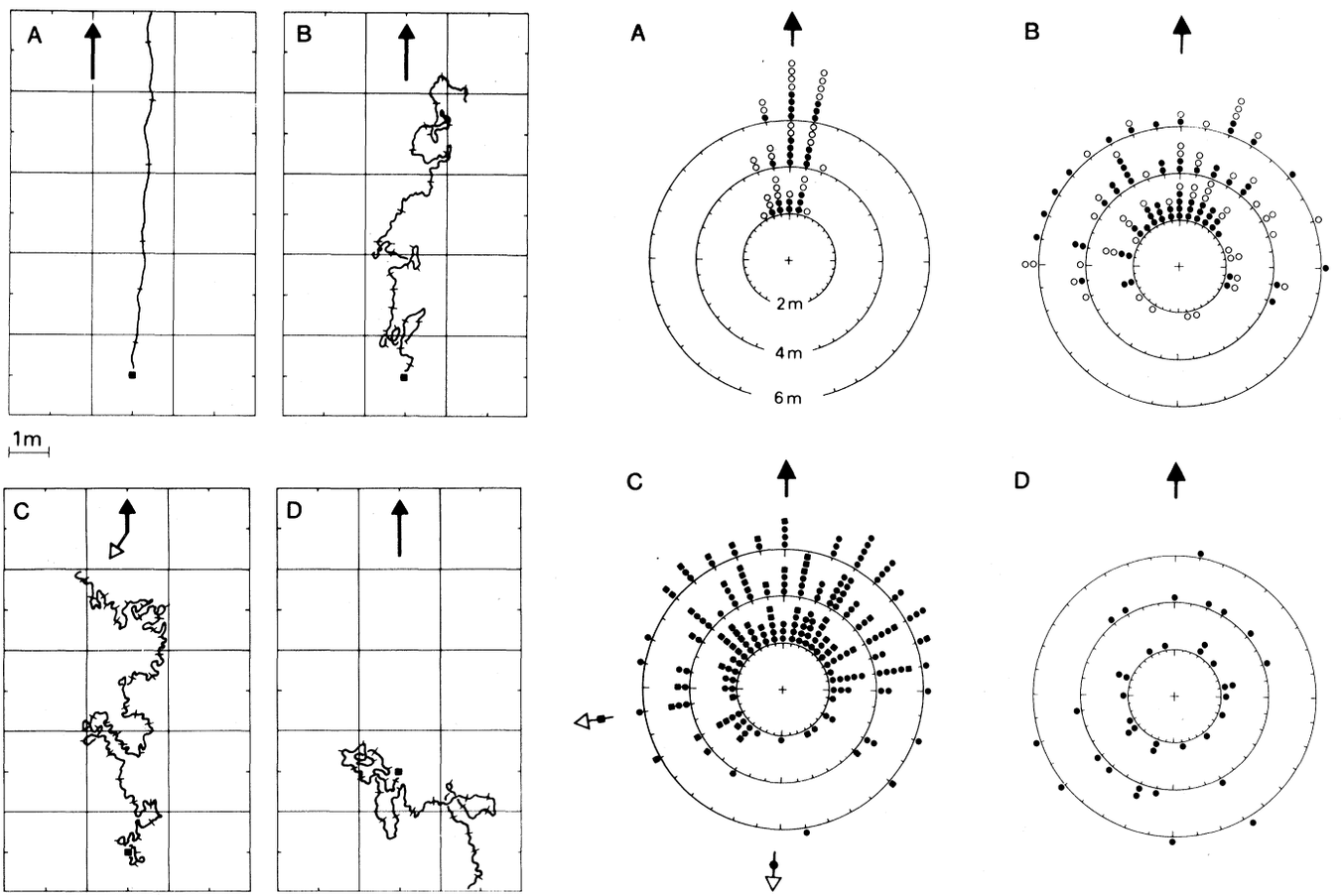

Fig. 1 (left). Homing paths of desert ants *Cataglyphis bicolor*, which were prevented from seeing landmarks and sun but could only view parts of the blue sky. (A) A COMP animal (ocelli occluded) viewing the natural blue sky; (B) an OC animal (compound eyes occluded) viewing the natural blue sky; (C) an OC animal viewing a single spot of artificially polarized light; and (D) a blind animal (compound eyes and ocelli occluded). The solid square is the point at which the ant was released; the black arrow is true homeward direction (in A, B, and D) or homeward direction as indicated by the E vector (in C); and the white arrow is the azimuth of the E vector. Time marks are given every 10 seconds. Fig. 2 (right). Return directions of ants that were allowed to view the natural blue sky (with the sun obscured) or individual E vectors. The ants' bearings are given for distances of 2, 4, and 6 m from the start (+). Black arrow (in A, B, and D) represents the homeward direction. (A) Controls (●) with neither compound eyes nor ocelli occluded and COMP animals (○) viewing the sky but prevented from seeing the sun. The two series do not differ in mean direction (Watson-Williams test, $P >> 0.1$) and deviation (F-test, $P >> 0.1$). (B) The OC animals tested as (in A). Two series (● and ○) that differ in the azimuth position of the sun relative to the homeward direction. The mean directions of the ants differ significantly from the sun's azimuth (Watson-Williams test, $P < 0.01$), thus excluding the possibility that the ants moved merely toward the brightest part of the sky. (C) The OC animals viewing a spot of artificially polarized light; E vector orientation, $\chi = -73°$ (●) or $-60°$ (■). The black arrow indicates the homeward direction that the ant should choose when relying exclusively on E vector information. White arrows are hypothetical homeward directions to be selected by the ants if they took the spot of polarized light for the sun. (D) Blind animals tested as in (A) and (B). Within the time interval of 5 minutes only 5 out of 19 blind animals moved as far as 6 m from the start.

How ants use the ocelli to detect the polarized light in the sky is a matter for speculation. We know from intracellular electrophysiological recordings that all photoreceptors of the *Cataglyphis* ocelli are ultraviolet receptors and that they are highly sensitive to polarized light (*12*), but it would be premature to design models of E vector detection until much more is known about how the analyzer directions of the photoreceptors are spatially arranged within the retina and how the photoreceptor axons converge onto the first-order interneurons (*13*). Electrophysiological measurements have shown that the ocelli of *Cataglyphis* look at regions of the sky that are closer to the horizon than to the zenith and that within the horizontal plane the visual axes of the left and right lateral ocelli deviate by 90° from the visual axis of the median ocellus (*14*). The ant's ocelli might then be thought of as a three-detector system that scans the sky for compass information. A scanning strategy involving widely separated detectors would correspond well with the striking behavior of ants in which the compound eyes have been occluded: the continual sideways movements resulting in tortuous walking trajectories.

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References and Notes

1. A. Forel, *Mitt. Münch. Entomol. Ver.* **2**, 1 (1878); E. Link, *Zool. Jahrb. Abt. Anat. Ontog. Tiere* **27**, 213 (1909); R. Demoll and L. Scheuring, *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere* **31**, 519 (1912); H. Homann, *Z. Vgl. Physiol.* **1**, 541 (1924); P. B. Cornwell, *J. Exp. Biol.* **32**, 218 (1955).
2. L. J. Goodman, in *Handbook of Sensory Physiology*, H. Autrum, Ed. (Springer-Verlag, New York, 1981), vol. VII/6C, p. 201; J. J. Milde, *J. Comp. Physiol.* **143**, 427 (1981); P. G. Mobbs *et al.*, *ibid.* **144**, 91 (1981); P. J. Simmons, *ibid.* **145**, 265 (1981); C. P. Taylor, *Brain Res.* **215**, 382 (1981); C. H. F. Rowell and K. G. Pearson, *J. Exp. Biol.* **103**, 265 (1983); J. J. Milde, *J. Comp. Physiol.* **154A**, 683 (1984).
3. A. Wolsky, *Biol. Rev.* **8**, 370 (1933); S. Bayramoglu-Ergene, *Z. Vgl. Physiol.* **48**, 467 (1964); B. Schricker, *ibid.* **49**, 420 (1965); W. B. Kerfoot, *Nature (London)* **215**, 305 (1967); R. Jander and C. K. Barry, *Z. Vgl. Physiol.* **57**, 432 (1968); J. L. Gould, *J. Comp. Physiol.* **104**, 161 (1975); M. Renner and T. Heinzeller, *J. Apicult. Res.* **18**, 225 (1979); K. G. Hu and W. S. Stark, *J. Comp. Physiol.* **135**, 85 (1980); K. Kral and H. Heran, *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere* **87**, 127 (1983).
4. R. Hesse, *Das Sehen der niederen Tiere* (Fischer, Jena, 1908), p. 44.
5. Ocelli are more likely to occur in good flyers than in wingless species [H. Kalmus, *Proc. R. Entomol. Soc. London Ser. A* **20**, 84 (1945); D. A. Parry, *J. Exp. Biol.* **24**, 211 (1947)].
6. M. Wilson, *J. Comp. Physiol.* **124**, 297 (1978); G. Stange and J. Howard, *J. Exp. Biol.* **83**, 351 (1979); G. Stange, *J. Comp. Physiol.* **141**, 335 (1981); C. P. Taylor, *J. Exp. Biol.* **93**, 1 (1981).
7. In *Cataglyphis* ants, the workers possess well-developed ocelli. In many other groups of ants, such as all European myrmicine ants, the workers lack ocelli [W. M. Wheeler, *Ants, Their Structure, Development and Behavior* (Columbia Univ. Press, New York, 1910), p. 66; C. J. Caesar, *Zool. Jahrb. Abt. Anat. Ontog. Tiere* **35**, 161 (1913)].
8. R. Wehner and B. Lanfranconi, *Nature (London)* **293**, 731 (1981); R. Wehner, *Neujahrb. Naturforsch. Ges. Zürich* **184**, 1 (1982); K. Fent, thesis, University of Zurich (in preparation).
9. This assumption is not completely arbitrary since it has been shown in bees that the compound eyes can derive compass information from spectral cues in the sky. [S. Rossel and R. Wehner, *J. Comp. Physiol. A*, **155**, 605 (1984); R. Wehner and S. Rossel, in *Experimental Behavioral Ecology and Sociobiology*, B. Hoelldobler and M. Lindauer, Eds. (Fischer, Stuttgart, 1985), p. 11. However, *Cataglyphis* ocelli possess only one spectral type of receptor (*12*).]
10. For distances of more than 1 m from the start, the directions of the ants' mean orientation vectors are always significantly different from the direction of the spot of polarized light [$P < 0.01$, Watson-Williams test on page 95 in E. Batschelet, *Circular Statistics in Biology* (Academic Press, London, New York, 1981) used for varying azimuth positions of the spot of polarized light] (Fig. 1C). Thus, phototactic responses that occasionally occur toward the spot of polarized light do not at all govern the response. Furthermore, the ants do not take the spot of polarized light for a point lying along the solar or antisolar meridian (Fig. 2C) [$P < 0.01$, Stephens test in E. Batschelet, *Statistical Methods for the Analysis in Animal Orientation and Certain Biological Rhythms* (American Institute of Biological Sciences, Washington, D.C., 1965), p. 29].
11. W. G. Wellington [*Science* **183**, 550 (1974)] suggested that insect ocelli might be able to detect the polarized light in the sky. His report describes only qualitative observations, and the data are not fully conclusive. For example, bumblebees are reported only to respond to polarized light displayed in the zenith, but then bimodal orientation is to be expected. None was observed. We show that *Cataglyphis* ants can read compass information from off-zenith E vectors present in the sky.
12. M. I. Mote and R. Wehner, *J. Comp. Physiol.* **137**, 63 (1980).
13. The ocellar retina of *Cataglyphis* does not exhibit an orderly arrangement of analyzer (microvillar) orientations. In this respect, it resembles more closely the ocellar retina of the honey bee than that of vespid wasps [K. Kral, *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere* **82**, 263 (1978)].
14. F. X. Geiser, in preparation.
15. We are grateful to A. Fent-Schlumpf and A. Meier for their continuous cooperation in the field and S. Rossel for discussion. Supported by SNF grant 3.073.081.

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Temperature Acclimation: Improved Sustained Swimming Performance in Carp at Low Temperatures

Abstract. *At low temperatures, the reduction in mechanical power output of the aerobic muscle forces cold-blooded animals, such as carp, to recruit their rapidly fatiguing anaerobic fibers at relatively slow swimming speeds. Previous experimental data have suggested that changes in the biochemistry and morphology of the aerobic muscle during cold acclimation might increase its output of mechanical power. The present experiments show that, because of these changes, carp can swim faster at low temperature using only their aerobic muscle, which results in an increase in their sustainable swimming speed. By modifying their musculature, cold-blooded animals can achieve some independence from the effects of seasonal changes in environmental temperature.*

Cold-blooded animals must generate the same mechanical power to locomote at a particular velocity irrespective of temperature (*1*), even though the maximum mechanical power that their muscle can generate decreases by a factor of two or three with each decrease of 10°C in muscle temperature (*2, 3*). We have shown that carp compensate for this loss of mechanical power by recruiting more muscle fibers and faster fiber types at low temperature (*1*). The neural mechanism appeared to be a "compression of the recruitment order" over a narrower range of swimming speeds at low temperature (*1*). The carp seemed to recruit motor units in the same order at low and high temperature; for example, at low velocities only the aerobic (red and pink) fibers were recruited, and as swimming velocities increased, the anaerobic white fibers were recruited as well. At low temperatures (10°C), however, the carp recruited all their aerobic red and pink fibers over a relatively small range of swimming velocities (15 to 26 cm/sec), whereas at 20°C the fibers were recruited over a greater range of velocities (15 to

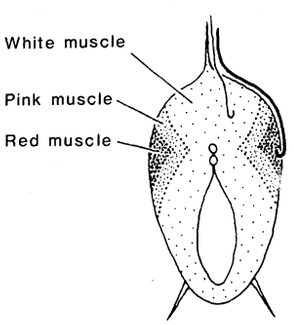

Fig. 1. Placement of the EMG electrodes. The three different muscle fiber types of the carp—white, red, and pink—are segregated into anatomically separated zones (cross-sections not drawn to scale). Fish were anaesthetized, and bipolar electrodes (teflon-insulated stainless steel wire, 75 μm in diameter) were implanted in the red muscle (heavy line) and white muscle (thin line), one set below the dorsal fin and the other 3 cm anterior to the caudal peduncle (See Fig. 2). These electrodes and a ground electrode placed intraperitoneally on the fish's ventral surface were brought forward to the first spine of the dorsal fin, where they were sutured and glued in place.