stored together in nerve terminal vesicles of sympathetic nerves (*8*).

2) Norepinephrine and ATP, when added exogenously to the vas deferens, produce contractions that are specifically antagonized by α_1- and P_2-receptor antagonists, respectively.

3) Stimulation of the motor nerves produces a biphasic contraction, and phases I and II are preferentially antagonized by the same α_1- and P_2-receptor antagonists.

4) Reserpine treatment does not abolish EJP's in the guinea pig vas deferens (*9*).

5) Adrenergic antagonists such as phentolamine, phenoxybenzamine, and prazosin readily antagonize phase II but are relatively ineffective in reducing EJP's at similar doses (*10*).

6) The P_2-receptor antagonist ANAPP$_3$ can preferentially block phase I of the contraction and the EJP's.

7) Since EJP's are enhanced by prazosin and blocked by ANAPP$_3$, it would seem unlikely that the two transmitters could interact in this fashion if they were released from different nerve populations. Furthermore, agents that selectively damage sympathetic nerves (such as 6-hydroxydopamine) can inhibit both phase I and phase II of the contractile response (*4*), indicating that both depend on release of transmitter from adrenergic neurons.

8) Finally, ATP and norepinephrine are synergistic in producing contraction when added exogenously, and exogenous ATP enhances contractile responses to nerve stimulation (*11*).

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References and Notes

1. N. Ambache and Zar M. Aboo, *J. Physiol. (London)* **216**, 359 (1971).
2. J. C. McGrath, *ibid.* **283**, 23 (1978).
3. G. K. Hogaboom, J. P. O'Donnell, J. S. Fedan, *Science* **208**, 1273 (1980).
4. J. S. Fedan, G. K. Hogaboom, J. P. O'Donnell, J. E. Colby, D. P. Westfall, *Eur. J. Pharmacol.* **69**, 41 (1981).
5. A. G. H. Blakeley, D. A. Brown, T. C. Cunnane, A. M. French, J. C. McGrath, N. C. Scott, *Nature (London)* **294**, 759 (1981).
6. G. D. S. Hirst and T. C. Neild, *ibid.* **283**, 767 (1980).
7. P. Sneddon, D. P. Westfall, J. Colby, J. S. Fedan, *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **41**, 1720 (1982).
8. K. B. Helle, H. Langercrantz, L. Stjarne, *Acta Physiol. Scand.* **81**, 565 (1971).
9. G. Burnstock, M. E. Hollman, H. Kuriyama, *J. Physiol. (London)* **172**, 31 (1964).
10. G. Burnstock and M. E. Hollman, *Br. J. Pharmacol.* **23**, 600 (1964).
11. T. Kazic and D. Milosavljevic, *ibid.* **71**, 93 (1980).

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Iron-Containing Cells in the Honey Bee (*Apis mellifera*)

Abstract. *Honey bees are sensitive to earth strength magnetic fields and are reported to contain magnetite (Fe_3O_4) in their abdomens. We report bands of cells around each abdominal segment that contain numerous electron-opaque, iron-containing granules. The iron is principally in the form of hydrous iron oxides.*

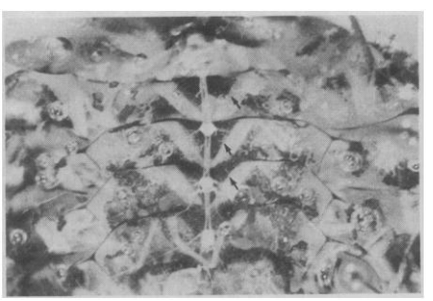
There is behavioral evidence that organisms as diverse as bacteria (*1*, *2*), homing pigeons (*3*–*5*), and honey bees (*6*, *7*) are sensitive to earth strength magnetic fields. In magnetotactic bacteria the response to magnetic fields is based on intracytoplasmic magnetite (Fe_3O_4) particles that impart a permanent magnetic dipole moment to these prokaryotes (*1*, *2*). The sensory systems that detect magnetic fields in homing pigeons and honey bees are still unknown. However, reports of magnetite in both homing pigeons (*8*) and honey bees (*9*) as well as in other organisms (*10*, *11*) suggest that this iron oxide could also be the basis of magnetic field detection in eukaryotes. Since magnetite in honey bees is reported to be localized in the abdomen (*9*), we have histologically examined tissues of the honey bee abdomen and looked specifically for those cells that contain iron and for connections between these cells and the central nervous system, a requirement for a sensory receptor.

We have found bands of cells in each abdominal segment of the honey bee that contain numerous iron-rich granules. We have localized the cells and the granules by both light and electron microscopy. For light microscopy we stained with Prussian blue, a reaction in which iron forms a blue precipitate in the presence of acidic potassium ferrocyanide. For electron microscopy we relied on electron opaqueness coupled with x-ray microanalysis to identify the iron granules. Using Mössbauer spectroscopy we identified the iron granules as consisting principally of hydrous iron oxides.

For gross examination of the honey bee abdomen (Fig. 1), adult foraging workers were pinned on dental wax, and their abdomens were cut and pinned open with stainless steel minutien pins. The abdominal contents were fixed and stained in situ (*12*). The dissected abdomens were then washed in distilled water and examined with a Zeiss dissecting microscope. The stained cells (Fig. 1) occur in a band under the epidermis in each abdominal segment. There is a higher concentration of cells in the ventral abdomen under each segmental ganglion. Sheets of this tissue were removed; examination revealed that the iron-positive staining cells form a reticular network within which is another population of smaller spherical nonstaining cells. In fresh, unstained tissue these two cell types are easily distinguished, and the iron-containing cells are seen to have granules of a yellowish color.

Examination of dissected whole abdomens stained with methylene blue shows that at each segmental ganglion a small nerve branch enters into the iron-positive tissue layer and ramifies throughout it. Mechanical movement of this small nerve trunk causes movement of this tissue layer but no other observable structures. Thus, it seems that this tissue is supplied with an efferent or afferent nerve supply (or both).

For light microscopy tissue was fixed and embedded in plastic. Sections (3 μm thick) were mounted on slides and stained for iron with the acidic potassium ferricyanide. The sectioned material (Fig. 2) shows the two cell types that



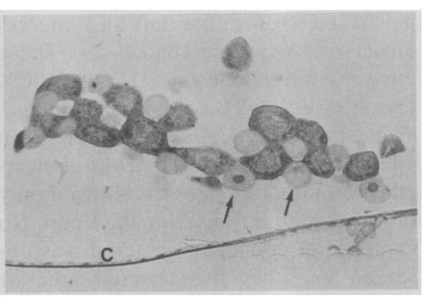


Fig. 1 (left). Honey bee abdomen pinned open and stained for iron. Arrows show large groups of iron-staining (dark) cells under segmental ganglion. Fig. 2 (right). Light photomicrograph of a section of the ventral portion of an abdominal segment containing oenocytes and fat cells (arrows). The oenocytes are characterized by a granular staining pattern; *c*, cuticle.

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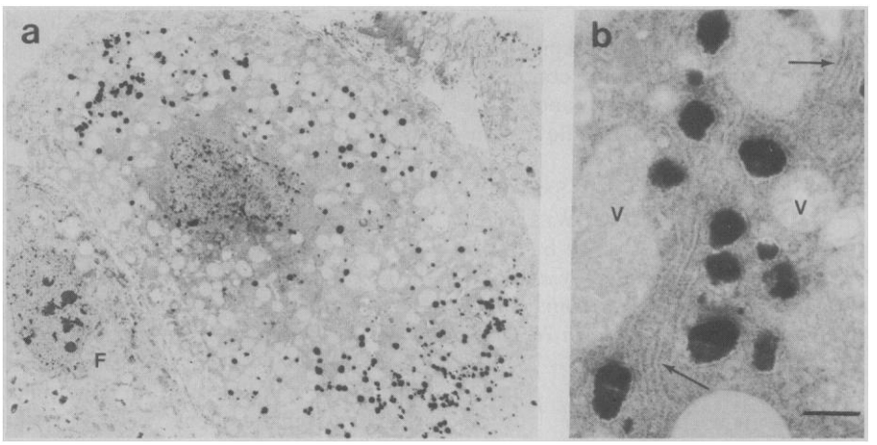

Fig. 3. (a) Low magnification transmission electron micrograph of iron-containing cell and neighboring fat cell (*F*). Dark granules are perinuclear iron containing granules. Many vesicles can also be seen (× 1,320). (b) High-magnification transmission electron micrograph showing an area containing iron granules, vesicles (*V*), and rough endoplasmic reticulum (arrows); scale bar, = 0.5 μm (× 19,200).

were observed in the whole mounts. The smaller cells never show any sign of a positive staining for iron, while the larger cells always show a granular staining pattern.

We also examined this tissue in the transmission electron microscope. Excised tissue was fixed and embedded conventionally. Silver sections were cut with a diamond knife and stained with uranyl acetate and lead citrate. Ultrastructurally one can distinguish the two cell types. The smaller, spherical cells have an abundant endoplasmic reticulum and contain many vesicles. These appear to be the fat cells described by Snodgrass (*13*). The other cells (Fig. 3a) are larger, more irregular in shape, and also have extensive rough endoplasmic reticulum free ribosomes, and many vesicles. These cells also contain many small (0.1 to 0.9 μm) round, very electron opaque particles. At high magnification (Fig. 3b) these particles do not seem to be membrane bound, and they do not have any obvious substructure.

The electron opaque particles in thick (1500 to 2000 Å) sections of unosmicated tissue embedded in Epon 812 were studied by electron diffraction and energy-dispersive x-ray microanalysis. These analyses were done on a JEOL 200CX operating at 200-kV accelerating voltage. The x-ray analytical system utilizes an energy dispersive Si(Li) detector. Selected area diffraction patterns showed only the weak diffuse rings from the Epon. No evidence of crystalline material was observed in either the selected area or microdiffraction modes. On the basis of the size of the particles, the section thickness, and the quantity of iron in the particles as suggested by the x-ray analysis (see below), a diffraction pattern would be expected if significant crystalline structure existed.

X-ray spectra were obtained in the STEM mode with a 200-Å spot counting for 200 seconds with the use of a low background graphite specimen holder with a specimen tilt of 40°. The spectra from an electron opaque granule (Fig. 4a) show a large quantity of iron present as compared to an immediately adjacent area devoid of granules (Fig. 4b). Spectra taken in the CTEM mode with a 0.1-μm spot gave the same results. These particles also contain calcium and phosphorus as seen in Fig. 4a.

To characterize the chemical state of the iron in the granules, ^{57}Fe Mössbauer spectroscopic measurements at 4.2, 160, and 300 K were made on bands of iron-rich cells that had been excised from honey bees and placed in distilled water and lyophilized. The Mössbauer spectrum (data not shown) of 180 mg of lyophilized cells pooled from 300 bees consists of a broadened quadrupole doublet at 160 and 300 K, based on a computerized, least squares fit to the data; the quadrupole splitting and isomer shift at 160 K are 0.65 mm/sec and 0.46 mm/sec (relative to iron metal at 300 K), respectively. At 4.2 K the spectrum shows evidence of nonhomogenous magnetic hyperfine splitting. These spectral characteristics indicate densely packed ferric iron with oxygen coordination similar to iron in biological iron storage materials including ferritin and others that contain amorphous iron oxides (*14*). In particular, hydrous iron oxide granules associated with calcium and phosphorus are known in the marine invertebrate *Molpadia intermedia* (*15*).

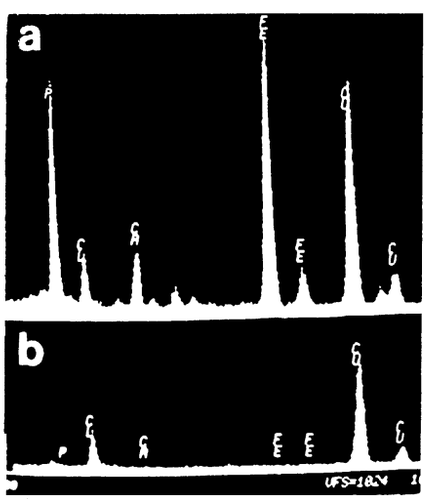

Fig. 4. (a) Energy dispersive x-ray spectrum of electron dense granules. STEM mode with a spot size of 200 Å at 200-kV accelerating voltage was used. Counts were for 200 seconds with a background of 20 to 40 counts. (b) Energy dispersive x-ray spectra of adjacent cell area devoid of granules; same conditions as (a).

The iron-rich granules occupy approximately 7 percent of the 3×10^{-8} cm^3 volume of the cells which contain them. Passage of trypsinized cells through a Coulter counter which selected for the large cells gives approximately 11,300 of these cells per bee. Thus the estimated volume of the granules is 2.5×10^{-5} ml per bee or 7.2×10^{-5} g, if the density is 3.0. Gould *et al.* (*9*) measured an average induced magnetic moment of about 2×10^{-6} E.M.U. per bee corresponding to at least 2.2×10^{-8} g of Fe_3O_4. Since hydrous iron oxides are typically paramagnetic at room temperature (*16, 17*) they would not contribute to the remanent magnetism of the bee. However, only 0.33 percent of the hydrous iron oxide present would have to be reduced to magnetite to account for the measured magnetic moment. Hydrous iron oxides are precursors to Fe_3O_4 formation in chitons and magnetotactic bacteria (*2, 18*). This small quantity of Fe_3O_4 would not be detected with any of our analytical techniques.

We believe that these iron-containing cells are the oenocytes of the honey bee as described by Snodgrass (*13*). These cells have been studied in the larvae of other insects [*Gryllus bimacultaus* (*19*) and *Calpodes ethilius* (*20*)] where they seem to be involved in steroid synthesis during development. Their function in the adult is at present unknown. There are no reports, however, that these cells contain either dense granules or iron in any insect except in our studies of adult bees.

In summary, the oenocytes of the adult foraging honey bee form an innervated sheet of tissue around each abdominal segment. Each cell of the sheet contains many electron-opaque iron-containing granules in the cytoplasm.

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References and Notes

1. R. Blakemore, *Science* **190**, 377 (1975).
2. R. B. Frankel, R. P. Blakemore, R. S. Wolfe, *ibid.* **203**, 1355 (1979).
3. W. T. Keeton, *Proc. Natl. Acad. Sci. U.S.A.* **68**, 102 (1971).
4. ———, T. S. Larkin, D. M. Windsor, *J. Comp. Physiol.* **95**, 95 (1974).
5. C. Walcott and R. P. Green, *Science* **184**, 180 (1974).
6. M. Lindauer and H. Martin, *Z. Vgl. Physiol.* **60**, 219 (1968).
7. H. Martin and M. Lindauer, *J. Comp. Physiol.* **82**, 145 (1972).
8. C. Walcott, J. L. Gould, J. L. Kirschvink, *Science* **205**, 1027 (1979).
9. J. L. Gould, J. L. Kirschvink, K. S. Deffeyes, *ibid.* **201**, 1026 (1978).
10. J. Zoeger, J. R. Dunn, M. Fuller, *ibid.* **213**, 892 (1981).
11. T. P. Quinn, R. I. Merrill, E. L. Brannon, *J. Exp. Zool.* **217**, 137 (1981).
12. Fixation was with either 4 percent Formalin or 2.5 percent glutaraldehyde in phosphate buffer. Staining was with a hot (60°C) 1:1 mixture of 0.5 percent potassium ferricyanide and 0.5 percent HCl for 15 to 30 minutes.
13. R. E. Snodgrass, *Anatomy of the Honey Bee* (Comstock Publishing Association, Cornell University, Ithaca, N.Y., 1956).
14. S. Ofer, G. C. Papaefthymiou, R. B. Frankel, H. A. Lowenstam, *Biochim. Biophys. Acta* **679**, 199 (1981).
15. H. A. Lowenstam and G. R. Rossman, *Chem. Geol.* **15**, 5-5 (1975).
16. A. Blaise, J. Chappert, J. L. Giravdet, *C.R. Acad. Sci. Paris* **261**, 2310 (1965).
17. J. M. D. Coey and P. W. Readman, *Earth Planet. Sci. Lett.* **21**, 45 (1973).
18. K. M. Towe and H. A. Lowenstam, *J. Ultrastruct. Res.* **17**, 1 (1967).
19. F. Romer, *Cell Tissue Res.* **151**, 27 (1974).
20. M. Locke, *Tissue Cell* **1**, 103 (1969).
21. B.W. is supported by grant GM 28804 from the National Institutes of Health. R.B.F. is partially supported by the Office of Naval Research. The Francis Bitter National Magnet Laboratory is supported by the National Science Foundation. We thank C. McKeon for help with tissue isolation and G. C. Papaefthymiou for help with the Mössbauer data analysis.

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A Specific and Enduring Improvement in Visual Motion Discrimination

Abstract. *Training improves the ability of human observers to discriminate between two similar directions of motion. This gradual improvement is specific to the direction on which an observer is trained, and it endures for several months. Improvement does not affect motion perception generally, nor does it depend on recognition of details of the movement.*

Practice can improve ability to discriminate among objects. This perceptual learning often simply reflects improved ability to pick out features distinguishing one visual target from another (*1, 2*). Other times, perceptual learning requires a change in the observer's use of verbal labels to describe his experience (*3*) or heightened attention or arousal (*4*). We report an enduring alteration in vision that is specific to the stimulus on which an observer is trained. Rather than resulting from an increased ability to pick out some critical feature of the stimulus, this form of perceptual learning may be related to changes in the selectivity of elements in the visual system.

Since previous work suggested that motion perception is plastic (*5, 6*), we set out to train an observer's discrimination of the direction of moving targets. Before training, we measured how well observers discriminated small differences in direction of motion. Discrimination was assessed around eight different directions: 0° (rightward), 45°, 90° (upward), 135°, 180°, 225°, 270°, and 315°. Hereafter, we refer to directions 0°, 90°, 180°, and 270° as principal directions and 45°, 135°, 225°, and 315° as oblique directions. Eight observers were tested: one was K.B. and six were naïve about our purposes.

Stimuli were bright, spatially random dots moving along parallel paths over the face of a cathode ray tube at 10° per second. At any one time, about 400 dots were visible within an 8° circular aperture. The dots, and their movement, were highly visible: the luminance of the dots was approximately 50 times that required for them to be just seen against a constant veiling luminance of 2 cd/m^2. Opposite ends of the display were linked electronically so that dots disappearing at one side wrapped around, to reappear at the opposite side. Full details of the display are given elsewhere (*6*). Observers viewed the displays binocularly, fixating a dark, stationary, central point. To guard against the possibility that observers might learn to identify details of our display, a new array of spatially random dots was used every 50 trials (*7*).

Each trial consisted of two 500-msec intervals. This pair of intervals was separated by a 200-msec period during which only the uniformly illuminated cathode-ray tube was visible. Two equiprobable types of trials, "same" and "different," were randomly ordered. On "same" trials, motion took the same direction during both intervals; on "different" trials, motion in one interval was in a direction differing by 3° from that of the other interval. The observer viewed both intervals and judged the two directions "same" or "different."

A block of 50 trials was characterized by one standard direction. This direction appeared in both intervals of "same" trials and in one interval of "different" trials. In the remaining interval of "different" trials, a random choice was made to present motion 3° either clockwise or counterclockwise of the standard direction. Whether the first or second interval contained the standard direction on "different" trials was also randomly determined. A tone after each correct judgment gave immediate knowledge of results.

The main experiment required seven sessions over 10 to 12 days. In sessions 1, 4, and 7, discrimination performance was measured for all eight directions. The order of testing was separately randomized for each session and observer. In sessions 2, 3, 5, and 6, an observer trained on just one of the eight directions, principal and oblique. At the start of the experiment, a different training direction was assigned each observer, who retained that assignment throughout the experiment. During a training session, an observer made 500 "same-different" judgments (ten blocks of 50 trials) with the assigned direction. For both training and test sessions, observers were rewarded with 2 cents for each correct response; 1 cent was deducted for each incorrect response.

Responses in a block of trials were reduced to a pair of proportions: the proportion of "different" trials correctly identified as such (hits), and the proportion of "same" trials misidentified as "different" (false alarms). These proportions were converted into d', a measure of discrimination performance (*8*). This measure granted immunity to spurious performance changes that would follow

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