

ELECTRIC FISH APPROACH STATIONARY SIGNAL SOURCES BY FOLLOWING ELECTRIC CURRENT LINES

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SUMMARY

African electric fish of a pulse species, *Brienomyrus brachyistius* (Mormyridae), housed singly in a large, circular arena, were presented with electrical stimuli which mimicked a conspecific intruder. Stimuli were produced with either dipolar or bipolar electrodes in three different geometries. We tracked the unconditioned approach response paths taken by the fish and compared tracks for each of the geometries. The results suggest that *B. brachyistius* can determine neither the distance nor the direction of an electric dipole from afar, but that they do manage to find the source by maintaining a precise alignment of their body axis parallel to the direction of the local electric field vector (parallel to current lines) while swimming. This behaviour ultimately leads to the current source. We propose that this behaviour may be a simple mechanism mediating the approach response of one electric fish to another.

INTRODUCTION

An essential element of the process of animal communication is the ability of the signal receiver to localize the source of signals. Once the recipient has determined the distance and direction of a signal source, it may orient its behaviour with respect to the position of that stimulus. Localization abilities are especially vital to the recipient when receiving long-distance calling signals which may elicit approach behaviour, or territorial signals which may evoke directed withdrawal. Both of these responses, and many others, require a response which is oriented with respect to the signaller.

For most of the common sensory modalities – such as vision, audition, chemoreception, vibration sense and surface-wave detection – a good deal is known about both the physical cues relevant to stimulus localization and the sensory processing of these cues (Hopkins, 1983c; Camhi, 1984; Wehner, 1981; Land, 1981; Erulkar, 1972; Konishi, 1977; Knudsen, 1980; Bell & Tobin, 1982; Markl, 1983; Bleckmann, 1980, 1986; Masters & Markl, 1981). In contrast, very little is known about the mechanisms of signal localization in electroreception, a sensory modality which is

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unique to some aquatic vertebrates (see Bullock & Heiligenberg, 1986). When an electric fish detects and locates a distant electric field generated by another electric fish, some other electrogenic organism or even an inanimate source, it is called 'passive electrolocation' (Kalmijn, 1974). This contrasts with 'active electrolocation', in which the fish senses conducting or non-conducting objects in the environment as *distortions* in the usual transepidermal current generated by its own electric organ discharge (see Heiligenberg, 1977; Bastian, 1986).

Mormyrid electric fish produce, by the action of a specialized electric organ in the tail region, an electric pulse, approximately 1 ms in duration. Both the instantaneous electric potential around a fish during a discharge, and the electric field determined as the gradient of the potential have been shown to match closely the potential from an electrostatic dipole source for distances greater than 10 cm from the fish's skin (Knudsen, 1975a). The electric signal does not propagate as an electromagnetic wave, but exists solely as an electrostatic field (Hopkins, 1986b). There are no delay times in propagation that might provide a cue to a recipient about the direction from which a signal is coming. In addition, the curved electric field lines, and the iso-electric current lines which are directly proportional to them, provide only ambiguous cues to the receiver about the distance and direction of the current source. Similar localization ambiguities do not occur with visual communication or with auditory communication in the 'far field', because in these modalities signals propagate in straight lines away from their sources. A. J. Kalmijn (personal communication) has suggested that a similar localization problem may exist when a receiver attempts to localize an acoustic dipole in the acoustic near field.

Because of these interesting differences between the electric modality and other better understood sensory modalities, we have investigated the mechanisms of passive electrolocation in mormyrid electric fish using an unconditioned approach response to an electric dipole stimulus mimicking a conspecific.

MATERIALS AND METHODS

Five African electric fish, *Brienomyrus brachyistius*, Mormyridae (Gill, 1862), ranging from 9 to 13 cm in length were used in these observations. Fish were housed individually or taken from community tanks. Each fish was tested in a large arena formed by bending a Lexan sheet 28 cm high into a circle of 55 cm radius and placing it in a 122×122×29 cm tank. Filled to a depth of 20 cm, the tank held approximately 275 l. A 13 cm disk of opaque plastic supported by three thin legs to a height of 7.5 cm located in the centre of the tank served as the sole shelter for the fish.

All the fish, when isolated in the arena, showed a natural tendency to seek and remain under the central shelter. During the experimental trials, the tank was illuminated with two 25 W, 110 V frosted blue bulbs controlled by a rheostat set between 20 and 70 V. We sought a light level bright enough to keep the fish underneath the shelter, yet dim enough so it would emerge for brief periods of exploration when stimulated electrically.

We produced an artificial 'mormyrid mimic' by generating single cycles of a 5.0 kHz sine wave (0.2 ms duration) repeated at intervals varying randomly from 50 to 100 ms (Wavetek 275 Generator). This stimulus roughly resembled the electric organ discharge (EOD) of a conspecific in both waveform and interval. The stimulus was passed through a variable attenuator and an isolation transformer. The floating output passed through a switching box and was delivered through a pair of Ag/AgCl wire electrodes wrapped around 1 cm Plexiglas tubing mounted 6.5 cm from the bottom. We used three different stimulus configurations: a tangential dipole, a radial dipole or a hemicircle bipole (see Fig. 1). The electrodes were set at a height that matched the normal swimming and resting height of the fish in the tank. This, together with the rather shallow depth of the tank, effectively restricted the three-dimensional localization problem to one of two dimensions.

A *tangential dipole* was formed by two electrodes placed 4.5 cm apart, just inside the circumference of the arena, with the axis of the dipole perpendicular to the radius of the arena. A *radial dipole* was formed by rotating the dipole by 90° so the axis was parallel to the radius of the arena. A *hemicircle bipole* consisted of two electrodes 110 cm apart on the diameter of the arena. Electrodes were placed at 45° intervals around the arena and could be selected at random using the switch box. Signal amplitude was adjusted to be suprathreshold (approximately 5–10 $\mu\text{V cm}^{-1}$) by attenuation. We attenuated most when using the hemicircle bipole, least for the radial dipole.

The fish were observed with a low-light-level television camera with a 25 mm f1.4 lens, mounted 2.5 m above the tank. Prior to each series of experimental trials, the fish was allowed at least 10 min of undisturbed electrical silence in the shelter. A pair of electrodes was then randomly selected and activated *via* a footswitch.

The fish typically made an unconditioned approach within 30 s of stimulus onset. We mapped the paths taken from the shelter to the active electrodes on clear acetate sheets placed in front of the video monitor. The stimulus was turned off as soon as the fish reached the electrodes; it then returned to the shelter. If the stimulus was on for more than 1 min with the fish failing to leave the shelter, the trial was rejected. The fish was allowed at least 1 min in the shelter before beginning the next trial.

We selected the active electrode pair at random from one of eight possible directions (four possible for the hemicircle bipole). After a series of trials, we made a composite with the active electrode positioned vertically by re-orienting our maps. We did not investigate the effects of the stimulus polarity in this study. We ran a maximum of 30 trials per fish on a given day, depending on habituation. The lights were progressively dimmed to maintain responsiveness as the experiment proceeded.

After the behavioural trials, electric field measurements were made with an assembly consisting of two small solder ball electrodes spaced 1 cm apart which slid along movable angle-iron rails above the tank. With the stimulator producing a 5 kHz sine wave, we measured x and y components of the electric field using a Grass P15 preamplifier and a Keithley 165 digital multimeter. Resultant electric field vectors were computed and are plotted in Fig. 1. Water conductivity averaged 560 μS (Horizon 1484-10 conductivity meter). Water temperature averaged 26°C.

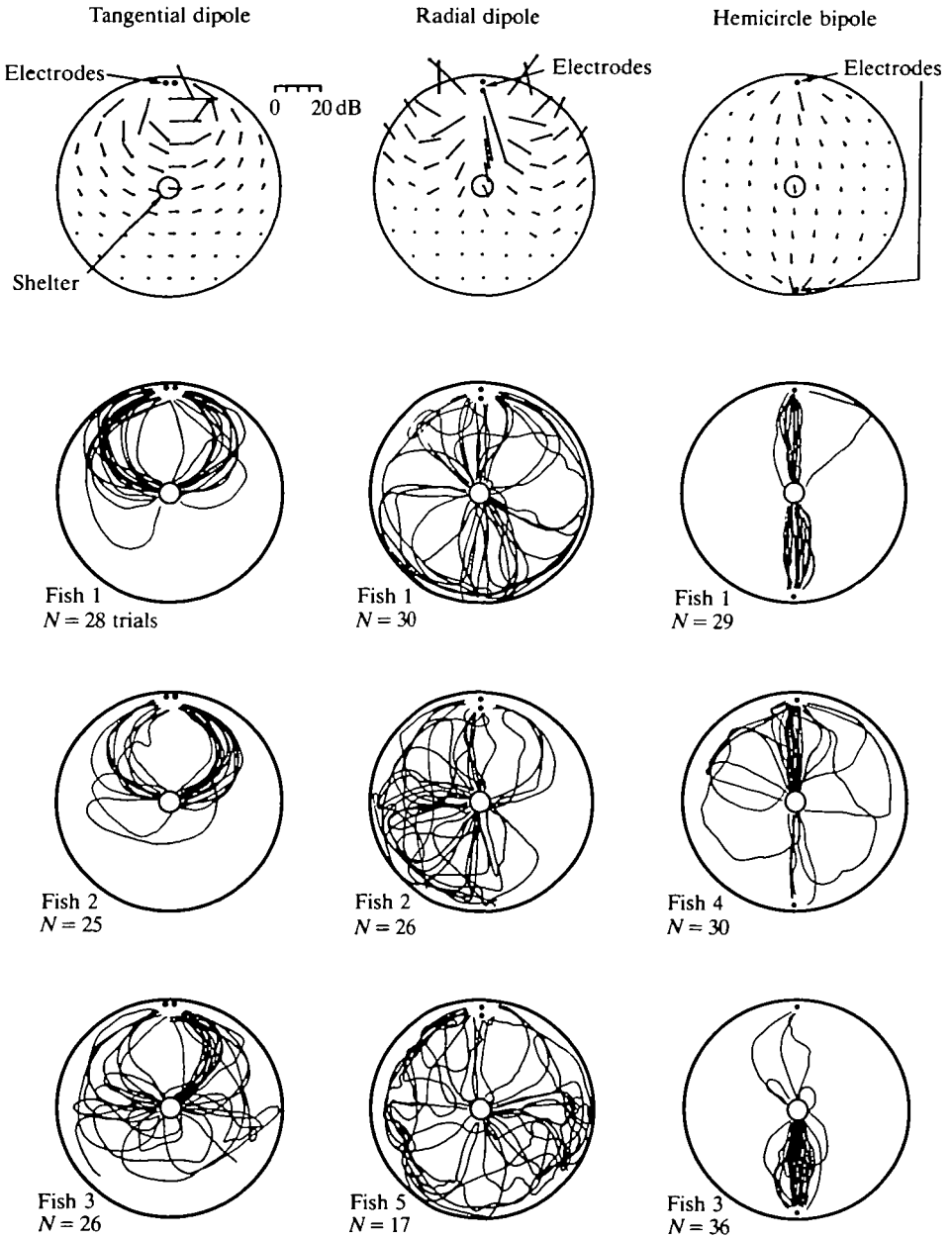
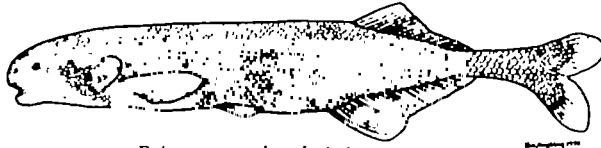


Fig. 1

RESULTS

The results of our three electrode configurations are summarized in Fig. 1. The magnitude and direction of the stimulus electric fields within the experimental tank are shown in the top row; the superimposed approach paths taken by the fish are below. The first column shows the results for the radial dipole, the second column, the tangential dipole, and the third column the hemicircle bipole electrodes. The three experimental paradigms may be compared by visual inspection of the superimposed tracks.

Tangential dipole

The superimposed maps show 79 tracks: 28 by fish no. 1, 25 by fish no. 2 and 26 by fish no. 3. Fish receiving the tangential dipole stimulus tend to follow a curved pathway leading either to the right or to the left of the most direct straight-line pathway to the electrodes. Occasional paths appear disoriented, as with the other stimulus geometries. We did not observe fish following the shortest path from start position to electrodes. Instead, they typically followed the longer, curved paths illustrated in Fig. 1.

Radial dipole

The superimposed maps show 30 tracks of fish no. 1, 26 of fish no. 2 and 17 of fish no. 5. Fish were less sensitive to the radially oriented dipole. We had to increase the stimulus amplitude 5–10 dB above the amplitude used in the tangential dipole orientation to get responses. We observed paths with directions which appeared random with respect to the direction of the dipole source. Most fish left the shelter by following a radius from the centre to the tank edge, and then turned to follow the plastic wall.

Hemicircle bipole

When one electrode pole was placed on one side of the tank and the other on the opposite side, the fish typically left the start position and swam directly towards one electrode or the other. The superimposed maps show 29 responses of fish no. 1, 30 of

Fig. 1. Top: the study species, *Brienomyrus brachyistius*, a mormyrid electric fish from Africa. Bottom: the fish is housed in a 1.1 m diameter circular arena and provided with an electrical stimulus which mimics a conspecific intruder, through electrodes in three geometric configurations: tangential dipole (left column), radial dipole (centre column) and hemicircular bipole (right column). The electrodes are indicated by filled circles, and the relative magnitudes and directions of the electric fields in each of the three geometries are indicated by the length and direction of the arrows in the first row of drawings. The beginning of each arrow shows the position of the measurement, the length of each arrow is proportional to the log of the electric field magnitude (see scale in dB; the reference level refers to the minimum recorded field strength in the matrix). The superimposed approach paths of *B. brachyistius* are shown in the second to fourth rows of drawings. Each diagram shows superimposed tracks for an individual fish. There is a close correspondence between the observed tracks of the fish as they approach the stimulus and the local direction of the electric field produced by the stimulus geometry employed.

fish no. 4 and 36 of fish no. 3. Presented with stimuli from a hemicircle bipolar electrode pair, the path was usually a straight line between the shelter and one of the bipolar electrodes. The seeming preference for one pole or the other by fish nos 3 and 4 is simply an artefact of the way in which we rotated the tracing of the track about the centre before superimposing the drawings. We observed no systematic preference for either of the two poles of any of the four pairs of electrodes actually used.

We observed a close correspondence between the vector direction of the electric field from the stimulus electrodes and the orientation of the approach pathway in all three stimulus orientations. For the tangential dipole, current lines cut through the centre of the tank, where the shelter is located, and arc towards the wall in a curved path. The fish were typically oriented parallel to field lines throughout their curved pathway. The electric field produced by the hemicircular bipole electrodes was nearly homogeneous in the tank centre, but bowed outwards at the edges of the tank. Again, the path orientations followed the current lines. Field lines for the radial dipole were the most complex. The shelter lies on the dipole axis and receives a very weak stimulus as a result. From the axis, field lines bend left or right and then arc back to the tank's edge. In all three cases, the fish followed the direction of the field lines, or the direction of maximum current density.

DISCUSSION

The results of these observations indicate that mormyrid electric fish are capable of finding a source of an electric field, like the one generated by a non-moving conspecific, using electrical cues only. To account for the observed responses, we suggest that the fish first orients parallel to the vector direction of the electric field, and then simply swims forward while maintaining the same alignment to the local electric field vector. Such a method is guaranteed to lead the fish to the source of the current, albeit on an indirect pathway. As a corollary, our hypothesis suggests that the fish can determine neither the distance nor the direction of a current source from a single point in space distant from that source, but must move to locate the source. If it had been able to predict the position of the electrodes, we would have expected to see more efficient approach paths, especially in the case of the tangential stimulus configuration, which provided a strong stimulus at the shelter.

How are these fish able to determine the direction of the local electric field vector in the first place? When a fish is oriented parallel to the field lines, current should pass inwards uniformly through electroreceptors in the anterior half of the body and outwards through receptors in the posterior half, with a phase reversal girdling the fish's mid-body like a belt. Oriented perpendicular to the field lines, the current should pass inwards through the left side and outwards through the right, with a phase reversal for the received stimulus along the midline. One possible mechanism of detection of electric field direction would involve detection of the alignment of the position of electroreceptors where the phase reversal occurs.

A second possible mechanism depends upon the fact that the fish is most sensitive to an electric field when it is oriented parallel to it. This is because the interior of

these freshwater fish is a relatively good conductor compared to the surrounding water, so that the body interior is nearly isopotential. When the body is parallel to the field lines, the head and tail occupy positions of greater potential difference with respect to each other than do the left *vs* right sides when oriented perpendicular to the field direction. As a result, the receptors, which lie embedded in a high-resistance skin, should pass the greatest current when head and tail differ in potential by the greatest amount (see Bennett, 1971). Our experiments do not tell us whether these fish are able to detect the direction of the local electric field vector without moving or 'hunting' for the maximum stimulus amplitude. Since the animals were free to move during the period of stimulation, they had ample opportunity to make successive comparisons of the electric field with different body orientations.

In mormyrids, the electroreceptors adapted to receive distant external electric fields in communication are the Knollenorgans (see Hopkins, 1981, 1986*a*; Bell & Szabo, 1986). Knollenorgans are distributed on the head, and on the posterior body walls near the anal and dorsal fins. Few are located on the skin in the mid-body near the pelvic fin region (Hopkins, 1983*b*). When the fish is aligned parallel to current lines, the polarity of the received stimulus should reverse at mid-body (approximately at the level of the pelvic fins where there are no receptors).

Knudsen (1975*b*, 1978) recorded from catfish midbrain (torus semicircularis) and found evidence for a somatotopic map of the ampullary electroreceptors in the skin which doubled as an electric field orientation-selective map; i.e. an organized map of cells which were selective to certain preferred electric field directions. When a catfish is stimulated with a low-frequency electric field, we would expect that only certain cells in this torus region would respond to the stimulus and that the stimulated region would change with the direction of the stimulus field. A similar result has been obtained for the ampullae of Lorenzini electroreceptors of the ray, *Platyrrhinoidis* (Schweitzer, 1986). Given the existence of such a map for ampullary receptors, it would not be surprising to find a similar map for the tuberous electroreceptors in mormyrids, the Knollenorgans, which are implicated in the behavioural response reported here (Hopkins, 1983*a,b*).

Determining the direction of an electric field by an E-vector map in the brain, or by a hunting strategy, would be expected to be much better in the horizontal plane than it is in the vertical midline plane. This is because the difference between the length of the fish and its width is much greater than the difference between its width and its height. Because the overall sensitivity of the receptor to a uniform electric field is determined by the separation of the receptors in the field, the horizontal plane gives the fish the strongest cues as to field direction. Similarly, hunting behaviour would require left-to-right motion for determining direction in the horizontal plane but rolling behaviour, an uncommon type of motion, to determine field direction in the vertical, midline plane. The fish might determine the vertical component of an electric field by pitching forward (head-down position).

Our experiments show a fish approaching a non-moving electric dipole. It is important to ask whether a mormyrid might approach a conspecific in nature using the same strategy seen here. Assuming the fish can approach a conspecific using

electrical cues only, the most important differences between our stimulus and a natural fish are that the stimulus is stationary and that a real fish typically turns around frequently. To the receiver, a rotating or moving dipole may provide additional cues that enable it to predict the direction and distance of the source more precisely or, alternatively, the cues provided by a moving fish may be so complex that the method of following isocurrent lines would be useless and the fish may have to fall back upon a more primitive localization strategy (i.e. random search with comparison of amplitudes at successive locations).

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REFERENCES

- BASTIAN, J. (1986). Electrolocation: Behavior, anatomy, and physiology. In *Electroreception* (ed. T. H. Bullock & W. Heiligenberg), pp. 577–612. New York: John Wiley & Sons, Inc.
- BELL, W. J. & SZABO, T. (1986). Electroreception in mormyrid fish. In *Electroreception* (ed. T. H. Bullock & W. Heiligenberg), pp. 375–421. New York: John Wiley & Sons, Inc.
- BELL, W. J. & TOBIN, T. R. (1982). Chemo-orientation. *Biol. Rev.* **57**, 219–260.
- BENNETT, M. V. L. (1971). Electroreception. In *Fish Physiology*, vol. 5 (ed. W. S. Hoar & D. J. Randall), pp. 493–574. New York: Academic Press.
- BLECKMANN, H. (1980). Reaction time, threshold values and localization of prey in stationary and swimming surface-feeding fish *Aplocheilichthys lineatus*. *J. comp. Physiol.* **140**, 163–172.
- BLECKMANN, H. (1986). Role of the lateral line in fish behaviour. In *The Behavior of Teleost Fishes* (ed. T. J. Pitcher), pp. 177–205. Baltimore, Maryland: The Johns Hopkins University Press.
- BULLOCK, T. H. & HEILIGENBERG, W. (1986). *Electroreception*. New York: John Wiley & Sons, Inc.
- CAMHI, J. M. (1984). *Neuroethology. Nerve Cells and the Natural Behavior of Animals*. Sunderland, MA: Sinauer Associates.
- ERULKAR, S. D. (1972). Comparative aspects of spatial localization of sound. *Physiol. Rev.* **52**, 237–360.
- GILL, T. (1862). On the West African genus *Hemichromis* and description of new species in the museums of the Academy and Smithsonian Institutions. *Proc. Acad. nat. Sci. Philad.* **14**, 134–139.
- HEILIGENBERG, W. (1977). Principles of electrolocation and jamming avoidance in electric fish. A neuroethological approach. In *Studies in Brain Function*, vol. 1 (ed. V. Braitenberg), 85pp. New York: Springer-Verlag.
- HOPKINS, C. D. (1981). The neuroethology of electric communication. *Trends Neurosci.* **4**, 4–6.
- HOPKINS, C. D. (1983a). Functions and mechanisms in electroreception. In *Fish Neurobiology*, vol. 1, *Brain Stem and Sense Organs* (ed. R. G. Northcutt & R. E. Davis), pp. 215–259. Ann Arbor, MI: University of Michigan Press.
- HOPKINS, C. D. (1983b). Neuroethology of species recognition in electroreception. In *Advances in Vertebrate Neuroethology* (ed. J. P. Ewert, R. R. Capranica & D. J. Ingle), pp. 871–881. *NATO ASI Series, A*: **56**.
- HOPKINS, C. D. (1983c). Sensory mechanisms in animal communication. In *Animal Behaviour* (ed. T. R. Halliday & P. J. B. Slater), pp. 114–155. London: Blackwell Scientific Publications.
- HOPKINS, C. D. (1986a). Behavior of Mormyridae. In *Electroreception* (ed. T. H. Bullock & W. Heiligenberg), pp. 527–576. New York: John Wiley & Sons, Inc.
- HOPKINS, C. D. (1986b). Temporal structure of non-propagated electric communication signals. *Brain Behav. Evol.* **487**, 43–59.
- KALMUN, J. (1974). The detection of electric fields from inanimate and animate sources other than electric organs. In *Electroreceptors and Other Specialized Receptors in Lower Vertebrates* (ed. A. Fessard), pp. 147–200. Berlin, Heidelberg, New York: Springer-Verlag.

- KNUDSEN, E. I. (1975a). Spatial aspects of the electric fields generated by weakly electric fish. *J. comp. Physiol.* **99**, 103–118.
- KNUDSEN, E. I. (1975b). Midbrain responses to electroreceptive input in catfish: evidence of orientation preferences and somatotopic organization. *J. comp. Physiol.* **106**, 51–67.
- KNUDSEN, E. I. (1978). Functional organization in electroreceptive midbrain of the catfish. *J. Neurophysiol.* **41**, 350–364.
- KNUDSEN, E. I. (1980). Sound localization in birds. In *Comparative Studies of Hearing in Vertebrates* (ed. A. N. Popper & R. R. Fay), pp. 289–322. New York: Springer-Verlag.
- KONISHI, M. (1977). Spatial localization of sound. In *Recognition of Complex Acoustic Signals* (ed. T. H. Bullock). Berlin: Dahlem Konferenzen.
- LAND, M. F. (1981). Optics and vision in invertebrates. In *Handbook of Sensory Physiology*, vol. VII/6B (ed. H. Autrum), pp. 471–592. Berlin: Springer-Verlag.
- MARKL, H. (1983). Vibrational communication. In *Neuroethology and Behavioral Physiology* (ed. F. Huber & H. Markl), pp. 332–353. Berlin, Heidelberg: Springer-Verlag.
- MASTERS, W. M. & MARKL, H. (1981). Vibrational signal transmission in spider orbwebs. *Science* **213**, 363–365.
- SCHWEITZER, J. (1986). Functional organization of the electroreceptive midbrain in an elasmobranch (*Platyrrhinoidis triseriata*). *J. comp. Physiol. A* **158**, 43–58.
- WEHNER, R. (1981). Spatial aspects of vision in arthropods. In *Handbook of Sensory Physiology*, vol. VII/6C (ed. H. Autrum), pp. 287–616. Berlin: Springer-Verlag.