

## SIGNALS AND NOISE IN THE ELASMOBRANCH ELECTROSENSORY SYSTEM

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Accepted 22 January; published on WWW 21 April 1999

### Summary

Analyzing signal and noise for any sensory system requires an appreciation of the biological and physical *milieu* of the animal. Behavioral studies show that elasmobranchs use their electrosensory systems extensively for prey detection, but also for mate recognition and possibly for navigation. These biologically important signals are detected against a background of self-generated bioelectric fields. Noise-suppression mechanisms can be recognized at a number of different levels: behavior, receptor anatomy and physiology, and at the early stages of sensory processing. The peripheral filters and receptor characteristics provide a detector with permissive temporal properties but restrictive spatial characteristics. Biologically important signals probably cover the range from direct current to 10 Hz, whereas the bandwidth of the receptors is more like 0.1–10 Hz. This degree of alternating current coupling overcomes significant noise problems while still allowing the animal to detect external direct

current signals by its own movement. Self-generated bioelectric fields modulated by breathing movement have similar temporal characteristics to important external signals and produce very strong modulation of electrosensory afferents. This sensory reafference is essentially similar, or common-mode, across all afferent fibers. The principal electrosensory neurons (ascending efferent neurons; AENs) of the dorsal octavolateralis nucleus show a greatly reduced response to common-mode signals. This suppression is mediated by the balanced excitatory and inhibitory components of their spatial receptive fields. The receptive field characteristics of AENs determine the information extracted from external stimuli for further central processing.

Key words: elasmobranch, electroreception, prey detection, mate recognition, navigation, noise suppression.

### Introduction

Elasmobranch electroreception is representative of the pleiomorphic electrosensory modality that existed across early vertebrate evolution. This form of electroreception still exists in all fish groups with the exception of the Neopterygii (Bullock et al., 1982). As a primitive representative, elasmobranch electroreception makes an interesting comparison with the secondarily evolved electrosensory systems of the gymnotids and mormyrids that make up the subject matter of the rest of this volume.

At approximately 800 extant species, elasmobranch diversity considerably outweighs the currently known number of gymnotid (62) or mormyrid (200) species (Helfman et al., 1997). Not only are elasmobranchs more diverse than the secondarily electroreceptive groups, they are arguably also more disparate (*sensu* Raff, 1996). They exhibit a wide range of body forms and live in a range of habitats, from shallow coastal seas to the deep ocean. Large-bodied planktivores, whale sharks, basking sharks, megamouth and mantas, contrast with formidable large pelagic predators, such as great whites and makos, and further contrast with smaller benthic invertebrate predators, such as the rays and dogfish.

To understand electroreception across such a diverse group requires an appreciation of the biological and physical *milieu* of the animals. To be fair, we have only begun to sample the diversity found across this fascinating group. The electroreceptors themselves are exquisitely sensitive, with behavioral thresholds below  $5 \text{ nV cm}^{-1}$ . Being so sensitive, the electroreceptors will respond to a wide range of extrinsic electric fields of both biological and inanimate origin. They will also respond to much else besides, including the animal's own bioelectric fields, electric fields generated by the animal's movements, movement *per se*, temperature and changes in the chemical composition of the sea water. Accordingly, some forms of stimulation will represent biologically useful signals whereas others will represent potentially confusing noise. Sorting out signal from noise is a challenge for both the neuroethologist and the signal-processing capabilities of the animal. Our starting point is to identify biologically important signals by looking at the behavioral capabilities of elasmobranchs that can be attributed to electroreception. Potential noise problems and their solutions are then identified and discussed.

### Electrosensory signals

The most common use of electroreception is likely to be in prey detection. This use is strongly indicated by the distribution of electroreceptive pores (Fig. 1), which parallels the distribution of the mechanosensory canals. Typically, the highest density of pores is around the mouth and on the ventral rostrum in front of the mouth. Despite this, there are only relatively few behavioral studies that unequivocally demonstrate the use of electroreception in prey detection. Kalmijn (e.g. 1982) has provided most of the direct evidence. In laboratory behavior experiments, both *Scyliorhinus canicula* and *Raja clavata* executed well-aimed feeding responses to agar-screened prey and to dipole fields. In field observations, the smooth dogfish *Mustelus canis* and the blue shark *Prionace glauca* attracted into an area by an odor source preferentially attacked an active dipole source. Tricas (1982) has shown that nocturnal predation on small fish by the swell shark *Cephaloscyllium ventriosum* is also mediated by the electrosensory system. Recent work with the little skate *Raja erinacea* demonstrates well-directed attacks at electrically simulated prey (M. D. B. Halstead, unpublished observations).

For small electrical sources at short range, it is likely that source location is determined simply by the area of the most strongly activated electroreceptors. Kalmijn (1997) describes it more formally by stating that, at close proximity, the precise position of the target is derived from the conspicuous non-uniformity of the field. In this instance, electrolocation would be akin to touch-at-a-distance, which is how the mechanosensory lateral line is often described (Montgomery et al., 1995). It is interesting that *R. erinacea* orienting to small

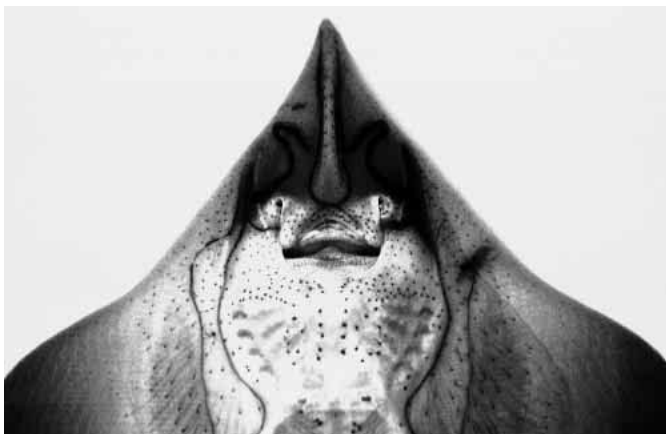


Fig. 1. Photograph of the ventral surface of a skate (*Raja nasuta*). Mechanosensory lateral line canals have been injected with ink to illustrate the distribution of canals. The injection site is evident on the right side of the photograph, and the canals are more extensively filled on this side. Electroreceptive pores are naturally pigmented and show up as black spots. In some cases, particularly the pores on the base of the pectoral fins, the jelly-filled canal leading away from the pore is evident. Note that the distribution of both systems centers on the mouth. Photograph by E. Skipworth, Experimental Biology Research Group, School of Biological Sciences, University of Auckland.

dipoles ignores the vertical dimension. Dipoles held above the pectoral fin induce a positioning of the mouth to the position on the substratum below where the stimulus was presented (M. D. Jarnot, unpublished observations). The skate has reduced source localisation to a two-dimensional problem. For larger electrical sources at a greater range, Kalmijn (1997) has proposed the following approach algorithm. When first noticing the bioelectric field of its prey, a shark must turn in such a fashion as to keep the spatially averaged direction of the field it receives constant with respect to the body axis (Fig. 2). It is possible that a shark could use an alternative strategy of turning to the side on which the electric field is strongest. However, Kalmijn (1997) comments that this would require the animal to have an appreciation of the distribution of the minute differences in the strength of the field over the electroreceptive skin area. Behavioral examination of approach paths and experimental manipulation of the electric field

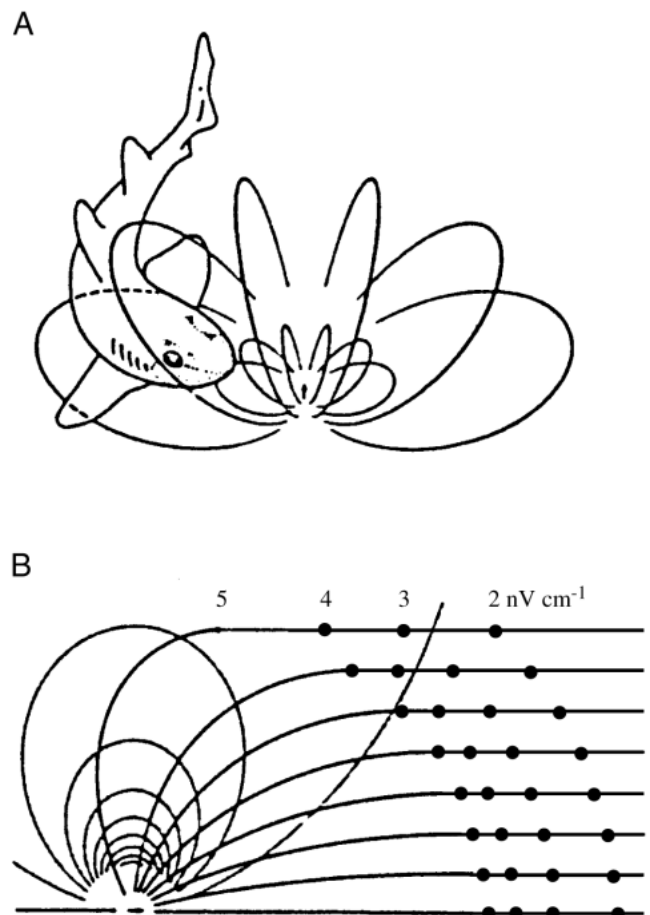


Fig. 2. Bioelectric fields and the detection of prey (taken from Kalmijn, 1997, with permission). (A) Three-dimensional representation of a dipole field simulating the bioelectric field of a prey item. (B) Section of the dipole field, and approach paths predicted by the suggested approach algorithm. The shark notices the field at the position of the first dot from the right and initiates the attack on reaching the position of the fourth dot (dots represent field strengths of 2–5  $\mu\text{V cm}^{-1}$ , respectively). The approach paths intersect the field lines at constant angles.

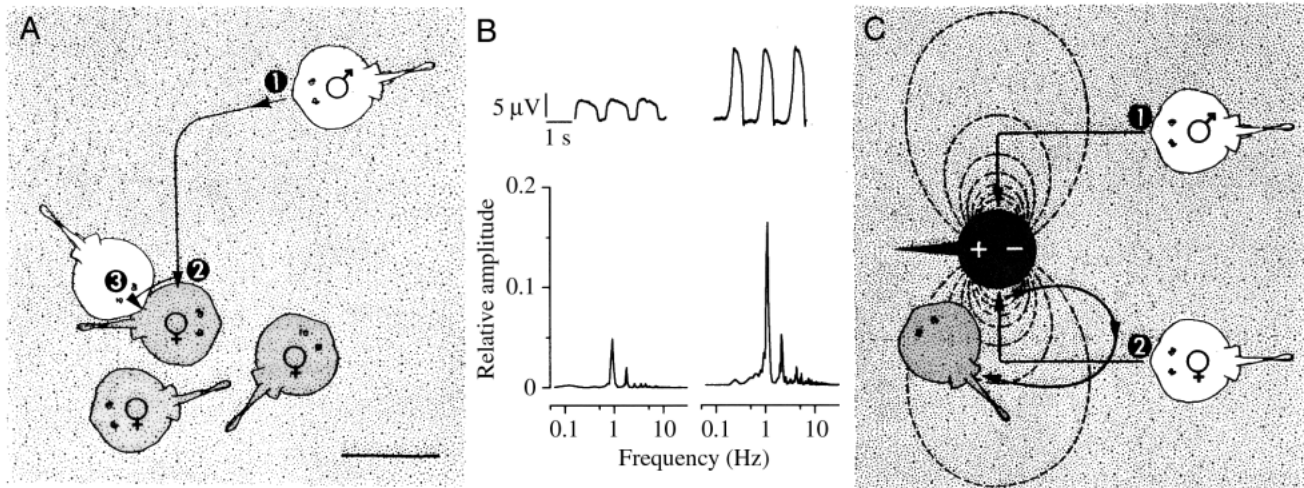


Fig. 3. Orientation responses by round stingrays (*Urolophus halleri*) to buried females and bioelectric simulations of conspecifics (taken from Tricas et al., 1995, with permission). (A) Males localize, orient towards and inspect buried females in the wild. The search path of a male (1) changes abruptly after detection of a female in the sand. Males inspect buried females with the rostrum placed over the margins of her body disc (2), pelvic fins (3) or sometimes her snout. Active courtship and copulation occur after the male has excavated the buried female. Scale bar, 25 cm. (B) Female bioelectric potentials recorded on the dorsal surface above the spiracle (top, left trace) and the ventral surface at the gill slits (top, right trace). The lower graphs are Fourier transforms that show the strong frequency components near 1 Hz that result from these ventilatory movements. (C) Orientation responses by round stingrays to a synthesized phasic bioelectric field. Recorded digitized waveforms were used to simulate the modulated electric field in playback experiments. Male stingrays (1) orient, approach and inspect the buried electric model (shown in black). Females orient towards and inspect the electric dipole model, but also frequently bury themselves close to it. The anode (+) and cathode (–) indicate the polarities of the buried electric dipole.

structure will be required to test the proposed approach algorithm. The receptive field structure of central neurons may also provide insight into which features of the electrical field are extracted to generate the approach behavior.

The second demonstrated use of electrosense in elasmobranchs is in mate detection (Tricas et al., 1995). The round stingray (*Urolophus halleri*) produces an electric field with a complex geometry that is modulated rhythmically by movements of the spiracles and gill slits during ventilation. Reproductively active male stingrays locate mates, and female rays locate buried conspecifics, using this weak stimulus (Fig. 3).

Orientation and navigation have been proposed as a third use for the elasmobranch electrosense (Kalmijn, 1978, 1981, 1984, 1988a,b, 1997). It is certainly the case that pelagic elasmobranchs undertake extensive migrations and can hold steady compass headings in the absence of other apparent cues (Carey and Scharold, 1990; Klimley, 1993). It is also the case that electric fields induced by the animal's movement through the earth's magnetic field will be within the range of sensitivity of the electroreceptors. Laboratory behavioral studies show that rays can be trained to orient to weak direct-current (d.c.) electric fields (Kalmijn, 1982), and preliminary field experiments provide some evidence that swimming direction can be changed by altering the direction of the electric field (Kalmijn, 1988b). On Kalmijn's analysis, elasmobranchs could have two modes of navigation using their electrosense. In the passive mode, the shark measures voltage gradients that develop through its body as a result of electric fields in the

environment. These fields are created by the flow of water through the earth's magnetic field. In the active mode, the shark measures voltage gradients that develop through the body due to its own swimming movements. Paulin (1995) has contributed to the theoretical analysis of active electronavigation by concentrating attention on the modulation of electrosensory inputs caused by head turning during swimming. He has shown that sufficient information is available to obtain directional cues from the electroreceptor voltage induced during head turns as the animal swims in different directions. In essence, a comparison of vestibular and electrosensory inputs could be used to determine compass heading (Fig. 4). More laboratory and field behavior experiments are required to show that elasmobranchs can navigate using imposed electric fields, and self-induced motional fields, and further to reveal the explicit mechanisms involved.

#### Potential noise problems

Elasmobranchs generate their own bioelectric fields as a necessary consequence of maintaining an internal ionic environment that differs from that of sea water (Bodznick et al., 1992). These self-generated fields are modulated by ventilatory movement probably due to variable shunting of an internal/external standing d.c. potential across the gills during opening and closing of the mouth and the spiracle. Both the d.c. and the alternating current (a.c.) components of these self-generated fields have the potential to interfere with the

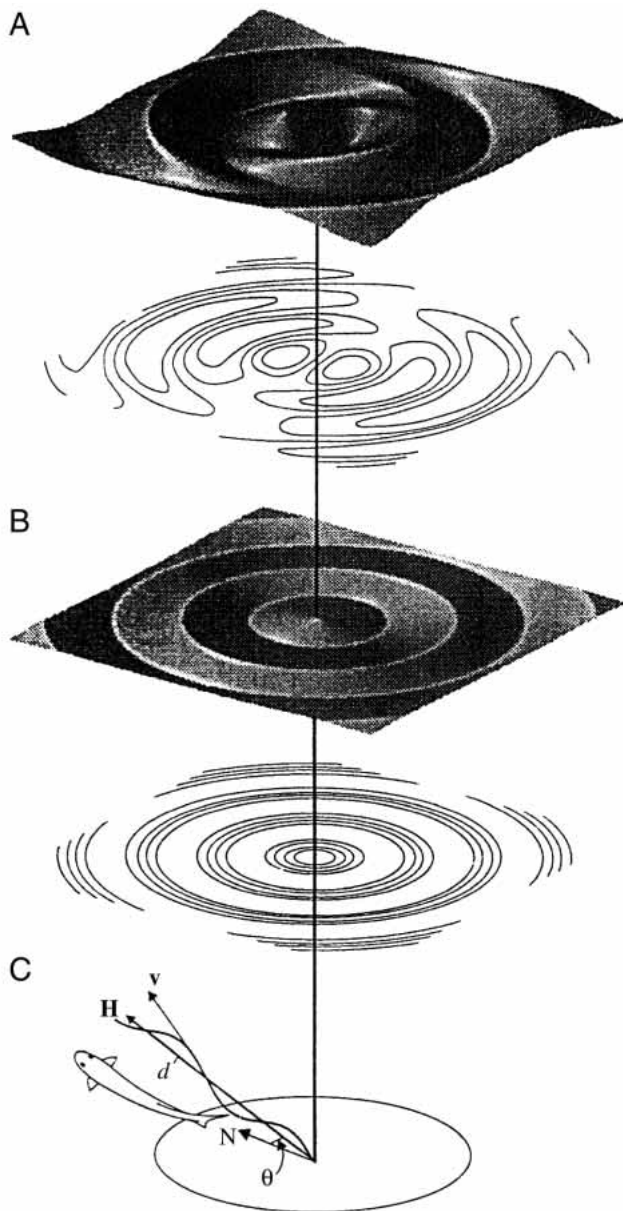


Fig. 4. Surface/contour plots of sensory afferent modulations due to head movements during swimming (taken from Paulin, 1995, with permission). (A) The height of the surface at distance  $d$  from the center of the plot in direction  $\theta$  represents the motion-induced receptor voltage at time  $t$  when the fish is swimming with heading  $\theta$ . (B) The corresponding point on this plot represents the rotational velocity of the head at the same time. (C) Swimming trajectory, N, north; **H**, vector in heading direction; **v**, velocity vector at time  $t$ ;  $\theta$ , heading.

detection of biologically important extrinsic signals. Experiments on freely ventilating animals show that electroreceptor afferents do respond very strongly during normal ventilatory movements, sometimes being driven over their entire dynamic range. Interestingly, because ventilatory potentials occur between the inside and the outside of the body, they are in effect common-mode over all electroreceptors (Montgomery, 1984b; Bodznick et al., 1992).

In addition to self-generated electric fields, elasmobranch

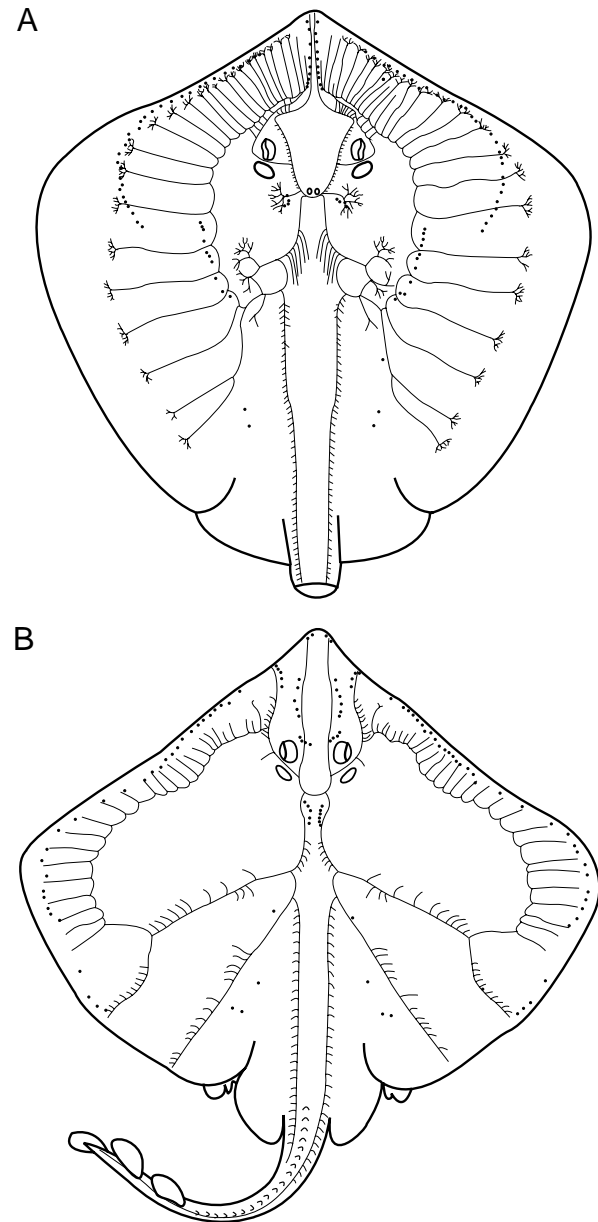


Fig. 5. A comparison of the distribution of electrosensory canals and pore openings on the dorsal surface of (A) the ray *Dasyatis akajei* and (B) the skate *Raja chinensis* (taken from Chu and Meng, 1979, with permission). Thin lines represent mechanosensory lateral line canals, dots represent the opening of the electrosensory canals of the ampullae of Lorenzini. Note that mechanosensory neuromasts are found in the main continuous canals rather than the tubules that connect these canals to the surface. Hence, both the electro- and mechanoreceptors extend out onto the fin tips on the skate, but not on the ray.

ampullary receptors respond to thermal, mechanical and chemical stimuli. Indeed, in the early days of electrophysiological investigation, these receptors were variously considered as thermo-, mechano- and chemoreceptors (Bullock and Szabo, 1986). Considering the normal physical environment of elasmobranchs, it is unlikely that temperature or chemo/salinity changes are a very important source of receptor stimulation. Moreover, they are likely to be

symmetrical across the whole population of receptors and, hence, common-mode. Mechanical sensitivity, however, could create significant problems. Movement of particular body parts, such as the pectoral fins of batoid elasmobranchs, could produce significant modulation of afferent activity. These responses would be due not only to the direct mechanical sensitivity of the receptors but also to movements of the receptor pores within the self-generated electrical field and by movements of the ampullary canals within the earth's magnetic field. It is likely that movement-induced self-stimulation is complex and highly dependent on the location of the particular receptor and on the detail of the particular movement.

**Noise-suppression mechanisms**

Noise-suppression mechanisms can be recognized at a number of different levels: behavior, receptor anatomy and physiology, and at the early stages of sensory processing.

Perhaps the simplest noise-suppression mechanism is to minimize the noise source. Electrical fields produced by elasmobranchs are typically of lower amplitude than those produced by bony fishes (Kalmijn, 1974). This is clearly related to the osmoregulatory mechanisms employed by elasmobranchs, which differ from those of teleosts, but whether the benefits of a lower bioelectrical field are simply fortuitous or somehow causally linked to osmoregulatory mechanisms is an unanswered (unanswerable) question. Electrosensory noise generated by movement can be minimized behaviorally and by receptor anatomy. The sit-and-wait predatory strategy of the swell shark *Cephaloscyllium ventriosum* (Tricas, 1982) is a good example of undertaking electrosensory prey detection while minimizing movement. Skates and electric rays also hold the body disc rigid while hunting for prey. Forward movement is produced by

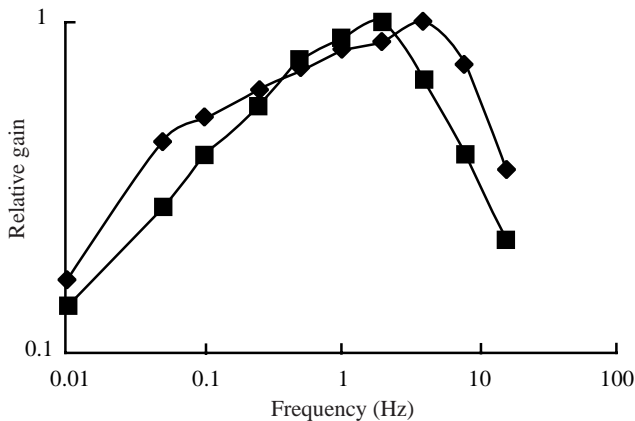


Fig. 6. Frequency response curves (double logarithmic scale) of primary afferent electrosensory neurons in the round stingray *Urolophus halleri* (■, data taken from Tricas et al., 1995) and the thornback ray *Platyrhinoides triserata* (◆, data from Montgomery, 1984a). Sinusoidal electric field stimuli were delivered at a range of frequencies, and neural responses were recorded as the change in firing rate of the unit in response to each stimulus. Neural responses were normalised to a gain of 1. The responses of the two species are quite similar, with relatively broad band-pass characteristics and a peak response in the range 2–4 Hz.

walking movements of modified pelvic fins called crura (Holst and Bone, 1993). Rays lack crura and generate gentle forward motion by movements of the tips of their pectoral fins. In these species, the electrosensory pores do not extend all the way out onto the lateral tips of the pectoral fin (Fig. 5).

Ampullary canals do have low-pass filter characteristics (Waltman, 1966) but, for canal lengths of less than approximately 10 cm, the filter properties of the receptor itself largely determine the response characteristics of the ampullary system. Receptor characteristics provide a broad-band detector (Fig. 6) with a frequency response range (response above half-maximal) of approximately 0.1–10 Hz. At the low-frequency end, the a.c. coupling of the receptors protects the system from saturation by internally generated standing d.c. potentials (Bodznick et al., 1993). External d.c. fields can still be detected as the animal moves into a spatially non-uniform field or as the receptor configuration is moved within a uniform field. It is not known whether the upper frequency limits of the ampullary system prevent the detection of any potentially useful signals or shield against any unwanted noise.

Behavioral strategies and peripheral receptor anatomy and physiology can reduce external and self-generated noise, but do not eliminate it. Some of the worst self-generated noise

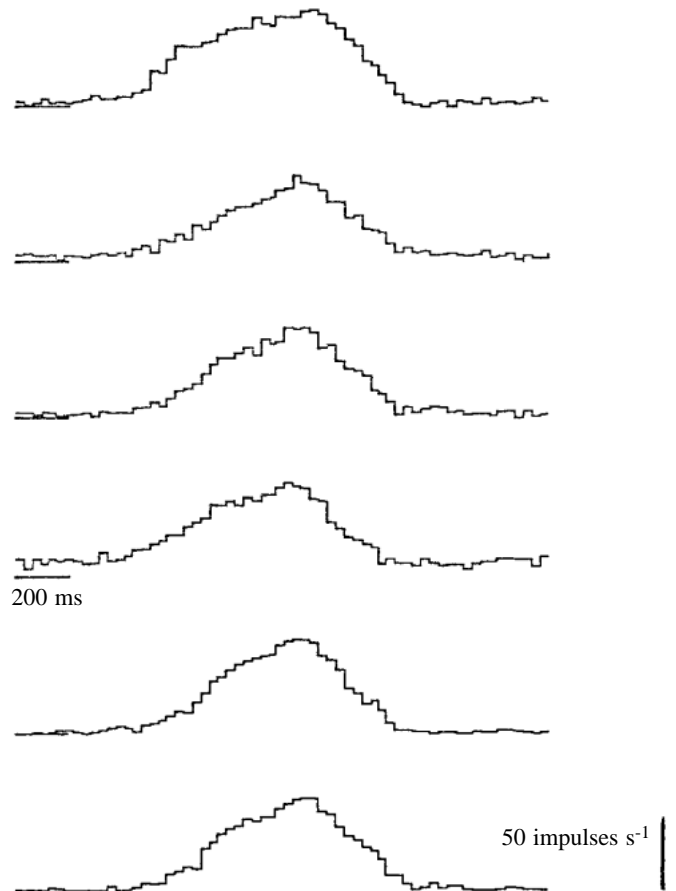


Fig. 7. Electrosensory primary afferent responses to ventilation in the little skate *Raja erinacea*. The method of preparation of the animal is given by Bodznick et al. (1992). Spike histograms show a uniform substantial increase in firing rate during exhalation.

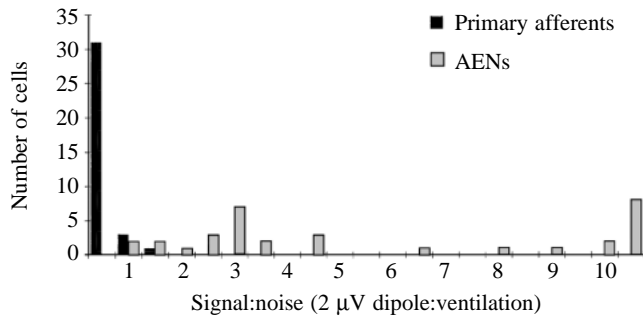


Fig. 8. Histogram of the signal-to-noise ratios of primary afferent neurons and ascending efferent neurons (AENs) in the little skate *Raja erinacea*. The signal-to-noise ratio was determined by comparing the amplitude of the response of the unit to a 2 μV dipole stimulus positioned in the center of the receptive field (the signal) with its response to ventilation (noise).

occupies the same bandwidth as the most important electrosensory signals. As mentioned above, recording of afferent activity in freely ventilating animals shows a very strong modulation of activity in time with ventilation (Fig. 7). As a general rule, it is usual to curarise animals as an integral step in preparation for electrophysiological experimentation, so it is likely that sensory reafference generated by movement is a common phenomenon in a range of sensory systems and circumstances. Movement-related sensory reafference is likely to be a very general phenomenon

that is typically missed or underestimated in conventional electrophysiological recording.

Ventilatory modulation of afferent activity is very similar in afferents that innervate receptors in different ampullary clusters, and in this sense is common-mode across the receptor field. Ventilatory modulation and other forms of common-mode noise could be reduced or eliminated by a common-mode suppression mechanism (Montgomery, 1984b). Studies specifically designed to test the common-mode hypothesis show that secondary neurons of the electrosensory pathway have a greatly increased signal-to-noise ratio (Fig. 8). These so-called ascending efferent neurons (AENs) of the dorsal octavolateralis nucleus respond very strongly to small localised dipole fields, but rarely show much response to ventilation. If a common-mode mechanism underlies this increase in signal-to-noise ratio, then it can be predicted that artificial common-mode inputs would also be cancelled, that AENs would have both excitatory and inhibitory components to their receptive fields and that the appropriate inhibitory network would exist in the dorsal octavolateralis nucleus. Each of these predictions has been verified experimentally (Bodznick et al., 1992; Bodznick and Montgomery, 1992; Montgomery and Bodznick, 1993).

The experimentally determined receptive field structure of AENs is interesting because it provides insight into the features of the external electric fields that are extracted for further processing. Receptive field structure has been determined for relatively few neurons in only two species, so it is a far from

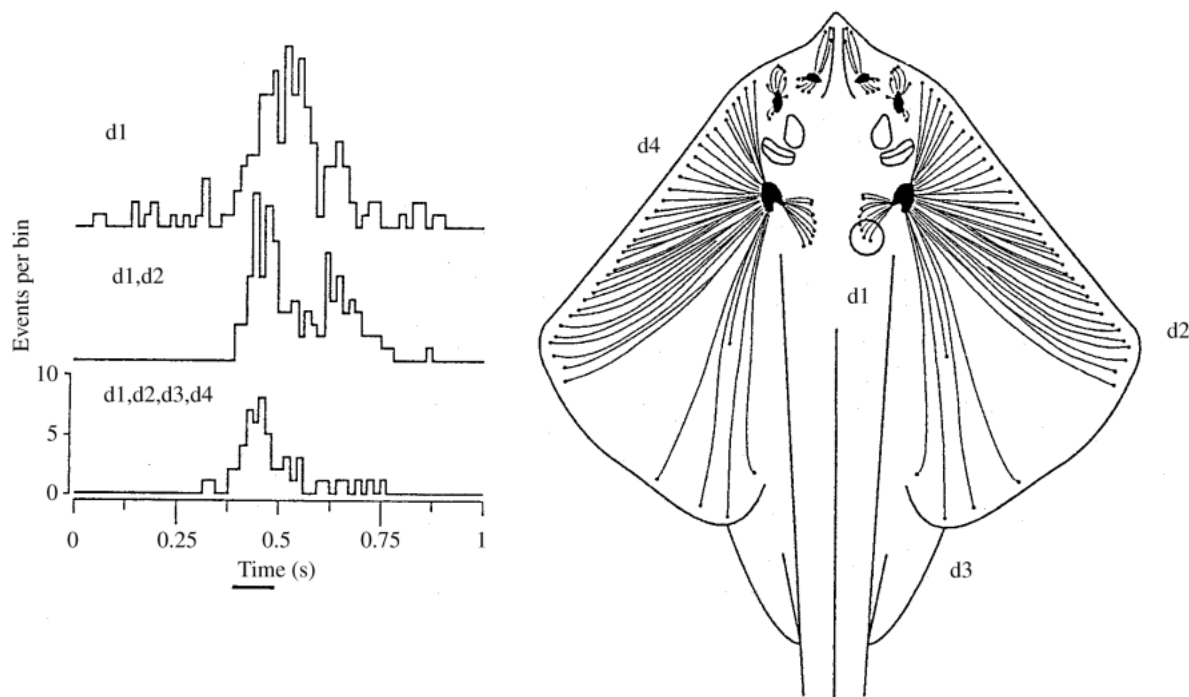


Fig. 9. Example of an ascending efferent neuron (AEN) with a discrete excitatory field (circle on the mid-dorsal surface of the fish) and a diffuse inhibitory field. The top histogram shows its response to a 1 Hz, 5 μV stimulus presented through dipole 1 (d1) located in the excitatory receptive field on the dorso-medial hyoid pore group. The middle histogram shows the suppressive effect of adding a 100 ms, 2 μV square-wave pulse (bar below histograms) through dipole 2 (d2) located near the lateral fin edge. Simultaneous activation of additional dipoles on the caudal and contralateral fin edges (d3 and d4) increases the degree of inhibition (lower histogram) (taken from Montgomery and Bodznick, 1993, with permission).

complete picture. However, the current picture is that AENs tend to have either a single discrete excitatory field center with a diffuse inhibitory surround or relatively closely situated discrete excitatory and inhibitory centres (Fig. 9). The effect of this is that the majority of AENs are sensitive to local dipole fields, but relatively insensitive to uniform fields. That the majority of AENs in these species seem suited to provide information on the precise location of small dipoles is perhaps not surprising. What remains to be seen is whether there are any central pathways in these or other species that specialise in the detection and processing of the navigationally relevant uniform fields.

### Discussion

Sensitivity without selectivity is a recipe for ambiguity. It is arguable that the extreme sensitivity of the elasmobranch electrosensory system can only be usefully employed within a system that optimizes the processing of behaviorally relevant stimuli and suppresses potentially confounding noise. Behavioral strategies, receptor anatomy and physiology and a common-mode suppression mechanism all contribute to improved signal-to-noise ratios at the level of the medullary electrosensory nucleus. But are these contributions enough? Modeling studies of the common-mode suppression mechanism using physiologically realistic assumptions (Nelson and Paulin, 1995) show that unavoidable delays introduced into the inhibitory pathway preclude perfect common-mode suppression of even perfectly common-mode noise. In addition, a common-mode network will not successfully cancel asymmetric noise inputs from receptor movement. The solution to these problems is a more sophisticated central processing mechanism.

### References

- Bodznick, D., Hjelmstad, G. and Bennett, M. V. P.** (1993). Accommodation to maintained stimuli in the ampullae of Lorenzini: How an electroreceptive fish achieves sensitivity in a noisy world. *Jap. J. Physiol.* **43** (Suppl. 1), 231–237.
- Bodznick, D. and Montgomery, J. C.** (1992). Suppression of ventilatory reafference in the elasmobranch electrosensory system: medullary neuron receptive fields support a common mode rejection mechanism. *J. Exp. Biol.* **171**, 127–137.
- Bodznick, D., Montgomery, J. C. and Bradley, D. J.** (1992). Suppression of common mode signals within the electrosensory system of the little skate *Raja erinacea*. *J. Exp. Biol.* **171**, 107–125.
- Bullock, T. H., Northcutt, R. G. and Bodznick, D. A.** (1982). Evolution of electroreception. *Trends Neurosci.* **5**, 50–53.
- Bullock, T. H. and Szabo, T.** (1986). Introduction. In *Electroreception* (ed. T. H. Bullock and W. Heiligenberg), pp. 1–12. New York: Wiley & Sons.
- Carey, F. G. and Scharold, J. V.** (1990). Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar. Biol.* **106**, 329–342.
- Chu, Y. T. and Meng, C. W.** (1979). *Monograph of Fishes of China (no. 2): A Study of the Lateral Line Canals System and that of Lorenzini Ampullae and Tubules of Elasmobranchiate Fishes of China*. Shanghai: Science and Technology Press (in Chinese with English Abstract).
- Helfman, G. S., Collette, B. B. and Facey, D. E.** (1997). *The Diversity of Fishes*. Malden: Blackwell Science.
- Holst, R. J. and Bone, Q.** (1993). On bipedalism in skates and rays. *Phil. Trans. R. Soc. Lond. B* **339**, 105–108.
- Kalmijn, A. J.** (1974). The detection of electric fields from inanimate and animate sources other than electric organs. In *Handbook of Sensory Physiology*, vol. III/3 (ed. A. Fessard), pp. 148–200. New York: Springer-Verlag.
- Kalmijn, A. J.** (1978). Electric and magnetic sensory world of sharks, skates and rays. In *Sensory Biology of Sharks, Skates and Rays* (ed. E. S. Hodgson and R. F. Mathewson), pp. 507–528. Washington: US Government Printing Office.
- Kalmijn, A. J.** (1981). Biophysics of geomagnetic field detection. *IEEE Trans. Mag.* **17**, 1113–1124.
- Kalmijn, A. J.** (1982). Electric and magnetic field detection in elasmobranch fishes. *Science* **218**, 916–918.
- Kalmijn, A. J.** (1984). Theory of electromagnetic orientation: a further analysis. In *Comparative Physiology of Sensory Systems* (ed. L. Bolis, R. D. Keynes and S. H. P. Maddrell), pp. 525–560. Cambridge: Cambridge University Press.
- Kalmijn, A. J.** (1988a). Electromagnetic orientation: a relativistic approach. In *Electromagnetic Fields and Neurobehavioral Function* (ed. M. E. O'Connor and R. H. Lovely), pp. 23–45. New York: Alan R. Liss.
- Kalmijn, A. J.** (1988b). Detection of weak electric fields. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 83–130. New York: Springer-Verlag.
- Kalmijn, A. J.** (1997). Electric and near-field acoustic detection, a comparative study. *Acta Physiol. Scand.* **638** (Suppl. 161), 25–38.
- Klimley, A. P.** (1993). Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini* and subsurface irradiance, temperature, bathymetry and geomagnetic field. *Mar. Biol.* **117**, 1–22.
- Montgomery, J. C.** (1984a). Frequency response characteristics of primary and secondary neurons in the electrosensory system of the thornback ray. *Comp. Biochem. Physiol.* **79A**, 189–195.
- Montgomery, J. C.** (1984b). Noise cancellation in the electrosensory system of the thornback ray: common mode rejection of input produced by the animal's own ventilatory movement. *J. Comp. Physiol. A* **155**, 103–111.
- Montgomery, J. C. and Bodznick, D.** (1993). Hindbrain circuitry mediating common mode suppression of ventilatory reafference in the electrosensory system of the little skate *Raja erinacea*. *J. Exp. Biol.* **183**, 203–215.
- Montgomery, J. C., Coombs, S. and Halstead, M. B. D.** (1995). Biology of the mechanosensory lateral line in fishes. *Rev. Fish Biol. Fisheries* **5**, 399–416.
- Nelson, M. E. and Paulin, M. G.** (1995). Neural simulations of adaptive reafference suppression in the elasmobranch electrosensory system. *J. Comp. Physiol.* **177**, 723–736.
- Paulin, M. G.** (1995). Electroreception and the compass sense of sharks. *J. Theor. Biol.* **174**, 325–339.
- Raff, R. A.** (1996). *The Shape of Life: Genes, Development and the Evolution of Animal Form*. Chicago: University of Chicago Press.
- Tricas, T. C.** (1982). Bioelectric-mediated predation by swell sharks *Cephaloscyllium ventriosum*. *Copeia* **1982**, 948–952.
- Tricas, T. C., Scott, W. M. and Sisneros, J. A.** (1995). Electrosensory optimization to conspecific phasic signals for mating. *Neurosci. Lett.* **202**, 129–132.
- Waltman, B.** (1966). Electrical properties and fine structure of the ampullary canals of Lorenzini. *Acta Physiol. Scand.* **264** (Suppl. 66), 3–60.