Ecological Functions and Adaptations of the Elasmobranch Electrosense

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ABSTRACT

Sharks and rays have a long evolutionary history as major predators in marine ecosystems, but the biological functions and selective pressures that shape the evolution of their ampullary electrosensory system are poorly known. The ampulla of Lorenzini is the functional electrosensory unit that consists of a small subdermal ampulla and a canal that projects to a surface pore on the head or pectoral fins. The sensory epithelium of the ampulla wall detects differences between the potential at the skin pore and internal potential of the animal, and stimulates neural transmission of information about the physical features of an external field to the brain. Natural weak electric stimuli include polar fields from bioelectric sources and induced fields from physical sources in the environment. Neurophysiological studies show that the ampullary electrosense responds to electric field gradients as low as 20 nV/cm, and behavioral studies show responses to gradients of 1-5 nV/cm. Elasmobranch fishes show behavioral responses to bioelectric stimuli produced by natural prey, mates, consexuals and potential predators. Numerous models exist for electrosensory navigation, but they remain to be rigorously tested. Recent work shows age-dependent changes in the response properties of the electrosense among embryo, juvenile and adult stages and are proposed to reflect ontogenetic adaptations to their changing environments. In addition, the electrosense response properties are seasonally modified by the periodic expression of gonadal steroids and may serve important modulation of sensory function during reproductive behaviors. Future work should continue to investigate different biological contexts in which the electrosense is used by elasmobranch fishes, and to test the selective forces that may have shaped the evolution of this remarkable sensory system.

Key words: Ampulla of Lorenzini, Behavior, Elasmobranch, Electroreception, Neuroecology, Ray, Shark, Sensory Biology

INTRODUCTION

The living elasmobranch fishes (sharks and rays) share with their ancestors many morphological characteristics that directly control their behavioral capabilities and influence their ecology.

Most sharks have a large mouth with well-developed dentition, a torpedo shaped body and paired fins like their predecessors that lived more than 400 million years ago. Thus, the sharks have evolved into highly adapted carnivores that are capable of rapid swimming or ambush movements to capture their prey. Similarly, the derived skates and rays (collectively known as the batoids) have retained the features of their ancestors of 100 million years ago that include ventral gill slits, expanded pectoral fins and a dorsally flattened body. This highly successful group has since diverged to primarily exploit the two-dimensional worlds associated with benthic habitats.

Sharks and rays also share with their ancestors several exquisite sensory systems that have evolved in response to numerous selective pressures within their natural environment. Selective forces that may shape the form and function of sensory systems include the efficient capture of prey that increases feeding success, and the capacity to detect and avoid predators during different phases of development. The ability to locate potential mates, engage in courtship behaviors and successfully mate may directly enhance reproductive success. In addition, there can be great fitness advantages for sensory systems that provide spatial details of their home range, or provide orientation cues during long migrations.

Of the many sensory systems possessed by sharks and rays, the ampullary electroreceptors are the most unique and enigmatic in terms of function in the natural lives of these animals. While much is known about the structure, proximate mechanisms of sensory transduction and encoding of weak electric stimuli by the ampullary receptors, only recently has experimental work begun to address a wide range of biological functions for the electrosense in natural settings. In this chapter we first review the gross anatomy of the ampullary system of marine elasmobranch fishes, the receptors, and the neurophysiological responses of electrosensory neurons. We then present a summary of the experimental and theoretical functions for the electrosense of the sharks and rays within some of the biological contexts in which they have evolved. Other reviews of the electrosensory system of marine and freshwater elasmobranchs, and teleosts can be found in Bullock and Heiligenberg (1986), Zakon (1988) and New and Tricas (1998).

MORPHOLOGY AND PHYSIOLOGY OF THE AMPULLARY SYSTEM

The functional unit of the electroreceptor system is a highly specialized structure known as the ampulla of Lorenzini. Each ampulla consists of small continuous alveolar sacs that are positioned around the base of a single canal (Fig. 1A). The canal is approximately 1 mm in diameter and extends from the subdermal ampulla through the dermis and terminates as a small pore on the skin. The wall of the ampulla contains the sensory epithelium that is innervated by primary afferent sensory neurons. Individual ampullae are arranged in 3-4 clusters on each side of the body with the canals radiating outwards to their surface pores of the head (Fig. 1B). Canals usually project in many directions from each cluster and their pores are distributed widely over the surface of the head, and in the skates and rays extend on to the expanded pectoral fins (Fig. 1C).
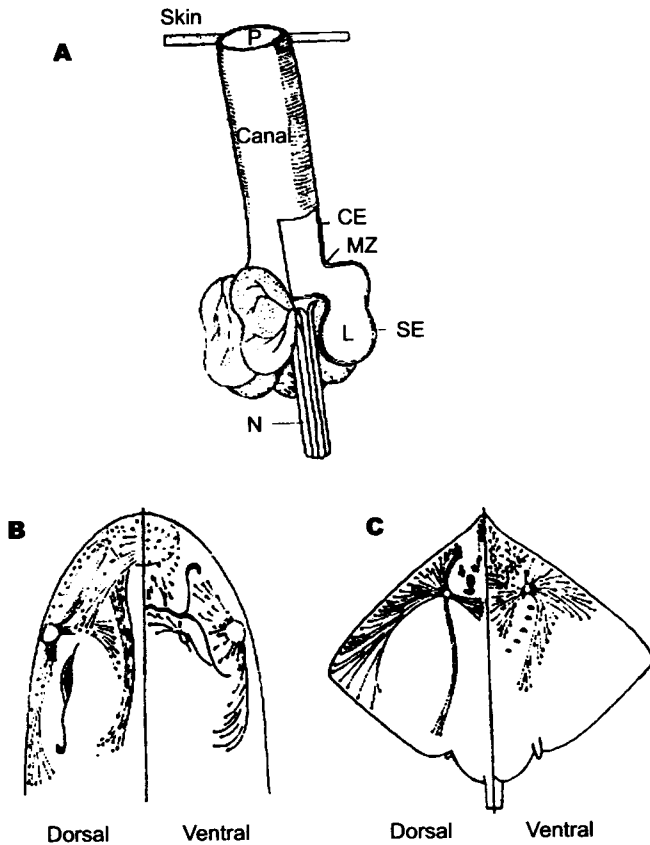
Fig. 1 The ampulla of Lorenzini system in marine elasmobranchs. A, Diagrammatic representation of the canal and ampulla that consists of several alveoli pouches. The ampulla walls are formed by the sensory epithelium (SE) that connects with the canal epithelium (CE) at the marginal zone (MZ), and is innervated by primary afferent neurons (N). The inner lumen (L) and subdermal canal are filled with a low resistive gel that form an electrical 'core conductor' and brings the lumen isopotential with the charge at the canal pore. (Modified from Waltman (1966). B, Representation of the ampullae of Lorenzini in the cat shark, *Scyliorhinus*. Ampullae are grouped into clusters in the head and have canals of different lengths that radiate in many directions. C, Representation of the horizontal distribution of ampullae of Lorenzini in the skate, *Raja*. Note that the canals project primarily within the horizontal plane of the head and pectoral fins due to the dorsoventrally flattened body. Figs. Modified from Murray (1960)

Receptor cells are flask shaped, and have a single apical kinocilium which projects directly into the lumen (Fig. 2A). Accessory (support) cells form the vast majority of the lumen surface and are bound to receptor cells by tight junctions that prevent ionic leakage between the lumen and basal portion of the epithelium. The receptor epithelium forms the thin (15 mm thick) wall of the ampulla, which is innervated in the basal region by primary afferent neurons (Fig. 2B). Tight junctions also occur around the apical surface of the cell but only a small fraction of the receptor cell surface (including the kinocilium) is exposed to the interior of the alveolus chamber. Both the canal lumen and the ampullary chambers are filled with a low resistivity,
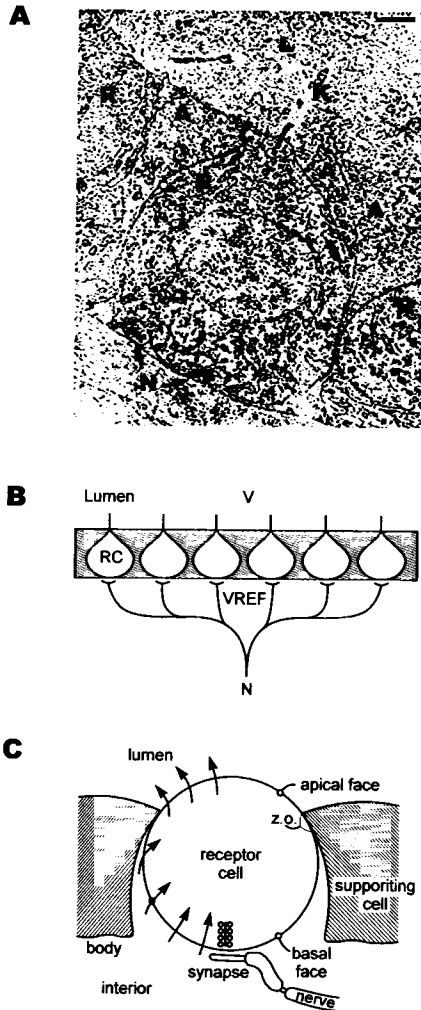
Fig. 2 Receptor cells of the ampullary electrosensory system. A, Transmission electron micrograph of the receptor cells (R) and adjacent accessory (support) cells (A) which are united by tight junctions. The kinocilium (K) projects into the ampullary lumen (L) and primary afferent neurons (N) innervate receptors at basal surface. Fig. modified from Waltman (1966). B, Diagram of the sensory epithelium. Receptor cells (RC) and adjacent accessory cells form the thin sensory epithelium layer. Tight junctions form a high electrical resistance barrier between the lumen of the ampulla and basal portion of the receptor cells. The difference between lumen voltage (V) and reference voltage (VREF) stimulates the small apical surface of the receptor cells and controls release of neurotransmitter onto primary afferent neurons (N). Fig. modified from Tricas (2001). C, Diagram of the ampullary receptor cell showing current flow during excitation. A cathodal (negative) stimulus relative to the basal region of the receptor excites the apical surface of the cell which causes an increase in outward current flow into the lumen (arrows). This in turn causes inward current at the basal region (arrows), release of chemical transmitter at the cell synapse, and excitation of the primary afferent nerve. Anodal potentials in the lumen will decrease outward current flow at the apical surface and subsequently decrease the rate of transmitter release. Modified from Bennett and Clussin (1977).

muccopolysacharrhide gel secreted by the superficial layer (Murray and Potts 1961, Waltman 1966). Each canal functions as a low-resistance conductor that provides charge at the ampullary lumen that is isopotential with that at the pore on the skin.

The tight junctions of the sensory epithelium concentrate a bias current flow that enters the receptor cells through their basal surface and exits into the lumen via the apical surface (Fig. 2C) (Obara and Bennett 1972). Receptor cells show a well-developed synapse for chemical transmission to afferent neurons at their basal surface. A single layer of transmitter vesicles covers the synaptic ribbon and releases chemical transmitter to depolarize the postsynaptic membrane of the primary afferent neuron. This regular release of neurotransmitter results in a regular pattern of neural discharge in the absence of externally applied stimuli. The receptor cells are excited by a cathodal (negative) stimulus applied at the apical surface (or skin pore) that further depolarizes the apical cell face. Regeneration of the apical membrane depolarizes the basal cell surface, which causes transmitter release into the synaptic cleft and an increased discharge rate in primary afferents. In contrast, applied anodal (positive) charges decrease the flow of bias current through the cell and results in a decrease of transmitter release onto primary afferents. There is no efferent projection from the brain to the basal region of electrosensory hair cells as occurs in the other octavolateralis sense organs (Roberts and Meredith 1989). Thus, changes in the polarity and intensity of the electric potential at the skin pore (and apical surface of the receptor cell) over time will modulate the resting discharge pattern of primary afferent neurons.

The electrosensory system of marine elasmobranchs can detect extremely weak electric fields within their environment. Murray (1962) reported neural responses of skate electrosensory primary afferents to a voltage gradient of approximately 1 μV/cm, and more recent experiments have extended this sensitivity to below 20 nV/cm (Tricas and New 1998). The neural response to a constant current field is robust, but adapts back to the resting discharge rate within a few seconds. Thus, ampullary electroreceptors show maximum responses to phasic fields delivered at frequencies from 1-10 Hz (Andrianov et al. 1984, New 1990, Montgomery 1984, Peters and Evers 1985, Tricas et al. 1995, Tricas and New 1998, Sisneros and Tricas 2000). Sensitivities of primary afferent fibers innervating ampullary electroreceptors to a uniform sinusoidal field range from 0.9 spikes/sec per μV/cm for the little skate, *Raja erinacea* (Montgomery and Bodznick 1993), 4 spikes/sec per μV/cm for the thornback guitarfish, *Platyrhinoidis triserata* (Montgomery 1984), 7.4 spikes/sec per μV/cm average for the Atlantic stingray, *Dasyatis sabina* (Sisneros and Tricas 2000a, 2002), 17.7 spikes/sec per μV/cm average for the clearnose skate, *Raja eglanteria* (Sisneros et al. 1998), and 24 spikes/sec per μV/cm average for the round stingray *Urolophus halleri* (Tricas and New 1998).

NATURAL PHYSICAL STIMULI OF THE ELECTRORECEPTOR SYSTEM

An ampullary electroreceptor responds to the difference between potentials at its apical surface (within the ampulla lumen) and basal surface (external surface of the ampulla). In some cases, ampullae are grouped into discrete clusters whereas other ampullae can be scattered across a

wide region of the head or fins. In the case of contiguous groupings of individual ampullae into distinct clusters, the receptors experience a common reference potential at their basal region (Fig.3). All sensory cells of a single ampulla experience the same apical voltage that co-varies with the potential at its skin pore. Thus, functionally the hair cells act as differential voltage detectors and stimulate primary afferent neurons as a function of the difference between potentials at the skin pore and internal potential of the animal.

The morphological arrangement of the ampullary canals permits detection of small local fields produced by biological organisms (Kalmijn 1974, Tricas 2001). Physiological processes in marine organisms result in an uneven distribution of ionic charges within the body that may produce weak standing or alternating multipole electric fields around the animal. When an adequate dipole stimulus from another organism such as a prey (e.g. Haine et al. 2001) nears a pore, the charge is conducted along the low resistance pathway of the canal interior and appears at the apical surface of the receptor cells within the single associated ampulla (Fig. 3A). This results in selective stimulation of ampulla receptors within the cluster, and depolarization of primary afferent neurons that are somatotopically mapped to the location of the pore on the skin. In this simple example, all ampullae have the same internal reference potential, are stimulated as a function of charge intensity at their respective surface pores, and have a neural response that is due primarily to the voltage drop across the skin and independent of canal length (Kalmijn 1974).

Sharks and rays can experience weak electric stimulation from fields that result from inter-actions with their environment (see Navigation section below), or when at the fringe of a large polar field. When the animal's body is within an extrinsic uniform field the low resistivity of the body admits the field to influence the internal reference potential (Kalmjin 1974). When a weak uniform field is applied along the length of the canal, the stimulus voltage in the lumen is determined by the linear separation between the ampulla and its canal pore. Thus, within a uniform field the primary afferent neurons associated with long canals receive stimulation across a greater spatial distance, are stimulated by a larger potential difference at their receptor cells, and exhibit the highest neural sensitivity (Tricas 2001) (Fig.3B).

Research on the spatial features of ampullary pores and canals on the body elucidate the importance of sensory system structure, ecology and behavior of individual species. Raschi (1986) compared anatomical characters of the ampullary system among 40 species of skate. He found that ampullary pore density was greatest in regions around the mouth probably to enhance prey capture, and that deep water species had larger (and presumably more sensitive) ampullae than did shallow water species. He also found inverse correlations between pore density and the mobility of natural prey. Tricas (2001) used a neuroecological approach to address adaptations of the electrosensory system in relation to the projection vectors of canals in the skate, *Raja laevis* and the great white shark, *Carcharodon carcharias*. This work showed that the body form and spatial arrangement of the ampullary system may set important functional constraints on the detection of natural electric stimuli. The dorsoventral compression of the batoid body limits the projection vectors of long canals to the horizontal plane. Thus the batoids can detect small dipole fields over a large surface of the body, but are mainly sensitive to the horizontal components of external fields. In contrast to the batoids, the
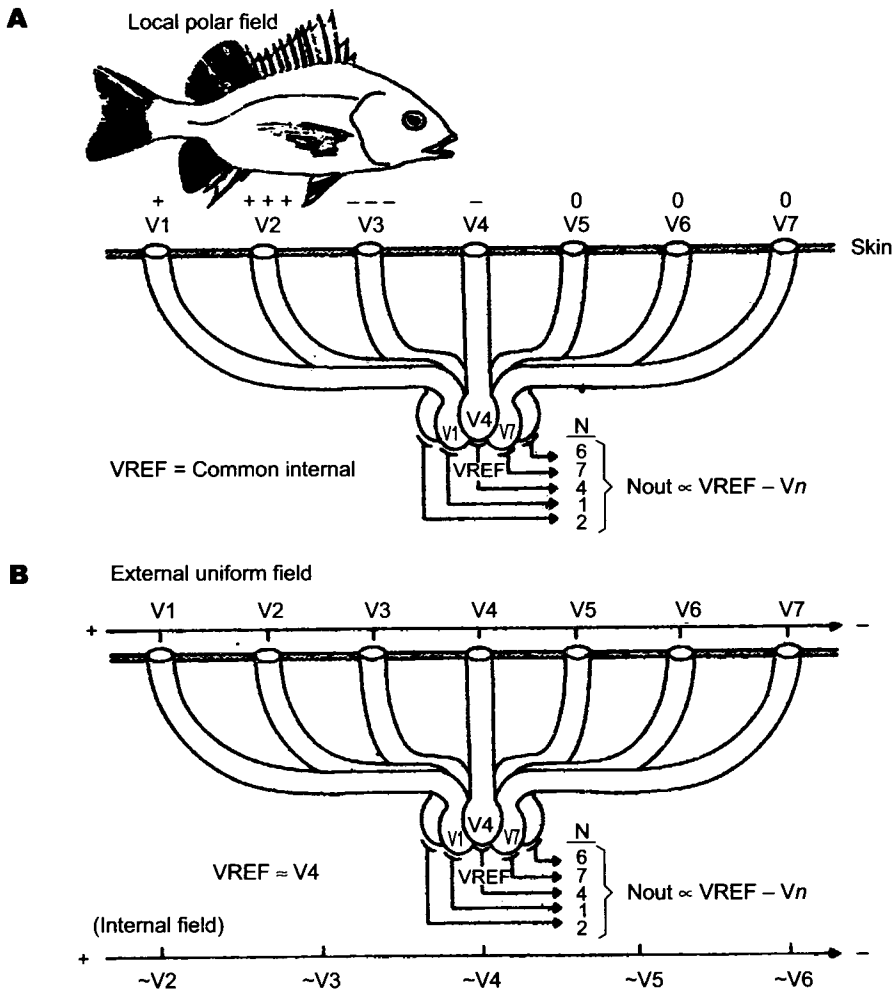
Fig. 3 Diagrammatic and simplified model for the encoding of weak polar and uniform electric fields by a subdermal cluster of ampullae of Lorenzini. A, individual ampullae are grouped in a subdermal cluster and their individual canals project beneath the skin to surface pores located over the head (and pectoral fins of batoids). A weak polar bioelectric field is produced by a prey organism (fish inset) and presents charges (+, 0, −) represented as voltage potentials at individual pores on the skin (Vn=V1 to V7). The potential at each skin pore is sampled by its conductive subdermal canal and results in an isopotential ampullary lumen (e.g. V1, V4, V7). Electroreceptors (not shown) that form the wall of a single ampulla are stimulated by the difference between the potential within the lumen and the independent internal potential located at the basal region of the receptor epithelium (VREF). Small populations of primary afferent neurons uniquely innervate each ampulla (arrows), are stimulated exclusively by the transreceptor potentials within their associated ampulla, and transmit somatotopic electric information to the brain via parallel neural channels (numbers indicated below N). The change in resting discharge rate output for each primary afferent neuron (Nout) is proportional to the difference between the common VREF and the potential at its associated surface pore. B, in the presence of a uniform field the low resistivity of the body admits a portion of the external field that also influences the common reference potential at the cluster. In this example, VREF is approximately equal to the external potential that is orthogonal to the internal field line (V4). Voltage potentials represented within the ampullary lumen (V1, V4, V7) are a function of canal length across the external field. From Tricas (2001).

ampullary canals of the white shark (and most sharks with a fusiform body) have canals that project into three-dimensional space rather than only the horizontal plane. This complex spatial arrangement provides electrosensory information about the charge distribution around the entire surface of the animal, and makes it possible for sharks to gain an image of a field in three-dimensional space. This study also showed that subgroups of canals within a single ampullary cluster have distinct projection vectors, and indicates that single clusters may serve multiple context-specific functions such as feeding and orientation behaviors.

BIOLOGICAL CONTEXTS AND BEHAVIORS

The first demonstrated biological function of the ampullary electrosense was for the detection of prey, and there is considerable theoretical work on the possible use in electric-mediated orientations. Recent experimental work has expanded functions of the electrosensory system to

Table 1   Biological functions for the electrosensory systems of sharks and rays.

Biological Function	Source
Prey detection	Kalmijn 1971; Tricas 1982; Blonder and Alevison 1988; Lowe et al. 1994; Haine et al. 2001; Kajiura and Holland 2002
Social communication	Bratton and Ayers 1987; Sisneros et al 1998
Detection of predators	Peters and Evers 1985; Sisneros et al. 1998
Detection of mates	Tricas et al. 1995
Geonavigation	Kalmijn 1974; Paulin 1995

include other contexts that occur during social and antipredator interactions (Table 1).

Detection of prey

The best-known function of the elasmobranch electrosense is for the detection of bioelectric fields produced by prey. Kalmijn (1971) performed a classic series of behavioral experiments in the laboratory on the catshark, *Scyliorhinus canicula*, and the Black Sea skate, *Raja clavata*, to show that elasmobranchs use the electrosense for prey localization. These fish executed well-aimed feeding responses to small flounder buried in the sand and were able to locate buried prey placed within an agar chamber that was permeable to its bioelectric field but not its odor. The ability to locate the prey was abolished when a thin plastic film that electrically insulated the field was placed over the agar chamber. These elasmobranchs also showed natural orientation responses toward buried active-dipole electrodes that produced simulated electric prey fields. Kalmijn (1982) later demonstrated in field experiments that free-ranging sharks such as the dusky smooth hound, *Mustelus canis*, and the blue shark, *Prionace glauca*, could be attracted by prey odor but would preferentially attack a weak electric dipole source (Fig. 4A). Tricas (1982) showed that in their natural habitat swell sharks, *Cephaloscyllium ventriosum*, use natural bioelectric fields to capture prey during normal nocturnal feeding (Fig. 4B). Other behavioral experiments using active dipole sources confirm the use of the electrosense for prey

detection in other species including the Atlantic stingray, *Dasyatis sabina* (Blonder and Alevizon 1988), the Pacific electric ray, *Torpedo california* (Lowe et al. 1994), the sandbar shark, *Carcharhinus plumbeus*, and the scalloped hammerhead shark, *Sphyrna leweni*, (Kajiura and Holland 2002). Collectively, these studies demonstrate that sharks and rays rely heavily upon their electrosense to locate natural prey at close range during the night or daytime, especially when prey are not in the field of view. However, because of the relatively small size of natural prey for sharks and rays and the polar nature of prey bioelectric fields, the field strength falls off quickly
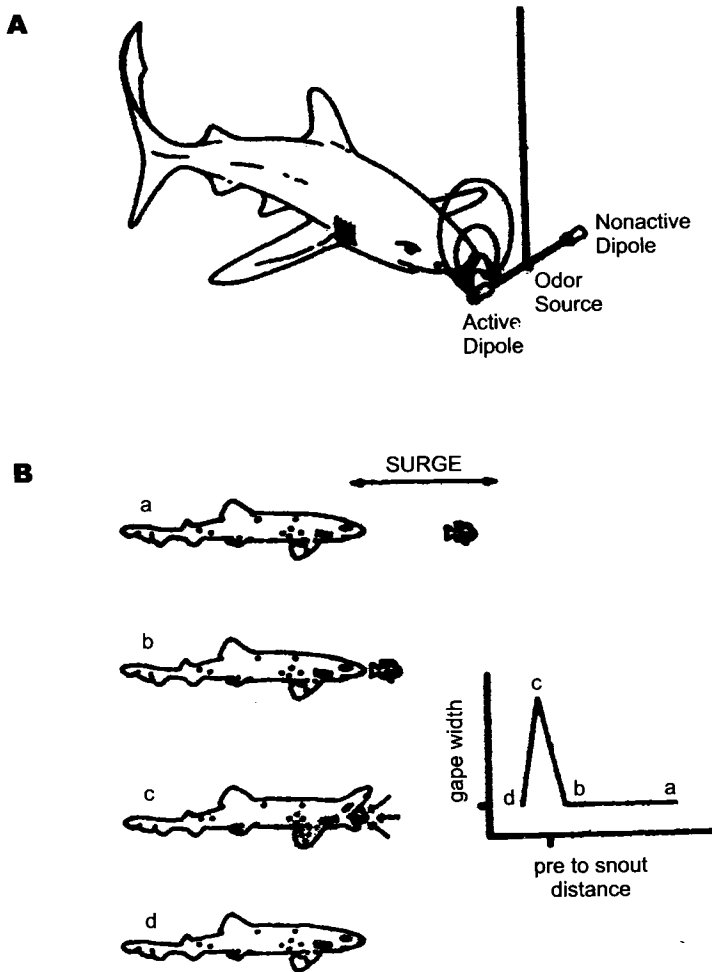

Fig. 4 Prey detection in elasmobranchs. A, Feeding response of the blue shark, *Prionace glauca*, on an active dipole source that electrically simulated prey. Blue sharks preferentially attacked the active dipole source rather than the prey odor source. (Modified from Kalmijn 1982). B, Gulp feeding response of the swell shark, *Cephaloscyllium ventriosum*, on blacksmith fish prey in the natural habitat. Sharks use an ambush predator strategy by lying on bottom at night and orient parallel to surge flow (a) and wait for blacksmith prey fish to swim near their snouts. Sharks wait until prey is within approximately 1-5 cm from the snout (b) and then "suck" into the mouth (c) and swallow fish (d). Modified from Tricas (1982).

with distance (Kalmijn 1988). Thus the effective distance of this sense in prey detection is usually limited to a distance of a few cm from the source.

Detection of conspecifics

Work on the non-electric stingrays has extended the role of elasmobranch electroreception to include social behavior. Tricas et al. (1995) showed that round stingrays, Urolophus halleri, use the electrosense to detect and locate conspecifics during the mating season (Fig. 5A). The main stimuli for conspecific localization are the weak bioelectric fields produced by cryptically buried females (Fig. 5B). Both males and females use their electrosense in a sex-specific context during the mating season, and orient towards buried conspecifics from distances of 0.1-1 m from the source. Male stingrays use their electrosense to detect and locate female mates, while females use the electrosense to locate and join buried conspecific females for refuge (Tricas et al. 1995, Sisneros and Tricas 2002b). Stingrays produce a standing dc bioelectric field that is partially modulated by the ventilatory movements of the spiracles, mouth and gill slits (Kalmijn 1974, Tricas et al. 1995). Both the static and modulated portions of this bioelectric field are attractive stimuli that can be used by searching stingrays to locate conspecifics buried in the substrate. The static portion of the ray's bioelectric field appears to vary at low frequency as the searching ray's electroreceptor system passes through it (sensu Kalmijn 1988). The modulated portion of the bioelectric field varies with the natural ventilatory movements of the ray ($\sim$ 0.5-2Hz) and because of the rapidly adapting nature of primary afferent discharges, may provide a significant electric stimulus especially when a receiver does not move such as occurs during inspection behavior. The peak frequency sensitivity of the electrosensory primary neurons in the round stingray matches the modulated frequency components of the bioelectric fields produced by conspecific stingrays (Fig. 5C). This match between peak frequency sensitivity of the peripheral electrosensory system and the ventilatory phasic signals produced by conspecifics indicates that the electrosense serves an important biological function in elasmobranch social behavior and that it can be used in sex-dependent contexts for conspecific localization during the mating season.

In addition to the non-electrogenic bioelectric fields, the weak electric organ discharges (EODs) of skates were proposed to serve an intraspecific communication function during social and reproductive behaviors rather than a defensive or predatory function (Mikhailenko 1971, Mortenson and Whitaker 1973, Braton and Ayers 1987). The peak frequency sensitivity of the electrosensory primary afferents in the clearnose skate, Raja eglanteria, is similar to the pulse rate of EODs produced by conspecific skates during social and mating behaviors (New 1994, Sisneros et al. 1998). A similar correspondence is seen between the peak frequency sensitivity of the electrosensory primary afferents in the little skate, Raja erinacea, and the EOD pulse rate produced by conspecifics of that species (Bratton and Ayers 1987, New 1990). Thus, the match between the electrosensory-encoding properties of the peripheral electrosensory system and the EOD pulse rate in these skates emphasizes the potential importance of the skate electrosense for electric communication during social and reproductive behaviors. However, much behavioral work remains to identify the specific social and sex-dependent contexts in which the skate EOD naturally function.
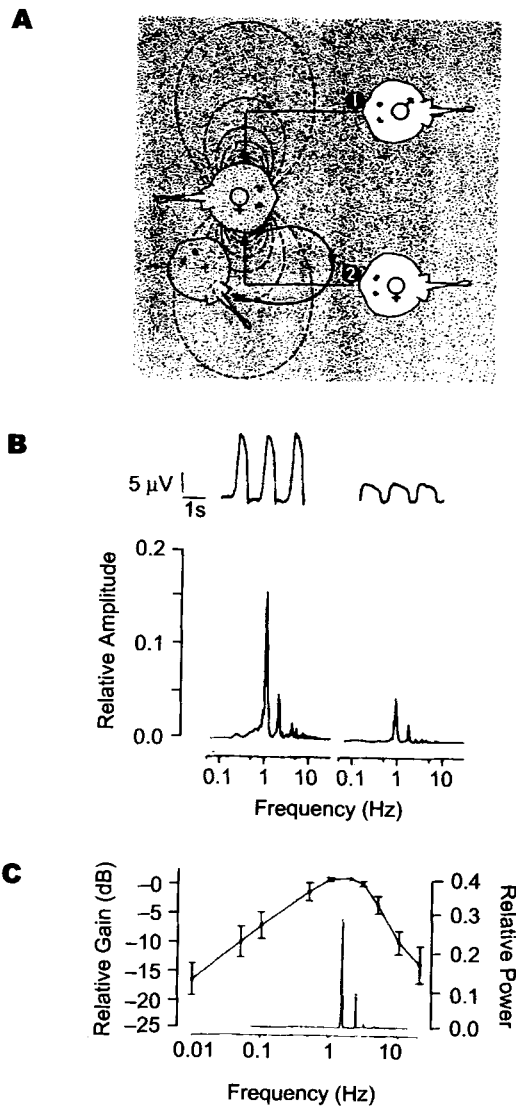
A

B

C

Fig. 5 Conspecific detection of mates, bioelectric stimuli, and the frequency response of the peripheral electrosense in the round stingray, *Urolophus halleri*. A, Diagrammatic representation of how male and female round stingrays use the electrosense to detect cryptically buried females during the mating season. Male rays use the electrosense to detect and locate females for mating while females use the electrosense to locate and join buried consexuals for refuge. B, Bioelectric potentials recorded from a female stingray on the ventral surface near gill slits (top, left record) and dorsal surface above the spiracle (top, right record). Recorded potentials vary part of the standing DC field and are similar for both male (not shown) and females. Fourier transforms of ventilatory waveforms (bottom) show strong frequency components near 1-2 Hz. C, Match between the peak frequency sensitivity of electrosensory primary afferent neurons and the frequency spectrum of the modulated bioelectric waveforms produced by round stingrays. The electrosensory primary afferents in *U. halleri* show greatest frequency response at approximately 1-2 Hz with a 3 dB bandwidth of about 0.5-4Hz. Data are plotted as the relative gain of mean discharge peak (± 1 SD) expressed in dB. Figs. A-C modified from Tricas et al. (1995).

Detection of predators

Another important function of the elasmobranch electrosense is for the detection of bioelectric fields produced by predators. Recent work on the clearnose skate, *Raja eglanteria*, not only demonstrates that the electrosense is functional in late-term egg-encapsulated embryos but also that their electrosense is most sensitive to the frequency spectrum that is produced by potential egg predators (Sisneros et al. 1998) such as produced by elasmobranchs, teleost fishes, marine mammals and molluscan gastropods (for review see Cox and Koob 1993). Late-term skate embryos vigorously undulate their tail in one corner of the egg case to create a continuous flow of seawater over their body for respiration (Fig. 6A) (Luer and Gilbert 1985). This tail undulating action draws fresh seawater through the egg case and creates a hydrodynamic streaming of seawater from the exit pore that can provide olfactory, electrosensory and mechanosensory cues to potential predators. The peak sensitivity of electrosensory primary afferent neurons in skate embryos is at the same frequency as the phasic ventilatory electric signals (0.5-2 Hz) produced by large fish predators, interrupts the respiratory movements of embryonic skates, and elicits an antipredator freeze behavior (Fig. 6B,C) (Sisneros et al. 1998). The freeze response exhibited by skate embryos stops the ventilatory streaming of seawater from the egg case and decreases the likelihood of olfactory, electrosensory, and mechanosensory detection by predators. Phasic electric stimuli of 0.1 to 1 Hz are also known to interrupt the ventilatory activity of newly post-hatched catsharks, *Scyliorhinus canicula* (Peters and Evers 1985), and this electrosensory-mediated behavior may represent an adaptive response during early life history to avoid detection by predators and enhance survival. Of potential significance is that a polar bioelectric field produced by a large predator would be strong compared to that of a natural prey item, but the effective distance for electrosensory detection of potential predators remains to be experimentally determined.

Navigation

The electrosense of elasmobranchs is known to mediate orientation to local inanimate electric fields and in theory is sensitive enough to function in geomagnetic navigation. Pals et al. (1982a) showed in behavioral experiments that the catshark, *Scyliohinus canicula*, could use dc electric fields to orient within a captive environment without light. Kalmijn (1982) also demonstrated that round stingrays, *Urolophus halleri*, orient within a uniform electric dc field, discriminate the direction of the dc field based on its polarity, and detect voltage gradients as low as 5 nV/cm. The electric field gradients used in the above experiments were of magnitudes similar to those produced by ocean currents (500 nV/cm, Kalmijn 1984) and tidal currents (8 μV/m, Pals et al. 1982b).

According to Kalmijn (1974, 1981, 1984), elasmobranchs may use the electrosense for two modes of electronavigation. In the passive mode, elasmobranchs detect the voltage gradient produced in their external environment such as occurs during flow of ocean water through the earth's geomagnetic field (Kalmijn 1988). In the active mode, elasmobranchs detect voltage gradients that are induced by the animal's locomotor movements through the earth's magnetic
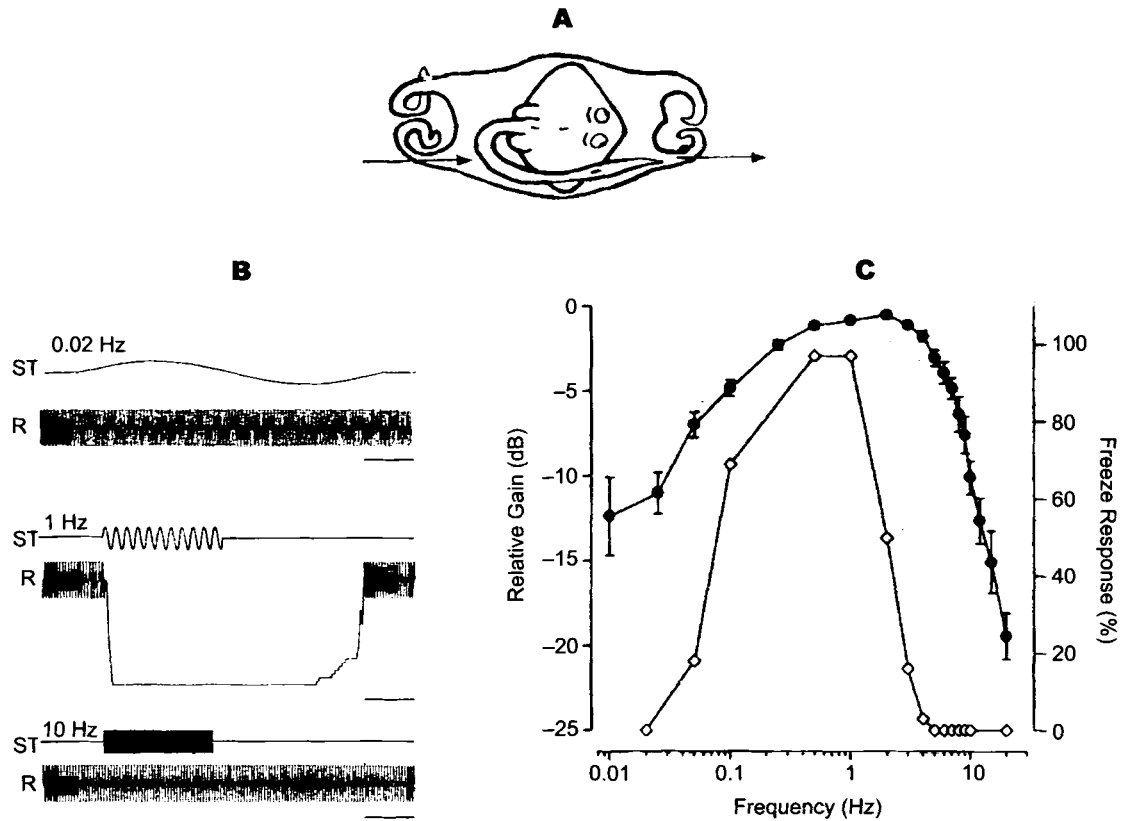
Fig. 6 Behavioral response of clearnose skate embryos, *Raja eglanteria*, to weak electric stimuli. A, Ventilation
behavior of skate embryos. Diagram depicts a late-term embryonic skate that drives seawater through
the egg case by undulating its tail near a ventilation pore in the horn. The tail beating action of the skate
draws fresh seawater through pores on the opposite end of the case and creates a localized vortex near
the exit pore by the tail. Arrow indicates flow of seawater. Modified from Sisneros et al. (1998). B,
Behavioral responses of embryonic skates to sinusoidal uniform electric fields at stimulus (ST) frequen-
cies of 0.02 Hz, 1Hz and 10 Hz. Stimuli were applied at an intensity of 0.56 nV/cm across the longitu-
dinal axis of the skate. The response (R) is expressed as a change in the peak-to-peak (PTP) tail displace-
ment within the egg case. Prestimulus tail displacement for each record was 10 mm PTP. At 1 Hz, note
the large tail displacement that occurs during coiling of the tail around the body after the onset of the
electrical ST and a period of no tail movement during and after stimulation. Time bars = 5 seconds. C,
Freeze response of skate embryos to weak electric stimuli. Behavioral responses (open diamonds) are
shown as a percentage of total ST presentation to 0.02-20 Hz. Note that the peak frequency sensitivity of
electrosensory primary afferent neurons (solid dots) for skate embryos is at 1-2 Hz and is aligned with the
freeze response peak of 0.5-1Hz. Figs. A-C were modified from Sisneros et al. (1998).

field (Fig. 7). Another active mode model by Paulin (1995) proposes that electrosensory and
vestibular canal information during head rotation are integrated and should provide
unambiguous directional cues during swimming. However, direct experimental tests of these
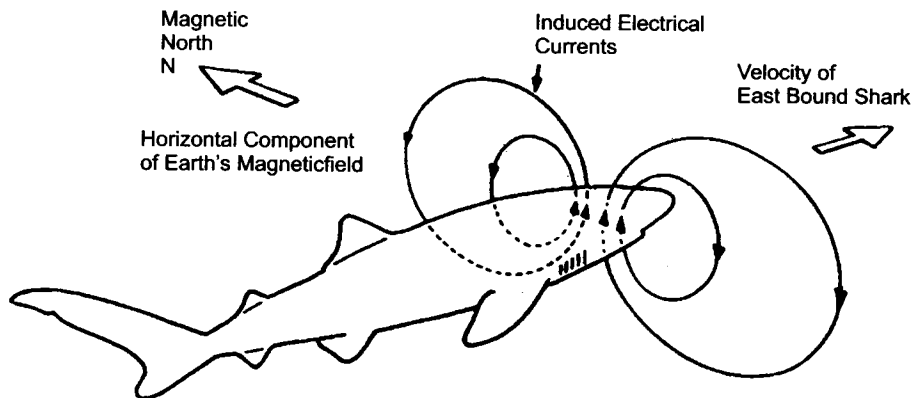active mode models await to be performed.

Fig. 7 Active mode induction of weak electric fields at the head as a shark swims through the horizontal component of the earth's magnetic field. This can provide a physical basis for an electromagnetic compass sense. From Kalmijn (1974).

Experimental evidence is consistent with the ability of elasmobranchs to use magnetic field information for electric orientation and navigation. Kalmijn (1982) showed that in the absence of an imposed electric field round stingrays, *U. halleri*, could be conditioned by food reward to locate and enter an enclosure in the magnetic east and to avoid an enclosure in the magnetic west. In addition, stingrays could discriminate the direction and polarity of the magnetic field. More recently Klimley (1993) showed that scalloped hammerhead sharks,*Sphyrna leweni*, swimming in the pelagic realm followed fixed, repetitive homing routes that correlated with the ambient pattern of geomagnetic anomalies associated with the ocean floor and he proposed that they may navigate by the use of geomagnetic fields. However, further experiments are needed to determine whether this orientation is mediated by direct magnetoreception or induced geomagnetic electroreception.

ONTOGENETIC AND SEASONAL CYCLES

Sharks and rays are large, long-lived fishes that can inhabit different ecological habitats during their life history. In addition, seasonal changes in behaviors such as migration or reproductive activity may result in seasonal variation in biological functions for the electrosense. Recent research has begun to address questions on temporal and spatial changes in electrosensory function.

Age-dependent effects on electrosensory responses

Physiological studies indicate that the ampullary electroreceptors in adult elasmobranchs are broadly tuned to low-frequency electric stimuli and respond maximally to sinusoidal stimuli from approximately 0.1 to 15 Hz (Andrianov et al. 1984, Montgomery 1984, Peters and Evers 1985, Tricas and New 1998). However, recent neurophysiological work on the clearnose skate, *Raja eglanteria*, and the Atlantic stingray, *Dasyatis sabina*, indicates that the discharge and

bandpass filtering properties of the peripheral electrosense change during ontogeny (Sisneros et al. 1998, Sisneros and Tricas 2002a). The resting discharge rate and regularity of the electrosensory primary afferents in these batoids increase with age and may serve to enhance the temporal resolution for encoding of low-frequency electrosensory stimuli (Sisneros and Tricas 2002a). Furthermore, during development the tuning properties of the peripheral electrosensory system shift to higher frequencies and sharpen. The −3 dB bandwidth of the peripheral electrosense in the Atlantic stingray is ~2Hz higher in adults (2.7-10.1 Hz) than in neonates (1.1-8.5 Hz). In addition, the −10dB bandwidth in Atlantic stingrays narrows from 1.1-28.7 Hz in neonates to 0.5-18.5 Hz in adults (a decrease in bandwidth by ~10 Hz). (The −3dB and −10 dB bandwidths are measures that describe the range of frequencies over which the sensitivity of the electrosensory system falls within the prescribed limits. In this case, the bandwidths of the peripheral electrosensory system are described as the range between frequencies at which the response is −3dB and −10dB compared with the peak response at midband.) Concurrent with the ontogenetic shift in −3dB bandwidth is an increase in best frequency (i.e. the frequency that evokes the maximum response from the electrosensory primary afferents) from 2-4 Hz in neonates to 3-5 Hz in juveniles, and 6-8 Hz in adults (Sisneros and Tricas 2002a). Similar ontogenetic shifts in −3 dB bandwidth and best frequency also occur in the clearnose skates, *Raja eglanteria* (Sisneros et al. 1998).

In addition to changes in the frequency response properties, the neural sensitivity (gain) of electrosensory primary afferents also increases with size during ontogenty in *R. eglanteria* and *D. sabina* (Sisneros et al. 1998, Sisneros and Tricas 2002a). Sensitivity in the clearnose skate is approximately five times greater in juveniles (mean total length = 17.4 cm) and eight times greater in adults (mean total length=52.3 cm) than in embryos (mean total length = 11.9 cm) (Sisneros et al. 1998). Sensitivity at best frequency in the Atlantic stingray is approximately three times greater in juveniles (mean disk width = 15.1 cm) and four times greater in adults (mean disk width = 25.0 cm) compared to neonates (mean disk width = 11.6 cm) (Sisneros and Tricas 2002a). As young batoids grow in size, an increase in sensitivity is expected due to the concurrent increase in canal length. The sensitivity of electrosensory primary afferents to uniform electric fields is positively correlated with canal length (Fig. 8) (Sisneros and Tricas 2000a), and therefore accounts for a large part of the observed increase in neural sensitivity through growth.

The adaptive importance of the ontogenetic changes in the response properties of the peripheral electrosense may be related to complementary functions during development to avoid predation and maximize prey detection. As discussed above, the peak frequency response of embryonic and neonate batoids is within the peak frequency band of phasic potentials produced by natural fish predators, corresponds to the same frequency stimuli that interrupt respiratory movements (Sisneros and Tricas unpublished data), and elicits an antipredator freeze response in embryonic skates (Sisneros et al. 1998). Such ontogenetic shifts in the frequency tuning of batoids may also affect a shift in foraging behavior and the diet of invertebrate prey. Infaunal prey such as polychaete worms and bivalves emit predominately unmodulated DC fields (Kalmijn 1974) as opposed to the modulated bioelectric fields
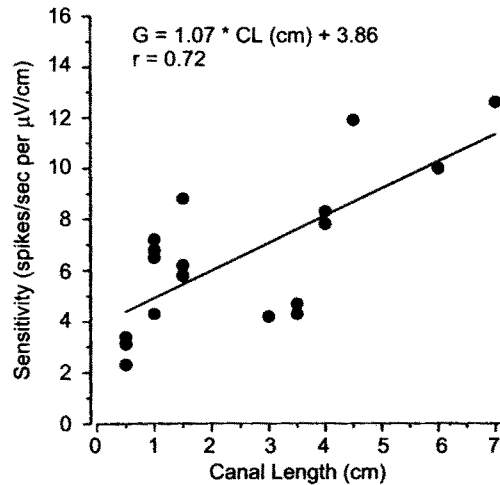
Fig. 8 Relationship between the sensitivity (gain) of electrosensory primary afferent neurons and the canal length of ampullary electroreceptive organs in the Atlantic stingray, *Dasyatis sabina*. Data are from male stingrays collected during the nonreproductive summer months. Note that the sensitivity (G) of the primary afferent neurons increases with ampullary canal length (CL). Neural gain is expressed as spikes per second (s/s) per unit of field intensity. Data replotted from Sisneros and Tricas (2000).

produced by small crustacean prey such as *Daphnia* and amphipods that generate rhythmic AC potentials at 8-10 Hz (Wilkens et al. 1997, Wilkens this volume). The AC signals from the latter prey are close to the peak frequency sensitivity of the electrosensory primary afferents in juveniles and adult batoids (Sisneros et al. 1998, Sisneros and Tricas 2002a). Weak AC signals may be important for the detection of crustacean prey, especially in cases where a batoid is at rest near a prey source and the detection of DC fields becomes difficult due to the rapidly adapting nature of electroreceptors to a constant current field. Small crustacean prey such amphipods, mysids and isopods form a major component of the diet in the Atlantic stingray, especially during the summer months when stingrays forage in the sea grass beds found seasonally in Florida lagoons. Thus, the ontogenetic changes in the response properties of the elasmobranch electrosense may represent sensory adaptations to enhance the avoidance of large predators as young, and as adults increase the probability of detecting the higher frequency information associated with small infaunal prey.

Seasonal hormonal cycles and electrosensory responses

Gonadal steroids are known to have important effects on the brain and behavior (Kelly 1982, Arnold and Gorski 1984) but very little is known about how the electrosense in sharks may be influenced by seasonal changes in hormone levels. Recent work on the reproductive biology and steroid cycles in the Atlantic stingray, *D. sabina*, provides the first look at how the electrosensory system function can change during the mating cycle in elasmobranchs. Females of this species undergo a 5-6 months period of egg development that begins in the fall and ends
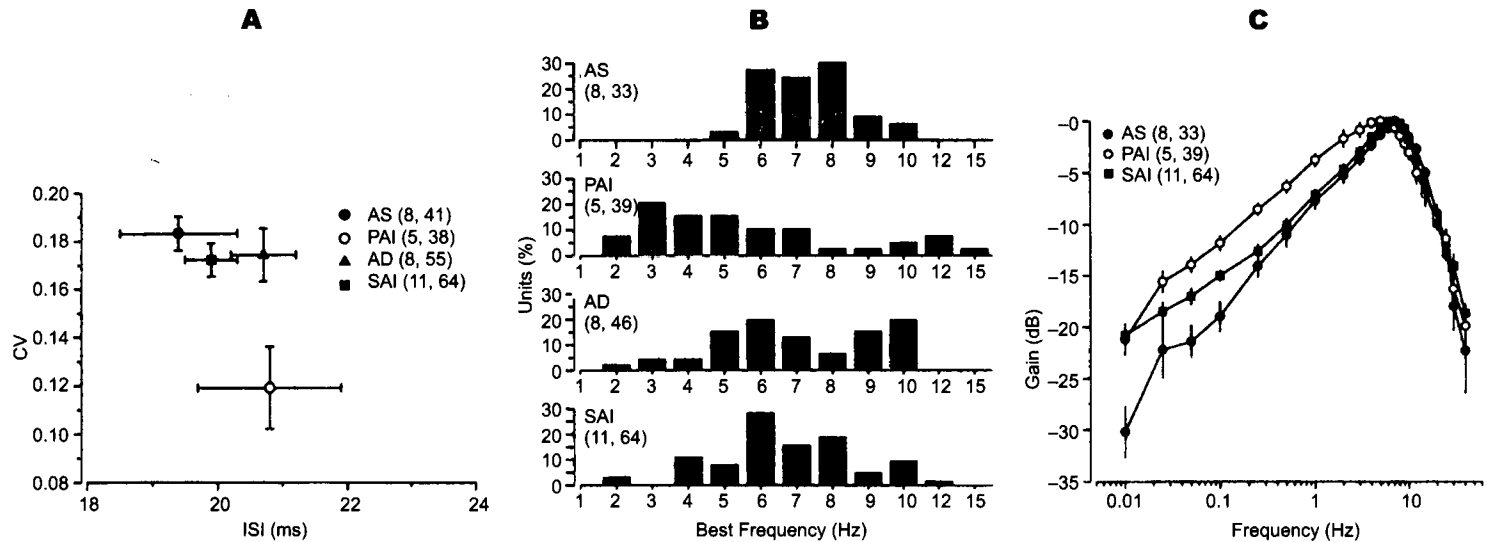
Fig. 9 Seasonal changes in the response dynamics of ampullary electrosensory primary afferent neurons in male Atlantic stingrays, *Dasyatis sabina*. A, Relationship between resting discharge variability and mean interspike interval for electrosensory primary afferent neurons in wild caught male stingrays. Rays were collected during the four phases within the annual androgen production cycle: (1) androgen suppression (AS), which occurs between reproductive seasons (April-July) during which the serum androgen levels are low and testes are inactive, (2) primary androgen increase (PIA), which occurs at the onset of the mating season and spermatocyte development (August-October), (3) androgen decrease (AD), which occurs after maximum testis growth and spermatocyte development (November-December), and (4) secondary androgen increase (SAI), which occurs at the end of the mating season and peak period of sperm maturation (January-March). Discharge variability is expressed as coefficient of variation (CV), a dimensionless ratio of standard deviation to mean interspike interval (ISA). Note the decrease in CV for PAI indicates an increase in discharge regularity during the onset of the reproductive season. The number of stingrays and electrosensory primary afferent neurons tested are indicated in parenthesis. All data plotted as mean ± standard error. B, Best frequency histogram for electrosensory primary afferent neurons recorded from male stingrays collected during annual periods of AS, PAI, AD and SAI. Number of rays and electrosensory primary afferent neurons tested are indicated in parenthesis. Note the decrease in best frequency for males collected during PAI at the onset of the reproductive season, and increased percentage of units with low best frequency. C, Bode plot for the frequency response of electrosensory primary afferent neurons recorded from male stingrays collected during annual periods of AS, PAI, AD, and SAI. Only data for males collected during AS and SAI are plotted for comparison with males collected during PAI. The number of rays and electrosensory primary afferent neurons tested are indicated in parenthesis. Peak sensitivity for males during PAI is 4-5 Hz and 7-8Hz during AS and SAI. Data were calculated from period histogram analysis and are plotted as the mean discharge peak. In order to control for absolute sensitivity of different units, data were normalized to a relative value of 0 dB assigned to the peak response for each unit and then expressed in relative dB. All data plotted as mean ±1 standard error. Note some standard error bars are obscured by symbols. Figs. A-C modified from Sisneros and Tricas (2000).
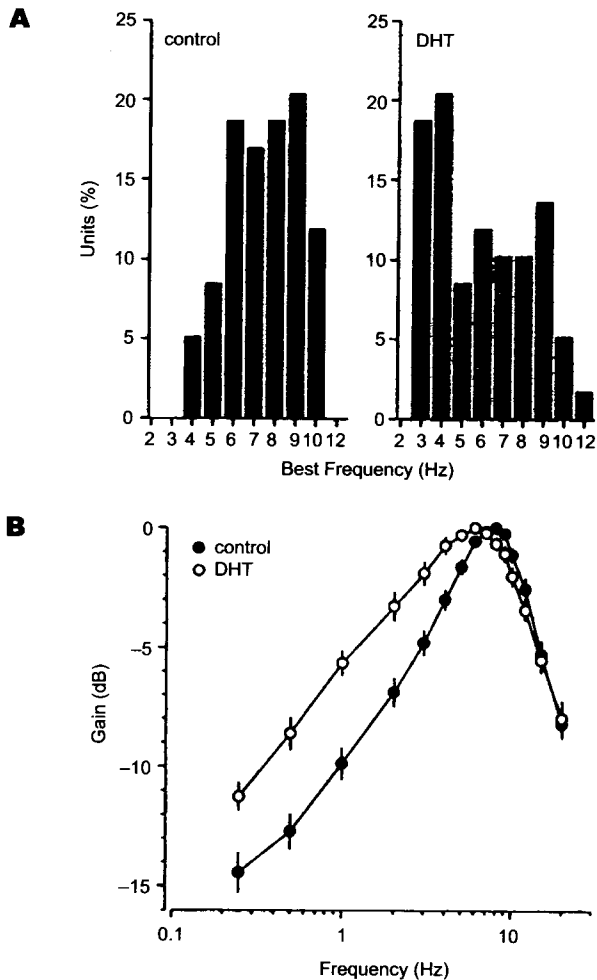
Fig. 10   Frequency response dynamics of electrosensory primary afferent neurons in control and dihydrotestosterone-treated male Atlantic stingrays, *Dasyatis sabina*. A, Best frequency (BF) histogram for electrosensory primary afferent neurons in control and dihydrotestosterone (DHT) treated male stingrays. Number of rays and electrosensory primary afferent neurons tested are indicated in parenthesis. Note that there is an induced downward shift in BFs of electrosensory primary afferents in DHT treated rays. B, Bode plot for the frequency response of electrosensory primary afferent neurons recorded from control and DHT-treated male stingrays. Peak frequency sensitivity of the electrosensory afferents is 7-8 Hz for control treated fish and 5-6 Hz for DHT treated fish. Number of rays and electrosensory primary afferent neurons tested are indicated in parenthesis. Data were calculated from the period histogram analysis and are plotted as the mean discharge peak. In order to control for absolute sensitivity of different units, data were normalized to a relative value of 0 dB assigned to the peak response for each unit and then expressed in relative dB. All data are ploted as mean ±1 standard error. Note some standard error bars are obscured by symbols. Figs. A & B modified from Sisneros and Tricas (2000).

with synchronous ovulation by all females in the spring (Maruska et al 1996). Male and female rays have a protracted mating season that completely overlaps the period of egg development (Kajiura et al. 2000). The onset of reproductive activity and egg development is accompanied by an elevation of androgen hormones in males and continues throughout the reproductive season (Tricas et al. 2000). At the beginning of the mating season, electrosensory primary afferent neurons in male rays exhibit an increase in resting discharge regularity, a downshift in best frequency and bandpass, and a greater sensitivity to low-frequency electric stimuli (0.01-4Hz) (Fig. 9) (Sisneros and Tricas 2000), which is similar to signals produced by conspecific mates (Tricas et al. 1995). The initiation of mating behavior and changes in the response properties of the peripheral electrosensory system in male stingrays coincide with the onset of spermatocyte production and the annual peak in androgen steroid levels for the population (Tricas et al. 2000, Sisneros and Tricas 2000). Experimental implants of dihydrotestosterone in non-reproductive male stingrays induced similar response shifts in electrosensory primary afferents that included a lowered best frequency and bandpass, and an increased sensitivity ($1.5\times$ increase) to low frequency stimuli from 0.5 to 2 Hz (Fig. 10). This androgen-induced plasticity of the male's electrosense may function to seasonally increase the probability of conspecific mate detection and localization during the mating season, and ultimately increase individual male fitness.

SUMMARY AND CONCLUSIONS

The electrosensory system of sharks and rays serves a wide range of natural functions including the location of prey, avoidance of predators, the detection of mates, social communication, and possibly geonavigation. These biological roles result from a highly specialized receptor system and the spatial arrangement of pores and canals on the body. The response properties and function of the electrosense may change with age and are associated with ontogenetic shifts in habitat use, foraging behavior and diet. The response properties of electrosensory neurons may change seasonally in reponse to gonadal steroid levels in the body that relate to reproductive activity and other seasonal behaviors. Future work should continue to investigate the biological contexts in which the ampullary electrosense is used, and to test the selective forces that may have shaped the evolution of this remarkable sensory system.

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