

# Neuroethology and life history adaptations of the elasmobranch electric sense

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## Abstract

The electric sense of elasmobranch fishes (sharks and rays) is an important sensory modality known to mediate the detection of bioelectric stimuli. Although the best known function for the use of the elasmobranch electric sense is prey detection, relatively few studies have investigated other possible biological functions. Here, we review recent studies that demonstrate the elasmobranch electrosensory system functions in a wide number of behavioral contexts including social, reproductive and anti-predator behaviors. Recent work on non-electrogenic stingrays demonstrates that the electric sense is used during reproduction and courtship for conspecific detection and localization. Electrogenic skates may use their electrosensory encoding capabilities and electric organ discharges for communication during social and reproductive interactions. The electric sense may also be used to detect and avoid predators during early life history stages in many elasmobranch species. Embryonic clearnose skates demonstrate a ventilatory freeze response when a weak low-frequency electric field is imposed upon the egg capsule. Peak frequency sensitivity of the peripheral electrosensory system in embryonic skates matches the low frequencies of phasic electric stimuli produced by natural fish egg-predators. Neurophysiology experiments reveal that electrosensory tuning changes across the life history of a species and also seasonally due to steroid hormone changes during the reproductive season. We argue that the ontogenetic and seasonal variation in electrosensory tuning represent an adaptive electrosensory plasticity that may be common to many elasmobranchs to enhance an individual's fitness throughout its life history.

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## 1. Introduction

Sensory neuroethologists seek to understand the neural basis of adaptive behaviors that animals use within their natural environment. Because this requires study of both neural mechanisms and behavior of the animal, multidisciplinary approaches are required. In many cases researchers focus on a single aspect of a neural system that controls behavior and employ a limited set of neurobiology techniques. In addition, behavioral studies are often necessarily limited to a single biological context in which to interpret the sensory system. As a result, it usually takes great time and effort to characterize the adaptive function of a neural system in relation to the natural behavior of the organism.

One example of an incompletely characterized system is the use of the ampullary electrosense by elasmobranch fishes to detect bioelectric stimuli. The ampullary organs were recognized long ago by Stenonis [57] and Lorenzini [34], but its physiological and behavioral functions remained unknown for centuries. The advent of modern neurophysiological techniques first produced evidence for multiple sensory functions until it was convincingly demonstrated to encode weak electric charges external to the animal [43,44]. A short time later researchers were able to experimentally demonstrate that sharks and rays could use this sense to successfully detect and locate bioelectric stimuli produced by their prey. However, these large fishes are wide ranging, difficult to maintain in the lab or observe in the wild thus there is only limited literature of their natural social, predatory, and anti-predatory behaviors. As a result, most neuroethology research on the ampullary electrosense of sharks and rays has focused on the response

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dynamics and central neuroanatomy, with relatively few new studies on other possible biological functions. The purpose of this paper is to present recent evidence that the electrosensory system functions in a wide number of behavioral contexts including social, reproductive and anti-predator contexts (Table 1).

## 2. The elasmobranch electrosensory system

All elasmobranch fishes (sharks, skates, and rays) possess an elaborate electrosensory system that consists

Table 1

Functions for the detection of bioelectric fields by the ampullary electrosense of elasmobranch fishes

Biological function	Source
Prey detection	[28,63]
Social communication	[13,14,55]
Detection of mates	[65]
Detection of predators	[55]

of subdermal groups of electroreceptive organs known as the ampullae of Lorenzini. Single ampullae of Lorenzini consist of a small chamber (the ampulla) and a subdermal canal that projects to a single pore on the surface of the skin (Fig. 1A). The wall of the ampulla is composed of a single-layer sensory epithelium that contains hundreds of sensory receptor and support cells [51,67] with only the apical surface of the receptors exposed to the ampulla chamber (Fig. 1B). Tight junctions unite receptor and support cells to form a high resistance separation of apical and basal surfaces of the sensory epithelium [53,67]. The basal surface of the receptor cell is innervated by multiple afferents of the anterior lateral line [31]. The wall of the canal is composed of two layers of flattened epithelial cells and is also highly resistive. The canal lumen and ampullary chamber are filled with a conductive low-resistance mucopolysaccharide to form an electrical core conductor such that the ampullary chamber is isopotential with a charge at the skin pore [18,45,67]. Many individual ampullae are grouped into separate bilateral clusters that send their canal projections to individual skin

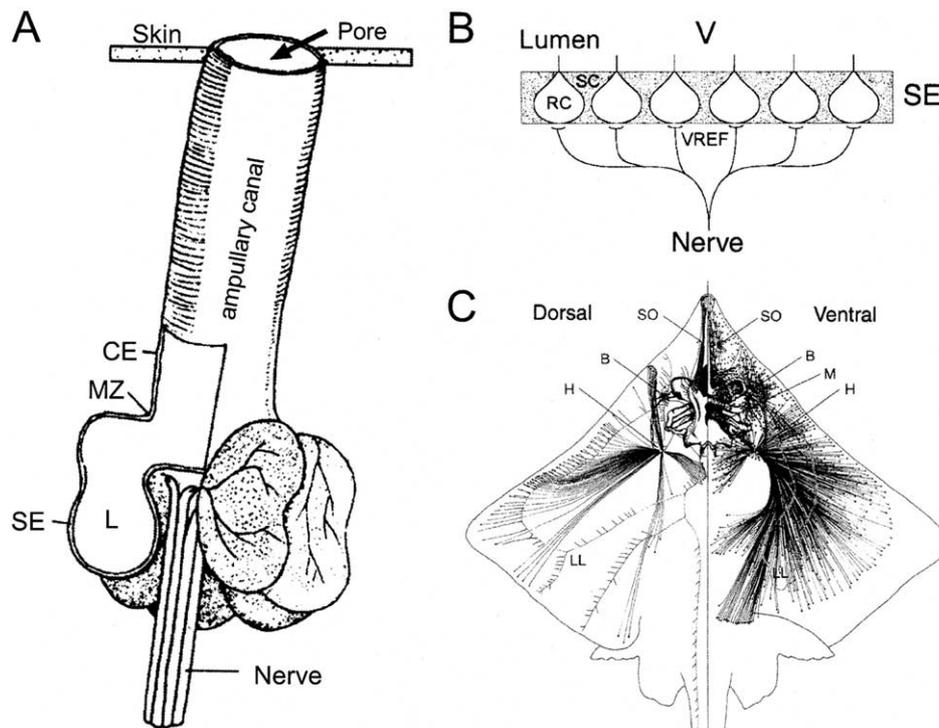


Fig. 1. Ampullary electroreceptor organ of the marine skate, *Raja*. A, The ampulla of Lorenzini consists of a small ampulla chamber composed of multiple alveolar sacs that share a common lumen (L) and a subdermal ampullary canal that projects to a single pore on the skin. Both the ampullary lumen and canal are filled with a highly conductive gel, which makes the lumen isopotential with voltages present at the pore. The sensory epithelium (SE) forms a highly resistance ampulla wall that connects with the canal epithelium (CE) at the marginal zone (MZ) and is innervated by primary afferent neurons of the VIIIth nerve. (Modified from Waltman [67]). B, Schematic representation of the sensory epithelium of the skate ampulla. In most elasmobranchs, the sensory epithelium (SE) consists of a single layer of receptor cells (RC) and support cells (SC). Tight junctions between the receptor and support cells form a high electrical resistance barrier between the lumen of the ampulla and basal portion of the receptor cells. The difference between the lumen voltage (V) and reference voltage (VREF) stimulates the small apical of the receptor cells and controls release of neurotransmitter onto primary afferent neurons (modified from Tricas [64]). C, Subdermal ampullary clusters and their radial canals which terminate at surface pores on the dorsal and ventral surfaces of the barndoor skate, *Raja laevis*. Ampullary clusters indicated by B = buccal, H = hyoid, M = mandibular, SO = superficial ophthalmic. LL = lateral line (modified from Raschi [50]).

pores on the head of sharks, and also the pectoral fins of batoids (Fig. 1C). These morphological features allow ampullary electroreceptors to detect potential differences between the common internal potential at the cluster and the somatopic charges on the skin. The morphological arrangement of the ampullary canals permits detection of both small local fields produced by small prey organisms and also uniform electric fields of inanimate or animate origins [29]. When a local-dipole stimulus is presented at a pore that is far away from its ampulla, the potential is conducted to receptor cells within the ampulla chamber and essentially measures the transcutaneous potential drop. However, when the body is positioned within an external field the low skin and body resistivities permit the field to influence the internal reference potential, thus the stimulus voltage depends upon the spatial separation between the ampulla and its canal pore. Long canals sample across a greater distance within a uniform field and provide a larger potential difference for receptor cells (and sensitivity) than do short canals.

### 3. The skate electrosense

#### 3.1. Electrogenic organs, physiology and behavior

Marine skates of the family Rajidae produce intermittently pulsed, weak electric discharges from spindle-shaped electric organs found bilaterally in the tail [22,52,56]. These electrogenic organs consist of disk- or

cup-like electrocytes that are arranged within the organ anterioposteriorly in series [16,23] and are depolarized by spinal electromotoneurons to generate a weak electrical discharge around the animal [3,10,33]. The discharges are controlled by descending input from an electric organ command nucleus located in the medulla [1,60,61].

The electric organ discharge (EOD) produced by skates is relatively low in amplitude, species-specific in duration [11,13,14] and has led to the suggestion that the skate EOD may serve a possible intra-specific communication function rather than a predatory or defensive function. Skate EODs generally consist of a monophasic, head negative waveform (Fig. 2) that varies in amplitude from approximately 20–40 mV [13] and are produced in a series of intermittent pulses. The relatively low amplitude of the skate EOD contrasts that of the strong EOD (30–60 V) produced by electric rays (family Torpedinidae) used during predatory and defensive behaviors [8–10,12,15,35]. Bratton and Ayers [13] reported that skates often produce EODs during physical contact and during behavioral interactions with other conspecific skates. EOD interaction is often greater among groups or pairs of skates than from isolated individuals [13,42]. In addition, the EOD pulse is characteristically different among skate species [14] and ranges from 31 ms to 216 ms in duration (Table 2). Skate electric organs also differ in length among species and may be sexually dimorphic [26,27]. Thus, the intermittent production and low amplitude of the skate EOD indicates that the EOD functions not for electrolocation, prey capture or defense, but more likely for social communication among conspecifics.

The skate electrosensory system is relatively broadly tuned to low frequency electric stimuli and is most sensitive to sinusoidal stimuli from approximately 0.1 to 10 Hz [2,46,55]. Skate electrosensory primary afferents exhibit peak frequency responses that range from 0.1 to 0.5 Hz in the black sea skate (*Raja clavata*) [2], 2–3 Hz in the clearnose skate (*R. eglanteria*) [55], and 1–5 Hz in the little skate (*R. erinacea*) [46]. While these differences in peak frequency response among species may represent species differences related to their behavior and natural ecology, the low pass characteristics observed in

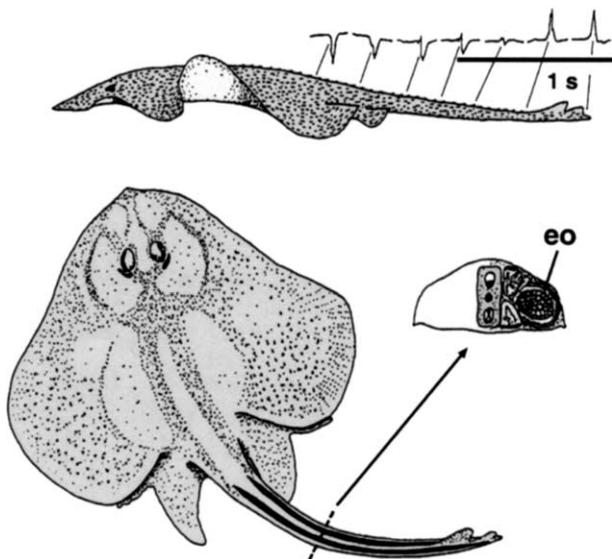


Fig. 2. Diagrammatic representation of the little skate, *Raja erinacea*, showing the position of the electric organ (eo; black) in the tail and the corresponding monophasic, head negative electric organ discharge waveform recorded 1 cm from the skin in the tail regions indicated. Note that the cross-section of the tail shows the position of the eo and lateral displacement of muscle bundles around the eo. (Modified from Bratton and Ayers [13]).

Table 2  
Species-specific pulse duration of electric organ discharges (EODs) from skates (family Rajidae)

Species	EOD pulse duration (ms)	Reference
<i>Raja montagui</i>	31	[14]
<i>Raja eglanteria</i>	33	[55]
<i>Raja microcellata</i>	34	[14]
<i>Raja clavata</i>	37	[14]
<i>Raja erinacea</i>	70	[13,14]
<i>Raja radiata</i>	92	[14]
<i>Raja ocellata</i>	217	[13,14]

skates and other batoids most likely represent physiological constraints of ampullary electroreceptor cells, i.e., membrane resistance and capacitance of the receptor epithelium, cable properties of the ampullary canals, and the ionic membrane properties of the receptor itself. Recent neurophysiological work shows that the skate electroreceptor system can encode weak EODs produced by conspecifics during social and reproductive interactions. In the clearnose skate (*Raja eglanteria*) the peak frequency sensitivity of electroreceptor primary afferents in adult clearnose skates (2–3 Hz) is aligned with average pulse rate of EODs (2.5 Hz) produced by conspecifics during social and mating behaviors (Fig. 3) [55]. Similarly, the peak frequency sensitivity (5–7 Hz) of electroreceptor primary afferents in the adult little skate (*Raja erinacea*) [46] is also aligned with the EOD pulse rate (about 5 Hz) produced during interactions with conspecifics [13]. Furthermore, the electroreceptor system in *R. erinacea* is also well suited to detect the spectral components of individual EOD pulses [47]. Such matches between the electroreceptor encoding capabilities and EOD properties of skates may serve to facilitate communication during social interactions.

### 3.2. Detection of predators

One important function of the skate electric sense, especially during the early life history, is for the detection and avoidance of predators. Work on the clearnose skate (*Raja eglanteria*) shows that the electroreceptor system of egg-encapsulated embryonic skates is well

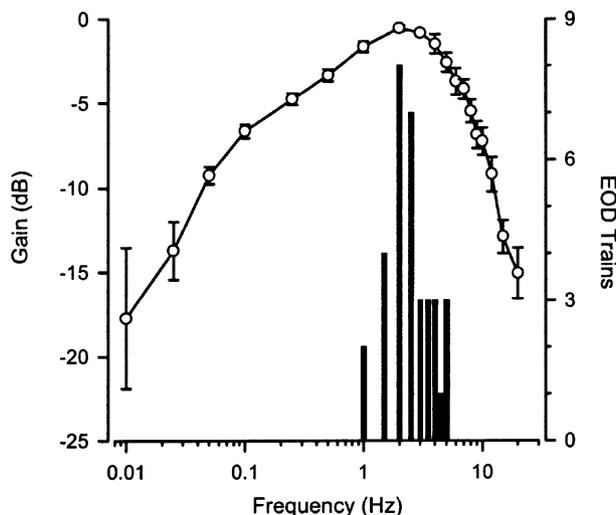


Fig. 3. The match between frequency sensitivity of electroreceptor primary afferent neurons and electric organ discharge (EOD) pulse rate produced by reproductively active clearnose skates, *Raja eglanteria*. The tuning curve of the skate electroreceptor primary afferents shows peak sensitivity at 2–3 Hz with a 3-dB drop at approximately 0.6 and 5.6 Hz. Pulse rate distribution of EODs shows that the mean EOD pulse rate ( $2.5 \pm 1.1$  SD Hz,  $n = 34$ ) matches the frequency of peak sensitivity for the clearnose skate electroreceptor system. (Modified from Sisneros et al. [55]).

suit to detect potential egg predators [55]. Embryos of egg-laying elasmobranchs spend their embryonic life in an oviposited egg case on or near the benthic substrate where they are vulnerable to egg predators, which include other elasmobranchs (sharks, rays and skates), teleost fishes, marine mammals and molluscan gastropods [17,21,37,58,59,62]. Late-term embryonic skates undulate their tail in one corner of the egg case to facilitate the circulation of fresh seawater through ventilation pores found in the horns of the egg case. This behavior results in the streaming of water from one horn of the egg case at velocities of approximately  $7 \text{ cm s}^{-1}$  [55] and creates a localized vortex near the egg which may provide olfactory, electroreceptor and mechanosensory cues that facilitate the detection and location of the skate by potential predators. The peak frequency sensitivity of electroreceptor primary afferents in embryonic clearnose skates matches the frequency of phasic electric stimuli produced during ventilatory activity of large fish predators (1–2 Hz) and also corresponds to the same frequency stimuli that interrupt respiratory movements and elicit an anti-predator freeze response (Fig. 4) [55]. Thus, the freeze behavior produced by egg-encapsulated embryonic skates will stop ventilatory streaming, decrease the likelihood of sensory detection, and thus “cloak” embryos from searching egg predators. Phasic electric stimuli of 0.1–1 Hz are also known to interrupt the respiratory movements of newly post-hatched dogfish, *Scyliorhinus canicula*, [49] and may reflect the perceived low frequency modulation of a d.c. field produced by an approaching predator as it moves relative to the embryo [30]. In sum, the match between peak frequency sensitivity of electroreceptor primary afferents and electric frequency stimuli that elicit a freeze response indicates that the electric sense of embryonic skates can efficiently mediate predator detection or avoidance, and may represent an adaptive response in skates and other elasmobranchs to enhance survival.

## 4. The stingray electric sense

### 4.1. Courtship and mating behavior of the round stingray

The round stingray, *Urolophus halleri*, is a relatively small stingray found from Point Conception, California to Panama Bay and is common throughout the Gulf of California [41]. Courtship and mating among many individuals of this species can readily be observed during the winter months (January–March) in the clear shallow waters near Bahia Kino, Mexico [48,65]. Each day before sunrise during the mating season, reproductively active female rays move into the shallow water habitat along the shoreline and bury in the sand bottom. Shortly thereafter, solitary male rays can be found

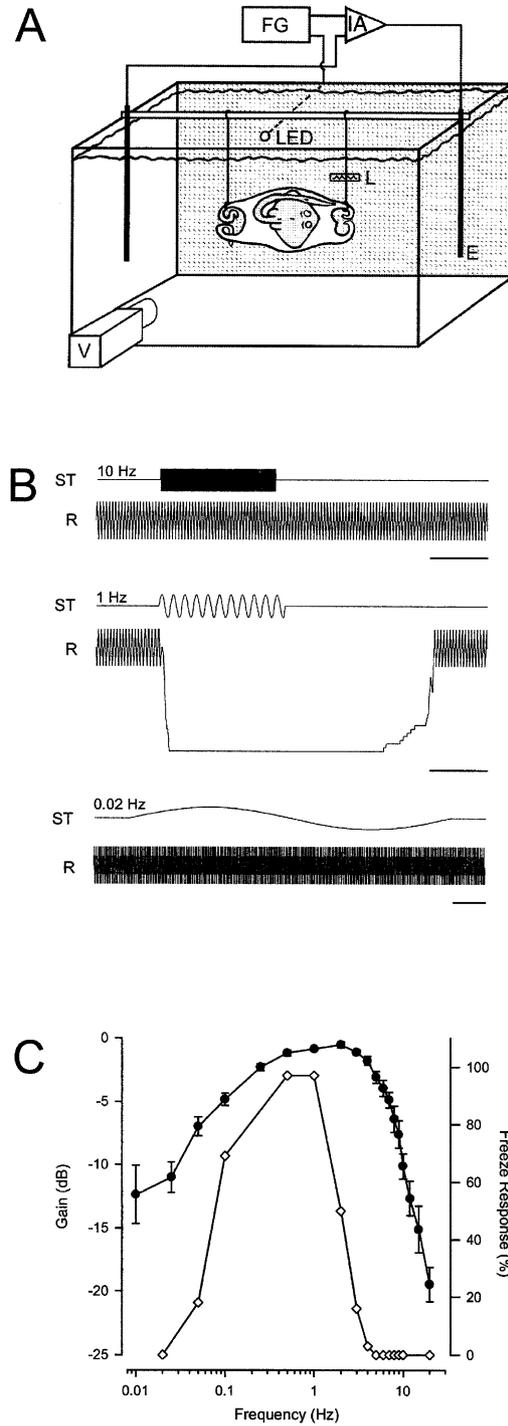


Fig. 4. Behavioral response of embryonic clearnose skates (*Raja eglanteria*) to weak electric stimuli. A, Experimental tank used to record the behavioral response of skate embryos to weak sinusoidal uniform electric fields. Embryonic skates encapsulated within the egg case were suspended in a glass tank between two carbon electrodes (E) separated apart by 34 cm and positioned along the longitudinal axis of the egg case. Electric stimuli were delivered to the electrodes by a function generator (FG) and an isolation amplifier (IA). Behavioral responses of the skate embryos were backlit by a continuous weak incandescent light source (L) and recorded by a video camera (V) while the stimulus synch output illuminated a LED for video synchronization. B, Behavioral responses of skate embryos to sinusoidal uniform electric fields at stimulus (ST) frequencies of 10, 1, and 0.02 Hz. Stimuli were applied at an intensity of  $0.56 \mu\text{V cm}^{-1}$  across the longitudinal axis of the skate. The response (R) is expressed as a change in the peak-to-peak (PTP) tail displacement of the skate 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 s. C, Freeze response of skate embryos to weak electric stimuli. Behavioral responses (open diamonds) are shown as a percentage of total ST presentation of 0.02–20 Hz. Note that the peak sensitivity of electrosensory primary afferent neurons (solid dots) for embryonic skates is at 1–2 Hz and is aligned with the freeze response peak of 0.5–1 Hz. (Fig. A–C were modified from Sisneros et al. [55]).

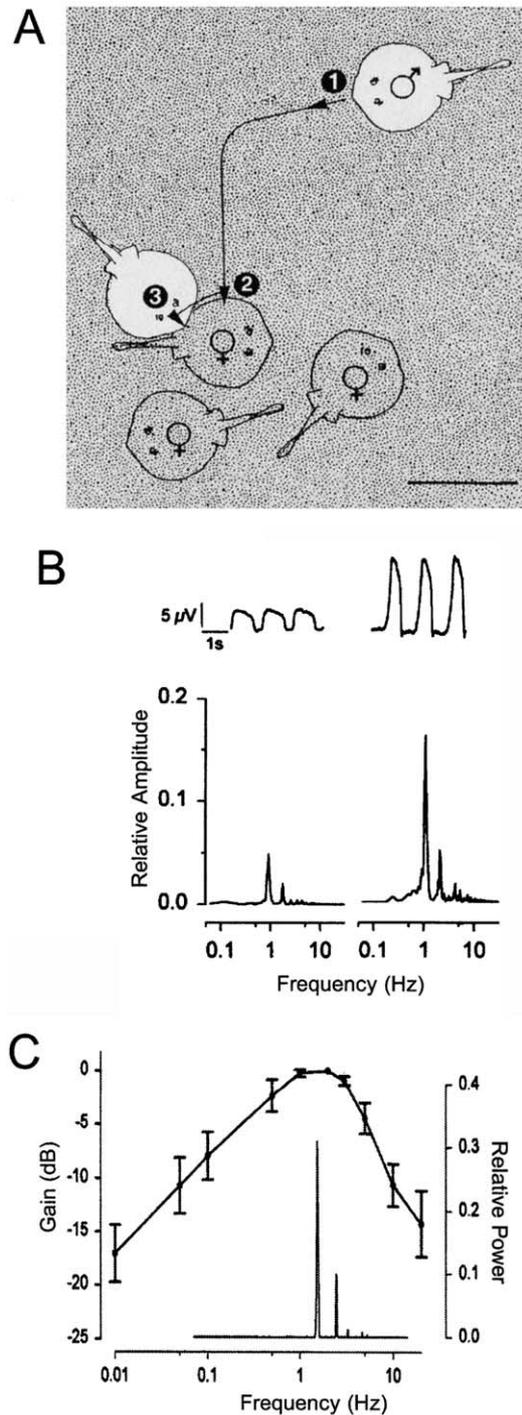


Fig. 5. Conspecific detection behavior, bioelectric stimuli, and frequency response of the peripheral electrosensory system in the round stingray, *Urolophus halleri*. A, Orientation responses by male round stingrays to buried conspecific females during the mating season (January–March) in the clear shallow waters near Bahia Kino, Mexico. Males localize, orient towards, and inspect visually cryptic females buried in the sandy bottom. Search path of the male ray (1) changes abruptly after the detection of and orientation to the buried female. Males inspect buried females near the margins of her body disk (2) and pelvic fins (3). Active courtship and copulation begins after the male excavates the buried female and grasps the female's body disk with his mouth. Scale bar = 25 cm. B, Bioelectric potentials recorded from a female stingray on the dorsal surface above the spiracle (top, left record) and ventral surface at the gill slits (top, right record). The positive field near the spiracle is often fully modulated relative to a reference point far from the ray. The ventral d.c. field is negative, much stronger and often >50% modulated. Recorded potentials are similar for both male (not shown) and female rays. Scales apply to both top records. Bottom graphs are Fourier transforms that show strong frequency components near 1 Hz that result from ventilatory movements. C, Match between the frequency sensitivity of electrosensory primary afferent neurons and the frequency spectrum of the modulated bioelectric waveforms produced by round stingrays. The response dynamics of the electrosensory primary afferents in *U. halleri* show best frequency sensitivity at approximately 1–2 Hz with a 3 dB drop at approximately 0.5 and 4 Hz. Data are plotted as the relative mean discharge peak ( $\pm 1$  SD) for six neurons at ten stimulus frequencies. (Fig. A–C modified from Tricas et al. [65]).

actively searching the area for visually inconspicuous buried females. Upon detection of a female ray, the searching male will abruptly change direction and orient towards the conspecific female and inspect the buried female with his rostrum placed over the margins of her body disk, pelvic fins, or sometimes the snout (Fig. 5A). Active courtship and copulation begins after the male excavates the buried female and grasps the female's pectoral fin with his mouth. Successful copulation occurs when the male pivots underneath the female while biting her pectoral fin, aligns his body in a ventral-to-ventral position, and then rotates his claspers forward and inserts one clasper into the female's cloaca. During copulation, the male will maintain his grasp with his mouth on the female's pectoral fin, usually on the anterior margin, and remain in a ventral-to-ventral position with the female on top of the male. Copulation can last between 1 and 10 min.

Early in the mating season, female rays will often aggregate next to one another in large groups (>20 rays) that contain individuals either completely exposed above the substrate or slightly buried with the body of each female overlapping several others. As the mating season progresses, heavily scared females from previous matings are often found buried by themselves or in smaller groups (<10 rays) near the shoreline in shallow water (<1 m deep). Group burying by females may represent a behavioral strategy for less-receptive females (identified by their multiple mating scars and in some cases missing spines which are often lost fending off persist males) to avoid searching males late in the mating season. Thus, small groups of buried female rays may provide a refuge for less-receptive females and create a "dilution" effect in which the probability that unreceptive female will incur unsolicited courtship and mating by a searching male is related to the inverse of the group size.

#### 4.2. Use of the electric sense for conspecific detection

Both male and female round stingrays in the wild use the electrosense to detect and locate conspecifics during the mating season [65]. The weak bioelectric fields produced by visually cryptic buried females provide the main stimuli for conspecific localization. Both stingray sexes use electroreception in a sex-specific context. Male stingrays use the electric sense to detect and locate conspecific females for mating while females use electroreception to locate and join other non-buried receptive females for mating or join buried less-receptive conspecifics for refuge. Like other fishes, stingrays produce a significant standing d.c. field that is partially modulated by the ventilatory movements of the mouth and gill slits [29,65]. Both the modulated and static portions of the d.c. field can be used by searching rays to locate buried conspecifics. The modulated portion of the stingray's

bioelectric field is an attractive bioelectric cue that varies with the natural ventilatory rate of the animal (~0.25 to 2 Hz) and should be a particularly important signal when the searching ray is at rest near a conspecific (Fig. 5B). The static portion of the dc field can also provide an adequate stimulus because it will appear to vary at low frequency as the stingray electroreceptor system passes through it (sensu Kalmijn [30]). Peak frequency sensitivity of the peripheral electrosensory system in *Urolophus* matches the peak frequency component of the bioelectric fields produced by conspecifics (Fig. 5C) [65]. Thus, the electric sense in the round stingray is an important sensory modality that is "tuned" to social bioelectric stimuli and used in a sex-dependent context for conspecific detection during the mating season.

The use of electroreception for conspecific detection in *U. halleri* has potential benefits for both sexes. For males, electroreception should enhance male reproductive fitness by increasing the probability of mate detection, which should ultimately increase the number of courtships and copulations with females. In contrast, conspecific detection via electroreception by females should allow females less receptive to mating to detect, locate and join buried conspecifics for refuge, especially during the progress of the mating season. In addition to creating a "dilution" effect (see above), groups of buried females may also create a "confusion" effect in which the overlapping bioelectric fields of buried females act to interfere with one another and decrease the ability of a searching male to locate a buried individual in a group. Future field studies that detail the use of electric sense for conspecific detection and examine female aggregation behavior will be needed to determine the potential benefits and trade offs for conspecific group burying by batoid elasmobranchs.

#### 4.3. Hormonal modulation of the electric sense

Recent work shows that in a wild population of Atlantic stingrays (*Dasyatis sabina*) the discharge and frequency response properties of the ampullary electrosensory system in males change with the androgen production cycle [54]. Populations of *D. sabina* exhibit a 9-month protracted mating season from August through April [36] during which male stingrays exhibit distinct reproductive activities associated with varying serum androgen levels [66]. During the primary androgen increase phase of the androgen production cycle, the electrosensory primary afferent neurons in wild male stingrays exhibit an increase in resting discharge regularity, a downshift in best frequency (BF) and band-pass, and a greater sensitivity to low frequency stimuli from 0.01 to 4 Hz (Fig. 6) [54]. Experimental implants of dihydrotestosterone (DHT) in male stingrays confirmed the androgen effect and induced a similar low-

ered BF and bandpass and increased sensitivity (by a factor of 1.5 $\times$ ) to low frequency stimuli from 0.5 to 2 Hz (Fig. 7), which is similar to the natural phasic signals produced by conspecifics [54]. The androgen-induced changes in the frequency response properties of the peripheral electrosensory system in male stingrays may represent an adaptation to seasonally increase the probability of conspecific detection and enhance the

detection of mates as well as the detection of conspecifics, which may be a target of intrasexual aggression during male competition for the access to females. The enhancement of mate detection by males should also ultimately enhance male fitness by increasing the number of male reproductive encounters with females.

The mechanism by which androgens modulate the frequency response properties of the elasmobranch

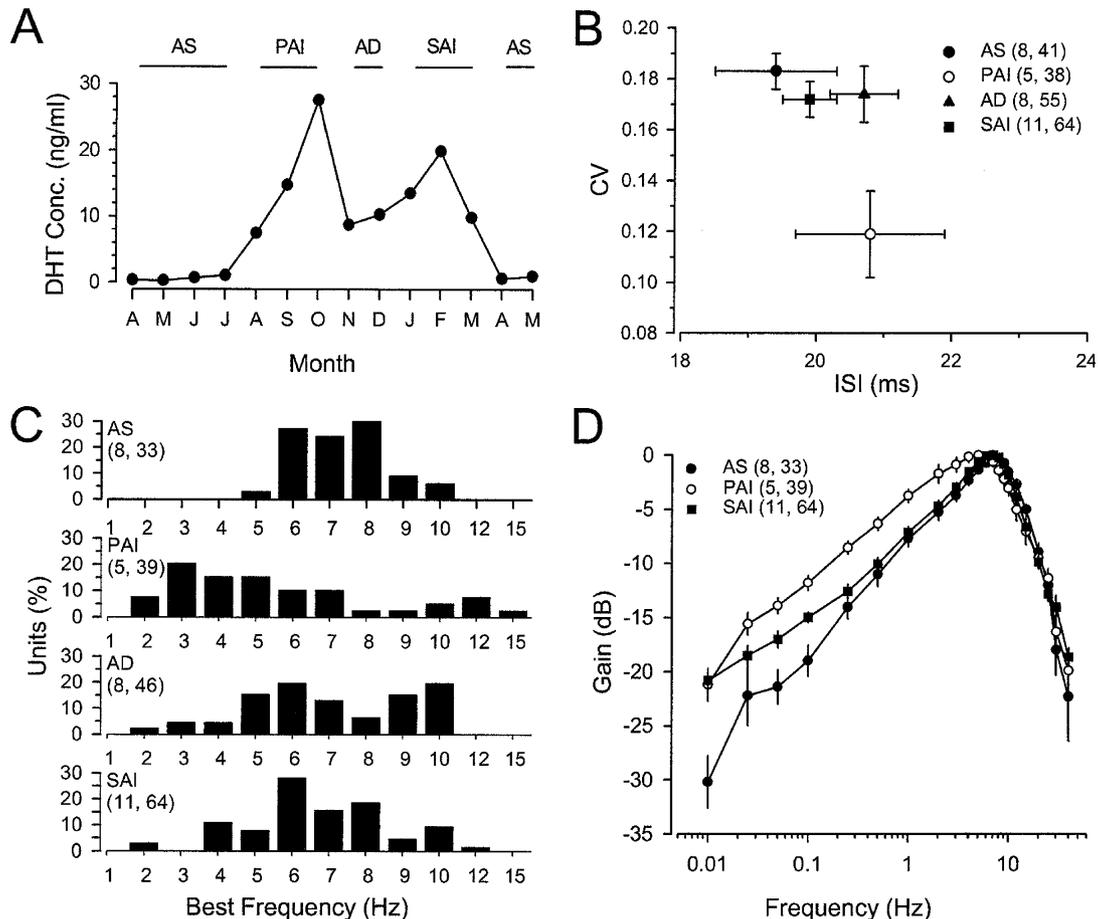


Fig. 6. Annual dihydrotestosterone (DHT) production cycle and response dynamics of ampullary electrosensory primary afferent neurons in male Atlantic stingrays, *Dasyatis sabina*. A, Annual cycle of serum DHT concentrations (median values) in male stingrays collected from the Banana River, FL between April 1993 and May 1994. Serum DHT levels in males show four phases within the annual 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 (PAI), 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). (Modified from Tricas et al. [66]). B, Relationship between resting discharge variability and mean interspike interval for electrosensory primary afferent neurons in wild male stingrays. Rays were collected during AS, PAI, AD, and SAI periods. Discharge variability is expressed as coefficient of variation (CV), a dimensionless ratio of standard deviation to mean interspike interval (ISI). 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  $\pm$  standard error. C, 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. D, 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 and 7–8 Hz 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  $\pm$  1 standard error. Note some standard error bars are obscured by symbols. (Fig. B–D were modified from Sisneros and Tricas [54]).

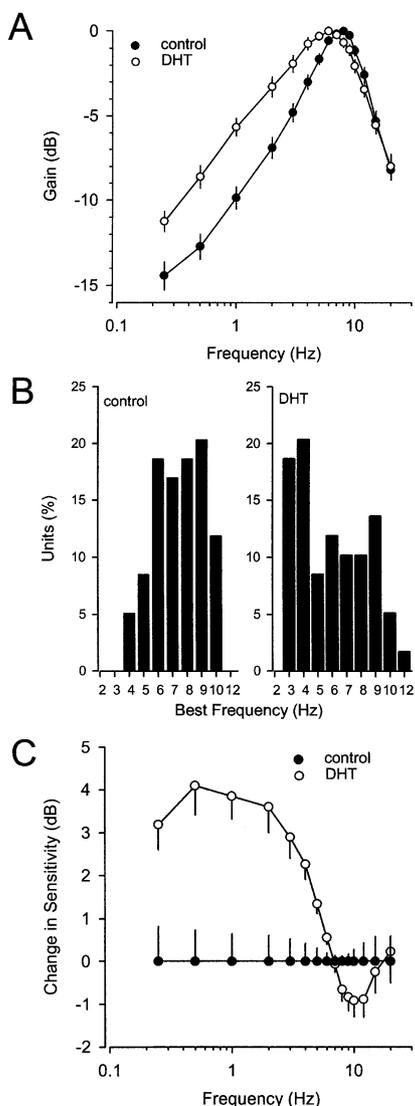


Fig. 7. Frequency response dynamics of ampullary electrosensory primary afferent neurons for control and DHT-treated male Atlantic stingrays, *Dasyatis sabina*. **A**, Bode plot for frequency response of electrosensory primary afferent neurons recorded from male stingrays following control and DHT implants. Peak frequency sensitivity 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 plotted as mean  $\pm 1$  standard error. Note some standard error bars are obscured by symbols. **B**, Best frequency (BF) histogram for electrosensory primary afferent neurons for control and 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 BF's of electrosensory primary afferents in DHT-treated rays. **C**, Frequency response of electrosensory primary afferent neurons between control and DHT-treated male stingrays. Data are normalized relative to the frequency response of electrosensory primary afferents in control rays. All data plotted as mean  $\pm 1$  standard error. Note that the neural response from 0.5–4 Hz in DHT-treated rays is approximately 2–4 dB higher than that in control rays. (Fig. A–C were modified from Sisneros and Tricas [54]).

ampullary electroreceptor system still remains to be demonstrated. Previous studies indicate that steroids can alter the tuning of tuberous electroreceptors and the electromotor properties of the electrosensory system of weakly electric fishes [4–6,19,24,32,38–40]. Recent evidence indicates that the steroid-induced changes in the electromotor system are mediated by steroid receptors within the electrocytes [7,19,20,25]. These steroid receptor mediated changes are thought to result in the genomic differential expression of multiple channel types (e.g., Na<sup>+</sup> and/or K<sup>+</sup>) that regulate the current kinetics of the electrocytes and produce the sexually dimorphic electrocommunication signals in weakly electric fishes. Similarly, the androgen-induced changes in the response properties of the elasmobranch ampullary electroreceptor system might also be mediated by androgen receptors. Unfortunately to date, no study has yet identified the location of steroid receptors in the either the teleost or elasmobranch electroreceptor systems. Thus, future studies that use steroid autoradiography, antibodies against steroid receptors, or oligonucleotide probes directed at the steroid receptor's mRNAs will be needed in order to determine the mechanism of steroid action in electroreceptor systems.

### 5. Summary and conclusions

Recent studies have experimentally demonstrated new uses of the ampullary electroreception in the natural behavior of sharks and rays that can be classified into four major categories (Fig. 8). The first function demonstrated for the shark electroreception was for the detection of weak bioelectric fields produced by living prey. Most if not all sharks and rays may use the electroreception in this context. The use of the electroreception to detect mates was recently demonstrated for non-electrogenic stingrays,

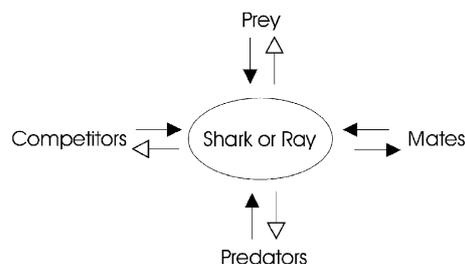


Fig. 8. Biological contexts in which the ampullary electroreception of sharks and rays can mediate natural bioelectric stimuli. The electroreception system was first shown to be sensitive to bioelectric fields produced by prey. Recent work shows that the electroreception can also be used to sense mates and potential predators. The use of the electroreception during competitive interactions with other species is probable. Closed arrowheads show sources of bioelectric stimuli and direction of information transfer. Open arrowheads indicate that the shark or ray could also provide bioelectric signals to the other organism during interactions with prey, predators or competitors that also have an electroreception system (e.g. other elasmobranchs).

and evidence is mounting that the weakly electric skates may use their EOD in social and mating interactions. Because social and mating behavior involves conspecific interactions both sexes likely use their electrosensory systems for this purpose. The electrosensory system of embryonic skates is capable of detecting weak bioelectric fields produced by an approaching predator. The electrosensory system may be used to avoid predation during other life history stages in many elasmobranch species. Finally, other conspecific and heterospecific ecological interactions such as competition over food items may be mediated by the electro-sense. This latter use of the electrosensory system remains to be further studied.

Neurophysiology experiments have revealed that the tuning properties of the electro-sense may change across the life history of a species, and also on a seasonal basis during the reproductive season. These changes in sensitivity are hypothesized to enhance individual fitness, but these adaptations still remain to be experimentally tested. For example, does the downward shift in BF and band pass in male stingray electroreceptors during the reproductive season confer an actual increase in their ability to detect and mate with females? These important questions must be addressed for a complete neuro-ethological analysis of the function of neural systems in the adaptive behavior of these fishes.

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