Environmental Biology of Fishes **60:** 77–92, 2001.

The neuroecology of the elasmobranch electrosensory world: why peripheral morphology shapes behavior

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Received 7 April 2000 Accepted 16 May 2000

Key words: ampullae of Lorenzini, batoid, ecomorphology, electric field, ray, skate, white shark

Synopsis

The adaptations of elasmobranch sensory systems can be studied by linking the morphological structure with the natural behavior and ecology of the organism. This paper presents the first step in a ‘neuroecological’ approach to interpret the spatial arrangement of the electrosensory ampullary organs in elasmobranch fishes. A brief review of the structure and function of the ampullae of Lorenzini is provided for interpretation of the organ system morphology in relation to the detection of dipole and uniform electric fields. The spatial projections of canals from discrete ampullary clusters were determined for the barndoor skate, *Raja laevis*, based upon a published figure in Raschi (1986), and measured directly from the head of the white shark, *Carcharodon carcharias*. The dorsoventrally flattened body of the skate restricts the projections of long canals to the horizontal plane. There is a distinct difference between dorsal and ventral projection patterns in all groups. Notable within-cluster features include a relatively long canal subgroup in the dorsal superficial ophthalmic (SOd) and dorsal hyoid (HYOd) clusters that are oriented parallel (bidirectionally) to the longitudinal axis of the body. It is postulated that this subgroup of canals may be important for detection and orientation to weak uniform fields. Ventral canal projections in the skate are primarily lateral, with the exception of the hyoid (HYOv) that also projects medially. This wide dispersion may function for the detection of prey located below the body and pectoral fins of the skate, and may also be used for orientation behavior. The mandibular canals located near the margin of the lower jaw (of both study species) are ideally positioned for use during prey manipulation or capture, and possibly for interspecific courtship or biting. The head of the white shark, which lacks the hyoid clusters, is ovoid in cross section and thus ampullary canals can project into three-dimensional space. The SOd and superficial ophthalmic ventral (SOv) clusters show strong rostral, dorsal and lateral projection components, whereas the SOv also detects rostral fields under the snout. In the sagittal plane, the SOv and SOd have robust dorsal projections as well as ventral in the SOv. Most notable are canal projections in the white shark buccal (BUC) ampullary cluster, which has a radial turnstile configuration on the ventrolateral side of the snout. The turnstile design and tilt between orthogonal planes indicates the white shark BUC may function in detection of uniform fields, including magnetically induced electric fields that may be used in orientation behaviors. These data can be used in future neuroecology behavioral performance experiments to (1) test for possible specializations of cluster groups to different natural electric stimuli, (2) the possibility of specialized canal subgroups within a cluster, and (3) test several models of navigation that argue for the use of geomagnetically induced electric cues.

Introduction

The 'neuroecology' of elasmobranch sensory systems

Functional morphology is a tool used to study organismal form and function, and provides important information for studies of adaptation, natural selection, and evolution. An outgrowth of functional morphology is the field of ecological morphology, often referred to as 'ecomorphology', which is based on the premise that the morphological design of an organism is associated with its ecology and behavior (see Wainwright & Reilly 1994, Motta et al. 1995). This approach is used widely to test hypotheses on feeding performance, prey selection and the evolution of feeding mechanisms in fishes (Turingan & Wainwright 1993, Westneat 1995, Hernandez & Motta 1997). The ability to link morphology and ecology relies on the identification of a quantifiable behavioral measure of 'performance' for the ecological phenotype such as prey capture success or processing ability. Remarkably, ecomorphology is infrequently applied to the study of sensory systems of fishes (e.g. Hueter 1990, Barry & Hawryshyn 1999). Like the performance measures used in feeding ecomorphology, the performance measures for sensory system ecomorphology can also be linked to feeding success or prey capture. However, since sensory systems are used primarily for pre-capture behaviors such as the detection, localization and capture of prey (rather than post-capture behaviors such as prey handling or processing), the specific performance measures will differ. Thus, the 'neuroecology' approach can be a useful complement to studies of feeding ecomorphology by establishing the constraints imposed by the sensory system morphology on the detection of natural stimuli, and in this manner they can provide new insight on behavioral adaptations.

Early anatomists who described the gross anatomical features of the ampullary organs of elasmobranchs (Stenonis 1664, Lorenzini 1678, Ewart & Mitchell 1891, Lamont 1916) were unaware of its ecological function. The discovery of the ampullary electrosense (Murray 1960, 1962, Dijkgraff & Kalmijn 1966) and its role in predation (Kalmijn 1971) has since given way to many unanswered questions that concern the ecological function and evolution of this extraordinary system. In his seminal work, Raschi (1986) compared anatomical characters of the ampullary system among 40 species of skates collected from a wide range of marine habitats. In those species examined there were more pores on the ventral than dorsal surface with pore density usually greatest around the mouth. In addition, the ampullary pores of piscivorous skates were distributed over a larger area of the body than those feeding upon benthic invertebrates, and the relative density of ventral pores was inversely related to prey mobility. Species that inhabit deep water had larger ampullae than did those in shallow waters, and were suggested to have higher sensitivity. The distribution of skin pores on deep water species may compensate for reduced visual function, and the increased pore density reflects an increased spatial resolution during predation. Such correlations and inferences about the distribution of canal pores among different species provide critical information for interpretation of function, ecology and evolution of the skate electrosense.

Raschi's (op. cit.) important work emphasized ecological associations of different spatial distributions of ampullary pores on the skin, but did not address other important functions such as directional sensitivity. This paper uses the neuroecological approach to interpret the behavioral and ecological functions of the electrosensory complex in the barndoor skate, *Raja laevis*, and white shark, *Carcharodon carcharias*. The fine structure and morphology of the ampullary system is reviewed to show how biologically significant electric fields stimulate the ampulla of Lorenzini. New morphological data are then presented on interspecific and intraspecific differences in the spatial arrangement of ampullary groups. These data are used to propose testable hypotheses on the behavioral and ecological functions of different ampullary groups in multidimensional space, the organization of the brain for information processing, and evolution of the ampullary electrosensory system.

The ampullary electrosensory system

All sharks and rays possess an electrosensory system that consists of subdermal groups of functional sensory units known as the ampullae of Lorenzini. Each functional unit consists of a small ampulla chamber that is formed by small bulbous pouches known as alveoli. A canal about 1 mm wide is attached to the ampulla and leads to the surface of the skin (Figure 1a). A layer of sensory hair cells and pyramidal support cells forms the lining of the alveoli (Waltman 1966). Each sensory hair cell has an apical kinocilium that projects into the lumen of the ampulla chamber (Figure 1b). Receptor and support cells are joined by tight junctions to form a high resistance electrical barrier between the apical and basal surfaces of the sensory epithelium. A double layer of squamous epithelial cells and connective tissue fibers form the canal wall and maintain the high electrical resistance between inner and outer surfaces. Both the ampulla and canal are filled with a high potassium, low-resistivity gel (Murray & Potts 1961, Doyle 1963). This arrangement forms an electrical core conductor such that the ampullary chamber is isopotential with a charge at the skin pore. Primary afferent neurons innervate the receptor cells, and encode stimulus amplitude and frequency data that are sent to the brain (Murray 1962, Montgomery 1984, Tricas & New 1998) (Figure 1c).

In marine species the ampullae are grouped into discrete subdermal clusters in the head (Figure 2) and are

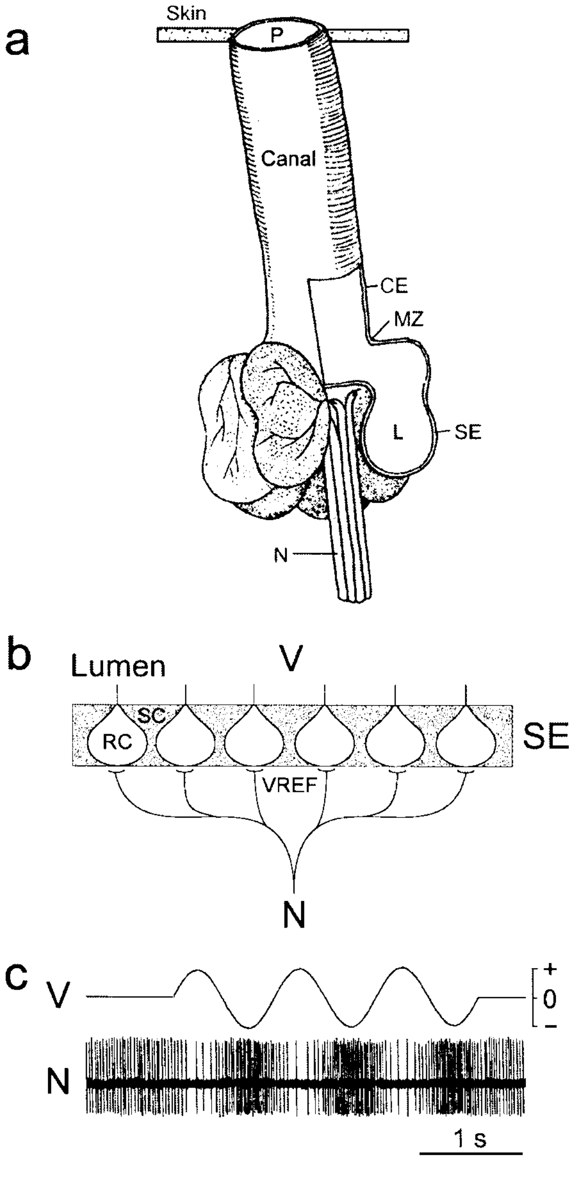

Figure 1. The ampulla of Lorenzini. a – the ampulla of the skate is formed by several alveoli that share a continuous lumen (L) and a subdermal canal that has a single pore on the skin. The sensory epithelium (SE) forms the highly resistive ampulla wall that connects with the canal epithelium (CE) at the marginal zone (MZ). The ampulla and canal are filled with a highly conductive gel. This arrangement forms an electrical 'core conductor' in which the potential within the ampulla lumen is isopotential with that at the surface pore. The sensory epithelium is innervated by primary afferent neurons (N) that conduct electrosensory information to the brain (Modified from Waltman 1966). b – in most elasmobranch species, the sensory epithelium is a layer of receptor cells (RC) and support cells (SC). Tight junctions between these cells 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). c – recording from a single primary afferent neuron shows that the resting discharge pattern is modulated by a varying lumen potential. Cathodal (−) stimuli increase neural discharges, whereas anodal (+) stimuli decrease discharges (modified from Tricas & New 1998).

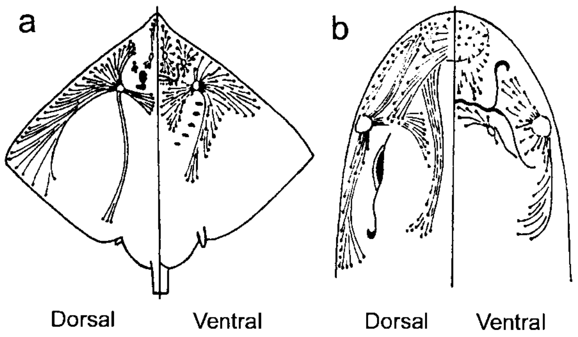

Figure 2. Diagrammatic representation of the horizontal distribution of ampullae of Lorenzini in the skate, *Raja,* and cat shark, *Scyliorhinus*. Ampullae are grouped into clusters in the head and have individual canals of different lengths that radiate in many directions. a – the body of the skate is dorsoventrally flattened, thus canals project primarily within the horizontal plane of the head and pectoral fins. b – the head of the shark is circular or elliptical in cross section, thus most canals in the shark head have projection components in multiple planes (modified from Murray 1960).

innervated by different branches of the anterior lateral line nerve (Norris 1929). Canals usually project in many directions from each cluster and their pores are distributed widely over the surface of the head (and pectoral fins in batoids). The contiguous grouping of individual ampullae into a single cluster results in a common potential at the basal region of all receptors. In contrast, all sensory cells of a single ampulla experience the same apical voltage that varies with the potential at its skin pore (Figure 3). The hair cells act as voltage detectors and release neurotransmitter onto their primary afferent neurons as a function of the difference between their apical (= pore) and basal (= internal) potentials. However, the potentials at surface pores are conserved within their respective ampullae, and the somatotopic distribution of the field is transmitted to the brain via parallel neural channels.

The morphological arrangement of the ampullary canals permits detection of both small local fields produced by biological organisms and large uniform electric fields of inanimate or animate origins (Kalmijn 1974). When a small localized dipole stimulus (such as that of a small prey) is presented at a pore that is far away from its ampulla, the potential is conducted to receptor cells within the ampulla chamber (Figure 3a). In this case, the receptor response is independent of canal length because the small spatial field does not influence the reference potential at the cluster. However, when the animal's body is within a uniform field (or at the fringe of a large dipole field) the body can admit a portion of the field that can influence the internal reference potential (Figure 3b). When the weak uniform electric field is parallel to the canal, the stimulus voltage at the apical surface of receptor cells is determined by the linear separation between the ampulla and its canal pore. Thus, long canals sample across a greater distance within the field and provide a larger potential difference for receptor cells than do ampullae with short canals. In addition, the strongest potential difference occurs when the canal is oriented parallel to the field and decreases as a cosine function as it deviates away from the direction of the field. Therefore, when an omnidirectional ampullary array is within a uniform field, the canals simultaneously sample the external potentials at different points on the body. Theoretically this can provide immediate information about the field's intensity, spatial configuration and possibly the direction of the source.

Laboratory and field studies demonstrate that the electrosense can mediate many natural behaviors of

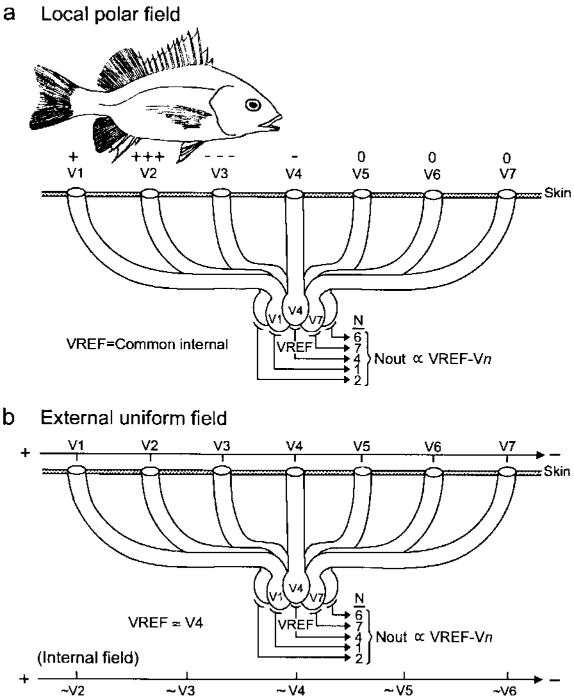

Figure 3. Simplified model for the encoding of extrinsic polar and uniform electric fields by the elasmobranch electrosensory system. a – any living prey produces a weak polar electric field formed by the differential distribution of charges on (or in) the organism. This creates weak potentials (+, −) in the water that surrounds the body of the prey. When the prey approaches, the surface pores of the ampullary system sample the field potentials (Vn) across the surface of the skin. The potentials at each pore are conducted to their individual ampullae and stimulate sensory neurons (N). In this scenario, the voltage gradient from the prey does not influence the common internal reference potential (VREF) at the ampullary cluster (and basal surfaces of receptor cells), and the effective stimulus for all ampullae is represented by the voltage drop across the skin. Neural output for each individual ampulla (Nout) is proportional to the difference between VREF and the voltage at its associated surface pore (Vn). b – when the shark or ray swims within a uniform field the field lines are parallel (and shown here as parallel to the surface of the skin). The body is more resistive than seawater but the relatively low skin resistance admits an only slightly weaker electric field through the body (Kalmijn 1974). The potential within each ampulla is isopotential with that of its pore (Vn), and is referenced to the common potential at the cluster (VREF). In this case, the stimulus within each ampulla is a function of the distance from its pore, i.e. canal length. Neural output for each ampulla (Nout) is also proportional to the difference between VREF and the potential at its associated surface pore (Vn).

rays and sharks. The ampullary receptor system can be used in the detection and capture of prey (Kalmijn 1971, 1982, Tricas 1982, Blonder & Alevizon 1988), the detection of potential predators (Sisneros et al. 1998) and in social behaviors (Tricas et al. 1995, Sisneros et al. 1998). In addition, theoretical models have proposed that geomagnetic induction of electric current could mediate orientation behavior (e.g. Kalmijn 1974, 1978, Paulin 1995). Despite these anatomical, physiological, behavioral and theoretical studies, few have interpreted the spatial arrangement of the ampullary complex in relation to the natural ecology of the animal (sensu Raschi 1986). The interpretation of specific features of the entire ampullary 'system' with the natural stimuli encountered in the wild is critical to understanding the morphological constraints of the electrosensory system, selective pressures, and specializations of different ampullary subsystems.

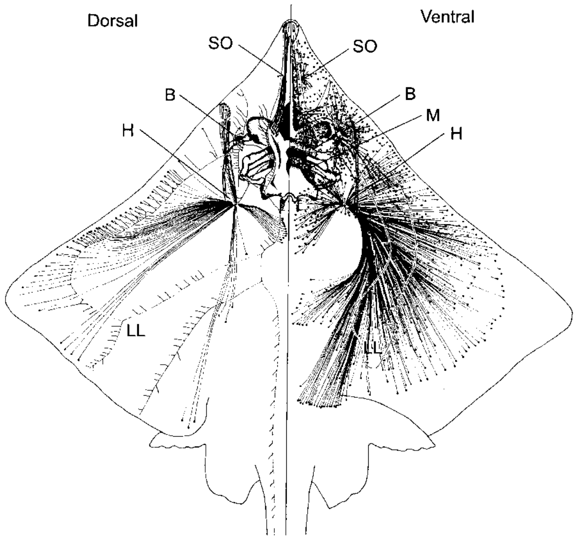

Figure 4. Ampullary clusters and canals on the dorsal and ventral surfaces of the barndoor skate, *Raja laevis*. Clusters indicated by B = buccal, H = hyoid, M = mandibular, SO = superficial ophthalmic. LL = lateral line (modified from Raschi 1986).

Materials and methods

Raja laevis

The two-dimensional spatial orientations of the ampullary canals in the barndoor skate, *Raja laevis*, were measured from the detailed morphological drawings provided by Raschi (1986) (Figure 4). Because of the dorsoventral flattening of the skate body, projection vectors for dorsal and ventral ampullary clusters were calculated only for the horizontal plane. A grid was superimposed over photocopy enlargements of the left dorsal and left ventral surfaces, and aligned with the longitudinal and transverse body axes. The center of the mandibular, buccal, hyoid and superficial ophthalmic clusters were marked as the origin for each canal projection. Angular projections from each cluster (rostral $= 0^\circ$) were measured to the nearest degree with a protractor and followed a counterclockwise rotation as viewed dorsally. The length of each canal was measured as the distance from the center of its cluster to the surface pore. Canal length measurements were converted to absolute values (nearest 1 mm) relative to the mouth width of $9.5\% \times 700$ mm TL $= 67$ mm as indicated by Raschi (1986). The vector angles for the complementary projections for the right side were calculated by subtraction of the measured angles from 360°. Vector data were then plotted in polar and Cartesian coordinates.

Carcharodon carcharias

The three-dimensional spatial orientation of ampullary canals was measured for the head of a juvenile white shark approximately 2.5 m total length. The entire head was fixed in a 4% formaldehyde solution and preserved in 50% isopropanol. The head was then clamped in a rigid stereotactic frame with the tip of the snout and the center of the eyes positioned in the horizontal plane to provide the longitudinal reference axis for the body. The skin was carefully removed on the left side to expose the ampullary canals of the mandibular, buccal and superficial ophthalmic clusters. The x (longitudinal), y (transverse) and z (vertical) coordinates for each surface pore and cluster center were measured with a caliper and ruler to a resolution of 1 mm. The measured coordinates for canals in each cluster were then converted to a common reference for the estimated center of each cluster $(0, 0, 0)$. Data were plotted in polar coordinates. As discussed above, canal length is the major character that determines the sensitivity of an ampullary unit in a uniform field. Furthermore, an ampulla encodes the strongest signal when its canal is oriented parallel to the direction of the uniform field. Therefore, the spatial orientation for each canal was expressed as the vector within the horizontal, transverse and sagittal planes. Vectors for canals were determined

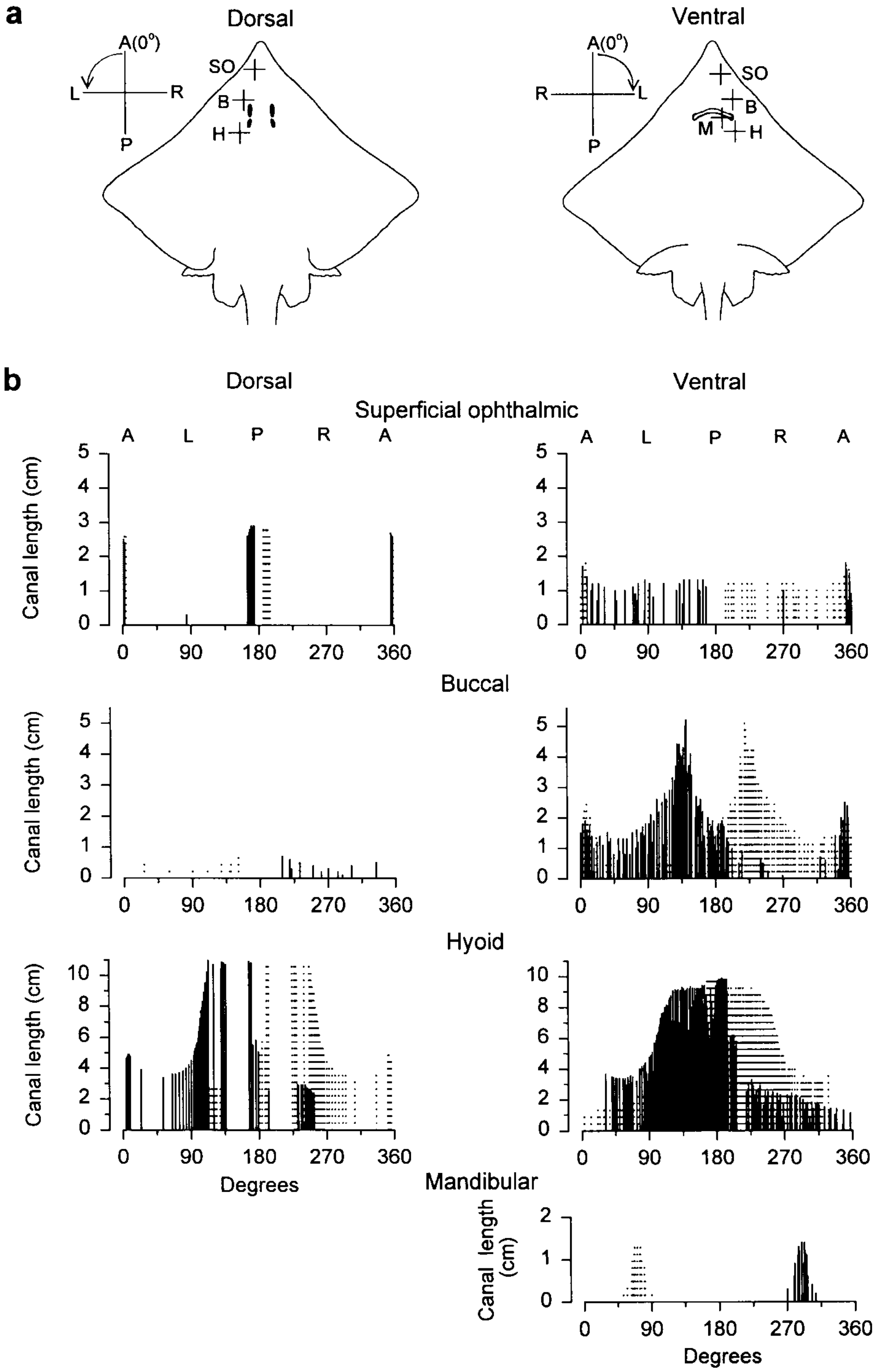

Figure 5. Projection vectors of ampullary canals in the barndoor skate, *Raja laevis*. a – dorsal and ventral locations of the four ampullary clusters on the left side of the body are indicated by crosses. All projections are referenced to 0° for the anterior (A) direction, 90° left (L), 180° posterior (P), and 270° right (R), and follow a left side rotation pattern (B = buccal, H = hyoid, M = mandibular, SO = superficial ophthalmic). b – plot of projection angle and length for individual canals from left (solid lines) and right (dotted lines) cluster pairs

for the three body planes by resolving the absolute coordinates into their respective canal lengths and projection angles. The vector angle for complementary canal projections for the contralateral side was calculated by subtraction of the measured angle from 360° and then adjusted to a 0° reference for rostral in the horizontal and sagittal planes, and a 0° reference for dorsal in the transverse plane. The bilateral distribution of canal vectors for each ampullary group was determined following a common angular rotation and then plotted in Cartesian coordinates. This analysis permits examination of angles of maximum sensitivity, null vectors where no projections occur, and possible sites for common mode rejection of electric field stimuli.

Results

The vector analysis of the ampullary canals provides information on the direction and lengths of ampullary canals in the separate ampullary clusters. The orientation data for each ampullary cluster are all presented relative to the major axes of the body, to allow comparison of relative sensitivities among ampullary groups.

The skate

The canal projections in *R. laevis* from the four discrete pairs of ampullary clusters can be reduced to the horizontal plane because of the dorsoventrally flattened body. The superficial ophthalmic (SO), buccal (BUC) and hyoid (HYO) clusters have canal projections to both the dorsal and ventral surfaces. These are subdivided into dorsal and ventral subgroups for analysis. The mandibular (MAN) projections are all concentrated on the lower jaw near the mouth.

The SO ampullary cluster is the most rostral and is located just anterior to the nasal capsule at the edge of the rostral cartilage (Figure 4,5a). Posterior to SO is the BUC cluster (= outer buccal of Raschi 1986) which is located lateral to the nasal capsule and anterior to the antorbital cartilage. The large HYO cluster is located immediately behind the hyomandibular cartilage and rostral to the branchial chambers.

There are major differences in dorsal projection patterns among clusters. The canals of the superficial ophthalmic dorsal cluster (SOd) are of approximately uniform length and have a pronounced longitudinal alignment in rostral and caudal projection groups (Figure 5b). This is in contrast to the buccal dorsal (BUCd) cluster, which has very short and medially directed canals. The canals of the dorsal hyoid (HYOd) group form a broad cruciform pattern and covers a wide area of the head and pectoral fins. The HYOd cluster also has seven canals that make a distinct caudal projection near 180°. These form two pore groups located near and approximately half the distance to the tip of the caudal disk margin. This is complemented by about 10 canals that project rostrally near 0° to the rostral margin of the disk. The lateral canals of the HYOd are the most abundant group and span an arc of about 45° around the tip of the pectoral fin. The ampullary pores along the anterior margin of the pectoral disk are positioned close to pores of the mechanosensory lateral line. A medial HYOd projection is formed by a group of the 12 shortest canals, which terminate in pores near the dorsal midline.

The ventral pores in *R. laevis* are more numerous than the dorsal surface, have a more profuse and omnidirectional projection pattern, and show distinct projection patterns among cluster groups (Table 1). The ventral superficial ophthalmic (SOv) canals are relatively uniform in length with widely spaced lateral

Table 1. Distribution of ampullae of Lorenzini within clusters in the barndoor skate, *Raja laevis*, and white shark, *Carcharodon carcharias*. Values indicate number of projections for a single ampullary cluster. BUCd = dorsal buccal, BUCv = ventral buccal, HYOd = dorsal hyoid, HYOv = ventral hyoid, MAN = mandibular, SOd = dorsal superficial ophthalmic, SOv = ventral superficial ophthalmic. In the white shark there is no hyoid cluster. Also, the white shark BUC is not divided into separate dorsal and ventral groups, thus total number of canals are given as BUCd. Canal numbers for *R. laevis* are estimated as counts taken from Figure 3 in Raschi (1986). np = not present.

Cluster	*Raja laevis*	*Carcharodon carcharias*
SOd	16	98
SOv	43	159
BUCd	12	33
BUCv	191	np
HYOd	66	np
HYOv	353	np
MAN	24	13

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on the dorsal and ventral surfaces of the body. The direction of projections as well as canal lengths differ greatly both among clusters and between dorsal and ventral surfaces. There is no mandibular projection to the dorsal surface. Note that plots for ventral canals are referenced to a dorsal view and angle rotation.

projections (Figure 5b). The ventral buccal (BUCv) canals also project in a broad lateral distribution but at a higher density than SOv. In addition, the BUCv shows longer canals (and higher sensitivity to uniform fields) in the posterior lateral quadrants at 135° and 215°. The most rostral canals of the ventral hyoid (HYOv) start their projection at about 45° from the midline and increase in length by more than 2-fold as they approach and pass the tip of the pectoral fin. The longest HYOv canals project caudally and share common projection angles with shorter canals. There is a prominent HYOv caudal subgroup made of approximately 20 canals with projections near 180° that extends to the posterior margin of the disk. Much shorter canals project rostrally and medially towards the snout to complete the nearly omnidirectional canal radiation pattern of the HYOv. The mandibular (MAN) ampullae arise from clusters located on the ventral surface of the lower jaw and have very short projections along the margin of the lower jaw.

The white shark

Unlike the dorsoventrally flattened batoids, the head of most sharks is cylindrical or ovoid in cross section, thus most canals of individual ampullary clusters show projection components in at least two planes. These vectors in *C. carcharias* are resolved into three planes in order to compare the relative sensitivity and directionality of individual ampullary clusters to uniform fields. The SO cluster shows a separation into dorsal and ventral projections, and therefore is subdivided into superficial ophthalmic dorsal (SOd) and superficial ophthalmic ventral (SOv) groups.

The SO cluster is positioned approximately midway between the eye and the tip of the snout, with the SOd ampullae dorsal to those of the SOv. The polar plot of the SOd ampullary pores shows a strong rostral, lateral and dorsal projection (Figure 6a). This cluster contains the longest canals (4–4.5 cm) that project rostrally and form a small group of skin pores just lateral to the tip of the snout (Figure 6b). The remaining canals project more laterally but not medially. In the sagittal plane, the canals project back towards the eye and follow the slope of the head to the tip of the snout. In the transverse plane the dorsolateral component is seen. This arrangement indicates a predominately rostral and dorsolateral sensitivity for the SOd that is aligned with a portion of the forward and lateral visual field.

The SOv cluster is located below the SOd (Figure 7a), and like its dorsal counterpart shows strong rostral and dorsal projections. As seen in the horizontal plane, these follow the lateral margin of the snout in front of the eye (Figure 7b) and a small area on the ventral surface of the snout. Canals in the sagittal plane project omnidirectionally, with the exception of the ventrocaudal quadrant because of the position of olfactory nares.

The BUC cluster is located near the ventral surface of the snout, behind the nares, rostral to the eye and dorsal to the upper jaw (Figure 8a). The canals of this cluster project in an unique omnidirectional 'turnstile' pattern that is situated on the ventrolateral surface of the snout. The longest BUC canals are about 4 cm long and project along a rostromedial-posterolateral line as seen in the horizontal plane (Figures 8a,b). A strong downward-directed vertical sagittal plane. In the transverse plane, the major projections are dorsolateral and ventromedial. This 'turnstile' arrangement and alignment at about 45° between the sagittal-horizontal planes and also the sagittal-transverse planes indicates that the BUC cluster may be sensitive to uniform fields in more than one direction.

The MAN cluster is located beneath the lower jaw near the corner of the mouth and consists of only 13 canals in our specimen (Figure 9a). Canals project rostrally and dorsally along the margin of the lower jaw up to about 3 cm from the center of the cluster (Figure 9b). This spatial arrangement is consistent with detection of electric stimuli near the lower jaw.

Discussion

The neuroecology of the skate electrosensory system

Living elasmobranch fishes are represented by more than 800 species, of which approximately 240 species are skates (McEachran & Miyake 1990). The body form and spatial arrangement of the ampullary system of these fishes set important functional constraints on the detection of natural electric stimuli. The dorsoventral compression of the body in batoids restricts the distribution of ampullary pores to the dorsal and ventral surfaces. In addition, the projections of long canals from ampullary clusters are essentially compressed in the horizontal plane. Thus the skates and rays can detect

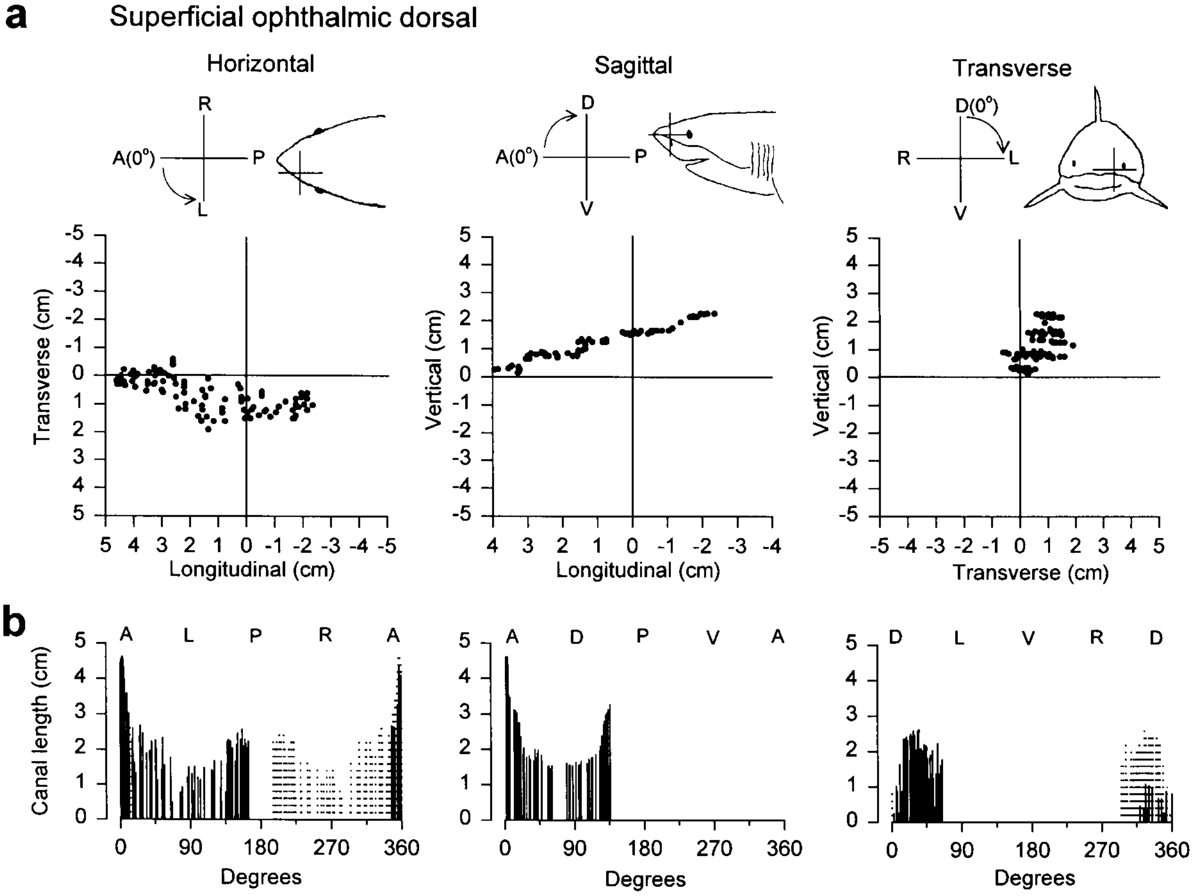

Figure 6. Projection vectors of the dorsal superficial ophthalmic ampullary group in the white shark, *Carcharodon carcharias*: a – polar coordinates for projections of the left ampullary cluster in horizontal, sagittal and transverse planes. Start of rotation (0°) is anterior for horizontal and sagittal planes, and dorsal in transverse plane. All projections are referenced to a rotation direction indicated by arrow. b – plots of projections for individual canals in horizontal, sagittal and transverse planes. Projection vectors are shown for both left (solid lines) and right (dotted lines) ampullary clusters. Note that the vertical projections are identical in the sagittal plane. Also, there are prominent rostral, dorsal and lateral projections in this group (A = anterior, D = dorsal, L = left, P = posterior, R = right, V = ventral).

small dipole fields, and are most sensitive to the horizontal components of uniform fields. Like their batoid relatives, the ampullary pores of most sharks are distributed over the surface of the head and can also detect small external polar fields such as those produced by prey. However, the head of most sharks is conical or slightly dorsoventrally flattened. As a result, ampullary canals can project omnidirectionally from clusters into three-dimensional space rather than only the horizontal plane. This complex spatial arrangement provides a potential sensitivity for a single canal to components of external uniform fields within three orthogonal planes.

One of the primary functions of the skate electrosensory system is to detect and locate bioelectric fields produced by their prey. Skates have a benthic lifestyle, a broad depth distribution and feed on a wide variety of prey primarily by a suction-grasping action of the mouth (Moss 1977). Raschi (1986) compared the ampullae of Lorenzini among 40 species of skates and showed that there were more pores on the ventral surface of the body, a feature related to their benthic feeding habits. In species that fed primarily upon benthic invertebrates, the ventral pores were more concentrated around the mouth and ventral pore density (not necessarily number of pores) was greater. Skates that fed upon more mobile fish prey had a large body size and lower pore density. The higher density of pores on the ventral surface of benthic invertebrate feeders

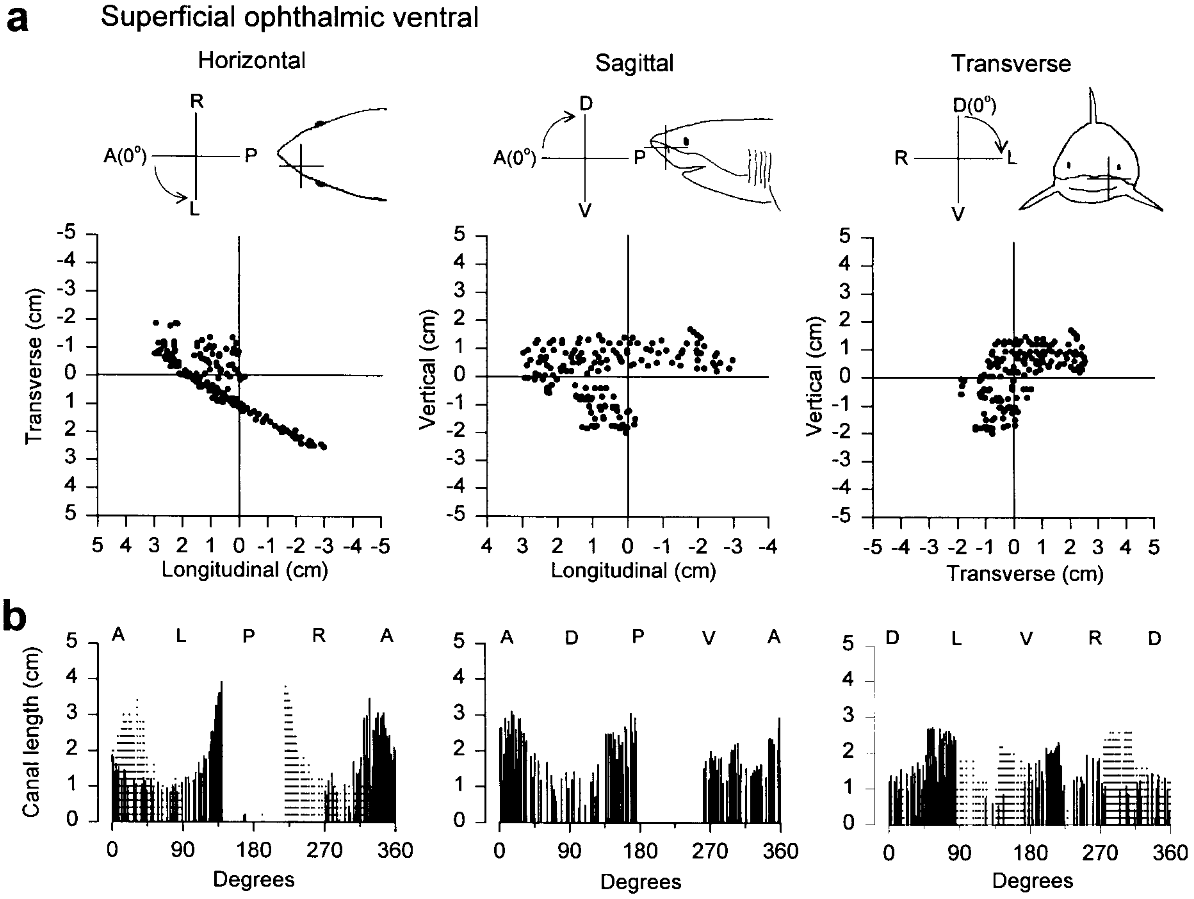

Figure 7. Projection vectors of the ventral superficial ophthalmic ampullary group in the white shark, *Carcharodon carcharias*: a – polar coordinates for projections of the left ampullary cluster in horizontal, sagittal and transverse planes. Start of rotation (0°) is anterior for horizontal and sagittal planes, and dorsal in transverse plane. All projections are referenced to a rotation direction indicated by arrow. b – plots of projections for individual canals in horizontal, sagittal and transverse planes. Projection vectors are shown for both left (solid lines) and right (dotted lines) ampullary clusters. Note that the vertical projections are identical in the sagittal plane. Also, there are prominent rostral and lateral projections in this group, and a near absence of projections due to the presence of the olfactory nares behind and below this cluster (A = anterior, D = dorsal, L = left, P = posterior, R = right, V = ventral).

provides a greater resolution for locating, manipulating and ingesting invertebrate prey that are excavated from the substrate.

The analysis of canal projection vectors for *Raja laevis* in this study provides further insight into biological functions of the skate electrosense. When a small prey field is presented at a canal pore and is small enough to not influence the reference potential at the basal region of the ampulla, sensitivity is independent of canal length. Thus ampullae with either long or short canals can provide information on the location of small prey relative to the surface of the skin. On the ventral surface of *R. laevis* the bilateral pairs of all ampullary clusters form an omnidirectional projection pattern (Figure 5) and pores cover a high proportion of the ventral body surface. This distribution would provide an excellent somatotopic map of small dipole fields near the skin surface.

In addition to bioelectric fields produced by prey, the ampullae can detect larger fields such as those produced by predators or conspecifics that are not positioned beneath the body. Weak standing bioelectric fields such as those that are produced by buried conspecific stingrays (Tricas et al. 1995) can stimulate electroreceptors from a distance, guide swimming movement towards the source and ultimately influence

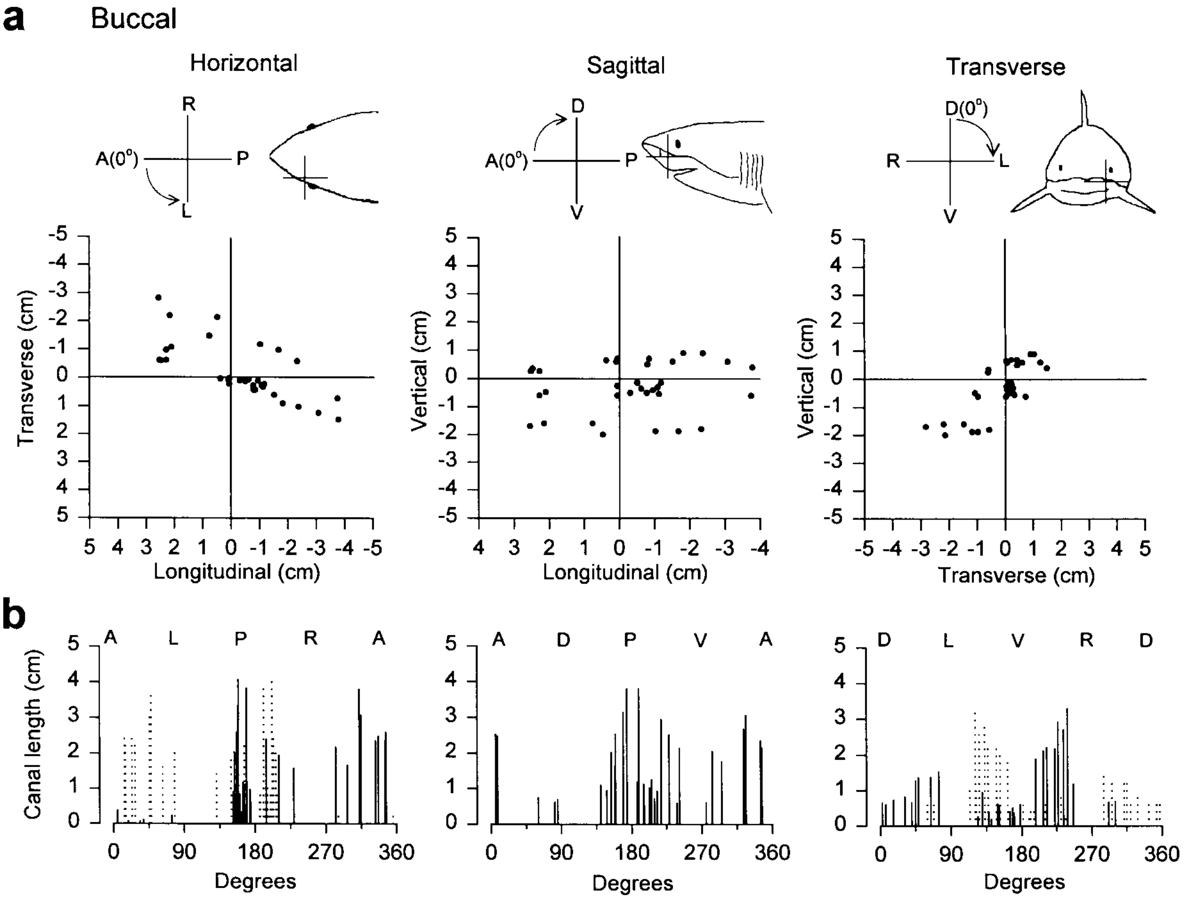

Figure 8. Projection vectors of the buccal ampullary group in the white shark, *Carcharodon carcharias*: a – polar coordinates for projections of the left ampullary cluster in horizontal, sagittal and transverse planes. Start of rotation (0°) is rostral for horizontal and sagittal planes, and dorsal in transverse plane. b – plots of projections for individual canals in horizontal, sagittal and transverse planes. Projection vectors are shown for both left (solid lines) and right (dotted lines) ampullary clusters. Note that the vertical projections are identical in the sagittal plane. The canal projections from this cluster project in a radial ‘turnstile’ pattern that follows the ventrolateral surface of the snout (A = anterior, D = dorsal, L = left, P = posterior, R = right, V = ventral).

both the voltage at the skin pore and the reference voltage at the ampulla. The voltage drop across the length of multiple canals could provide good directional information about the precise location of the source. In *R. laevis* a sensitivity bias based upon canal length is seen in the posterior quadrants of the BUCv and HYOv, whereas the SOv ampullae are approximately equally sensitive in the lateral direction. On the dorsal surface of *R. laevis* the SO canals are aligned with the longitudinal body axis and may provide an excellent sensory channel for orientation behavior. A similar longitudinal (and lateral) directionality exists in the HYOd group. The short medial projections of the BUCd canals indicates they may best detect strong fields above the body and between the eyes, probably when the animal is close to the source. The weakly electric organ found in the skates may serve important communication functions during social interactions (Bratton & Ayers 1987, Sisneros et al. 1998). The subgroup of the BUC could mediate inspection or approach behaviors towards the tail of a discharging conspecific. Mapping of the spatial configuration and strengths of these active discharges are needed to interpret the possible co-evolution of the electrosensory and electrogenic organ communication systems. In addition, ethological analyses of orientation behavior used in natural social settings are needed to determine any special functions for ampullary subgroups.

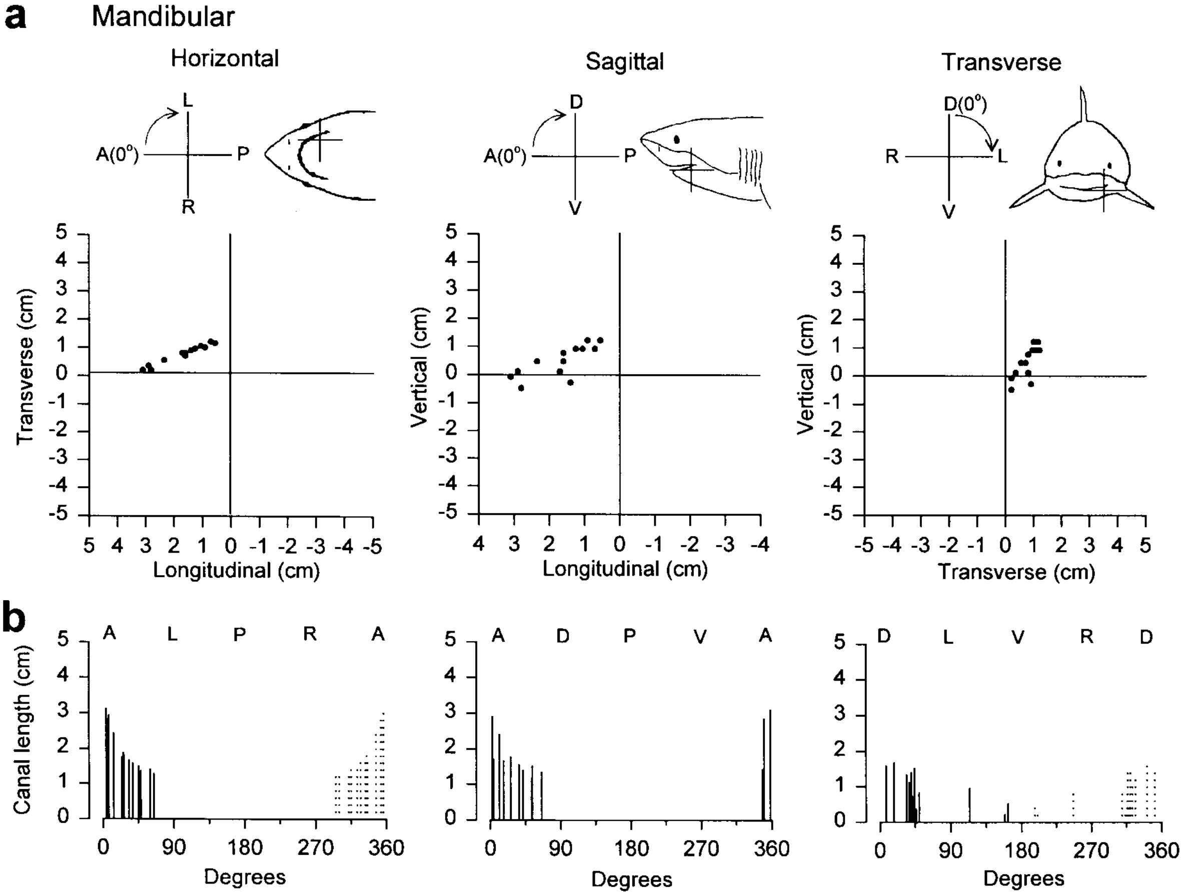

Figure 9. Projection vectors of the mandibular ampullary group in the white shark, *Carcharodon carcharias*: a – polar coordinates for projections of the left ampullary cluster in horizontal, sagittal and transverse planes. Start of rotation (0°) is rostral for horizontal and sagittal planes, and dorsal in transverse plane. b – plot of projections for individual canals in horizontal, sagittal and transverse planes. Projection vectors are shown for both left (solid lines) and right (broken lines) ampullary clusters. Note that the vertical projections are identical in the sagittal plane. These canals project along the margin of the lower jaw (A = anterior, D = dorsal, L = left, P = posterior, R = right, V = ventral).

The features of canal length and projection angle are also important when the animal encounters externally generated uniform fields. Kalmijn (1974, 1984) proposed the 'passive mode' model in which a horizontal electric field is induced by the movement of surface waters through the vertical component of the earth's magnetic field. With this system, charges of opposite polarity accumulate along the sides of a drifting shark and stimulate the ampullae. The restriction of ampullary subsystems to the horizontal plane in the skate could make an excellent comparator of charges across the body under such conditions. Differences in charge strength among the rostrally and caudally directed canals in the SOd and HYOd could sum at higher processing centers and serve as null detectors to indicate an orientation perpendicular to the flow of the stream. Alternatively, the two opposite inputs could be maximized for orientation parallel to the stream flow.

The 'active mode' model (Kalmijn 1974, 1984) proposes that a vertical electromotive field is induced as a shark swims through the horizontal component of the earth's magnetic field in an east or west direction. This results in a differential distribution of positive and negative charges on the dorsal and ventral surfaces of the body. The lack of vertically directed ampullary canals in the skate would not permit efficient detection of electric field gradients, but the charge stimuli on the two surfaces would be of opposite polarity and intensity would vary as a function of swimming speed and direction. Like the passive mode model, the ampullary groups responsible for detection of either of these stimuli would require specific organizations of the neural network in the brain. The somatotopic arrangement of ampullary clusters are conserved in the input pathways to the brainstem (e.g. Bodznick & Schmidt 1984), but the details of neural connectivity to support these models remain to be identified.

The neuroecology of the white shark electrosensory system

The barndoor skate and white shark share similar ampullary systems (white sharks lack the hyoid group) but differ greatly in body form, habitats and life style. The white shark is widely distributed in temperate coastal waters of the world. Adults are a major predator of marine mammals, especially pinnipeds (Le Boeuf et al. 1982, Ainley et al. 1985) and cetaceans (reviewed by Long & Jones 1996). Many studies have documented adult attack behavior on pinnipeds that are at rest on the surface as involving a visually-mediated search behavior followed by a rapid ambush attack from below (Tricas & McCosker 1984, McCosker 1985, Klimley et al. 1996). Just before the rapid attack, the eyes are rolled back into the orbit to reduce injury and the animal is momentarily without visual input. The electrosensory system was postulated to possibly provide information on the location of the prey during the final moments of the attack, during post-attack manipulation or pursuit of prey, or to detect changes in the disposition of the prey such as bleeding (Tricas & McCosker 1984). Many of the SO pores on the dorsal, ventral and lateral regions of the head and snout are within the visual field. Their position and concentration in this region would provide good spatial resolution for detection and tracking of a nearby prey at night, when the eyes are closed or the prey is beneath the snout. In comparison, juvenile white sharks feed primarily upon small bottom dwelling elasmobranchs and bony fishes (Tricas & McCosker 1984). White sharks are known to routinely swim near the bottom (e.g. Strong et al. 1986) and may use their SOv ampullary system to detect visually cryptic prey such as the cabezon, *Scorpaenichthys marmoratus*, that is associated with rocky inshore and kelp habitats (Limbaugh 1963). In this case the long anterior projecting canals of the SOd and SOv could detect these prey as the shark's snout passes over them.

The white shark ampullary system would also be well adapted to detect extrinsic and self-generated uniform fields. Orientations to horizontally induced fields in the passive mode (see above) could be mediated by some of the BUC or SO ampullae, most notably the laterally projecting SOv canals. In the active mode, the upward projecting SOd canals could encode the polarity and magnitude of weak charges on the dorsal surface of the head, as could components of the SOv. Most notable is the BUC cluster which sends radial projections that lay on the sloped ventral surface of the snout. The round shape of the snout tilts the BUC turnstile approximately midway between the sagittal and horizontal planes, whereas the pointed snout rotates the BUC toward the tip of the snout. This dual tilt feature theoretically makes the ampullae in the BUC equally sensitive to vertical, horizontal or oblique fields. Thus, if the SO or BUC function in detection of uniform fields, it is predicted that the neural circuitry to encode them should differ among clusters because of their different spatial organization.

Paulin (1995) proposed a model for geomagnetic induced orientation in sharks that integrates input from the vestibular labyrinths with changes in the induced voltages on the head during lateral swimming motion. Similar to Kalmijn's active mode, the induced vertical fields could be detected by the SOd, SOv, and/or BUC canals with vertical projection components. More work is clearly needed to verify the encoding of horizontal and vertical uniform fields by individual ampullary groups. In addition, there must be specific central processing pathways for encoding such information, and these remain to be characterized.

This paper has presented the first step of a neuroecological analysis, which is a detailed description of the spatial organization of the canals from different ampullary groups. In the discussion above numerous proposals were made as to how different ampulla groups and subgroups could function in the life of the skate and white shark. The next step is to identify biological contexts in which the system operates such as feeding, magnetic orientation, or the detection of mates or predators. An appropriate performance measure, such as distance of orientation from prey, can be chosen and experimental tests performed to demonstrate differences in performance within or among species.

Future direction

As outlined in the discussion, there exists numerous hypotheses on the function of the elasmobranch electrosensory system in natural settings. However, there are only a few studies that have attempted to test these models. Suggestions for future work with a 'neuroecology' emphasis are described below.

The stimulus specialization hypothesis

An efficient electrosensory system can enhance fitness in many biological contexts. This implies that selection may exist for a particular spatial configuration of the ampullary receiver system. For example, in order to determine how a sensory system imparts selective advantages during feeding, it is first critical to determine the prey species that make up the diet set. Live prey could then be brought into the laboratory and the spatial and intensity maps of their bioelectric fields constructed as done initially by Kalmijn (1974). These bioelectric configurations can be used to assess whether they differ enough so that elasmobranchs could use electric signatures to discriminate between prey species. A similar approach could be used to answer questions on electrosensory function in social behaviors or predator avoidance. Information about the spatial arrangement and intensity of these biologically important fields can be compared to the spatial features of ampullary clusters so that possible evolution of the ampullary receiver system to specific signals can be inferred and tested.

The functional subunit hypothesis

A broad range of theoretical and experimentally demonstrated functions for the electrosensory system are known, but there is almost no information on how the ampullary system may be subdivided for different behavioral functions. Anatomical studies clearly show differences in sizes, locations, pore distributions and projection patterns among elasmobranch species (Chu & Wen 1979). For example, the superficial ophthalmic cluster of the barndoor skate has a small but prominent number of long canals that are aligned with the main body axis. Do these form a functional subunit that serves a specific function such as orientation to horizontal uniform fields? Experimental studies where subunits are manipulated and the effects on behavior recorded can be conducted to address these questions. Differences in behavioral function can be confirmed by identifying different projection patterns of neurons from such subgroups.

Geomagnetic induction orientation hypotheses

There are currently a number of models which propose that elasmobranch fishes can use the ampullary electrosense to detect induced fields derived from the earth's magnetic field (Kalmijn 1974, 1984, 1997, Paulin 1995). Extensive field work has shown that sharks in open waters can make large scale directed movements in the absence of visual bottom landmarks (Sciarrotta & Nelson 1977, Carey & Scharrold 1990, Klimley 1993). However, well-designed, replicated and reviewed experiments are needed to demonstrate that these theories actually model what elasmobranchs do in the field. New technologies for in situ monitoring, recording and transmitting information about ambient electric fields and associated movements of the animal will make this possible. Furthermore, technical advances in the monitoring of sensory processing pathways in the brain of behaving animals are needed. Such field studies are a critical complement to laboratory studies in which the animal is isolated in the lab and specific variables are manipulated.

Acknowledgements

I thank Brook Swanson and Russ Brodie for their assistance in data collection, Mike Thursby for his discussions on antenna theory, David Bodznick and John New for their reading of the manuscript, and John Montgomery and Mike Paulin for discussion on biological matters. I also thank Ralph Turingan, Phil Motta and Peter Wainwright for their comments and annual thumping of ecomorphology at the F.I.S.H. meetings. This work is dedicated to the memory of Don Nelson who mentored me to doubt the obvious, swam by me in the face of danger and introduced me to bullshot.

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