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Electroreception in Elasmobranchs: Sawfish as a Case Study

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Key Words

Electroreception · Ampullae of Lorenzini · Elasmobranchs · Sawfish · Shark

Abstract

The ampullae of Lorenzini are the electroreceptors of elasmobranchs. Ampullary pores located in the elasmobranch skin are each connected to a gel-filled canal that ends in an ampullary bulb, in which the sensory epithelium is located. Each ampulla functions as an independent receptor that measures the potential difference between the ampullary pore opening and the body interior. In the elasmobranch head, the ampullary bulbs of different ampullae are aggregated in 3–6 bilaterally symmetric clusters, which can be surrounded by a connective tissue capsule. Each cluster is innervated by one branch of the anterior lateral line nerve (ALLN). Only the dorsal root of the ALLN carries electrosensory fibers, which terminate in the dorsal octavo-lateral nucleus (DON) of the medulla. Each ampullary cluster projects into a distinctive area in the central zone of the DON, where projection areas are somatotopically arranged. Sharks and rays can possess thousands of ampullae. Amongst other functions, the use of electroreception during prey localization is well documented. The distribution of ampullary pores in the skin of elasmobranchs is influenced by both the phylogeny and ecology of a species. Pores are grouped in distinct pore fields, which remain recognizable amongst related taxa. However, the density of pores within a pore field, which determines the electroreceptive resolution, is influenced by the ecology of a species. Here, I compare the pore counts per pore field between rhinobatids (shovelnose rays) and pristids (sawfish). In both groups, the number of ampullary pores on the ventral side of the rostrum is similar, even though the pristid rostrum can comprise about 20% of the total length. Ampullary pore numbers in pristids are increased on the upper side of the rostrum, which can be related to a feeding strategy that targets free-swimming prey in the water column. Shovelnose rays pin their prey onto the substrate with their disk, while repositioning their mouth for ingestion and thus possess large numbers of pores ventrally around the mouth and in the area between the gills.

Introduction

Electroreception is a sensory modality that is present in early vertebrates, including Agnatha, Chondrichthyes, Sarcopterygii, early Actinopterygii, and three orders of Teleostei [Bullock et al., 1982, 1983]. It is also present in some Amphibia and Monotremata [Bullock et al., 1983; Fjällbrant et al., 1998]. It is probably the only major vertebrate sensory system that evolved more than once, as it

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evolved in early fishes and was subsequently lost in early actinopterygians and re-evolved twice in teleosts [Bullock et al., 1982, 1983; Bodznick and Boord, 1986; Collin and Whitehead, 2004]. Electroreceptive structures can be divided into tuberous and ampullary systems. Tuberous structures exist only in two teleost taxa, the Mormyriformes and the Gymnotiformes. Both teleosts and non-teleosts possess ampullary systems of different morphologies. Teleost ampullary organs are morphologically more diverse than those of non-teleosts [Szabo, 1974]. All ampullary structures possess a jelly-filled canal that connects the sensory structure with a somatic pore.

The ampullae of Lorenzini are the electroreceptors of the Chondrichthyes, non-teleosts (Petromyzontiformes, Dipneusti, Crossopterygii, Polypteriformes, Chondrostei), and some amphibians (Urodelea and Apoda). These ampullary structures differ from the general teleost *bauplan* insofar as the receptor cells of the sensory epithelia possess kinocilia [Waltman, 1966; Bullock et al., 1983; Wueringer et al., 2009]. Moreover, the preferred stimulus polarity of ampullae of Lorenzini differs from that of other ampullary organs, and thus all ampullae of Lorenzini are considered homologous [Bennett and Clusin, 1978].

Historically, the identification of the electroreceptive role of the ampullae of Lorenzini in elasmobranchs required the combination of various biological disciplines. Ampullary pores and canals were first described in the 17th century, and they were thought to be mucus-producing organs [Raschi, 1984]. Sand [1938] reported that ampullae respond to changes in temperature as small as a tenth of a degree, by altering the spontaneous resting discharge in both directions according to temperature changes. Hensel [1955] confirmed this and stressed the anatomical similarity with mammalian thermoreceptors. Murray [1960] revealed the ampullae to be mechanoreceptive, but later doubted this, as they were less sensitive than receptors of the lateral line. Murray [1962] showed that changes in salinity and electric currents cause alterations in the resting discharge of the organ. However, when Dijkgraaf and Kalmijn [1963] described behavioral responses of elasmobranchs to weak electric fields, which were lost after denervation of the ampullae, it became clear that the ampullae of Lorenzini were electroreceptors. Three hundred years after the first description of the ampullae of Lorenzini, Kalmijn [1966] demonstrated for the first time that sharks were capable of detecting the bioelectric fields of prey in the absence of any other sensory cues.

The present review will focus solely on the ampullae of Lorenzini and electroreception in elasmobranchs, which comprise all sharks, skates, and rays. The proposed function of the ampullae of Lorenzini as magnetoreceptors [Kalmijn, 1978] is beyond the scope of this review.

Fine Structure of the Ampullae of Lorenzini

Elasmobranchs can possess thousands of ampullae, but each ampulla is an independent organ that can detect external electric fields [Raschi, 1984; Tricas, 2001]. In the skin of the head and pectoral fins of elasmobranchs, the ampullae are visible as minute somatic pores (fig. 1b). Each pore is the opening of a jelly-filled canal that ends in a group of alveolate bulbs embedded in subcutaneous tissue (fig. 1a) [Boord and Campbell, 1977].

The canal wall generally consists of two layers of squamous epithelial cells separated from multiple layers of collagen fibers by a basement membrane [Waltman, 1966; Zakon, 1986; Wueringer et al., 2009]. These cells are connected with each other through tight junctions and desmosomes, creating a smooth surface within the canal wall [Szabo, 1974; Waltman, 1966]. The tight junctions in the luminal region between superficial cells of the canal wall insulate the canal [Waltman, 1966]; therefore, each ampulla of Lorenzini is a well-insulated core conductor [Bodznick and Boord, 1986; Brown et al., 2002].

The sensory epithelium of the ampullae of Lorenzini is restricted to the inside of the alveolate bulbs [Murray, 1974]. The epithelium is single layered and contains receptor and supportive cells [Waltman, 1966; Murray, 1974; Wueringer et al., 2009]. In marine elasmobranchs, an ampulla can contain several hundred sensory cells [Szabo, 1974]. The oval or pear-shaped sensory cells are encircled by several supportive cells [Murray, 1974; Szabo, 1974; Wueringer et al., 2009]. Apically, desmosomes and tight junctions connect receptor cells with supportive cells and supportive cells with each other. In marine elasmobranchs, only 1% of the apical surface of receptor cells is exposed to the lumen [Szabo, 1974] and a single kinocilium extends from this surface [Waltman, 1966; Murray, 1974; Wueringer et al., 2009]. The kinocilium is surrounded by numerous microvilli extending from the apical surface of the supportive cells [Waltman, 1966]. Waltman [1966] assumes the kinocilium to be of no importance to electroreception. The cilium shows the unusual pattern of 8 + 1 fibers in the body and 9 + 0 in the base and does not have an apparent basal body [Boord and Campbell, 1977; Wueringer et al., 2009]. The basal surface of sensory cells possesses multiple ribbon-shaped presynaptic bars, along which synaptic vesicles are aligned [Murray, 1974; Boord and Campbell, 1977; Wueringer et al., 2009]. This structural formation has

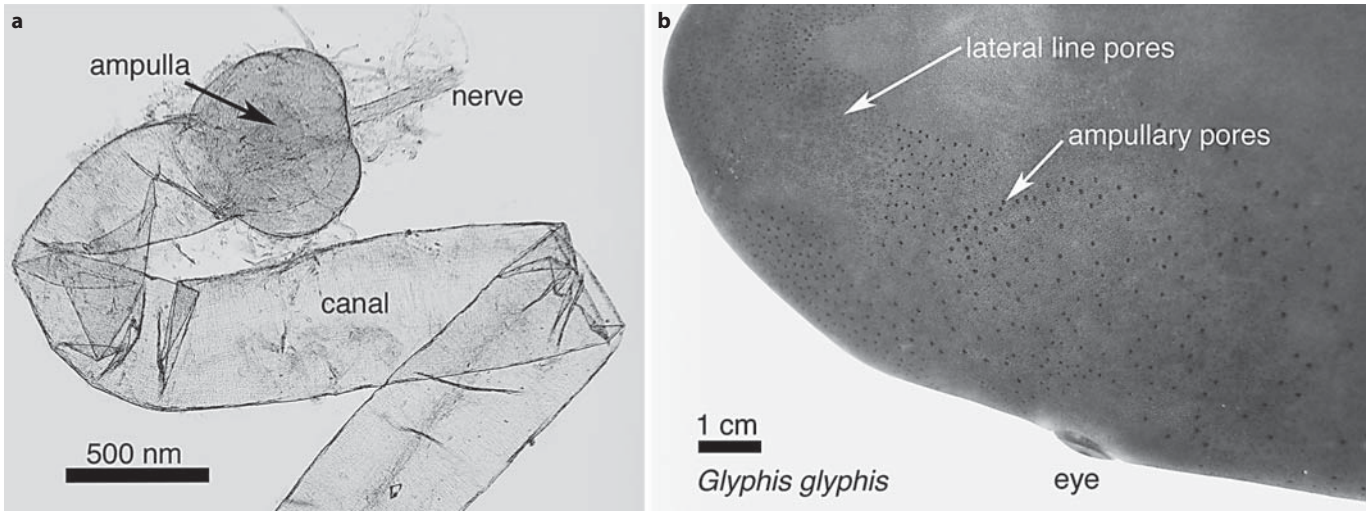

Fig. 1. Electroreceptive structures of elasmobranchs. **a** A single ampulla of the narrow sawfish *Anoxypristis cuspidata* that has been removed. During preparation, the canal became bent. The different regions of the electroreceptor are visible, namely the ampulla, which consists of alveoli and the canal. The nerve extends from the ampulla. **b** Ampullary pores on the surface of the head of a spear tooth shark, *Glyphis glyphis*. Note that smaller lateral line pores intermix with ampullary pores.

been termed ribbon and gutter [Murray, 1974], or tongue and groove [Waltman, 1966; Wueringer et al., 2009]. The synapse connects with afferent nerve fibers that lose their myelinated sheath as they enter the ampulla and spread out over each alveolus [Waltman, 1966]. There are no efferent fibers leading to the receptor cells.

The supportive cells of the sensory epithelium secrete a gel into the ampullae of Lorenzini [Szabo, 1974]. It is a species-specific muco-polysaccharide gel [Murray, 1974] that is rich in ions and possesses electrical properties approximating those of seawater with one exception: the values of voltage noise are reduced [Brown et al., 2002]. The gel may aid in maintaining the geometry of the canals and prevents infections of otherwise vulnerable and open structures [Brown et al., 2002].

The canals of the ampullae of Lorenzini can reach up to half the disk width in some species of rays [Chu and Wen, 1979], which allows the ampullary bulbs of different ampullae to occur in distinct clusters [Murray, 1974]. A cluster consists either of a loose aggregation of ampullae or an aggregation of ampullae within a connective tissue capsule [Aadland, 1992; Wueringer and Tibbetts, 2008; Wueringer et al., 2011]. Aggregations of ampullae and capsules ensure that different ampullae share a common internal reference potential [Kalmijn, 1974]. Each cluster is innervated by only one branch of the anterior lateral line nerve (ALLN).

Ampullary clusters were first described by Ewart and Mitchell [1891] and Norris [1929], who named them after the origins of their innervation and established a terminology that has been used ever since. Carcharhiniform and lamnid sharks possess three clusters on each body side, which are bilaterally symmetric, while rajids skates possess four [Ewart and Mitchell, 1891; Norris, 1929; Aadland, 1992], and rhinobatids and pristids possess five [Norris, 1929; Wueringer and Tibbetts, 2008; Wueringer et al., 2011]. Interestingly, the largest cluster present in batoids, namely the hyoid cluster [Raschi, 1978; Wueringer and Tibbetts, 2008; Wueringer et al., 2011], is missing in carcharhiniform and lamniform sharks [Raschi, 1984]. Moreover, ampullae of a particular area of innervation are found loosely aggregated in sharks and clustered together within the same connective tissue capsule in skates [Raschi, 1984].

Somatic pores visible on the skin of elasmobranchs may be divided into several pore fields that are useful for comparisons between different taxa. One pore field may contain ampullary pores from more than one cluster [Raschi, 1978; Wueringer et al., 2011]. Ampullae from one cluster can project to more than one pore field, like the hyoid cluster, which projects to four to six pore fields in rhinobatids and three pore fields in pristids [Wueringer and Tibbetts, 2008; Wueringer et al., 2011].

As the number of pores does not seem to increase ontogenetically, pore densities decrease with age and size of

the animal [Kajiura, 2000; Wueringer and Tibbetts, 2008; Wueringer et al., 2011]. This ontogenetic decrease of resolution might be compensated by increasing sensitivity, as growing ampullae increase both the length of their canals and the number of receptor cells [Raschi, 1986; Kajiura, 2000].

Conduction of an Electric Stimulus

The physiological response properties of the ampullae of Lorenzini are linked to the passive electrical properties and the structure of the organ [Kalmijn, 1974]. The connections between cells of the canal wall and the alveolar receptor epithelium provide a very high electrical resistance between the inside and the outside of the ampullary structures [Waltman, 1966; Murray, 1974], and so the ampullae are well-insulated core conductors [Bodznick and Boord, 1986; Brown et al., 2002]. The average capacity of the canal is 0.4 $\mu F\ cm^{-2}$, while the resistance of the canal wall is 6 $M\Omega\ cm^2$, and the resistance of the gel is around 25–31 $M\Omega\ cm^2$ [Waltman, 1966; Murray, 1974]. These values result in negligibly small attenuation values for dc voltages along the canals [Murray, 1974]. When exposed to a low frequency, weak electric field, the receptors inside the ampullae measure the potential difference between the water at the skin pore, which equals the ampullary interior, and the body interior at the receptor epithelium [Bodznick and Boord, 1986].

Receptors isolated from the ampullary receptor epithelium exhibit regular ongoing resting discharge rates that are modified by external electric fields [Murray, 1962; Waltman, 1966; Bodznick and Boord, 1986]. In live animals, resting discharge rates are also modulated by electric fields caused by ventilation [Bodznick and Boord, 1986]. A decrease or increase of the spontaneous resting discharge depends on the polarity of the field; ampullae of Lorenzini are excited by a cathodal pole presented to the opening of the pore and inhibited by an anodal pole [Murray, 1962; Szamier and Bennett, 1980; Bodznick et al., 1992].

An excitatory stimulus causes the following sequence of activity in the receptor cells, while supporting cells remain passive (after Bennett and Obara [1986] and Clusin and Bennett [1979a]): depolarization of the apical membranes by an excitatory stimulus causes an apical Ca^{2+} influx into receptor cells. The Ca^{2+} influx then leads to the depolarization of the basal faces of the cells, which, in turn, causes opening of basal Ca^{2+} channels and Ca^{2+} influx. This initiates transmitter release into the synapse, and also activates Ca^{2+}-activated K^+ channels on the basal surface, causing K^+ efflux from the receptor cell, which leads to repolarization of both the apical and basal surfaces. The repolarization deactivates the Ca^{2+} flow on both surfaces, which then deactivates the K^+ flux in the basal face. This results in repolarization and thus restoration of excitability. In the presence of an ongoing excitatory stimulus, the cell produces an oscillation of responses, with waves of depolarization and repolarization followed by one another. Each oscillation generates an action potential, which in turn generates a postsynaptic potential. The oscillations are essential for electroreceptor function [Clusin and Bennett, 1979a].

The ampullae are tonic receptors that adapt to dc fields within seconds [Kalmijn, 1974, 1978; Aadland, 1992]. The adaptation to dc fields has two consequences: first, the animal has to move with respect to the dc field in order to detect it, and second, it enables elasmobranchs to detect weak, modulated voltage gradients in the presence of their own bioelectric field [Kalmijn, 1974, 1978; Bodznick and Montgomery, 2005]. However, the ampullae of Lorenzini are low-frequency electroreceptors that detect electric fields of frequencies near dc to at least 15 Hz [Bodznick and Boord, 1986]. Ampullae with the longest canals are most sensitive to electric fields [Kalmijn, 1974]. Moreover, each ampulla is directional, responding best to fields oriented parallel to the canal [Murray, 1962; Bodznick and Boord, 1986; Camperi et al., 2007].

Neurological Aspects of Electroreception

In elasmobranchs, both the ampullae of Lorenzini and the cephalic lateral line system are innervated by the anterior lateral line nerve (ALLN) [Bodznick and Boord, 1986]. This nerve is considered a branch of the branchiomeric cranial nerve VII [Boord and Campbell, 1977]. The ALLN forms three rami, which are named ophthalmic, buccal, and hyomandibular [Norris, 1929]. The buccal ramus can further branch into the inner and outer buccal branch, the ophthalmic ramus can branch into the superficial ophthalmic and the profound ophthalmic branches, while the hyomandibular ramus can further branch into the hyoidean and mandibular branches [Raschi, 1986]. Upon entering the cranium, each ramus further subdivides into a dorsal and ventral root, all of which terminate in the medulla. The dorsal root carries only electrosensory fibers and terminates in the dorsal octavo-lateral nucleus (DON), while the ventral root contains only mechanosensory fibers and terminates in the medial octavo-lateral nucleus [Boord and Campbell, 1977; Bodznick and Boord, 1986]. Presence of the DON is regarded as an indicator of electroreceptive capacity among non-teleosts [Boord and Campbell, 1977; Bullock et al., 1982]. As the

histological organization of the DON is similar to that of the cerebellum and processes sensory information, it is considered a cerebellum-like structure [Bell, 2000].

The elasmobranch DON consists of a central zone, a peripheral zone and an overlaying molecular layer. The DON of *Raja* receives afferents from five sources [Bodznick and Boord, 1986]: Primary electroreceptive fibers project into the central zone, where they synapse with the smooth dendrites of large multipolar cells. Importantly, each ramus of the ALLN, and thus each ampullary cluster, projects into a distinct division of the central zone. These divisions are separated by compacted cell plates and the size of each division is proportional to the number of electroreceptors pointing to it. Moreover, the arrangement of projection terminals of the rami and individual afferents are somatotopically arranged. The large multipolar cells also receive inputs from other sources of the DON and are thus key in electrosensory processing in the medulla [Bodznick and Boord, 1986].

The central and peripheral zones of the DON receive projections from commissural axons, which terminate within a narrow layer of the peripheral zone. Afferents from the dorsal granular ridge project to the molecular layer of the DON. These afferents carry proprioceptive and electroreceptive information and are topographically arranged. They also carry motor corollary discharge signals. Additional afferent fibers project from the nucleus B and the paralemniscal nucleus of the medulla to the DON.

Projections from the DON are far-reaching [Bodznick and Boord, 1986]: axons from central and peripheral zones of the DON enter the contralateral dorsal nucleus. Axons of the large multipolar cells form the lateral line lemniscus, which ascends via the ventrolateral wall of the brain stem to the mesencephalon and terminates in the lateral mesencephalic nucleus and the central zone of the optic tectum. Some fibers project into the lateral portion of the nucleus of the lateral line lemniscus, while others ascend to the midbrain in the ipsilateral lateral line lemniscus or to the nucleus B of the cerebellar peduncle.

The electroreceptive system evolved in various taxa independently and without efferent innervation [Bennett and Clusin, 1978; Bodznick, 1989; Coombs and Montgomery, 2005]. The reason for this phenomenon is that the subtraction of common mode received signals is sufficient for noise reduction [Bodznick and Boord, 1986; Bodznick et al., 1992; Montgomery and Bodznick, 1999; Montgomery et al., this issue]. This is achieved in the DON, where predicted signals such as cyclic respiratory changes are subtracted from sensory input [Bell, 2000].

Biologically Important Stimuli and Their Origins

Electric potentials are generated at boundaries between chemically or physically different materials. These might even reach intensities larger than electric fields from animate sources [Wilkens and Hoffmann, 2005]. Wilkens and Hoffmann [2005] illustrate two examples: (1) when a metal is put into saltwater, it will attract or lose electrons depending on its electrochemical force compared to that of the water. Equilibrium is reached soon after and results in a steady DC potential without further current flow. (2) Between two liquids, on the other hand, where all charges are moving freely, a dynamic equilibrium is reached and a steady current will flow. A rich electrical landscape is thereby formed [Wilkens and Hoffmann, 2005]: a water body is surrounded by a boundary made of different materials, creating regional or global fields that are quite stable and could be used for orientation. Seasonal and daily variations are affected by water stratifications, salinity, and temperature changes. One possible advantage of electroreception is that the electrical landscape combines stimuli from both salinity changes and temperature changes. Moreover, the movement of charged particles in a magnetic field induces an electric field with magnetic flux lines perpendicular to the electric flux lines. In the earth's magnetic field, the movement of an animal in saltwater as well as the movement of saltwater itself creates an electric field [Kalmijn, 1974].

In the aquatic environment, the presence of a localized dipole electric field equates to the presence of an organism [Bodznick et al., 2003]. The bioelectric fields that surround living organisms originate from three sources: the direct contact between membranes and the external medium creates DC potential differences, contractions of body cavities create low-frequency AC currents with frequencies of less than 10 Hz, while muscle action potentials cause ac currents with frequencies higher than 20 Hz [Kalmijn, 1972, 1974; Haine et al., 2001; Kimber et al., 2011].

The question arises if organisms can camouflage themselves electrically from electroreceptive predators. It appears that bioelectric fields are a necessity of life. However, Kalmijn [1972] found that crustaceans have low-frequency potential fluctuations that follow the rhythm of respiration. In various crustacean taxa, a phenomenon called 'pausing' is known, which means that both ventilation and the heartbeat of these animals can be interrupted [Gribble and Broom, 1996]. Pausing can occur in regular intervals in inactive animals, but it can also be controlled by exogenous stimuli [Gribble and Broom, 1996]. One possible exogenous stimulus is the experimenter entering the room, where the crab's aquarium is located

[Gribble, pers. commun.]. However, whether a crab 'pauses' in the presence of a predator, and if/how this influences its electric detectability, remains to be tested.

Interestingly, the bioelectric fields of sharks and rays are up to one order of magnitude weaker than those of their teleost prey [Kalmijn, 1974], which may be due to the low resistance of their skin [Murray, 1974].

Behavioral Responses of Elasmobranchs to Electroreceptive Stimuli

The electric field detection thresholds of marine and freshwater fishes have been recently summarized [Peters et al., 2007]; those of freshwater elasmobranchs are in the range of 0.1 mV cm^{-1}, whereas their marine relatives can detect fields in the range of 5 nV cm^{-1}. Generally, the high sensitivity of the ampullae of Lorenzini is related to the spontaneous resting potential being very close to the threshold that activates an action potential [Bennett and Clusin, 1978]. Moreover, central processing of input from all ampullae can decrease behavioral thresholds, as it enables differentiation of spontaneous activity from externally imposed electric fields [Clusin and Bennett, 1979b]. However, individual ampullae are less sensitive and respond to voltage gradients of 1 μV/cm [Murray, 1974], which may be caused by experimental trauma [Bennett and Obara, 1986].

Since the first description of the reactions by elasmobranchs towards localized weak electric fields [Kalmijn, 1966, 1971], various uses of electroreception have been identified: object localization and discrimination [Johnson et al., 1984], prey detection and localization [Kalmijn, 1974, 1978, 1982; Haine et al., 2001; Kajiura and Holland, 2002], navigation [Kalmijn, 1982; Paulin, 1995], electrocommunication, including mate detection [Bullock and Szabo, 1986; Tricas et al., 1995], and predator avoidance [Sisneros et al., 1998].

Two approach algorithms for elasmobranchs towards their prey have been proposed, which were based on near-field acoustical pathways, as the acoustical near-field can be calculated with the same equation as the dipolar electric field [Kalmijn, 1997; Kalmijn et al., 2002]. After detection of the localized electric field of prey, the shark will arrive at the source of the electric field by correcting its course constantly to maintain the initial angle between its body axis and the equipotential surfaces of the electric field. On the other hand, a shark may arrive at the center of an electric dipole field through constant analysis of the field configuration, which allows it to turn and approach the field center. Both approach pathways have been confirmed behaviorally in sharks [Kajiura and Holland, 2002; Kajiura, 2003] and rays [Wueringer et al., 2011].

The study of the use of electroreception in feeding has received the most attention. From a distance of around 40 cm between predator and prey, electroreception guides the predatory strike [reviewed in Peters et al., 2007]. Detailed ethograms of predatory strikes and subsequent prey manipulation behaviors exist for sphyrnid and carcharhinid sharks and rhinobatid and pristid rays [Kajiura and Holland, 2002; Kajiura, 2003; Wueringer et al., 2012]. Sharks and rays display innate feeding responses towards prey-simulating weak electric fields [Tricas, 1982; Kajiura, 2003; Wueringer et al., 2012]. One behavioral study indicates that the small spotted catshark *Scyliorhinus canicula* is unable to distinguish the biological electric fields of crustaceans from artificial dipole fields of the same strength [Kimber et al., 2011].

Materials and Methods

The main body of this work compiles information on electroreception in sharks and rays. Following is a case study, with new results highlighting the interplay of ecological and phylogenetic influences on the distribution of the ampullae of Lorenzini over the skin surface. For this, previously separately published ampullary pore field data of two species of shovelnose rays *(Aptychotrema rostrata* and *Glaucostegus typus)* [Wueringer and Tibbetts, 2008] and three species of sawfish *(Pristis microdon, P. clavata*, and *Anoxypristis cuspidata)* [Wueringer et al. 2011] are compared. Pristids and rhinobatids are compared, as these two taxa share a common shovelnose ray-like ancestor [Schaeffer, 1963; Cappetta, 1974; Wueringer et al., 2009; Aschliman et al., 2012]. As the ampullae of Lorenzini are distinctively abundant on the rostra of rhinobatids and pristids, this analysis may provide clues on the evolution of the elongated rostrum. Compared to rajids, the rostrum of rhinobatids is elongated, but the rostrum of pristids is the longest of any batoid. The rostral cartilage can comprise up to 22% of the total length in adult small tooth sawfish, *Pristis perotteti* [Thorson, 1982].

Wueringer et al. [2011] and Wueringer and Tibbetts [2008] differentiated electroreceptive pore fields of sawfishes and shovelnose rays according to the grouping of ampullary pores (pore fields) and innervation of their ampullary clusters. The distribution of ampullary pore fields determines the overall receptive field of a species, while the number of ampullary pores within a pore field determines its spatial resolution [Wueringer and Tibbetts, 2008]. For the present comparison, pores of all pore fields that are innervated by the same branch of the ALLN are summated, and the following pore areas are distinguished: hyoid ventral, mandibular ventral, buccal and ophthalmic ventral, hyoid dorsal, and ophthalmic dorsal. The mean pore numbers might differ from those previously published [Wueringer and Tibbetts, 2008; Wueringer et al., 2011], as only samples in which all commonly innervated pore fields were counted were used. Moreover, ventrally, the buccal and ophthalmic innervation areas were placed into one category, as data from Wueringer and Tibbetts [2008] prevented exact separation of the two nerves.

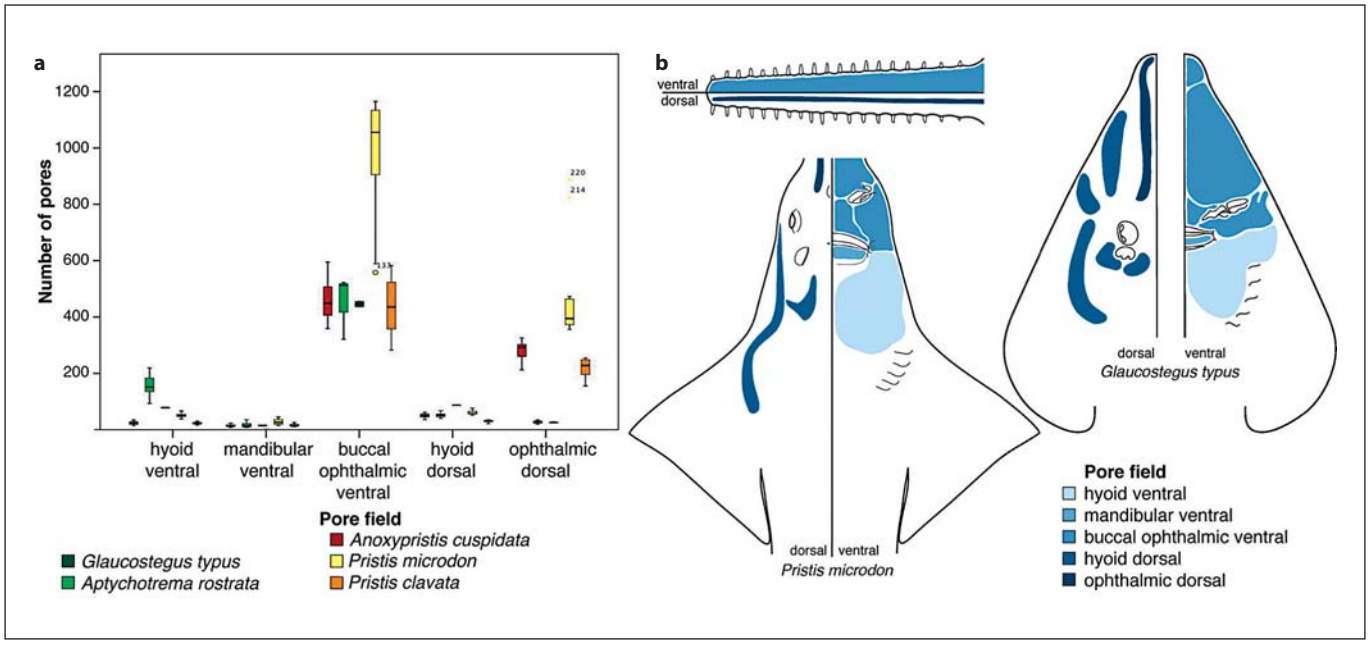

Fig. 2. a Mean number of ampullary pores per pore field for five species of batoids belonging to the rhinobatid shovelnose rays *(Rhinobatus typus, Aptychotrema rostrata)* and pristid sawfish *(Anoxypristis cuspidata, Pristis microdon, P. clavata)*. Major differences exist between the two families in the ophthalmic dorsal region, where sawfish possess significantly more pores than shovelnose rays. **b** Distribution of pore fields in pristids and rhinobatids, grouped by their innervation.

To test for interspecific differences in pore numbers in corresponding pore fields, a one-way ANOVA was conducted. If a Levene's test for equality of variances found that population variances were unequal, the Browne-Forsynthe statistic is reported instead of the ANOVA. If pore counts differed significantly between species, a Dunnett C post-hoc test determined which pore counts were different.

Results

Both sawfishes and shovelnose rays possess a well-developed electroreceptive sensory system [Wueringer and Tibbetts, 2008; Wueringer et al., 2011]. However, major differences between the five study species are apparent (fig. 2; table 1). Freshwater sawfishes *(Pristis microdon)* possess almost double the number of pores in any pore field compared to the two marine species of sawfish examined.

Both species of shovelnose ray possess more pores than any species of sawfish (fig. 2; table 1) in the ventral hyoid region (1), which is located between the mouth and the gills. The mean pore numbers of the mandibular region (2) and the ventral buccal and ophthalmic group (3) are comparable between shovelnose rays and sawfish, with the exception of *P. microdon*. The ventral buccal and ophthalmic group comprises pores located ventrally anterior to the mouth and extending to the tip of the rostrum. As a result, the electroreceptors of sawfish are spaced further apart on the ventral side of the long rostrum, and their spatial resolution in this region is decreased compared to that of shovelnose rays.

The numbers of pores of the dorsal hyoid group (4) are significantly different from each other in almost all five species. Differences between the two families in mean pore numbers of the dorsal ophthalmic group (5) are the most interesting: both species of shovelnose ray possess ten times less pores than two species of marine sawfish, *Anoxypristis cuspidata* and *P. clavata*, while freshwater sawfish possess double pores than the marine sawfish.

Discussion

Most morphological studies of the electroreceptors of elasmobranchs examine shifts in total ampullary pore numbers (and thus ampullae) between the dorsal and

Table 1. Mean number of pores per pore field (per body half), presented as mean ± SD

Pore field	*Glaucostegus typus*	*Aptychotrema rostrata*	*Anoxypristis cuspidata*	*Pristis microdon*	*Pristis clavata*	Stat. significance
(1)	**151.9 ± 42.5**	**77.0 ± 1.0**	22.2 ± 5.8	**49.6 ± 8.4**	22.4 ± 4.5	$p_1 = 0.000$
(2)	15.8 ± 9.8	13.3 ± 2.1	13.1 ± 4.7	**27.2 ± 10.7**	15.0 ± 4.8	$p_1 = 0.000$
(3)	451.3 ± 113.8	445.0 ± 12.7	460.8 ± 72.9	**977.3 ± 209.4**	436.3 ± 108.7	$p_2 = 0.000$
(4)	50.9 ± 8.5	**88.0 ± 3.6**	48.2 ± 7.1	**59.7 ± 7.8**	**29.0 ± 4.2**	$p_2 = 0.000$
(5)	24.8 ± 5.1	24.7 ± 2.1	*276.8 ± 41.3*	**474.0 ± 182.4**	*218.4 ± 35.7*	$p_1 = 0.001$
Dorsal	**75.8 ± 11.5**	**114.0 ± 0.7**	**326.9 ± 44.0**	**528.8 ± 189.4**	**247.3 ± 37.5**	$p_1 = 0.000$
Ventral	433.4 ± 239.3	536.5 ± 10.6	495.6 ± 70.9	**1,054.0 ± 214.4**	474.0 ± 114.6	$p_1 = 0.000$
Total	713.7 ± 152.0	647.5 ± 9.2	797.7 ± 54.5	1,580.4 ± 104.0	721.3 ± 142.8	/

Pore counts for dorsal, ventral, and total are presented per body half. If pore counts differed significantly between species, a Dunnett C post-hoc test determined which pore counts were different (indicated in bold, italic). Values differ from those reported by Wueringer and Tibbetts [2008] and Wueringer et al. [2011], as pore fields were added up according to their common innervation, which could only be done for a specimen if values existed for all pore fields needed. Pore fields: (1) hyoid ventral, (2) mandibular ventral, (3) buccal and ophthalmic ventral, (4) hyoid dorsal, (5) ophthalmic dorsal.

p_1 refers to the Browne-Forsynthe test of equality of means, while p_2 refers to the results of a one-way ANOVA.

ventral surfaces, which can then be related to physical parameters of different marine zones [Raschi, 1978; Kajiura, 2000; Kajiura et al., 2010; Kempster et al., 2012]. Total ampullary pore numbers were recently reviewed for all species of sharks and rays assessed to date [Kajiura et al., 2010; Kempster et al., 2012] and will not be further discussed here. Instead, a more detailed examination of pore numbers grouped by innervation will be used to demonstrate functional shifts based on predatory behavior.

The differences in ampullary pore distributions between shovelnose rays and sawfish are related to their predatory tactics: shovelnose rays possess more electroreceptors ventrally around the mouth compared to sawfish. During prey manipulation, the crustacean and teleost prey of shovelnose rays is still alive when it is pinned onto the substrate with the pectoral disc [Wilga and Motta, 1998] and, therefore, mouth repositioning has to be fast and accurate. In sawfish, free-swimming teleost prey has been stunned and wounds may have been inflicted with the rostral teeth during lateral swipes of the rostrum, before the animal repositions its mouth to ingest the prey [Wueringer et al., 2012].

Ventrally, the number of pores along the rostrum of sawfish is comparable to shovelnose rays, although the sawfish rostrum comprises at least 20–22% of the total length [Thorson, 1982; Taniuchi et al., 1991]. Pores are spaced further apart and the electroreceptive resolution in this region is decreased in sawfish compared to shovelnose rays. However, it is important to note that pore numbers on the ventral and dorsal side of the sawfish rostrum are quite comparable, thus providing the animals with a good electroreceptive resolution around and along their rostrum.

Along the dorsal rostrum, pore numbers of marine sawfish are at least ten times higher than in shovelnose rays, while those of freshwater sawfish are 20 times higher. The combination of an increased pore number with the elongation of the rostrum enables sawfish to detect the exact location of prey suspended in the water; a strategy, which is used when aiming and striking at electric dipoles [Wueringer et al., 2012].

Ecological Adaptations of Electroreceptors

Adaptations to Saltwater and Freshwater Environments

Andres and von Düring [1988] divide the electroreceptive structures of elasmobranchs into three groups, due to their overall size. The ampullae of Lorenzini of marine elasmobranchs are macroscopic and thus referred to as macroampullae. Freshwater rays possess miniampullae that are reduced in overall size and length of the canal, and holocephalans and hexanchid sharks possess microampullae, which only occur in restricted areas of the head. The canals of microampullae vary between 1.5 and 10 mm in length, depending on their location. Freshwater rays possess miniampullae with canals of about 450 μm in length [Andres and von Düring, 1988]. However, various authors use the term microampullae for the electroreceptors of potamotrygonid freshwater rays [Szabo,

1974; Szamier and Bennett, 1980; Raschi et al., 1997; Jørgensen, 2005].

In marine elasmobranchs, the skin has a low resistance compared to that of teleosts, as isotonicity with the environment is maintained by depositing urea in muscle tissue [Murray, 1974]. However, as elasmobranch muscle tissues are less conductive than the surrounding seawater, electric fields extend throughout the body gradually [Murray, 1974]. Ampullary canals, which are isolated core conductors, are long in order to reach the gradient required for voltage comparison between the surroundings and the inside of the body to be made [Murray, 1974]. In potamotrygonid freshwater rays, on the other hand, the skin resistance is high and externally imposed electric fields are almost excluded from body tissues [Kalmijn, 1974; Murray, 1974]. As a result, ampullae possess short canals and ampullary bulbs are positioned within the dermis, as they measure the potential difference between the surroundings and the inside of the animal right under the skin [Murray, 1974].

The electrosensory systems of euryhaline elasmobranchs, like the bull shark *Carcharhinus leucas,* the stingray *Dasyatis sabina,* the estuarine whipray *Himantura dalyensis*, and all pristid sawfishes, resemble those of their marine relatives, with long ampullary canals and macroampullae [Whitehead, 2002; McGowan and Kajiura, 2009; Marzullo et al., 2011; Wueringer et al., 2011]. In saltwater, these animals display reaction thresholds, which are as low as those of their marine relatives [McGowan and Kajiura, 2009; Wueringer et al., 2012]. In freshwater, *Dasyatis sabina* shows a reduced sensitivity and initiates behavioral reactions towards weak dipole electric fields at much shorter distances and larger field strengths [McGowan and Kajiura, 2009]. Comparison of the geometry of dipole electric fields in salt- and freshwater shows that the electric fields of the same strength spread further in freshwater, and decrease more rapidly in saltwater [McGowan and Kajiura, 2009]. Even though the absolute voltage in freshwater is greater, the slope or voltage change is much smaller, which represents the stimulus that elasmobranchs detect [Clusin and Bennett, 1979b; McGowan and Kajiura, 2009].

Adaptations to Feeding in Low-Visibility Habitats

Interrelation of the visual and electroreceptive system explains eco-morphological variations of the electrosensory system of elasmobranchs. Both sensory modalities are used in foraging behavior and the capture of prey. In batoids, a ventrally positioned mouth and dorsally positioned eyes mean that the visual system alone does not provide the necessary input to guide a batoid to its prey. Raschi [1984, 1986] correlates the pore density in rajids with the mobility of their prey and habitat visibility. Rajid predators, specialized in capturing cryptic prey, possess increased densities of pores ventrally, with the highest densities found around the mouth, compared to species feeding on mobile prey [Raschi, 1984, 1986]. Species adapted to the deeper, aphotic waters of the continental shelf have a high percentage of pores shifted to the dorsal side, where they compensate for a generally lower visual input [Raschi, 1984, 1986]. In sharks, visual fields are larger than those of rays [McComb et al., 2009], but eyes are often protected during the final stages of prey capture. White sharks, *Carcharodon carcharias,* roll their eyes in their orbits during prey capture, but the high number of ampullae of Lorenzini positioned within the visual field seems to facilitate the repositioning of the mouth during this crucial stage [Tricas, 2001]. Amongst galeoid sharks, species inhabiting murky waters possess more alveoli than species inhabiting clear pelagic waters, which presumably use visual input for the capture of prey [Raschi, 1984; Raschi et al., 2001]. Freshwater sawfish possess twice as many pores as any other species of sawfish assessed, which can also be related to habitat visibility. Neonate freshwater sawfish travel upstream into freshwater [Whitty et al., 2009], where visibilities can fall below 25 cm, while all other species of sawfish remain in marine to brackish waters, where visibilities are slightly higher [Wueringer et al., 2011].

Future Directions in Electroreceptive Research

Humans impact global elasmobranch populations through over-fishing, habitat destruction, pollution, and climate change. But, as the world moves towards renewable energies, manmade electrical pollution may also affect sharks and rays [Gill and Taylor, 2001]. While electrically shielded underwater cables do not generate an electric field, they do produce a magnetic field, which in turn induces an electric field around the cable. The intensities of these electric fields lie well within the detectable range of elasmobranchs [Gill and Kimber, 2005] and their effect on elasmobranchs has yet to be evaluated.

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