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The pit organs of elasmobranchs: a review

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Elasmobranchs have hundreds of tiny sensory organs, called pit organs, scattered over the skin surface. The pit organs were noted in many early studies of the lateral line, but their exact nature has long remained a mystery. Although pit organs were known to be innervated by the lateral line nerves, and light micrographs suggested that they were free neuromasts, speculation that they may be external taste buds or chemoreceptors has persisted until recently. Electron micrographs have now revealed that the pit organs are indeed free neuromasts. Their functional and behavioural role(s), however, are yet to be investigated.

Keywords: pit organ; neuromast; lateral line; mechanoreceptor; shark

1. INTRODUCTION

The remarkable sensory abilities of elasmobranchs (sharks and rays) have inspired a great deal of research, literature and popular entertainment. As top predators, their sensory biology is of interest to fishers and ecologists as well as physiologists. One sensory system of elasmobranchs, however, remains little known. The pit organs are tiny sensory organs (in the order of 100 μm diameter) found scattered on the skin, mainly along the dorsal surface, in species-specific patterns (Johnson 1917; Budker 1938; Tester & Nelson 1967; Maruska & Tricas 1998). They are classified as part of the lateral line, a sensory system of fishes and larval amphibians (Blaxter 1987). Details of the morphology of pit organs, however, are scarce, and their functional and behavioural role(s) are still obscure.

The lateral-line system is mainly responsible for detecting water motions of various kinds (see Blaxter's (1987) review, and citations therein). The lateral-line organs, called neuromasts, are mechanoreceptors found either on the skin surface or enclosed in subsurface canals. Neuromasts typically contain sensory hair cells, supporting cells and mantle cells, sitting on a basement membrane and capped by a gelatinous cupula into which the sensory hairs project. Neuromasts found on the surface are called free or superficial neuromasts, and these may be divided into at least two categories with different probable evolutionary origins (Coombs *et al.* 1988). Although elasmobranch pit organs have been identified as free neuromasts (Tester & Nelson 1967; Peach & Rouse 2000), it is unclear which category they belong to, or indeed whether they are functionally equivalent to the free neuromasts of other vertebrates. The nomenclature of free neuromasts is somewhat confused, with various types of free neuromasts being described as 'pit organs' or occurring in 'pit lines' (for further discussion of this issue see Coombs *et al.* (1988)). For the sake of clarity, 'pit organs' will be used in this paper only to refer to the organs of elasmobranchs, although the term may elsewhere refer to free neuromasts in other vertebrates.

Pit organs were initially called 'nervenhügel' or 'spaltpapillen'; the term 'pit organ' first appeared in the late 1800s. Various lateral-line researchers in the 19th and early 20th centuries (cited in Budker 1938) noted the existence of the pit organs, and some made observations on their location, innervation and/or histology. In all of these studies, however, the main focus was on the lateral-line canal organs. Budker (1938) was the first to attempt a synthesis of knowledge of the pit organs ('cryptes sensorielles'), and to illustrate the generalized distribution of pit organs over the body surface of a shark. Budker's diagram of a cross-section through a pit organ showed sensory cells reaching all the way from the apical surface to the basement membrane, a characteristic of vertebrate taste buds. Budker also reported some experiments where fish-meat extract applied to the pit organs elicited behavioural responses. Given this evidence, Budker suggested that the pit organs had a gustatory function.

Interest in pit organs was revived in the late 1960s when Tester & Nelson (1967) mapped the distribution of pit organs on 15 species of sharks, and also examined their morphology and histology. Like Budker, they recognized several distinct groups of pit organs—the most numerous on the dorsolateral and lateral surfaces, a pair anterior to each endolymphatic pore, a mandibular group and an umbilical group. They noted that the pattern of pit organ distribution varied among species, and sometimes one or more of the groups was absent.

Based on their light microscopical observations, Tester & Nelson (1967) were fairly certain that the pit organs were ordinary free neuromasts, not external taste buds. They observed that the sensory cells did not reach all the way to the basement membrane as Budker had claimed, and that the sensory cells appeared to bear apical hairs extending into a cupula-like body, unlike the cells of taste buds. They were unable to adequately visualize the cupula, however, despite trying a number of methods.

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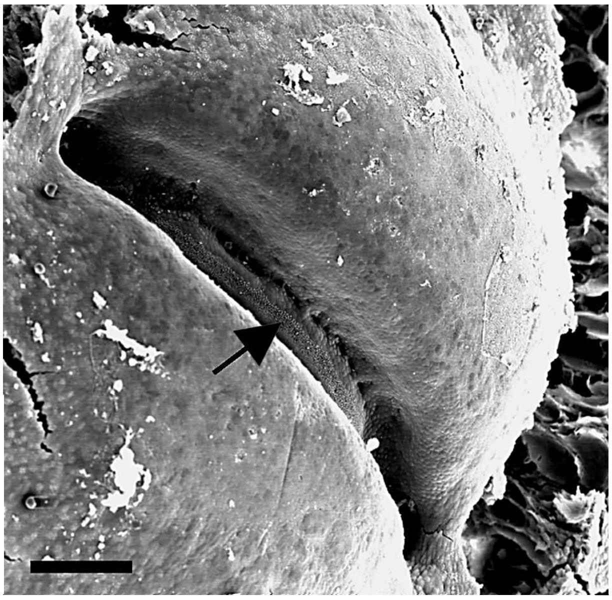

Figure 1. Pit organ of the stingray *Pastinachus sephen*. Arrowhead indicates edge of neuromast. Scale bar, 100 µm.

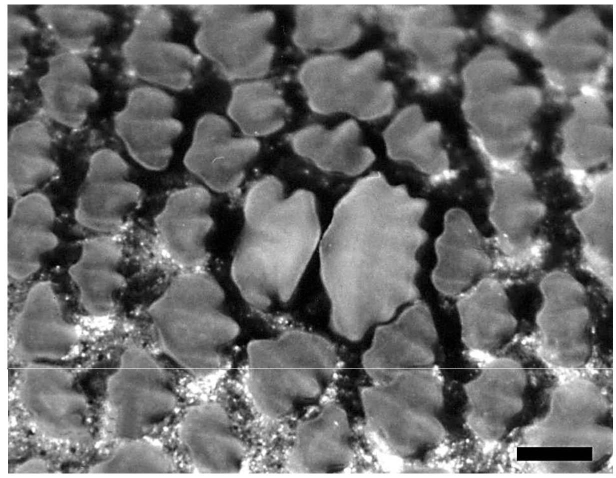

Figure 2. Two large modified denticles covering the pit organ of the epaulette shark *Hemiscyllium ocellatum*. Scale bar, 100 µm.

Soon afterwards Tester & Kendall (1967) examined the innervation of pit organs in two species of sharks. Like earlier researchers who had focused on the lateral-line canals (e.g. Johnson 1917), they found that the innervation of the pit organs was intimately associated with that of the canal neuromasts.

Shortly afterwards, Katsuki *et al.* (1969) published the results of their electrophysiological experiments to investigate the possible gustatory function of pit organs. They recorded responses to various ions, a mechanical stimulus, and to substances that stimulate the taste buds of mammals. They reported that the pit organs responded quite differently from the canal neuromasts to many of these stimuli, but their results were more qualitative than quantitative, and did little to clarify the functional properties of pit organs. The mechanical stimulus they used, although unclear, was described as 'touch', and their method for distinguishing pit organ and canal nerves seems to have been somewhat unreliable. In addition, the chemical stimuli they used may have been confounded by mechanical stimuli as the organs were 'flooded' with solutions (again, the exact method was unclear). They concluded that pit organs were more sensitive to changes in salinity and cation concentrations, and less sensitive to mechanical stimulation, than canal neuromasts. As the responses to salinity changes seemed especially marked, they speculated that the pit organs might function as salinity detectors.

Katsuki & Hashimoto (1969) did some further experiments on the enhancement of mechanosensitivity in pit organs by potassium ions. They speculated that the lack of a conventional cupula (as suggested by Tester & Nelson) might account for the marked chemosensitivity of pit organs. They also observed that the pit organ nerves sometimes showed burst discharges synchronized with the respiratory gill movements, as well as exhibiting spontaneous activity. Evidence was mounting that the pit organs had similar functions to other lateral-line organs, but Katsuki & Hashimoto (1969) apparently considered that their chemoreceptivity was functionally significant, rather than just a by-product of receptor physiology.

After Tester & Nelson's (1967) paper, the hypothesis that pit organs were ordinary free neuromasts received fairly wide acceptance in the scientific community. Speculation that pit organs were taste buds, however, still appeared from time to time in popular literature. The conclusions of Katsuki and his colleagues that the pit organs had a chemoreceptive function perhaps lent some resilience to Budker's theory. In an echo of Budker's behavioural experiment, Katsuki *et al.* (1969) found that the pit organs of sharks showed dramatic neural responses to the application of meat or blood. Although the words 'blood' and 'shark' together in a sentence may be evocative, it is difficult to imagine of what behavioural use this might be.

The nature of pit organs remained uncertain for so long partly because their structure had only been documented using the light microscope, which did not provide sufficient resolution to determine whether they were typical neuromasts. Although Hama & Yamada (1977) mentioned unpublished data indicating that the pit organs appeared similar to canal neuromasts, it was only recently that the morphology of pit organs was fully investigated at the electron microscope level (Peach & Rouse 2000). We have now documented the morphology of the pit organs of a variety of elasmobranch species, confirming that in most respects they have the structure of typical neuromasts (Peach & Marshall 2000).

2. RESULTS AND DISCUSSION

The pit organs of some elasmobranchs can be detected with the naked eye, due to their association with enlarged and modified placoid scales (denticles), with grooves in the skin, or sometimes (*Mustelus antarcticus* and *Etmopterus* spp.) with distinct patterns of pigmentation (Budker 1938; Reif 1985; M. B. Peach and N. J. Marshall, unpublished data). The functional significance of these accessory structures is unclear, but possibly includes protection against abrasion or direction of water flow towards the sensory surface. The few rays so far documented have their pit organs located within

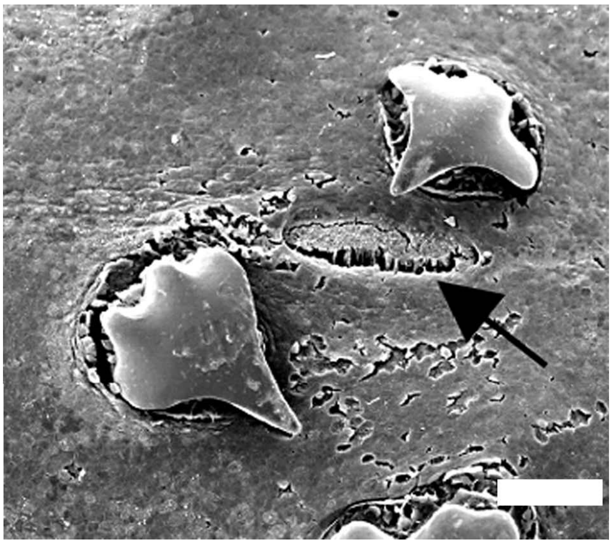

Figure 3. Pit organ of the shovelnose ray *Rhinobatos typus*. Arrowhead indicates edge of neuromast. Scale bar, 100 μm.

grooves, and exposed to direct water flow, while the pit organs of most sharks are covered by more or less imbricate denticles (Budker 1938; Reif 1985; Maruska & Tricas 1998) (figures 1 and 2). Although these denticles clearly have some effect on the hydrodynamic environment of the pit organ, water flow around and underneath them has yet to be modelled.

A few sluggish, mainly bottom-dwelling sharks (the angel shark *Squatina*, the lantern shark *Etmopterus*, the sevengill shark *Notorhynchus*, the sawfish *Pristis* and sawshark *Pristiophorus*) are known to have pit organs in grooves, like those of rays (Daniel 1934; Budker 1938; Reif 1985). In some of these sharks, the pit organs are also associated with modified denticles nearby, although these do not usually cover the pit organs. The shovelnose ray *Rhinobatos* and the guitar-fish *Rhynchobatus* also have modified denticles adjacent to their pit organ grooves (figure 3). Although these data suggest that exposed pit organs in grooves are related to a bottom-dwelling lifestyle, more typical pit organs covered by imbricate denticles have been recorded on other bottom-dwelling and demersal sharks (e.g. *Hemiscyllium*, *Ginglymostoma* and *Mustelus*). Thus the morphology of the pit organs and their accessory structures may relate more strongly to phylogeny than to ecology. In some other sharks (*Chlamydoselachus*, *Euprotomicrus*, *Isistius*, *Echinorhinus* and *Mitsukurina*) the pit organs have not yet been located, as there is no modification of the denticles or skin to indicate their presence (Reif 1985).

The number of pit organs appears to remain constant during ontogeny, but may vary among conspecific individuals as well as among species (Tester & Nelson 1967). The number of pit organs on one side of the body ranges from about 77 in (1 in = 0.025 m) *Squalus acanthias* to over 600 in *Sphyrna lewini* (Tester & Nelson 1967). The pit organs of rays are apparently less numerous than those of sharks (Budker 1938) but their distribution has been completely documented only for *Dasyatis sabina* (Maruska & Tricas 1997) and *Rhinobatos typus* (Peach & Marshall 2000). Because the data set is fairly small and includes mainly pelagic sharks, relationships between pit organ abundance and phylogeny or ecology are difficult to discern. Reif (1985), however, did note a positive correlation between pit organ abundance and swimming speed in sharks.

The behavioural role of pit organs remains mysterious. Tester & Nelson (1967) suggested that they may play a role in prey capture under dim light conditions, while Katsuki and his colleagues focused on their chemoreceptive properties and suggested that they may be detectors of salinity changes. This seems unlikely, as very few elasmobranch species migrate between salt and fresh water, although most if not all elasmobranchs possess pit organs. Reif (1985) suggested that the pit organs might function as detectors of swimming speed. This seems feasible, as the free neuromasts of other fishes and amphibians are directly exposed to water motion, and detect velocity (citations in Blaxter 1987). It is not yet clear, however, whether the pit organs of sharks, for the most part well shielded by overlying denticles, receive the same kind of stimuli as the free neuromasts of other vertebrates. Maruska & Tricas (1998) noted that the pit organs of stingrays were well placed to detect water movements generated by tidal currents, conspecifics or predators.

Ironically, it seems to have been clear to the earliest researchers that the pit organs belonged within the lateral-line system. The influential work of Budker initiated the confusion that has persisted until recently. A number of approaches can now be taken to improving our understanding of pit organs. Electrophysiological recordings from the pit organ nerves, in the presence of controlled mechanical stimuli, could establish whether the pit organs have frequency response characteristics similar to those of the free neuromasts of other vertebrates. Behavioural experiments, where the pit organs are occluded by chemical or mechanical means, could determine whether the pit organs are important in rheotaxis or prey detection. Modelling of the immediate hydrodynamic environment of the pit organs, and how this is affected by the accessory structures, would help to clarify the relevant stimulus. Work is currently under way to document the distribution and morphology of pit organs on more species of elasmobranchs, especially bottom dwellers (Peach & Marshall 2000).

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