The Senses of Fish
Adaptations for the Reception of Natural Stimuli
I love fish and when asked to write this Foreword was very happy to be given the opportunity to welcome this exciting tome on “The Senses of Fish: Adaptations for the Reception of Natural Stimuli”, edited by Profs. Gerhard von der Emde, Joachim Mogdans, and B.G. Kapoor. My enthusiasm was briefly damped when a graduate student of mine, whom I told of the task allotted to me, remarked “Who still reads books these days?”. Temporarily stunned, I hastened to reply “Smart people do, of course!”.

This volume contains such a wealth of information and presents such a wonderfully balanced variety of contributions by experts in their own fields, each and all expanding their subject one or another, that I could have added “This book makes smart people smarter still—and that’s why smart people will read it”. The topics covered fall neatly into six categories. The first two chapters, by Barbara Evans and Arnold Sillman & David Dahlin, provide the reader with exciting new details on fish eye adaptations and the reasons behind such adaptations. Eyes and vision in fish are finely tuned to the photic environment and as a consequence of this relationship as well as the wide range of habitats that fish occur in, a variety of modifications to the eye’s optics, development, retinal organization, photopigments, absolute and spectral sensitivities have evolved. Without a thorough examination of these adaptations, we would be unable to make much sense of the visual behavior of fish.

Recent years have seen an upsurge of interest in the chemosensory abilities of fish and three chapters, one each by Anne Hansen & Klaus Reutter, Tine Valentinèë, and Gabrielle Nevitt & Andrew Dittman, testify to this fact. Using behavioral responses and a comparative approach, Tine Valentinèë shows that predatory fish with functional olfactory and taste receptors do not necessarily use these senses during food procurement. Visual hunters use the taste system solely during oral food evaluation. The situation for the detection of underwater smells is somewhat different as Hansen and Reutter demonstrate. However, that olfaction in migratory species plays a maior role has been known for a long time, but how, for instance, imprinting in juvenile
Salmon might work, in contrast to imprinting in mammalian species, is investigated by Nevitt and Dittman. The two authors provide evidence that odor memories may also be retained peripherally and that olfactory receptor neurons could be “selectively tuned” by responding to specific odors present “during a hormonally linked sensitive period”. This is an exciting concept and one can expect more fascinating discoveries in this fertile field of ‘developmental neuro-etho-ecology’.

A fascinating overview of the sensory systems and sensory brain areas in deep sea fish by Hans Joachim Wagner allows the reader not only to appreciate the specializations that are present in the denizens of deep water, but also to see the developmental parallels in fishes of other habitats (cf., for instance, Meyer-Rochow & Coddington, 2003, In: Fish Adaptations, eds. Val A.L. & Kapoor B.G., Oxford and IBH Publ. M/s Sci. Publ., Enfield, New Hampshire, pp. 339-383). This chapter by Wagner, placed in the centre of the book, thus connects the more detailed treatments of selected senses and sensory adaptations, preceding and following Wagner’s chapter, with each other and, like the fish’s brain, has an integrative function.

Aspects of sound production and hearing in fish are dealt with in another fascinating section of this book. Far from being silent creatures, Friedrich Ladich introduces us to the ‘noisy’ underwater world and describes how and why fish produce sounds. Little known and poorly studies is the ability of some species of fish to detect sounds as high as 180 kHz. Adaptations responsible for this remarkable feat, in particular within the Clupeiformes, and possible ecological consequences of ultrasound detection are being reviewed by Dennis Higgs. But how the acoustic signals in the end are ‘heard’ and processed by the fish’s nervous system is the topic of Zhongmin Lu’s chapter. Concentrating on what has been discovered on the goldfish’s sound detecting pathways, Lu also examines acoustic communication and directional hearing in the mormyrid Pollimyrus adspersus, the midshipman Porichthys notatus, and other species. Hong Young Yan then summarizes the current state of knowledge with regard to hearing in fishes and emphatically draws attention to the fact that despite considerable progress, many aspects of sound perception in fish are still poorly understood.

A very comprehensive treatment by John Janssen is given to the role of the lateral line, especially in species that inhabit dark environments or turbid waters. Yet, how the different species of fish integrate the signals coming from the lateral line with those being received through channels of the other senses is still largely unknown. Joachim Mogdans, Sophia Kröther, & Jacob Engelmann in their chapter touch upon this problem, but deal primarily with recent findings on the lateral line brainstem’s responses to a variety of stimuli. Two subsystems, consisting of superficial neuromasts whose function is impaired in running water, and canal neuromasts, whose function remains unaffected in running water, were discovered and led the researchers to conclude the presence of a clear form-function relationship for the lateral line.

Finally, the enigmatic electric sense of some fish: That topic forms the subject of chapters by Lon Wilkens, Tim Tricas & Joseph Sisneros, Clifford Keller, and Mary Hagedorn. Wilkens introduces us to the paddlefish, a fish that rarely features as an experimental subject. However, as Wilkens ever so ably demonstrated with his remarkable research, the paddlefish uses rostrally located electoreceptors to detect plankton and to investigate its environment. A form of
"passive electroreception", and what exactly this term entails, is revealed in the chapter by Tricas and Sisneros. The two researchers have chosen skates as their experimental subjects, marine species in other words, which, unlike the weakly electric fish (dealt with in the chapter by Keller), are not at all famous for communicating electrically. Keller leads us into an alien world of senses, into a world in which signals familiar to us humans have become largely replaced by electrical stimuli. Aimed primarily at conspecifics, such signals, like Mary Hagedorn explains, can also be a powerful incentive to those adventurous human beings, wishing to work with fish in remote jungle settings.

Although the contributors to this book hail from several different countries and presumably were not brought up in the same cultural environments, their fascination for fish unites them all. As someone who was born under the sign of Pisces, I too, have a "soft spot" for fish of all kinds: I like them fried, cooked, and smoked, and I regularly enjoyed ‘gefilte fish’ as a boy in my grandmother’s home. But I am equally fond of them when I find them cut open in the dissection dish, under the microscope, or placed in some apparatus designed to reveal their physiological secrets. I love watching them dart around in my aquarium at home and have gone diving to see them in their natural habitats. I even have a collection of coins that feature fish and I know people, who possess thousands of fish stamps from all over the world. Obviously, as the enthusiasm has shown, with which this book’s contributors have written their chapters, there are many different ways to express one’s adoration for fish.

What makes fish so attractive to humans? Where does this age-old fascination for the slippery creature of the aquatic domain come from? Is it because we all pass through fish-like stages in our embryological development? Is it because the class Pisces outnumbers all other vertebrate classes with regard to the number of species (at least 25,000 species have been described to date)? Or is it, because fish are seen as inhabitants and messengers of a world alien, and maybe even threatening, to humans? I guess there isn’t a single reason why humans since ancient times have found fish captivating, but fact is that the humble fish, as a symbol, has had a very long history and occurs in cultures and religions throughout the world. So fond must the early English have been of fish (or were they simply bad observers?) that they even lent this term to animals, which have little to do with real fish (witness shellfish, starfish, crawfish, jellyfish, cuttlefish, crayfish, and silverfish).

Christians revere the fish as a symbol of Christ and in Jewish lore the fish, being customarily consumed on the Sabbath, symbolizes prosperity. Pre-Christian Germanic tribes ate fish in honor of the great mother goddess Freya, a habit that according to some scholars persists to this day in the tradition of many a European to have a meal of fish on Fridays. In India a reincarnation of the goddess Durga, known as Meenakshi, was respectfully called ‘the beautiful fish-eyed one’ and the first Indian coinage of 600-300 BC has many examples of fish motifs. Several other non-Indian deities like Isis, Apollo, and Poseidon (the God of the Sea) were also associated with fish. Amongst the Maya of the New World different species of fish held different meanings: hags were seen as spies and destroyers, catfish represented cleaners and renewers, and other species were invoked in local systems of counting. In Japan, on the day known as ‘kodomo no hi’ (May 5th each year), even today tall bamboo poles with carp kites and streamers are erected in the
gardens of many a home, for to the Japanese the carp embodies strength and determination. On the other hand, fear and panic have nowadays, unfortunately, become almost synonymous with sharks around the world. However, actual shark-worshippers still inhabit some remote islands like Malaita of the Solomons in the West Pacific.

Clearly, fish have accompanied humanity and human culture from their beginnings, and this has also found numerous reflections in the arts. Poems in praise of fish have been written and set to music (F. Schubert’s composition “Die Forelle” comes to mind), fish paintings (e.g., Paul Klee’s “Golden Fish”), fish sculptures (the Olympic fish of Barcelona beating them all with its gigantic size), and nowadays even fish movies, fishing competitions, and fish games exist. Stories, fairy tales, and fables involving fish, often rooted in antiquity (who would not have heard of Aesop’s ‘Fisherman and the Little Fish’) have a long history, but they are still popular today and they are being told in virtually all parts of the world.

This book, although anything else but a collection of mere fishy stories and fables, does follow that long tradition of human fascination with fish and there is no doubt that the scientific research, reported in this volume, represents the fruits of years of patient and dedicated study. The authors, editors, and publishers must feel privileged to share in the production of so worthy a text as I do to have been called to welcome it on its appearance. As we gather more and more data on the wondrous ways the fishes ‘function’, we slowly start to grasp why, for at least 400 million years, these animals have managed to flourish and been able to live through geo-historic crises and environmental changes too profound for us to comprehend. We are reminded of the fact that almost three quarter of the Earth’s surface are the domain of our friends, the fish. And we are realizing that we are in the process of understanding, what kinds of adaptations have allowed them to succeed in occupying every conceivable niche of their watery realm and what roles their sensory capacities have played to guarantee their survival through the ages.

Much of what we know today about the senses of fish, represents abilities and adaptations almost unimaginable to us ‘mere humans’ only a few years ago. This is a fact and there is nothing ‘fishy about that. However, none of the exciting discoveries can diminish the deep respect we hold for our ‘scientific quarry’. On the contrary, the discoveries have served to enhance our appreciation of this formidable creature of Nature and sometimes may even cause us to take a deep breath and reflect on our own imperfections.

Before I end this Foreword with a translation of that fitting and famous poem “Die Forelle/The Trout” by Christian Schubart, I should like to emphatically state: This book cannot fail to give great pleasure to all those people smart enough to pick it up and read it thoroughly!
The Trout

Beneath the limpid water
I saw a jolly trout
As swift as arrow darting
And flashing in and out.
I stood upon the margin,
All in the morning cool,
And watch'd the fish disporting
Down in the crystal pool.

Near by there stood an angler,
With rod and line and hook,
And saw the trout a-swimming
Down in the crystal brook.
With shine upon the water
Unbroken, so I thought,
In vain will be his angling,
The fish will not be caught.

At last the thievish angler
Impatient grew. With guile
The water clear he ruffled,
And in a little while
He jerk'd his rod in triumph.
And struggle, struggle as it may,
The poor outwitted victim
Upon the greensward lay.

Animals have to be able to perceive external sensory stimuli and generate appropriate behavioral responses in order to live successfully in their environments. On an ontogenetic scale, behavioral responses to sensory stimuli are either innate or learned. Learning enables an animal to respond to changing stimuli through experiences made during life. On a phylogenetic scale, organisms also 'learn' to adapt to changed signals in their environment. Evolutionary learning works in a different time frame, however, that is from generation to generation. Its motor is selection, and its result is an adaptation of the sensory apparatus and the nervous system. During this adaptation process, ‘communication’ with the environment is maintained, enabling the animal to gather important signals coming either from the surroundings or from other animals, like prey, predators, or conspecifics.

In this book we use fish as model systems to demonstrate how evolutionary learning has shaped various sensory systems. Why fish? There are three main reasons for this: First, ‘fishs’ comprise a huge and diverse group of animals. There are about 25000 extant fish species that live in such diverse environments like the deep sea or shallow freshwater puddles in the Himalayas. Closely related taxa may live in different habitats and thus under completely different environmental conditions. They have adapted to these diverse environmental conditions not only in their external body features, but also by modifying their sensory apparatus. Second, fish possess more senses they many other animals. They are equipped with the well known senses that humans have, but in addition they possess at least three more senses. Third, fish stand at the basis of vertebrate evolution. While shaping the senses of fish, evolution worked on the very ‘blueprint’ of vertebrate organisation, which forms the basis of all other vertebrates, including humans. Fish thus can serve as model systems for vertebrate evolution in general, including the evolution of sensory systems and their adaptations to environmental conditions.

We brought together scientific experts from different areas, who report about the sensory systems of fish and unravel their physiological and ecological evolutionary adaptations. The first two chapters deal with vision, one of the most important senses of vertebrates. However, vision in different aquatic habitats has to cope with quite diverse photic conditions and thus requires fundamental adaptations of the eyes and their sensory receptors. Chemoreception, dealt with in chapters three to five, may be one of the “oldest” senses of vertebrates. Yet again,
environmental conditions differ in the various habitats fish live in, and this requires adaptations of the olfactory and taste systems of the different groups. An interesting case study of olfactory specialization is olfactory imprinting, which can be found in several groups of fishes. The best-known example may be olfactory imprinting in the service of homing in salmons as described in chapter five. Chapter six does not deal with a particular sensory system, but takes a look at several groups of fish living in an extreme environment: the deep sea. Here, the chemical senses, vision, and the lateral line system are especially developed and adapted to the different niches in this ultimate environment. That fish are not deaf is well known since the days of Karl von Frisch, and chapters seven to ten discuss several aspects of underwater hearing. Related to hearing, sound production by fish (chapter 10), mainly in the service of intra-specific communication, is an important evolutionary factor shaping fish hearing organs. The lateral line system of fish compromises two main sub-systems: the mechanosensory lateral line, dealt with in chapters 11 and 12, and the electrosensory lateral line (chapters 13 to 16). The latter can be divided still further, depending on the type of stimuli that are perceived: low frequency electric signals for 'passive' electrolocation through ampullary electroreceptor organs (chapters 13 and 14), and high frequency signals, actively produced and thus involved in 'active' electrolocation (chapter 15). Finally, chapter 16 stresses an important 'human' point: science is made by people, sometimes under extreme conditions. Especially when studying environmental adaptations of animals, it is necessary to go out into the field and get information directly from the source. This can be dangerous at times and may require personal sacrifices by the scientists that are often forgotten and not mentioned in scientific reports, thus making scientific results look simple and 'easy' to obtain. That this is often not the case is highlighted by our final essay-chapter.

Gerhard von der Emde
Joachim Mogdans
B G Kapoor
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