

## Preface

Kara E. Yopak

School of Animal Biology and the UWA Oceans Institute, University of Western Australia, Crawley, W.A., Australia

To the general public, the term ‘shark’ is often synonymous with mystery, fear, and morbid fascination. To an evolutionary neuroscientist, however, sharks and their relatives (skates, rays, elephant sharks, and chimaerids) represent a key a stage in the evolution of gnathostomes, with the appearance of the first fully formed neural ‘bauplan’ that is present in all extant jawed vertebrates. Building on the fascination with this basal vertebrate lineage (Class Chondrichthyes), participants in the 2011 Karger Workshop, which took place on November 10 in Washington D.C., have spent significant portions of their academic career bridging the gap between our understanding of the sensory biology, central processing, neural development, connectivity, and ecology of this unique group of fishes.

This issue of *Brain, Behavior and Evolution* contains reviews and original papers based on the presentations at the Karger Workshop. This workshop brought together the world’s experts on the central nervous system of cartilaginous fishes, including well-established scientists and tenured faculty, as well as students and early career researchers, who all added new insights and enthusiasm to the field. These investigators pursue research in various subject areas and subdisciplines, with overarching attention to a better understanding of the architecture, function, and variability in the brains of chondrichthyans.

Cartilaginous fishes are comprised of nearly 1,200 species and are widely distributed in a variety of marine niches. Although once thought to have empirically simple brains, research by the members of this symposium have collectively shown that cartilaginous fishes possess a battery of highly-developed sensory systems, relatively enlarged brains, and complex neuromorphological characteristics. Using a range of histological methods, tract tracing, cladistics, electrophysiology, and molecular genetics, these scientists are uncovering the evolutionary processes acting on the chondrichthyan brain and subsequent implications for behavior.

Though an oversimplification of a complex idea, the theme that surfaced multiple times during the course of the workshop and the subsequent publications in this issue was reminiscent of an ancient French proverb by novelist Jean-Baptiste Alphonse Karr (1808–1890): ‘The more things change, the more they stay the same’. Although clearly not Alphonse Karr’s intent when he made this statement, this strikes me as being highly relevant to the nervous system, particularly that of cartilaginous fishes, whereby, despite broad taxonomic divergence and widely disparate ecological niches and behavioral repertoires, which are linked to interspecific variability in peripheral and central anatomy, there are still noted neural commonalities that evolved at least as early as the cartilaginous fishes and persist across all vertebrates.

### KARGER

Fax +41 61 306 12 34  
E-Mail [karger@karger.ch](mailto:karger@karger.ch)  
[www.karger.com](http://www.karger.com)

© 2012 S. Karger AG, Basel  
0006–8977/12/0802–0077\$38.00/0

Accessible online at:  
[www.karger.com/bbe](http://www.karger.com/bbe)

Kara E. Yopak  
University of Western Australia  
School of Animal Biology and the UWA Oceans Institute (M317)  
35 Stirling Highway, Crawley, WA 6009 (Australia)  
Tel. +61 8 6488 4509, E-Mail [kara.yopak@uwa.edu.au](mailto:kara.yopak@uwa.edu.au)

Moving from the outside in, so to speak, a Special Issue on the nervous system of cartilaginous fishes is incomplete without a full understanding of the peripheral anatomy and the sampling of environmental signals encountered by a species in its preferred ecological niche. Shaun P. Collin provides an extensive review of the sense organs mediating vision, olfaction, gustation, lateral line, electroreception, and audition in cartilaginous fishes. Coupled with Barbara Wueringer's detailed description of the electrosensory system, its innervation and central termination, these two papers emphasize the need for a full understanding of the influence of external stimuli, the sensitivity of each of the peripheral sense organs, the integration of sensory input within the central nervous system, and how all of these are coupled to determine a species' behavioral response. Using a comparative approach, both Collin and Wueringer highlight that the relative importance of each sense may differ between species, both inter- and intraspecifically, as they encounter different ecological niches during their life history. This variability in the anatomy and behavioral sensitivity thresholds of each species raises many questions about the quantitative levels of sensory input reaching the CNS and the evolutionary pressures acting on both the brain and the sensory organs. In an applied sense, a better understanding of the peripheral sense organs can have far reaching implications with respect to the effects of anthropogenic noise and other environmental sensory perturbations, and even their susceptibility to fishing pressures and the future development of more effective repellents.

Variability in the relative importance of individual sensory systems in cartilaginous fishes has been advancing in concert with widespread interspecific variability in the development of major brain regions, with commonalities in brain organization found in species that share various ecological niches and life-histories. Kara E. Yopak and Thomas J. Lisney focus on the midbrain and provide a review of our understanding of the dorsally positioned optic tectum (analogous to the superior colliculus of mammals and the primary visual center of the brain), and the ventral tegmentum mesencephali. Due to the variability in the size of these brain areas across cartilaginous fishes, they speculate that the relative size of the optic tectum and tegmentum reflects the importance of vision and sensory processing. However, there are still many gaps in our knowledge of the tectum in cartilaginous fishes; we are still lacking definitive conclusions regarding the extent of the retino-thalamo-telencephalic visual pathways, the level of variability in the number of

tectal laminae and tectal thickness, and the functional implications for this variation, highlighting the need for further study of the visual system in cartilaginous fishes.

Although there are some documented instances of ontogenetic shifts in brain organization in cartilaginous fishes, little is known about embryonic neural development in this group. In a paper lead by Isabel Rodríguez-Moldes' group, the development of the telencephalic subpallium is traced through embryonic and postembryonic stages, using *Scyliorhinus canicula* as a model species. The authors analyzed the patterns of innervation of this brain area using tract-tracing techniques in an effort to postulate on the equivalence of regions and nuclei among elasmobranchs and to support homologies with other vertebrates. Quintana-Urzaínqui and coworkers review the chemoarchitecture, connectivity, and development of the subpallium of *Scyliorhinus canicula* and reveal that the striatal and pallidal subdivisions have a similar embryological origin and genetic specification to those of tetrapods, thereby supporting the homology of these regions with the basal ganglia. However, further studies are needed in order to establish clearer relationships between the genoarchitecture of the subpallium of shark embryos and the basal ganglia of adults, taking into account other subpallial regions and interspecific differences.

Beyond general interspecific variability and the characteristics of the embryonic brain that have remained conserved through evolutionary time, the connectivity and functionality of two major brain areas remain the subject of intense research activity, likely due to their cognitive associations: the telencephalon and the cerebellum.

Michael H. Hofmann and R. Glenn Northcutt explore the organization, connectivity, and function of the telencephalon in elasmobranchs. Although once thought to essentially serve an olfactory function, the telencephalon was later found to be more similar to the telencephalon of other vertebrates, contributing greatly to the processing and moderation of other sensory modalities and higher cognitive functions. Hofmann and Northcutt reassess the intrinsic and extrinsic connections of the telencephalon in two elasmobranch species. Tracers were injected into various parts of the forebrain to trace the olfactory pathways. Based on their data, Hofmann and Northcutt urge a reconsideration of the dorsal pallium as a nonolfactory brain center and suggest that many telencephalic centers, including the dorsal pallium, are involved in olfactory orientation. However, due to the level of interspecific variability in the size and complexity of the telencephalon across cartilaginous fishes, more work on olfac-

tory pathways is required before definitive statements can be made regarding ascending and descending projections in chondrichthyans.

Our special guest, John C. Montgomery of the University of Auckland, concludes this Special Issue with an insightful analysis of perhaps the most mysterious of brain regions – the cerebellum – that occupies a large portion of the brain. Even the function of the cerebellum is still an area of considerable debate. As this brain area appeared first in early chondrichthyans, it is itself an additional innovation to the central nervous system in the Devonian. Montgomery and collaborators (Bodznick and Yopak) review the current knowledge of the anatomy and function of the cerebellum and what they propose to be the evolutionary antecedent to the cerebellum, called the cerebellum-like structures. Given the fundamental similarities of the molecular layer between these two structures across basal vertebrates, they propose that the cerebellum arose through a change in the genetic-developmental program amounting to a duplication of an existing structure. They also discuss a relatively new idea, drawing a parallel between neural architecture and autonomous robot design. Along this line, they present the cerebellum as an evolutionary advancement in gnathostomes that is literally superimposed on pre-existing un-

derlying brain structures and pathways, thereby paving the way for some aspects of higher neural function in the evolution of vertebrate brains.

As Guest Editor of this Special Issue, I speak on behalf of all of the workshop participants in sincerely thanking *Brain, Behavior and Evolution* and the Karger Publishing Company for their immense support of the production of this issue and their continued support of evolutionary neuroscience. We are extremely grateful to Alice Powers and the rest of the J.B. Johnston Club for Evolutionary Neuroscience Executive and Program Committees for their efforts in making the annual meeting a great success. I would like to personally thank the contributors to this workshop and Special Issue for their tireless efforts to push the field forward. I would also like to extend special thanks to Georg Striedter for his encouragement and generous assistance through this process.

We sincerely hope the readers appreciate the collaborative merging of the wide breadth of expertise encompassed in this issue and work to develop a better understanding of how the shark nervous system has evolved, how these animals receive and process information from their environment, and the implications these variations have for evolutionary adaptations in sensorimotor function in vertebrate nervous systems.