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"ORGANISMAL" VS. "MECHANISTIC" BIOLOGY

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ABSTRACT: Gerhard Roth's new book, *Visual Behavior in Salamanders*, illustrates the advantages that an organismal perspective brings to physiological studies in general, and to sensory neurophysiology in particular. While many "mechanistic" biologists hope optimistically that the "system" they study will provide a general "model" for vertebrates as a whole, an organismal perspective emphasizes the unique qualities of each species, within its particular system of developmental and functional constraints. By comparing many species in the context of their phylogenetic relationships, it is possible to make well supported statements about the distribution of physiological characteristics among groups of vertebrates. While the cost of this approach is relatively high in terms of the time and effort necessary to gather data on a number of different species, an understanding of the ontogenetic and physiological basis for evolutionary transformation is absolutely necessary for an understanding of functional diversity.

VISION is extremely important to most vertebrates (for example, in avoiding predators, finding food and mates), so it is not surprising that a large portion of the vertebrate brain is associated with receiving and processing visual input. Since Ramon y Cajal's (1892) famous work, there has been a large amount of research on the comparative neuroanatomy of vision in vertebrates. Neurophysiological studies, begun in the 1940's and 1950's, uncovered two trends that appeared to characterize the evolution of vertebrate vision: first, that primitive vertebrates lack binocular vision, and the extent of binocularity has increased during vertebrate phylogeny; and second, that visual processing in the brain of primitive vertebrates takes places primarily in peripheral visual areas such as the retina, whereas in "higher" verte-

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brates there is relatively less peripheral processing and relatively more secondary processing of visual information.

A recent book provides new insights into the neurobiology of vision in "lower" vertebrates.

> Visual Behavior in Salamanders. By Gerhard Roth. Studies of Brain Function Series, Vol. 14, Springer Verlag, Berlin, 1987, 301 pp. $110.00.

This book is a compendium of recent studies on the visual system of salamanders, covering topics ranging from optics of the eye, to retinal and tectal processing of visual input, and the elusive neurological problems of depth perception and sensorimotor interfacing. Virtually every aspect of visual behavior is covered from a point of view emphasizing that salamanders are unique among vertebrates, rather than representative of the "primitive" vertebrate condition.

The first chapter of the book is a review of the taxonomy, distribution, and ecology of virtually all living genera of salamanders, organized taxonomically and written from a strongly phylogenetic perspective. For each family of salamanders, the geographic distribution, ecological attributes, and major lineages that comprise the group are reviewed. Major evolutionary trends within the salamanders, such as loss of the free-living larval stage, lunglessness, paedomorphosis and miniaturization, are also discussed. The author is determined to leave the reader with an overall impression of the varied life-histories and evolutionary fates of the diverse families of salamanders—data which prove invaluable in interpreting much of the neuroethological research which comes later.

Chapter two deals with the range of visually-guided behavior that salamanders exhibit, primarily feeding behavior. The first part of this chapter treats the functional morphology of feeding mechanisms of salamanders in some detail. Especially with regard to the mechanisms of feeding, all salamanders are not equal. Derived species of salamanders exhibit highly projectile tongues that must be wielded with millisecond accuracy (familiar to many from the widely reprinted photos by the author), while relatively primitive salamanders, such as *Ambystoma,* have relatively slow, unspecialized, short-range tongues. The basic parts that comprise the tongue are similar among salamanders, but the functional characteristics of tongue projection are not, and the data on functional diversity presented in this chapter have important implications for sensorimotor interfacing, discussed in a later chapter.

Given this range of feeding morphologies, it is not surprising that salamanders also exhibit a diversity of natural diets, and of prey preferences (measured in the laboratory using various neuroethological techniques). What emerges from these neuroethological studies is that there is a reasonable correspondence between preferred prey stimulus configuration and natural diets, which is supported by a relatively large amount of field and laboratory data. Salamanders can be divided into at least two major categories on the basis of preferred prey: those that prefer elongate, slow, continuously-moving stimuli and those that prefer faster, compact, discontinuously-moving prey. Stimulus preferences are strongly affected by both the velocity and the continuity of stimulus motion. Evidence that experience modifies stimulus preferences is also presented.

In this chapter, we also learn that salamanders (and toads) can, in fact, detect stationary prey, and that there is a complex interaction between olfaction and vision in controlling feeding behavior. While the chapter is mostly concerned with feeding behavior, visual mate recognition, depth perception, and optokinetic nystagmus are briefly treated.

The third chapter covers the morphology and function of salamander eyes, including visual acuity, accommodation, and an interesting study of the effects of miniaturization on eye structure. Among the smallest of land vertebrates, miniaturized salamanders with extremely small eyes solve their vision problems in a variety of ways (Linke et al., 1986). Roth compares the morphology of retinal elements, including photoreceptors, bipolar cells, amacrine cells, and retinal ganglion cells, among species of salamanders, and he also draws comparisons between salamanders and frogs.

Chapter four treats the anatomy of the salamander brain in general, and the anatomy of visual projections in particular. Perhaps the most striking new information contained in this chapter is the observation that, in direct-developing salamanders of the family Plethodontidae, there is a strong binocular projection from the retina to the optic tectum. These derived salamanders are the only known amphibians that have evolved frontal eyes and binocular vision that parallels the binocular vision of amniotes. Furthermore, binocularity develops early in bolitoglossine embryos, so that a fully binocular optic tectum is present at the time of hatching (Rettig et al., unpublished). A second interesting comparison is made between frogs and salamanders in the structure of the optic tectum. Salamanders have long been thought to possess a primitive, unlayered optic tectum in which there is little structural or functional differentiation of cell types, in contrast to the highly layered, differentiated tectum of frogs and amniotes. Roth's analysis of the salamander tectum shows, however, that the cell types and the secondary and tertiary visual pathways are essentially similar in salamanders and frogs, the difference lying primarily in the fact that a single population of tectal neurons fails to migrate in salamanders (Roth et al., 1989).

Chapter five is a detailed account of the neurophysiological properties of visual neurons and the role of visual neurons in prey recognition. This area of research is controversial. Early studies of the response properties of retinal ganglion cells (RGC's) led to the idea of "detector" neurons, individual cells which, like the proverbial "grandmother neuron", respond strongly to highly specific stimuli. Electrophysiological recordings from the frog retina suggested the presence of "bug detectors", RGC's that respond strongly to small, compact, visual stimuli (Lettvin et al., 1959, 1961; Maturana et al., 1960). Later, RGC's that responded to elongate, visual stimuli (e.g., "worm-detectors") were also found (Ewert, 1974). These discoveries eventually led to the idea that prey recognition in amphibians was performed mostly (if not solely) by retinal detector cells, whose output formed a command system for the motor program leading to prey capture.

Numerous recent electrophysiological studies of the response properties of visual neurons in the amphibian retina and optic tectum have provided new evidence that prey recognition in amphibians is more complex than earlier experiments had suggested (Ewert, 1987; Grüsser and Grüsser-Cornehls, 1976; Grüsser-Cornehls and Himstedt, 1973). The new interpretation stems chiefly from the observation that the stimulus preferences of individual visual neurons are strongly velocity dependent. A single neuron may prefer "bugs" at high velocities but "worms" at lower velocities. Furthermore, the response properties of different neurons change with velocity in different ways. The bottom line is that most individual neurons in the retina and in the optic tectum have response properties that preclude them from being "detector cells", because their preferred stimulus orientations change with stimulus velocity or with distance from the retina (see below). These new data suggest that, contrary to previous interpretations, object recognition must result from the activation of a network of neurons that possess many different kinds of response properties, rather than the activation of a population of detector neurons with response properties that correspond to particular types of prey items in the environment. In the book, Roth proposes a new "recognition module" model, in which the integrated output of many different tectal neurons functions as a prey recognition network. Thus, it appears that object recognition in amphibians is more complex, and more like amniotes, than previous work has suggested.

A second argument that also works against the "detector cell" hypothesis is that neither retinal ganglion cells nor visual neurons in the optic tectum are capable of distinguishing large stimuli that are far away from small stimuli that are closer to the retina (i.e., these visual neurons lack size constancy). These neurons respond only to the relative size of the image on the retina, not to the absolute size of the object (taking its distance from the retina into account). At some stage between image reception and motor output, the distance of the object must be estimated, and the distance information must be integrated with other properties of the stimulus in order that only stimuli of the appropriate absolute size trigger motor commands for feeding. If an object of a given size on the retina is, in fact, a large object far away rather than a small object nearby, a motor command that triggers prey capture may be entirely inappropriate. Sticking the tongue out at an approaching predator is clearly a futile waste of precious escape-time.

Roth discusses this and other issues in his sixth and final chapter, "Conclusions and speculations on the neural guidance of visual behavior in salamanders." Two additional problems that are discussed in detail are depth perception and the integration of sensory input with motor output in the feeding system.

For those readers who are primarily interested in herpetology, this book is an excellent overview of the latest studies on salamander vision, as well as a review of the basic anatomy and physiology of the amphibian visual system. For those readers interested in neurobiology as well, this book provides a stimulating and controversial view of neural integration in the amphibian visual system. Most importantly, this book exemplifies a research strategy that combines "organismal" and "mechanistic" studies, a research program that is directed toward a mechanistic explanation for the evolution of biological diversity.

ON THE NECESSITY OF MECHANISTIC ORGANISMAL RESEARCH

Of the many, diverse goals of basic biological research, perhaps the best understood by non-biologists is the necessity of understanding the mechanistic basis for the diverse physiological processes that sustain life. [I use the term "mechanistic" here to include explanations of function based on molecular, biochemical, and cellular processes within organisms.] A second goal that is perhaps less appreciated both within and beyond the community of practicing biologists is an understanding of "organismal" processes, such as evolutionary diversification. [I use the term "organismal" to refer to that body of research concerned with studying processes involving whole organisms, in contrast to processes occurring within organisms.]

These two goals are currently pursued largely independently, without reference to each other, for a variety of different reasons. On the one hand are physiologists, who have focused their attention on understanding a few, hopefully representative "systems", and elucidating general principles from intensive studies of a small number of species, justly claiming that their work is too time-consuming to lend itself to a comparative approach in which many species are studied. Often, this approach leads to over-generalization of the results, when concepts derived from studies of a single species are optimistically applied to members of much larger taxonomic groups.

On the other hand are organismal biologists, who have concentrated their efforts toward understanding evolution, and have directed their interests primarily toward explaining why evolution has occurred in terms of fitness and natural selection. Current research in organismal biology has seen a flowering of studies in which hypotheses of phylogeny have been integrated with ecological and/or morphological research. Despite this recent emphasis on phylogenetic (or "transformational") analyses (Lauder, 1982), the question "why are organisms the way they are?" and the answer "because natural selection has made them that way" have dominated much of modern organismal biology (but see, for example, Wake, 1982).

The research strategy of Gerhard Roth and colleagues addresses a question that is central to an understanding of both physiological mechanisms and evolutionary processes, a question that has been largely overlooked by modern evolutionary biology. This is the question of the physiological and ontogenetic basis of evolutionary transformation, or "how" differences arise between ancestor and descendant. The fundamental question is, "how can an ancestral developmental program be modified to produce the diversity that is observed among descendant species?" ["A favorable mutation arises," is the superficial explanation that has directed attention away from this interesting problem.] It is highly desirable to know, step by physiological step, the mechanistic basis for developmental modifications that result in evolutionary diversification—the physiological details of changes in the developmental program that account for the differences between a descendant and its ancestor.

The question of how differences arise between ancestors and their descendants is philosophically allied to the structuralist school (including both pure morphology and transcendental morphology), in that the phenomenon to be explained is the process of transformation of structure. In contrast, most modern evolutionary biologists (allied to the functionalists) explain why a structure was transformed, in terms of fitness effects and natural selection.

What does one need to know in order to answer the "how" question for a given characteristic within a given lineage? First, one needs a hypothesis of the phylogenetic relationships of species within the lineage (i.e., a cladogram). Second, one needs to know the distribution of the ecological, behavioral, physiological, and ontogenetic (etc.) characteristics that have evolved within the lineage. Third, one needs to know the physiological and ontogenetic bases for observed variation in the characteristic(s) of interest. This is the new part. From a combination of these different types of information, we can construct mechanistic explanations for how descendant species come to develop characteristics that are different from those of their ancestors. This goes beyond the phylogenetic approach of identifying transformational events (i.e., incorporating cladograms into our research), by investigating the physiological and ontogenetic bases for the transformational events we have identified. This is, more or less, the approach that is exemplified by Roth's research on aspects of visual behavior in salamanders, and why his book on the visual system contains so much information on salamander ecology and phylogeny.

Two examples from Roth's book illustrate the value of studying the ontogenetic and physiological bases of evolutionary transformation: (1) lamination (or lack thereof) in the optic tectum of salamanders; and (2) ontogenetic repatterning and the evolution of binocular vision in salamanders.

Herrick (1948) described in detail the laminae of the optic tectum of salamanders. He noted that salamanders have reduced lamination of the tectum and fewer different types of tectal neurons than frogs, leading numerous comparative neurobiologists (cf. Leghissa, 1962) to state that salamanders possess the most primitive tecta found among vertebrates. Recent work by Roth and co-workers, on a large number of salamander species (Roth et al., 1989) has shown that, while it is in fact true that the salamander tectum has fewer laminae and fewer cell types than most other vertebrates, primary, secondary, and even tertiary visual pathways are virtually identical in frogs and salamanders. In frogs, the tectum becomes laminated primarily because small-field neurons migrate laterally into final positions that correspond to the outer laminae. Furthermore, the salamander tectum appears unlaminated because these cells fail to migrate. This research has identified a phylogenetic transformation (i.e., from a laminated tectum in the common ancestor of salamanders and frogs to an unlaminated tectum in living salamanders), and a developmental mechanism (i.e., failure of small-field neurons to migrate). Current research in Roth's laboratory is examining the cellular and molecular bases for failure of migration.

A second example is the evolution of binocular vision in salamanders. Prevailing dogma holds that, in salamanders, the eyes are strongly lateral with non-overlapping visual fields and the retinal ganglion cells project to the contralateral optic tectum (Romer and Parsons, 1986). Rettig, Roth, and Wake (unpublished) discovered that plethodontid salamanders in general, and bolitoglossine salamanders in particular, exhibit a much greater ipsilateral retinofugal projection than other anamniotes (i.e., each retina projects to both sides of the optic tectum). Furthermore, whereas in most plethodontid salamanders the ipsilateral projections continue to develop late into ontogeny, they are fully developed in bolitoglossine plethodontids at the time of hatching. The phylogenetic transformations here are from contralateral to bilateral retinofugal projections in the common ancestor of the plethodontid salamanders, and from late-developing to early-developing ipsilateral retinofugal projections in the common ancestor of bolitoglossine salamanders. Future research on the ontogenetic and physiological mechanisms of retinal ganglion cell development in these salamanders, if successful, will reveal the mechanistic basis for the evolution of binocular vision in this group.

Because every species is the product of a unique evolutionary history and a unique ontogenetic program, it is naive of physiologists to proceed in their research as if the species that they study had no evolutionary history, and no developmental or functional constraints. The current physiological function of any existing species is a product of its ancestry, its ontogeny, and constraints imposed by the integration of the organism as a whole.

Because of phylogenetic and developmental constraints, it is naive of evolutionary biologists to ignore the problem of *how* new phenotypes arise. The fitness of a particular phenotype depends upon the background of other characteristics within the whole organism and is, therefore, species- or lineage-specific. Whether or not a particular phenotype will, or can, arise depends not only upon selective factors acting on the organism, but also on its compatibility with the developmental program. The only mechanism for the production of new phenotypes is modification of existing developmental programs. There are many conceivable developmental and physiological routes to adaptedness, and it matters *how* you get there, as well as why.

It is refreshing to see that, at a time when there is so much antagonism between "mechanistic" and "organismal" biology, some researchers are attempting to integrate these fields to provide a new set of developmental and physiological explanations for biological diversity. While there are clearly many interesting questions in evolutionary biology that require a mechanistic answer, their formulation requires an organismal perspective.

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