

**Goals of neuroethology.** Theodore H. Bullock.  
*BioScience* v40.n4 (April 1990): pp244(5).

**Full Text:**COPYRIGHT American Institute of Biological Sciences 1990

## **Goals of Neuroethology**

As early as the beginnings of rational medicine, people have sought connections between brain and behavior. The Edwin Smith surgical papyrus of about 1700 BC, itself a copy of a much older document, suggested that human behavior anomalies such as aphasia, paralysis, and seizures are functions of the brain. Phrenology and its excesses in the 1800s grew out of solid evidence of cortically localized speech functions. In this century, Sir Charles Sherrington (Nobel laureate in 1932) elucidated the neural basis of walking and scratching in dogs. Walter Rudolph Hess (Nobel laureate in 1949) discovered hypothalamic centers for emotional expression and mood switching in cats. Long before the term neuroethology was introduced in the 1960s, some workers in the broad field of neuroscience (a term introduced about 1960) were motivated by a concern to understand behavior. The number of these workers has multiplied from perhaps a few dozen before 1900 to thousands today, most of whom identify with the field of psychology, perhaps a thousand with neuroethology.

## **Neuroethology defined**

The invertebrate physiologist Graham Hoyle (1970, 1975, 1984) advocated a strict definition; neuroethology is the accounting for proven innate behavior in terms of single, identified cells. But if neuroethology is what neuroethologists do, the dues-paying membership of the International Society of Neuroethology votes to define this young science broadly. In the broad sense in which it is generally used today, neuroethology includes studies on protozoans and humans, reflexes and cognition, ion channels and brain/body ratios, learning in snails, and the innate understanding of squirrel monkey calls by squirrel monkeys.

From molecular to cognitive, neuroethology demands the full technical armamentarium of modern neuroscience. It is not a parallel to neurophysiology, neuroanatomy, or neurochemistry, which are defined by a discipline applied to a system. Neuroethology has two faces. Viewed from one side, it is any neuroscience applied to species-characteristic behavior. Viewed from the obverse, it is any ethology that explicitly seeks to make statements about the neural causation, ontogeny, and evolution of a behavior.

There is no sharp line separating neuroethology from psychobiology, behavioral neurobiology, and similar terms in common use. Species-characteristic behavior is not necessarily purely innate and does not exclude learned behavior or the process of learning, even when the task acquired is artificial or maladaptive. The term neuroethology is used when there is emphasis on or relevance to the understanding of natural behavior.

Neuroethology is not only concerned with causations and functions. For example, how does echolocation work in terms of neurons? It is also concerned with development and evolution, in terms of molecules, motor control, and mental events. The field is inevitably both reductionist and integrative, both comparative and general,

though usually not in the same study.

### **Basic issues, not only natural history**

Because the usual material for neuroethological research is some discrete, obviously adaptive piece of natural behavior, often species-peculiar, such as singing, echolocating, or communicating by feeble electrical pulses, neuroethology is sometimes mistakenly defined in terms of elucidating the peculiar cases chosen. In this way, it has to some degree acquired the image of natural history--significant to bird lovers, bat buffs, and fish fanciers, but not worth the attention of mainstream neurobiologists. This view implies that neuroethology does not have broad goals, questions that tie it together, and tough issues that belong to the interdisciplinary perspective. The main message of this article is that neuroethology has such goals, some of which may be uniquely valuable as access to questions of the most general significance.

Let me tip my hand by naming two of these questions here. One is whether there are principles of operation in the brain hitherto unfamiliar in communication science. Another is whether, in spite of a prevailing counteropinion, evolution has created systems with greater and greater complexity.

The goals of neuroethology that extend beyond curiosity about particular species and their peculiar habits of life might be shoehorned into three rubrics, or three Rs: roots, rules, and relevance.

### **What are our roots?**

Roots refers to the goal of achieving perspective on the place in nature accorded to the brain of any given species. What are its antecedents? Within this brain, what is new and what is old? Brain and behavior, compared to any other systems or functions I know of, have evolved the greatest distance (of course, neither smoothly nor always). Compared to the difference between counting on fingers and on a giant computer or between atoms and galaxies, the span of complexity is far greater between the humblest nervous systems in sea anemones and the brain in humans.

Leaving aside the how and why of brain evolution, consider the what: the crucial novelties in structure and physiology of the brain in the higher animals. This organ is the outstanding achievement of animal evolution; inquiry into the differences between successively more advanced levels of animal organization is a major and relatively neglected chapter in biology.

Two strategies must be distinguished: comparing higher taxonomic categories for macro-level differences in brain structure and function and in behavior and comparing lower taxonomic categories for micro-level differences. The former is more likely to encounter different major grades of complexity, not necessarily or obviously adaptive. The micro-level, dealing with lateral divergence or radiations, is more likely to deal with discrete adaptations at approximately the same grade of complexity.

### **What are the rules?**

Rules refers to the goal of achieving insights into the nuts and bolts of neural mechanisms are often best revealed mechanisms are often best revealed in specially favorable species.

The rules or mechanistic insights may be reductionist (component oriented) or focused on higher-level systems. The inquiry may be oriented either top-down or bottom-up, that is, starting from a behavior and dissecting its components or starting from the cellular or subcellular level to predict consequences. Each of these approaches has its value and advantages. In any case, the strategy under this rubric is largely aimed at

uncovering principles that might apply widely among species.

### **What is the human relevance?**

Relevance refers to the goal of discovering roots or rules that bear on some human problem. Preferably, the problem is recognized by the man in the street in his role as taxpayer and as a potential supporter or adversary to the laboratory use biological materials, whether animals or fetal tissue.

Human problems are not confined to disease; they include how the mind develops in undernourished infants, in environments impoverished in stimuli, or when exposed to substances toxic in low doses over long times. Relevant discoveries are often serendipitous, but planned hunting among taxa is now widespread, particularly in neurochemistry.

### **Range of neuroethology**

What kinds of findings or assertions satisfy the goals of neuroethology? I pointed out already that it cuts across levels and disciplines, uses them all, and is not identified with only one approach such as unraveling the circuits of identified cells--though this approach is certainly a source of many advances.

From its central focus on the neural analysis of species-characteristic behaviors, neuroethology ranges widely: reductionist approaches extend to the cellular, subcellular, and molecular levels and coexist with systems analyses of cells, from small sets up to large assemblies. The explanatory insight for the behavior under study may come by identifying chemical components, anatomical arrangements, or physiological proclivities at each organizational level. Properties of single cells and of the separate loci within single cells, such as the relative abundance of different kinds of ion channels and the distribution of receptors for different transmitters and modulators, grade into connectivity and the distribution of many distinct forms of integrative capabilities of the cells. In the matter connection, I like to refer to cells' personality traits, to emphasize their variety.

Some species are favorable for analysis in terms of identifiable cells, particularly among nematodes, leeches, insects, decapod crustacea, and pulmonate and opisthobranch gastropods. Other taxa are favorable for analysis in terms of cell groups (known as subnuclei and nuclei, laminae, modules, and maps of several kinds); density of synapses; degrees of synchrony among cell assemblies; rhythms and resonances; the fine structure in gray matter and neuropile; and, on the scale of fractions of millimeters and fractions of seconds, cooperativity among cells--for which several measures are in use, such as domains of coherence and fractal dimensions.

### **Diversity among neuroethologists**

Neuroethologists are far from a club of like-minded researchers. They can differ fundamentally in mind set. Workers divide on the issues of the most favorable taxa and the best approach. Some advocate mammals, as close as possible to humans; others emphasize the special advantages of simpler systems and concentrate their efforts either on soft-bodied gastropods or leeches (known as squishies) or on hard-bodied arthropods (crunchies). Some approaches are relatively neglected, out of fashion, or out of touch with the others, although not necessarily without promise.

The debate continues, as it did in the days of Jacques Loeb (1900), as to whether the prime approach for a behavior physiologist is reductionist or integrationist: whether unraveling neuronal circuits is a more opportune strategy than going directly to the complex mammalian cerebral systems and subsystems, and whether single-unit recording or compound field potential recording is more advantageous. Should the research have a

chemical or an electrical emphasis, study rhythms of the stomach or mating dances, emphasize motor versus sensory versus cognitive aspects of behavior, or employ empirical experiments or modeling or the use of nonlinear dynamical analysis?

### **Sampling of recent advances**

This special issue of BioScience presents a series of exemplary studies in neuroethology. These are not balanced by taxonomic representation or by behavioral domain. Most of them deal with insects, fish, or frogs doing unfamiliar things that proved favorable for analysis.

Andrew Bass (page 249 this issue) describes vocalizing fish and the central, as well as peripheral, machinery evolved for production and control of acoustic signals. Catherine Carr (page 259 this issue) also chooses fish and social communication, but in a different modality. She describes feeble electric pulses discharged at controlled rates, night and day, and serving both in communication and in locating objects (electrolocation) through separate, parallel systems of central sensory analyzers.

Communication is also the theme of the article by Peter Narins (page 268 this issue) on another unfamiliar modality: seismic signaling among frogs. This system, like that of electrolocation, has such incredible sensitivity that we may be distracted sensitivity its achievements in signal-in-noise discrimination and recognition of ethologically important sign stimuli.

Darcy Kelley and Dennis Gorlick (page 275 this issue) show how such discrimination of social signals--for aggression in Siamese fighting fish and courtship in African clawed frogs--is under the control of hormones. David Ingle and Karin Hoff (page 284 this issue) analyze the brain mechanisms in another form of behavior in frogs, the avoidance reactions to visual stimuli that include presumptive threats. Although the behavior is stereotyped in form, these authors find evidence that it uses both short-term and long-term memories in guiding direction, manifesting the two aspects of triggering and biasing stereotyped behavior. Alexander Borst (page 292 this issue) looks into the ways available and the means employed by flies to recognize the gestalt of moving visual images that guide its behavior in the apparently simple act of landing.

### **Tips to other good bets**

I hope this selection of six stories, based on three classes of animal, will stimulate you to seek further among the wealth of equally interesting stories, all unfinished, like whodunits cut off in mid-yarn. For example, George Mackie (in press) compares the sets of giant axons that mediate the jet-propelled swimming of the jellyfish, *Aglantha*, and the squid, *Loligo*, pointing out a series of similarities and a series of differences. Malcolm Burrows and his coworkers (1988) carefully scrutinize individual unidentified neurons in the locust, *Schistocerca*, compiling a list of cells that perform their functions in the neural circuit without nerve impulses--as is true of most neurons in the vertebrate retina. Eric Kandel and his coworkers (1989), Daniel Alkon (1987), and others have carried to the subcellular and molecular level the identification of mechanisms underlying learning in opisthobranchiate gastropods such as *Aplysia* and *Pleurobranchia*.

Among the vertebrates, fish and anurans are features in the articles in this BioScience issue. Reptiles have also proven uniquely valuable. They have given behavioral context to the widespread vertebrate sensory system, the vomeronasal receptors (Halpern 1987). Sparrows, canaries, and other finches have been studied for the elegant neural bases for learned song (Gahr and Konishi 1988, Goldman and Nottebohm 1983, Konishi 1985, Konishi and Akutagawa 1988, Margoliash and Konishi 1985, Margoliash 1986, Nottebohm et al. 1976) and owls for their accurate localization of sound sources, both in azimuth and in elevation (Knudsen 1988,

Knudsen and Knudsen 1989, Olsen et al. 1989, volman and Konishi 1989).

Not to neglect the mammals, I point to the great advance in bringing circadian rhythm research inside the head when Robert Moore and his colleagues (see Johnson et al. 1988a,b) showed in rats the special involvement of the tiny suprachiasmatic nucleus, the principal hypothalamic target of direct optic nerve fibers. I have already referred to the classic discoveries Hess made of the several hypothalamic centers for affective behavior in cats.

Human neuroethology embraces the landmark find (1860s and 1970s) of aphasia, an inability to speak or understand speech, produced by restricted lesions in brain regions that now bear the names of their discoverers, Paul Broca and Carl Wernicke. Neuroethologists are active on many fronts today. For example, there is the split-brain research into the segregation of function between hemispheres (Gazzaniga 1985), the study of congenitally deaf users of sign language who suffer strokes or localized lesions causing signing aphasia (Poizner et al. 1987), and the demonstration using xenon imaging showing increased blood circulation in the supplementary motor cortex when a patterned sequence of finger movements is thought through over and over again (intention), without actually willing the movement (Roland et al. 1980, Roland and Friberg 1985).

### **But most questions are unsolved**

To counterbalance an impression of euphoria--that we have plenty of new insights--a few of the myriad of unsolved puzzles might be listed.

\* What are the roles of brain control of the retina and of hair cells in the inner ear? The widespread occurrence of both suggests we have to deal with the evolution of a significant process.

\* What do the great size differences of different brain areas mean in terms of behavioral correlates, for example the differences in cerebellum among species of elasmobranchs? What is the meaning of the great differences in degree of lamination of the dorsal cochlear nucleus among species of rodents? Must we assume everything is adaptive?

\* What are the physiological bases of slothfulness in sloths? Are they quite different from laziness in cats or sluggishness in the slow loris?

### **Implications basic to evolutionary biology**

Why do I claim that neuroethology has implications basic to neuroscience, cognitive science, philosophy, and evolutionary biology? Let me start with evolution. Consider the assertion that, more than any other system or function of animals, the nervous system and behavior manifest a distinction between evolutionary adaptive radiation and advance in level of complexity.

The vast majority of evolutionary changes are called adaptive radiations and concern lower taxa--species, genera, and families. These changes can be considered as lateral moves into different niches, because there may be specialization but no necessary or inarguable increase in complexity of the organisms. The small minority, but for our purposes the interesting evolutionary changes, are vertical leaps. They have created, or allowed to survive, higher taxa that may or may not be specialized but are on a new plane of complexity--by a potentially rigorous definition.

I use complex here in its dictionary meaning: having more parts, processes, interrelations, aspects, and details.

Complexity can be estimated by the count of parts, processes, and so on, or by the number of bits of information necessary to describe the system under consideration.

My assertion then can be restated this way: the nervous system and behavior, more than any other system or functional domain, manifests occasional advances (as well as occasional regressions) in grade of complexity between some of the higher taxa--some phyla, some classes, and some orders. Higher animals can be defined as those that are more complex than lower species--not necessarily better adapted or more perfect but simply using more parts, processes, and interrelationships. The great resistance to using the terms higher animals and lower animals, reflected in some recent literature, can be seen as a leaning over backwards to avoid misunderstood meanings of these basically neutral words. They carry no automatic connotations of value or anthropocentricity.

The reason this assertion is so important for evolutionary biology is that the dimension of complexity has generally been overlooked, downgraded, or denied and is not today recognized as a major problem in biology, whereas the span of complexity is in fact so great in the nervous system and behavior. Although Protozoa are highly successful, and sponges and other lower invertebrates have great survival value, insects are vastly more complex, cephalopods still more so, and some vertebrates, at least mammals, higher yet. Obviously, there is no clear relation to adaptation, reproductive potential, or survival value.

It is not essential to agree on the value or even the description of what has been achieved--adaptability, ecological dominance, or some other imagined, unmeasured candidate value. There would certainly be disagreement if we tried to rank lower, or even many higher, taxa, such as genera or families, in respect to complexity.

The great relevance to neuroethology of this assertion is that the obvious advances of insects over jellyfish and of mammals over insects have not yet been scientifically documented in objective assessments of behavior; they rest mainly on neuroanatomy. Neurophysiology, apart from anatomy, is farther behind than behavior. Although the evolution of vastly increased complexity in brain and behavior, from the simplest phyla to the most advanced, is one of the great facts of nature, it has been astonishingly neglected as a research subject. Recognizing, cataloging, and characterizing the advances in anatomy, physiology, and behavior among taxa far enough apart to show unequivocal differences in level of complexity, and then attempting to distinguish these traits from lateral radiations, surely constitutes a major set of tasks and challenges for biology.

### **Even wider implications**

Another assertion is behind the claim of relevance of neuroethology to neuroscience, cognitive science, and philosophy. As an article of faith, a large but reasonable prediction of the progeny to be expected from the marriage of modern neural computation and experimental neuroethology (if we choose the correct species, brain system, technical approach, and method of analysis) is that we will discern new principles in the brain's operation, its handling of data, its segregation of functions, and its forms of representing information.

I am quite sure new principles are there, waiting to be uncovered--principles unfamiliar to contemporary communications theory, computer theory, and neural network theory. The most unfamiliar ones are likely to involve higher cognitive functions. But even relatively lower level processing, such as cerebellar and tectal computation, now seem likely to embody fundamental novelties.

When such novel principles are discerned--perhaps vaguely at first, probably little by little--or at least when they are implicated in cognitive functions, another domain classically reserved for philosophers will have moved into the domain of objective science. Churchland (1986) has pointed out that this shift has already

happened with the phenomenal progress of higher central neurophysiology, causing some anguish on the part of "those who suppose that science and humanism must be at loggerheads." She opines, "It would be amazing if the new theories and the new discoveries did not contain surprises of such magnitude as to constitute a revolution in understanding. . . at least the equal of the Copernican and Darwinian revolutions."

### References cited

- Alkon, D. 1987. *Memory Traces in the Brain*. Cambridge University Press, Cambridge, UK.
- Bass, A. 1990. Sounds from the intertidal zone: neuroethology of vocalizing fish. *BioScience* 40: 249-258.
- Borst, A. 1990. how do flies land? *BioScience* 40: 292-299.
- Burrows, M., G. J. Laurent, and L. H. Field. 1988. Proprioceptive inputs to nonspiking local interneurons contribute to local reflexes of a locust hindleg. *J. Neurosci.* 8: 3085-3093.
- Carr, C. E. 1990. Neuroethology of electric fish. *BioScience* 40: 259-267.
- Churchland, P. S. 1986. *Neurophilosophy*. MIT Press, Cambridge, MA.
- Gahr, M., and M. Konishi. 1988. Developmental changes in estrogen-sensitive neurons in the forebrain of the zebra finch. *Proc. Natl. Acad. Sci.* 85: 7380-7383.
- Gazzaniga, M. S. 1985. *The Social Brain: Discovering the Networks of the Mind*. Basic Books, New York.
- Goldman, S. A., and F. Nottebohm, 1983. Neuronal production, migration, and differentiation in a vocal control nucleus of the adult female canary brain. *Proc. Natl. Acad. Sci.* 80: 2390-2394.
- Halpern, M. 1987. The organization and function of the vomeronasal system. *Annu. Rev. Neurosci.* 10: 325-362.
- Hoyle, G. 1970. Cellular mechanisms underlying behavior-neuroethology. *Adv. Insect Physiol.* 7: 349-444.
- Hoyle, G. 1975. Identified neurons and the future of neuroethology. *J. Exp. Zool.* 194: 51-74.
- Hoyle, G. 1984. The scope of neuroethology. *Behav. Brain Sci.* 7: 367-412.
- Ingle, D. J., and K. vS. Hoff. 1990. Visually elicited evasive behavior in frogs. *BioScience* 40: 284-291.
- Johnson, R. F., R. Y. Moore, and L. P. Morlin. 1988a. Loss of entrainment and anatomical plasticity after lesions of the hamster retinohypothalamic tract. *Brain Res.* 460: 297-313.
- Johnson, R. F., R. Y. Moore, and L. P. Morin. 1988b. Running wheel activity in hamsters with hypothalamic damage. *Physiol. Behav.* 46: 755-764.
- Kandel, E. R., P. Goelet, V. F. Castellucci, P. Montarolo, N. Dale, and S. Schacher. 1989. Initial steps toward a molecular biology of long-term memory. Pages 119-148 in S. Chien, ed. *Molecular Biology in Physiology*.

Raven Press, New York.

Kelly, D. B., and D. L. Gorlick. 1990. Sexual selection and the nervous system. *BioScience* 40: 275-283.

Knudsen, E. I. 1988. Sensitive and critical periods in the development of sound localization. Pages 303-320 in S. S. Easter Jr., K. F. Barald, and B. M. Carlson, eds. *From Message to Mind: Directions in Developmental Neurobiology*. Sinauer Associates, Sunderland, MA.

Knudsen E. I., and P. F. Knudsen. 1989. Vision calibrates sound localization in developing barn owls. *J. Neurosci.* 9: 3306-3313.

Konishi, M. 1985. Birdsong from behavior to neuron. *Annu. Rev. Neurosci.* 8: 125-170.

Konishi, M., and E. Akutagawa. 1988. A critical period for estrogen action on neurons of the song control system in the zebra finch. *Proc. Natl. Acad. Sci.* 85: 7006-7007.

Loeb, J. 1990. *Comparative Physiology of the Brain and Comparative Physiology*. G. P. Putman's Sons, New York.

Mackie, G. O. In press. Giant axons and control of jetting in *Loligo* and *Aglantha*: why squid aren't jellyfish. *Can. J. Zool.*

Margoliash, D. 1986. Preference for autogenous song by auditory neurons in a song system nucleus of the white-crowned sparrow. *J. Neurosci.* 6: 1643-1661.

Margoliash, D., and M. Konishi. 1985. Auditory representation of autogenous song in the song system of white-crowned sparrows. *Proc. Natl. Acad. Sci.* 82: 5997-6000.

Narins, P. M. 1990. Seismic communication in anuran amphibians. *BioScience* 40: 268-274.

Nottebohm, F., T. M. Stokes, and C. M. Leonard. 1976. Central control of song in the canary, *Serinus canarius*. *J. Comp. Neurol.* 165: 457-486.

Olsen, J. F., E. I. Knudsen, and S. D. Esterly. 1989. Neural maps of interaural time and intensity differences in the optic tectum of the barn owl. *J. Neurosci.* 9: 2591-2605.

Poizner, H., E. Klina, and U. Bellugi. 1987. *What the Hands Reveal About the Brain*. Bradford Books, MIT Press, Cambridge, MA.

Roland, P. E., and L. Friberg. 1985. Localization in cortical areas activated by thinking. *J. Neurophysiol.* 53: 1219-1243.

Roland, P. E., B. Larsen, N. A. Lassen, and E. Skinjoj. 1980. Supplementary motor area and other cortical areas in organization of voluntary movements in man. *J. Neurophysiol.* 43: 118-136.

Volman, S. F., and M. Konishi, 1989. Spatial selectivity and binaural responses in the inferior colliculus of the great horned owl. *J. Neurosci.* 9: 3082-3096.

Theodore H. Bullock is a professor in the Department of Neurosciences, University of California, San Diego, CA 92093. [C] 1990 American Institute of Biological Sciences.

**Source Citation:**Bullock, Theodore H. "Goals of neuroethology." *BioScience* 40.n4 (April 1990): 244(5). *Expanded Academic ASAP*. Thomson Gale. UC Riverside (CDL). 18 May. 2006  
<[http://find.galegroup.com/itx/infomark.do?&contentSet=IAC-  
Documents&type=retrieve&tabID=T002&prodId=EAIM&docId=A9147810&source=gale&srcprod=EAIM&userGroupName=ucriverside&version=1.0](http://find.galegroup.com/itx/infomark.do?&contentSet=IAC-Documents&type=retrieve&tabID=T002&prodId=EAIM&docId=A9147810&source=gale&srcprod=EAIM&userGroupName=ucriverside&version=1.0)>.

**Thomson Gale Document Number:**A9147810

© 2005 Thomson Gale, a part of The Thomson Corporation.  
Thomson and Star Logo are trademarks and are registered trademarks used herein under license