NEUROETHOLOGY

Neuroethology is the evolutionary and comparative approach to the study of animal behavior and its underlying mechanistic control by the nervous system. This interdisciplinary branch of behavioral neuroscience endeavors to understand how the central nervous system translates biologically relevant stimuli into natural behavior. For example, many bats are capable of echolocation which is used for prey capture and navigation. The auditory system of bats is often cited as an example for how acoustic properties of sounds can be converted into a sensory map of behaviorally relevant features of sounds. Neuroethologists hope to uncover general principles of the nervous system from the study of animals with exaggerated or specialized behaviors.

As its name implies, neuroethology is a multidisciplinary field composed of neurobiology (the study of the nervous system) and ethology (the study of animal behavior in natural conditions). A central theme of the field of neuroethology, delineating it from other branches of neuroscience, is this focus on natural behavior, which may be thought of as those behaviors generated through means of natural selection (i.e. finding mates, navigation, locomotion, predator avoidance) rather than behaviors in disease states, or behavioral tasks that are particular to the laboratory.

Philosophy

Neuroethology is an integrative approach to the study of animal behavior that draws upon several disciplines. Its approach stems from the theory that animals' nervous systems have evolved to address problems of sensing and acting in certain environmental niches and that their nervous systems are best understood in the context of the problems they have evolved to solve. In accordance with Krogh's principle, neuroethologists often study animals that are "specialists" in the behavior the researcher wishes to study e.g. honeybees and social behavior, bat echolocation, owl sound localization, etc.

The scope of neuroethological inquiry might be summarized by Jörg-Peter Ewert, a pioneer of neuroethology, when he considers the types of questions central to neuroethology in his 1980 introductory text to the field:

1. How are stimuli detected by an organism?
2. How are environmental stimuli in the external world represented in the nervous system?
3. How is information about a stimulus acquired, stored and recalled by the nervous system?
4. How is a behavioral pattern encoded by neural networks?
5. How is behavior coordinated and controlled by the nervous system?
6. How can the ontogenetic development of behavior be related to neural mechanisms?

Often central to addressing questions in neuroethology are comparative methodologies, drawing upon knowledge about related organisms' nervous systems, anatomies, life histories, behaviors and environmental niches. While it is not unusual for many types of neurobiology experiments to give rise to behavioral questions, many neuroethologists often begin their research programs by observing a species' behavior in its natural environment. Other approaches to understanding nervous systems include the systems identification approach, popular in engineering. The idea is to stimulate the system using a non-natural stimulus with certain properties. The system's response to the stimulus may be used to analyze the operation of the system. Such an approach is useful for linear systems, but the nervous system is notoriously nonlinear, and neuroethologists argue that such an approach is limited. This argument is supported by experiments in the auditory system, which show that neural responses to complex sounds, like social calls, cannot be predicted by the knowledge gained from studying the responses due to pure tones (one of the non-natural stimuli favored by auditory neurophysiologists). This is because of the non-linearity of the system.

Modern neuroethology is largely influenced by the research techniques used. Neural approaches are necessarily very diverse, as is evident through the variety of questions asked, measuring techniques used, relationships explored, and model systems employed. Techniques utilized since 1984 include the use of intracellular dyes, which make maps of identified neurons possible, and the use of brain slices, which bring vertebrate brains into better observation through intracellular electrodes (Hoyle 1984).

Critics of neuroethology might consider it a branch of neuroscience concerned with 'animal trivia'. Though neuroethological subjects tend not to be traditional neurobiological model systems (i.e. *Drosophila*, *C. elegans*, or *Danio rerio*), neuroethological approaches emphasizing comparative methods have uncovered many concepts central to neuroscience as a whole, such as lateral inhibition, coincidence detection, and sensory maps. The discipline of neuroethology has also discovered and explained the only vertebrate behavior for which the entire neural circuit has been described: the electric fish jamming avoidance response. Beyond its conceptual contributions, neuroethology makes indirect contributions to advancing human health. By understanding simpler nervous systems, many clinicians have used concepts uncovered by neuroethology and other branches of neuroscience to develop treatments for devastating human diseases.

Modern neuroethology

The International Society for Neuroethology represents the present discipline of neuroethology, which was founded on the occasion of the NATO-Advanced Study Institute "Advances in Vertebrate Neuroethology" (August 13–24, 1981) organized by J.-P. Ewert, D.J. Ingle and R.R. Capranica, held at the University of Kassel in Hofgeismar, Germany (cf. report Trends in Neurosci. 5:141-143,1982). Its first president was Theodore H. Bullock. The society has met every three years since its first meeting in Tokyo in 1986.

Modern advances in neurophysiology techniques have enabled more exacting approaches in an ever-increasing number of animal systems, as size limitations are being dramatically overcome. Survey of the most recent (2007) congress of the ISN meeting symposia topics gives some idea of the field's breadth:

- Comparative aspects of spatial memory (rodents, birds, humans, bats)
- Influences of higher processing centers in active sensing (primates, owls, electric fish, rodents, frogs)
- Animal signaling plasticity over many time scales (electric fish, frogs, birds)
- Song production and learning in passerine birds

- Primate sociality
- Optimal function of sensory systems (flies, moths, frogs, fish)
- Neuronal complexity in behavior (insects, computational)
- Contributions of genes to behavior (Drosophila, honeybees, zebrafish)
- Eye and head movement (crustaceans, humans, robots)
- Hormonal actions in brain and behavior (rodents, primates, fish, frogs, and birds)
- Cognition in insects (honeybee)

Application to technology

Neuroethology can help create advancements in technology through an advanced understanding of animal behavior. Model systems were generalized from the study of simple and related animals to humans. For example, the neuronal cortical space map discovered in bats, a specialized champion of hearing and navigating, elucidated the concept of a computational space map. In addition, the discovery of the space map in the barn owl led to the first neuronal example of the Jeffress model. This understanding is translatable to understanding spatial localization in humans, a mammalian relative of the bat. Today, knowledge learned from neuroethology are being applied in new technologies. For example, Randall Beer and his colleagues used algorithms learned from insect walking behavior to create robots designed to walk on uneven surfaces (Beer et al.). Neuroethology and technology contribute to one another bidirectionally.

Neuroethologists seek to understand the neural basis of a behavior as it would occur in an animal's natural environment but the techniques for neurophysiological analysis are lab-based, and cannot be performed in the field setting. This dichotomy between field and lab studies poses a challenge for neuroethology. From the neurophysiology perspective, experiments must be designed for controls and objective rigor, which contrasts with the ethology perspective – that the experiment be applicable to the animal's natural condition, which is uncontrolled, or subject to the dynamics of the environment. An early example of this is when Walter Rudolf Hess developed focal brain stimulation technique to examine a cat's brain controls of vegetative functions in addition to other behaviors. Even though this was a breakthrough in technological abilities and technique, it was not used by many neuroethologists originally because it compromised a cat's natural state, and, therefore, in their minds, devalued the experiments' relevance to real situations.

When intellectual obstacles like this were overcome, it led to a golden age of neuroethology, by focusing on simple and robust forms of behavior, and by applying modern neurobiological methods to explore the entire chain of sensory and neural mechanisms underlying these behaviors (Zupanc 2004). New technology allows neuroethologists to attach electrodes to even very sensitive parts of an animal such as its brain while it interacts with its environment. The founders of neuroethology ushered this understanding and incorporated technology and creative experimental design. Since then even indirect technological advancements such as battery-powered and waterproofed instruments have allowed neuroethologists to mimic natural conditions in the lab while they study behaviors objectively. In addition, the electronics required for amplifying neural signals and for transmitting them over a certain distance have enabled neuroscientists to record from behaving animals[7] performing activities in naturalistic environments. Emerging technologies can complement neuroethology, augmenting the feasibility of this valuable perspective of natural neurophysiology.

Another challenge, and perhaps part of the beauty of neuroethology, is experimental design. The value of neuroethological criteria speak to the reliability of these experiments, because these discoveries represent behavior in the environments in which they evolved. Neuroethologists foresee future advancements through using new technologies and techniques, such as computational neuroscience, neuroendocrinology, and molecular genetics that mimic natural environments.

Case studies

Jamming avoidance response

In 1963, Akira Watanabe and Kimihisa Takeda discovered the behavior of the jamming avoidance response in the knifefish *Eigenmannia* sp. In collaboration with T.H. Bullock and colleagues, the behavior was further developed. Finally, the work of W. Heiligenberg expanded it into a full neuroethology study by examining the series of neural connections that led to the behavior. *Eigenmannia* is a weakly electric fish that can generate electric discharges through electrocytes in its tail. Furthermore, it has the ability to electrolocate by analyzing the perturbations in its electric field. However, when the frequency of a neighboring fish's current is very close (less than 20 Hz difference) to that of its own, the fish will avoid having their signals interfere through a behavior known as Jamming Avoidance Response. If the neighbor's frequency is higher than the fish's discharge frequency, the fish will lower its frequency, and vice versa. The sign of the frequency difference is determined by analyzing the "beat" pattern of the incoming interference which consists of the combination of the two fish's discharge patterns.

Neuroethologists performed several experiments under *Eigenmannia*'s natural conditions to study how it determined the sign of the frequency difference. They manipulated the fish's discharge by injecting it with curare which prevented its natural electric organ from discharging. Then, an electrode was placed in its mouth and another was placed at the tip of its tail. Likewise, the neighboring fish's electric field was mimicked using another set of electrodes. This experiment allowed neuroethologists to manipulate different discharge frequencies and observe the fish's behavior. From the results, they were able to conclude that the electric field frequency, rather than an internal frequency measure, was used as a reference. This experiment is significant in that not only does it reveal a crucial neural mechanism underlying the behavior but also demonstrates the value neuroethologists place on studying animals in their natural habitats.