

REVIEW

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Neuroethology, its roots and future

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Abstract Scholars in a particular scientific field should be familiar with its historical roots. Such knowledge will put their own research into a historical perspective, and, in addition, will allow them to assess current strengths and weaknesses in their particular area of research. To keep an exciting field like neuroethology alive and close to fast moving scientific frontiers, it is necessary to constantly adapt and broaden its approaches to newly emerging ideas from other fields, and to quickly incorporate new methodologies. The following article tries to expose some of the roots of neuroethology, and, in addition, will present some evidence as to why the authors think this field needs a broader definition than that formulated in the past. Doing so after the 5th International Congress of Neuroethology in San Diego in August 1998 seems to the authors the most appropriate time.

Introduction

The word neuroethology itself is a merger between ethology, according to Konrad Lorenz (1981) “the comparative study of behavior which applies to the behavior of animals and humans”, and neurophysiology (or neurobiology, to use a different definition), “the study of the function of the nervous system”. Therefore, in its simplest definition neuroethology is the study of the neural mechanisms underlying behavior. Thus, it was only when general knowledge of the morphology and function of the nervous systems in humans and animals became available and was accumulated in the 19th century by pioneers such as Ramon y Cajal,

Johannes Müller, and Emil du Bois-Reymond, that the foundations were laid for linking behavior with events in the nervous system.

Historical roots of behavioral biology

The field of ethology was established by pioneers such as Oskar Heinroth, Konrad Lorenz, Niko Tinbergen and Karl von Frisch. Behavior was described and analyzed by careful observation of animals in their natural habitat or natural-like habitat in captivity. A major difficulty in any behavioral study, the high inter-individual variability of behavioral expressions, was reduced by focusing on particular forms of behavior and on the selection of animal species. Rhythmic motor behaviors (walking, flying, swimming) and communicative behaviors (particularly in the context of courtship) were predominantly studied (see also Camhi 1984; Hoyle 1984; Burrows 1996). These behaviors are to a great extent inherited, and thus vary less between individuals. They are released or controlled by rather fixed stimuli and are displayed by the animals rather stereotypically. Birds and insects were the animals of choice by many ethologists. Erich von Holst (1969, 1970) pioneered behavioral physiology (Verhaltensphysiologie) by focusing on the elements of rhythmic behavior and examining the function of the nervous system by localizing and analyzing the mechanisms of release and expression of these elementary forms of behavior.

Ethologists developed the concepts of “fixed action patterns” and “sign stimuli”, a connection between stimulus and response which could also be applied for rather complex stimuli and elaborate behavioral patterns. Both the strength and the weakness of classical ethology is expressed in these concepts. On the one hand, the focus on inherited behavior provided researchers with valuable and reproducible data sets, but on the other hand, guided them away from the other major source of information underlying behavior – individual learning. This aspect of behavioral biology was

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studied intensively by the American school of experimental psychology (behaviorism) (Skinner 1938; Hull 1943) and from a different vantage point by the Russian scientist Ivan Pavlov (1927). Behaviorism and Pavlov's reflexology dealt differently with behavior variability, namely by bringing the animal to the laboratory, reducing the complex environment to a small number of external variables, and focusing on simple behavioral patterns which are easily learned by the animal under constrained conditions. Behaviorism has been extremely valuable to behavioral biology by setting standards and procedures for experimentation with animals. The experimental paradigms developed belong to the core of modern behavioral biology, but neuroscience in general and neuroethology in particular have gained little on the conceptual level from behaviorism. This is because the nervous system was conceptually eliminated by behaviorists on two grounds: (1) little can be said about the nervous system when only input-output relationships are studied, and (2) the output is thought to be fully controlled by the input with the nervous system considered to be a mere computational machine working according to rules defined by the input. The concepts of ethology were different in this respect. The intrinsic productivity of the nervous system was a basic notion; evidence was established for spontaneous and input-independent activity ("creativity") of the nervous system. The dependence of behavioral expressions on the internal status of the animal (including the nervous system) was considered to be a major component in the expression of behavior and its variability. Thus, ethology has been conceptually closer to the roots of modern cognitive neuroscience, but the school of behaviorism has nevertheless helped enormously to avoid simple anthropomorphism and to establish a tradition of critical experimentation.

Where are the questions coming from?

A bat flying in total darkness; a bee orienting its flight path according to the polarized light pattern of the blue sky; a blue jay finding stored food items at hundreds of places – behavior of animals confronts us with endless questions about how this is achieved, what the underlying neural mechanisms are, how it was developed in the course of evolution, and how it suits the animal's needs. Neuroethologists find their questions outdoors but have to bring them into the laboratory for analysis. This is a quite complex process, often with limited success. The major questions need to be reduced to smaller, workable ones, and there is a danger that the overriding question might be lost by the constraints posed by limited methods. Probing the brain for neural correlates of behavior imposes enormous restrictions and eliminates a large proportion of the quite exciting problems, and thus may reduce the relevance of the finding to the original question. Although great methodological advances have been made over the last 20 years it is still nearly

impossible to record intracellularly from neurons in a performing animal, and aiming for particular individual neurons is still limited to small nervous systems or chopped-off (sliced) portions of bigger ones. Multiple recordings from single neurons are possible only in rare cases in behaving animals (e.g., place cells in hippocampus), and optical recording from ensembles of neurons, a necessity for understanding the spatial and temporal organization of a large number of neurons during perceptual and behavioral performances, is still a goal to be reached. The techniques are still rather dissatisfying, compared to the secrets we want to unravel. However, acceleration in the development of new methods and the improvement of existing ones is impressive. Therefore, we should continue to defend our stronghold and search for questions by careful observation of animals in the wild, despite the unavoidable consequence that we have to make so many compromises.

Comparative studies

Each species has neighbors on an evolutionary scale, and they are potential sources of information when we want to understand a neural mechanism and the design principles of the underlying networks. The reason is that modifications induced by adapting to a particular ecological niche can indicate which structures and functions are more closely related to the performance involved. Comparative studies are a specific realm of biological sciences. Their value for the research process is not always fully appreciated, because arguments based on comparison are correlative in nature and do not provide a direct insight. However, analysis of (closely) related species will open our eyes to the multitude of relationships between structure and function, and provide hints about neural strategies. For example the study of brain structures in song and non-song birds provides insight into how the nervous system had to undergo morphological and physiological changes to achieve the new task of controlling singing in birds.

In favorable cases evolution might have led to the development of specialized or reduced systems which may be more easily accessible using techniques at hand. Imprinting, for example, could be considered as a special form of learning or a special form of epigenesis, and such a mixed system provides us with the opportunity to study the relationship between genetically controlled developmental processes and experience-dependent modifications.

Phylogenetically less advanced nervous systems come with a smaller number of neurons and often solve rather similar problems as do those with a large number of neurons. For some unknown reason, such small nervous systems often contain particularly large neurons which can be individually identified in favorable cases. Such a situation is particularly appropriate for current electrophysiological and anatomical techniques. Using such

systems, it has been possible to probe the rich capacity of single, dedicated neurons. An additional advantage of these systems is that they may produce, at least partially, behavior under the restrained conditions in the laboratory and unravel the complex functions of individual neurons.

The true ethologist may be taken aback when even movements of internal organs such as intestines, hearts or ventilatory muscles are subsumed under behavior (Selverston and Moulins 1987; Harris-Warrick et al. 1992), but the fact is that without such studies, influential and useful concepts such as those of the identified neuron and the central pattern generator could not have been formulated.

The identified neuron concept still proves useful for circuit analysis, in which individual neurons are identified as components of neural circuits by (1) their structure, (2) their physiological response, and (3) often by their immunoreactivity (see Burrows 1996). Some particularly conspicuous neurons, better known as giant neurons, could be identified as command neurons whose activity is necessary and sufficient to trigger the initial fast parts of, for example, the escape behaviors of crayfish, earthworms or squids (Edwards et al. 1999).

Studies on individual neurons have proven that for a functional analysis it is necessary to know the identity of a particular neuron not only with respect to its structure or position in a neuronal circuit but also with respect to its involvement with ion channels or intracellular signaling pathways (see also Baro et al. 1997). This is a completely new area which has not yet been fully integrated into neuroethology.

However, the notion that single large neurons implement rather stereotyped and fast functions of the nervous system reflects only one aspect. Single, dedicated large neurons can also represent a complex function (e.g., the rewarding components in appetitive learning; Hammer 1993) and can be highly adaptive.

But neurons do not work in isolation, and functionally flexible ensembles of neurons are most likely the building blocks of the nervous system (see below).

Learning and memory

Experience-dependent modification of behavior has not been at the center of ethology, and behaviorism has not provided any concepts about the neural implementation of learning and memory (see above). It is thus not surprising that memory research routes derive from a different line of historical development in neuroscience. A major question in neurology during the last century was that of localization of function. Franz Josef Gall divided the human cortex into 27 faculties, each residing in different parts of the cortex (phrenology). Although this attempt was not backed up by experimental results or objective observations, it initiated the search for mechanistic relationships between cognitive capacities and brain structures. This view was substantiated by Brocca

and Wernecke who discovered areas in the temporal lobe of the human brain essential for speech production and recognition. Memory is a cognitive faculty, and the question of where it resides in the brain was an important one for neurologists who were exposed to severe form of memory deterioration (e.g., Alzheimer, Korsakov syndrome). From 1920 to 1950 Karl Lashley (1942) dominated the scene. His failure to identify particular brain regions that were specific to, or necessary for, memory storage called for alternative approaches in memory research, and these were initiated by the psychologist Donald Hebb (1949) and the neurologists Brenda Milner and Wilder Penfield. Hebb postulated that cognitive functions can indeed be distributed, because dynamic assemblies of neurons work together to represent and store information, rather than a fixed architecture of nerve nets. Milner and Penfield discovered the contribution of the hippocampal complex to recent memory and the establishment of stable knowledge about facts, faces and spatial layout, although old memories were intact in patients who had their hippocampi dissected (Milner et al. 1998).

The notion that memory is not an integrated faculty but is divided up both into temporal phases *and* with respect to its contents, facilitated the identification of brain structures as substrates of these capacities. It was only after these discoveries on patients that animal studies again became important in memory research. Meanwhile, we know that different memory phases are a property of nervous systems in general and somehow reflect the self-organizing dynamics of the brain (Squire 1987). However, we barely understand why such dynamics evolved, and which ecological and behavioral conditions can be better coped with when final memory formation is postponed. A typical domain of neuroethological research, the comparative approach, will provide us with clues to these puzzles, and observations of animal performances under natural conditions will ultimately help us to ask the right questions. Memory contents determine the location of the memory trace not only with respect to the sensory and motor channels involved but also with respect to multimodal and cognitive integration levels. For example, the hippocampus or/and its phylogenetically related structures serve as an integration and storage site for spatial orientation in fish, birds and mammals. Does this mean that neural mechanisms underlying spatial representation and storage in vertebrate brain are homologue faculties, which are elaborated when behavioral demands are greater, and reduced if less demanding behavioral strategies are applied? Support for this notion comes from comparative studies in food-storing and non-storing-birds (Clayton and Krebs 1994). These studies are an excellent case for the strength of neuroethological research. Not only do we learn more about structure-function relationships, but we also gain insights into the evolutionary process leading to higher brain performances.

Following this research strategy we might in the future even understand why and how declarative forms of

memory in humans (those memories which we consciously recollect) are related to the same brain structure, the hippocampus.

Single neuron versus ensembles of neurons

The concept of the single neuron being the substrate of complex integration and decision making in the brain reminds us of the ethological notion of sign stimuli and innate release mechanisms. Would it not be wonderful if nervous systems had the sign stimuli/release mechanisms implemented in superneurons residing with a network of handshaking cells in a hierarchically organized nervous system? Indeed, there are neurons which cause the animal to perform a fully integrated piece of behavior (e.g., tailflip in decapods; Edwards et al. 1999) when one of them produces one spike. There are also neurons which respond rather selectively to particular combinations of inputs (e.g., face neurons), and – as mentioned above – there is a neuron that serves the reward function in appetitive learning (the VUMmx1 in honeybees). Are these dedicated neurons exclusive models of brain functions? Certainly not, since overwhelming evidence indicates that many neurons have to co-operate in the extraction and coding of sensory features and the control of motor patterns. The response profile of each of these neurons is determined by many other neurons, and this interactive process can be highly dynamic. But neural processing is likely to be even more dynamic, leaving each single neuron only the capacity of being a member in an assembly, from which transiently interacting groups of neurons are selected. Group selection on the basis of variability at the level of single neurons resembles interesting formal features of evolutionary processing (neural Darwinism; Edelman 1993), and has been proposed to explain the fact that interactive nets of many rather similar, non-dedicated neurons appear to be responsible for feature extracting and coding.

Again, the comparative attitude in neuroethology and the fascination of researchers by the multitude of nervous systems as they appear at all phylogenetic levels will provide us with most encouraging perspectives. Is the proportion of non-dedicated neurons assembling in flexible groups related to the complexity of neural performance, and does it depend on the phylogenetic level? Do different organizational principles of nervous systems (e.g., in invertebrates versus vertebrates; in different groups of vertebrates) lead to different proportions along the scale from dedicated to non-dedicated neurons, from morphologically composed circuits to flexible and multifunctional aggregates, and from specialized solutions to productive compositions with emerging properties? It is obvious that theories of brain functions capture only small parts of these overwhelming prob-

lems (Singer and Gray 1995). The analogy with a computer has been creative and stimulating, but it also limits the view to pre-designed, restricted circuits. The call for more general theories of nervous functions is certainly one of the most pressing ones, and again the comparative attitude of neuroethologists with their conceptual foundations in evolutionary theory may be a creative driving force behind the pursuit of such a theory.

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