Introduction 1

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This book introduces the reader to the fascinating field of **neuroethology**. As other disciplines studying animal behavior, a major task of neuroethology is to understand the causal factors that lead to the production of behavior. There are two principal approaches to achieve this goal. One approach aims at a "software" explanation of behavior. As shown in Fig. 1.1, the animal is treated as a black box, which, in response to a biologically relevant stimulus, generates a behavior. Such an approach is used by all behavioral sciences, including ethology, one of the founder disciplines of neuroethology. The second approach, which is employed by neuroethology, aims at understanding how the central nervous system translates the stimulus into behavioral activity. In other words, neuroethology seeks a "hardware" explanation of behavior by elucidating the structure and the function of the black box.

Neuroethology attempts to understand how the central nervous system controls the natural behavior of animals.

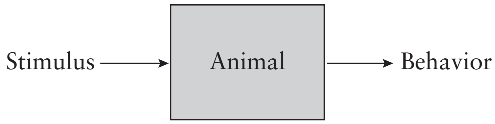

Figure 1.1 The black-box approach. Scientific disciplines restricting their research to the behavioral level treat the animal as a black box that, upon stimulation with a biologically relevant stimulus, produces a behavioral pattern. Such disciplines, thus, provide "software" explanations of behavior. In contrast, neuroethology attempts to give hardware explanations by exploring the structure and function of the black box, in relation to the production of behavior. (Drawing by Günther K. H. Zupanc.)

Neuroethology: the synthesis of neurobiology and ethology

Neuroethology has its roots in both **neurobiology** and **ethology**. The synthesis of these two disciplines, which created a new area of study, was and continues to be challenging. This is mainly due to the rather diametric approaches employed by the two founding disciplines. Neurobiologists have traditionally worked on anesthetized animals, isolated parts of tissue, or even single cells. They are primarily interested in the structure and function of such particular cells or tissues. The species is often chosen based on technical considerations, such as the presence of large nerve cells, and the ease by which the animal preparation can be obtained. Ethologists, on the other hand, employ a **whole animal approach**, with the animal kept under conditions as natural as possible. Preferably, at least part of their observations should be conducted in the field. If this is not possible, then the animal is transferred to, or bred in the laboratory, where it is kept under semi-natural conditions to minimize the occurrence of unnatural behavior.

Despite the obvious differences between neurobiology and ethology, the success of neuroethology is based on the incorporation of a blend of neurobiological and ethological approaches into its own scientific armory. Particularly, its focus on "natural" and biologically relevant behavioral patterns makes neuroethology distinct from other disciplines studying the neural basis of behavior. As part of the overall strategy, this should include investigations of the animal in its natural habitat. The researcher can then simulate the field conditions in the laboratory and apply more natural stimuli in the experiment than would be possible if studying the behavior in the laboratory only.

In recent years, such **field studies** have been eased by many technological developments, such as the availability of battery-powered laptop computer, which allow the researcher to characterize the animal's natural behavior with an unprecedented degree of precision. With the enormous advances made in the miniaturization of instruments, it is not unthinkable anymore that neuroethologists will, at one point in the future, be able to obtain physiological recordings from animals living a relatively normal life in their natural habitat!

On the other hand, neuroethologists investigate rather simple behaviors. This is sometimes to the disappointment of ethologists, who are typically interested in more complex behaviors. However, the intrinsic conceptual and technical difficulties make such a self-applied restriction not only unavoidable, but also desirable.

Neuroethological research combines both neurobiological and ethological approaches.

In the latter respect, one could compare the situation of today's neuroethology with that of physics in the seventeenth century. The initial restriction to simple models to analyze the motion of objects (e.g. neglecting air resistance when examining falling objects) led to the discovery and establishment of many fundamental principles, such as the Newton's laws of motion. An attempt in the early days of mechanics to analyze more complex systems, although closer to reality, would almost certainly have failed and tremendously delayed the further development of the physical sciences.

Choosing the right level of simplicity

Progress in neuroethology is crucially dependent upon choosing the right level of simplicity. Thus, although the ultimate goal of neuroethology is to understand the neural mechanisms underlying behavior, it would at present not be sensible to examine the entire behavior of an animal.

In any animal, the behavior consists of many individual elements. It involves not only what is generally associated with behavior, movements of the body in particular, but may also include specific body postures, production of sound, color changes, electric discharges, and even glandular activity, for example the secretion of pheromones. The entire behavioral repertoire of an animal is called the **ethogram**. As immediately evident, this entire set of behavior is too complex to be analyzed by the neuroethologist, or even by the ethologist. Therefore, the behavior of an animal has to be split into its individual components, referred to as the individual behaviors or behavioral patterns. As a first step, the total behavioral repertoire is often divided into major groups representing functional categories, for example "sleep," "feeding," "courtship," or "aggression." Yet, these categories are still too large to be quantified and analyzed in a meaningful way. This makes a further subdivision necessary.

Ethogram: the entire behavioral repertoire of an animal species.

Example: *Cichlids are a family of more than two thousand teleost fishes. They are well known for their highly developed aggressive, courtship, and parental care behavior. As illustrated in Fig. 1.2, the behavior subsumed under the term "aggression" actually consists of a number of individual behavioral patterns, including chasing, butting, frontal display, lateral display, and mouth wrestling.*

Obviously, by dividing the behavior of an animal further and further down, a hierarchical arrangement results. Niko Tinbergen, one of the founders of ethology (see Chapter 2), calls the different levels within this hierarchical system **levels of integration**. The lateral display of cichlids, for example, involves alignment of the fish beside its opponent, typically

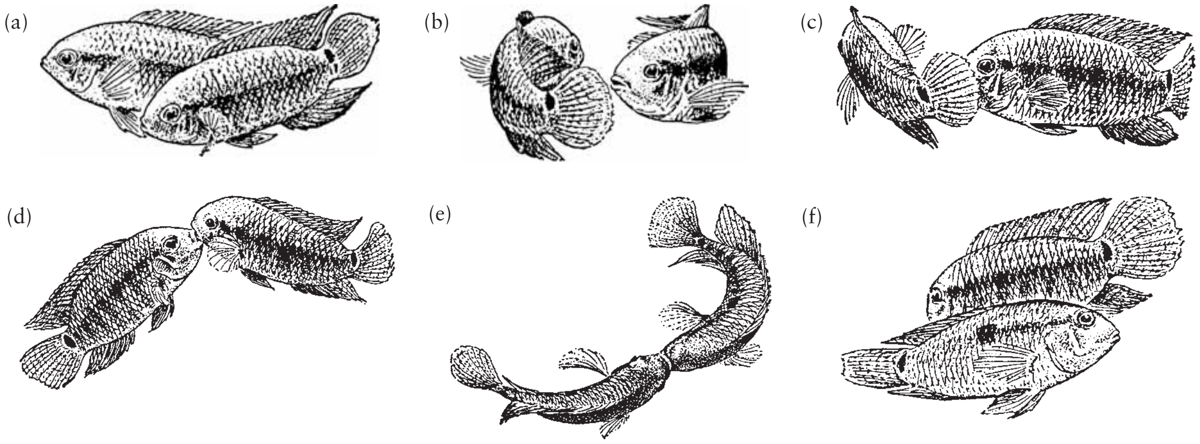

Figure 1.2 Aggressive behavior of the blue acara (*Aequidens pulcher*), a teleost fish of the cichlid family. a: Lateral display. The fish align beside each other, spread the dorsal, anal, and pelvic fins, and intensify the coloration of their bodies. These threats are accompanied by light tail beats. b: Circling. While circling each other, the fish have the ventral part of the mouth lowered. c: Tail beating. One fish beats its tail against the head of the opponent. d: Mouth grasping. The fish grasp each other at the lower or upper mandible. e: Mouth pulling. Each fish tries to pull the opponent, after having grasped each other's mouth. f: Defeat. The fish in the front gives up. It folds its fins, adopts a pale coloration, and swims off. (After **Wicker, W.** (1968). *Das Züchten von Aquarienfischen: Eine Einführung in ihre Fortpflanzungsbiologie*. Franckh'sche Verlagshandlung, Stuttgart, page 59 (fig 13.)

within a few centimeters, and a rapid, powerful sideways thrust of the tail. During this display, the dorsal, anal, and pelvic fins are erect and the opercula extended. The erection of the fins, on the other hand, is defined by the action of the individual fin rays, whose movement is the result of the contraction of muscle fibers controlled by neural motor units. Figure 1.3 illustrates this stepwise subdivision of behavior into smaller and smaller elements.

Dividing the behavior of an animal into components of decreasing complexity results in a hierarchical arrangement with different levels of integration.

While it hardly makes sense to undertake a study aimed at elucidating the neural basis of "aggression" in a cichlid fish, one would likely succeed, with the techniques available, to identify the structures within the central nervous system that control the movements of the dorsal fin. Operation at this lower level of integration not only reduces the number of neuronal structures involved in the control of a behavioral pattern, but also provides the investigator with behavioral elements typically much better defined than those encountered at a higher level of integration. This makes it markedly easier to quantify behavioral patterns—a prerequisite for many types of analysis at both the behavioral and the neurobiological level.

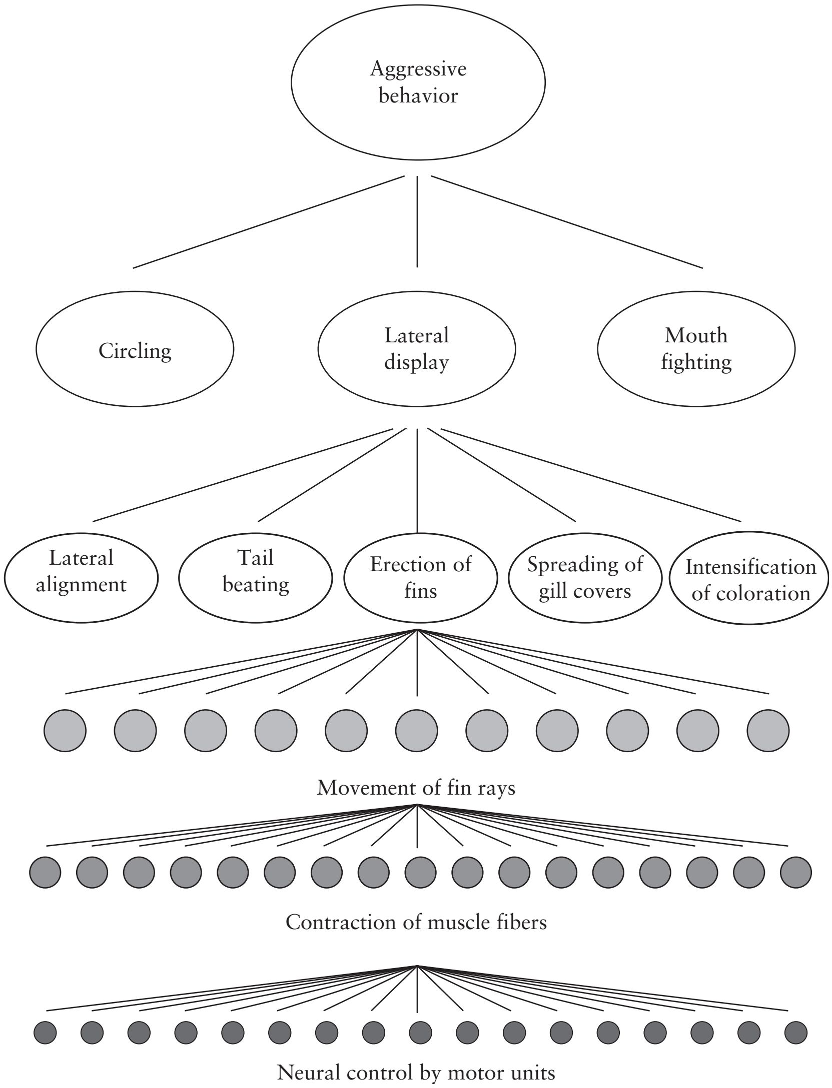

Figure 1.3 Splitting the lateral display, an aggressive behavioral pattern of cichlid fish, into individual elements. This leads to a hierarchical arrangement in which various levels of integration are distinguished. (Drawing by Günther K. H. Zupanc.)

Quantifying behavior: a prerequisite for neuroethological research

In general, behavioral patterns can be quantified using their rate of occurrence ("how often is the dorsal fin erected?"), their duration ("how long is the dorsal fin kept in an erect position?"), and/or their intensity ("is the dorsal fin erected maximally, with the fin rays almost perpendicular to the dorsal edge of the fish's body, or do the fin rays adopt positions intermediate between the maximal and the minimal angle?"). A similar attempt to quantify the lateral display would be very difficult, particularly because

A behavioral pattern can be quantified using its rate of occurrence, duration, and/or intensity.

of the complexity of the different actions involved in the execution of this behavior. Since not all individual actions are necessarily executed simultaneously during lateral display, a main problem would be to identify the endpoints of this behavior. Lack of such information makes it virtually impossible to determine the parameters, "rate of occurrence" and "duration". Also, measurement of the intensity would be difficult: is the behavior more intense when a larger number of individual actions are displayed, or when the degree of execution of individual patterns is maximized?

Finding the right model system

The above considerations underline the importance of choosing the right **model system**. Such systems are *not* primarily studied to provide insights into the neural mechanisms underlying the behavior of the respective species. Rather, their characterization enables the neuroethologist to extract principles applicable to many, if not all, animals. This is possible, because there are, probably in any case, only a finite number of solutions to a given behavioral problem. Keeping the body oriented, for example, requires the analysis of geophysical invariants, but the number of options available is limited to a very few, such as the measurement of the direction of the incident light or of the animal's angle relative to gravity (see Chapter 4).

Many solutions to such problems were invented very early in evolution, so that frequently the neural implementation of these solutions are **homologous** in different species. Such homologous developments are a major reason why many fundamental cellular mechanisms underlying learning and memory are very similar among animals, including both vertebrates and invertebrates. On the other hand, these universals of life make it possible to establish principles of learning and memory processes by studying the rather simple neural network of the sea slug *Aplysia*, although ultimately most researchers would like to understand more complex systems, including those of humans (see Chapter 11).

Ideally, when choosing a model system, the behavior under scrutiny should be simple and robust, readily accessible and ethologically relevant. The animal displaying this behavioral pattern should be inexpensive, suitable for examination in the laboratory, easy to maintain, and possible to breed. These requirements are far from trivial to meet, and the right choice of a suitable model system always demands profound knowledge in both animal biology and husbandry.

Example: *Two orders of teleost fish produce, by means of a specialized organ, electric discharges of low voltage. As will be demonstrated in detail in Chapter 7, these so-called electric organ discharges are quite*

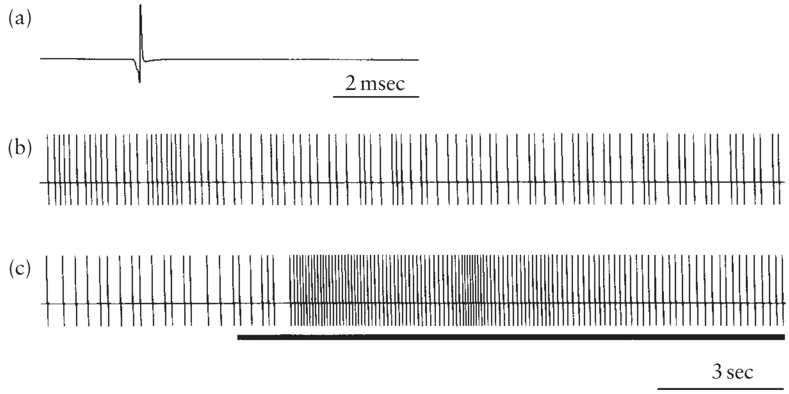

Figure 1.4 Electric organ discharge of the elephant nose, *Gnathonemus petersii*. a: Each discharge results in a brief electric pulse, which is highly constant in terms of duration, amplitude, and waveform. b: Resting discharge pattern at slower time scale. As the individual pulses are highly constant, this behavior can readily be quantified by counting the number of pulses (here represented as vertical bars) produced per second and by analyzing the pattern of discharge. In the example shown, approximately five pulses per second are generated, and the intervals between the individual pulses are somewhat irregular. c: After stimulating an isolated fish with the discharges of a second elephant nose (indicated by the horizontal bar below the trace), the discharge pattern changes significantly. In the example shown, the fish discharges at almost three times the resting rate, and the pattern of pulse production becomes more regular. The result of this experiment underlines the ethological relevance of the electric organ discharge. (After **Zupanc, G. K. H. and Banks, J. R.** (1998). Electric fish animals with a sixth sense. *Biological Sciences Review*, **11(2)**, 23–27, A: page 24, fig. 2a; bc: page 26, fig. 6.)

simple, in terms of their biophysical properties, highly robust, and they can readily be monitored by placing recording electrodes near the fish. Their rate of occurrence, duration, and intensity can easily be measured, thus allowing the researcher to quantify this behavior. This is illustrated by Fig. 1.4, which shows the discharge pattern of the elephant nose (Gnathonemus petersii). This mormyriform fish produces very brief electric pulses, which are, even over hours and days, highly stable in terms of their physical appearance (Fig. 1.4a). However, the fish are able to modulate the discharge pattern, for example by altering the pulse repetition rate, or by changing the mode of regularity (Fig. 1.4b,c). These modulations are, for example, used to encode information in the context of intraspecific communication, such as during aggressive encounters (Fig. 1.5a–f). In addition, the fish employ their discharges for object detection. The electric behavior, therefore, meets the above requirement of ethological relevance. Moreover, many weakly electric fishes can be kept in aquaria under semi-natural conditions; several species have even been successfully bred in the laboratory. Taken together, these properties make them ideal subjects for neuroethological research.

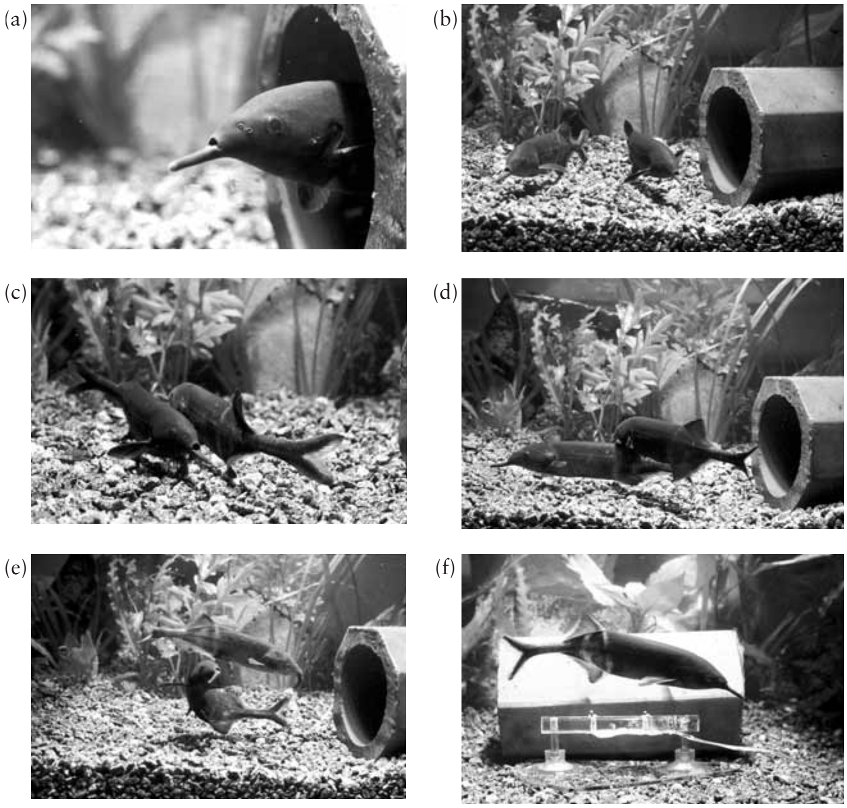

Figure 1.5 The elephant nose shown in various behavioral situations. a: At rest, the fish likes to stay in caves or, in this case, in a clay pipe. In such a situation, the fish typically emits only a few pulses, separated by rather irregular intervals. b: If a second fish is introduced into the tank, both fish stay initially at a short distance from each other. c: They then frequently adopt a head-to-tail stance alongside each other, with their "chin" appendage (sometimes incorrectly called a "nose") projecting rigidly forward. d: If the intruder fails to move off, the territory-holder attacks and rams the intruder. e: Finally, the intruder is beaten by the territory-holder. The defeated fish turns light brown. Now, both fish have curled in their chin appendages. The social interactions shown in b–e are accompanied by specific patterns of electric organ discharges which clearly differ from the resting discharge. f: Elephant nose fish, like other electric fish, can be stimulated by mimics of the discharges of a neighboring fish played back via an electric fish model. This model consists of plexiglass (perspex) rods with built-in electrodes. (Reproduced from **Zupanc, G. K. H.** (1982). *Fische und ihr Verhalten*. Tetra Verlag, W. Germany, pages 126, 128, 129.)

This and other examples of good neuroethological model systems are discussed in detail in the following chapters of this book. Their exploration over the last decades has greatly advanced our understanding of how the brain controls behavior. Moreover, and equally important, this research has also deepened our appreciation for the biology of the whole animal.

Summary

- Neuroethology attempts to understand the neural mechanisms governing animal behavior by employing approaches derived from ethology and neurobiology.
- A crucial requirement for neuroethological research is the choice of suitable model systems. These systems are characterized by behavioral patterns which, although simple, robust, and readily accessible, are also ethologically relevant.

Recommended reading

Martin, P. and Bateson, P. (1993). *Measuring behaviour: an introductory guide*. Second Edition. Cambridge University Press, Cambridge.

An excellent guide to the principles and methods of quantitative studies of behavior, with emphasis on techniques of observation, recording, and analysis.

Tinbergen, N. (1951). *The study of instinct*. Oxford University Press, London.

A classic. Even half-a-century after publication of its first edition, still a source of inspiration.

Questions

1.1 You intend to apply for a research grant to develop a novel neuroethological model system. What animal species and which behavior would you propose to examine? Justify your choice using the above criteria.

1.2 Songbirds produce, particularly during the breeding season, characteristic songs which subserve a variety of behavioral functions. How would you split the songs into individual behavioral patterns? How would you quantify these behaviors?

1.3 Any model system is a simplification of reality. Using one of the model systems presented in this book, discuss aspects which, in your opinion, were neglected for the sake of simplicity. How would have inclusion of one or several of these aspects impeded neuroethological analysis? On the other hand, how could consideration of such aspects provide more realistic explanations of the neural mechanisms underlying behavior?