

The scope of neuroethology

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Abstract: Neuroethology, an interdisciplinary subdivision of neuroscience, has emerged in recent years. Since 1976 there has been a regular session under this heading at the annual meeting of the Society for Neuroscience. In 1980 two introductory texts in English were published on the subject (Ewert 1980; Guthrie 1980), and a third (Camhi 1984) was published recently. There is widespread interest in neural mechanisms underlying behavior, but they encompass such a vast array of often unrelated topics that proponents do not share common goals. This article describes the emergence of ethology as a discipline, pointing out that its practitioners were successful because they confined their research to stereotyped, complex, nonlearned, innate behavioral acts. A limited number of profoundly significant principles emerged. Each of these is redefined. The major concepts of earlier ethology were embodied in a simple hydraulic model used by Konrad Lorenz in 1949 (Lorenz 1950). It is pointed out that this model implies the existence of common neurophysiological mechanisms and neuronal circuitry. This model has now been made obsolete by neurophysiological progress, but with appropriate modifications an updated version may still be useful in focusing attention on possible principles. The initial aim of neuroethology should be to examine the neurophysiological events in a variety of behaviors, exhibited by diverse animals from different phyla, which meet the criteria of innate behavioral acts. The behaviors should be sufficiently complex to interest ethologists, yet they should be addressable with neurophysiological methods down to the cellular level. In the case of vertebrates this may mean working with brain slices as well as whole animals, but for some invertebrates recording should be possible in the nearly intact animal during execution of the behavior. The work will be exacting and very difficult, and it is not likely to get done at all unless neuroethologists recognize that they should both train and discipline themselves and restrict their attention to well-defined goals.

Keywords: behavioral biology; behavior patterns; ethology; fixed action patterns (FAPs); instinct; learning; Lorenz; motor programs; neuroethology

Historical origins of ethology

A scientific discipline of neuroethology could not have existed either before the term “ethology” had become established or before neuroscience had developed to the point where both neuroanatomical and neurophysiological methods were available that could be used to attack ethological questions. There is a strong tendency to equate neuroethology with the neural bases of behavior in the broadest sense. To do so encompasses such a broad spectrum of phenomena that the extremes are virtually unrelated and can only be linked by the widest stretches of imagination. Such links are too tenuous. If the term “neuroethology” is to serve the useful purpose of identifying a group of active scholar–investigators sharing common goals, to bring them together and stimulate their research, it must be relatively narrowly defined. There are clearly dangers in defining any subject too narrowly, because this can lead to the arbitrary exclusion from serious consideration of information, especially of that yet to be discovered, that is truly relevant and significant for the mainstream. But the danger is much less than that associated with using a definition that is too broad. Unless the focus is restricted, the subject matter expands into a diffuse vapor without any substance at all.

The first potential trap is to assume that the term is merely a faddish one, culled to draw attention to a previously nameless but ancient line of inquiry. The first

experimental investigations into the possible functional relations of a nervous system to behavior were undoubtedly those of Galen made 1,800 years ago. There is a direct line from his unparalleled starts, through the ideas of Descartes and the experiments of Francis Glisson and Albrecht Haller, via Charles Bell and François Magendie, to those of Johannes Müller and his pupil Emil du Bois-Reymond, who can be considered to have founded modern experimental neuroscience. Spice the above with some Galvani, Hall, Helmholtz, Weber and Bernstein; then mix with some Gall (no pun intended), Fechner, Wundt and Titchener, and finally, a liberal dash of Pavlov and Sherrington, bake, cool, then top off with an icing of Cajal and Golgi, and you have neuroscience cake.

The point is that here we have the product of the combined histories of much of physiology, medical neuroanatomy, and psychophysics. But still this was not nearly enough to provide a satisfactory basis for the understanding of behavior, although in many circles, especially Russian and British ones, it was considered more than adequate. Even a generation of American pioneers in the study of behavior, Whitman (1819), Craig (1918), McDougall (1923), Russell (1934) and eventually B. F. Skinner [see special issue on the work of B. F. Skinner, *BBS* 7(4) 1984], had failed to realize that something important had been left out. Fortunately, careful and systematic examination of examples of the behavior, in natural rather than laboratory settings, of a variety of

animal species, especially of relatively lowly forms including invertebrates (though mainly insects), enabled a group of Middle-European zoologists to detect some very important missing ingredients in the mixture.

For the animal kingdom as a whole, the majority of even the most complex behaviors, the ones with the longest sequences of coordinated movements and the subtlest interactions with other individuals of the same species, fall into the category of instinctive acts. They require no experience of the behavior in its context, nor learning, for their perfect execution. Such behavioral sequences can be broken down into a few discrete components, each a distinct act or subroutine. Some of the acts could be recognized as also being performed by related, but different, species in which they occurred in a different sequence. In a few instances it has been possible to show that Mendelian laws apply to the inheritance of the ability to perform these acts.

The realization that there is genetic involvement with chunks of behavior provided a major breakthrough in the understanding of how complex behaviors have evolved. Natural selection clearly acts on the totality of the behavior. But at some evolutionary stage, what eventually became a subroutine must have been a complete behavior. Possibly an entire subroutine can appear as a mutation and become incorporated in a sequence if it confers selective advantage. But in spite of the simplicity and fundamental importance of these findings, they sank into the minds of a majority of both behavioral scientists and physiologists very slowly. In fact, it was not until the 1973 Nobel Prize for physiology or medicine was awarded to Konrad Lorenz, Niko Tinbergen, and Karl von Frisch for their pioneering studies in these aspects of behavior that the majority of psychologists and biologists interested in behavior even accorded the work any attention. When the news broke in the United States, it did not receive the customary plaudits associated with Nobel prize announcements in most of the relevant quarters. Quite the contrary! While the furor was still raging, students of animal behavior were crowding libraries trying to find out what these “unknowns” had discovered; indeed – what was the fuss all about? Details may be found in a fascinating historical account by Thorpe (1979).

Lorenz, who was Tinbergen’s source of inspiration, and who was clearly the first person to understand the significance of what the Middle-European naturalists were discovering, frequently used the term *Ethologie* to designate the subject of his interest. He first used it in the title of a 1931 paper, published when he was 27 years old, on the behavior of crows (the uniquely European one he worked with is called a jackdaw). The term “ethology” had been around in various contexts for more than half a century before Lorenz used it. Wheeler (1902) had used it in a context somewhat similar to that of Lorenz, but it was still confused with purely descriptive natural history observations and even with ecology. Clearly Lorenz did not start out making penetrating generalizations: Indeed, his avowed first love was studying the natural history of birds, simply because he *enjoyed* watching them and was curious about their behavior. Such was the unlikely path which led to intellectual distinction and the ultimate in scientific recognition. It was Niko Tinbergen, however, who was responsible for the successful publicizing of ethology. The subject came to be well known shortly after

his book was published in 1951. He referred to *The Study of Instinct* as a “programme for ethology” in spite of the title.

The word “instinct” is derived from the Latin *instinctus*, past participle of *instinguere*. The origin of this word was associated with the use of a pointed stick, and it can mean “to prick.” *Instinctus*, as used by Cicero, is to be incited, or fired up – doubtless equivalent to the responses engendered by being jabbed. This is very clearly a reflex action. Paradoxically, that is not what Lorenz wanted to convey. The whole “point” of the ethological movement was that it uncovered a multitude of common behaviors that are not akin to reflexes, even when triggering is involved. To emphasize the difference ethologists sometimes referred to the behavior as “endogenous” – generated from within. A reflex will occur at all times unless it is either habituated or centrally suppressed during the execution of other behavior. An instinctive behavior will occur only when there is a central nervous system readiness. Lorenz termed this the “action specific energy” for that particular behavior. Thorpe (1979) and others have done ethology a disservice by erroneously attributing to Lorenz the designation “reaction specific energy,” which connotes reflex action. Lorenz thought in terms of a gradual accumulation of a “reservoir of energy” for the behavior in question, which must be full, or nearly so, or the behavior will not occur at all. But no catchy word or phrase has yet been coined that adequately conveys the endogenous aspect. Since the success of the Lorenz–Tinbergen studies, the term instinct has come to be used differently from the way it was formerly, and it now carries with it the implication of at least partially endogenous generation. The aspect of releasability and the implication of spontaneous appearance were, even in Roman times, associated with the word *instinctus*. Those were times when emperors, in particular, used to “fly off the handle.”

In Germany, there had been a move toward a science of neuroethology in Erich von Holst’s Max Planck laboratory of *Verhaltensphysiologie* (founded at Seewiesen, where Lorenz already had an *Abteilung*); this laboratory nurtured cybernetics pioneer Horst Mittlestaedt. But this movement was content to treat the nervous system as a “black box.” It was successful in uncovering some new principles about nervous system function, the most important being that for a short time a memory of motor output, the *efference copy*, is established and heeded. The prevalence and importance of feedback, especially the *reafference*, was also emphasized. But in spite of the functional importance of the efference copy, we still have no direct knowledge of its nature more than 30 years later. There was a marked lack of interest in direct neuroanatomical/neurophysiological investigation. Unfortunately, this line of progress was finally stilled when von Holst became preoccupied with improving the sounds produced by asymmetrical violas. Fortunately, this situation is being rectified, particularly within the last few years and especially by Lorenz’s successor at Seewiesen, Franz Huber, and by Ulrich Bässler, Norbert Elsner, and Gernot Wendler.

I first began to think of the possibility of a science of neuroethology in 1951, when I was learning about and beginning to practice neurophysiology, and after I had experienced the impact of the Lorenzian/Tinbergenian

concepts. The research question I was asking was a specific, simple one, suggested to me as a thesis project by Bernard Katz, "How can a phytophagous insect produce nerve impulses when its blood contains large amounts of potassium and very little sodium?" The insect I worked on was the locust, and I spent a lot of time simply observing the insect's behavior. My friend and colleague at the time, Peggy Ellis, was intensively studying the *marching* behavior of nymphal locusts. She had discovered how to induce them to march routinely under laboratory conditions. *Marching* is the form of field behavior shown by immature (flightless) locusts, in place of swarming. Huge bands of immature locusts walk together, as do naturally wingless species as adults. This behavior has some aspects of the kind of stereotyped behavior, termed a "fixed action pattern" (FAP), which was the cornerstone of the ethology movement.

In marching both the posture adopted and the style of locomotion are different from those of ordinary walking. Special conditions, a fair amount of elapsed time, a minimum number of animals per unit space, and the absence of food are required before marching will commence, but given these circumstances, it is quite certain that marching will occur. Once it is well under way, the accessibility of food will not stop it; the insects simply pass over and ignore the food until they are exhausted. Then they stop and eat voraciously.

My physiological work showed that the neuromuscular junctions, but not the nerves, which are protected by a regulatory sheath, would be affected by the ionic composition of the blood. Therefore, if a FAP were initiated in a locust in the manner implied by the Lorenz model, the expression of the output would be affected by the blood ion concentrations. Theoretically, the range would be from no behavior at all, through feeble mimicking, with poor posture, to supranormal intensity, depending on the potassium, which is high after feeding. Peggy Ellis and I tested this hypothesis experimentally (Ellis & Hoyle 1954; Hoyle 1954), with affirmative results: Locusts that have recently fed do not, and cannot, march. Starved ones march the most vigorously. John Pringle (1939) had shown for the cockroach, and I confirmed for the locust, that the innervation of insect muscles is extremely simple, some muscles of functional importance in behavior receiving but a single excitatory axon. Therefore, the neural output is easily recordable and quantifiable. That realization was for me the beginning of a neuroethological approach. This may not have been considered to be a new field of inquiry, but it certainly felt like one. I know of no precedent for the experiments I did with Peggy Ellis, or for our interpretation, which was backed by a film shown to the Society for Experimental Biology.

The principle of a dependence of behavioral expression on peripheral as well as central factors should apply to other animals, including man. That this is true is amply evident in the behavior of persons suffering from episodic hyper- and hypokalemias. Complete motor paralysis occurs in humans, as it does in locusts, when blood potassium levels are at their highest (Creuzfeldt, Abbott, Fowler & Pearson 1963).

Peripheral neuromuscular events, which are easily and precisely understood, turned out to be key ones in locusts and humans, and it was important to have drawn attention to the ability of altered peripheral transmission to

play a role in determining behavior. To my knowledge, this was a possibility that had not previously been considered, and for me it derived directly from the Lorenz model. Now, how to proceed directly to work out the CNS (central nervous system) events? Sherrington (1906) advanced knowledge of central nervous mechanisms indirectly by studying movements. Words to the effect that "movements provide us with a window into the nervous system" indicate the principle that guided him. I decided to adopt this principle for use with arthropods (see Hoyle 1970). It proved possible to record from several different muscles of insects at the same time, during several kinds of behavior, including courtship songs of crickets and grasshoppers, and associated movement sequences. These turned out to be perfect examples of FAPs. The study in turn helped to define the FAP concept. This line of work has since been developed by many investigators to the state of a fine art, especially by Norbert Elsner in Germany (see Elsner & Popov 1978). The myograms provide a simple, quantitative measure of precisely what the nervous system puts out in order to cause the behavior. From the data a great deal can be inferred about the nervous system strategies involved in determining particular behaviors. Such data are of value in comparing related species (Elsner & Popov 1978; Ewing & Manning 1966; Lindberg & Elsner 1977), and in studying genetic aspects of behavior control (Bentley 1971; Bentley & Hoy 1972; Hoy & Paul 1973). There are some behaviors of some organisms, notably some nudibranch molluscs, in which the discharge of some identified interneurons is obligatorily and precisely reflected in the execution of a particular movement. Myographic data can in such cases be dispensed with in neuroethological analysis, but for arthropods and vertebrates, which have articulated skeletons, and which therefore use a balance between forces in cooperating agonists with those in cooperating antagonists, myograms are essential. This is because exactly similar movements are produced, at different times, by widely different, detailed motor patterns. In order to understand the rules underlying control, it is necessary to know these details and how they relate to the movements. In such cases the CNS must either be using proprioceptive input extensively or making very sophisticated calculations of the movements that should result from various combinations of motor output (see Selverston 1980).

These requirements place constraints on the level of analysis that is possible for any given system. There are so many motor neurons active when any vertebrate makes a movement that precise, comprehensive myography is impossible. Only in arthropods is precision possible, and then only for those muscles that have, or use in a given movement, no more than four excitatory axons per muscle (though with computer analysis it is possible to increase this limit).

The next-higher step concerns the premotor interneurons. Prior to the introduction of intracellular dyes in 1968, studies of this stage were restricted to guesswork except with a few molluscs that had unusually large, pigmented neurons. The latter organisms are mostly aquatic and lack limbs. Their "behavior" is restricted to the bending of their soft, unarticulated bodies in water, so it is necessarily less complex, with fewer adaptive variants, than that of terrestrial animals locomoting on legs.

This is not to say they have nothing to contribute to neuroethology. The only demonstration that any CNS can produce a FAP in the absence of inputs other than a trigger (or releaser) has come from one of them, the nudibranch *Tritonia* (Dorsett, Willows & Hoyle 1973). Much of our knowledge of basic cellular neuronal properties has been derived from *Aplysia*. The technical advantages offered by the giant neurons of the abdominal ganglion have led to an extensive exploration of the limited movements controlled by this ganglion (Kandel 1976; 1979). But the reflex movements studied by Aplysiologists unfortunately do not represent the kind of behavior that constitutes the science of ethology.

Future research needs to combine the study of behaviors that have been of sufficient complexity to excite the serious interest of the giant pioneers of ethology with analysis of the neuronal circuitry underlying *those behaviors*. This is a tall order, but thanks to intensive efforts during the seventies and continuing today, the circuitry underlying one modest FAP, the leap of the grasshopper, has now been worked out. There may be neurons other than those currently known to be involved in the jump, but they are unlikely to be playing more than minor roles. A circuit diagram of the neurons is shown in Figure 1. The behavioral features of a jump have been described (Heitler 1974). The jump can be elicited by many different modalities of stimuli. A brief change in any of a wide range of external factors, such as movement in the visual field, light intensity, temperature, sound, air puff, touch, or chemical stimuli, can cause a jump. The insect will also jump spontaneously, meeting the vacuum-activity requirement for qualification as a FAP; unevoked jumps are likely to occur in conflict situations, for example, when a competing male appears during a courtship approach. This behavior may be analogous to what has been called displacement activity in vertebrates. It should be borne in mind that a jump is not simply a reflex response. Either flexion or fast extension of a single hind leg tibia occurs as reflex responses to appropriate stimuli but results in either kicks or preparation for jumps only. There is no known condition under which a jump is bound to occur: At times grasshoppers will fry to death on a hot plate, suffer death by crushing, or be eaten rather than jump.

We do not yet know what the central factors are that determine the readiness to jump, but there is increasing knowledge about modulatory neurons that seem likely to be involved, and answers to the question should soon be forthcoming. Although it is certainly possible that a grasshopper's brain can "command" the insect to jump (or not jump), such a command is certainly not necessary for a jump. The neural machinery necessary and sufficient for a jump resides within the third thoracic ganglion alone. Lateral, ascending, and descending inputs converge on this circuitry and may, individually or cooperatively, set it into motion. [See also Kupfermann & Weiss: "The Command Neuron Concept" *BBS* 1(1) 1978.]

It may be argued that the parallel development of interest in various aspects of neuroscience, from developmental (e.g., Coghill 1929) to cellular, in the 1920s, 1930s, and 1940s simply merged with ethology, so that at no stage was there a conscious emergence of neuroethology. As it happens, we can easily see that this is incorrect. At the same Cambridge meeting in 1949 at

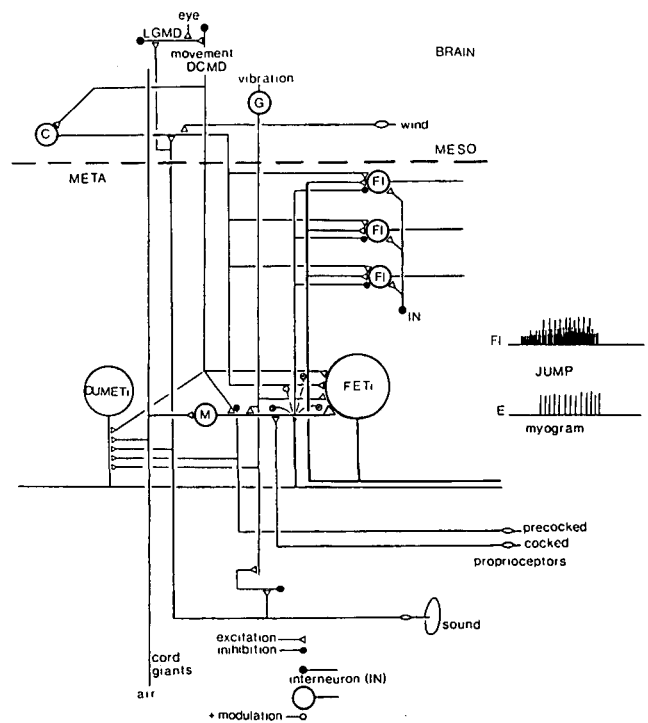


Figure 1. Diagram of specific identified neuron circuitry involved in the locust/grasshopper jump. This is a simple, unitary fixed action pattern (FAP) of behavior. Several laboratories have contributed details. The neurons are as follows:

1. *Motor neurons*. Fast extensor tibiae (FETi – Hoyle 1953). Three sets of flexor tibiae (F1 – Burrows & Hoyle 1973).

2. *Interneurons*:

Visual. Lobular giant movement detector (LGMD – O’Shea & Williams 1974). Descending contralateral movement detector (DCMD – Rowell 1971).

Vibration/sound. Giant interneuron sensitive to both vibration and sound with a cell body in the mesothoracic ganglion, traveling from the metathoracic ganglion up to the brain (G – Rehbein 1976).

Multimodal. (a) Supplier of coactivation to flexors and extensor tibiae (C – Pearson & Robertson 1981). (b) Supplier of excitation to the extensor but inhibition to the flexor, the last link in the chain, the jump-trigger interneuron (M – Pearson, Heitler & Steeves 1980).

3. *Modulatory neuron*. Overall humoral-type excitatory modulation, both central and peripheral, is provided by a dorsal, unpaired median neuron innervating both regions of neuropil in the ganglion and the extensor muscle (DUMETi – Hoyle 1974). The substance synthesized and released is the phenolamine equivalent of norepinephrine, *octopamine*.

which Lorenz presented a hydraulic model (to be described below), the collected views of the traditionalists were summarized by Paul Weiss (1950). Weiss produced a rather vague diagram (Figure 2) full of cross-connecting arrows linking component “centers” for the generation of complex behavior. There are levels, from inputs to outputs, in terms of specific motor neurons. The most significant aspect, which certainly was universally accepted at the time, was that there was a strict hierarchy, with tiers of control systems. The diagram is also notable for its open-loop character: There were no feedback elements anywhere in the system. It should be recalled, however, that this was only one year after the publication of Norbert Wiener’s *Cybernetics* (1948), in which he took physiologists to task for not understanding the signifi-

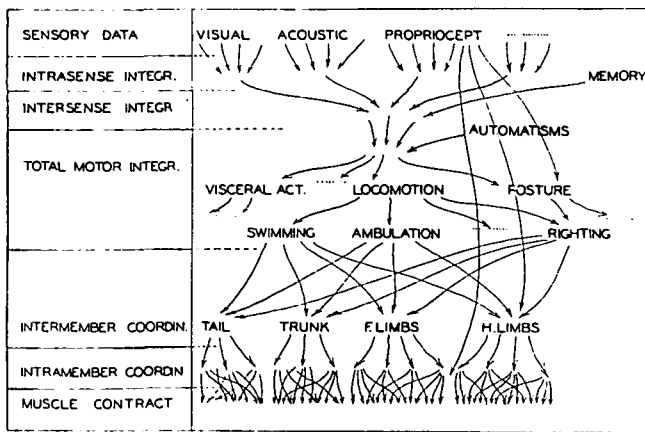


Figure 2. Early hierarchical concept of control of behaviors of a typical quadrupedal vertebrate (from Weiss 1950).

cance of the control systems they had discovered to be widespread in all forms of animals. The ethologists were as naive about the neurophysiological significance of their findings as the neurophysiologists were about the behavioral implications of theirs.

When stripped of the vast foliage of observations on individual behavioral acts of a wide variety of species, the core of strictly ethological knowledge boils down to a very few, profoundly simple, statements. The ethology pioneers left a legacy of novel classificatory terms, each of which conjures up a clear image of the relevant behaviors. Within each category, examples of these behaviors are found in men, other mammals, birds, reptiles, amphibians, fish, insects, crustaceans, some molluscs, some flatworms, and even some sea anemones, thereby encompassing all levels of neuronal organization yet evolved. Therein lies the profundity of the findings. These terms are presented below, with simple, widely accepted definitions, and remarks relative to the discussion that follows.

Definitions of key concepts

1. Fixed action pattern (FAP). This is a complex, coordinated movement or sequence of movements that recurs in a similar manner whenever it is performed. There is a beginning, a middle, and an end for a sequence, and the components occur only in one order. A sequence never begins in the middle. The act as a whole has adaptive significance. It is generally performed only in a specific, biologically significant context. At a given temperature the time-relations of components are very nearly constant whenever the FAP occurs. Only minor variations occur in response to external stimuli applied during the movement. Most or all of the components of a FAP are expressions of inherited factors and are subject to the Mendelian laws of inheritance as wholes. Examples are escape swimming in some sea anemones and also in some molluscs, nest-building in some insects, fish, and birds, courtship and sexual behavior in some molluscs and many arthropods, facial expressions in primates, and a wide range of territorial, aggressive, defensive, and sex-related acts in all vertebrate orders.

FAPs are elicited only by highly specific situations or stimuli (releasers), except on rare occasions when they

may occur spontaneously or in an inappropriate, stressful situation. The recognition and specification of FAPs has been by far the most important outcome of the work of ethologists.

There are also numerous examples of behaviors that in most respects resemble FAPs, but in which a part, parts, or the whole are not always performed with equal vigor. They may have reduced excursion amplitude, reduced force, less speed, or fewer cycles of repetition. Several examples are described by Tinbergen (1951), and the matter has been specifically addressed by Schleidt (1974). Should these behaviors be given a different designation? Most ethologists say not, thinking the adjective "fixed" as best applied rather loosely. Some of these behaviors are compounded of FAPs and interspersed reflex actions or of learned actions with or without reflex components. In such cases it is better to consider the entire behavioral act as a complex that includes FAP components rather than to weaken the basic concept, which otherwise has a precise meaning. If the entire sequence is stereotyped but has components that vary a great deal in amplitude or frequency, it is still possible that it should be considered a FAP. Only a detailed study of the causes of the variations could decide the true nature of the control mechanisms.

The waggle dance of the bee is a FAP that is modified quantitatively in relation to the messages to be conveyed: directions, distance, and quality of food (von Frisch 1967). However, this behavior is clearly a FAP, not a reflex. Purposive modulation of a FAP for information-transfer is a very different matter from variation in the vigor with which a male robin attacks different models of a male robin.

2. Displacement act. This term is a corollary of the FAP concept and applies to a fixed action pattern when it is performed in a context that is definitely inappropriate. This commonly occurs when for some reason a more appropriate FAP cannot be expressed, or when the situation is marginal for each of two different behaviors, or deserves the connotation "stressful." It is often difficult to make a satisfactory assessment of appropriateness or otherwise, and mistakes have been made. The important aspect is that a situation that might release a FAP is often one that causes widespread general arousal, paying attention, and the like so that one or another FAP is likely to occur. If the cues are those appropriate to more than one FAP, especially FAPs that are fundamentally opposite, such as attack/withdraw, displacement acts are especially likely to occur.

3. Releaser. A key concept of ethology, a releaser may be defined as a specific single organismic or environmental feature, complex of features, or context, or a behavioral act or sequence of behavioral acts, performed either by another individual or by a group of animals, that elicits a FAP. Releasers range from a simple sign, such as the red spot on the lower mandible of a herring gull, to an entire complex sequence of combined auditory and visual displays.

The fact that so many of the behaviors that have been studied in the name of ethology require a releaser has been the basis of the more cogent criticisms of ethological theory, because the releaser → FAP relation appears to resemble classical reflex action (e.g., Kennedy 1954;

Schneirla 1952). There is no difficulty when, as is often the case, FAP expression is an all-or-none one. But what about a stereotyped behavior whose amplitude is directly proportional to some quality of the releaser such as its size or color? Such behaviors have greatly occupied the research attention of some prominent ethologists (especially Tinbergen among early ethologists, 1951), who were proud of the way they quantified the behavior. Another controversial aspect concerned the presence of more than one releaser, particularly when the releaser was an object and the released behavior directly related to the releaser. In such a situation the animal generally makes a choice and “selects” or displays a preference. This may be for an artificial object such as a pot egg rather than a real one, because it is bigger or has more spots or whatever. The artificial object may elicit constant amplitude behaviors, in which case the FAP concept clearly applies. The situation is moot for all behaviors in which the amplitude or intensity is proportional to releaser quality. The answer to the question, Is this a reflex?, for such behavior may be “yes,” but can, in principle, only be decided on the basis of knowledge of the neurophysiological underpinnings.

4. Vacuum activity. A complex FAP may sometimes be performed by an animal in spite of the lack of any external releaser. Although, in most cases, the possibility of an invisible internal “prick” cannot be ruled out, the sudden appearance of complex behavior suggested to Lorenz the then-new concept of “action specific energy.” He chose to think of the tendency to show a behavior as proportional to an accumulation of its energy; that energy is confined within restraining boundaries from which it is increasingly trying to force its way out. Occasionally the restraint is overcome spontaneously and the pent-up energy rushes out, causing action that was appropriately termed “vacuum activity.”

5. Consummatory act. There is often a terminal element in a behavioral sequence that is clearly recognizable as the objective of preceding preliminary behavior. This is termed the “consummatory act,” and it may be defined as a fixed or relatively fixed act that follows a FAP, a sequence of FAPs, a sequence of reflex actions, or mixtures of FAPs and reflexes, and that is followed by quite different behavior, or none at all. The entire sequence is clearly at an end after the consummatory act. This may be, for example, completion of a nest, orgasm following mating, or feeding following capture of prey. A consummatory act is especially common after behavior to which the adjective “appetitive” may be applied unequivocally. It is the logical climax of appetitive behavior.

The expression “consummatory act” may appear somewhat quaint or old-fashioned to most modern ethologists. For many behaviors there is an entire sequence of movements, or the repetition of a movement, before termination, and a lot of possibility for feedback influences. A small amount of good-tasting food may be as satisfactory as a huge quantity of poor-tasting stuff in quenching food-seeking behavior. Some birds overbuild their nests while others underbuild. Is it the sight of the nest, the feel of it, the amount of work done on it, the availability of nest-building material, or combinations of all of these that leads to termination? Even lowly animals seems to make

compromises. But however difficult it may be for ethologists trying to quantify their data to handle this particular concept, it is easy to understand what is meant in general. Termination could be due to a running out of the neural substrate for drive (see below), or an inhibition based on performance, especially the consummatory act, or a combination of the two. Each of these possibilities invokes neurophysiological phenomena that are amenable to analysis in suitable subjects.

6. Drive and mood. I am well aware that both of these terms seem quaint to modern ethologists and psychologists. In Gallistel’s (1980) *The Organization of Action*, the index entry for “drive” advises the reader to “see Motivation.” Nevertheless, drive is defined in the glossary; mood, however, is missing from both glossary and index. Yet there is no point in dwelling on mere semantics: Nobody truly has any difficulty understanding both terms and translating them into their personal experience of behavior. The sight and smell of food are not going to elicit food-related behavior in an animal that has just finished filling its stomach with attractive food. There are strong fluctuations in the tendency of any measurable appetitive behavior to be expressed. Therefore, we can easily define both drive and mood and attempt to determine their physiological underpinnings. [See also multiple book review of Gallistel’s *The Organization of Action* *BBS* 4(4) 1981.]

Drive is the probability of occurrence of an appetitive FAP. Drive is weakest immediately following the relevant consummatory act and strongest when the consummatory act has not been carried out for a long time. Secondary, capricious variations in strength are superimposed, so that even when drive is strong, a releaser may not elicit the behavior. Mood is a quantitative variation in expression of a behavior under apparently constant conditions.

Lorenz and his model of instinctive behavior

Lorenz made but one brief excursion into the larger domain of physiology, which was also the occasion of his introduction to a broader audience than that of his native land. This was in 1949, when he accepted an invitation to address the British Society for Experimental Biology at its Fourth Annual Symposium in Cambridge. The topic was “Physiological Mechanisms in Animal Behavior.” Lorenz departed from his usual procedure by presenting a model summarizing ethological findings that he thought would make them clear to neurophysiologists. The model, the sole illustration of his article (Lorenz 1950), was presented in a stunningly powerful yet simple diagram (Figure 3). This model quickly became famous, or in some circles infamous. It is known as the “water” or “toilet” (“hydraulic”) model and indeed, actual domestic porcelain objects have been used in dramatic “live” simulations. Lorenz wrote of his model that “it is able to symbolize a surprising wealth of facts really encountered in the reactions of animals.” He further justified it with the statement, “As an instrument for the quantification of external and internal stimulation, this model has proved to be of some value” (p. 255).

The toilet model has come to symbolize neuroethology

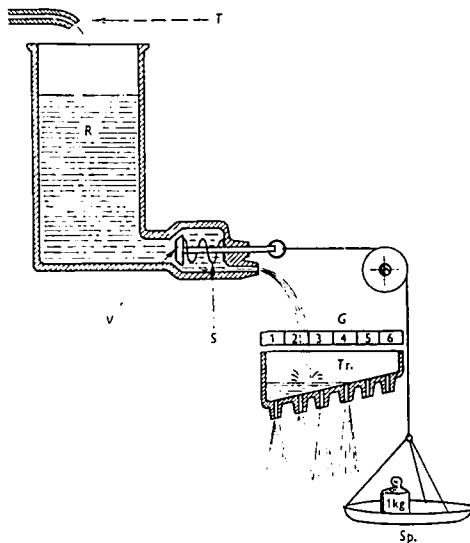


Figure 3. The famous Lorenz (1950) hydraulic model, illustrating the concepts of the generation of instinctive behavior developed by ethologists.

whether persons who call themselves neuroethologists like it or not, so it can serve the purpose of providing us with a synopsis for the ethology side of our coin. The model intentionally implied a physiological underpinning for FAPs and their “release.” In the model, behavior is simulated by water jets, at the lower right. The rigid sequence of component behaviors of a specific FAP is indicated by the slope of the trough (Tr.), and the actual sequence by the numbered scale (G). The central nervous system gradually builds up drive for execution of this FAP, symbolized by a trickle of water (T) gradually filling up a tank or reservoir (R) of “action specific energy” for the behavior. The energy tries to express itself as movement by leaving the tank and entering the trough, but is blocked by the spring-loaded valve (V). The spring (S) symbolizes neural inhibition, and it is also the route for mood, in the form of variations in its stiffness. Releaser action for the FAP is symbolized by a weight added to the scale pan (Sp.).

By putting a series of the reservoirs side by side, and allowing some parallel or “leaky” plumbing, one could bring displacement acts into the scheme. The traditional problem of explaining the utilization of the same movements in several different overall complex behaviors is also incorporated.

Linking the reservoirs also leads to thinking about a major problem, that of how an appropriate behavior is “selected” from the repertoire following the completion of a complex releaser signal, perhaps sharing some sensory components with releasers of different, inappropriate behaviors.

The delight of the Lorenz model was that one could immediately think of a large number of behaviors, in species from the lowliest diploblastic Metazoa to man (as witness *The Naked Ape*, by Desmond Morris, 1967) that could be fitted into the scheme. It provided all the magical joy of a great generalization: the illusion of comprehensibility. But was it in this case no more than a poetic mirage? The water in the model is real enough, and the physiologist, though unable to specify a precise neurophysiological equivalent, could at least envisage some

possible candidates. The output stages in the model were very easily understood in physiological terms, since each is a muscular contraction. The releasers were in principle equally easy to translate. At their simplest they are signs that are either present or absent. The sign details often needed multiple-channel sensory coding: shape, size, color, and the like sometimes being compounded. But the final step in information processing could be a 1, 0 choice – a single bit of information. A translation of instinctive behavior into basic neurophysiology of cells loomed as a realizable possibility, at least for the simpler invertebrate nervous systems. The science of neuroethology cannot fairly be considered to have predated the Lorenz hydraulic model of 1949. Neuroethology could thereafter be conceived of, and its principal purpose stated. Its pursuit could be equated with testing the model and, if validated, with the elucidation of the neural equivalents of the structural and functional features of the Lorenz model.

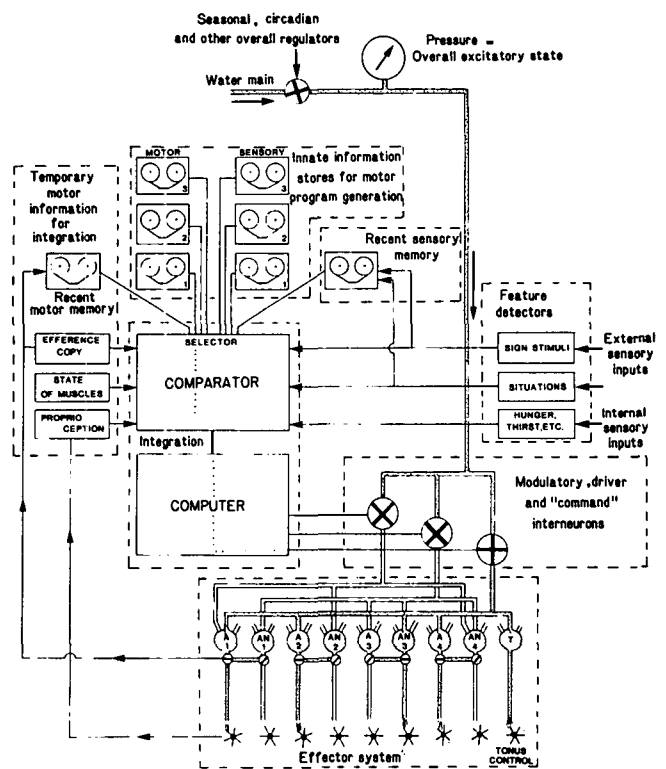


Figure 4. A 1984 hydraulic model of behavior generation, with special reference to targets for budding neuroethologists. Agonists in a movement, which is part of a FAP, are indicated as A₁, A₂, etc., and their reciprocating antagonists as AN₁, AN₂, etc. Modulatable forms of tonus (see review by Hoyle, 1983) are indicated by T. In the simplest form of truly fixed FAPs, direct motor tape control without involvement of feedback, the stored information (simulated tape program 1) is first selected, then turned on, and via a direct pathway (indicated by dotted line) activates the relevant interneurons (symbolized by regulators directing water to appropriate effectors). Other, more varied FAPs, especially those carrying recently learned information (as in performance of the honeybee dance) involve complex central integration of inputs by a neural comparator, and subsequent modification of the “taped” instructions by a neural computer. A motor program can also be produced by reference to stored innate sensory tape information, in conjunction with incoming sensory and motor information.

I am told by an eminent ethologist that the “flush toilet model is not taken too seriously anymore.” Clearly, among other omissions, it lacks the multitude of feedback processes as well as all the modulatory influences that we now take for granted as being important factors in all nervous systems. No allowance is made for behaviors that are not diminished by performance, especially those in which there is enhancement from the first in a series of closely spaced FAP repetitions, to the next.

A modified Lorenz model, which substitutes modulation of neural elements of the FAP-generation circuits for water filling the tank and incorporates secondary modulations via feedback, both proprioceptive and extrinsic, will do nicely as a modern substitute. In Figure 4 I have attempted to draw such a model, again using water, partly to relate to the Lorenz model but also because a flow of water is so easy to grasp, but adding a valve-controlled, pressurized basic system, with electronic controls and memory, such as we now know are built into even the simpler nervous systems.

Defining modern ethology and neuroethology

The simplest logic demands that neuroethology be the study of the neural mechanisms underlying the behaviors that constitute the science of ethology. To determine what these behaviors are the neuroscientist should first read at least the major works of professional ethologists. A survey of the behaviors and the distribution of species that are addressed in reviews and textbooks, in the name of ethology, is revealing. For example, in his classical work, *The Study of Instinct*, Tinbergen (1951), by my count, referred to 473 animal species. Their distribution according to major classes is shown in Table 1. There is a strong emphasis on insects and birds, which is not surprising, as Tinbergen loved to watch birds and to experiment with insects. However, in the second edition of a popular introductory text published much later, Manning (1972), referring to some 225 species, yields almost identical percentages of birds, which take first place easily with 37%, and insects, with 19%, as runners-up. This was in spite of the fact that Manning trebled the proportion of mammals referred to, from a meager 10% in Tinbergen. Molluscs formed less than 3% of the total in each, and these were almost entirely cephalopods.

Table 1. *Distributions by class of animals referred to in two books on general principles of ethology, Tinbergen (1951) and Manning (1972)*

Class of animal	Tinbergen	Manning
Mammal	10.0	32.6
Bird	38.0	37.0
Reptile	1.7	0.4
Amphibian	5.0	0.9
Fish	15.0	5.0
Insect	20.0	19.0
Crustacean	4.6	0.4
Mollusc	2.5	2.2
Other invertebrates	2.1	2.2

An in-depth, independent research program has been undertaken by a neurophysiologist and his coworkers to describe the behavior of a lowly gastropod mollusc, *Aplysia* (Kandel 1979), this species being easy to study neurophysiologically. There is, nevertheless, no sign that the remarkable successes in the physiological aspects of this endeavor have won over ethologists. The ethologists were there first and are in a position to call the tunes. To reach them, and thereby promote the unquestionably exciting and important field of neuroethology, it will be necessary for neurophysiologists to address the same organisms and behaviors as do ethologists.

Before proceeding with a discussion of specific goals and strategies, let us pause to consider how modern ethologists see themselves and define their subject.

Some authors choose to define ethology very broadly. The broadest definition is that of S. A. Barnett in *Modern Ethology* (1981): “the scientific investigation of behavior by all means and by all kinds of people.” Barnett quotes John Passmore’s familiar passage from *The Perfectibility of Man* (1970): “To write anything worthwhile is to arouse opposition, controversy.” Let me beg to disagree with him. Even though the great “ethologists” defined their field loosely, it is very clear both from the subject matter of their research and their view of their findings that they in practice came to apply a restricted meaning. Barnett defines almost everything associated with the study of behavior except the most important thing of all – he fails to define what he means by the word “behavior” itself! My dictionaries offer a variety of choices, of which the simplest is “movement.” Clearly, Lorenz was not a student of movement. Another definition in Webster is “an organism’s muscular or glandular responses to stimulation,” that is, a reflex. The very word made Lorenz and Tinbergen recoil. The whole point of the ethologists’ findings was that there is more to behavior than reflex action, and I doubt very much that the intellectual aspects of gastric secretion ever stirred their minds. The dictionary does go on to qualify the definition with, “especially movements that can be observed.” There are several scientists who are intensively studying ganglia such as the one that controls the internal mincing of food by lobster stomachs, which they regard as a model for the generation of behavior (e.g., Selverston, Russell, Miller & King 1976). I concede that what these investigators are discovering may provide valuable basic information about the ways in which neurons can be interconnected, and also about the properties that enable neural circuits to function efficiently. I also concede that this knowledge may some day serve to guide neuroethologists in some aspects of their studies, but I emphatically deny that such research is to be considered part of neuroethology.

An ethologist friend who thinks exceptionally clearly and whose work I admire says that he views ethology as a “broad concern with what real animals do in real situations.” However, close examination of what this ethologist takes the time to study in detail shows that it is quite restricted: The animals he studies are all furry and warm-blooded (a fraction of 1% of the animal kingdom), and only one act of behavior is targeted. It is a major disadvantage of the field that an in-depth study of even one behavior can demand the full-time attention of an investigator plus students. Never has there been a field of

scientific endeavor where cooperation by experts in different disciplines is more essential.

A program for would-be neuroethologists

We should start by disclaiming the notion that the behavior of interest to ethologists is to be equated with *any kind of movement*. This route quickly leads to the absurdity of including in neuroethology a great deal of physiology and biophysics as well as much of neuroscience. The dictionary definitions of behavior also include "manners," "deportment," and "moral conduct." While these again take us out of the actual realm of the research interests of Lorenz, they at least introduce the notions of complexity, of restriction to recognizable clusters, and of interaction with other behaving entities.

Let us then examine what types of events interested Lorenz. As we have seen, these were stereotyped sequences of coordinated movements. They were always ones that were repeated exactly, or very nearly exactly, not only by any given individual, but by other individuals of the same species. They were movement clusters strongly related to survival: escape, defense, attack, territoriality, feeding, courtship/mating, cooperation. These are all behaviors that relate to the achievement of *goals*, and when they occur in man, they are associated with *emotion*. They are all classifiable under the term "instinctive," that is, *complex goal-related innate behaviors*.

A careful consideration, and above all, one hopes, a rational acceptance, of these constraints is important if we are to agree upon a working definition of neuroethology that will promote the development of a useful body of natural knowledge. Let us enumerate those parts of physiology that can be ruled out and relegated, as they always have been in the past, to their appropriate subdivisions of traditional physiology, and along with them the related neuroanatomy. Neuroethology will doubtless draw strength and information from some of the rejects, but should maintain firmly its "exclusiveness." There will be many occasions on which a legitimate neuroethological study overlaps with some of the other disciplines of more limited scope. For example, I think we should exclude reflexology, even though some FAP sequences incorporate reflex actions, and also all forms of fundamental and applied sensory physiology. However, the triggering of many FAPs depends upon *feature extraction*, so releasing cannot be fully understood without knowing the details of this subsidiary action of the sense organs involved.

Neuroethologists will encounter novel as well as traditional membrane processes down to the level of ion channels, synaptic transmissions, and electrical and chemical modulations. They will come across familiar, but also novel, neuronal anatomies and circuits. The involvement of nonneural cells associated with nervous systems could become a significant phenomenon for neuroethologists. How, then, will they be distinguishable from the host of basic physiologists, biophysicists, and biochemists? Inevitably, neuroethologists wear second, third, and more hats associated with these disciplines. It will only be by their assertion of different, more global, principal goals that they will be recognized. When they

talk to other neuroethologists, all of them will know that their common purpose is understanding *the generation of particular kinds of complex behavior*. There will be a very few major goals and they will be common. It should be possible for neuroethologists to avoid losing sight of the woods because there are so many interesting trees, but only if the goals are delimited.

It may be argued that, as knowledge of neuroanatomy and cellular physiology expands, understanding of the neural bases of behavior in general, and therefore also of its subdiscipline, neuroethology, will inevitably achieve the same objectives, and that this would happen without any specific focusing on a separate endeavor labeled neuroethology. I argue against this view. Neuroethology is quite likely to revert to some earlier dogmas (such as those of reflexology), or find new ones, if left to the random pursuits favored by current neuroscience. For, in neuroscience, we are dealing with a kind of knowledge that is based on an enormous number of concurrently interactive, time-dependent variables, in biophysical systems of enormous complexity. The time required to describe a nervous system adequately is something new to science. No matter how much effort is expended, it will take hundreds of years just to work out the elemental details. Perhaps, as more data accumulate, a general theoretical framework, which we lack completely at present, will be developed. There is an existing field of neural modeling that is beginning to expand because of its potential for practical use in robotics. I expect this to be highly interactive with neuroethology of the kind I shall advocate.

The advantage of defining more limited goals is that a measure of real understanding at an intellectually satisfying level could probably be achieved within a human lifetime. There are other potential advantages. The insight of the major ethologists I have mentioned prevented a continuation of the blind following of false leads. A major outcome of their thought was the realization that there was more to complex behavior than the compounding of reflexes. The reflex schools of physiology, established by Sherrington and Pavlov, totally dominated both thinking and experimenting for more than half a century. Paul Weiss (1941) was thought slightly ridiculous when he dared to ask, though in a less-than-global journal, "Is the sensory influx a constructive agent, instrumental in building up the motor patterns, or is it a regulatory agent, merely controlling the expression of autonomous patterns without contributing to their differentiation?" (p. 592) Sir James Gray was on much firmer ground in 1949, thanks to growing understanding of the findings of the Lorenz school, when he asked the same question in the form: "Can an animal initiate and maintain patterns of coordinated muscular movement without reference to the outside world?" (Gray 1950, p. 112).

The decline in the dominance of reflexology was not far away. Major credit for experiments that led to rejection of a false dogma must go to a very small group of invertebrate neurobiologists, especially the late Donald Wilson (1972; also see review by Delcomyn, 1980). But the way to widespread acceptance of their findings had to a large extent been prepared, albeit unwittingly, by the European ethologists. As we have noted, ethologists mainly worked on and wrote about birds and insects; they treated

examples from each class as if they provided equivalent variations on the common themes of animal behavior. The general principles expounded were meant to apply across the board to behaving animals, whether they had a backbone or not. These ideas about the generation of many of the behaviors the ethologists studied were clearly incompatible with reflexology, though they did not make a major issue of this incongruity.

As long as physiologists subscribed to the Sherringtonian/Pavlovian dogma that the most complex behaviors could, in principle, be understood on the basis of the compounding of reflex actions, there was hardly any need for an elaborate, prolonged attack on the question of how behaviors are generated by investigators armed with microelectrodes. The relatively recent realization that many, perhaps most, complex behaviors are generated by endogenous neuronal activities has completely changed the requirements. We must now admit that we have no understanding of the neural mechanisms underlying a majority of behaviors. The only way a behavioral act can be fully understood is in terms of the actual functioning of the individual neurons producing the output/commands and of the circuits in which they operate. That is a very tall order. It is virtually unapproachable for most vertebrate behaviors: There are far too many cells and they are too inaccessible to permit obtaining the kind of information that is needed. This is not to say that we cannot obtain information of relevance to the central questions from vertebrates, but that definitive information that will allow a comprehensive understanding of all but the simplest movements may be forever beyond our reach.

For some behaviors of some invertebrates there are no known barriers to eventually obtaining all the knowledge needed. This is because the relevant neurons are addressable during the execution of the behavior. By combining cellular neuronal knowledge from invertebrates with whatever can be obtained from vertebrates we should eventually be able to achieve a satisfactory overall understanding of the principles underlying the generation and control of behavior by nervous systems. The closest we have yet come to obtaining complete explanations of FAPs is for a few behaviors of invertebrates from different phyla. One such behavior is the escape swimming of the nudibranch mollusc *Tritonia* (Getting 1983; Willows et al. 1973). This has the singular advantage of being obtainable in the isolated nervous system, along with being recordable from the intact animal. The presence of the rest of the animal is not necessary for the swimming motor neural program to occur; nor does the rest of the animal influence the production of the program when it is present. Doubtless many small, specific cellular details remain unknown, but both the triggering (or releasing) mechanisms and the major details of the patterning are known. Although this FAP is generally elicited by the experimenter with a chemical agent (common salt), it can occur spontaneously. Another instance of the study of fictive behavior (i.e., motor output comparable to that occurring in the natural condition, but in a semi-isolated state) is oviposition digging by female grasshoppers (Thompson 1982). There are some parallels between the neural mechanisms of digging and of *Tritonia* swimming. The locust/grasshopper jump, whose neural circuit was referred to above (see Figure 1), is different in every possible way from escape swimming, leading one to

wonder just what the range for arrhythmic behaviors is. In spite of the relatively lowly levels of these behaviors, it is reasonable to consider these studies neuroethological.

Goals for neuroethologists

Following the lines of thinking outlined above, the primary target for neuroethologists becomes the study of the cellular events underlying fixed action patterns and related instinctive acts. Although it may seem a trifle redundant, and certainly rather naive, it may be desirable to spell out precisely which aspects of neuroethology most need to be tackled. These are:

1. Description of motor neural circuits and the ways they function in the generation of a wide range of *complex behaviors*, especially different behaviors using common musculature.
2. The precise roles played by proprioceptive, tactile, and visual feedback in determining behavioral details.
3. The nature and location of the efference copy, which, one can deduce, plays a major role in determining motor control of some complex behaviors and in learning motor skills.
4. Neural events of association between reafference and the efference copy in behaviors using both.
5. The locations and nature of inherited stores of information, which can be called upon as "motor tapes" to produce species-specific behaviors. (Examples are uncapping of cells in a hive containing dead bees and removing the corpses, two separate behaviors, each of which is genetically determined and subject to Mendelian laws of inheritance; Rothenbuhler 1964a; 1964b).
6. The locations and nature of inherited stores of information, which can be called upon as "sensory tapes" to guide the production of species-specific behaviors. (Examples are offered by conspecific recognition of song by insects and by birds, and the "image" of the final product used in the construction of patterned webs and nests by spiders, insects, fish, and birds.)
7. Elucidation of the changes occurring in a nervous system, which determine the progressive change in the probability that a particular behavior will occur.
8. Determination of the neural factors underlying variation in drive for behavior in general and for specific behaviors.
9. Identification of the neural and associated mechanisms generating circadian and circannual behavioral cycles.
10. Determination of neural determinants of changes in drive following execution of a consummatory act.
11. Analysis of the mechanism of "switching on" of behaviors by their releasers.
12. Determination of the locations and nature of information stores (memory) acquired by experience that are used to modulate innate behavior.
13. Determination of the means by which memory information is utilized in the execution of behaviors.

Hard choices about target animals and behaviors

There has long been a debate in private, and to some extent in public, about the optimal species/behavior targets for analysis (e.g., Hoyle 1975; 1976), and the

question is as far from resolution now as when it was first raised. Many investigators refuse even to face the question, resorting to bizarre “justifications” of choices made for no good reason. I still feel that large insects offer by far the most promising compromise among interest, significance, and feasibility. I confess to feeling somewhat negative about the enormous amount of research being published on *Aplysia*, though the depth of the work is exemplary. Kandel and Schwartz (1982) refer to this behaviorally boring glob of squishy protoplasm as a “higher invertebrate.” If this is so, the humblest insect must sit at the right hand of God! The research emphasis on *Aplysia* has been dictated solely by the easy accessibility of its large, naturally colored abdominal ganglion cells. If some of the immense effort devoted to *Aplysia* could be diverted to one or a few truly higher invertebrate(s), we might see some giant strides in neuroethology. As it is, there seem to be no principles of integrative or intrinsic neural functioning that we can extrapolate from *Aplysia*. The work is valuable at the cell and membrane level, of course, but can lead to oversimplifications or can even be misleading if extrapolated to the behavior of animals with legs. Cellular descriptions of events in habituation, sensitization, and simple classical conditioning need to be complemented with information about the cellular mechanisms of the long-lasting forms of learning.

There are such major basic gaps in fundamental neurobiological knowledge that some effort to channel efforts toward resolving them is justified. For example, what is an efference copy in cellular terms? Where is it located? Which neurons are addressed when a behavioral “species memory” of a simpler invertebrate is utilized in a fixed action pattern requiring specific sensory input? Exactly how do any of several well-known “command” interneurons evoke walking? What really is the “flight motor” of a flying insect? Where in the nervous system of a bee are the waggle dance instructions located? One could go on and on because the list is so long.

The crustacean stomatogastric ganglion and *Aplysia* visceral ganglion have been regarded as “model systems,” but models of what has not been stated. It is indeed possible that some neuronal generators of movement cycles in other organisms will be found to work like the neurons controlling a single locomotor movement of *Aplysia* (and like others, such as the stomatogastric ganglion neurons). But these are at best examples of what *may* be found elsewhere. They cannot be taken as models of what actually happens in another system until the other system has been at least partially explored. A model-T Ford engine is a good model for even the most complex 16-cylinder Ferrari engine, but it cannot tell us anything about a turbojet. Even a cursory examination will suffice to indicate whether or not an unknown engine can be modeled by the model-T, but the direct inspection must first be made.

So neurophysiological strategy must involve the exploration of many systems, in addition to in-depth examination of a few. My judgment is that the choice of the ganglia of *Aplysia* and the crustacean stomach as targets for so much attention is not justified on the basis of the significance of the behaviors they generate. The same arguments apply even more cogently to neural circuits controlling hearts, which are also intensively studied, most recently in the leech by Peterson (1983a; 1983b). Much of

our current knowledge of neural events in relation to behavior has been obtained from a few insects, notably locusts and crickets, which are rather limited in repertoires. However, the brains of bees, whose behavior certainly commands widespread interest (and respect), have recently been shown to be amenable to study with intracellular dye-filled electrodes (Erber 1983). We should all like to know what goes on in insect brains – aside from the processing of visual, chemoreceptor, and wind sensory information – especially what roles they may play in generating and controlling behaviors. Bees, ants, and wasps are guided by species-specific “species memories” of both individual and group activities. Where in their nervous systems do they store this information? How do they utilize it to generate relevant movements? Until the bee brain has been more intensively examined, there is still a great deal that we can learn about learning, using preparations that have proven amenable to cellular analysis. With insects, we can study operant conditioning using a paradigm that eliminates many of the experimental objections raised to “learning” the association of two stimuli, one or even both of which may be aversive (Forman 1982; Hoyle 1980). The results may be slower in coming, because the experiments are much harder to carry out, but the results should take us beyond such phenomena as habituation, sensitization, and short-duration associations.

An instinctive behavior of worker bees prompts them to “record” flight direction and distance and then to use the stored information for the subtle modulation of an inherited basic movement pattern. The latter, the waggle dance, is a good example in the best sense of a FAP. There is no difficulty recognizing it, it cannot be confused with any other behavior of the bee, and it is a set sequence of movements; however, a few key elements are capable of variations based upon recent experience. These quantitative modifications are the critical features of the contribution of information: The dance (FAP) is merely a vehicle for the expression of recently acquired information, by way of the variations. The entire question of how insects acquire any form of new information, store it, and later use it to modify their behavior is wide open, but it is certainly amenable to cellular analysis in some species. Major criticisms of the FAP concept have come from experiences in which a part of the total expression of a stereotyped instinctive behavior was shown to be clearly due to learned behavior. A particularly clear example is imprinting, in which the inherited stereotyped behavior allows for a major element – the object to be followed – to be learned. There is nothing in the nature of a FAP that forbids its being altered over the long term by experience, or even by immediate sensory input. Likewise, one FAP could be followed by another sometimes (but not routinely) or be mixed with reflex actions.

In addition to their jump, there are other activities of grasshoppers for which the neural events are at least partially known, including flying, maneuvering in flight, the elemental stepping of walking, digging/egg-laying, and a variety of courtship stridulations. Some of these behaviors use common motor neurons, yet the motor neurons appear in each case to be themselves participants in the circuits. The circuits are complete in headless animals, so the carrying out of these complex behaviors does not require input from the head except as a source of

general excitation. The most significant finding to have emerged from these cellular and circuitry analyses is that there is no evidence for hierarchies. Each behavior is the result of the interactions of a small number of neurons, which includes some key interneurons located in the same ganglion as the motor neurons, and the motor-neurons themselves. There is no trace of the kind of hierarchical organization (in the big-business sense) envisaged by Paul Weiss (1950) and others. What the known nervous system examples actually do is what is done in modern computing, that is, parallel processing of information. We need theoretical work, combined with modeling, which will enable us to understand parallel processing.

Prospects for neuroethology of vertebrates

I have generally been very pessimistic about the prospects for the neuroethology of vertebrates – and have often been chided for expressing this view: Presumably, it all depends what it is that one wants to know. There is no difficulty in generating data on vertebrates in the name of neuroethology – quite the contrary. The problem is whether any of it helps in resolving the major questions raised above. Even knowledge of neurons and their circuits is of little value for neuroethology, except in the context of the behaviors they are associated with. Since I have called for extensive cell-level knowledge of events occurring during behaviors as a prerequisite for understanding the neuroethology of invertebrates, how can less be required for vertebrates? The major retort has been that invertebrates have relegated significant major functions to single neurons, whereas the equivalent functions in vertebrates are associated with masses of what are presumed to be approximately equivalent neurons. Because of the anticipated similarity, it is supposed that knowledge from any one within a cluster may be transferred to the others. This might be more believable if it had been demonstrated to be true for any given cluster, in a behavioral context. The possibility of testing the validity of the assumption as a principle at least looms a little larger since the introduction of cellular work on slices of brains, but the work remains to be carried out. Bullock (in personal communications) keeps suggesting to me that I pay attention to the work of his laboratory on vertebrates, which he calls “honorary invertebrates,” namely, electric fish. It is certainly true that weak electric organ discharge patterns are complex, interactive, and subtle. Furthermore, the motor aspect – generation of the discharge – is quantifiable, and the sensory return is addressable all the way into the brain. However, as “behavior” electric organ activity is highly specialized, does not involve limbs, and seems remote from the majority of “behaviors” in which the motor output is expressed as movements.

If we address the relevance of vertebrate studies from the standpoint of, “It is what neuroethologists who work on vertebrates do,” what comes up? I have two colleagues who like to be called neuroethologists, J. Simmons, who works exclusively on echolocation in bats (Simmons 1980), mainly behaviorally, and R. Fernald who studies features in the visual system of a cichlid fish (1983), mainly neuroanatomically. Two prominent scientists working in the United States who like the neuroethology

label are Fernando Nottebohm, of Rockefeller University, and Mark Konishi, of the California Institute of Technology. The former works exclusively on brain anatomy in relation to the generation of songs by birds (Nottebohm, Stokes & Leonard 1976), and the latter on auditory location of prey by owls and the cortical representation of the spatial field (Konishi 1983). Neither is able to address the motor control questions raised above.

For another source of what is regarded by some as neuroethology, we can consult the subject matter of two books on neuroethology, one by Ewert (1980) and one by Guthrie (1980). Ewert (1980), in the English translation of his 1976 German text, defines the goal of neuroethology as relating activity within groups of interconnected nerve cells to behavior. He defines behavior as “spatially and temporally coordinated patterns of movement” (p. 1). This objective is woolly and, as a dyed-in-the-wool champion of first finding out how invertebrate nervous systems work, I feel cynically committed to pointing out that this may be the best that can be hoped for from studies on vertebrates. (I am mindful of the demonstration carried out by the late R. C. Gary for his medical students at the University of Glasgow. He asked that every student in his class think up a different sensory input for a cat – any kind of odor, region of touch or pull, local temperature change, stretch or flexion, movement, sound, and the rest. Having amassed a long list, he produced a decerebrate cat with a needle electrode implanted in its anal sphincter, and started to work through the list. Every stimulus produced a burst of spikes!) Featured in Ewert’s book, apart from his own work, are studies on object location by electric fish and behaviors elicited by local electric stimulation of the brains of several vertebrates besides toads. The longest chapter (pp. 71–128) is devoted to “recognition and localization (in brains) of environmental signals.” Ewert’s own research has been on the basic prey-catching behavior of toads, including factors eliciting it and its habituation. He has also examined both the effects of lesions on the behavior and of focal electrical stimulation, via flexible implanted leads, in toads free to move. These are fine examples, but of *Verhaltensphysiologie* rather than neuroethology, at least as I have defined it here.

The author of the other text, D. M. Guthrie, has worked on invertebrate animals, but he has devoted about half of his book to vertebrates. Major topics covered are Roeder’s work (1967; 1975) on bat/moth interrelationships, various visual discrimination(s), association of regions of brains with sensitivity to specific modulators, and the production of motor output by mammals.

A cursory inspection of the vertebrate data that are included in these textbooks, combined with the work actually being performed by researchers who gladly accept the label of neuroethologist, shows that none of the data or work arises out of the classical period of Middle-European dominance in ethology. The investigators are interested, not in behavior in general, but in very highly specialized aspects peculiar to certain classes. The favored animals are all specialists: Only song birds sing; only bats echolocate; only electric fish electrolocate; only owls can hunt in total darkness. There is a surprisingly strong emphasis on the relevant special sensory input. Much of classical ethology is concerned with the acts, not with releaser details. The connections of these investiga-

tors with each other's research domains are so tenuous as to be invisible. These investigators are not to be separated from those among their colleagues who are solely interested in the specific behaviors of the relevant species, and not at all in either neurophysiology or neuroanatomy.

Recently a large, multi-author volume was published on *Advances in Vertebrate Neuroethology* (Ewert, Capranica & Ingle 1983). Although it is true that much of the work reported has neuroanatomical/neurophysiological implications, very little of it was directly concerned with getting at the critical problems of the neural machinery of behavior. Tinbergen's term *Ethophysiology* (Tinbergen 1951) much more aptly describes what is in the book than does neuroethology, in my opinion.

What is needed is focus on both behavioral and neural circuit functioning. There should be no leaning toward the principles of neurophysiology, with its reductionism and intense concern for novel cellular processes. There should be total commitment to the common themes in the generation of instinctive behavior listed above. Control of flow of the water in the Lorenz model is the heart of the matter of ethology, water that represents basic but still unknown neurophysiology, neurochemistry, and information flow in neural circuits. These things are knowable, and their pursuit provides just as big a challenge today as it did in 1950. The prospects for successful investigations have been greatly enhanced by the development of new techniques. The most important of these are the intracellular dyes, which are making it possible to develop maps of identified neurons, and the use of brain slices, which has brought vertebrate brains within range of intracellular electrodes.

Is a general theory of neural circuit function possible?

Unfortunately, in spite of an explosion of research activity in neuroscience in the 34 years since the Cambridge meeting, there has been little advance in its conceptual underpinnings. The single general framework that has ever existed, the McCulloch–Pitts (1943) binomial model of neural function, had to be abandoned when intracellular recording revealed the widespread occurrence and importance of analog information processing and signaling (reviewed in Pearson, 1976). But the vacuum left behind has yet to be filled with even a tentative new model. Neuroscience came to be the art of the do-able, with expediency ruling the day, rather than a soundly based intellectual domain. Three generations of neuroscientists have now been trained without any link to a widely accepted general theory of neural circuit function and neural integration. They have been given to believe that they are engaged in a massive fact-finding operation guided only by the relative softness of the seams in the body unknown that happened to face their individual picks! Science without larger questions provides a dismal prospect to a truly inquiring mind. Of course, to those who would make careers out of providing random facts, nothing could be nicer, so varied and so complex are nervous systems. There is enough material to occupy armies of such persons for centuries. But without some strong delineations neuroscience will continue to explode

into myriad fragments. We shall end up with masses of descriptive minutiae of many nervous systems without advancing our overall understanding of how they do the job for which they evolved.

Although I see no prospect of an all-encompassing theory, there are some neuroscience clusters for which it seems possible that theoretical frameworks might be devised. First, there is learning, especially the unknown cellular events associated with *memory*, its acquisition, storage, retrieval, and utilization. Second is *feature detection* by sensory systems. Most anatomy and physiology of sensory systems is trivial from the point of view of the major ethological themes. There is just too much sensory information available to most animals, and their nervous systems have been at pains to reduce it to significant fragments. It is only the extracted key features that seriously concern behavior.

The third cluster is *motor control*. There is, happily, a great deal of common ground in existing approaches to the general questions of the control of posture and locomotion in all kinds of animals. For historical reasons, this area has kept sight of the possibility of a theoretical framework, most recently in tensor theory application (Ostriker, Pellionisz & Llinas 1982), and ideas have been usefully adopted reciprocally between students of "higher" and "lower" forms of life. However, this framework is apparently inadequate. In the 1982 abstract of a Neurosciences Society Workshop on motor control, it is stated that "Experimentation in this area cannot proceed without theories" and "the predominant, almost extreme, empiricism which characterizes research in motor control might in the long run be disadvantageous for progress" (Ostriker et al. 1982, p. 155).

The fourth cluster is the most global: *information processing*. We know that nervous systems are real-time, clock-controlled, gated devices, having mixed hard-wired circuitry and plastic modulability, in which both digital and analog information is handled simultaneously and consecutively. Thinking critically about information processing in such complex systems should not be left to aged oscilloscope watchers, accustomed to 10-hour days making and pushing electrodes. There are professional theoretical physicists who win Nobel prizes from couches in rooms furnished only with paper and pencil and a computer terminal. Neuroscience desperately needs a comparable coterie. Existing neural modelers are concentrating their efforts on working out computer programs capable of mimicking known cellular events, plus evaluating quantitatively the effects of changes in the form of dendritic spines, changes in synaptic conductances, and the like. These may be necessary steps, but in addition some thinking about, and modeling of, circuits, especially ones with lots of feedback and parallel processing, is long overdue. I have little doubt that, should a theoretical branch become firmly established and attract good minds, it would not only benefit neuroscience but also, in a very short time, completely revolutionize the science of computing. Of course, laboratory neuroscientists should keep a close watch on these anticipated theorists to make sure they keep to the facts and propose valid experiments.

The fifth cluster is *development*. Spectacular progress has recently been made in this field by young scientists, some of whom started out by working in invertebrate

neuroethology (e.g., Goodman & Spitzer 1979). Goodman is taking advantage of identified neurons discovered by insect neurobiologists, determining when they appear in the embryo and how they hook up with each other, and discovering previously unidentified neurons as a result of following the genesis of neurons. This information is bound to help in the understanding of neural circuitry, so this is a bidirectional service. But at its present stage, discovering the elemental facts of development, this field can properly be left, as it has in the past, to specialists in developmental biology. Most of the transferees from neuroethology to neural development have quickly lost sight of their original goals. They are now interested in development per se, and molecular/genetic concomitants. Fine. Let them work out the details of development at all levels. When enough is known about any specific nervous system, the details may well prove valuable to the neuroethologist. But let us, until much more is known, stop pretending we belong in the same guild. We all belong to the same city; our activities interact to some extent, but we each have very different jobs to do for the time being.

There are other neural matters, too, that can be left to other kinds of professionals. Kinesis, tropism, and taxis are in the domain of experimental zoologists. Membrane biophysics has more than enough independent professional adherents. Medically oriented neuroscience produces relevant information but is clearly not of primary concern. Neuroanatomy I have left out, because it is best if the relevant anatomy is done, as needed, in combination with the physiological studies, rather than, as has been the case in the past, as a separate branch of neuroscience. Neuroendocrinology and neuropharmacology are likewise not valid intellectual subdivisions of neuroethology: They have their own axes to grind.

Qualifications and justifications

Much has been written during the last decade on the oversimplification implicit in early ethological concepts. Hardest hit of all has been the very cornerstone of ethology, the releasable, inheritable FAP, merely because it was found on closer examination that for many supposed FAPs, the "fixed" aspect is highly suspect (reviewed by Wolf Schleidt, 1974, and by Barlow, 1977). Among the most detailed studies are those by John Fentress and his associates on facial grooming in mice (Fentress 1980). This is a nice example because it is a regularly repeated act, and the basic movements occur in the stumps of mice from which the forelegs have been removed late in development. The detailed studies showed that both early and late stages of a grooming sequence in a normal intact mouse are subject to a lot of variation. The middle stages are much less variable. Furthermore, the details of grooming behavior are different in mice examined in familiar territory, compared with similar mice in unfamiliar territory. The imposition of a load during the grooming may abruptly halt grooming, or lead to progressive increase in force developed by the restrained muscles.

It is quite unreasonable to hold the view that such findings have rendered the "fixed" aspect redundant, even if it emerges that no instinctive behavior of a

vertebrate is played out in strict conformity with the open-loop motor tape concept. There are undoubted instances in invertebrates, notably the escape swimming sequences of sea anemones and of some molluscs and the courtship songs of some insects, where no variations or negligible ones occur. Possibly the ancestral version of facial grooming in mice was equally fixed. We already know that there is a full spectrum in the behavioral repertoires of invertebrates, from ones in which there is no significant variation in performance under standard conditions to ones with as much leeway as there is in facial grooming of mice.

Several people have toyed with the idea of simply dropping the "F" (fixed) and calling these behaviors "action patterns." This would be invalid because every kind of goal-oriented movement is an action pattern. The original term is well worth keeping as long as the aspects I discussed above are kept firmly in mind. It is the fixed aspects of a FAP with variability that are the most significant ones for classification. No amount of variability in a FAP alters the fundamental fact that, at some time in each behaving organism's evolution, a genetic change occurred that added a new aspect to the behavioral repertoire for each movement sequence for which we can now designate a concise descriptive term, such as escape swimming, courtship song, facial grooming, etc.

There were probably many different routes to any one of these end points in the evolution of behavior in terms of the kinds of neural anatomy and physiology involved. Furthermore, there may be unique special adaptations peculiar to one phylum or another. However, these are not possibilities to be either second-guessed or despaired of. The very essence of neuroethology should be to determine, for representative orders of animals from diverse phyla, precisely what the possibilities are.

In all cases the behavior arose initially as a mutation, or concurrent set of mutations, which caused novel neuronal circuitry and connectivity, as well as cell and synaptic properties and associated modulabilities, to arise during development. In some cases, these must have occurred in pathways that already possessed a great deal of variability due to competing convergent inputs. In others, they will have affected routes with no other inputs and so led to fixed actions. The point I wish to emphasize is that, although the final outcomes will be seen to be markedly different quantitatively in the variants, the underlying mechanisms and genetic bases may be found to be similar.

Even now, when we know very little about the neural generation of FAPs, I would hazard the guess that there is at least one widespread common feature in the mechanism of their generation in both vertebrates and invertebrates. This feature is the involvement of one or more interneurons releasing a neuromodulator substance (see my commentary on the *BBS* article by Dismukes, 1979, for definitions) at specific neuropilar sites. I envisage the appropriate parts of a central nervous system as acting like a keyboard, which, being struck in certain chord combinations, produces each specific phrase of a behavior. The same notes in different combinations produce different phrases. Striking a particular chord is the role of a specific interneuron (i.e., the command neuron) or cluster thereof. Where there is cyclical repetition of the movement, the cycling is likely to be caused by reciprocal

inhibitory relationships of the agonists in the movement with their antagonists. The cycling will continue as long as the modulator influence persists at a suprathreshold level.

This hypothesis may be given the tentative label, to facilitate discussion, of the *orchestration/modulator hypothesis*. The timing of sequences within the behavior will depend, in this hypothesis, in part upon the relative timing of excitation of the modulators, and in part upon the length of time their effects take to become apparent. This sequence is in no way at odds with the motor tape concept (Hoyle 1964), but rather is a specific proposal as to the neural substrate of a tape.

It is easy to see, with this model, how variation and evolution of behavior might come about. Furthermore, the wide range of “fixity” of a FAP observed is especially easily understood. The mechanism proposed is compatible with the known facts of *Tritonia* escape swimming (Dorsett et al. 1973; Getting 1983) and with a recent discovery in my own laboratory by Sompong Sombati (1983) that minute amounts of the natural neuromodulator substance octopamine iontophoresed from a micropipette into locust neuropil evoke bouts of specific behavior at very precise locations only.

Conclusion

No matter how many of the major themes of neuroscience are removed from the specific domain of neuroethology, what remains is still a vast spectrum of specialties that calls for the careful assignment of priorities in determining which need to be studied most urgently. Regardless of their choice of animal species, neuroethologists might consider concentrating first on in-depth analyses of the neural machinery producing FAPs. Once understanding of the common neuronal events underlying a sufficient number of FAPs has been obtained, several other major subdivisions of ethology – elucidation of the neural bases of mood, drive, displacement, and vacuum acts – should be resolvable as corollaries. So far, research on the neural underpinnings of FAPs has been regrettably very scarce, probably because it takes a great deal of intensive research before any single behavior can be adequately understood. But to progress, there is no alternative: Some choices should be made now and backed with resolve. May granting agencies see the ultimate wisdom of supporting the endeavor.

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Neuroethology: A call for less exclusivity and more theory

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Less exclusivity. I share Hoyle’s enthusiasm for neuroethology as a well-defined area of neuroscience that emphasizes animal

behavior rather than circuit properties of neurochemistry per se. I also agree that the working out of explicit neural circuits for insect locomotion (as in Hoyle’s Figure 1) is an exciting chapter in neuroethology. But why must Hoyle exclude much excellent work that many of us would accept as enriching neuroethology? Hoyle defines neuroethology as “the study of the neural mechanisms underlying the behaviors that constitute the science of ethology,” giving an almost mystical primacy to work in the preneural canon of ethology. Kandel’s (1979) illumination of the cellular mechanisms of learning is dismissed (admittedly in wickedly amusing rhetoric) because *Aplysia* does not exhibit behaviors that interest Hoyle. Ewert’s (1980) book on *Neuroethology* – which includes an exposition of the studies of how a toad brain recognizes prey and enemy that I have used in my own work on what I had thought to be (theoretical) neuroethology – is dismissed as *Verhaltensphysiologie*. Ewert defines the goal of neuroethology as the experimental analysis of the neural releasing and control mechanisms of behavior. Hoyle, using criteria I find inscrutable, finds this “woolly” – but it seems to me just as illuminating as his own definition, and all the better because it does not rely on a prior definition of what constitutes ethology. Hoyle gives the game away when he confesses that, while *he* is not woolly, *he* is a “dyed-in-the-wool champion of first finding out how invertebrate nervous systems work.”

All this is unnecessarily divisive. Let us accept both Hoyle’s and Ewert’s definitions as useful approximations; and that some neuroethologists like molluscs, some prefer insects, but that many see neuroethology as a path to understanding the human being, so that many vertebrate systems (spinal mechanisms of locomotion in cat or visual systems in frog, toad, cat, or monkey) become central to their study. Researchers into neural control of locomotion have learned the value of rich communication between students of vertebrate and invertebrate systems. I urge a similarly ecumenical view of neuroethology.

More theory. I am delighted that Hoyle is a strong advocate of the development of theory in neuroethology, but distressed that he has not read any of the literature since “the McCulloch–Pitts (1943) binomial [*sic*] model of neural function.” I will offer here a brief selection of entry points to the subsequent literature of brain theory, and I will give a number of references to studies on vision, learning, and control of movement. I do not argue that all (or most) of them lie within theoretical neuroethology proper, but only that they provide relevant concepts for the construction of a theory of neural mechanisms that addresses the integrating of action and perception in animal behavior. Hoyle says that “laboratory neuroscientists should keep a close watch on . . . theorists to make sure they keep to the facts and propose valid experiments.” I argue, however, that the brain theorist has at least *two* roles: not only to construct tightly constrained models tied to quantitative experiments, but also to conduct *gedanken* experiments to enrich our vocabulary for analyzing animals in the laboratory and the field: What are the possible mechanisms of depth perception? How might limb movements be controlled? How can an animal learn from experience? The latter models may be seen as exploring the “style” of the brain, and they are, I claim, as relevant to the understanding of the human brain as is the study of invertebrates. Another dimension is what might be called “applied brain theory” – as brain theorists collaborate with workers in robotics and artificial intelligence to explore ways to make increasing use of parallelism in the next generation of computer systems. My own overview of multilevel approaches to brain theory is given in Arbib (1972; 1981); another argument for not restricting brain theory to the consideration of detailed neural modeling only is given by Marr and Poggio (1977).

Szentagothai and Arbib (1975) provide both a functional and a structural overview of the nervous system, then lay out experimental and theoretical studies, presented at a Neurosciences Research Program work session, on neural mechanisms for

stereopsis and on the role of the cerebellum in the adjustment and learning of motor patterns. The style of visual modeling given there has been developed by Marr (1982) and his coworkers. Stent (1981) has lauded Marr's work as if it were *sui generis*, but it is, in fact, just one chapter in the dynamic field of computer vision, which has seen much interaction among neuroscientists, psychophysicists, and computer scientists, and which is ably summarized in the recent texts by Ballard and Brown (1982) and Nevatia (1982). The proceedings edited by Amari and Arbib (1982) contain Ito's report on current experimental support for aspects of the Marr–Albus model of learning in the cerebellum; Amari's review of competitive and cooperative aspects in the dynamics of neural excitation and self-organization; and the work by my colleagues and me on modeling neural mechanisms of visuomotor coordination in frog and toad (see also Lara & Arbib 1983). Another important study of visually guided behavior is the work of Reichardt and Poggio (1976) on visual control of the behavior of the fly.

Hinton and Anderson (1981) offer a collection of papers on the "connectionist" approach to both brain theory and artificial intelligence, seeking to understand how computations can be executed quickly if they are distributed over a network of parallel processors. Here the emphasis is on memory mechanisms, but subsequent work applies connectionism to problems in vision and the control of movement.

As a body of work, these volumes chart the emergence of a paradigm of "competition and cooperation in highly parallel neural networks" that will greatly contribute to our growing understanding of the neural mechanisms of animal behavior.

Neuroethology: An overnarrow definition can become a source of dogmatism

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I like most sections of Hoyle's target article, especially the historical parts (although the role of von Holst is not correctly described), those dealing with the lack of concepts and theories, and, of course, those favoring insects. I also agree that the discipline that studies the neural basis of innate behavioral acts should be defined and could be called "neuroethology." (In Germany, the term *Sensomotorik* covers most of this field.) But some aspects of the definition in the target article (sometimes those only read between the lines) exclude topics of strategies that could become relevant for this discipline in the future. Such aspects are:

1. Exclusion of reflexology. Within the last 10 years a large number of reflexes have been found in which direction or intensity depends on the behavioral context (e.g., Bässler 1983). The more investigators have looked for such phenomena, the more examples have been described. Perhaps the distinction between reflexes and the release of FAPs will disappear in the future, and reflexes can then be used as models for the release of FAPs.

2. Exclusion of behavioral physiology (ethophysiology, Verhaltensphysiologie). The study of the neural basis of a particular behavior can be started either from the higher level of complexity (behavior) or from the lower one (neurophysiology). The first strategy can normally be divided into three stages: (a) quantitative description of the behavior (which can also be attributed to ethology); (b) relating the behavior to the activity of one system or a few unambiguously defined ones (in other words, one tries to show that the behavior in question is a characteristic of a specified, but only functionally defined system); (c) elucidation of the neural basis of this system (for more details of this strategy, see Bässler, 1983). Stage (b) very often uses methods of

behavioral physiology. At the moment it is an open question which of these two strategies is the more successful one. Hence, one should not exclude one of them by definition.

3. Restriction to cellular events. Although I favor the single-cell approach in my own research, I am not sure that we will find any generalizable statement at this level. Perhaps such generalizations are only possible at the level of groups of neurons. As an example, the walking movements of mammals and insects are certainly not produced by the same kinds and numbers of neurons, but perhaps by functionally similar groups of neurons. As each science is only valuable when it produces statements of some general applicability, one should not exclude by definition a possible – eventually, the only possible – source of generalization.

Perhaps my view is wrong, and the elimination of these aspects may not hinder future research. If the target article only seeks to demarcate a certain kind of neuroethology from other related disciplines, then investigators dealing with the aspects mentioned above (as I do myself) would no longer be called neuroethologists. This would be no disadvantage if it were only a matter of classification, but I fear that such a line of demarcation could also be used – in contrast to its original intention – to establish new kinds of dogmatism and then to suppress new ideas. In my opinion, therefore, it is too early to define a certain segment of our discipline in such an absolute manner.

Flow diagrams and hydraulic models

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Hoyle's approach has something in common with the hydraulic model he admires so much. It is provocative and amusing, external considerations play no role in keeping it going, and, in general, it is wrong. For all its defects, though, Lorenz's hydraulic model had a number of virtues, as Hoyle rightly notes. It was simple and vivid. It treated behavioural organisation as a coherent system. Above all, it was a software account of how behaviour might be controlled, not a proposal for what the hardware might be like. A flow diagram in more than one sense! It would have been reasonable to expect that nobody would try to relate the cistern's contents to some analogous fluid in the central nervous system such as a neurotransmitter. No such luck, since many people did.

Lorenz's model was unsatisfactory in dealing with feeding behaviour for some of the reasons that Hoyle mentions, and it was actively misleading in accounting for sexual and aggressive behaviour (Hinde 1970). Hoyle hopes that he can deal with these difficulties by incorporating some fancy-looking hardware and some feedback circuits into the model. He does not seem to realise that he has lost the simplicity and vividness that made Lorenz's model so attractive. Hoyle's updating is baroque, unfalsifiable, and no better than numerous other models that could be (and have been) devised. What is worse is that, like others before him, he seems to be in serious danger of believing that the working parts of the model bear some straightforward relationship to those bits of the nervous system that he seeks to study as a neurophysiologist.

Although it is much less central to his interests, it is worth noting that when Hoyle writes so glibly about innate behaviour, he has wedded himself to yet another outmoded body of thought. Even Lorenz (1965) abandoned the learning–instinct dichotomy in the face of cogent criticism and drew a fresh distinction between phylogenetically adapted and ontogenetically adapted behaviour. Behaviour adapted during the course of evolution sometimes requires a learning process, such as imprinting, during the development of an individual. So

Lorenz's category of phylogenetically adapted behaviour is not the same as unlearned behaviour. The notion of unlearned behaviour is not implausible, providing one remembers that "experience" in a general sense is inevitably involved as a necessary condition in the expression of such behaviour. However, unlearned behaviour is not easily and unequivocally identified in practice, because to do so involves proving a negative. Even if this difficulty is brushed aside, as it often is nowadays, the belief that adult behaviour can invariably be dissected into learned and unlearned components is certainly wrong (Bateson 1983). So is the conviction that behaviour is distributed bimodally into two clusters, one of which is learned and the other of which is not. Hoyle's insects may not seem to learn much, but their capacity is easily underrated simply because nobody has looked very hard for behavioural plasticity. When someone does, the capacity for behavioural change may be greater than naive preconceptions suggest.

Hoyle evidently looked at some modern textbooks on animal behaviour and showed a draft of his article to practicing ethologists. Why did he not heed their advice? I find it difficult to believe that he persisted in misrepresenting the modern state of ethology through an obstinate sense of his own rectitude. Perhaps the clue is to be found at the end of his article where he refers to the support of granting agencies. Does he knowingly tell a misleading story in an attempt to corner meagre research funds for his own brand of research? If so, he is wicked. But even if that were the case, it would be difficult to be really cross with him. Among physiologists, he is very unusual in wishing to link his work with more complex levels of organisation rather than, as he puts it, "leaning toward the principles of neurophysiology, with its reductionism and intense concern for novel cellular processes." I like that. Instead of biting the hand that is extended towards us, we ethologists should guide its owner to problems that seem genuinely tractable to his neurophysiological skills. A question remains: Will he let us?

Neuroethology: In defense of open range; don't fence me in

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Programmatic science is an old story. Before Hoyle, many others with worthy goals have aimed at persuading, reasoning with, luring and coercing scientists to choose their material and their approaches toward a common problem. By and large, the best science has been undirected and unfettered, whether by choice of material or approach or by someone's definition of the preferred scope. I understand and empathize with Hoyle's goals. I sit at the same time in an oceanographic institution, where some oceanographers would like everyone to work on the oceans, and in a medical school, where some medics would like more concentration on medical problems as they define them. Fortunately for the standing of both, the prevailing policy is broader, and the lesson of Julius Comroe (1977) is accepted. Comroe (see also Comroe & Dripps 1976) showed by historical research that if you identify a series of advances in science, chosen as the most important insights with respect to some defined goal (medicine in his case; but we may substitute the neural basis of species-characteristic behavior), the key research that opened the way to those insights would, in a high percentage of cases, have been considered at the time so remote from the area it eventually illuminated as to be quite irrelevant.

This is my short-form comment on one of Hoyle's main points, namely, that for key insights into the neural mechanisms of locomotion we should work on locomotion, or at least animals with legs! The whole history of biology is eloquent testimony against such a restriction.

The other main point of the target article, namely, that research should not be called neuroethology unless it is obviously centrally relevant, pales in cogency under this light. What's in a name? Usage of the term "neuroethology" will vary, in spite of Hoyle's considerable influence, just as perceptions of its history and utility may differ (Bullock 1983). Since Hoyle is aiming at neural mechanisms at the cellular and circuit levels, the key insight might well come from spikeless neurons in crabs' legs or fish retinas, from plateau potentials or regenerative repolarization in stomatogastric ganglia, or from reciprocal synapses in rabbit olfactory bulbs. No one hoping for real understanding will be content for long merely to search in a behaving animal for the distribution of items on a list of known circuit variables that has been frozen as of 1983 – given the spectacular growth of that list over the years.

Like Hoyle, I find some approaches more exciting than others; but unlike him, I hate to admit it, and I try to overcome it – on the sound old principle that you're down on what you're not up on. Much of Hoyle's target article is a confession of preferences. In many impassioned discussions the giveaway to the presence of a question of taste, about which there is no disputing, is the phrase, "the question is . . ." – or the set of questions, or the relevant approach.

But there is a position for which I have even less taste, expressed as some form of, "Let us first understand this simpler level and then investigate the more complex." I used to hear that from biochemists and "general" physiologists who were impatient over money spent on research of only special interest, such as on flying in grasshoppers or on the visual cortex – as though the world would wait for them, and as though their findings could simply be scaled up to explain speech.

It is not simply tolerance of other people's approaches, levels, and materials I am urging, but a genuine and humble appreciation of the absolute necessity, for the sake of the best science, that the curiosity, ingenuity, rigorous thought, and creativity of many scientists, with diverse talents and tastes, should be encouraged to range freely! However, not to worry; even an article in *BBS* won't stop them.

Difficulties and relevance of a neuroethological approach to neurobiology

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Hoyle has always been a sort of barrister defending and promoting behavior (1975; 1976; etc.). In this article he attempts to make a synthesis of the ethological approach to animal activities, particularly of invertebrates, with modern neurobiological studies. In a sentence, the paper states, it is time we knew what neuronal systems are used for! This is true, and insufficiently understood by neuroscientists, even by those whose speciality is invertebrate studies. For most of them, invertebrate preparation is merely an isolated system useful as a membrane model or for deciphering cellular mechanisms. A striking example of such an attitude is presented by the studies on the swimmeret beating in decapod Crustacea. Since the pioneering works of Davis (1968), this preparation has been limited to a consideration of the connectivity of the different motoneurons, comparing the cellular membrane properties to analogous models. This is, of course, useful, but it is curious that until now (Cattaert & Clarac 1983), the relation of the beating and the behavioral activity of the animal had never been studied. This is of particular interest if we remember that the swimmerets are a vestigial locomotor system, which is no longer involved in displacement (Bent & Chapple 1977). It was demonstrated that swimmeret beating is linked to thoracic locomotion and, at the same time, associated with very different behavioral situations. For each of

these, the number of muscles implicated, the frequency of the rhythm, the amplitude of the movements, and the force exerted are different and characteristic of each situation. The role of this heretofore ignored rhythm will soon be known. Several other motor systems must be studied at this level of complexity in order to make the association between a motor system and a given behavior.

Since I fundamentally agree with the importance and the scope of neuroethology as presented by Hoyle, my main comments will describe the difficulties encountered by such an approach. When Hoyle edited a book entitled *Identified Neurons and Behavior of Arthropods* (1977) in honor of C. A. G. Wiersma, the *and* was a very important detail. In the present paper, the goal of the neuroethologist seems to be to study the neurons of behavior; this of course has to be done, but several dangers must be outlined.

By definition neuroethology is a "vertical" science, whose main interest is to link the results obtained from many different levels of complexity in the nervous system. We know that each level has its own logic and its specific rule. When Hoyle presents a general diagram of the jump (Figure 1) as a FAP, he does not emphasize the behavioral laws regulating the motor processes. A neuroethological diagram must incorporate adaptations to the constraints of the environment. I disagree with the author's contention that the circuitry of the jump has been worked out to the exclusion of possible minor modifications. New neuronal networks may yet be found whose function is an expression of behavior.

We can reproach Hoyle for this aggressiveness in attacking certain isolated neuronal preparations as being invalid material for neuroethological studies while he himself proposes other preparations that still have not reached the desirable level for a neuroethological approach. When he later proposes that the scientists working on mammals use slices, he becomes a reductionist (!), a criticism he must try to avoid.

Locomotion is involved in a behavior when we consider that displacement is included in an oriented action, such as in searching for a prey or a partner for mating. . . . In recent reviews on this subject by Grillner (1981) and Wetzel & Howell (1981), the authors always took great care to distinguish the level at which the results were obtained; an example in characterizing this attitude is the success of the term "fictive locomotion," used for the first time by Perret, Millanevove, and Cabelguen (1972). In itself, "fictive" does not have a very satisfactory meaning, but it does permit one to consider all the work done on central pattern generators and to propose a possible relation with the data obtained from the intact animal. The question of the possibility of making generalizations about data obtained at the cellular level is enunciated by Selverston in his *BBS* article, asking "Are central pattern generators understandable?" (1980).

In order to link the different levels of neuronal complexity and to give us a good idea of behavior we must: (1) have all the parameters of behavior in our preparation, and not in the form of a largely dissected and "pinned" preparation, just a poor imitation; and (2) work on the properties of the higher level of complexity that corresponds to the laws of behavior.

With that in mind, the explanation of some behavioral laws lies at the level of the individual cell, as demonstrated by Hoyle himself (1980); the tonically firing coxal adductor involved in the leg-movement learning paradigm can be trained to fire at different rates by operant conditioning controlled by a computer. In the same manner, when Kupferman, Cohen, Mandelbaum, Schonberg, Susswein, and Weiss (1979) defined the metacerebral cell as an "arousal cell" controlling the feeding behavior of *Aplysia*, they opened the large field of neuromodulation, which is particularly useful to a neuroethologist. [See also Dismukes: "New Concepts of Molecular Communication among Neurons" *BBS* 2(3)1979.]

The ensemble of neurobiology could be just an opposition of several branches of science such as biophysics, biochemistry,

cell biology, pharmacology, physiology, or ethology, as at the annual meeting of the Society for Neuroscience. If we refer to the number of communications and posters under the heading of neuroethology, we find that the neuroethologist is a rare specimen! Because of the difficulty of the job, the neuroethologist must take the different parts of the neurobiological puzzle and place them in their proper order, relating the lower levels of organization to the more complex.

In order to obtain an adequate knowledge of neuroethology, we need some conceptual approach that allows us to keep the hierarchical complexity of neuronal organization. In considering motor control, we have several models presented by "mammalian scientists," which are very instructive even for "invertebrate scientists," because their functional diagrams present the order of complexity of neurobiology. MacKay (1980) and Paillard (1960; 1983) offer some interesting approaches to the organization of motor behavior. In his model, MacKay considers motor behavior as a system of conditional loops with several levels of instructions; the complexity of this hierarchical structure depends on its level of evolution. Then, even in the simplest FAP, it is possible to consider a motor organization sequence composed of the following elements: selection of the goal, selection of the muscles, timing the relation, force regulation; all these elements converge to permit a movement adapted to the environment. This kind of approach preserves the behavioral level and leaves it in its proper place. This is the software of a computer, whereas the majority of scientists only study the hardware!

There appears to exist among research scientists a kind of gravitational force that compels them to explain their problems in more and more detail. As their descriptions reach more and more precise mechanisms, the behavioral aspect becomes less and less evident. In opposition to these descending analyses, a neuroethologist must have an ascending vision linking lower-level mechanisms with more integrated processes. Hoyle's target article, then, is necessary, if it presupposes behavior as the underlying basis of our work, but it misses the point, if it is taken only as a justification of work done at the cellular level.

Neuroethology: Why put it in a straitjacket?

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As one of the earliest, most enduring, and least flappable proponents of neuroethology, Hoyle deserves credit. His target article serves the useful purposes of drawing attention to this budding transdiscipline and outlining the views of one of its most outspoken adherents. Especially laudable is Hoyle's call for the development of general principles of neuroethology (see below). Beyond these broad generalizations, however, the present treatment is in major respects unsatisfying, leaving us with many more questions than answers.

Perhaps the central unanswered question is why we should attempt in the first place to define the scope of neuroethology. Aside from creating arbitrary new labels and pigeonholes, it is not clear what this exercise in intellectual territoriality accomplishes. Hoyle's purpose seems to be to deny certain individuals their rightful place in the Hallowed Halls of Neuroethology. Hoyle thereby reveals himself as a scientific elitist. In contrast, I am a populist. Let us open wide the Hallowed Halls to all who would enter by defining neuroethology broadly and simply as the study of the neural mechanisms of animal behavior. Much needless time and argument can thereby be saved for more substantive tasks, such as closing the present gulf between biophysics and behavior. Any study that contributes to this end is rightfully classified as neuroethology, including certainly the elegant analyses of motor pattern generation by Selverston

(1980) and colleagues (Selverston, Russell, Miller & King 1976), and the classic studies on the neural and biophysical mechanisms of habituation and sensitization by Kandel and collaborators (Kandel 1976; 1979; Kandel & Schwartz 1982).

Perhaps the effort to build boundaries around neuroethology could be justified under the banner of formulating broad new goals and approaches to the topic. Hoyle's article contains much that is broad, but little that is new. First, we are treated to a highly personalized "history" of ethology, the purpose of which is to provide a model for the development of neuroethology. The history would flow differently from a different pen, but no matter, for the parallels are not persuasive. Ethology developed as a pioneering science, faced with a constant demand for breaking new ground and establishing new principles in a relative conceptual vacuum. The neurosciences followed a similar course, and are presently at a younger stage in their evolution. In contrast, neuroethology is a hybrid, the "progeny" of two comparatively mature disciplines. The different etiology renders a different developmental history inevitable; one cannot provide a model for the other.

When it comes to goals and approaches, one is left wondering where Hoyle stands. From ethology he draws the lesson that success stems from focusing on "stereotyped, complex, non-learned, innate behavioral acts," and he proposes that neuroethology do the same. But in listing the goals of neuroethology, Hoyle identifies no fewer than 13 areas that deserve attention, beginning with neural circuitry, coursing through the labyrinth of drive and motivation, and finally terminating with learning and memory. I concur with the desirability of breadth, but am perplexed by Hoyle's apparent inconsistency. Similarly, his Abstract encourages the study of "diverse animals from different phyla," but he suffers a later relapse into phylogenetic chauvinism, with yet another plea for neuroethologists to focus on Hoyle's choice of preparations, namely, "large insects" (read "locusts"). The locust is without question a fine neuroethological preparation, but so are the sea slug, crayfish, lobster, praying mantis, lamprey, the owl and the pussycat. Imagine the state of neuroethology without the insights provided by studies on these organisms! Diversity is prerequisite to evolution by natural selection. Let us hope that diversity remains the basis of the evolving science of neuroethology, diversity in technical and conceptual approach, and diversity in the choice of experimental subjects. Long live hybrid vigor!

Politicians have developed the strategy of making opposite and contradictory statements in order to appeal to the fullest spectrum of opinion. In this sense, Hoyle's target article is a success. There is something here for everyone, except perhaps *Aplysiologists* (take heart, *Aplysia pleurobranchaea* does not even receive dishonorable mention). Hoyle's strongest suit is his evident appreciation for general principles. The ability to formulate unifying principles, that is, those that have application across many neurons, networks, and phyla, is one index of the intellectual maturity of the discipline. Such principles furnish a conceptual framework for the design and conduct of experiments, and they can represent the "larger questions" Hoyle seeks for the "truly inquiring mind." As Hoyle recognizes, the field of neuroethology is ripe for such formulations. We would do well to get on with the task, and to desist from divisive and diversionary attempts to confine neuroethology to a definitional straitjacket.

Can neuroethologists be led?

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What we have here is a clarion call to arms in defense of the emerging field of neuroethology. The question is, what is the nature of the war?

On the one hand, if the target article is meant mainly to establish a commonly accepted definition of an emerging field, I think Hoyle is a general without an army. Fields are established by bodies of workers who share common research goals and methods. A developing field can be helped along by its workers who help publicize its name and concepts, as Hoyle himself has done in the titles of two reviews, "Cellular Mechanisms Underlying Behavior – Neuroethology" (1970) and "Identified Neurons and the Future of Neuroethology" (1975). Its content can also be shaped by example, as Kenneth Roeder did before the term even came into use (1963). But it cannot be directed along a specific path merely by the opinions of a single individual.

Part of Hoyle's difficulty is that few others will share his particular vision of the field. Hoyle seems to "know" what ought to be part of neuroethology and twists and shapes his definition until it fits his own mental image. Why else dismiss Ewert's fine work on prey-capture in toads as "comparative physiology," just because analysis of the system has not yet reached the cellular level? Why else include the simple movements that constitute the jump of a locust while excluding the complex behavior involved in kinesis? Is it just because we have been able to analyze jumping in terms of the activity of individual neurons, while our understanding of kinesis has languished? I could give other examples, but there is no sense in belaboring the point. In the end, neuroethology will constitute the kind of work done by investigators who call themselves neuroethologists, not just the kind of work that a single individual believes should be included.

On the other hand, there are other factors that can shape a field these days. If Hoyle's article is meant mainly as a device to attract funding and recruits to the emerging field, then he may indeed have a cause, but the campaign may be like the Children's Crusade of medieval times. Hoyle's last sentence is, "May granting agencies see the ultimate wisdom of supporting the endeavor." But will they? And will researchers tackle the hard problems Hoyle defines as the heart of the field? Jobs, grant support, even peer recognition depend on a steady – some might even say voluminous – output of research results. How many researchers are willing to invest 2 or 3 years in a difficult project with the very real prospect of having little to show for their efforts at the end? As long as all the stakes go to those who can demonstrate rapid progress, Hoyle's attempt to lead his colleagues into taking a longer view of their work seems to be as likely to succeed as were the youthful crusaders of so long ago. One may applaud the effort, without much expectation of its success.

Disregarding vertebrates is neither useful nor necessary

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If Hoyle's target article had closed with the paragraphs on "Goals for neuroethologists," I am confident that it would be widely accepted as presenting a consistent and sagacious review of the foundations, limits, and goals of neuroethology. The shortened article would not only have been in consonance with Hoyle's own definition of neuroethology ("the study of neural mechanisms underlying the behaviors that constitute the science of ethology," with ethology defined by Konrad Lorenz, 1981, p. 1, as "the comparative study of behavior, which applies to the behavior of animals and humans") and with his illustrative model of behavior generation (Figure 4), but also with recent views of neuroethology summarized in Ewert, Capranica, and Ingle (1983) and Huber and Markl (1983). For me, dissonance within this article itself (see below) and with the opinions of many other students in the field of neuroethology (in the books mentioned above) is introduced and provoked not so much by

stressing invertebrates, especially insects, as the first-choice animals to study within the rubric of neuroethology, but by (1) concluding that neuroethological research in vertebrates has been irrelevant (or even nonexistent) so far, and (2) proceeding to set the rules by which behavior of vertebrates might fit (if at all) into "true" neuroethological research.

And all this because of seemingly necessary consequences from the ethological side of neuroethology! As little as the science of ethology, as defined and discussed by Lorenz (1981), is restricted to the observation and quantification of movement or fixed action patterns, the science of neuroethology has to be restricted to the study of the neural circuits of such movement patterns. There can be no doubt that ethological work encompasses the stimulus configuration for releasing certain sequences of movement (sign or key stimuli) as well as internal and external modulatory influences on and learning and memory in the execution of, for example, prey-catching, courtship behavior, mating, and brood care. The neural bases of all such complex, goal-related, naturally occurring behaviors, which can be described by Hoyle's model (Figure 4) and which are in consonance with his "Goals for neuroethologists," have been pursued in vertebrate research, which, consequently, has to be called neuroethological work. Studies on bats, electric fish, and barn owls, especially, which are disregarded in Hoyle's article for being too specialized, have highlighted principles of neural representation of stimulus parameters and feature extraction in the brain, which are necessary prerequisites for initiating and guiding a behavioral sequence toward its goal (e.g., catching prey). Although we have to admit that, as Scheich (1983, p. 8) says, "the art of neuroethology of vertebrates is hardly beyond the stage of a comparative neurology of sensory systems," these sensory systems are (1) equally part of Lorenz's hydraulic model of behavior generation and, as I understand it, are (2) investigated with the ultimate goal of getting insight into the generation of a certain behavioral sequence that often is, in fact, a fixed action pattern, and (3) lead, on a comparative basis, to well-coordinated approaches of sensory-motor interfacing in vertebrates. It is therefore clearly inconsistent (and herein lies the incoherence of the article) that, on the one hand, neuroethology and its goals are discussed in a comprehensive way, and, on the other, the scope of neuroethology is restricted mainly to insect studies.

It may be easier for neuroethologists involved in invertebrate work to wear all the hats of physiology, biophysics, and biochemistry at the same time, because they are dealing with systems with only a relatively small number of elements. Possibly, progress can be made faster and thus the goal (of understanding a certain behavior) can be more obviously linked to every publication of results. The investigator of complex vertebrate behavioral sequences is more likely to be forced to wear the hats one after the other and to work for subgoals that, together with work in other laboratories, can add up to major progress in understanding animal behavior. But insofar as the biology of behavior is the principle that guides the research through the labyrinth of the different methodological approaches and subgoals, there is no obvious reason the research should not be termed neuroethological. A flourishing and widely recognized neuroethology cannot be restricted to invertebrates or to the study only of motor coordination. The major goal of neuroethology is, as Huber (1983, p. 91) says, "to provide an understanding of behavioral strategies of animal species in terms of operations of their nervous systems at *all* levels."

Neuroethology or motorethology?

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After reading Hoyle's article, I had the impression that "real" neuroethology deals with the study of motor systems in

locusts. The primary goal for neuroethologists, according to Hoyle, should be the "study of the cellular events underlying fixed action patterns and related instinctive acts." If one consults the ethological literature, one finds that neither locusts nor fixed action patterns (FAPs) are the main target of ethological research. In a recent textbook on the principles of ethology, even Lorenz (1982) devotes more space to the modification of behavior than to fixed action patterns. This apparent discrepancy probably has two causes: Hoyle's definitions are too narrow, and the techniques of neuroethology restrict this discipline to a small range of experimental animals and behaviors.

The model Hoyle proposes as a modern substitute for the old Lorenz model [reproduced here as Figure 1 of Hoyle's accompanying Response, *q. v.*] clearly states his primary interest in motor systems. His statement that an eminent ethologist does not take the old Lorenz model too seriously any more could refer to Lorenz himself, who has published a modified version of his model that differs markedly from the old one (Lorenz 1982). This new model assumes that the releaser does not act by opening the spring directly, but that it fills the reservoir together with a number of "charging" and endogenous stimuli. Hoyle's model, in my view, is a detailed description of the water trough of the Lorenz model. It is remarkably vague about the function of the comparator and computer. As the software of the computer is not described, I cannot see how this model could be tested experimentally.

The central problem of neuroethology is whether an analysis of the neural mechanisms controlling natural behavior is possible at all. The limiting factor is not whether an animal has legs or whether it is a "glob of squishy protoplasm," but whether it performs the behavior under the restricted experimental conditions of a neurophysiological experiment. The logical starting point of a neuroethological analysis has to be a careful observation of the behavior *under natural conditions*. The next necessary step is a behavioral analysis under laboratory conditions. And this is when the problems begin. In most cases, laboratory behavior differs significantly from free, undisturbed behavior under natural conditions. If the experimenters proceed at this point with the analysis, they have to be aware that the neural mechanisms they are going to study apply to behaviors that are only loosely correlated with the original natural behavior. Neuroethology, in my view, presently analyzes in a first crude approximation the real neural events that control natural behavior. For many behaviors, it will be impossible to perform a neuroethological analysis. One example is the waggle dance of the bee. Unlike Hoyle, I do not see a possibility of studying this form of communication with neurophysiological techniques, simply because a bee does not exhibit it under laboratory conditions.

Another point where I disagree with Hoyle is in the emphasis he puts on the analysis of the motor system and the secondary role he assigns to the analysis of sensory information processing. The functional role of a releaser and the mechanisms of eliciting a specific behavior with specific stimuli can only be understood after performing a careful analysis of the processing of sensory information at the level of the receptors and higher-order interneurons (Boeckh & Ernst 1983; Huber 1983). Exclusion of sensory physiology at the different neuronal levels is such an extensive restriction that we ought to rename this discipline "motorethology."

Hoyle's new view of neuroethology: Limited and restrictive

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Hoyle points out that neuroethology could not have been developed before ethology was established and ethological concepts had been worked out. This argument is reasonable in one

respect (Ewert 1984), although I would agree with the broader view put forward by Bullock (1983), namely, that neuroethology did emerge from an eclectic confluence of many streams originating from a wide assortment of traditions of ethology, comparative physiology, comparative neuroanatomy, and clinical neurology. In this context, I am greatly surprised that Hoyle devotes more than 10% of his target article to the description and discussion of Lorenz's hydraulic model, even saying, "The toilet model has come to symbolize neuroethology." In no place does he mention the pioneering work by C. A. G. Wiersma (1974), who has shown us how to discover individual, recognizable, and behaviorally meaningful nerve cells, thus laying the foundations for neuroethology.

Hoyle, calling himself "a dyed-in-the-wool champion of first finding out how invertebrate nervous systems work," strictly distinguishes among neuroethology, ethophysiology, and *Verhaltensphysiologie*, but unfortunately gives no definition for the latter two disciplines. A main point in Hoyle's definition of neuroethology seems to be the type of behavior under investigation; that is, neuroethology should not be concerned only with "the neurophysiological fundamentals of behavior" and also no longer with "the cellular mechanisms underlying behavior (cf. Hoyle 1970)," but now with "the study of the cellular events underlying fixed action patterns." Again, I think that this view is too narrow and much too dependent on the definition of FAP, which is itself disputed. Hoyle himself seems to invalidate his concept by pointing out that FAP sequences may incorporate reflex sequences; and then we are in trouble because he suggests excluding reflexes from neuroethological investigation. But how can one know whether a behavior is a FAP or a reflex without analyzing the neuronal circuitry?

Regarding the working program, Hoyle points out that neuroethologists will encounter novel as well as traditional membrane processes down to the level of ion channels. Some paragraphs later in this target article he denies the value of related data for neuroethology, if they have been obtained in *Aplysia* – since the investigated behavior does not – according to Hoyle – represent the kind of behavior that constitutes the science of ethology. Is it because these animals "lack limbs"? Hoyle himself began to think of the possibility of a science of neuroethology when he found that the leg neuromuscular junctions responsible for marching behavior in grasshoppers were affected by the ionic composition of the blood. The realization that the neural output was recordable and quantifiable was for him already the beginning of a neuroethological approach (although he was aware at that time that the behavior he was investigating had only some aspects of a FAP). Thus, he emphasizes the recordings of myograms and muscle potentials from the legs of freely moving grasshoppers, pointing out, "This line of work has since been developed by many investigators to the state of a fine art." The jamming avoidance response of weakly electric fish, on the other hand, does not appear to be adequate for neuroethological research in Hoyle's view, since, as he says, "as 'behavior' [it] is highly specialized" and "does not involve limbs," albeit he realizes that "the motor aspect – generation of the discharge – is quantifiable, and the sensory return is addressable all the way into the brain." The possibility that, for example, our knowledge of behavior-related neural principles obtained in electrosensory systems of these specialists (e.g., time domain analysis of frequency-related information by coincidence circuits) might contribute to the understanding of general rules (e.g., in auditory systems) is not considered by Hoyle.

The main goals of neuroethology listed by Hoyle are not much different from the ones described elsewhere in the literature of vertebrate neuroethology, except that he has partly reversed the sequence (priority?) of the topics. Indeed, invertebrate neuroethology and vertebrate neuroethology tend to use different research strategies. Whereas the first often approaches the functional properties of neuronal networks controlling behavior from the motor side, the latter has first focused its interest on sensory and motivational aspects. Of course, there is no *right*

place to begin, since all are parts of an integrated whole (cf. Hoyle 1977). In this context, I think, the analysis of the sensory and motor aspects of releasing mechanisms – innate, modified innate, or acquired – is an important task of neuroethology, since it involves studies on the neuronal basis of (1) stimulus feature extraction, (2) stimulus localization, (3) sensorimotor interfacing and feedback interaction, (4) modulatory functions and storage processes, and (5) motor pattern generation. Hoyle avoids the term releasing mechanism, although it is linked with an important concept of ethology (Schleidt 1962). He even suggests excluding sensory physiological research from neuroethology, but at the same time he correctly realizes that "the triggering of many FAPs depends upon *feature extraction*, so releasing cannot be fully understood without knowing the details of this subsidiary action," and some pages later he even emphasizes that it is "only the extracted key features that seriously concern behavior."

Regarding the question of how the central nervous system works, Hoyle considers some basic ideas of the "command system concept" introduced by Kupfermann and Weiss (1978) under his new labels "keyboard" or "orchestration/modulator" action; we had applied these to the prey-catching sequence (multiple-action system) of the toad: "Operation of each command system requires simultaneous activation of all of its command elements" (i.e., tectal output neurons with recognition properties like class T5-2, neurons with localization properties like classes T1 and T3, and neurons with arousal properties like class T4).

Command systems differ from each other by a distinct combination of command elements () which can be shared by the different command systems [], for example [(T4)(T5-2)] → ORIENT, or [(T5-2)(T1-3)(T3)] → SNAP. . . . An AND-condition between two command elements subserving similar functions might be altered to an OR-condition based on learning or due to the influence of other modulatory elements. (Ewert 1980, pp. 125, 299–300)

Evidence that the classes of tectal neurons mentioned above project down to the motor systems (putative motor pattern generators) has been provided recently by antidromic activation of these cells in response to electric stimulation applied to the tectobulbar/spinal pathways at the level of the caudal medulla oblongata (Satou & Ewert 1984).

I think that Hoyle misses or misinterprets an important aim of neuroethology, that is, the exploration of neural principles in animals of different ecological and behavioral adaptations. The *comparative* neuroethological approach – in particular, including those animals that are adapted to extreme environmental conditions and have developed special strategies – may contribute to the understanding of general rules and concepts. As predicted by Bullock (1983), we are going to realize that investigating interspecies differences in terms of neuroanatomy, neurophysiology, and ethology – including their ontogenetic developments – will provide important insight into general neurophysiological principles underlying behavior.

Neuroethology according to Hoyle

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Neuroethology is an emergent discipline in which the rich collection of methodologies from the study of the nervous system and the brain are applied to scientific questions derived from careful behavioral observations of animals in their natural habitats (Fernald 1984). Most scientists are engaged in neuroethological research as a result of pursuing interesting scientific questions beyond the narrow boundaries of conventionally defined disciplines, which are often characterized only by a collection of related techniques (e.g., neuroanatomy, neurophysiology, etc.). Hoyle, with characteristic evangelistic zeal,

argues that certain neuroethological research directions, when carried out on his favorite organisms, large insects, are intrinsically more worthwhile than others. He offers, in support of this idea, a highly selective "history" of the development of ethological ideas, spiced with self-congratulatory reminiscences. Although Hoyle personally has played an important role in the field of neuroscience through the analysis of neural circuitry of identified neurons in insects, as well as by training several students who are now productive neuroscientists, this discussion of neuroethology is seriously wrong in several regards.

First, Hoyle's summary of the history of ethology excludes many significant contributions and exaggerates others, resulting in a very distorted perspective on current ethological thinking. For example, Lorenz's hydraulic model was a conceptual construct summarizing Lorenz's views about the organization of endogenously generated behavior, and was intended to motivate other scientists to begin thinking about the immediate causation of such behavior. It was not a model covering the "generation of instinctive behavior" in its entirety, but an attempt to schematize the motivational forces postulated to underlie certain behavioral acts. Discussions of the applicability and generality of this model certainly stimulated ethological thinking by providing a focus for observational and experimental analysis. The model has been supplanted in time by more intricate representations based on more data about the many influences on the behavior of specific animals (e.g., Baérends 1976).

In urging neuroethologists to elucidate the neural equivalent of an updated hydraulic model, Hoyle misses one of the important lessons to be learned from discussions about the Lorenz model: There is no *generally* applicable description of the forces underlying "animal behavior." Rather, the enormous complexity and diversity of the behavior of animals requires specific models for analysis of specific issues. For interested readers, Hinde (1982) offers an insightful, balanced analysis of the relationship between ethology and other scientific disciplines, identifying the complementarity and convergence of ideas from different disciplines.

Second, Hoyle offers six terms as the key concepts of ethology, when in fact these terms are neither of a comparable level for discussion among themselves nor do they represent the "core of strictly ethological knowledge" as claimed. The undisputed contribution of the ethological pioneers, most notably, Lorenz, Tinbergen, and von Frisch, was to recognize important central principles in the otherwise bewildering complexity and diversity of animal behavior. The first was that there is selective responsiveness to particular stimulus characteristics known as sign stimuli. Sign stimuli may be called releasers if upon seeing them the animal consistently performs particular behavioral acts. The second was the discovery that each species has stereotypical movements, termed fixed action patterns, which are as characteristic of the species as are morphological features. These correspond to Hoyle's numbers 3 and 1. The remainder of the terms listed by Hoyle are of quite a different nature.

Displacement activities (2) are behavioral patterns that appear inappropriate or irrelevant for a given situation. Displacement activities need not be fixed action patterns, as Hoyle claims, and are interesting primarily as a window into the motivational state of an animal in a conflict situation. It is not a central concept of modern ethology, but a descriptive term primarily of interest to ethologists studying the immediate causes of apparently irrelevant behavior.

Vacuum activity (4) and consummatory acts (5) are also terms of limited use and usefulness, each describing categories of events, not central principles of modern ethology. Finally, the terms "drive" and "mood" (6) are qualitative descriptors of the inferred state of an animal. While early investigators emphasized the importance of the internal state in understanding what animals do, definitions of drive and mood are certainly not at the core of ethological knowledge.

Finally, I strongly object to the suggestion that neuroethologists should follow the goals laid out by Hoyle and by implication adopt his unjustified prejudices against certain research directions. Whereas goal-directed scientific research may be the *modus operandi* for attacking major commonly agreed upon medical problems, basic research in general and neuroethological studies in particular do not fall into a similar category. The major task of scientists is not to find the solution to questions adopted from a list of chosen goals, but to select only the most important questions to pursue from the many that one confronts in scientific work. In this context, I am particularly concerned by Hoyle's loudly proclaimed bias against research on *Aplysia*. *Pace* Hoyle, detailed studies on various aspects of *Aplysia* have led to important discoveries that are highly relevant to neuroethological inquiry, including studies of the neural basis of learning (Carew, Abrams, Hawkins & Kandel 1983). More recently, control of an important "real" behavior in *Aplysia*, namely egg laying, has been traced to the genome (Scheller, Rothman & Mayeri 1983).

Arguing from this same narrow perspective, Hoyle claims that studies on vertebrates have provided little of use in the past and promise little in the future for neuroethology. That this is patently wrong should be evident from the literature, but let me offer one example. Hoyle argues that one goal of neuroethology should be the elucidation of the efference copy. A neural representation of efference copy has in fact been found in vertebrates – fish (Bell 1981). Moreover, evidence for efference copies is amply available in other species as well (Angel 1976; McClosky, Colebatch, Potter & Burke 1983; Zaretsky 1982).

In conclusion, Hoyle's myopic view of neuroethology offers little useful information or guidance for scientists interested in understanding the machinery of the nervous system responsible for initiating or modulating behavioral acts important for survival of the animal.

Neuroethology and theoretical neurobiology

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Hoyle's leadership role in neuroethology is well represented by his list of 13 sensible and important goals that he has targeted for neuroethologists in the years ahead. This list reflects his clear appreciation of the fact that "what is needed is focus on both behavioral and neural circuit functioning."

This enlightened atmosphere is darkened by the remarks that Hoyle directs against all vertebrate experimentalists. After noting Ewert's definition of behavior (1980) as "spatially and temporally coordinated patterns of movement," Hoyle blasts the entire vertebrate field with the statement that "this may be the best that can be hoped for from studies on vertebrates." This remark reflects a serious breakdown of scientific communication between behavioral and neural experimentalists who study different organisms, or even different systems within the same organism. This type of breakdown is inevitable when an experimental science does not have at its disposal theories powerful enough to bridge the gap between its distinct experimental paradigms. Hoyle clearly realizes this through his use of quotations such as "Experimentation in this area cannot proceed without theories."

Hoyle goes on, however, to make the inaccurate claim that "in the 34 years since the Cambridge meeting, there has been little advance in its [neuroscience's] conceptual underpinnings. The single general framework that has ever existed [was] the McCulloch-Pitts (1943) . . . model. . . . But the vacuum left behind has yet to be filled with even a tentative new model." Coming from an experimentalist of such distinction, an attack on

the huge field of vertebrate experimental studies and a total ignorance of recent theoretical progress may be viewed as serious problems for the field as a whole. I believe that they reflect the same problem.

Due to the complexities of behavioral and brain data, most experimentalists have retreated into experimental paradigms that are sufficiently narrow to support a "personal replication" criterion of truth: If you don't believe or understand a piece of data, you can then at least do the experiment over for yourself. Or you may trust the results of a small group of colleagues who studied with the same respected teacher, worked at some time in the same lab, and so on. Given a personal-replication criterion of truth, data from other paradigms tend to be ignored as irrelevant, and an appreciation of theories capable of unifying several paradigms becomes inconceivable.

To illustrate how different the data and theoretical landscape look to me, I will briefly comment on some theoretical results that are relevant to both invertebrate and vertebrate studies.

One sweeping claim deserves another. Significant theoretical progress has already been made on *all* of the 13 topics that Hoyle targets for neuroethology. Moreover, the theoretical principles that support this progress enable specialized circuits to be derived and used to analyze both vertebrate and invertebrate data. A few recent examples and two older examples of this theoretical progress will illustrate my claim.

Theoretical work on the neural mechanisms underlying reinforcement, drive, and incentive motivation led to a theory of opponent processes, called *gated dipole theory*, in which slow chemical gating reactions (e.g., involving norepinephrine) modulate cellular reactions to rapidly varying phasic cues and tonic arousal shifts (Grossberg 1972; 1975; 1982b; 1982c; 1983). These opponent processes were interpreted as simple models of hypothalamic circuits. Contrary to Hoyle's claim that "water . . . represents basic but still unknown neurophysiology," these circuits are part of a larger brain-behavior theory that addresses all of the issues raised by the water models in his Figures 3 and 4 (Grossberg 1982a). My theory does not merely mimic a water analog. For example, it disagrees with such claims as, "Drive is the probability of occurrence of an appetitive FAP." This statement implies that a hungry animal will attempt to eat with equal probability in the presence or absence of food. In my theory, incentive motivation is closer to the concept that Hoyle seems to intend: It is sensitive to a number of factors other than drive, notably, the reinforcing properties of sensory cues, and the competitive balance that exists among all external cues and internal drives at any time.

With the appetitive hypothalamically interpreted circuits of gated dipole theory as a starting point, G. A. Carpenter and I realized that a specialized gated dipole circuit has circadian clocklike properties. We have now quantitatively simulated many of the important data that are ascribed to the circadian pacemaker in the suprachiasmatic nuclei of the mammalian hypothalamus (Carpenter & Grossberg 1983a; 1983b; 1984a; 1984b). Carpenter and I also realized (Carpenter & Grossberg 1981; 1983a) that an intracellular gated dipole process, in which the gating chemical models an intracellular Ca^{++} process, can quantitatively fit parametric intracellular data that were collected from turtle cones (Baylor & Hodgkin 1973; 1974; Baylor, Hodgkin & Lamb 1974a; 1974b). Putting together findings on photoreceptors and circadian rhythms, it is now clear, at least formally, how an intracellular gated dipole circuit of the photoreceptor type can be modified to create a circadian pacemaker circuit. A circadian pacemaker has, for example, been reported in the eye of *Aplysia* (Jacklett 1969). Thus, a theory now exists in which a general design principle and sharply articulated circuit instantiations of this principle have contributed to the explanation of complex data about photoreceptor transduction, circadian rhythms, and motivated behavior across several species. Of particular interest to neuroethologists is the fact that these results derive from an analysis of how the behavior of individual

organisms adapts to environmental contingencies on a moment-by-moment basis.

Another recent theoretical contribution of this type was made with my colleague Kuperstein (Grossberg & Kuperstein 1984), a contribution to motor control whose significance again cuts across neural systems and species. The behaviors in question are saccadic eye movements. In considering these movements, we had to derive explicit circuits for the computation of efference copy, as well as many other processes that are of general importance in motor control. This work illustrates one reason I disagree with Hoyle concerning the claim that invertebrates are always simpler to understand than vertebrates. Neuroethology teaches us that neural circuits are organized to generate adaptive goal-oriented behaviors. Without a behavioral linkage, no amount of superb neurophysiological experimentation can lead to an understanding of brain design, because this type of work, in isolation, does not probe the functional level on which an organism's behavioral success is defined. Vertebrate behavioral experiments are much more plentiful than invertebrate experiments – there are thousands of them on every conceivable topic – and vertebrate behaviors are often highly structured and paradoxical. These data provide just the type of structure and paradox that force theoretical conclusions when they are confronted by a prepared theoretical mind.

As an active theorist myself for 25 years, I am eager to study good data from all paradigms. As a matter of historical fact, however, most of the anatomical and physiological results that I have read in the invertebrate literature were already familiar to me from theorizing about vertebrate data. Nevertheless, the elegance and clarity of a completely worked out invertebrate circuit is a thing of beauty and a joy forever. I still believe, however, that the greatest benefits from invertebrates will derive from their suitability for a biochemical analysis of learning and memory on the intracellular level. Working out a circuit is just a preparatory step, albeit one that requires great imagination and virtuosity, for identifying the cells on which a biochemical analysis should be carried out.

To illustrate my claims about prior familiarity with invertebrate results and, more generally, that the theoretical life has gone on for some time since McCulloch and Pitts (as also is indicated by several thousand pages in print), note how theory bears upon some important recent experiments about *Aplysia*.

A major issue in psychology and neuroscience concerns the relevance of invertebrate learning studies to the understanding of vertebrate learning, notably human learning. The important invertebrate studies of Carew, Hawkins, and Kandel (1983), Hawkins, Abrams, Carew, and Kandel (1983), and Walters and Byrne (1983) have bridged the gap between experimental facts and theoretical models concerning the neural substrates of associative learning. The theoretical models suggest that the cellular mechanisms of learning disclosed by these experiments may be universal, but the anatomies in which these mechanisms are expressed in invertebrates and vertebrates may differ in important ways. One illustrative difference is indicated below in the context of a general associative prediction.

On the mechanism side, the experiments support a 1968 theoretical prediction (Grossberg 1968; 1969a) that the action of an unconditioned stimulus (US) on presynaptic conditioning of a pathway activated by a conditioned stimulus (CS) is mediated by a Ca^{++} current. On the anatomical side, Hawkins et al. (1983) suggest that a US activates a facilitator neuron that presynaptically modulates each CS-activated synaptic knob. In neural systems wherein secondary conditioning can occur, a conditioning experiment enables a CS to act like a US in later conditioning experiments (Wike 1966). If the anatomical substrate of conditioning were universal, then every such CS could activate a facilitator neuron that could modulate all the CSs with which it could be conditioned. The wiring diagram of Walters and Byrne (1983) accomplished part of this requirement by letting the US activate a single facilitator neuron that nonspecifically modu-

lates the excitability of all CS-activated synaptic knobs. Their network confirms a 1969 theoretical prediction (Grossberg 1969b; 1971; 1975; 1982c).

A secondary conditioning capability also requires an anatomical feature that is not reported in the invertebrate experiments. In order to acquire US properties, a CS must send a conditionable pathway to its facilitator neuron. The CS must be able to effectively activate this pathway after learning occurs but not before learning occurs. Hawkins et al. (1983 p. 403) report that a CS cannot activate a facilitator neuron because "paired presentation of the CS and the US produced no more total firing of the facilitators than did unpaired presentation." Their observation is compatible with a general prediction that is of independent interest and whose verification would imply that the anatomical substrate of conditioning reported in the invertebrate studies is not universal: Either a neural system is incapable of secondary conditioning, or a CS will cause increased total firing of its facilitator neuron as CS-US pairing continues.

Thus, two of the most important recent experimental findings about *Aplysia* were theoretically anticipated 15 years ago. Many more theoretical predictions have recently received experimental support. One can only speculate how different the mind and brain sciences would be today if the available means of theoretical communication, unification, and prediction were already assimilated by the experimental community.

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Can the aims of neuroethology be selective, while avoiding exclusivity?

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Hoyle's intention in trying to place well-defined targets before neuroethologists is a timely one. Unfortunately, his enthusiasm leads him to propose such a wide variety of goals that the result is inevitably rather confusing. His 13 goals seem to cover most aspects of behavior, including so far totally intractable ones, like memory.

His remarks on vertebrate neuroethology are especially baffling, as despite a number of successful single-neurone studies on vertebrate brains, some of them in animals with a degree of movement (Everts 1976; Markowitsch & Pritzel 1978), Hoyle persists in seeing the only hope for further advance in brain slices. Indeed, one begins to suspect that it is the success of vertebrate neuroethology as evidenced by recent publications like *Advances in Vertebrate Neuroethology* (Ewert, Capranica & Ingle 1983) that has led him to conduct a rearguard justification of invertebrate (that is to say, insect) studies. The hard fact is that ethology has been largely founded on the study of vertebrates, whose well-ordered and easily observed behavioral sequences have offered hope of analysis, in the first instance, by behavioural methods. Most of the animals referred to by Tinbergen (1951) and Manning (1972) and cited in Table 1 are vertebrates – 70% and 76% of the samples respectively – and it is easy to see why this is so. Paradoxically, Hoyle's strongest condemnation is reserved for the humble sea hare *Aplysia* – "this behaviorally boring glob of squishy protoplasm." An internationally known pharmacologist who works mainly with mammals remarked, after hearing Kandel talk recently at Cambridge, that this was in his opinion a uniquely valuable system. Like many of us he was mainly impressed by the positive aspects of *Aplysia* research.

Over the question of cell size and its effect on the accessibility

of neurones to electrophysiological techniques, it is worth noting that most nervous systems, including that of *Aplysia*, contain some relatively small cells (say, less than 20 μ). As Hoyle suggests, it would be interesting to know what goes on in the insect brain, but one is put off by the difficulty of studying the 2–5 μ globuli cells that compose many significant structures like the corpora pedunculata. In the fish I currently study, neurones range in size from the Mauthner cell (400 μ by 30 μ) to the 4–5 μ cells of the optic tectum. At present, there is unavoidable variation in the degree of detail we can resolve at different points in such systems.

If neuroethology is to make progress, a pragmatic approach must be fostered, that is, one aimed towards practical outcomes. Systems that mediate limited and well-defined behaviours and that offer reasonable hope of detailed analysis at the neurone level should be a prime object of study in whatever organism they appear. I believe Hoyle is right when he says, "The time required to describe a nervous system adequately is something new to science," and I would agree that the FAP occupies a central position in neuroethological thinking. It is nevertheless possible that the FAP will prove something of a millstone when the freer, more exploratory types of behaviour come within the scope of neurophysiological analysis.

The suggestion that systems engineers, robotics designers, and artificial intelligence (AI) technologists, together with the odd Nobel prizewinner in physics, might be useful in giving some theoretical backbone to neuroethology is an attractive one. Hoyle rightly stresses the information-processing side of neuroethological problems. In my (limited) experience, information technologists exhibit rather varied reactions to the idea of collaboration with biologists. Some AI researchers find such contacts interesting and potentially valuable, like those working on the OMS vision system (Brown, Boveri & Cie 1982–83); others design information-processing stages that turn out to be very similar to those proposed for biological systems. The parallelism between the Ohta image analysis system (Ohta 1982) and the processing steps suggested by Marr (1982) for human vision may be taken as an example of the latter; at the same time, the Alvey report, signalling a new initiative in information technology in the United Kingdom, specifically excludes collaboration of this kind.

The value of the recent initiative that has occurred under the label of neuroethology is that it has concentrated the minds of those whose main aim is to elucidate the neuronal substrates of behaviour, towards the idea of working on particular well-defined examples of behaviour. It has also had the effect of making them pay some attention to the methods and goals of ethologists, with ethology's inevitable bias towards the study of vertebrates.

Generalized model systems, like that of Lorenz and the updated version put forward by Hoyle here, are often useful mainly in providing material for review articles. They are usually insufficiently specific to have very much predictive force. For example, the quantified ideas concerning feedback and feedforward seem to have come from servosystem engineers and applied mathematicians (Black 1934; Nyquist 1932; West 1953) originally, and were then imported into physiology (Bayliss 1960; Merton 1953) after further development through automatic gunnery control systems (1939–1945). In this example, the electrical and mechanical ideas were disseminated in engineering circles at first, and had little effect in telling biologists what to look for; but once the analogy had been grasped, the ideas proved seminal for the interpretation of the corpus of knowledge concerning spinal reflexes that had accumulated by then.

Hoyle's orchestration/neuromodulator hypothesis underlines our present interest in neuromodulating substances, but it is not clear from the model whether each substance corresponds precisely to a major section of taped programme, or whether it is simply producing what used to be called "set," predisposing the

animal to a certain type of behaviour in a persistent way. The octopamine example would indicate the former. I would agree, though, that the opening up of research in the field of neuropeptides and similar substances offers an especially exciting prospect for neuroethology.

Ethology has progressed

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In attempting to understand the diverse phenomena of the living world, scientists must classify them into manageable groups, and they may use explanatory concepts whose utility subsequently turns out to be limited to a small range of phenomena or to a particular level of analysis. The progress of scientific understanding depends upon using these categories and concepts judiciously, valuing the advances they make possible, while at the same time recognizing their limitations. Hoyle's target article fails on the latter count, because it sadly neglects the advances in ethology over the last 30 years. The concepts of the 1940s and early 1950s provided the foundations on which ethology was initially built, and all honour to the pioneers who laid them. But the growth of the structure has required major modifications to those foundations. If neurophysiologists find the concepts of 40 years ago useful, good luck to them – but let them not write as though ethology had stood still for 40 years. Such concepts may still have a certain value if attention is confined to what Hoyle likes to call "stereotyped, complex, nonlearned, innate behavioral acts," and it may indeed be wise for the neuroethologist to limit his immediate goals – but ethology itself is not so confined.

On the descriptive level, it is no longer useful to make an absolute distinction between instinctive acts and reflexes, as though some types of behaviour were never subject to modifications of threshold, while for all others modifications of threshold were of primary importance. (Hoyle is actually confused about his concept of "instinctive act," which he sees as embracing interactions with other individuals. Interactions have emergent properties not relevant to an individual's "act.") It is no longer useful to imply an *absolute* distinction between activities that occur "in vacuo" and those that occur as a consequence of external stimuli. It is also no longer useful to make an *absolute* distinction between behaviours that can be labelled as displacement activities and behaviours that occur under the normal motivational conditions (i.e., between autochthonous and allochthonous activities, to use Tinbergen's terms). It is essential to recognise that "releasers" may not only release responses, but also stimulate or guide responses, bring them to an end, and more. It is indeed "quaint" and "old-fashioned" to discuss consummatory acts with the implication that it is their actual performance, rather than the accompanying stimuli, that is always responsible for bringing behavioural sequences to an end, though this is convenient for Hoyle in permitting him to retain, even in 1984, the hydraulic model with its draining away of impulses. Of course, it may be useful to focus on the *properties* to which these several terms refer when investigating the neural bases of particular instances of behaviour, but it must not be implied that the distinctions are absolute. In some but not all cases, Hoyle does imply this, and yet he writes as though the categories were natural ones.

Hoyle wants to perpetuate not only the descriptive categories of early ethology, but also its explanations. It is surely not necessary to hark back to the manner in which the "as if" hydraulic model of Lorenz failed to account for displacement activities and, as Hoyle describes it, failed to take cognisance of feedback. Nor should it be necessary to emphasise how the

hydraulic model led to facile implications about neurophysiological mechanisms. In constructing his influential hierarchy of nervous mechanisms, Tinbergen (1951) simply translated the reservoirs into nervous centres, and the action specific energy into motivational impulses. In attempting to account for displacement activities, Bastock, Morris, and Moynihan (1953) attributed them to "sparking over," thereby translating the hydraulic energy of the original Lorenz model into electrical energy with its special properties. Careful reading of their paper shows that it was sometimes nervous or motivational impulses, sometimes the nervous system or the behaviour, and sometimes even the fish that were said to "spark over"! Again, the treatment of the concepts of drive and mood provided by Hoyle seems almost incredibly naive. Mood, for instance, is defined as variation in the expression of behaviour, rather than being used as a concept to explain such variations.

Hoyle also sadly neglects the developmental issue. He perpetuates the distinction between genetically determined and learnt behaviour, speaking of the components of a fixed action pattern as expressions of inherited factors.

Finally, it is necessary to put the record straight concerning the history of ethology. First, a jibe about von Holst's unfortunately becoming "*preoccupied* with improving the sounds produced by asymmetrical violas" reveals a lack of understanding of the way von Holst worked; and Huber [q.v.] who Hoyle implies took up neurophysiological work "in the last few years especially," has been at it since the fifties. More important, Hoyle describes Lorenz as Tinbergen's source of inspiration, and Tinbergen's primary role is reduced to that of "successful publicizing of ethology." Nothing could be further from the truth. Tinbergen was active in research before he met Lorenz. It is Lorenz who has been the publiciser and Tinbergen the hard-headed scientist. Certainly Tinbergen learned much from Lorenz, but the reverse was also true. Tinbergen took up some of Lorenz's concepts and refined them or recognised their limitations. As their more recent writings show, Lorenz (e.g., 1981) has sought to retain the 1930–1940 conceptual structure of ethology, while Tinbergen has moved with the progress of the subject. The result has been differences of emphasis among ethologists. Lorenz and those influenced by him have continued to use the hydraulic model, have continued to emphasise the distinction between "innate" and "learned" behaviour, and have continued, in discussing the evolution of behaviour, to talk in terms which imply group selection. By contrast, Tinbergen and his followers have come to discuss the causation of behaviour in terms more directly amenable to links with neurophysiology; they have endeavoured to understand the development of behaviour in interactional terms and have kept up with trends in evolutionary thinking.

Hoyle's paper is to be welcomed in so far as it encourages work in the field of neuroethology, but it is essential to recognise that the clear-cut categories and concepts on which he wishes to base his work, though useful in some contexts perhaps, are not ubiquitously so.

Neuroethology, according to Hoyle

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It was Hoyle's considerable achievement to open a new phase of quantitative ethology almost 30 years ago, with his electromyographic recordings from freely walking insects. He was also one of the first to succeed in applying the technique of intracellular recording, long in use with other invertebrates, to the motoneurons of insects, and was thus one of the founders of the cellular analysis of insect motor systems.

Here, as in some of his earlier essays, Hoyle pleads for a narrowly defined field (his version of "neuroethology," but a name such as "field X" or "neuromotor behavior" would perhaps serve as well) in which the participants have nearly or entirely common goals; thus mutual reinforcement, and hence progress, might in some sense be optimal. Any civilized means of promoting cooperation, fruitful concentration, and intellectual self-discipline would seem praiseworthy – how can one disagree? The results of cooperative work on the locust motor system are impressive. We await the next great jump forward.

The rub is, of course, that Hoyle chooses to usurp the term "neuroethology" for his purposes; most of us who think of ourselves as neuroethologists use the term rather more broadly. This does not mean that we all descend to the level of Hoyle's vividly described collectors of "random facts." There are, of course, mechanisms other than the optimization of designated-field breadth (which, in practice, ought to be achieved by the organizers of workshops and symposia) by which wonderful concentration is brought about. New questions, and new methods for answering them, arise continually; when any one of these combines broad interest, challenging complexity, and enticing tractability, it is the question itself that provides the focus and motivation for concerted interdisciplinary effort by many workers. The molluscan and stomatogastric work, bird-song production, arthropod motor system, owl hearing, insect movement perception, bat sonar, fish electroreception, frog hearing, insect chemoreception, and (dare I say) cricket phonotaxis all come to mind, among many others. To debate whether each is a cluster within neuroethology or whether only some subset of them is to be granted imprimatur under the rubric of "neuroethology" does not seem helpful to me at this stage of our adventure. We are gaining understanding of interactions among the levels we are learning to reach, and have little idea now which approaches will be the cornerstones of more general formulations. Despite the behavioral significance of "fixed action patterns," surely the actions of neuroethologists cannot be as fixed as Hoyle recommends.

Finally, the bit of rhetoric ("unfortunately, this line of progress was finally stilled when von Holst became preoccupied with improving the sounds produced by asymmetrical violas") Hoyle uses in referring to the late Erich von Holst's fascinating experiments on the structural acoustics of stringed instruments is rather uncharitable. Hoyle also seems not to consider as "progress" the contributions of this great man to remote brain stimulation in populations of free birds during his final years of ill health. One may as well complain in vain that Isaac Newton spent too much time reorganizing British coinage, or, perhaps, that Sigmund Freud turned from his early work on crayfish to other matters.

Vertebrate neuroethology: Doomed from the start?

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Hoyle's feisty treatment of issues inherent in neuroethology is a useful provocation to rethink long-term goals in this still-burgeoning infant discipline, although he seems to feel that, for the sake of a healthy future, the weak sibling, vertebrate neuroethology, should be abandoned in some harsh landscape to wither away. For those of us whose careers would suffer from such an outbreak of infanticide, Hoyle's "straight-and-narrow" sermon forces us to justify our own programs explicitly. This is ironic for those of us who have already taken a "holier-than-thou" attitude toward much work in physiological psychology that appears to have little relationship with the real-life challenges for which brains have evolved. Now, instead of basking in

the warm assurance that we alone are studying "real behavior," we are asked to explain how we can ever hope to find our way between sensory and motor domains within the still vaguely charted core of the vertebrate brain.

Hoyle is quite right in asserting that vertebrate ethology is overbalanced toward the study of sensory systems. There is a certain pleasure in imagining how objects may be encoded and represented by animals with strange sensory systems – bats, electric fish, pit vipers – which at present distracts us from linking these unique sensory filters with overt behavior. There is a distinct thrill obtained from recording in the frog's thalamus single cells that encode the universal auditory characteristics of "mate" or astonishment at the discovery of "face detector" cells in the temporal cortex of rhesus monkeys. Most of us are still working hard to determine the sensory definition of objects and space, and are not yet ready to connect these "representations" with useful activities such as movements or emotions. Yet, since many important connections from sensory systems into limbic or motor systems are now being adequately defined, it seems likely that some of us will march on across these borders in the not-distant future.

Nonetheless, I personally sympathize with Hoyle's insistence that a focus upon the organization of behavior (the generation of action patterns and their selection or modulation by motivational states) should be the core of neuroethology: that is, looking from the overt morphology of behavior back to the antecedent eliciting events rather than inward from the sense organs. Indeed, in the very volume that Hoyle has dismissed as lacking promise, *Advances in Vertebrate Neuroethology* (Ewert, Capranica & Ingle 1983), I reviewed several new studies on the interfacing of visual pathways with motor patterns, and concluded that visuomotor output pathways for consummatory and taxic components of behavior of frogs can be distinguished (surely in line with the thinking of the founding fathers of ethology!).

Progress has also been made in relating the sensory control of the electric organ discharge of certain fish. The "jamming avoidance response" has been elegantly analyzed by Heiligenberg's group (Heiligenberg 1982), using behavioral, anatomical, and recording methods and always keeping the output pattern of electrical signals as the reference point for defining the group's questions about mediating events. Furthermore, the ability to uncouple the output of these organs (by curarization) from the "anticipation" of their sensory effects has enabled Curtis Bell (1982) to describe three different categories of corollary discharge modifications of electrosensory systems. Hoyle seems to have overlooked this work of a fellow Oregonian in his implication that useful studies of corollary discharge have not been undertaken by vertebrate neuroethologists.

Although lower vertebrates (fishes, amphibians, and reptiles) most clearly exemplify the operation of innate releasing mechanisms and fixed action patterns that characterize old-time ethology, some basic discoveries have been made using mammalian preparations as well. The systematic work of the late John Flynn (1972) is exemplary in combining anatomical, physiological, and behavioral methods in working out brain pathways relating to the display of aggression in cats. His studies of restrained cats during hypothalamic stimulation revealed that induction of a "motivational state shift" would result in "tuning" of certain visual and tactile reflexes (orienting, biting, or paw-swiping) that are components of prey-attack. The studies of Donald Pfaff and others (Pfaff, Lewis, Diakow & Keiner 1973) on the fixed patterns of lordosis in the rat also show that reflexes can be sensitized by hormone treatment (which perhaps also reflects activation of a diencephalic tuning system). These insights might be compared with the discovery by Ewert that prey-catching responses of frogs and toads are either inhibited or released by modulation of the optic tectum by the caudal diencephalon (Ewert, Capranica & Ingle 1983). Recently, Gerald Schneider (Schneider, Jhaveri, Edwards & So 1984) has

shown that predator-avoidance behavior of hamsters is tightly dependent upon the function of optic tectum (as in the frog) and little upon the high-level computations of the visual cortex. Since efferent tectofugal systems are similar among higher and lower vertebrates, the circuitry underlying avoidance behavior appears to be a tractable problem in several vertebrate species.

In summary, I submit that Hoyle has ignored some actual achievements of vertebrate neuroethology and has underestimated the potential for detailed analysis of circuitry defining the sensorimotor interface in vertebrates (including mammals). Finally, I charge that the fallacy of "invertebrate ethocentrism" is just as dangerous as the NIH (National Institutes of Health) practice of mammalocentrism. We have good reasons to believe that design features of vertebrate and invertebrate brains are different in many details. We do not know whether motor patterning or drive interaction or hormonal facilitation operate in the same manner within the two universes. While I recognize that quick breakthroughs in linking sensory and motor mechanisms are the more likely with certain invertebrate preparations, their relevance to an understanding of human perception, decision making, and action patterns must be validated by vertebrate neuroethologists who study neural systems with a more certain resemblance to our own. Some balance between our dual goals of elegance and relevance must be worked out; I do not believe that Hoyle has found that balance, despite his telling arguments concerning the goals of neuroethology.

They are really complex when you get to know them

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Within a scholarly discussion of neuroethology Graham Hoyle revives his mischievous and, some might say, malicious argument that his hard and crunchy is better than your soft and squishy (Hoyle 1976). Hoyle maintains that the amount of research on *Aplysia* has somehow obstructed research on truly interesting arthropod invertebrates, and that the research effort on *Aplysia* is not justified by its potential to explain complex behaviors of the type ethologists are interested in. To gain some perspective on this thesis, I have tried to obtain a rough estimate of the relative proportions of specific organisms currently being studied by neurobiologists. I analyzed the keyword index of the abstracts for the last Society for Neuroscience annual meeting. By also examining a random sample of 100 abstracts, I obtained an estimate of the proportion of abstracts that did not include a given organism in the title, which permitted me to adjust the figures from the keyword index to better reflect the actual organisms used. The analysis (Table 1) indicates that vertebrates were used in 88% of the research reports (4,344 out of 4,920). Rodents (primarily rats) accounted for 51% of all research, while nonmammalian vertebrates (one of the central concerns of ethology) were mentioned in 6% of the abstracts. Invertebrates accounted for 5% of the total (not including 17 reports on olives). Of the total number of invertebrate papers (Table 2), I estimated that 38% were on molluscs and 44% were on arthropods. Of course, these percentages include all types of research, in neuroethology as well as in other areas of neurobiology. Since molluscs, compared to arthropods, are more often used for cellular or biophysical studies, my figures probably underestimate the relative proportion of arthropod studies directly relevant to neuroethology.

Reports using *Aplysia* and closely related gastropod molluscs constitute 92% of all reports using molluscs. By contrast, among the arthropods, no group clearly predominates. Thus, one can

Table 1 (Kupfermann). Estimate of number of reports of given organisms reported on at Neuroscience Society meeting, 1983

Organism	Adjustment factor ^a	Adjusted no.
<i>Vertebrates</i>		4,344
Mammals		4,069
Rodents		2,520
Rats	2.1	2,248
Mice	1.2	212
Other	1.0	60
Nonhuman primates		315
Humans	3.3	396
Cats	1.8	588
Other mammals	1.0	150
Birds	1.0	73
Cold-blooded vertebrates	1.0	202
<i>Invertebrates</i>	1.0	227
<i>Miscellaneous or unknown</i>		349
Total estimated reports		4,920

^aThe number of organisms reported in the index was multiplied by the adjustment factor to compensate for those titles that did not cite the organism used. The adjustment factor was calculated on the basis of inspection of a random sample of 100 abstracts and their titles.

conclude that the arthropods are not being ignored by neurobiologists, although, presumably for various reasons, arthropod researchers have not chosen to concentrate their efforts on any one type of organism. This diffuseness of effort among arthropod researchers provides for a broad biological perspective, but may hinder the attempt to solve specific scientific questions of general interest.

Regarding the assertion that the behavior of *Aplysia* and gastropod molluscs is dull and irrelevant to neuroethologists, I would like to point out that there is substantial evidence that gastropod molluscs exhibit beautiful examples of complex behaviors. I will cite one set of examples concerning feeding, a behavior that I am most familiar with (for a sample of some of the work on feeding behavior in *Aplysia*, see Carefoot, 1967; Jahanparwar, 1972; Kupfermann, 1974; Preston & Lee, 1973; Susswein, Weiss & Kupfermann 1978; and Weiss, Koch, Koester, Mandelbaum & Kupfermann 1981). Feeding in *Aplysia* is elicited by highly specific features of their preferred food, seaweed. The behavior initially consists of an appetitive phase in which the animal locomotes and searches for food. Direct contact with food triggers a consummatory response (fixed action pattern) that consists of a stereotyped sequence of movements that involve the precise coordination of over a dozen different muscles used in grasping and swallowing the food (Cohen, Weiss & Kupfermann 1978). Both the appetitive and consummatory phases occur spontaneously when animals have been food-deprived for a long period. Feeding in *Aplysia* is highly dependent upon arousal state, mood, satiety level, learning experiences, and competing behaviors. In short, feeding in *Aplysia* (and many other gastropod molluscs) exhibits virtually every behavioral phenomenon of interest to ethologists. To varying degrees, other behaviors of *Aplysia* and gastropod molluscs also

Table 2 (Kupfermann). Estimate of number of reports of given invertebrate organisms reported on at Neuroscience Society meeting, 1983

Organism	No.
Molluscs	86
Gastropods	79
Tritonia	2
Aplysia	60
Hermissenda	7
Pleurobranchia	4
Limax	2
Snail	4
Nongastropods	7
Arthropods	100
Crustaceans	42
Lobster	4
Crab	8
Barnacle	4
Crayfish	26
Insects	58
Grasshopper	10
Drosophila	15
Insect	8
Cricket	4
Manduca	9
Locust	8
Cockroach	4
Annelids	27
Other Invertebrates	14
Total invertebrates	227

exhibit the complex features that interest ethologists. No amount of research on molluscs will provide a complete explanation of courtship in ducks; but arthropods will not solve this problem either. Nevertheless, invertebrates have already provided, and will continue to provide, insights into the neural mechanisms of general classes of behavior that appear to be common among virtually all animals. Hoyle's deriding the behavioral capacities of a particular group of animals seems antithetical to the essential features of ethology, namely, understanding, appreciation, and reverence for the true behavioral capacities of animals.

The squishy revisited: A call for ethological affirmative action

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Hoyle emphasizes, quite correctly, that both ethological and neurophysiological studies on the same behaviors and species are needed if neuroethology is to prosper. He argues, however, that this should be accomplished by restricting neurophysiological attention to a few ethologically respectable species and

behaviors. The reason for this is hard to understand. The principles of ethology, as set forth by Lorenz, Tinbergen, and their disciples, were meant to be generally applicable. It is true that ethological studies have emphasized a small number of taxa, but this should not imply that other taxa are somehow uninteresting to ethologists. It is much more likely that they simply have not been studied yet by ethologists. We need both neurophysiological studies of ethological favorites and, perhaps more important, ethological studies of any and all species whose nervous systems appear particularly accessible to neurobiological study.

Gastropod molluscs, particularly opisthobranchs such as *Aplysia*, possess what Jonathan Copeland (personal communication) calls the "Cadillac" of nervous systems. It is true that these "Cadillacs" have been used primarily for studies of the cellular properties of neurons and the control of relatively simple movements. It is unjust, however, to suggest that the animal is somehow to blame for this. Opisthobranchs do not lack behavior: They have lacked ethologists. Over the past two-and-one-half years we have been working to remedy the situation by conducting detailed observations of the spontaneous behavior of *Navanax inermis* and *Aplysia californica*. We have constructed ethograms for both species and found that their behavior agrees quite closely with ethological models and is complex enough to be interesting in its own right (Leonard & Lukowiak 1982; 1983; in press a; in preparation). Most opisthobranchs are slow moving relative to insects or vertebrates. This may be largely responsible for the idea that they don't do anything. However, with time-lapse techniques it becomes obvious that they do a great deal.

Both *Navanax* and *Aplysia* have respectable repertoires of FAPs. Our ethograms for *N. inermis* and *A. californica* currently contain 28 and 45 FAPs, respectively. We can expect to find more as we look in more detail at juvenile stages and behavior in the more complex environment of the field. In particular we have established that in *Navanax*, normal sexual behavior involves the active alternation of sexual roles by the members of a pair during bouts of copulation (Leonard & Lukowiak 1982; in press b; in preparation). Sexual roles in both *Aplysia* and *Navanax* are behavioral states, and each role involves the execution of a complex series of FAPs. Either species has tremendous potential for physiological tests of ethological models, and our results suggest that these opisthobranchs may be ideally suited for the study of male-female conflict with respect to reproductive strategy, a burning issue in ethology today. Our observations suggest that opisthobranch behavior is comparable in complexity to that of insects and other crustaceans. An overview of the scattered literature on gastropod behavior reveals instances of male-male competition for mates, parental care, territory, and everything but eusociality. All animals face the same challenges from their environment, and being animals they use behavior to meet them. To be adaptive, behavior has to be complex.

Ethology is necessarily a comparative science, and neuroethology must be also. As such, the disciplines cannot afford to rely on observations from only a small number of "model systems." For neuroethology to enter a golden age, we need, not a narrower focus of our attention, but broader training. A competent neuroethologist must be a courtier with both ethology and neurobiology. It would be foolish for the neurobiology of the 1980s to pursue the neuronal bases of the ethology of 1950. Hoyle is obviously familiar with the ethological literature, but his definitions of ethological terms are quite idiosyncratic and in no way represent a consensus of current ethological opinion. In fact, it is highly unlikely that a consensus could be reached on the definition of such terms as FAP. We will only have a science of neuroethology when we have a generation of scientists trained as such – as neither neurobiologists nor ethologists. In the meantime, we all have to do a lot of reading and communicating.

We are making good progress in the neural analysis of behaviour

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I do think that it is worthwhile for neurobiologists to keep examining the issues raised in Hoyle's target article. This said, I find myself in disagreement with most of its major conclusions. I will limit my comments to a few of the general principles raised rather than make specific criticisms of the way the literature has been interpreted.

Acceptable goals for neuroethologists. At least some of the goals on the list would be present in the minds of most behavioural neurobiologists. However, as Medawar (1967) has said, "research is surely the art of the soluble." It is unfair and inaccurate to imply that the large body of workers in this area is simply on a random fact-gathering spree. The overwhelming message that I get from reading the introductions to so many neurobiology papers is that a serious and directed effort is being made to tackle those parts of the goals that are presently accessible. When I read the discussions at the end of these papers, I find that a valiant effort is being made to interpret the results in a way that will help to bridge the gap between neurobiology and ethology. This effort largely fails. Unlike the author of the target article, I do not feel that this is because the wrong questions are being asked. I believe this failure reflects a shortage of basic materials with which to build and bridge. Aspiring young neurobiologists must see at the outset of their careers the accolades awaiting anyone who can deal with the listed goals effectively. The fact that they choose to deal with the less spectacular but more accessible parts of the underlying mechanisms means that both they and their supervisors agree with my position. There are times in science when an extreme opposing view eventually prevails over a more generally supported one. The fact that we are making sound progress by using our present approach suggests that this will not be one of those times.

Who may properly call himself a neuroethologist? There are two problems with the argument presented in the target article. First, is there any merit at all in imposing a rigid definition on a field still in flux? As work progresses a consensus may emerge concerning the limits of neuroethology, but judgements attempted at this stage are almost certain to be irrelevant. In the absence of any true bridge between neural analysis and ethology, intent or rationale forms the only criterion. Second, the basis of the proposed definition is unsound. No modern ethologist would be sympathetic towards Hoyle's view of the bounds of ethology or accept the outmoded definitions of fixed action pattern and other ethological terms (Dewsbury 1978; Hinde 1982). The discipline of ethology has not remained static (Hinde 1982) as the target article would suggest. Even if an attempt to define the field of neuroethology at this time can be justified, the use of such out-of-date sources to derive the definition cannot.

Target animals and behaviours. The author has argued on several recent occasions for concentration of our efforts on fewer species (Hoyle 1976), and, indeed, one can make a powerful case against the haphazard proliferation of experimental animals simply because a particular animal has not yet been studied. However, it is also true that many researchers end up asking the right question of the wrong animal simply because it is available in the home laboratory, because there is a tradition of using it there, or because there is pressure to concentrate the field on selected species. It is entertaining that this author in particular should now be supporting this position so vigorously, when the literature abounds with examples of his equally vehement defense of the opposing view (Hoyle 1967; 1977). He has argued cogently in the past that the field of muscle physiology was held

back for years because experiments were confined to "one or two laboratory animals, especially the frog, and soon, in the way that men have, 'vergleichende' became almost a word of contempt among the misguided" (Hoyle 1967, p. 152). There can be few senior neurobiologists today who could demonstrate more effectively than Hoyle the productiveness of the comparative approach. Indeed, there can be few neurobiologists who have worked on a greater variety of animals and few laboratories that have spawned graduate and postdoctoral research on a wider range of species than his. If one animal or preparation were demonstrably superior to most others for behavioural neurobiology, most laboratories would soon focus upon it. This has happened with locusts and grasshoppers in the field of neural development. The last 20 years of work has shown that a variety of preparations is necessary. That situation is unlikely to change suddenly. What *Aplysia* has told us could not have been as effectively learned from *Shistocerca*. What we have learned about sensory processing from compound eyes could not have been found by studying cercal input.

In conclusion, I find myself at variance with the tone of the target article, with the message that progress has been slow because we have failed to impose guidelines of various sorts upon our field. I believe that we are making satisfactory progress and that, in a new field, work will be concentrated naturally on those projects and species which prove themselves capable of yielding the most rapid advancement of our understanding.

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Neuroethology: Not losing sight of behaviour

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Hoyle has been an extremely important figure in the development of neurobiology, and I yield to nobody in my admiration of his achievements. I also like his direct approach to questions and his total lack of reticence in expressing his opinions – a non-nonsense trait that owes a lot to his cultural origins in the North of England, where spades are called spades and not wrapped up in the deferential circumlocutions of the South.

I say all this at the outset because, while he has written a number of important reviews in this field (e.g., 1964; 1976), this target article does not number among them. There are still some useful insights to be found here, but I'm afraid Hoyle's tendency – often highly productive – to concentrate only on the issues that he considers fruitful is here carried to unfruitful extremes.

Hoyle is justified in his criticism of the scope and nature of much that is called neuroethology. So many people who start with *behavioural* questions in mind soon drop down through the levels of analysis to end up juggling with the complexities of synaptic transmission out of all sight of these questions. Often they never return. But Hoyle's arguments to encourage a more behavioural focus are greatly weakened by his idiosyncratic view of what constitutes "behaviour." At times he seems to equate it not just with movement but with the movement of limbs. Hence, he is led to dismiss, or at least underrate, the importance of Kandel's work (e.g., Kandel 1979) with *Aplysia* and Bullock's on electric fish (e.g., Bullock 1977), both of which endeavours seem to me to embody many of the behavioural and information-processing virtues that Hoyle calls for elsewhere in his review.

I am certainly not a neuroethologist and therefore can only guess how someone working in the field will react to Hoyle's conception of it. However, it is clear that his view of neuroethology derives from his view of ethology itself. This latter

view I find very strange, for I cannot understand why he chooses to ignore so much of modern ethological thinking. In keeping with his obsession with behaviour as movement, he chooses to emphasise releasers and the fixed action pattern (FAP) and set them firmly in the 1950s mould of action specific energy and psychohydraulics.

I wholly agree that scientists in pursuit of the current fashions often neglect original basic concepts. In fact, the FAP is indeed a remarkably robust and useful concept – there is much that modern ethologists have to say concerning it. But for Hoyle, “Control of flow of the water in the Lorenz model is the heart of the matter of ethology.” This carries tradition too far! He quotes an ethological colleague who tells him that nobody pays much attention to psychohydraulics now. The reason is that it does not model behaviour adequately. Hoyle himself recognizes that the model has its drawbacks, because it lacks feedback control and also conspicuously fails to account for the patterning of much aggressive and exploratory behaviour. As ethology has matured, it has come to recognise that many of the grand old generalisations no longer work. We have to accept, for example, that the performance of any behaviour may have both incremental and decremental effects on its subsequent performance. The updated model Hoyle provides may be useful – he doesn’t explain it enough – but I am uneasy with its grafting of electronic components onto hydraulic ones. It seems unnecessary, and I am reminded of the criteria that Deutsch (1960) argued must be met by behavioural models if they are to be useful.

With reference to the FAP itself, I think that Hoyle’s (1964) ideas concerning “motor” and “sensory tapes” in their control have been most useful. I do not understand why he insists on making such a clear division between reflexes and FAPs. After all, the same nervous system is operating and motor patterns are resulting. Reflexes and FAPs share many properties (some of which I have tried to illustrate – following Sherrington, 1906, and Precht, 1956) in Chapter 1 of Manning (1979). I agree with Hoyle that we must assume a large genetic component in the control of FAP development. They are clear examples of phylogenetic units that it has proved possible for natural selection to modify in relative isolation from other such genetically programmed units. However, we must admit that our evidence for genetic control in FAP development is almost all indirect – we can usually put forward only soft arguments, which are not based on adequate genetic analysis. Hence, when Hoyle asserts that, “Most or all of the components of a FAP are expressions of inherited factors and are subject to the Mendelian laws of inheritance as wholes,” he is propounding an act of faith, not a balanced assessment of the evidence. I wish it were so simple as his suggestion that subroutines within FAPs may arise by mutation. I recommend a careful study of Bentley and Hoy (1972) to reveal the kind of impasse that we have reached at times.

Finally, I suppose one of my problems in relating Hoyle’s neuroethology to its mother field is that I don’t really have a clear picture of ethology as a proscribed field of endeavour. It is the *approach* to the behaviour of the whole animal in its whole environment that represents ethology’s great achievement and has made it so influential. For all my criticisms, I like the way Hoyle refuses to lose sight of behaviour itself among all the nerves and muscles.

The ethology of neuroethology

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Hoyle’s contributions to the study of the neural bases of animal behavior can hardly be overestimated. He himself would seem to be the last to do so, as this brilliantly written target article

testifies. In addition to his having made many original investigations and important discoveries on his own, he has been and continues to be a leading pioneer in the methodology of single-neuron work on – more or less – “behaving” animal preparations; and he has been a continuous source of stimulation for a large number of researchers in the field described in this article.

A first-hand introduction to how one of the founding fathers of neuroethology sees its claims and aims is therefore to be welcomed, even if it cannot be denied that it displays a somewhat personal, at places even idiosyncratic, view of the matter. Autobiography (and autohagiography) cannot replace unbiased historical representation of a scientific development, even if written by scholars who have themselves helped to found and decisively shape this development. To someone who has watched the impressive advances of the investigations of the neural mechanisms of animal behavior rather closely, the following reactions suggest themselves: Hoyle’s entirely justified emphasis on the methodological importance of the intracellular identified neuron approach as a source of progress in neuroethology seems to obscure or even underrate the immense *conceptual* stimulation and encouragement provided for this field of research by, for example, von Holst’s early and admittedly rather crude neurophysiological work on central pattern generators, or Roeder’s demonstrations that even rather sophisticated-looking natural behaviors of insects are not too complex to be fruitfully studied at the basic neuronal level; or Bullock’s and his coworkers’ success in showing that even in vertebrates one need only pick a really suitable experimental preparation to go right down to the neuron level in explaining the mechanisms behind highly specialized behavior.

Being strongly insect-biased myself, I need not be convinced that insects are marvelous animals for investigating many basic physiological and behavioral problems. However, it seems odd to find this widely accepted fact all but discredited by an almost group-chauvinist downgrading of research on other (especially more squishy) phyla. As far as some of the major aims of neuroethology, as stated by Hoyle, are concerned: memory (but note that he defines neuroethology first as the study of the neurophysiological events behind innate behavioral acts!), feature detection, motor control, information processing, and development, it is true that work on the neural circuitry of invertebrate fixed action patterns can contribute to all of these; however, to demarcate the field so that neurophysiological work on fish electrolocation, bird-song control and development, bat echolocation, amphibian visual or acoustical pattern recognition, or the ontogeny of cat visual information processing is either relegated to the periphery or even expelled seems not only somewhat arbitrary, but might even turn out to be downright deleterious to the very aims of the field of neuroethology so aptly formulated by Hoyle, if his advice were followed to the word. The same holds true for the study of the endocrine and especially neuroendocrine mechanisms of behavior: How could “water-level control” in the Lorenzian motivation model ever be fruitfully investigated without clarifying the endocrine effects on the neural machinery as well as elucidating the workings of this machinery itself? Focusing forces on those problems that can at present be attacked with the highest expectation of success is certainly an excellent short-term research strategy. However, in the long run, a field of investigation has to define itself by the full breadth of the phenomena – here of animal behavior – and not lose in scope what is gained by concentration. Hoyle’s view of neuroethology seems to gain exclusivity of focus by restricting its interests in animal behavior to the most narrow, and only historically relevant, definition of what ethology is all about. The point of reference should not be classical ethology, but the full range of animal behavior.

Altogether, this commendable article also reads to the outsider as strangely possessive and defensive; strangely, because the Hoyle-type neuroethological approach seems to be so well accepted and thriving both in the United States and in Europe.

Then, why write at such length in battling tones if no one earnestly denies neuroethology in invertebrates its ranking place in modern biology? I can only understand this as a particularly nice demonstration of human ethology in science. The article seems an effort to rally the tribe, to stake out its territorial claims in order to monopolize its resources, to define the defended boundaries against intruders (and defectors), to affirm precedence of occupation, to throw out foreigners or to relegate them to lower services, to give its members a feeling of historical identity by deriving their unifying tribal goals from the gospel of sanctified, Nobel-prized founders, to erect common linguistic and conceptual totem poles for the society of friends, and, finally, to christen the true believers through the psycho-hydraulic flush toilet handed down to the British Society of Experimental Biology in 1949! And why all this? Now, economic sociobiology may not be beneath even the most high-spirited endeavors of the human mind! The last sentence gives it all away: "May granting agencies see the ultimate wisdom of supporting the endeavor." Optimal foraging in the world of academia, the ethology of neuroethology. Which is not to say that I would not fully agree with this *videant consules* message of Professor Hoyle.

Resurrecting Lorenz's hydraulic model: Phlogiston explained by quantum mechanics

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Sciences during their development pass through necessary stages of oversimplification, of elementary models and catchy concepts. As understanding proceeds, more and more qualifications are introduced; the appealing clarity of the original concepts is obscured and is replaced by a more accurate but more tedious description. Ultimately, the original concepts drop out of use, and with luck are superseded by a new formulation at a deeper level of analysis. Within the field, the original concept is at best relegated to a useful shorthand in communication among practising scientists who understand its problems, but outside the field, it often remains long enshrined in the works of popularisers and in the thought processes of scientists in other areas. Examples abound, from phlogiston to Newtonian physics, in the homunculus and in Mendelian genetics, in the ethological terminology of the 1950s and (to cite a tiny example from our own field) in the command neuron. [See Kupfermann & Weiss: "The Command Neuron Concept" *BBS* 1(1) 1978.]

My first major criticism of Hoyle's article is that it resurrects a simplified parody of the ethology of the 1950s, claims it represents the real behaviour of animals, and holds up this illusory construct as a desirable target for modern neurobiology. He proposes, in short, to explain phlogiston with quantum mechanics. An outsider to behavioural science and imprinted upon the ethological concepts of his youth, he takes some of these (though ignoring others, such as ritualisation and intention movements, which fit less readily into his scheme) and elevates them to a peak of reification barely contemplated even by their originators 35 years ago. He dismisses offhand the careful work of two subsequent generations of ethologists who have revealed the limitations and evaluated the uses of this terminology and of the Lorenzian hydraulic model, and, incredibly, wheels the latter back on stage. This mummy, dusted and superficially decorated with neurophysiological terms and with the difficult parts concealed in labels such as "computer" and "comparator," is to be investigated through modern circuit analysis.

I cannot believe that this would be a fruitful approach. True, it would indeed be nice to have a unifying theory of neurobiology to "explain" the profusion of alternative designs, but this one will not do it. Natural theologians collected natural history and

life history data for 300 years before the Darwinian theory of evolution rationalised the hopeless diversity, and that theory would not have originated in satisfactory form had it not been for their labours. Patience, neurobiology – better no theory than a retrograde one, one which has already delivered its contribution.

For it is simply not true that neurobiology and ethology have not previously met, and this is my second major criticism of the target article. Hoyle grossly understates the extent to which neural circuit analysis has already provided a basis for the understanding in neural terms of those aspects of behaviour which "interested the founders of ethology." To give one example: There are some behavioural components well described as "fixed action patterns" in the original sense, and there are some neurons that fit the original concept of "command fibre." For 38 years we have known that one command fibre and its associated postsynaptic circuitry is the basis of one FAP – Kees Wiersma's brilliant work (1947) on the crayfish lateral giant fibre made this clear and established *him* as the authentic founder of the sort of neuroethology Hoyle advocates. By the time the ethologists were working the same conceptual ground 10 to 20 years later, it was already clear to Wiersma and to other pioneers of the neural basis of instinctive behaviour, such as Roeder, that much behaviour is not organised in this way, even in crayfishes or moths. In this area, neurobiology had preceded ethology: In others, the corresponding neural investigations have been made subsequently, as the necessary techniques and self-confidence developed.

An outstanding feature of Hoyle's target article is the number of highly relevant neurophysiological studies he ignores. We have, for example, detailed studies at the synaptic level of how stimulus filtration is achieved in both insects and vertebrates, especially within the visual system (e.g. Barlow & Levick 1965; Hubel & Wiesel 1974; Rowell, O'Shea & Williams 1977, among many others). We understand in many preparations the activation of complex circuits by key stimuli of external origin, circuits producing either episodic or cyclically repeated behaviour; e.g. the release of the various tailflips or alternatively of swimming in the crayfish (reviewed by Wine and Krasne 1982) or of escape swimming in *Tritonia* (Getting 1976; Lennard, Getting & Hume 1980). Some of the longest coherent sequences of fixed action patterns known, the moulting programmes of arthropods, have been analysed in depth in moths (e.g. Truman 1979), locusts (Hughes 1980), and crickets (Carlson 1977): The release of this behaviour through key stimuli of internal origin (hormonal secretion) is being actively investigated (e.g. Truman, Mumby & Welch 1980), as is the comparable release of the egg-laying behaviour of the seahare (reviewed by Scheller, Rothman & Mayeri 1983). We have descriptions of identified intraganglionic interneurons in locusts which each drive discrete but overlapping assemblages of motor neurons, producing elemental complex movements (Burrows 1980), a phenomenon which would surely have delighted Tinbergen in 1950. Particularly puzzling is Hoyle's distaste for the stomatogastric preparation, apparently due to the fact that the movements of the lobster stomach were not described by Lorenz. In my laboratory, we are currently investigating the circuits that allow a flying locust, equipped with a relatively rigid central pattern generator for flight and associated sensory feedback, to integrate exteroceptive information with this mechanism and make adaptive corrections to the flight path, or steer at will towards or away from objects (reviewed by Reichert, in press). I am not sure that this work would qualify for Hoyle's brand of neuroethology (though if locust jumps and seaslug swims do, surely locust flight is allowed in); but if it does, then it is piquant that the most useful source of comparative information for our analysis is certainly – the stomatogastric preparation.

In the space allowed it is impossible to rise to all of Hoyle's deliberate or unintentional provocations. I think it should be mentioned, however, that his article may give a false impression

that ethology stagnated without fertilising a new and active interdisciplinary science. Nothing could be further from the truth. The great achievement of classical ethology was to make biologists realise to what a huge extent behaviour, even the complicated behaviour of the higher vertebrates, is based on species- (or other taxon-) specific genetic instructions, and, so based, is directly subject to classical selection. Ethology may not have revolutionised neurobiology (though the interaction was certainly more fruitful than Hoyle appears to realise), but it was instrumental in causing the present-day fusion of behaviour, ecology, population genetics, molecular biology, and evolutionary biology that has become probably the most exciting area of biology since Darwin. Whole new fields of investigation (e.g., sociobiology, optimal foraging strategy theory, and so on) have arisen as the direct consequence of this fusion. The Nobel prizes to the ethologists were certainly appropriately awarded. It is likely to be a long time before neurobiology makes advances as seminal.

Points of congruence between ethology and neuroscience

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Let us assume that ethology is the subdiscipline of biology that deals with the behavior of organisms (following the proposal of Lorenz, 1981), and that neuroethology is the subdiscipline of biology that deals with the sensory, neural, muscular, and glandular substrata of behavior (following the intent of Hoyle's target article). Even though any one behavior is supported by a specific substrate, behavior and substrate can be investigated independently, at least in principle, and either investigation has the potential to come up with its own explanations. We will not seek to explain behavior by its underlying structure, as attempted by ontological reductionists, even though we may find indications that the underlying structures set specific limitations on the range of potential behaviors. However, we do accept the conclusion that only the overt behaviors and structures are directly subject to natural selection, and that any substrate within the organism can be reached by natural selection only through the surface (Schleidt 1981). Accordingly, we must not ignore the close correspondence between overt behavior and its internal-substrate, and must deal with it, not as ethologists or neuroscientists, but as biologists.

In my view, the essence of a scientific explanation is to provide some kind of map that shows the relevant objects and their features while omitting irrelevant clutter. "To explain something" means, literally, to lay it out flat, so that it becomes obvious and nothing remains hidden. Any particular scientific topic can be represented not only by its topographic map, but also by one of the traditional forms of scientific description, such as verbal explanations, working models, or sets of equations. Each form of description has advantages and disadvantages. Transparency, eloquence, and ability to minimize redundant information and noise vary, but ultimately, all forms are mutually translatable. The idea of a "map," and correspondingly, the idea of scientific investigation as a "mapping process," has the advantage of representing the attempted congruence between "the real world" and the selected "scientific topic." Thus, whenever congruence is absent we are alerted to the fact that our attempted explanation has failed. In order to clarify the relation between ethology and neuroethology, I want to point to two kinds of inappropriate explanations: The first corresponds to the use of the wrong map, comparable to the attempt to navigate the streets of Vienna with a street map of Washington, D.C. The second is equivalent to the use of a map on which the con-

gruence is coincidental or only partial, as in using the storm sewer system map when a street map is needed.

In comparing the scope of ethology with that of neuroethology the problem of congruence is most important, since both types of erroneous application of "maps" have created confusion in both fields, and have raised false hopes and expectations. We tend to ignore basic behavioral and structural differences among members of different animal phyla, and we confuse relations among behavioral elements with relations among anatomical structures that we suspect are important for behaving.

First, we have to remind ourselves that the basic theoretical framework of ethology, including the concept of the fixed action pattern (FAP), was conceived mainly from studies of vertebrates, mainly birds and mammals. To this date, no fine-grained comparison of different taxa exists that allows us to decide whether or to what extent the particular features emphasized as significant in birds (e.g., Lorenz 1932; 1970) are also significant in other classes, such as hydrozoans, crustaceans, snails, or cyclostomes. In fact, until recently, even a format for fine-grained descriptions of behavior that could make such a comparison feasible was lacking (e.g., Drummond 1981; Finley, Ireton, Schleidt & Thompson 1983; Schleidt & Crawley 1980). However, some differences in the behavior of the members of different taxa are too obvious to be ignored. For instance, birds and mammals show a wide variety of adaptive modifications of behavior (Lorenz 1965) that are blatantly absent in insects. This difference in learning ability may well indicate a fundamental difference in the overall organization of behavior in these taxa. The differences in anatomical structure are too obvious to require any further emphasis. Thus, the assumption that a better understanding of insect behavior will help us understand human behavior is unfounded, except for the very general fact that we understand principles by comparing different items such as systems or organisms. Or, more aggressively phrased: If we want to understand human behavior, we should focus on the study of other primates, and possibly other vertebrates. But the greater the genetic distance, the less immediate will be the applicability of the results to the human case.

Second, we must not forget that the original prototypes of the FAP are the grunt-whistle of the mallard and the fly-catching of the starling (and, unofficially, the sexual act of the human male). The patterns of locomotion in fish, worms, and centipedes were added with the physiological explanation for their spontaneity in mind (von Holst 1939; Lorenz 1937). The "flush toilet model" of the FAP (Lorenz 1950) was introduced as a challenge to the persistence of Pavlovian-Sherringtonian thinking in terms of reflexes, and as a logical alternative to the Cartesian idea of stimulus control. The model emphasized the internal production of excitation, and showed how internal and external control could be integrated, with the method of "dual quantification" (Lorenz 1943) in mind. However, it was certainly not intended as a hypothetical blueprint for a particular neural subsystem. It was inspired mainly by the inventor's intimate knowledge of the anatomy and physiology of both the motorcycle, including its carburetor, and the human body, including its urogenital tract, but not especially by his knowledge of brain anatomy (documented in Lorenz 1936). This is not mere inference on my part, but an authentic statement in the sense that I was privileged to assist Konrad Lorenz in designing the first drafts of the model and executing it in pen and ink.

I believe that progress in our understanding of the FAP and the implications of its model can be made by correcting erroneous assumptions (e.g., Lorenz 1981, p. 181, Fig. 18b); by analyzing the model's assumption in greater detail and mapping it onto a different frame of reference (Figure 1); and by checking the features against those of a particular animal's behavior (e.g., Schleidt 1964; 1965; 1974). But to elaborate on the fine details of the old "psychohydraulic model" and to represent a particular function by combining a variety of electronic, hydraulic, and logic symbols (e.g., Hoyle's Figure 4) is confusing. Although the

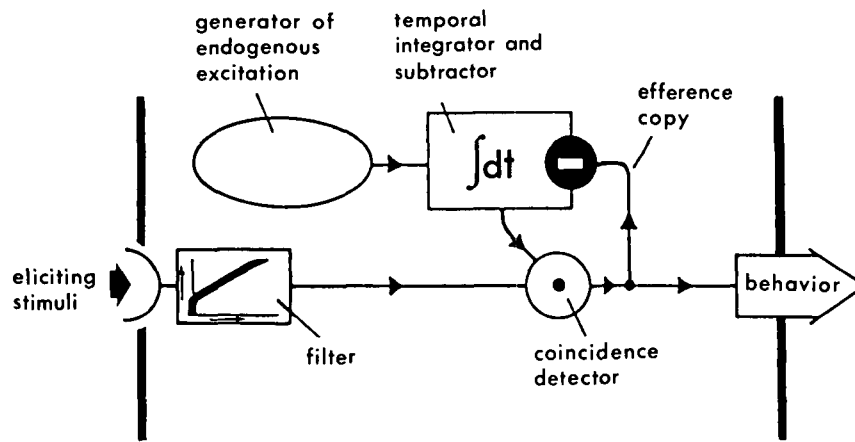


Figure 1. (Schleidt) Functional diagram of the "psychohydraulic model" (Lorenz 1950), according to Hassenstein (1983).

1984 model fails to *explain the behavior* any better than did the original 1950 version, it leaves me in a state of awe about the hypothetical neural structures and functions, and evokes visions of Rube Goldberg's creations (Marzio 1973).

The ethologist's conceptual map of the FAP could conceivably be as different from the map envisioned by the neuroscientist as the street map of Vienna is from the map of its sewers. Navigating the streets of any city with the help of its sewer map or navigating the sewers with the help of the street map would be equally confusing, in spite of the obvious partial congruence between the two maps. Ultimately, we must widen our scope and think as biologists. We need to have available and use *both maps* with equal skill in order to make a novel contribution to our understanding of the neural underpinnings of ethology. This is not just a matter of finding the neural mechanisms that support behavior, but locating among all the clutter the particular points of congruence.

Neuroethology – how exclusive a club?

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For anyone who has been acquainted with Professor Hoyle over the past 20 years, the argument that insects are the only salvation for neuroethology is not entirely new. Indeed, he has spread this view at every opportunity, and my initial response to this particular effort was that there is very little new here. But, in fact, I think it can be said that neuroethology is at some kind of crossroads in its development, and an examination of future progress in this relatively new discipline might be worthwhile.

For me, the application of rigorous neurophysiological techniques to ethology has always been a natural progression toward understanding the fundamental determinants of behavior. Since there are interesting behaviors in all phyla, and a mechanistic explanation of them would provide the basis for testing the principles that have emerged from purely ethological studies, I have never felt the need to restrict the field to a few especially favored organisms. But if we are to apply the techniques of neurophysiology, then the animals selected and the behaviors scrutinized have to be experimentally tractable. If we accept the recommendations in Hoyle's target article, it is only insects that have both really interesting behaviors and nervous systems that will yield to the microelectrode. In a marvelous exposition of biased, confused, and contradictory thought, Hoyle rejects most other preparations, including many that have added to our knowledge of neuroethology. *Aplysia* is treated with contempt, while a close kin, *Tritonia*, is held up as the only animal that has come close to providing us with a complete explanation for a fixed action pattern. Are we to believe that only preparations

with which Hoyle has been associated are worthy of study?

Hoyle has, of course, also labored mightily and for many years on insects, but where is the progress? Has he produced a neurophysiological explanation for locust marching, a project he began over 30 years ago? To be fair, this explanation is still missing . . . and why?

The neuroethological approach I was taught as a graduate student was to first study the behavior quantitatively, making ethograms and the rest. Then one examined the muscles and the neuromuscular apparatus so as to establish a transfer function between the nervous system and the movements. Particularly useful was recording from the muscles while the behavior was occurring and then correlating this information with films of the movements or outputs of movement detectors. This was about all one could do with what were essentially noninvasive techniques, and for many today, such methodology remains the end point for the physiological analysis of an ethological problem. Further progress required a semi-intact or isolated CNS preparation in order to work out the circuitry and the mechanisms underlying the movements, and when this was achieved, to try and relate it all to the behaving animal. It was at this point that the two mutually contradictory features of neuroethology became apparent. The animals with the ethologically most obvious and complex behaviors had the most difficult nervous systems to work on experimentally, and those animals with large, easily accessible neurons were, indeed, usually less interesting from an ethological point of view (but only for those investigators who were shortsighted). Hoyle's prescription for reconciling these opposing truths seems, at first glance, to be entirely reasonable.

His primary target for aspiring neuroethologists would be a description of motor neuronal circuits and the role of proprioceptive feedback in shaping the final motor programs. He would also like to know how they are turned on and off and controlled at a cellular level. But what are the *requirements* for the attainment of these worthy goals, and how do insects in particular measure up?

1. All of the motor neurons have to be identified. Not too hard, thanks to the development of backfilling techniques.

2. All of the premotor interneurons involved in generating the behavior must be located. Extremely difficult. They are small, numerous, and the cells must be penetrated and held while the behavior is in progress. Furthermore, it must be shown that perturbing their activity has an effect on the motor output program.

3. All of the ephaptic and synaptic connections between the interneurons themselves and between the interneurons and the motor neurons must be identified and characterized in terms of their effectiveness and temporal properties. In addition, they must be rigorously proven to be monosynaptic.

These last two requirements have usually become the Waterloo of insect neurophysiologists, even if they have survived the

battle of finding all the cells involved. The main reason is that, in order to obtain the necessary data, dual penetrations must be made between pre- and postsynaptic neurons that have been previously identified. There are only a few laboratories in the world able to perform this feat routinely (and unfortunately Hoyle's is not one of them). There are two more requirements:

4. The neuronal and hormonal inputs to the pattern generating circuits must be located and characterized.

The inputs play a key role in interfacing the circuits to the environment, even in the case of fixed action patterns. For insects, many workers feel that some of the proprioceptive pathways may actually be part of the motor pattern generator. Because such inputs can easily be manipulated experimentally (being peripherally located), they are easier to deal with than premotor interneurons – the CNS largely remains a black box.

5. Finally, knowing all of the cells and circuits involved, it is still necessary to determine the algorithms that are used by the circuit in the production of behavior. This usually means the formulation of an experimentally testable hypothesis, and this can be even more difficult than unraveling the circuit.

While these practical problems might not be of interest to a deep thinker, the goals Hoyle hopes to achieve will be difficult to attain without considering them realistically, and this he has failed to do.

The example given in the target article, concerning the locust jump circuit, is among the best examples of what is possible with insects, but it should be pointed out that this is a relatively simple behavior compared with courtship and mating, for example, that all of the neurons and synapses involved have still not been identified, and that a description of how this circuit *actually works* is not available. A circuit is a necessary start – but it alone is not sufficient to explain a behavior.

If the complex circuits of insects are so refractive to thorough electrophysiological analysis, can the circuits of other invertebrates with less wonderful behaviors be of value to neuroethologists? Even if, by Hoyle's definition, some researchers are restricted from admission into the neuroethology club, I think the elucidation of how many motor circuits work might be at least of academic interest to some comparative neurobiologists. It will certainly be of value to vertebrate physiologists as model systems.

The motor patterns produced by the lobster stomatogastric ganglion drive the teeth and because the movements (unlike limbs) cannot be seen, Hoyle feels their study lies outside the scope of neuroethology. However, the neuromuscular apparatus and the observed motor patterns are in fact precisely identical to the systems and the behaviors that he has formally blessed. There is no a priori reason to think that the mechanisms underlying such varied motor patterns as snail feeding, leech heartbeat or *Tritonia* swimming may not share features common to cyclic motor patterns in insects. Evolution is probably more conservative than Hoyle would have us believe.

Then, what is the future of neuroethology, and who should bring this field to new shores? The discipline may constrict its horizons to meet Hoyle's restrictive requirements. I hope that it does not. I think its future lies not in exclusion but in diversity. I am seriously concerned that, without the insights gained from a wide spectrum of preparations that combine the best features of interesting and complex behaviors with experimental tractability, neuroethology may become a discipline which will not only have been born but will also have died in our lifetime.

Keep the scope of neuroethology broad

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The contributions of ethology to our understanding of the mechanisms of behavior are considerable, and it rightly belongs

among the disciplines that constitute the neurosciences. It can be distinguished from psychological approaches to behavior in general terms by its strong insistence upon studying the natural behaviors of animals in their normal environments. This reveals a more direct concern with evolution than is characteristic of psychology. Comparative psychology has at various times in its history professed to do the same, but it has frequently failed to work comfortably with either a broad spectrum of species or a biologically sound selection of behaviors to study. It has, however, participated in the long and rich conceptual development of psychology, which surpasses a narrowly defined ethology in the sophistication of its theoretical constructs. *Verhaltensphysiologie*, which is distinguished from comparative psychology by being truly comparative and concerned with natural behavior, has converged upon psychology in its theoretical constructs. This process of convergence has proceeded so far that the study of some topics, such as song learning in birds, requires the language of cognitive psychology to express some of its ideas.

In his article on the scope of neuroethology, my colleague, Professor Hoyle, argues that neuroethology should take a relatively narrow, although certainly highly focused, definition of itself. It is true that ethology can be distinguished from psychological approaches to behavior in specific terms by its concept of the fixed action pattern as the most basic, biologically relevant element of behavior. Because the fixed action pattern is a functional unit, representing an adaptive behavior that has emerged genetically and been shaped in evolutionary processes, it is a key concept for uniting understanding of internal and external causes of behavior. This concept is a significant achievement and represents an enduring contribution to the ideas of neurosciences. And, surely, no one can fault the assertion that one ought to study an organism's natural behaviors evoked under natural conditions.

The definition of neuroethology as the study of the neural mechanisms underlying the behaviors that constitute the science of ethology is also quite reasonable. The subject matter of ethology is, therefore, the issue at hand in attempting to delineate neuroethology from other components of the neurosciences. These points are nicely made by Hoyle in his target article. The article seems, however, self-defeating in its attempt to chart a future course for neuroethologists. The source of this difficulty appears to be the inconsistency between a narrow and restrictive identification of the subject matter of ethology and a broad and advanced identification of its goals.

For example, it is argued that current research on the neural mechanisms of bird song, visual pattern recognition in fish, visual orientation to prey in toads, and echolocation in bats really represent *Verhaltensphysiologie* rather than neuroethology. The study of jumping and flying in grasshoppers is neuroethology, however. The approach, which has worked so well in determining how the nervous system of a locust controls walking or flying, consists of specifying at each stage (or cell) in the process exactly what happens during execution of the fixed action pattern. This amounts to measuring the transfer functions of the components and integrating them to then describe how the system they compose actually works. This is entirely appropriate, but it is unlike the practices of scientists who have so far contributed the most to developing theories of information processing in the nervous system. Such theories have emerged most frequently from the study of higher-order behavioral phenomena and have represented an attempt to extract some principles of brain function from sophisticated relationships between stimuli and responses.

The most interesting models of information processing in the brain come primarily from psychology, where the most sophisticated stimulus-response relationships have historically been addressed. Examples include the electric-field model of the brain, which emerged from Gestalt psychology; the sensory-quality models specific to vision and hearing which emerged from psychophysics; and the extraordinary theory of Hebb

(1949), which emerged from a variety of psychological themes, including the work of Lashley (1929), the observations of clinical neurophysiology, and research on perceptual development. These theories all result from taking the intellectual risks that are a big part of the business of science – attempting to describe the mechanisms underlying phenomena before it becomes technically feasible to think of describing these mechanisms from direct, unambiguous measurements. Great though the achievements of modern neuroscientists may be in measuring such things as the response properties of sensory neurons and piecing together the neural representation of stimulus features, the concepts corresponding to feature detection and stimulus processing may have been more difficult to come by in the beginning, when they were deduced from psychophysical data. Which is the greater intellectual step: discovering that the properties of perception require the brain to exhibit interactive properties such as can be modeled as electric fields, or carrying out very difficult measurements to demonstrate such interactions in neural responses? I do not know the answer to this kind of question.

I think that it is preferable to live with the manifest plurality of interests within, and overlap among, the disciplines that study behavior and the nervous system. It may be less tidy than being able to specify without ambiguity the content of ethology, comparative psychology, and *Verhaltensphysiologie*. It is true that working out the neural mechanisms of behavior will demand discipline and dedication to the task, but these qualities are not absent from what has already been done. The kinds of ideas driving ethology, psychology, and *Verhaltensphysiologie* are too similar, and the concepts these disciplines create are too much alike to consider them as parallel and independent activities.

As a footnote to the proposed exclusion of research on echolocation in bats from neuroethology, I am reliably informed that Karl von Frisch once expressed regret that he had not discovered and studied it.

The proper domain of neuroethology

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I am in agreement with Hoyle's general sentiments about the present standing and future prospects of neuroethology. I, too, have been puzzled by the liberal (mis)application of the term "neuroethology" to seemingly random (from an ethologist's viewpoint) pieces of neuro- or behavioral physiology, and I am disappointed by how relatively little attention is given (especially in higher vertebrates) to the neural bases of FAPs and related phenomena. I suspect that a major reason for this inattention to ethological concepts as theoretical guides in physiological work is that concepts like the FAP have largely fallen into disrepute (especially in America) as useful explanatory constructs for the behavior of higher vertebrates (e.g., primates). (Witness the heated reaction to sociobiology in America!) Along with Hoyle, I maintain that such concepts are appropriate in the neurophysiological analysis of complex behaviors in all vertebrate orders, including primates, and I will provide some relevant examples from areas that Hoyle, unfortunately, considers as lying outside the proper domain of neuroethology.

Hoyle draws the boundaries of the discipline rather sharply, dismissing in a few sentences the entire fields of development, neuroendocrinology, and neuropharmacology as not having any valid intellectual subdivisional status. It seems to me that neuroethology overlaps significantly with all of these fields insofar as they contain specialists interested in understanding "the generation of particular kinds of complex behavior." There

has been a thrust in recent years to elucidate the neural-developmental bases of species-typical behaviors (including such phenomena as imprinting) in a variety of vertebrate species (e.g., Gottlieb 1973; 1976). This work has proved extremely valuable in clarifying the role of experience in the development of species-typical behaviors. Admittedly, this work has not (to my knowledge) led to the identification of neural circuitry responsible for the execution of FAPs, but it should nonetheless be encouraged, as it will continue to bring improved clarity to these widely used and much misunderstood key ethological concepts.

One particular area of neuroembryology that holds much promise for contributing to neuroethology is fetal neurosurgery. The work by Taub (1977) stands as a particularly compelling demonstration of the existence of FAPs (or something very close to them) in a higher primate species: Complete unilateral forelimb deafferentation (by dorsal rhizotomy) in fetal rhesus monkeys at the end of the second trimester does not impair use of the deafferented limb in the complex, coordinated movements of ambulation and reaching at 3 to 5 months of age. Similarly, bilateral forelimb deafferentation at birth leaves intact spontaneous motor responses like walking, running, climbing, and reaching, even after blindfolding. These data strongly suggest that motor programs may be "hardwired" into the primate CNS before birth. Without this type of developmental analysis, however, there would be no point in exploring the primate brain for the location of innate motor programs for complex behavior.

Certain work by reproductive neuroendocrinologists (much of which includes neuropharmacology) also fully qualifies as neuroethology (in the sense defined by Hoyle). What springs to mind is work on the role of gonadal hormones in motivation and sensory-motor function. Pfaff's recent monograph (1980) details the neural circuitry and hormonal basis of the female rat's lordosis response and makes explicit how this behavior pattern fits the classic ethological model of FAP, IRM, and (some will shudder) even Lorenz's hydraulic model of motivation. In brief, the lordosis response of the estrous rat has all the features of the classic FAP, being highly stereotyped, species-typical in form, and released by highly specific stimuli (i. e., localized cutaneous pressure). The release of this pattern is dependent upon the action of estrogen (which is the motivational variable) on specific hypothalamic nuclei, which in turn provide a descending influence on brainstem and spinal cord such that in the presence of cutaneous pressure on the female's posterior, lordosis behavior will occur.

I think this neuroendocrinological approach to the physiological basis of motivation underlying species-typical behavior patterns holds great promise also for species with complex nervous systems, including primates. Aspects of the neuroendocrine system (e.g., steroid uptake sites) and neurochemical projection systems show substantial conservatism among the major groups of vertebrates, which may indicate commonalities in the physiological mechanisms of motivation. The estrogen facilitation of central neuronal responsiveness to regional cutaneous pressure described by Pfaff (1980) for the female rat has, for example, also been described for female squirrel monkeys, who like the rat (but unlike higher primates) have sharply circumscribed estrous cycles (Rose & Michael 1978).

The specific motor and sensory effects produced by electrical stimulation of the cat hypothalamus or midbrain in the context of predatory attack (Flynn, Vanegas, Foote & Edwards 1970, for review), appear fundamentally similar to the steroidal influence on neural tissue described above. Stimulation facilitates local reflexes (e.g., head orientation, biting, pawing) that are incorporated into the species-typical predatory motor pattern. A type of sensory biasing appears to be responsible, so that, under brain stimulation, visual field responsiveness to moving objects is enhanced – Flynn et al. (1970) suggest this is mediated by direct hypothalamic influence on visual cortex cell activity – and

peripheral sensory fields are enlarged, making tactile stimuli applied to the muzzle, for example, effective in eliciting head orientation and mouth opening. Such changes in sensitivity to sensory stimuli can also be produced by amygdaloid stimulation (Block, Siegel & Edinger 1980): Depending on electrode location, sensory fields of the cat's lip can be either expanded or constricted and attack facilitated or suppressed, respectively. Finally, gonadal steroids have been shown to affect brain stimulation – elicited attack behavior in both cats (Inselman-Temkin & Flynn 1973) and rhesus monkeys (Perachio 1978). It seems entirely appropriate that one of the earlier uses of the term “neuroethology” was by two Swiss investigators in describing their work on brain stimulation – evoked attack in the cat (Brown & Hunsperger 1963).

Since gonadal hormones have been shown to have significant effects on the processing of stimuli by the CNS in both man and other animals (Candelman 1983, for review), it seems probable that some of the physiological mechanisms of motivation described above are common to man and other animals. It is conceivable, for example, that basic emotions selectively bias attention toward salient sensory stimuli, such that the latter serve to “release” prepotent motor responses. Furthermore, such sensory biasing mechanisms could have an evolved basis (or innate components, as is likely in the decoding of primate facial expression, Sackett, 1966), and hence be proper targets for ethological study.

Substantial progress has been made in recent years in elucidating the neural bases of (visual) attention mechanisms in the primate brain (e.g., Lynch 1980), including the demonstration of direct hypothalamic connections with neocortical sensory areas (Mesulam, Mufson, Levey & Wainer 1983); and proposals have been made about the role of opiate systems in sensory stimulus filtering (Lewis, Mishkin, Bragin, Brown, Pert & Pert 1981). All of these findings have direct relevance for a neuroethology of large-brained mammals, but I suspect that it will take some convincing for neuroscientists to accept traditional ethological concepts as appropriate for the analysis of higher mammalian behavior patterns.

Ethology and neuroethology: Easy accessibility has been and still is important

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Hoyle has presented a clear and interesting vision of neuroethology. Several of his assumptions, however, undermine the ambitious program for “budding neuroethologists” that he lays out. Particularly troublesome is the assumption that only those categories of behavior and those species that have been studied by the classical ethologists are worthy of neuroethological analysis. This assumption is combined with a hasty dismissal of the large amount of work on *Aplysia*, which “has been dictated solely by the easy accessibility of its . . . cells.” I think there is an interesting irony here. It is true that the *Aplysia* nervous system permits extensive access to various identified neurons with well-defined functions, and that this easy access has encouraged the neurobiological study of *Aplysia*. Although I am not an ethologist, it seems to me that easy accessibility was as important for the classical ethologists in their selection of species and behaviors for study as it has been for cellular neurobiologists. The ethologists have been primarily interested in incorporating behavior into the framework of zoology and evolutionary biology (e.g., Lorenz 1950; Manning 1972; Tinbergen 1951). I submit that they selected species and behaviors for study, not because each was “of sufficient complexity to excite . . . serious interest,” or “goal-directed,” or likely to be

amenable to neurophysiological analysis, but because some animals and behaviors allowed relatively efficient collection of data appropriate to the particular scientific questions the ethologists were asking. These questions appear to have revolved largely around the role of behavior in evolution. Thus “species-specific” behaviors, such as mating rituals (which lent themselves to analysis of behavioral homologies), were of more evolutionary interest than behaviors, such as flexion reflexes, locomotion, or scratching, that appear identical across many species. Stereotyped, all-or-none behaviors were useful because they simplified quantification and optimized observability. The species selected were almost always easily accessible for naturalistic observation. As bird watchers, butterfly collectors, and naturalists well know, colorful, diurnal, flying animals with dramatic behavioral displays (i.e., many birds and insects) are easy for people to observe in the wild. That does not mean that these same species and behaviors are also optimal for neuroethology, nor does it mean that ethology should restrict itself to the convenient classical preparations. As modern ethologists have extended their studies to less theatric behaviors and animals, they have found that restrictive definitions of ethological terms such as fixed action pattern, releaser, and consummatory act have limited applicability in many situations (Hinde 1970). Moreover, these definitions are really of less importance than the larger goals of ethology, which are to understand the biological adaptiveness of behavior and its role in evolution (Lorenz 1958).

Hoyle seems to have overlooked the zoological and evolutionary heart of ethology in his prescription for neuroethology. Instead, he offers a set of goals that fits better into other areas of neurobiology: motor control and pattern generation, sensory and perceptual physiology, learning and memory. These areas of neuroscience are defined by functional questions, not by a priori definitions of innate fixed action patterns or by simple reference to the supposed tastes of the field's pioneers. If there is to be a science of neuroethology distinct from the rest of neurobiology, it must first identify the central goals (rather than the methods and prejudices) of ethology that will benefit from neuronal analysis. I submit that these goals should not be directly concerned with the physiological mechanisms of behavior (which are the province of neurophysiologists and neuropsychologists), but instead with the complex interactions among evolution, the nervous system, and behavior. Such goals might concern the processes by which the nervous system provides adaptation to an animal's niche; the neural substrates by which phylogeny, ontogeny, and learning interact to produce adaptive behavior; and the sites of neural change underlying changes in behavior during speciation. Having set general goals, the neuroethologist then selects the preparations that promise “easy accessibility” to the specific questions asked in order to move toward each goal. Preparations that are practical for the combined analysis of genetic, developmental, and cell biological correlates of behavior should be especially useful for neuroethology, and I agree with Hoyle that insects are attractive for certain neuroethological questions.

However, different neuroethological questions will lend themselves to different preparations, and it seems premature to discard most of the animal kingdom in favor of anybody's “optimal” neuroethological preparation. Despite Hoyle's suggestion that “no principles of integrative or intrinsic neural functioning” have come from *Aplysia* (which seems strange in view of his other statement, “Much of our knowledge of basic cellular neuronal properties has been derived from *Aplysia*”), a variety of general principles of neural function related to the scope of neuroethology have come from *Aplysia* and other gastropods. My pet example is activity-dependent neuromodulation, which was first discovered in *Aplysia* in its tail sensory neurons (Walters & Byrne 1983) and shortly afterward in the siphon sensory neurons (Hawkins, Abrams, Carew & Kandel 1983). This mechanism allows the selective addressing

of hormones or neurotransmitters to functionally active cells, providing a mechanism for associative learning and offering the possibility that similar addressing of trophic signals occurs during development. Activity-dependent neuromodulation may be quite general, having also been found in the crayfish (Breen & Atwood 1983); suggestions of it have been reported in the mammalian brain as well (Woody, Swartz & Gruen 1978).

Although (as I have defined neuroethology) few neuroethological questions have been addressed directly in the easily accessible gastropod nervous system, the gastropods seem well suited to a neural examination of at least one of the ethological questions that most occupied Lorenz, that of the relationship between innate and learned adaptation to the environment, sometimes viewed as the “nature–nurture” controversy (Lorenz 1965). The fact that gastropods show fixed action patterns that can be regulated by associative learning (e.g., Walters, Carew & Kandel 1981), as well as surprisingly complex forms of classical conditioning (Sahley, Rudy & Gelperin 1981), and memories that can last for weeks or months (Croll & Chase 1977; Pinsker, Hening, Carew & Kandel 1973) augurs well for the possibility of obtaining insights on the cellular level into the processes by which learning interacts with instinct. In addition, the gastropods provide easy accessibility for the zoological, developmental, and genetic investigations (Kandel 1979; Kriegstein 1977; McAllister, Scheller, Kandel & Axel 1983) that will be necessary for securing answers to this and other general neuroethological questions.

Is neuroethology wise?

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I cannot help continuing to feel out of sympathy with the attempt to construct a distinct science of neuroethology. I agree with the need to correlate studies of natural behaviour with their neural backgrounds. It is clearly valuable to recognise sub-routines such as fixed action patterns (FAPs). But what is gained by making a special science of this study and isolating it from other studies of behaviour? In particular, it seems most unwise to concentrate so much on the inherited component of behaviour. Hoyle himself seems confused about this. His definition of primary targets for neuroethology deals with “instinctive acts.” But by the second paragraph of “Is a general theory of neural circuit function possible,” “memory” is the first of his possible neuroscience clusters. Presumably, this is not to be part of neuroethology, since memory is not instinctive.

Another danger in isolating the study of FAPs is that it obscures the need for the study of coding. Hoyle rightly castigates those who limit themselves to small parts of the nervous system and regrets the lack of a general framework to replace the “McCulloch–Pitts (1943) binomial model.” Surely this lack is due to overattention to *simple* systems in which the coding problem seems soluble. He rightly says that we need attention to the *difficult* problems of complex systems. Yet the program of neuroethology concentrates on simple problems almost by definition. He puts “in-depth analyses of the neural machinery producing FAPs” as his first priority.

A further worry about neuroethology is that it has encouraged people to work only with animals that have large cells that allow intracellular recording. The really deep problems are in the systems with small cells; if they cannot be analysed by way of electrodes, we must find other methods. In fact, each animal and group of workers contributes differently. Hoyle ridicules *Aplysia* as a “glob of squishy protoplasm,” but, with it, Kandel (1976) has taught us the only hard facts we know about memory, because of one *small* cell in it. Now we need the study of *many*

small cells in a truly “higher invertebrate,” which I could easily suggest.

Surely we study simple systems for two reasons: (1) because they are important in themselves, for example, in insects, and/or (2) because they help us to understand the nervous system and behaviour. For this latter purpose, neuroethology has presented us with some fine analytical tools, especially fixed action patterns and releasers. But its more general theoretical models, such as action specific energy, seem to me to obscure the problem and hinder proper analysis. Hoyle’s criticism of “reflex physiology” and the rest seems old-fashioned when experimenters like Mountcastle and Zeki, theoreticians like Marr, surgeons like Ojemann, and psychologists like Weiskrantz and Milner are greatly advancing our knowledge of the difficult problems of the nervous system. Unfortunately, most zoologists pay no attention to such people. They would do better to heed them and stop criticising poor old Sherrington and Pavlov, who did well enough in their day. I fear that emphasis on “neuroethology” will further isolate zoologists, which would be a pity.

Hoyle himself has done splendid work on memory, which seems to me to contradict the whole tenor of his target article here.

Author’s Response

Neuroethology: To be, or not to be?

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First, I should like to thank all of the commentators for taking the time to read my article and to prepare such an interesting array of commentaries, not forgetting the several persons whose commentaries were received late and are not included here for lack of time and space. Perhaps I shall have the opportunity to reply to you in Continuing Commentary. I feel greatly honored by the interest of so many distinguished scholars in my (as several of you wrote) “idiosyncratic musings.” My only comfort in the face of this presumed criticism is that this expression would apparently have been equally applicable to others among you, had you been the author. I am grateful that the titles of only two of the commentaries included the inevitable reference to the best-known bearer of the family name!

It does not surprise me that very few of you are empathic with my specific proposals. Some of you, like one of my ex-Ph.D. students, **Macmillan**, a major mentor, **Young**, and **Erber**, detect “contradictoriness, inconsistency and dissonance.” Perhaps this apparent fickleness is inevitable when one is groping for articles of faith: I would truly like to be a disciple of a coherent discipline of neuroethology. The commentaries made it clear that it is at best going to be much more difficult than I had thought for us to achieve a consensus as to the kinds of studies to be incorporated under the rubric neuroethology. **Clarac** addressed the intrinsic difficulties of making neuroethological studies no matter how we define them, while **Young** believes it unwise even to consider the use of this designation as a subdivision of neuroscience.

The most commonly expressed objection to my proposals was a desire to remain free to adopt any connotation now, or at any time in the future. **Bullock** aptly expressed this view with his “don’t fence me in” title. However, neither **Bullock’s** arguments nor those of the others expressing this viewpoint, notably **Bässler**, **Davis**, **Ewert**, **Steklis**, **Simmons**, and even **Huber** (who, like myself, works on insects and is also now pushing for identified neuron work) have persuaded me away from my premise, that restriction is necessary. I willingly concede that my own definitions and list of goals are open to criticism. If there were a consensus as to what we should do in the name of neuroethology I should be glad to conform and either follow or alternatively adopt the label of whatever branch of neurobiology you assign to me. **Bässler** suggests *Sensomotorik*, but while this expression is true of what most of us do in practice, the missing element is clearly the dedication to behavior. I want a close relation to the search for, and the understanding of, *general principles* (always assuming there indeed are any) underlying the neural *generation* of behaviors. It is apparent that you all share my unease with the situation in which we currently find ourselves, in identifying the subject matter of neuroethology, whatever your individual bias, in both research and in teaching. Some of you are content to let matters drift for the time being, as though they will sort themselves out quite naturally, with time. Of course, I strongly dislike this viewpoint, as my target article emphasized, perhaps because time is running out.

To **Young** I assert that since the term *neuroethology* is now the title of four books, albeit each with very different contents, it is unlikely to fade away. Incidentally, the newest to arrive on the scene (**Camhi** 1984) provides another difficult pill to swallow. Expressly avoiding the desperately needed “broad, comprehensive treatment covering a great many of the animals that have been studied” (from the Preface), **Camhi** provides us with a largely elementary introduction to neurobiology as a whole, rather than a well-defined subdivision. The intrinsic paradoxes of attempting to define neuroethology and to prepare experimental protocols arising out of the definition were addressed by several of you, perhaps most eloquently by **Bateson**. Although I took a strong stance, which was at least in part based upon personal conviction, admittedly biased, and of the die-hard variety, I hoped to provoke you into suggesting alternatives, one or another of which might become widely accepted. This was my principal disappointment with the commentaries. Although most of you grumbled about my specific proposals, none of you presented comprehensive alternatives.

Erber objects to my lack of details on the hypothetical “comparator” and “computer” elements of the updated hydraulic model I proposed in Figure 4 of the target article, for which several of you expressed dislike. Of course, nobody knows what the elements might be, but the terms have been used quite frequently in recent years by neural theorists, so there seemed no need to explain them. My intention was to draw attention to the urgency for experimental neuroethologists to be aware of the need to provide some substantive locales for these processes in the simpler invertebrates which possess them. If any sets of neurons serving these functions can be found, studying

how they work would become a major research target for neuroethologists. **Erber** refers to the new hydraulic model of **Lorenz** (1981), which is reproduced here in Figure 1. **Lorenz** chastises himself in his new book, *The Foundations of Ethology*, for not having realized that his early model (Figure 3 of the target article) had what he chooses to call a major deficiency – the model misleadingly implied a qualitative difference between events that fill the tank with “energy,” and those that release the behavior, when they in fact “differ only in quantity.” I found this “confession” and “correction” quite sad, because the old model closely depicts the situation for some behaviors with which I have worked whereas the new one does not. The new **Lorenz** model is a throwback to the dark ages of total reflexology! If we have found anything at all that is truly worthwhile in the name of neuroethology it is that there are many behaviors for which the readiness to execute a particular behavior is determined by endogenous mechanisms that are totally independent of particular kinds of sensory input or even, perhaps, any input at all.

Lorenz reiterates that “some sort of motor excitability accumulates while a motor pattern is not performed and then used up by its performance” (p. 286). He also states emphatically that “the concept of a specific quantity of excitability obviously corresponds to a physiological reality” (**Lorenz** 1981, p. 122). With both of these statements I agree, except that, as **Lorenz** himself points out elsewhere in his book, the first would have been more inclusive had it read: “some sort of motor excitability accumulates in *some* behaviors when motor patterns are not performed and then used up by their performance.”

Lorenz avoided stating what he thought might be the neural substrate of action-specific energy (which he now prefers to call action specific potential, ASP), although hinting at the involvement of neuroactive substance(s).

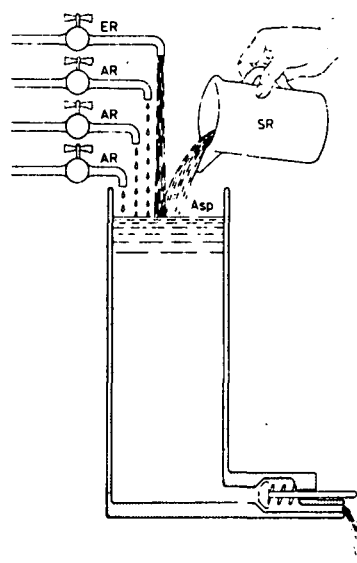


Figure 1. **Lorenz’s** (1981) revised version of his classic hydraulic model (see Figure 3 of the target article). **ASP** represents Action Specific Energy, **ER** an endogenous readiness agent, **AR** accessory readiness agents, and **SR** the releasing stimulus. In the earlier model **SR** was depicted as weights added to a scale pan attached via a pulley wheel to the stop at the base of the tank. From **Lorenz** (1981); reprinted by permission of the publisher.

The gradual accumulation of ASP from the constant dripping of the endogenous source is readily associated with a gradual build-up of a neuromodulator in appropriate neurons, as outlined in my own orchestration hypothesis. When a behavior is released, the appropriate cluster of modulator neurons is excited. Their stores of modulator substance are depleted as the behavior, which they help to generate, unfolds.

The emergence of the new model from Lorenz further emphasizes my key point, which is that the core of neuroethology should be to examine the model in relation to a variety of behaviors, from diverse phyla, in depth, by way of cellular neurophysiological analysis.

In his new account, Lorenz has made another shift in position which I consider to be a serious error from the point of view of neuroethology. He has chosen to substitute the expression fixed motor pattern (FMP) for fixed action pattern (FAP). This is most unfortunate, because the former expression begs an important question. In the parlance of (Hoylean) neuroethology, a FMP means that the CNS produces a motor output that is tightly controlled in regard to the numbers and timing of motor impulses. Highly stereotypic outputs are known, for example, in cricket songs, as demonstrated first by Ewing and Hoyle (1965), and then very beautifully developed using genetic procedures by Bentley and Hoy (1974). An even more remarkable example of stereotypy occurs during courtship behavior of the tiny male grasshopper *Gomphocerippus rufus* and its relatives, reviewed by Elsner and Popov (1978). These studies have shown that a nervous system can produce stereotyped motor output accurate to the level of a single nerve impulse, with ± 1 millisecond accuracy in timing. Such sequences are true FMPs; some are produced in the absence of any external stimulus, others only when a specific *single* releaser (sight of female) is present.

Fixed action pattern (FAP) is the appropriate general term because, for a majority of stereotyped movements, even in insects, the underlying motor patterns (which is to say, the electrical activity in the motor neurons causing the movements) are *not fixed* even though the movements (actions) are. In 1954–55, I recorded the electromyograms of several thousand visually identical, stepping movements from locusts induced to march under laboratory conditions (Hoyle 1957). Off and on since then I have repeated this work and have recorded from walking insects of other species also. The almost incredible fact is that no two out of the thousands of EMGs recorded – these indicate the motor patterns causing limb movements, which even high-speed cinematography shows to be identical in space and time – have exactly similar underlying motor patterns. There are periods when only intrinsic muscle tonus, a very significant but totally neglected factor, together with inertial and gravitational forces, are the only antagonist to phasic agonistic action (Hoyle, 1984). At other times there is constant-frequency antagonist excitation, requiring much more powerful agonist excitation to achieve the same movement (Figure 2). At yet other times, perfect reciprocity of antagonists, with no overlap, occurs, or there can be extensive overlap.

The point is that the movements can be “fixed” even though the motor output is anything but fixed. These experiences led me to propose (Hoyle 1964) that in many

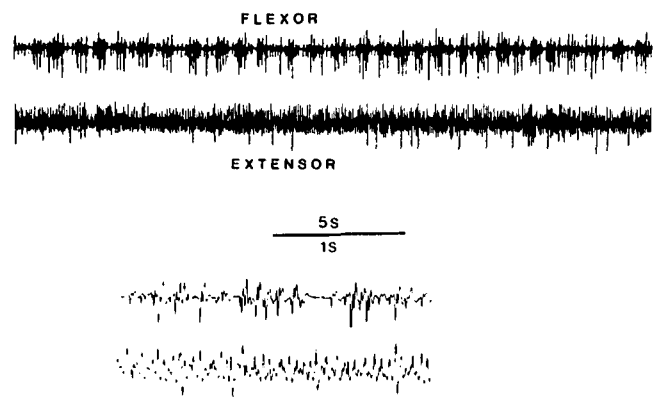


Figure 2. Electromyographic activity in the antagonist muscles causing alternating flexion and extension of a locust hindleg extensor tibia, during a bout of rhythmic stepping at a mean frequency of 1.2 per second. The flexion movements were caused by bursts of impulses in a complex of three intermediate flexor and three fast flexor motor neurons. The individual contributions of these neurons were different for each flexion. Extension was produced during each waning of flexor activity, because the slow extensor motor neuron SETi fired throughout at a nearly constant frequency averaging 19 Hz. Thirty stepping movements are included in the record shown (top traces – excerpt at higher speed below), each of which was visually identical. From Sombati and Hoyle, unpublished.

FAPs the motor program must be guided by a CNS store of sensory information. This I termed a “sensory tape” mode of operation, the information content being equivalent to a score, consisting of the appropriate sequences of sensory inputs associated with the movements to be programmed. The store of information is conceptually equivalent to musical notation. Neuroscientists often think of musical notes as motor instructions, which they are not. They are no more than sensory guidelines, indicating what has to be achieved by an independent comparator with computer feedback and a motor output device.

In presenting his new hydraulic model Lorenz presciently foresaw my own version of his model when he wrote, “The simulation could be brought closer to the real physiological process by adding a few gadgets.” In my model, replete with gadgets, and in the text, I also placed a high priority on understanding the locations and natures of stored information, whether inherited or acquired, and how such data are addressed and fed into the nervous system as needed. This has been attacked by Bateson as being both naive and irrelevant. It is indeed possible that there is no separate section of a nervous system which is, as it were, set aside specifically to take care of these functions, and that they are distributed among the entire neuron population. Yet Young approached the *Octopus* nervous system as though it were compartmentalized and found that this was indeed the case. We need comparable studies on other organisms. If equivalent data were available for an invertebrate with complex behavior, yet a nervous system well described at the identified neuron level, then I believe we could, for the first time, get an in-depth grasp of how nervous systems produce complex behavior.

Fernald and Ingle both accuse me of being unaware of the elegant work of fellow Oregonian Bell, on “efference

copy" in weakly electric fish (Bell 1981). I am sure, however, that Bell would be the first to come to my rescue, since he knows that I admire his work, and likewise that of **Bullock's** associates on these fish. Bell provided incontrovertible but indirect evidence in a vertebrate for the existence of an efference copy of motor output (to the weak electric organ). Many years earlier I showed that a locust ganglion must keep an efference copy of any significant trends that occur in mean frequency of its tonic motor output (Hoyle 1965). If such shifts in frequency are consistently correlated with aversive inputs, then an adaptive process is set in motion, which reverses the trends. One of my pleas in the current target article was for work to be attempted on the physical location and *cellular nature* of efference copies, a matter which Bell has not addressed, and about which nothing is known. Knowing the physiology of efference copies is profoundly important for understanding the neural details of behavior generation.

To **Rowell** I should like to say that I was a close personal friend of Wiersma from 1955 until his death; I worked with him at Caltech in 1956–57, and as Rowell knows, since he was there, I organized a Wiersma *festschrift*, which was published in 1977. I am certain that Wiersma enjoyed as great an intellectual intimacy and empathy with me as with any other scientist. He greatly influenced my thinking, but there was also a lot of intellectual traffic in the other direction. I am the last person in the world who would willfully denigrate Wiersma's pioneering efforts. However, I am certain that at no time did he ever think along the same lines I have, or published concerning the neural bases of behavior. Incidentally, he was as dismayed as I have been at the frequent misuse of his concept of "command" interneurons. [See Kupfermann & Weiss: "The Command Neuron Concept" *BBS* 1(1) 1978.]

Ewert accuses me of missing out on comparative aspects, but I should like to remind him that I have published neuroethological data on sixteen species, from six different phyla. However, while I greatly enjoy the diversity, it has given me less than I had hoped for in the way of worthwhile insights into what I really want to know about how nervous systems work, because so much is always unknown. It will be essential for many investigators to stick with related aspects of one species for a very long time if the requisite depth of information is to be attained. Of course, that which is indeed general *must* be extracted after making comparisons, as I have often emphasized. A major "message" of my target article is that many of those collecting data in the name of neuroethology are not yet even trying to collect the most needed data, because they do not adequately focus their efforts on core problems. The vertebrate neuroethologists among you acknowledge that they are concentrating on sensory aspects because of technical difficulties in bridging the all-important gap to the CNS integrating regions, with their memory stores, comparators, and computers.

In a positive vein, may I say that I appreciated the wisdom offered by **Steklis**, **Walters**, and my colleague, **Simmons**. You have tempered my steel! I am more than grateful to **Manning**, **Grossberg**, **Huber** and especially **Markl** for the much needed kind remarks interspersed among their legitimate criticisms. Even in Science an

ounce of praise sometimes produces more useful activity than a ton of kicks!

In reply to **Guthrie's** inquiry regarding the orchestration hypothesis, we are working intensively on this, and its consequences, in the locust, and we have had some very exciting results, but we are a long way from being able to present a complete picture for any single behavior. One of the orchestrated behaviors we are studying is flight (see commentary of **Rowell**). In the locust, to our knowledge, there are only two substances which mediate the orchestration of metathoracic ganglion behaviors: octopamine and proctolin. There are about 90 octopaminergic neurons and only a few that are proctolinergic, so octopamine is by far the more important. Vertebrates have a whole pharmacopoeia of modulators. I do not consider that a modulator substance corresponds to a section of a "tape." Each modulator is discretely released at from one to several highly localized sites, in a precisely timed sequence, by from one to several modulator neurons. These events in totality represent the tape playback. A single synchronous burst of excitation of a subcluster of modulator neurons, whether using the same or different substances, elicits the equivalent of a single tape section. Where the store of information is located that permits control of the activity of the modulator neurons seems likely to become a key question for neuroethology.

What may I say in attempting to annul the bad taste I consciously courted by my acrid remarks concerning the future of vertebrate neuroethology? **Ehret** tells me, simply and clearly, how I could have modified the target article so as to make it widely acceptable, which of course I should have liked, but only up to a point. The worldwide ratio of neuroscientists working on vertebrates to those working on invertebrates is greater than 30:1. The size of the splash made by invertebrate neuroscientists in the last decade is out of all proportion to the share of the total funds made over to them, and is a real tribute to both the accessibility of identifiable neurons in some invertebrates and the strategies adopted for exploiting them. **Young**, and indeed some other commentators, too, associate neuroethology largely or exclusively with invertebrates because of this. I'm sorry that after devoting a lifetime of unparalleled, superb work on cephalopod brains, which are the most advanced physically among invertebrates, **Young's** efforts are not being rewarded in the form of any cellular-level progress made with them.

The principal reason for adopting the position I did regarding vertebrate studies is that the more one knows about what it is that has to be known before one can satisfactorily describe how a behavior is generated and controlled, the more the focus becomes cellular. Diagrams such as that of **Weiss** (1950) (Figure 2 of the target article), which was adopted by **Baerends** (1976) and included by **Lorenz** in his new book, may be conceptually expressive. But they are meaningless in terms of neural anatomy and physiology while implying the contrary. In the long run there can be no substitute for knowledge of the properties of individual neurons, their connections and interactions and modulations thereof, which are active in behavior. None of these can be second-guessed, but must be determined directly. Furthermore, while we may find it useful to build tentative models on the basis of early findings even in systems with few neurons, we must

insist that no neuronal “stone” remain unturned. In the latest appraisal of functioning of the 30-neuron lobster stomatogastric ganglion, no fewer than 5 different modulators, dopamine, NA, 5-HT, and two peptides, have become implicated (Eisen & Marder, in preparation). All early models are currently being overthrown in light of findings about the actions of neuromodulators. Someday, a better understanding of the contributions of intracellular rather than extracellular information transfer is likely to have even more profound effects on our thinking.

Ingle, and others of you who work on vertebrates cannot expect any sympathy from me! There may be a case for associating neuroethology specifically with invertebrates, but for the converse exclusivity, as expounded in the recently published book, *Advances in Vertebrate Neuroethology* (Ewert, Capranica & Ingle 1983), I can find no justification. There are marked differences in neuronal organization, of course, between vertebrates as a whole and any single invertebrate phylum. The almost universal tendency to lump invertebrates together is biologically absurd. There are greater differences between molluscs and arthropods than there are between arthropods and vertebrates, because molluscs lack a skeleton and jointed legs. The range of neural organizations seen within a single phylum, especially the molluscs, which is the most diverse of all, is vast. But in the matter of the principles of behavior generation, which I maintain is the major objective of neuroethology, who among you expects major differences to be found? Once again I reiterate that we should focus on possible common principles.

Our endeavor, almost unique in biology today, has the opportunity to benefit from a genuinely comparative approach, which I do indeed favor strongly. This should not be seen as yet another dissonance on my part. In-depth studies on vertebrate neurobiology are going to continue no matter what. It is support for the invertebrate studies that needs understanding and sympathy because it will always be fragile and vulnerable and can so easily suffer from neglect in the future. Even if studies on invertebrates do continue to prosper, unless there is intellectual reciprocity, both between those who study them, interphyletically, within invertebrates, and between each of these persons and the majority, who are studying vertebrates, we shall never have a true science of neuroethology.

Curiously, some of the greatest discord is to be seen among those who work exclusively on a single invertebrate species. Each waves the flag of chauvinism, espousing some “unique advantage,” but actually trying to draw attention to his or her own work. To a large extent it relates to the demeaning practice of being required to “justify” the expenditure of money on basic research.

A major secondary consideration in this regard is laziness. It is easiest to avoid burdening our overloaded brains with the work of others, concentrating instead on “getting results” and “getting them published.” When the work of others directly relates to our own because it is on the same part of the same species, we must pay attention. But otherwise? We are producers, but where are the consumers? The only possible consumers are ourselves; we should all consume a lot more than we do currently if we are to survive.

Of longest acquaintance, and a most trusted friend is

Manning, who pointed out that perhaps you need to understand the sociology of the dominant Viking element in northern England in order to appreciate a target article written by one of them! Yet at the north-country grammar school which most shaped my character, almost the first lesson was that we should follow Socratic principles: Dialectic was said to be the essential basis for any intellectual endeavor! When my first debate teacher, a very tall Scotsman named Murdoch, with bright blue eyes and a shock of red hair, first addressed me, he said: “Young Hoyle, you’re enthusiastic about the time-honored sport of fox hunting, are you not?” “Oh no, sir,” I pleaded passionately, “I believe it to be cruel, beastly, socially irresponsible, and in every way obnoxious!” “Splendid,” he retorted, “for next week’s debate you will be the proposer of the motion *that this house strongly favors the perpetuation of fox hunting.*” Trying desperately hard, at a tender age, to understand the other person’s point of view and defending it in public debate with a professional advocate’s urgent desire to win as a matter of principle (we lost) was an invaluable lesson for life. No wonder I am an ardent supporter of *BBS*.

So I especially thank those of you from whom I learned a new viewpoint: **Arbib**, **Bateson**, and **Grossberg**. You are absolutely right about our exclusivity and lack of cross-fertilization. I have started to immerse myself in your lists of references, insofar as these are available to me. You may be surprised at how few are to be found in the library of the university where I work, a major, state-supported university no less. This is an important point: The serious theoretical work in neuroscience, which I strongly advocate in my target article, must be published in *commonly available journals of neuroscience*, not hidden in “U. Mass. Technical Reports,” “Air Force Office of Scientific Research Reports,” and obscure books which impoverished university libraries cannot afford to purchase.

We certainly need to get together more, and often. A splendid beginning was made more than two decades ago in the symposium, which I was fortunate enough to attend, held at Ojai, California, in 1962, which led to the book edited by the late Reiss entitled *Neural Theory and Modelling*. Some of the papers published in this pioneering blend of theoretical and experimental approaches are still referred to quite often today. But where are the sequels that might have kept this early interdisciplinary endeavor up-to-date? Theorizing is not an aspect which has stood still; it is contact with the rapidly advancing knowledge of nerve cells and circuits – especially motor circuits – which has lagged. At this point I should like to defend my not paying much attention to the work of von Holst. In part this was because of the direction his work has taken, as exemplified by his student, colleague and successor at Seewiesen, Mittelstaedt, who has, with others, made theorizing about neural function in behavior an end in itself. This activity is doomed to sterility unless it can be linked to identified neurons. It has fostered a specific subdiscipline boasting two journals, *Kybernetik* and *Biological Cybernetics*. I shudder when I think back on the time I have spent struggling through the often mathematically difficult papers in these journals in search of illusive enlightenment.

One can but marvel at the versatility of Poggio and his associations with the late, prophetic David Marr, on the

one hand, and Reichardt, on the other. The latest paper by these authors (Reichardt, Poggio, & Hansen 1983) is tantalizingly subtitled "towards the neural circuitry" (of the flight control of a fly by visual input). May I live to see the day when these worthy theoreticians guide a capillary electrode into a neuron! They will certainly be welcome additions to the inner core of neuroethologists.

Similar thoughts go out to Hampson and Kibler (1983) in their efforts to establish a Boolean neural model of adaptive behavior; likewise to Pellionisz and Llinas (1979), Morasso (1981), and now even the psychologist Fentress (1981), in their very different approaches to the question of recognizing that behavior is a three-dimensional movement domain. It would be of no value to imply, given the minuscule amount we currently know about nervous systems, that strictly artificial intelligence research is outside the range of neuroethology. Few of us have failed to be impressed or even influenced by Minsky and Papert's (1969) classic book on perceptrons, or Klopff's recent *The Hedonistic Neuron* (Klopff 1982), which shows that at least some theoreticians know and relate to some cellular neuroscience.

Some of you, notably **Hinde, Manning, Schleidt, and Fernald**, protest that I have not kept up with the progress in ethology. This is doubtless true, and perhaps I misread the various articles recommended to me by way of catching up, including those in the series *Perspectives in Ethology* edited by Bateson and Klopffer. Or it may be that I was unable to tear my mind away from early ethological imprintings. It seemed to me that recommended articles were providing evasions, circumlocutions, apologies, and reinterpretations of the most diffuse kind. They did not replace old concepts with new ones: The basics clearly remain the same. If there are no hard-core general principles underlying behaviors, then the party is over: There can indeed be no neuroethology, at least not a worthwhile intellectual endeavor demanding serious effort. However, I was not convinced of this by what I read. I believe that the program for neuroethology which I propose in my target article has the merit that at least it would help to settle the question of whether or not there are common principles of behavior, which cannot be resolved by strictly behavioral research. Disciplined neuroethology would be of inestimable help to ethologists in the long run. Because of the constraints dictated by neural functions it would clarify the nature of the different kinds of behaviors studied by ethologists, and promote rational classification.

To the highly perceptive **Markl**, and also to **Delcomyn** and **Bateson**, go my special commendations for, as it were, seeing through me. The article was indeed a kind of sermon. This field needs a new kind of funding: assured basic funding for long periods, preferably measured in terms of a human working lifetime.

To those of you who have worked intensively on a ganglion selected entirely for its manipulative convenience, specifically **Kupfermann, Leonard & Lukowiak** for the *Aplysia* visceral ganglion, and **Selverston** for the stomatogastric of spiny lobsters, may I say only "please render unto Caesar . . ." I greatly admire your beautiful work, which I always read carefully, and I do listen to your sessions at meetings of the Society for Neuroscience, as you surely know. What is available in the catalogue of cellular and synaptic mechanisms and modes of hooking up of neurons is potentially core material for neu-

roethology. However, I note that these sessions tend to be dedicated to "transmitters," "synaptic transmission," and "circuitry." Also, you show a preference for the *Journal of Neurophysiology* as a publication outlet. As I see it, your goals seem to have been primarily toward exposing cellular events as ends in themselves: Where is the dedication to understanding the broad principles of behavior? Where are the comparisons and discussion of the relevance of your findings to those of others working on different phyla? Admittedly, there is a seductive cellular trap (and a comfortable one, because considered significant), that I also fall into, as I pointed out in the target article. When I was preaching in the target article, it was as much at myself as at any of you.

The plea is for us to recognize the possibility of a subdivision of inquiry that is more than something thrown in as an afterthought, as so often appears to be the case with our existing neuroethology. The objectives of neuroethological research should be clearly stated and relentlessly pursued, in animals selected for their relevance, not the convenience of some small part of their nervous system. The "behavior" of *Aplysia* has been concocted by neurophysiologists, not, as **Leonard & Lukowiak** point out, by ethologists. The latter are not about to switch to studying *Aplysia*, and elevation of the movements performed by this mollusc to the presumed status of serious ethological interest, if done solely by the neurophysiologists themselves, is not likely to cut any ice.

My final specific reply is reserved for ethologist **Bateson**. Yes, I am truly willing to let ethologists be the pipers and call the tunes. But in exchange, they must read the work of neuroethologists closely, understand the capabilities and limitations neurophysiologists face technically, and be willing to focus their own attention on behaviors of neurophysiologically tractable animals.

I am ready to take seriously any model which treats nervous systems as devices for the intrinsic generation of behavior as their primary purpose. Inputs which promote general or specific behaviors, or which modify ongoing behavior, or which are anticipated and incorporated into the generation of specific behaviors, are superimposed upon an intrinsic capability. We must reject all models (they are the majority) that treat nervous systems as if they were input/output devices.

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