well differentiated in this species. It is to Ewert's everlasting credit that he recognized early the importance and potential of the model and that he has devoted his life to it. No other vertebrate model system that involves the entire sensory-to-motor continuum has been so well described. It is clear that the monumental work of Ewert and his collaborators represents the foundation for the detailed, exciting work that lies ahead.

The future will no doubt include defining the detailed synaptic relationships and functions of all neuronal types involved in prey-catching as well as the ontogenetic development of structures and behavior. Comparative studies on other species will provide further important clues about structure-function relationships. In order to better understand Ewert's work, it is perhaps meaningful to identify some specific aspects in the future development of Ewert's prey-catching model.

There is a tendency to associate specific neuronal aggregates with specific functions because of the behaviors elicited by electrical stimulation or the deficits observed after selective lesions. Ewert has provided us with clues about the roles of various brain structures on that basis, but he has also shown that given aggregates are involved in many functions through their interaction. Thus, prolonged electrical stimulation of the pretectum (posterior thalamus) [close to the rostral tectum] results in a broad range of behavioral responses, ranging from escape behavior to orienting and snapping. The potential variables responsible for such responses are too complex to be dealt with here; suffice it to say that the circuitry of the region stimulated is very complex indeed. In fact, the details of bypassing and afferent and efferent connections are essentially unknown. A detailed Golgi-EM study of the region would provide some of the requisite information about how synapses from various sources are related to one another on a given neuron, and which effects are caused by unrelated responses from the inadvertent modulation of bypassing fibers.

Ewert's interesting finding that pretectal lesions result in indiscriminate (often inappropriate) responses to visual stimuli suggests to him that the toad with such a lesion suffers from a visual agnosia. This is in line with the interpretation that the pretectum in toads serves an associative function and has an integral part in the analysis of visual images. The region contains essential elements for certain "discrimination filters." In fact, the high degree of differentiation of the region is thought to be related to the functions of the T5(1) and T5(2) cells in the optic tectum (Ewert 1984b). The answer to the question of how the associations are accomplished eludes us; clearly the next generation of experiments should include a precise analysis of excitatory-inhibitory interactions of inputs to the relevant neurons with a concomitant structural analysis of the circuitry of any given neuron so that the interactions of all circuits in the function can be understood. This analysis would include: (1) identification, at the ultrastructural level, of the sources of all inputs on a given neuron; (2) identification of the neurotransmitters of the various inputs; and (3) the precise localization of the projections of the pretectal neuron. This is a tall order indeed, but because of the relatively high degree of parcellation of cell groups in the toad pretectum, the task should be much easier in this species than in others.

It is important to understand that in the target article Ewert deals primarily with prey-catching in adult toads and only secondarily with the apparent similarities in other vertebrates. Space obviously will not permit further description of the ontogenetic development or the interspecific variability of the components of prey-catching. It should be stressed that the pertinent neural mechanisms do change in both the ontogenetic and evolutionary time domain. Ewert (1984b) has himself provided evidence for the parcellation theory (Ebbesson 1980; 1981; 1984; in press). This theory predicts that parcellation of brain nuclei and specialization of neurons is accomplished by restricting the types of afferents to given neurons in evolution and ontogeny. This results in finer tuning of a given function and

explains, for example, how "discrimination filters" are added between sensory input and motor output and how more and better quality filters would result in a more appropriate behavior in response to a given stimulus.

A comparison of the thalamotectal circuitry in anurans and urodeles reveals distinct differences in which the urodele configuration appears as the less parcellated one with only a single identifiable cell group (lateral posterocentral nucleus, PC) in the caudal dorsal thalamus. It is interesting that only T5(1)-type neurons have been recorded from the fire salamander's optic tectum (Finkenstädt & Ewert 1983a). In contrast, this cell group is represented in adult anurans by two parcellated nuclei (posterolateral nucleus, PL, and lateral posterocentral nucleus, LPC) which in turn determine the property of configurationally sensitive tectal T5(1) neurons and configurationally selective T5(2) neurons by selective inhibition. Class T5(1) and T5(2) cells may, in conjunction with inputs from other cell classes (Tx), activate motor pattern generators for different types of behavior. It is especially noteworthy that the ontogenetic parcellation of LPC and PL from a single nucleus is completed 6–12 months following metamorphosis. This parcellation may be related to the remarkable improvement in configurational prey-selection after metamorphosis, the final acuity of which is not reached until one year after metamorphosis (Ewert, Capranica & Ingle 1983). Thus, during ontogeny the thalamic-pretectal region of frogs and toads transiently exhibits a functional organization similar to the one primitive amphibians such as urodeles show as adults.

Surely a research program to study the ontogeny of prey-catching behavior in relation to changes in its structural and physiological substrates will be very important not only in studying how T5(2) cells develop, but in trying to understand neuronal plasticity in general.

Although Ewert's analysis of prey-catching is thorough, it is wonderful to realize that much remains to be done. I venture to say that many more types of neurons and interactions are responsible for a given behavior than Ewert's circuit diagrams suggest. As Ewert has pointed out, determinants of behavior are not only the direct visual circuitry, but also the neuronal activity of superimposing systems such as those relating to nutrition, hormone levels, circadian rhythms, and so on.

Because of my belief in the great value of a detailed and comprehensive characterization of synapses and circuits, I was delighted to see the beautiful cobalt-stained tectal neurons from which Ewert et al. (1985) and Matsumoto et al. (1986) have recorded (Figure 18). Such studies reveal aspects of the complexity of neuronal circuits. For example, when one considers the location and dendritic spread of the stained tectal neurons in relation to (1) the physiological properties and location of retinal afferents (Ebbesson 1970; Lettvin et al. 1959), (2) the variety and distribution of terminal types on the given neurons (Ito et al. 1980; Lázár 1984), and (3) the origin and distribution of the terminals on a given neuron (Ito et al. 1980), it is clear that Ewert and his collaborators have many wonderful years ahead for refining their knowledge and insights. Considering that ultrastructural studies are needed for each type of neuron involved in the circuitry, one realizes the enormity of the task that lies ahead. The value of Ewert's contribution is in the soundness of the foundation he has laid and in his ability to stir the imagination of others to continue the building and refining of a truly worthwhile model.

Networks with evolutionary potential

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It is fascinating to see a state-of-the-art neuroethological analysis of an instinct (an innately goal-directed behavior) that describes

the encoding of a hierarchical chain of fixed action patterns in a nonhierarchical way in overlapping neuronal circuits and loop-controlled networks in the toad's brain. The release of pertinent adaptive behavior by key stimuli depends on the spatiotemporal activity patterns in neuronal networks that share many elements. There is obviously no single class of neurons that could be related to "making a decision" about which behavior to display or which stimulus to recognize because the behavior to be produced – which is interpreted as "recognition" by a human observer – is the result of the probability distribution of activity in several neuronal elements of differing specificity. The concept of "grandmother neurons" has been abandoned. Thus, the demonstration of network function in prey-catching of toads is of general significance and may reflect principles of economy and safety of information processing and response release in the vertebrate brain. But to what extent can prey-catching in toads and the proposed neural circuits serve as a general model for the release of instinctive behavior in vertebrates?

1. It is well known that instinctive behavior occurs in decerebrated cats if the diencephalon and lower centers of the brain are left intact (e.g., Gallistel 1980). This corresponds favorably with the present data on toads, which do not indicate contributions of cerebral telencephalic structures to prey-catching.

2. The superior colliculus, which is the mammalian homologue of the optic tectum, is regarded as a sensorimotor interface which translates sensory information into motor commands that compensate mainly for space-related errors in the motor system relative to the goals to be achieved by the action (e.g., Sparks 1986). The same idea is reflected in Ewert's "command releasing systems" with T5(2) neurons as links to motor nuclei. The superior colliculus, however, is known as a substrate for multimodal sensory integration (e.g., Meredity & Stein 1986), which does not seem to be true for the optic tectum in toads. The question arises whether auditory and somatosensory aspects of visual stimuli representing prey, predators, or mates converge on circuits shown in Figures 22–25; or could multimodality of the tectum (superior colliculus) be an evolutionarily new achievement common to mammals yet absent in amphibians? [See also Foreman & Stevens: "Relationships Between the Superior Colliculus and Hippocampus" *BBS* 10(1) 1987.]

3. It is especially interesting that arousal, attention motivation, and associative learning are suggested to influence prey-catching networks in the toad's tectum, and how they do so. Attention and arousal have been shown to alter neural activities in the auditory midbrain of rats (e.g., Disterhoft & Stuart 1977; Gonzalez-Lima & Scheich 1984). These mammalian data correspond well with attentional effects on tectal T5(2) neurons so that prey detection is enhanced by a higher level of activity in prey-selective neurons due to attentional factors. The introduction of attention into tectal circuits may be described by a network model proposed by Fukushima (1986) who suggests that attention has facilitating effects on the afferent visual pathway and that visual afferents gate the attentional influence at the same time.

Motivation and associative learning are a different subject, however. Sensory-motivational integration as well as associative learning in mammals are assigned to neural networks and functions of the forebrain (e.g., Thompson et al. 1978; Thompson 1980). While tecto-prosencephalic loops are included as sources of modulatory effects on prey-catching in Ewert's analysis (Figure 24), sensory-motivational interfacing and associative learning seem to take place in the tectum itself – at least they are introduced to the prey-catching circuits via T5(2) neurons. Thus these neurons function as sensory-motivational and associative interfaces. It is surprising to find neurons with such highly integrative properties in the tectum and not in the forebrain. Could it be that the prey selectivity of T5(2) neurons does not arise in the tectum itself but through forebrain loops indicated in Figure 24? And could it hence be that T5(2) neurons become tectal relays of a descending command releas-

ing system for prey-catching whose major components, however, the ones that generate prey selectivity, are located in the forebrain? The function of T5(2) neurons as output cells of a forebrain-tectal loop would be to contribute to the occurrence of taxis components of the instinctive prey-catching pattern (orientation, approach, fixation as in Ewert's original schema). The association of spatial attributes in the optic tectum to key-stimulus information descending from the forebrain would be in formal agreement with the initiation of saccadic eye movements for fixation of an interesting stimulus by mammals (e.g., Sparks 1986). If integration of sensory, motor, motivational, and associative aspects of instinctive behavior should actually take place in the optic tectum of amphibians, however, this would point to an important evolutionary perspective. It might indicate that during the evolution from amphibians to mammals object recognition and spatial localization have separated from a common tectal origin in amphibians to forebrain (motivational and learning-related aspects) and midbrain (spatial localization) mechanisms in mammals.

Ethological invariants: Boxes, rubber bands, and biological processes

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The search for invariants that account for the processes of behavioral change represents one of the most fundamental conceptual problems in the behavioral and brain sciences. Classically, ethologists have approached this problem through the construction of basically static conceptual boxes that were in turn connected with fixed arrows. "Fixed action patterns," "innate releasing mechanisms," central versus peripheral mechanisms, and genes versus experience are obvious examples. Connecting boxes with arrows can be very useful as an initial heuristic, but the tradition can also get in the way of more refined analyses. Boxes become things, things become centers, centers become inherited, and so on.

The difficult issue to come to grips with is that when these "boxes" are interconnected they may change one another's properties. Actions can become coarticulated, mechanisms can be modulated, central processes can influence peripheral processes (as well as the reverse), and gene products depend upon developmental contexts. The buffers that define our distinctions are often relative rather than all-or-none, and they can change over time when placed in different contexts, and so on. This gives the investigator a framework rather like interconnected rubber bands that pull on one another, thereby distorting each other's properties. Rubber band models are difficult to work with!

But they may give a hint. The hint is in the invariance of relations as opposed to individual properties. One can add a dynamic to this without destroying the idea of invariance simply by studying invariances in rules of change (in relations) over time, and so on (Bohm 1969). Stabilities become relative, relational, dynamic, and multileveled (Fentress 1986).

There is something frustrating about such notions, for the closer we look for invariances, the more slippery they often appear. So we go back to boxes. I recall that when my late friend, Graham Hoyle, was preparing his *BBS* article on neuroethology with an invertebrate focus, plus his subsequent response to commentators (Hoyle 1984), he and I were at odds about this form of boxology. The result was that I became transformed from an ethologist in his target article to a psychologist in his response to critics; this was not, I believe, intended as a compliment! Yet Hoyle himself had many years before provided one of my favorite examples of the point I wish to make. When