

Neuroethology of releasing mechanisms: Prey-catching in toads

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Abstract: “Sign stimuli” elicit specific patterns of behavior when an organism’s motivation is appropriate. In the toad, visually released prey-catching involves orienting toward the prey, approaching, fixating, and snapping. For these action patterns to be selected and released, the prey must be recognized and localized in space. Toads discriminate prey from nonprey by certain spatiotemporal stimulus features. The stimulus-response relations are mediated by innate releasing mechanisms (RMs) with recognition properties partly modifiable by experience. Striato-pretecto-tectal connectivity determines the RM’s recognition and localization properties, whereas medial pallio-thalamo-tectal circuitry makes the system sensitive to changes in internal state and to prior history of exposure to stimuli. RMs encode the diverse stimulus conditions referring to the same prey object through different combinations of “specialized” tectal neurons, involving cells selectively tuned to prey features. The prey-selective neurons express the outcome of information processing in functional units consisting of interconnected cells. Excitatory and inhibitory interactions among feature-sensitive tectal and pretectal neurons specify the perceptual operations involved in distinguishing the prey from its background, selecting its features, and discriminating it from predators. Other connections indicate stimulus location. The results of these analyses are transmitted by specialized neurons projecting from the tectum to bulbar/spinal motor systems, providing a sensorimotor interface. Specific combinations of such projective neurons – mediating feature- and space-related messages – form “command releasing systems” that activate corresponding motor pattern generators for appropriate prey-catching action patterns.

Keywords: action patterns; command systems; connectionist networks; feature analysis; neuroethology; neuromodulation; prey capture; releasing mechanisms; sensorimotor interface; sign stimuli; toad; vision

1. Introduction

1.1. Topic

Animals see things and can then respond on the basis of what they see. What neural operations connect a particular visual stimulus to a corresponding action pattern? For the past 20 years my coworkers and I have investigated neuroethologically the visual cues and releasing mechanisms involved in prey-catching by toads (for a review see Ewert 1984a). The present target article integrates a body of behavioral and neurobiological data in an attempt to understand the neuronal basis of prey recognition. This work has yielded some interesting insights into more general questions concerning sign stimuli, feature detection, releasing mechanisms and command functions, and their dynamic properties.

In ethological terms, stimuli are referred to as “sign stimuli” (see Appendix) if they consistently release specific patterns of behavioral responses whenever the motivation of the animal is appropriate. These stimulus-behavior relations are mediated by releasing mechanisms (RMs) whose recognition properties are largely innate, but can be partially modified by experience (Schleidt 1962). The concept of “innate releasing mechanism” was introduced by Lorenz (1935; 1943) and Tinbergen (1948; 1951) to describe the input/output characteristics of a

“black box” that performs specific sensory analysis and triggers a corresponding motor program as a function of prior phylogenetic adaptation to predictable, behaviorally meaningful stimulus situations. Investigating the neurophysiological bases of sensorimotor transformations in such specialized systems has a variety of advantages (e.g., Bullock 1983; Capranica & Moffat 1983; Ewert 1974; 1985; Heiligenberg 1983; Huber 1983; Suga 1984). Amphibians are especially appropriate experimental animals for the following reasons: (1) Toads and frogs have a limited behavioral repertoire that includes fixed action patterns; (2) in response to relatively simple sign stimuli, toads and frogs consistently exhibit predictable behaviors whenever their motivation is appropriate; (3) stimulus-response relationships can be analyzed quantitatively by changing certain stimulus parameters in simulated natural objects or dummies, thereby identifying effective features; (4) toad and frog neuroanatomy are reasonably well understood (e.g., Kicliter & Ebbesson 1976; Lázár 1984; Neary & Northcutt 1983; Wilczynski & Northcutt 1983a; 1983b); this is a prerequisite for neurobiological recording, labeling, stimulation, and lesion experiments.

The visually released prey-catching behavior of toads (Eibl-Eibesfeldt 1951; Ewert 1968; 1984a; Ingle 1968; 1983a; Schneider 1954) is particularly suitable for a neuroethological analysis of sensorimotor function (see Ap-

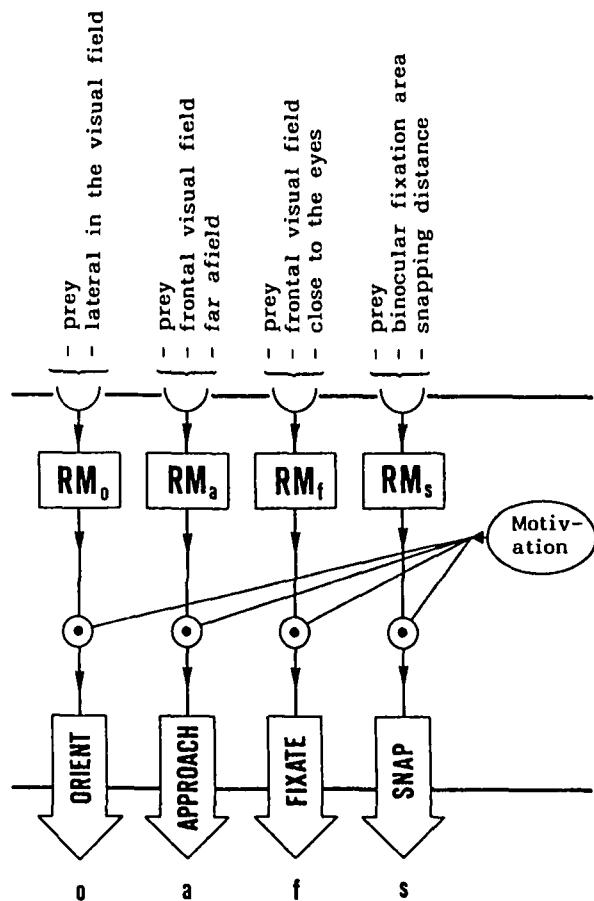


Figure 1. Upper, photo: Toad *Bufo bufo spinosus* in its natural environment fixating an earthworm (photo by H. Burghagen). Lower, diagram: Releasing conditions for prey-catching action patterns; depending on prey and its location in visual space, the various action patterns orienting (*o*), approaching (*a*), fixating (*f*), and snapping (*s*) are activated by appropriate releasing mechanisms (RMs). (Simple flow chart according to a scheme by B. Hassenstein in Czihak et al. 1981.)

pendix). Toads respond to prey with distinct behavioral patterns – orienting *o*, approaching *a*, fixating *f*, and snapping *s*, – which often yield a sequence *o,a,f,s* (Figure 1). Prey-catching thus calls for certain perceptual operations by the RMs concerned with stimulus recognition, stimulus localization, and sensorimotor transformations. The investigation of such mechanisms touches on questions of general significance not only to neuroethologists but also to scientists working in neighboring fields such as ethology, psychology, neurophysiology, and systems neuroscience.

Controversy surrounds terms such as feature detection and command function. Apart from semantic problems (arising because we lack clear definitions), discussion is often too theoretical, sometimes philosophical and even emotion-laden, not taking experimental findings suffi-

ciently into account. In the present article, I hope that such problems will be minimized by the presentation of a reasonable amount of experimental detail to support and motivate the concepts (although this has unfortunately made the paper somewhat long).

1.2. Questions

We note that behavioral sequences are often hierarchically organized (Tinbergen 1951). We must accordingly test whether during prey-catching one particular action must first be accomplished before another can begin. Is such an action necessary and/or sufficient to trigger a subsequent response? Or does the release of each action pattern depend on the ongoing stimulus situation, drawing on operations related to both stimulus

recognition and stimulus localization? The answers to these questions are important for an understanding of the prey recognition system.

Given that the visual environment of the toad is structured, the basic question arises as to how signals (prey) are distinguished from noise (background). What are the releasing (visual) features of prey? Is there in the visual domain a unique prey sign stimulus, or do the features that release prey-catching consist of a certain range within a stimulus continuum?

We must ask whether the perceptual operations required for prey selection are performed by a "feature detector" (Figure 2A), which has often been proposed as a necessary component of innate RMs (for a discussion see Capranica 1983; Scheich 1983), or by a "feature-analyzing network" (Figure 2B). The feature-detector approach (e.g., Hubel & Wiesel 1962; 1965; Konorski 1967) usually postulates distinct "hierarchical" feature-extracting processes: The higher the level of convergence on feature-sensitive neurons (Figure 2A), the higher the degree of feature selectivity. At one extreme, highly selective gnostic neurons (say, a "grandmother cell" in man's brain) would only respond if a complex signal occurred (say, a specific set of individual facial features). In such a system, information flow would be from a level of lesser selectivity to one of greater selectivity. The network-analyzer hypothesis, on the other hand, involves "parallel" information processing in a neuronal network: Here, an ensemble of different classes of interconnected feature-analyzing neurons would be responsible for the recognition of a visual object (Figure 2B). Unlike in a feature detection system, the feature-selective properties of neurons in such a network would be determined by mutual interactions. In addition, a class of neurons, through interconnections, could take part in different ensembles (Figure 2B), thus contributing to the recognition of different objects. Here, the same basic network, but with distinct spatiotemporal activity patterns, could take part in the analysis of different visual objects (e.g., Creutzfeldt in Szentagothai & Arbib 1974; Hebb 1949; 1959; John & Schwartz 1978; Mountcastle 1957). Network analysis raises the question of how the signal-related information is read in the brain, transferred to the appropriate motor

systems, and translated into a motor pattern. Finally, we will have occasion to ask whether the "detector" and "network-analyzer" concepts are mutually exclusive, or whether the (toad's) brain might be taking advantage of both parallel and hierarchical principles of information processing to recognize visual objects.

The question arises as to how RM circuitry mediating stimulus-response relations is influenced by modulatory circuits signalling attentional variables, motivational states, and learning (as defined by Kandel et al. 1979). In this context it is important to ask whether both circuits work independently (except at their point of convergence), or whether there is substantial overlap, so that certain neurons may be used for both mediation (coupling an appropriate behavioral response with a given stimulus) and modulation (influencing the mediation).

1.3. Approach

The research is multidisciplinary, from behavior to neuron, involving: (1) behavioral studies on innate and learned aspects of prey stimuli; (2) neurobiological investigations of brain structures and their interactions in prey-catching; (3) the evaluation of feature-analyzing and space-monitoring neurons as putative components of RMs; (4) the study of sensorimotor links between visual pattern analyzing and motor pattern generating systems; (5) the investigation of neural loops in the modulation of RMs as a function of attention, motivation, habituation, and learning.

We begin with a global black box study in a behavioral paradigm and then analyze functionally related brain structures and interacting subsystems down to single cell responses and underlying changes in membrane potential. We then propose a conceptual synthesis that leads to integrative and interacting functional units (cell assemblies) as putative components of cooperative (releasing) systems – the central core of the behavioral black box.

From a methodological point of view, the advantage of this approach is that a variety of questions (pertaining to feature analysis, sensorimotor access, modulatory function) are directed at the same subject (visually controlled prey-catching behavior in toads and frogs), so a uniform system can be described and understood without having to "fill gaps" by borrowing data from other domains. The multimethodological nature of the approach also elucidates various ethological, neurophysiological, and neuroanatomical aspects of one coherent functional framework and confirms that the same principles emerge with different experimental paradigms and techniques.

2. Behavioral sequence: Conditions of release

The four components of prey-catching behavior, *o,a,f*, and *s*, are activated by corresponding releasing mechanisms (RMs) that recognize prey and monitor its location in space.

2.1. Action patterns

Goal-directed behavior often consists of two components: the target-oriented appetitive response(s) and the consummatory act (Manning 1979; Tinbergen 1951). The former can vary in the shape and order of its constituents;

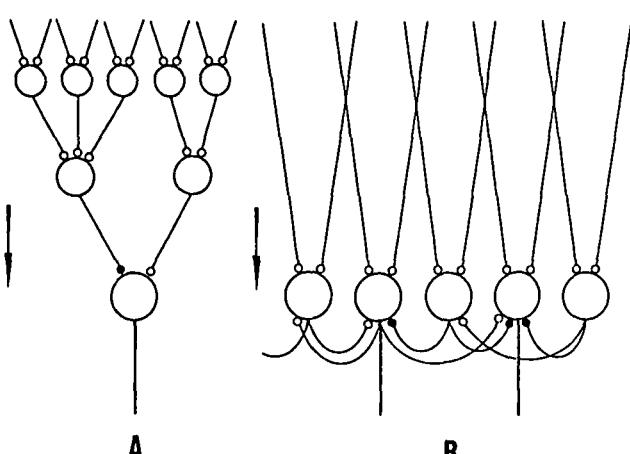


Figure 2. Neuronal wiring principles underlying a "feature detector" (A) and a "feature-analyzing network" (B). Smallest black and white circles represent different types of synapses, here arbitrarily chosen.

the latter is relatively rigid. Both depend on motivation. The toad's visually guided prey-catching behavior fits this description: orienting toward prey (*o*), approaching (*a*), and fixating (*f*) are directed appetitive behaviors, whereas snapping (*s*) is the consummatory act (Figure 1).

2.2. Releasing mechanisms

Postmetamorphic prey-naive common toads (the tadpoles are vegetarian) raised in the laboratory from the egg exhibit prey-catching patterns immediately after their transition to terrestrial life, although precise acts are subject to maturation (Ewert 1985; Traud 1983). The "standard" prey-catching sequence *o,a,f,s* can be regarded as a series of stimulus-response cycles (Figure 1). The components of prey-catching are activated by different RMs which use comparable prey recognition processes but are distinguishable by mechanisms that locate the visual stimulus in space (Ewert et al. 1983).

The notion that visual perception of "what" and "where" precedes prey-catching behavior in toads and frogs (Ewert 1974) has to be evaluated with reference to the ballistic, programmed character of the action patterns emphasized by various authors. Once triggered by an appropriate stimulus in the peripheral visual field, orienting toward the prey proceeds to completion – in conjunction with proprioceptive inputs (Comer et al. 1985) – without feedback from the target during the turning movement (Grobstein et al. 1983). Toads also program the route of the approach toward prey to some extent before they start to move (Collett 1983). If the prey disappears during a critical phase of fixation, toads snap accurately at the empty stimulus site (Hinsche 1935). It is noteworthy that the subsequent ingestive behavioral patterns (gulping and mouth wiping) also occur, despite the absence of the prey. This suggests that certain motor programs are somehow connected in the brain (Ewert 1967b). In this context it is important to note that frogs and toads also possess various "compound motor coordinations," for example, jumping/snapping. These too are ballistic, but may involve feedback-guided correctional maneuvers (Gans 1961).

2.3. What are the conditions of sequential release?

Hierarchical influences among releasing mechanisms or motor pattern generating structures (Baerends 1976; Tinbergen 1951) are not essential for the sequential activation of prey-catching patterns (Ewert et al. 1983). It is not the previous action, but the ongoing stimulus situation – "prey sign stimulus and its locus in space" – that determines the subsequent response. If the distance between prey and toad is short, prey-catching consists of *o,f,s*; if the prey suddenly appears close to the animal, only *o,s*, or *f,s*, or just *s* is elicited; if the prey flees, the toad's appetitive pursuit responses occur – depending on the prey's behavior – in variable succession, such as *o,o,o,a,o,a,f,a,f,f,o,f,s*; if, in an experimental paradigm (Ewert 1969a), a prey object is moved around the toad at a constant distance from the animal, then *o,o,o,o,o...* is the pattern. Studies in which frogs readily snap toward prey even though their orienting is blocked by selective transection of the tectospinal pathways show that orienting is not a prerequisite for eliciting snapping (Ingle 1983a; Kostyk & Grobstein

1982). All these experimental findings contradict Grüsser-Cornehls's (1984, p. 238) suggestion that the recognition of prey is the result of central processing in which the motor acts play an essential role.

The release of each action pattern *o,a,f*, or *s* requires the analysis of prey features (Ewert et al. 1983); the choice of action, that is, the capture "strategy," further requires the localization of the stimulus in the x-y-z coordinates of the visual field. This means that the RMs of prey-catching use the same recognition processes, but their localization mechanisms differ. Triggering a compound motor coordination also presupposes appropriate stimulus recognition and localization before the animal can start to respond.

These results imply that in a motivated (hungry) toad, orienting to and/or snapping at a visual object (during a given time interval) correlate with the degree of resemblance of that object to prey.

3. Sign stimuli: Configural properties

The ethological analysis of prey recognition is concerned with quantitative measurements of prey orienting (and/or snapping) in response to moving two-dimensional stimuli (dummies) with variable features. RMs distinguish prey from nonprey based on *configural* stimulus properties. "Configuration" is used to refer to a combination of stimulus features having certain specific internal relations: In the present case these internal relations are the spatial extents of a stimulus pattern parallel and perpendicular to its direction of movement. This perceptual ability is called "configural selectivity" (see Appendix).

3.1. Natural stimuli

Before we begin to analyze and describe features of visual prey quantitatively, some remarks on natural prey are necessary. Metamorphosed common toads are carnivorous.

From investigations of stomach contents it is known that anurans feed on earthworms, slugs, millipedes, beetles, and other small invertebrates (Porter 1972). All these have more or less elongated shapes and their longer body axis is oriented parallel to the direction of movement. Usually objects must be moving in order to be categorized as prey; a nonmoving retinal image fails to elicit a prey-catching response. In the analysis of prey recognition we will accordingly focus on moving stimuli that contrast with their background. We will ignore color, since common toads are active during twilight and nighttime.

3.2. Structured environment

The visual environment of the toad includes objects like leaves, branches, and stones, some of which are the size of prey. Why does the toad ignore any moving retinal image as potential prey when the source is a stationary structure in front of which he moves his head (which of course makes the retinal image move), as shown in Figure 3A or 3B? Two explanations come to mind: First, the many moving retinal images may suppress the capture response because of "surround inhibition" through inhibitory interactions among corresponding projection areas in a central visual map. Second, the brain of the moving

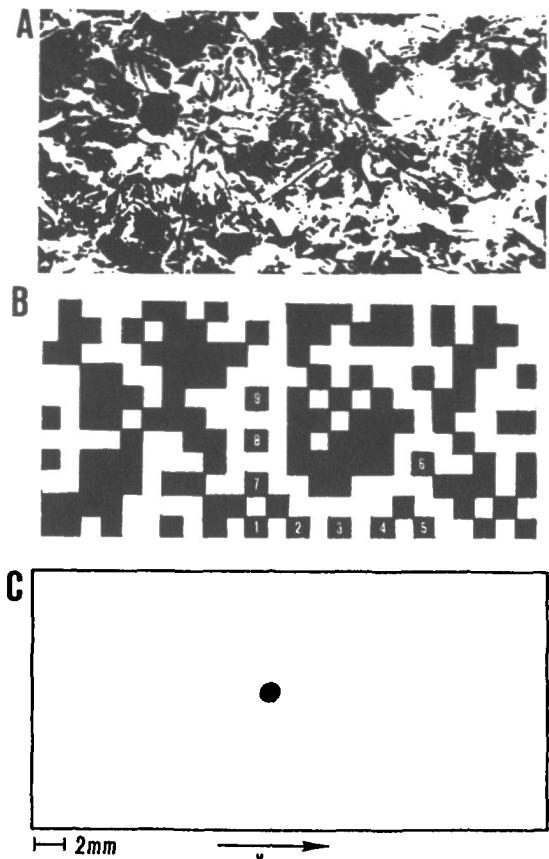


Figure 3. Visual environments: (A) ground in a forest; (B) artificial structure; (C) homogeneous white surface surrounding a small stationary black stimulus. Arrow indicates direction of movement of retinal image; for explanations see text.

toad may anticipate information about corresponding moving retinal images, which is cancelled by means of the "reafference principle" (von Holst & Mittelstaedt 1950) [See also Berkinblit et al.: "Adaptability of Innate Motor Patterns and Motor Control Mechanisms" *BBS* 9(4) 1986; Gyr et al.: "Motor-Sensory Feedback and Geometry of Visual Space" *BBS* 2(1) 1979; Roland: "Sensory Feedback to the Cerebral Cortex During Voluntary Movement in Man" *BBS* 1(1) 1978.] The observation that for a moving toad the self-induced motion of the retinal image of a single stationary stimulus against a contrasting homogeneous background (Figure 3C) readily elicits prey-catching (orienting and snapping) favors the inhibitory surround hypothesis (Burghagen & Ewert 1983; Frost 1982). The "swarm phenomenon" is an ethological example of inhibitory surround effects; a toad's prey-catching is generally inhibited when many simultaneously moving visual stimuli originate from the presence of multiple prey (Schneider 1954). This phenomenon has been investigated quantitatively with simulated prey (Ewert & Härter 1968; 1969). The inhibition of the toad's attack under these conditions is not necessarily caused by "interocular (intertectal) competition" or "confusion" owing to too many visual releasers. It has been demonstrated experimentally that a double stimulus (presented in the animal's monocular visual field) can be inhibitory even if one of the two stimuli is subliminal for the release of prey capture. Detailed quantitative experimental studies show that these inhibitory effects depend on the spatial arrange-

ment of images on the retina in relation to their direction of movement (Ewert et al. 1970). This effect may arise from certain properties of interacting central nervous processes. This leads to our "interaction concept."

3.3. Innate correspondence between stimulus features and releasing mechanism

3.3.1. The "interaction concept." Suppose a toad is sitting in front of the stationary structure shown in Figure 3B. How could a signal with the features of a prey object emerge? It must be different from the rest of the structure in certain spatiotemporal properties; if just one small stimulus object (S1) is moving, while all others are stationary, the toad responds with prey-catching. The probability of responding increases – within limits – with the number of such stimuli, provided they move at the same speed and are aligned parallel to the direction of horizontal movement at a short interstimulus distance: S1-S2-S3-S4-S5. But if two stimuli move simultaneously and are aligned perpendicular to the direction of movement (S1-S7), the toad's prey-catching activity level is lower than with a singly moving stimulus; it decreases further the greater the extent of the pattern perpendicular to the direction of movement: S1-S7-S8-S9. If a further stimulus (S6) is added to the optimal prey stimulus pattern S1-S2-S3-S4-S5 (Figure 3B), the entire configuration's capacity to release prey-catching is markedly reduced and may even become zero (for quantitative details, see Ewert et al. 1970; 1982).

Thus, to distinguish prey from nonprey, RMs may take advantage of certain interacting central processes: (1) Many simultaneously moving, randomly distributed retinal images of small visual objects have masking effects on the perception of a single image because of inhibitory interactions in the central visual system ("inhibitory surround"); (2) several small moving images aligned at small distances parallel to the direction of movement are interpreted as prey because of excitatory interactions in the visual system; (3) the arrangement of small images perpendicular to the direction of movement signals nonprey because of inhibitory interactions in the visual system. Property (1) allows toads to select prey from structured backgrounds and to discriminate object motion from self-induced motion. Properties (2) and (3), applying to patterned as well as to continuous shapes, determine the configural features of prey.

It is obviously the geometry of a visual pattern in relation to its direction of movement that plays a critical role in prey selection, as expressed by different levels of prey-catching activity. Systematically varying the area of a two-dimensional rectangular object in different transformation groups of a stimulus continuum (cf. Figures 4 and 5Aa-c) shows that the relationship between the edge lengths parallel [$xl(1)$] and perpendicular to [$xl(2)$] the direction of movement is critical (Ewert 1968; 1969a): Successively extending $xl(1)$ (for $xl(1) : xl(2) > 1$ and $xl(2) = \text{constant}$) increases the releasing value of prey (Figure 5Aa), whereas extending $xl(2)$ (for $xl(1) : xl(2) < 1$ and $xl(1) = \text{constant}$) progressively decreases this value (Figure 5Ab). In fact, the configural properties of a stimulus (expressed by the ratio of $xl(1) : xl(2)$) are more important than the area (expressed by $xl(1) \cdot xl(2)$) within a relatively wide range (Ewert 1968); for example, a $2 \times 20 \text{ mm}^2$ and

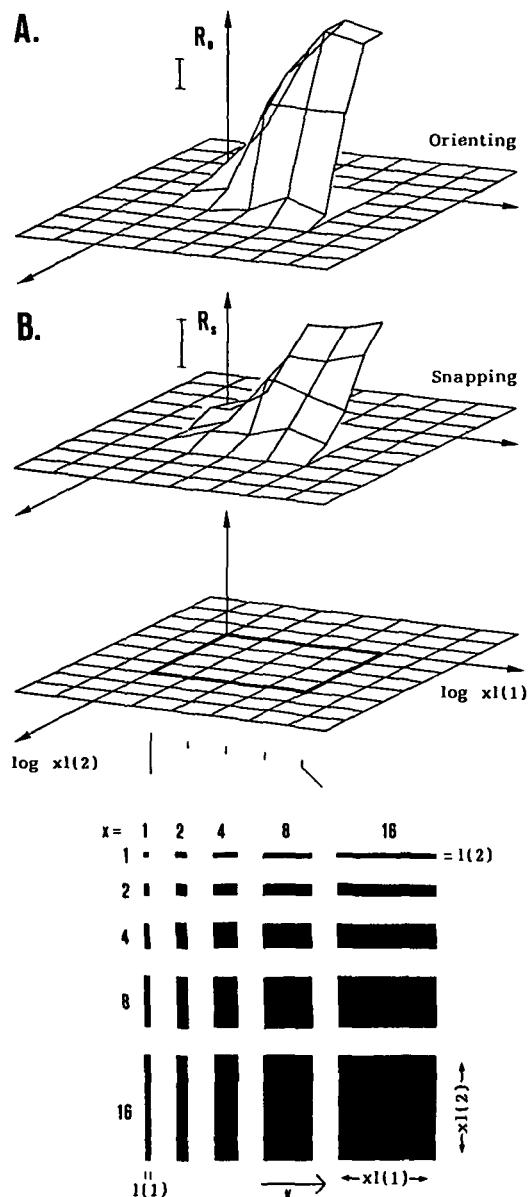


Figure 4. Experimental analysis of prey sign stimulus in the common toad *Bufo bufo*. Bottom: Range of a stimulus continuum of two-dimensional rectangular black objects (5 by 5), each moving against a white background at constant velocity of $v = 10^\circ/\text{sec}$; $xl(1)$ is the length of the edge oriented parallel to the direction of movement and $xl(2)$ that of the edge oriented perpendicularly; $l(1) = l(2) = 2.5\text{mm}$; magnification factors $x = 1, 2, 4, 8$, and 16; arrow indicates movement direction (see also Appendix Figure 27). Above: Corresponding grid consisting of a 5 by 5 array serving as a coordinate frame; the range of the stimulus continuum that contains the 25 objects shown below is surrounded by thick lines. (A) Orienting activity R_o in response to single stimulus objects as shown below; computer-processed data of Figure 5A; intermediate values are approximated. (B) Snapping activity R_s . Scales on the ordinate refer to 5 responses per 60 sec (R_o) or 30 sec (R_s). The distance between the stimulus and the toad's eyes was 70mm in (A) and 20mm in (B).

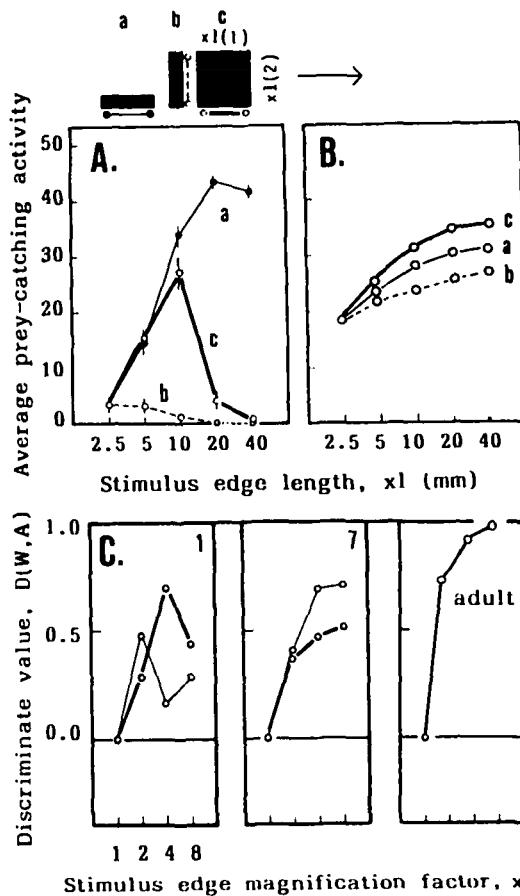


Figure 5. Prey-catching orienting activity of common toads in response to a black two-dimensional stimulus moving horizontally (see arrow) against a white background. During the experiment the toad sat in a cylindrical glass vessel; the stimulus object was moved mechanically around the vessel at a constant angular velocity (v) and constant distance (d). The toad's orienting activity (number of successive turning movements per time interval) correlates with the degree of resemblance of that object to prey (for details see Ewert 1969a; in this procedure, the subsequent action patterns of prey-catching usually failed to occur because of the lack of appropriate stimulus conditions according to Figure 1, provided that the distance, d , was relatively long). Stimulus objects with different configurational features were investigated: (a) Wormlike stripes of 2.5mm width whose longer axis $xl(1)$ is oriented parallel to the direction of movement and (b) antiwormlike stripes of 2.5mm width whose longer axis $xl(2)$ is oriented perpendicular to the direction of movement; the length $xl(1)$ and $xl(2)$ was variable, respectively; (c) squares of comparable edge length $xl(1,2)$; $l(1) = l(2) = 2.5\text{mm}$; $x = 1, 2, 4, 8$, and 16; $v = 10^\circ/\text{sec}$; $d = 70\text{mm}$. Average prey-catching orienting (turning) responses per time interval measured (A) in normal toads (from Ewert et al. 1983 according to corresponding results for $v = 23^\circ/\text{sec}$ after Ewert 1969a, see Appendix Figure 27) and (B) in toads following a pretectal lesion (from Ewert & von Wietersheim 1974b). (C) Maturation of worm(W)/antiworm(A) discrimination calculated by the discriminant values $D(W,A)$ in young postmetamorphic common toads during the first (1) and the seventh (7) day of their terrestrial life. Thick lines: animals were caught in a pond as they approached land; thin lines: control animals raised in the laboratory singly from eggs in a homogeneous white environment. These were not fed after metamorphosis. Test stimuli: stripes of 0.7 mm width and variable length xl for $l(1) = l(2) = 0.7\text{mm}$; $x = 1, 2, 4$, and 8; $d = 20\text{mm}$ (from Traud 1983).

an $8 \times 80 \text{ mm}^2$ black stripe have about the same releasing value for prey-catching, provided each one moves along its longer axis at a given speed.

However, if stimuli are "configuration neutral" in the present respect ($\text{xl}(1) : \text{xl}(2) = 1$), as with squares (Figure 5Ac) or disc-shaped objects of different sizes, prey-catching exhibits a nonlinear interaction between the influences of both configurational features $\text{xl}(1)$ and $\text{xl}(2)$. The area then becomes important for discriminating prey from nonprey, which requires estimating absolute size (Ewert & Gebauer 1973; Ingle 1968). When the area of such a moving object exceeds a critical range, it is categorized as a predator (Ewert & Rehn 1969).

3.3.2. The Gestalt approach. A simple way of fundamentally altering the "Gestalt" (configuration) of a visual stimulus (while preserving its shape and area) is to move a small $2.5 \times 30 \text{ mm}^2$ stripe either parallel or perpendicular to its longer axis (Ewert 1968). The two configurations have different releasing values. Whereas the former (called the "worm configuration") is an optimal prey signal, the latter (the "antiworm configuration") is treated as nonprey and may even be regarded as a threat, since toads sometimes freeze in their postures or avoid such a stimulus. The selective response to a stripe moving in a worm (W) or an antiworm (A) configuration can be quantified by the expression $D(W,A) = (R_W - R_A) / (R_W + R_A)^{-1}$, in which R_W and R_A are the prey-catching activities in response to worm and antiworm, respectively (Figure 5C, adult). The discrimination value is positive and increases (within limits) with stripe length magnification x : $D(W,A) = f(x)$ (Ewert 1968; Ewert et al. 1978). That is, for positive values of $D(W,A)$, wormlike stripes are preferred to the same stripes presented in antiworm configuration. The important point here is that two identical stripes (i.e., of the same shape and size) are discriminated by the toad depending on the orientation of their longer axes relative to the direction of movement (determining their configuration).

Since the efficacy of a stimulus as a prey signal depends on its intensity (e.g., velocity and contrast), the question of invariance in worm/antiworm preference has to be investigated. If the speed of movement (Figure 6B) (Burghagen 1979; Burghagen & Ewert 1983; Ewert et al. 1983), movement pattern (Borchers et al. 1978), direction of movement (Figure 6A) (Beck & Ewert 1979; Ewert, Arend, Becker & Borchers 1979), or contrast between stimulus and background (Ewert et al. 1979) are changed equally in both W- and A- configurations, the $D(W,A)$ values remain positive, although their magnitudes may vary; that is, the "basic pattern" of the stimulus-response relationships shown in Figure 5A is not altered. If, however, such a stimulus parameter is changed differently in W- and A- configurations (e.g., the contrast direction with the background "white/black" vs. "black/white"), the $D(W,A)$ value can be positive and significantly different from zero only up to a certain ratio $\text{xl}(1) : \text{xl}(2)$. Invariance in configuration preference thus requires a "minimal ratio" of the configurational features.

Moderate changes in prey-catching motivation (e.g., those related to hunger or to the season) are expressed by the general level of prey-catching activity; the basic stimulus-response relationships are maintained (Ewert

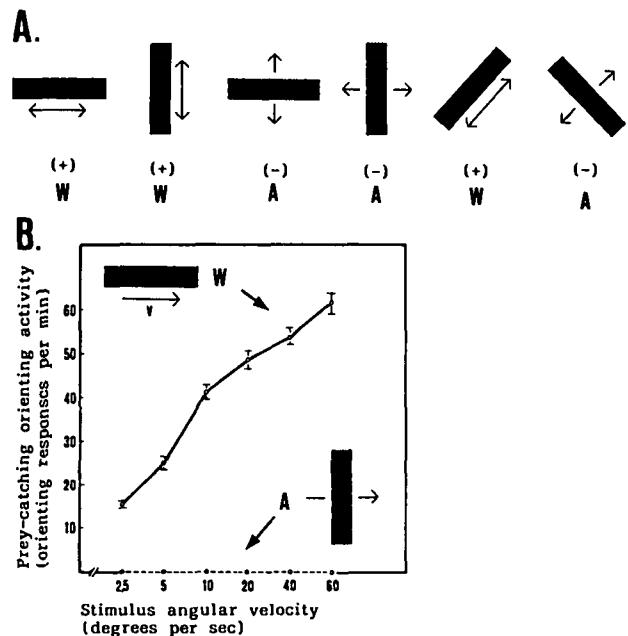


Figure 6. (A) Directional invariance of common toad's worm (W) versus antiworm (A) preference: (+), prey-catching; (-), no response. The direction of movement of the $2.5 \times 30 \text{ mm}^2$ black stripe is indicated by arrows; movement velocity was 25 mm/sec (from Ewert, Arend, Becker & Borchers 1979). (B) Velocity invariance of toad's worm versus antiworm preference for a $2.5 \times 40 \text{ mm}^2$ black stripe; response per min/2 (from Burghagen 1979; Burghagen & Ewert 1983).

1984a). The $D(W,A)$ values, for example, decrease with increasing prey-catching motivation, but remain positive.

3.3.3. Ontogenetic and phylogenetic considerations. The worm/antiworm preference is innate in common toads. At the completion of metamorphosis (immediately after the transition to terrestrial life) the RMs of the prey-naive toads are already functional, although the acuity of configurational stimulus discrimination (Figure 5C), distance estimation, and snapping performance improve with maturation (Ewert & Burghagen 1979a; Traud 1983; for results in salamanders see Himstedt et al. 1976). It has been further shown that the $D(W,A)$ values are positive irrespective of whether an animal was raised from the egg in a homogeneous white environment or in differently structured environments consisting of stationary or moving wormlike stripes or moving antiwormlike ones (Traud 1983). In the course of the first postmetamorphic year both sensory and motor performances improve (Ewert & Burghagen 1979a) in parallel with special neural differentiations in the central visual system (Clairambault 1976; Ewert 1984b). Configural discrimination in adult toads is rather robust; the stimulus-response relationships in test animals freshly caught in the forest display the same basic pattern (illustrated in Figure 5A) as in those kept for several months (or years) in the laboratory and fed exclusively on mealworms (Herbst & Ewert, unpublished data).

In the subspecies *Bufo bufo bufo* there are no obvious interindividual differences in configural prey discrimination (even if the responses of the small males and the large

females are compared). Other subspecies (*B. b. spinosus*), species (*B. asper*, *B. viridis*), or genera (*Hyla arborea*, *Rana temporaria*) show some variations with respect to optimal sizes of worm and square-shaped objects, but the basic response patterns according to Figure 5A are comparable (Burghagen 1979; Ewert & Burghagen 1979b; see also Finkenstädt & Ewert 1983a and Himstedt 1982 for results in urodeles).

3.4. Learned correspondence between stimulus features and releasing mechanism

Various visual features of natural prey objects allow toads to link these with individual experience and to store this information in order to recall it when faced with the corresponding stimulus (e.g., Birukow & Meng 1955; Brower et al. 1960; Cott 1936; Eibl-Eibesfeldt 1951; Eikmanns 1955; Freisling 1948). Depending on stimulus events, these experiences may be concerned with stimulus-specific habituation or associative conditioning.

3.4.1. Successive stimulus events. With the repeated release of the prey-catching orienting response (*o*) by the same prey object during a long-term series of presentations, the toad habituates specifically to certain visual cues varied within wormlike dimensions (Birukow & Meng 1955; Ewert & Kehl 1978). For example, after the habituation of prey orienting in response to a small rectangular triangle with the small cathetus (vertex) leading in the direction of movement, the toad immediately responds to the mirror image of the triangle (i.e., when the object is moved with its sharp tip leading in the same direction). Since the releasing values of both stimulus objects (measured separately in terms of the initial response rates per minute) are almost the same, it can be concluded that a stimulus-specific property of habituation keeps the prey-catching RMs responsive to "novel" prey stimuli. Motor components of prey-catching are not responsible for habituation.

3.4.2. Concurrent stimulus events. Associative conditioning in toads may involve different processes that (1) add new stimulus selecting properties or (2) permanently modify the innate ones. As an example of addition (1), toads for whom the smell of mealworms has been associated with prey respond either to the prey stimulus or to the combination "prey odor" and "any visual moving stimulus" (Ewert 1968; Shinn & Dole 1978). In the presence of known prey odor, the D(W,A) values become smaller. Furthermore, surround inhibition is decreased. For example, toads may respond with prey-catching to components of the kind of moving structured background shown in Figure 3B. In the absence of a known prey odor, surround inhibition is effective and visual stimuli are sharply classified according to the RM's original properties. Other studies in which toads associated negative experience with particular cues of specific prey animals have been reported elsewhere (e.g., "bee avoidance," Cott 1936).

As an example of modification (2), toads that have been fed several times on mealworms presented by hand finally respond to the hand alone, suggesting an association between food and hand (Brzoska & Schneider 1978). This phenomenon is not "hand specific," since Burg-

hagen (1979) has shown that it involves the extension of the entire spectrum of potential prey to include even large black square objects which normally elicit escape. The D(W,A) values are decreased but positive, and surround inhibition is attenuated. This modification in prey recognition often persists for several months. If in a comparable experiment the mealworm is presented several times together with an antiwormlike moving holder (Päsel & Ewert, unpublished data), toads become less cautious with the A-stimulus and finally respond to it alone with prey-catching. Here too, the D(W,A) values are significantly less than in unconditioned controls, but they remain positive, which means the preference is not inverted in favor of the A-configuration.

Recalling the "interaction concept" in configural selection, we conclude that the underlying neural mechanisms can be modulated by special inputs related to motivation and learning.

3.5. How are objects sorted into categories?

3.5.1. What do we measure? We must take into account the fact that the frog's or toad's "peripheral" visual system displays a variety of peculiarities: They have no retinal foveal pit (Gordon & Hood 1976), no mammalian-type involuntary saccadic eye movements (Autrum 1959), nor any voluntary scanning or overt eye movements. This does not mean that the anuran eye is completely motionless; however, they have only optokinetic (and vestibular-coupled) nystagmus, and movements concerned with binocular adjustments or monitoring the stationary environment (e.g., for such things as obstacles; see Grüsser & Grüsser-Cornehl 1976 and Dieringer 1986 for reviews). The toad's prey-catching behavior (or escape) is usually released by moving visual objects; prey recognition is feasible in any part of the large visual field, and perceptual decisions related to prey or nonprey precede the corresponding ballistic behavior patterns (Ewert et al. 1983). If a visual stimulus has none of the features of prey, the goal-oriented turning in a prey-motivated toad fails to occur or, rather, the probability of its occurrence is extremely low. Hence, the frequency of orienting and/or snapping in response to a visual stimulus can be taken as a measure of its resemblance to prey. When an experimentally simulated prey object circles around the toad at a constant distance and angular velocity, the path δ in the visual field through which the stimulus is displaced to elicit a prey-oriented turning movement decreases as the resemblance of the dummy to prey increases (Ewert 1969a). Thus, in this procedure smaller values of δ are concerned with greater orienting activity (responses per time interval) and vice versa. More specifically, the effective displacement δ depends on the response latency, which is inversely correlated with prey features. That is, the less the stimulus fits the prey category, the longer the animal takes to decide to turn toward a prey object (which follows the "all-or-none principle"). Since the stimulus-response relationships measured for orienting to prey (Figure 5A) are maintained for approaching, fixating, and snapping at it (e.g., Figures 4A and B; Ewert et al. 1983), we conclude that prey recognition processes are basically the same in the corresponding RMs (Figure 1).

3.5.2. What is prey in visual configural terms? Before we can discuss visual features, some remarks on the terminology of form perception are necessary. According to Zusne (1970), the term "recognition" refers to an ability to decide whether forms are different from those previously seen, whereas "identification" is concerned with the identity of a known form labeled by a name. In the present study, the term recognition (comparison with stored image) will refer to a genetically determined "information store"; consider a prey-naïve toad raised in a homogeneous visual environment. At the completion of metamorphosis, such an animal responds preferentially to particular visual stimuli with motor patterns related to prey-catching; we hence infer that this is based on comparing the incoming signal with a "prey image" that has emerged and been established in the toad's visual system during its evolutionary history (Ewert 1985; Traud 1983). More generally, visual pattern recognition is defined here as the assignment of space time-dependent contrast distributions (features) from the visual environment to innate or learned categories that have behavioral significance ("invariants" or "universals"). The origins of categories can also be both phylogenetic and ontogenetic. How organisms sort objects in their environment into different categories according to invariant features is one of the most basic questions of cognitive science: "The problem is very general, for an 'object' can be any recurring class of experience . . . and 'sorting' can be any differential response to the object category. . . . Categorization hence plays a critical role in perception, thinking, and language" (Harnad 1987a, p. 1).

What defines categories? In toads, the stimulus parameters of contrast and movement are prerequisites for categorizing the retinal image of a visual object as prey or predator. Within wide ranges of variation of these parameters, prey is distinguished from nonprey by size and configural features (see Appendix). An impressive example of configural properties is the fact that an optimal wormlike stripe loses its efficacy as prey if a small spot (itself subliminal for prey-catching) is placed just above the stripe (Ewert et al. 1970). The fact that a stripe is differently categorized by the toad depending on the orientation of its longer axis relative to the direction of movement is another convincing example of configural selection (see also Appendix Figures 26Ca and Cb). A stimulus object, however, has to be evaluated not only by itself but in comparison with the set of stimuli it is assigned to, by variation of its features along a physical continuum (see also Garner 1966; Gibson 1950; 1951). Studying the effect on prey-catching (Figure 4 top) of variations in configural features, $xl(1)$ and $xl(2)$, through their continuous transformation (Figure 4 bottom) allows us to describe the range of the prey category in the stimulus continuum (see also Appendix Figure 27A). More specifically, it is the proportion $xl(1) : xl(2)$ of an object – also taking into account its area $xl(1) \cdot xl(2)$ – that determines the degree of resemblance between that object and prey. This implies that prey categorization is *approximate* and that it involves a schema in which prey objects are represented in terms of "characteristic" spatiotemporal features, rather than being precisely copied. The boundaries of the prey category within the stimulus continuum (as well as the acuity of stimulus discrimina-

tion and the accuracy of recognition) are influenced by motivation and learning.

There is consequently no such thing as a unique "prey feature." The worm and antiworm Gestalts tested experimentally can be interpreted as invariant configurations reflecting the extremes of two transformation groups of a two-dimensional stimulus continuum (Figure 4 and Appendix Figure 27A). Hence, neither the worm nor the antiworm really appears to exist in the toad's visual world; that is, they may not be explicitly represented in the brain by specific detectors. But worm and antiworm are behaviorally significant features of moving objects. (There are also other possible features not considered here.) In the terminology of Suga (1984), $xl(1)$ and $xl(2)$ are "information-bearing parameters" essential for determining the range in a stimulus continuum which carries the visual information that is important for a species in the service of category formation. Worm and antiworm resemble abstract symbols sufficiently generalized to "describe" different categories of significant forms without being too specific. Worm selectivity is thus not limited to worms, but includes a variety of other invertebrates, such as beetles, millipedes, and slugs. The antiworm configuration accentuates an object's surface extension perpendicular to the direction of movement, which, to the toad, obviously means "be cautious." This feature, in combination with an appropriate size for the side of the stimulus parallel to the direction of movement, fits the category "predator" (e.g., moving shadows simulating airborne predators such as owls, or large looming objects simulating ground predators such as hedgehogs; Ewert & Traud 1979). The image of a snake – the "archenemy" of toads – includes many such antiwormlike features (e.g., coils of the body); in addition, the raised head and "neck" often assume a position perpendicular to the movement of the body (Ewert & Traud 1979). The notion that antiwormlike features in "threat postures" may serve as vital signals for intra- and interspecific communication in the animal kingdom (e.g., Eibl-Eibesfeldt 1979; Tinbergen 1951) suggests that there might be comparable configuration-analyzing systems in different perceptual tasks. [See also Eibl-Eibesfeldt: "Human Ethology" *BBS* 2(1) 1979.]

The observation that sign stimuli are defined by characteristic relationships between different features (configurations) accords with many other examples reported in the ethological literature. For gaping blackbird nestlings, the feeding parent is characterized by a 1:3 ratio of a head-rump schema (Figure 26A) (Tinbergen 1951). For a female treefrog (to mention an example in the auditory domain), the calling male is characterized by certain low- and high-frequency tone components of its mating call which, in order to be optimal, must occur in a particular ratio (Capranica & Moffat 1983; Gerhardt 1981).

3.5.3. General conclusions. From a teleological point of view, I think that a highly specific representation of a behaviorally meaningful object by a specialized innate recognition system would have an adverse effect on an animal's survival. Representation by a "schema" allows the recognition of a variety of objects belonging to a category by their shared defining features. With a "prey schema" (flexible within a limited range) the probability of correct decisions in anurans is high enough to guaran-

tee behavioral success, and there is also room for adaptations based on individual experience. In songbirds it has been suggested that an innate "song template" only crudely defines the species song, leaving considerable freedom for imitation, improvisation, and invention (Konishi 1985). [See also Baker & Cunningham: "The Biology of Bird Song Dialects" *BBS* 8(1) 1986.] In human speech, correctness of categorization also turns out to be an approximate rather than an exact matter, which is regarded as an advantage rather than a handicap; approximateness gives the verbal labeling system the potential for the universal expressive power of natural language and guarantees that meaning revision will always converge (see Harnad 1987b).

A few remarks about "innateness" are also in order at this point. The controversy surrounding this term is enormous; currently at least four meanings are associated with it: (1) something that is present at birth, (2) something that is unlearned, (3) something that is phylogenetically adapted, and (4) something arising from genetic differences. In the case of the toad's configural prey recognition, meaning (3) seems the appropriate one, although many authorities in developmental ethology would disagree as to whether that means "genetically determined," since genes alone may not be sufficient for the expression of a property. In my view, the prey configuration selecting behavior of an adult toad has been established as a result of genetic dispositions (designed neural network properties) involving maturational processes (the programmed development of neural connectivity) and behavioral practice (perceptual sharpening). The term "established" may be preferable to "innate" in this context as it leaves open a variety of factors and substrates that might be involved in RMs.

4. Interactions and integrative functions of central visual maps: An approach to behavior-correlated brain structures

The x-y coordinates of visual space are topographically represented by a multiplicity of maps in different laminae of the optic tectum and in various structures of the thalamus (Figure 7). Hence there are different "visual channels," but these are not isolated. Central visual maps may be mutually connected so that they can communicate with and influence one another. Intrinsic tectal excitatory processes, together with thalamic (pretectal) inhibitory input, determine the functional properties required for visual information processing in (1) surround inhibition, (2) prey/background extraction, (3) configural prey selection, and (4) prey/predator discrimination. The integration of prosencephalic inputs makes this putative innate system adaptive (within limits) to internal states and external stimuli.

The neuroethological analysis of behaviorally relevant brain areas is pursued using two experimental methods: (1) the study of regional glucose utilization in the brain of the behaving toad by applying the (^{14}C)-2-deoxy-D-glucose (2DG) method; (2) functional evaluation of anatomically defined structures through brain stimulation and lesioning.

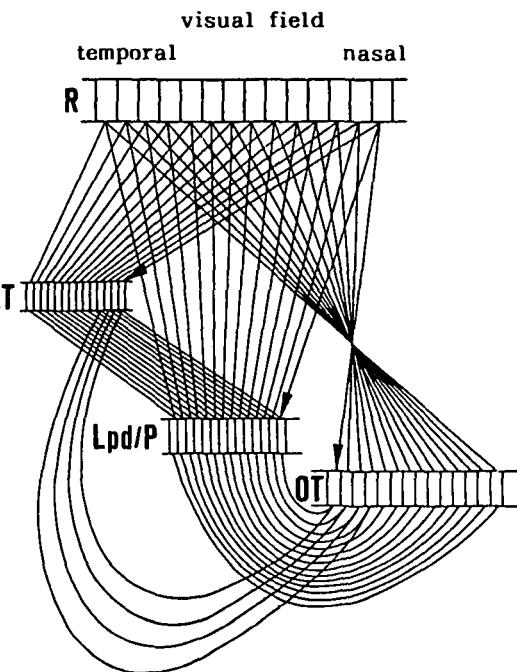


Figure 7. Schematic diagram of central visual maps in anurans, illustrating central projections from the contralateral eye and ipsilateral interactions among the projection fields in the visual system. These relationships are not precisely "point-to-point" as regards convergence and divergence (e.g., see Figure 10C). R: retina; AT: anterior thalamus; OT: optic tectum; Lpd/P: pretectal nuclei; "nasal" and "temporal" refers to visual field positions (according to Ewert et al. 1974; Fite & Scalia 1976; Gaze 1958; Lázár 1971; Neary & Northcutt 1983; Scalia 1976; Weerasuriya & Ewert 1983; Wilczynski & Northcutt 1977).

4.1. Regional distribution of brain activity

The question of whether central visual maps (Figure 7) and related structures are involved in various kinds of visual behavior can be investigated by the 2DG method. Figure 8 shows that prey-catching in response to a worm-like moving stripe (W), predator avoidance in response to a moving large square (S), and no motor response to an antiwormlike moving stripe (A) are associated with different patterns of increase and decrease in 2DG uptake in various brain structures (Finkenstädt et al. 1985; 1986; see also Ewert 1985). In view of the distinct releasing properties of the W-, S-, and A-stimuli, the following suggestions can be made: If the uptake of ^{14}C -labeled 2DG in a given brain area is different in S- and W-experiments ($^{14}\text{C}_S \neq ^{14}\text{C}_W$), a correlation with prey-catching or predator avoidance, respectively, can be inferred (e.g., see thalamic pretectal lateral posterodorsal [Lpd] nucleus); if, in addition, $^{14}\text{C}_A \neq ^{14}\text{C}_W$, the structure under investigation may also be involved in stimulus-feature analysis (e.g., see optic tectum [OT], thalamic pretectal lateral posterodorsal [Lpd] nucleus). Cases in which $^{14}\text{C}_S = ^{14}\text{C}_W$ indicate a correlation with prey-catching and avoidance behavior; for example, striatum (STR), cerebellum (CB) (for details see Finkenstädt et al. 1985; 1986).

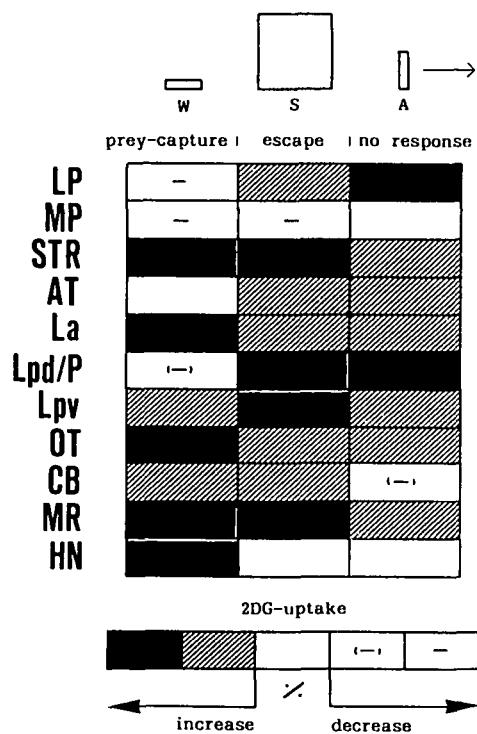


Figure 8. Regional patterns of brain activity measured with the 2DG autoradiographic technique in common toads which were repetitively orienting toward a moving prey object (wormlike $4 \times 28 \text{ mm}^2$ black stripe, W), avoiding a moving predator object (square $84 \times 84 \text{ mm}^2$ black object, S), or sitting motionless before a moving nonprey object (antiwormlike $4 \times 28 \text{ mm}^2$ black stripe, A). The patches indicate relative uptake of 2DG in various brain structures in comparison with reference structures and controls. AT: anterior thalamus; CB: cerebellum; HN: hypoglossal nucleus; La: lateral anterior thalamic nucleus; Lpd: lateral posterodorsal thalamic nucleus; Lpv: lateral posteroventral thalamic nucleus; LP: lateral pallium (posterior part); MP: medial pallium (posteroventral division); MR: medial reticular formation of the medulla oblongata; OT: optic tectum; P: posterior thalamic nucleus (lateral part); STR: striatum (ventral division). Lpd, Lpv, and P are pretectal nuclei; nomenclature of diencephalic structures according to Neary & Northcutt 1983 (for details see Finkenstädt et al. 1985; 1986; Finkenstädt & Ewert, submitted).

4.2. Functional relevance of visual maps and related structures

4.2.1. Behaviorally effective brain areas. Results from brain stimulation experiments with chronically implanted electrodes in freely moving toads indicate that (1) central programs for prey-catching and avoidance behaviors exist; (2) the former can be triggered by tectal stimulation and the latter mainly by posterior thalamic (pretectal) stimulation. The optic tectum is responsible particularly for "visual grasping," to use the general term of Akert (1949), whereas posterior thalamic nuclei participate in different types of "avoidance" related to a visual predator (escape), a stationary obstacle (detour), or vestibular input from body tilt (maintenance of posture).

There are topographic relationships between brain stimulation sites and behavioral patterns. Depending on the position of the electrode in the tectal visual map,

approximate orienting responses are directed toward appropriate loci of the visual field of the contralateral eye (Ewert 1967b; 1967c; 1974). The tectal area from which snapping can be elicited is smaller (Figure 9 A,B; cf. also C) and represents the animal's visual snapping region as determined in behavioral studies (Ingle 1976). Electrical stimulation of the posterior thalamus elicits avoidance behaviors such as ducking, ipsiversive turning, moving backward, jumping, running, "freezing" in body posture, puffing up and assuming a stiff-legged avoidance posture accompanied by secretion of the skin glands, sidestepping, or tilting the body along its sagittal or transverse axes (Rehn 1977; cf. also Ewert 1984a; for comparable results in the fire salamander see Finkenstädt & Ewert 1983b). In the posterior thalamus, stimulation sites for changes in body posture and detourlike movements are distributed in median regions; those for directed escape are found more laterally.

4.2.2. Thalamic/tectal interactions. Based on the effects of various tectal lesions, it is likely that the optic tectum participates in both prey-catching and predator avoidance behaviors (Bechtereck 1884; Rehn 1977). The coordinated control of both types of behavior requires thalamic/tectal interactions.

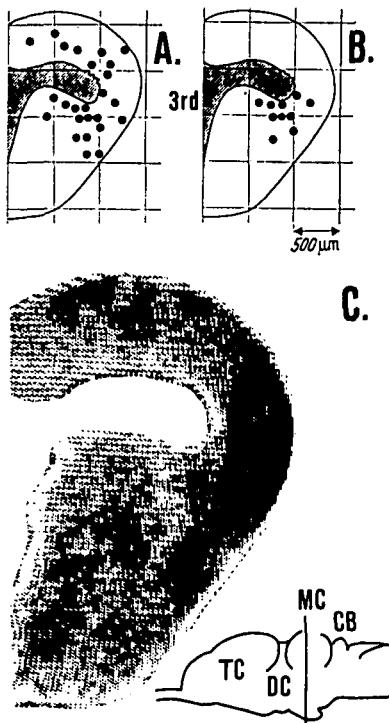


Figure 9. Areas relevant to snapping behavior in the common toad's midbrain shown in transverse section. (A) Reconstruction of sites which, when electrically stimulated, elicited snapping (B) and/or orienting (A) (from Ewert 1967b). (C) "Snap evoking area" labeled by means of the 2DG method during repetitive release of snapping with a wormlike object moving to and fro close to the toad in the frontal visual field. Note the "spatial convergence" of 2DG uptake from superficial to central tectal layers in the computer-processed autoradiographic image; CB: cerebellum; DC: diencephalon; MC: mesencephalon; TC: telencephalon; 3rd: third ventricle (from Finkenstädt et al. 1985).

Hints of functional thalamotectal connections are provided by electrical stimulation experiments; prolonged repetitive stimulation with trains of impulses in an area between the optic tectum and the ipsilateral pretectal neuropil close to the rostral tectum initially elicits escape, then with an increase of the escape threshold it leads to nonresponsiveness and may finally release orienting and snapping (Ewert 1968). It is interesting that after repetitive pretectal electrical stimulation toads often respond to large moving visual stimuli with prey-catching behavior as well. Tetanization of posterior thalamic (pretectal) neurons has presumably reduced their excitability, thus facilitating the visual responses of tectal neurons in the ipsilateral hemisphere. Rehn (1977) has supported this hypothesis with experiments using two stimulation electrodes; the threshold for electrically elicited prey-catching in the tectum decreased when tectal stimulation was preceded by long-term repetitive stimulation of the ipsilateral posterior dorsal thalamus.

Evidence regarding the behavioral significance of thalamotectal interactions is provided by lesion studies (Ewert 1968; Ewert et al. 1974). After unilateral lesions in the posterior dorsal thalamus, toads respond to any stimulus moving in the visual field of their contralateral eye with prey-catching; the effect resembles a sort of "agnosia"; retinotectal pathways are intact but visual pattern recognition is disturbed. This "disinhibition syndrome" is characterized by: (1) impairment of configural prey discrimination (Figure 5B); e.g., $D(W,A) \approx 0$; (2) failure of prey/predator discrimination (Figure 5Bc; e.g., an increase of prey-catching activity in response to successive elongation of the edge of a moving square stimulus); (3) strong attenuation of surround inhibition (e.g., prey-catching response to moving background structures); (4) loss of discrimination between object motion and self-induced motion in a structured environment; (5) eventual occurrence of sustained poststimulus activities in orienting behavior (Ewert 1967a; 1968; 1969b; Ewert et al. 1970; Ewert & von Wietersheim 1974b; for comparable results in the fire salamander see Finkenstädt 1981; Finkenstädt & Ewert 1983b).

These effects must be related to disorders in the central visual system, since the threshold for tactually elicited turning or snapping (Grobstein et al. 1983) is not reduced in thalamic-lesioned toads with subsequent bilateral optic nerve transection (Weerasuriya, unpublished data). The sources of the putative inhibitory thalamotectal influences (Figure 10B) are the anterior dorsal thalamus (AT), the pretectal (PT) lateral posterodorsal thalamic nucleus (Lpd), and the lateral portion of the posterior thalamic nucleus (P), respectively, but not the median part of P. This has been studied with various lesion techniques using either sagittal microknife cuts, electrocoagulation, or the axon-sparing neurotoxins kainic acid or ibotenic acid (Ewert 1984a; Ewert et al. 1983; Finkenstädt & Ewert 1983b; Schürg-Pfeiffer et al., submitted). Median transections of the posterior or tectal commissures are not effective in this context. Since it has not yet been possible to distinguish between effects of lateral P and Lpd, in the following I will be referring to "pretectal" (Lpd/P) lesions.

It is important to note that the above-mentioned "agnostic" phenomena produced by unilateral anterior thalamic lesions are always restricted to the frontal visual

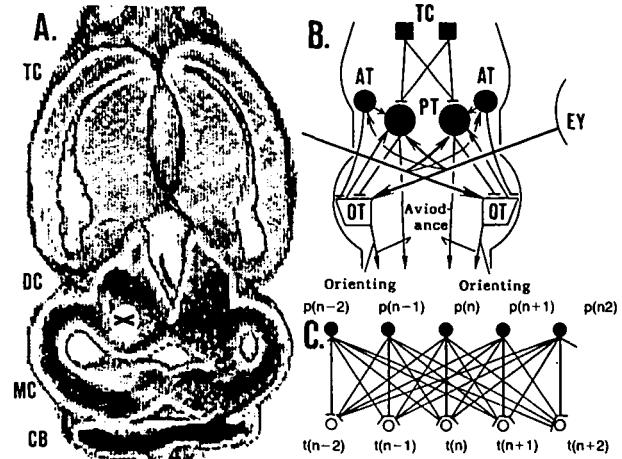


Figure 10. Central interactions in the control of prey-catching and predator avoidance behavior in common toads. (A) Glucose utilization in the brain of a toad with unilateral pretectal lesions measured with the 2DG method during repetitive release of "disinhibited" prey-catching orienting in response to an anti-wormlike stripe moving in the horizontal visual field of either eye. The 2DG uptake shown in the autoradiographic image of a horizontal brain section was much stronger in the left medio-caudal tectal lobe ipsilateral to the pretectal lesion (see "x") than in the tectal lobe of the right hemisphere in which the pretectal region (PT) displayed considerable 2DG uptake. Note that the anterior thalamus (AT), which is thought to inhibit the rostral tectum, was strongly labeled bilaterally (T. Finkenstädt in Ewert 1985). (B) Integrative and interactive aspects of information processing related to visually guided prey-catching and predator avoidance, derived from brain stimulation and lesion studies (Ewert 1967a; 1967b; Ewert et al. 1983). Arrows indicate putative excitatory influences, and lines with cross bars indicate inhibitory influences. AT: anterior thalamus; OT: optic tectum; PT: pretectal Lpd/P nuclei; TC: telencephalon (striatum). (C) Proposed principle of central lateral inhibition; p: prethalamic neurons; t: tectal neurons; lines with cross bars: putative inhibitory connections; retinal inputs to p and t are not shown (from Ewert 1981 according to Ewert & Härter 1968).

field, whereas those after pretectal lesions can pertain to any portion of the entire visual field of the contralateral eye, with an emphasis on extrafrontal regions (Ewert et al. 1983). The effects produced by a small unilateral Lpd/P lesion correspond to a small circumscribed region in the visual field resembling the reverse properties of a scotoma (Ewert et al. 1974). Evidence of ipsilateral inhibitory pretectotectal influences is provided by 2DG studies showing strong glucose utilization in the tectum ipsilateral to a unilateral pretectal lesion (Figure 10A). Here, the size and position of the "agnostic visual field" coincides with increased 2DG uptake in a topographically corresponding area of the tectum (Finkenstädt & Ewert, in preparation). Anatomical connections between anterior thalamus, pretectum, and tectum (Figure 10B) have been described in frogs (Lázár 1984; Neary & Northcutt 1983; Trachtenberg & Ingle 1974; Wilczynski & Northcutt 1977) and toads (Weerasuriya & Ewert 1983), suggesting that structures of the rostral thalamus project to the rostral third of the tectum whereas the pretectal projections include the mediocaudal tectal regions.

Telencephalic influences on the release of prey-catching are inferred from brain stimulation, lesion, and 2DG

studies (cf. Diebschlag 1935; Ewert 1967a; Finkenstädt et al. 1986; Finkenstädt & Ewert, submitted). The results suggest that striatal and medial pallial structures, via thalamic/pretectal nuclei, determine and modulate tectobulbar/spinal output (Figure 10B) (see also sect. 6.4.5). After removal of both telencephalic hemispheres, the putative inhibitory pretectotectal influences appear to override the tectal prey-catching system, leading to visual neglect of prey and a decrease in the visual threshold for escape. After a further large bilateral pretectal lesion, visual prey-catching is hyperexcited (" disinhibited"), whereas predator avoidance fails to occur (Ewert 1967a).

4.3. What is the neural basis for visually guided behavior?

It must first be emphasized that the release of a relatively simple, mainly visually oriented behavior (prey-catching) in the toad involves various structures throughout the brain. This implies that different visually guided behaviors are regulated by the same "macronetwork" with different spatiotemporal patterns of excitation and inhibition (Figures 8 and 10B); I therefore hasten to suggest that it would be dangerous to investigate the release of behavior in terms of the sensory properties related to just one structure. Although various (sub)systems appear to be important in the control of certain visually guided behaviors, these "visual channels" do not all operate privately, to the exclusion of others: (1) Prey-catching is controlled by the optic tectum, depending on inhibitory influences from thalamic-pretectal nuclei (Figure 10B; Ewert 1968; 1974; 1984a); (2) predator avoidance is controlled by thalamic-pretectal nuclei in conjunction with excitatory influences from the optic tectum (Figure 10B; Ewert 1968; Ewert & von Wietersheim 1974a); (3) a startle response may be triggered mainly by the optic tectum (Ewert et al. 1983; Ingle 1983; (4) barrier avoidance appears to be mediated mainly by median pretectal nuclei (Ewert 1971; Ingle 1971; 1977; 1980; 1983; and (5) optokinetic nystagmus is guided by the basal optic nucleus and portions of the large-celled pretectal gray (Fite et al. 1983; Katte & Hoffmann 1980; Lázár 1973).

Recalling the "interaction concept" of visual pattern recognition, I suggest that the toad's configural stimulus discrimination can be traced back to a property inherent in interacting pretectal/tectal networks (Ewert 1967a; Ewert et al. 1970). In this context, inhibitory pretectotectal connections play a prominent role and probably act according to the principle of lateral inhibition (see also sect. 5.3.4). There is indirect evidence to show that pretectal inhibition not only is related topographically to tectal cells but also spreads with decreasing strength over large tectal areas (Figure 10C; Ewert 1968; 1981; Ewert & Härtter 1968; 1969; Ewert et al. 1970). I further suggest that pretectotectal inhibition interferes with intrinsic reverberatory processes of lateral excitation in the tectum (Ewert et al. 1970; Ewert & von Seelen 1974; Ingle 1975; Székely 1973) and that both pretectal and tectal activity relate configural features of prey to a certain range in a stimulus continuum, as shown in Figure 4.

According to the "interaction hypothesis," a moving retinal image of a small object weakly activates pretectal structures, thus producing less inhibition to corresponding tectal structures than several randomly distributed

images which would strongly activate the pretectum. If small retinal images are narrowed (or a corresponding compact image is extended) parallel to the direction of movement, the putative excitatory reverberating mechanisms of the tectum are maximally activated; if the same images are aligned (or an appropriate compact image is extended) perpendicular to the direction of movement, pretectal activation increases and pretectotectal inhibition overrides the relatively weak tectal excitatory processes. In response to overall extended images, the tectal and pretectal effects interact appropriately. Such perceptual operations take the size of the stimulus area into consideration in relation to the direction of movement; the processing principle, however, is invariant under changes of the direction in which the stimulus moves.

Superposition of corresponding anterior thalamic input on the pretectotectal inhibitory processes presumably influences visual discrimination with special reference to the frontal visual field, thus providing a sort of "central fovea." Modulatory inputs to thalamic/pretectal structures arriving from the telencephalon (e.g., medial pallium) may determine dynamic properties of their interaction. These influences could, for example, attenuate anterior thalamic and pretectal effects, thus allowing surround inhibition to decrease and discriminatory processes to adapt to appropriate internal or external signals (Figure 10B) in relation to motivational states and learning.

5. Feature-analyzing neurons and integrative functional units: A cellular approach

The cellular approach to the analysis of configural features is guided by neuroanatomical studies of the cytoarchitecture of retinal, pretectal, and tectal structures in conjunction with extracellular microelectrode recordings from single neurons (combined partly with electrical stimulation and electrolytic lesioning) in paralyzed or freely moving animals. Intracellular recording and iontophoretic staining allows the identification of neurons and the evaluation of their responses in terms of changes in membrane potential. It can be shown that selectivity for configural stimulus properties is accomplished by feature-analyzing neurons in interacting pretectal/tectal networks which receive specific combinations of retinal input.

5.1. Information processing in the retina

The question of what the frog's retina tells its central projection fields – given Cajal's (1894) cytological treatise on the retina and the groundwork by Hartline (1940) and Barlow (1953) – was systematically examined by Lettvin et al. (1959) and quantitatively investigated by Grüsser and Grüsser-Cornehls (1968; 1976; for comparative studies in toads see Ewert & Hock 1972).

In the frog's and toad's retina there are at least four different classes of ganglion cells (R1–R4) that mediate the output of functionally connected retinal neurons. Ganglion cells send their axons to the superficial layers of the optic tectum (classes R1–R4) (Gaze 1958; Grüsser & Grüsser-Cornehls 1976), to the pretectal neuropil (probably classes R1, R3, R4) (Ewert 1971; Ewert et al. 1974),

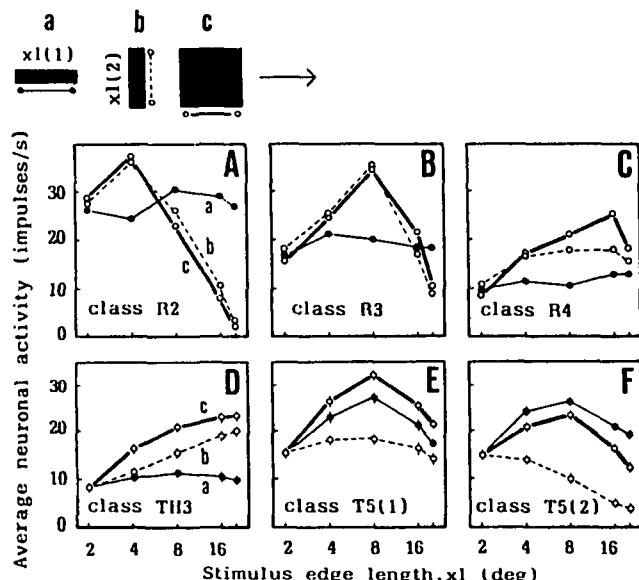


Figure 11. Activity of retinal ganglion cells (A-C) and central visual neurons (D-F), recorded extracellularly in paralyzed common toads in response to black wormlike (a), antiwormlike (b), and square (c) stimuli each traversing the centers of the excitatory receptive fields of single neurons at $v = 7.6^\circ/\text{sec}$ against a white background; $l(1) = l(2) = 2^\circ$; $x = 1, 2, 4, 8$ and 10 (from Ewert & Hock 1972; Ewert & von Wietersheim 1974a).

and to other diencephalic targets (Lázár 1971). The various ganglion cell classes exhibit different sensitivities to the stimulus parameters of movement and contrast. Furthermore, as a result of the different angular sizes of their excitatory visual receptive fields (ERF) and the strength of the adjoining inhibitory receptive fields (IRF), these neurons display various preferences for the area of a moving stimulus: Class R1 and R2 neurons ($\text{ERF} \approx 4^\circ$ diam.) are activated maximally by relatively small compact moving objects of about 4° diameter, class R3 neurons ($\text{ERF} \approx 8^\circ$) by such objects about double in size, and class R4 neurons ($\text{ERF} = 12-16^\circ$) by large dark objects against a bright background (Figure 11A-C,c). With a moving background structure, class R2 neurons are less activated than class R3 and R4 neurons (Tsai & Ewert, in press).

In the analysis of retinal ganglion cell responses of common toads we have taken advantage of testing configurational stimuli known from behavioral studies (Ewert et al. 1978; Ewert & Hock 1972). The results of these (Figures 11A-C and 12, R2-R4) and other investigations, together with the arguments presented by Grüsser and Grüsser-Cornehls (1970) and Hood and Gordon (1981), invalidate a retinal "prey detector" concept (Barlow 1953; Lettvin et al. 1959) according to which a particular class of retinal ganglion cells should exert the function of a prey detector:

(1) The behavioral (Figure 5A) and neuronal stimulus-response relationships do not accord well for any class of retinal ganglion cell (Figure 11A-C); (2) the $D(W,A)$ values are negative for stripes with an edge length of $xl = \text{ERF(diameter)}$, both in R2 and R3 neurons (cf. Figures 12 and 5C adult), the "prey detectors" proposed by Lettvin et al. (1959) and Barlow (1953), respectively; (3) if during chronic recording from an R2 or R3 neuron in the freely moving prey-motivated toad a small black stripe of

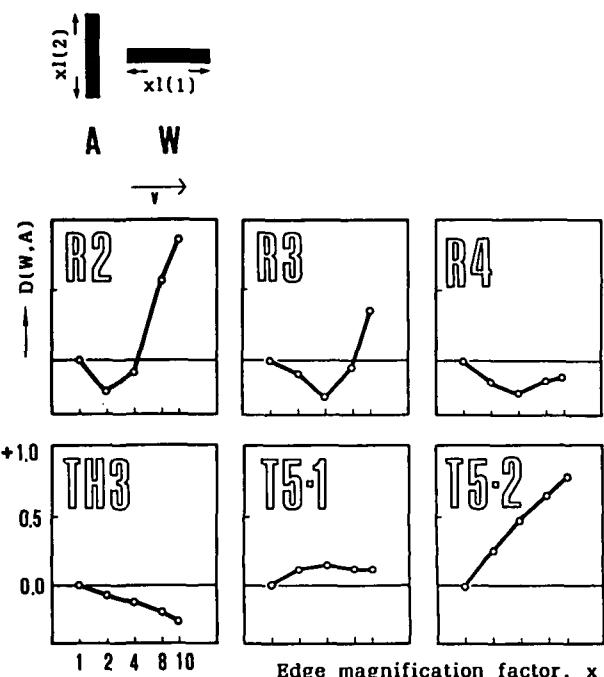


Figure 12. Discrimination values $D(W,A)$ for stripes moving in W - or A -configuration as a function of x for retinal (R2, R3, R4), pretectal (TH3), and tectal (T5(1), T5(2)) neuron classes in common toads; $l(1) = l(2) = 2^\circ$ (from Ewert et al. 1978).

$xl \approx \text{ERF(diameter)}$ traverses the receptive field center in A-configuration, the neuron will be optimally activated, while the probability of prey-catching is zero. The same stripe in W-configuration slightly reduces the neuronal discharge frequency (cf. also Figure 11Aa,b for $xl = 4^\circ$ and 11Ba,b for $xl = 8^\circ$), whereas the toad responds readily with prey-catching (Borchers & Ewert, unpublished observations); (4) the behavioral phenomenon of surround inhibition cannot be explained solely by inhibitory receptive fields in retinal (class R2) ganglion cells, because behavioral inhibition is strongly reduced in toads stimulated with the odor of prey and is almost abolished in toads with pretectal lesions (Ewert 1968; Ewert et al. 1970; cf. sect. 4.2.2), although retinal IRF properties are unaffected (Ewert & von Wietersheim 1974b).

What is the function of the various retinal ganglion cell classes? They obviously transmit to the optic tectum and to other central visual structures information regarding different stimulus parameters (e.g., contrast, movement, area), with each cell class emphasizing various aspects of these. Prey-feature analysis, however, is carried out together with tectal and pretectal structures.

5.2. Feature-analyzing tectal and pretectal neurons

Single cell recordings from retinal projection fields in the optic tectum and pretectum allow us to describe classes of neurons that exhibit different kinds and degrees of sensitivity to variation in the configurational features $xl(1)$ and $xl(2)$.

5.2.1. Morphological and physiological survey. The optic tectum consists of a laminated structure (Figure 13Aa). Based on Golgi studies, Székely and Lázár (1976) have

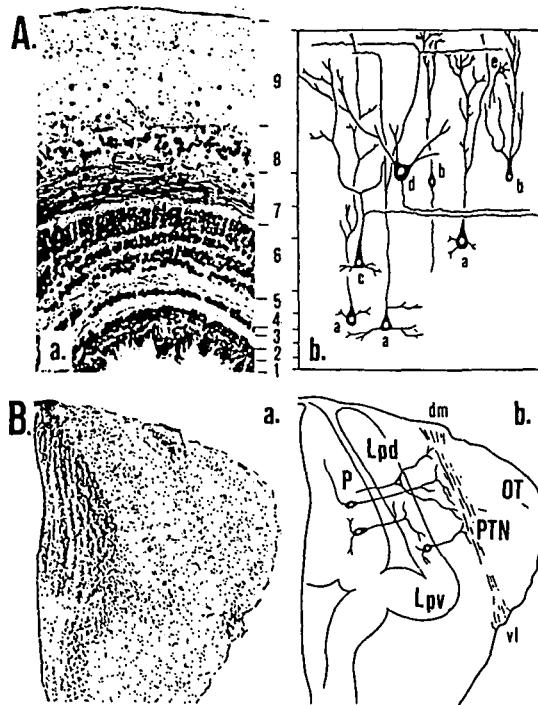


Figure 13. (A) Cytoarchitecture of the anuran optic tectum (cut-out). (a) Klüver-Barrera stain from a transverse section of the tectum showing the laminar structure, layers 1–9 (Ewert et al. 1983); (b) neuronal morphologies from Golgi studies; a, b: pear-shaped neurons; c: pyramidal neuron; d: large ganglionic neuron; e: stellate neuron (drawing after Székely & Lázár 1976). (B) cytoarchitecture of the anuran pretectal region. (a) Nissl stain from a transverse section (Ewert et al. 1983); (b) some morphological types from Golgi studies (drawing after Lázár 1979); dm, vl: dorsomedial and ventrolateral optic tract, respectively; PTN: posterior thalamic (pretectal) neuropil; for other abbreviations see Figure 8.

described morphologically distinct types of tectal neurons which are suitable for collecting retinal inputs, processing these by intrinsic links, and mediating the output of the tectum to bulbar/spinal structures (Figure 13Ab). In the pretectal Lpd/P region (Figure 13Bb), neurons pick up retinal input from the adjacent posterior thalamic (pretectal) neuropil and others provide connections between Lpd and P nuclei (Lázár 1979). Investigations of thalamic/tectal connections have shown that cells from Lpd/P nuclei project to the tectum (Neary & Northcutt 1983; Weerasuriya & Ewert 1983; Wilczynski & Northcutt 1977), whereas some tectal cells of layer 6 (top) and layer 8 send axons to pretectal and rostral thalamic nuclei (Antal et al. 1986; Bieger & Neuman 1984; Lázár et al. 1983).

Applying various physiological criteria, extracellular microelectrode recording studies in awake paralyzed toads and frogs have led to a classification of posterior thalamic pretectal (TH1–TH10) neurons (by Ewert 1971) and tectal (T1–T9) neurons. (The classification T1 to T7 by Grüsser and Grüsser-Cornehls, 1970, considered shape, size, and location of the ERF of a neuron, and the presence of monocular or binocular inputs; Ewert's classification of T5-type "small field" neurons, T5(1) to T5(4), takes notice of their different selectivities in response to changes of configurational features of moving visual stimuli

For reviews see Grüsser & Grüsser-Cornehls 1976; Ewert et al. 1983; Ewert 1984a.)

Among pretectal neurons (Figure 14A–C), many types are optimally activated in visual stimulus situations suitable for releasing avoidance behaviors: turning away from a large moving object (e.g., class TH3) or a looming

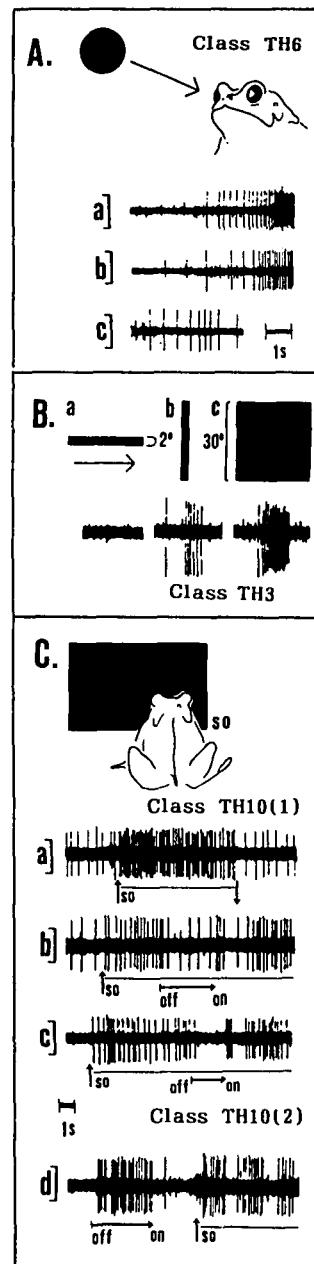


Figure 14. Response properties of extracellularly recorded pretectal neurons in the toad *Bufo americanus*. (A) Selective sensitivity of a TH6 neuron ($ERF \approx 180^\circ$) to a large object approaching the toad's eye from the dorsal (a) or lateral (b) visual field; the neuron was weakly activated (c) if the object moved around the toad in the horizontal plane at constant distance. (B) Selective sensitivity of a TH3 neuron ($ERF \approx 45^\circ$) to different configural moving stimuli (a–c). (C) Sensitivity of TH10-type neurons ($ERF = 30\text{--}90^\circ$) to a stationary obstacle (so); (a,b) records of TH10(1) neurons with spontaneous activity and (c) without; the response to the obstacle ceased after the room lights were turned off and was regained when they were turned on; (d) a TH10(2) neuron responding to a stationary obstacle (so) or to offset of the room lights (from Ewert 1971).

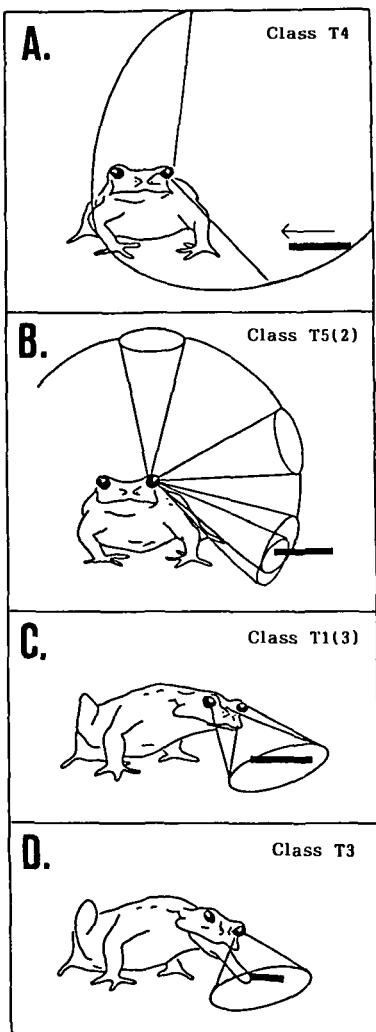


Figure 15. Receptive fields of tectal neurons in frogs and toads, suitable for discovering (A) and localizing (B–D) visual objects such as prey. (A) class T4, wide-field neuron ($ERF \approx 180^\circ$); (B) class T5(2), small-field neurons ($ERF \approx 27^\circ$); (C) class T1(3), binocular neuron ($ERF \approx 25^\circ$); (D) class T3, approach-sensitive neurons ($ERF \approx 25^\circ$) (according to Ewert 1974; Ewert & Borchers 1971; Grüsser & Grüsser-Cornehl 1970; Lettvin et al. 1961). Note that the release of each prey-catching action pattern requires cooperation (combination) of different classes of tectal neurons in which prey-feature selective T5(2) cells are involved (see sec. 6.3. and Figure 22).

approaching object (class TH6), or detouring around a stationary obstacle (e.g., classes TH10(1) and TH10(2)). The responses of other pretectal neurons display wide fields (e.g., class TH4), they are flexible (e.g. class TH5(2)), and some cells even seem to have memory (class TH9). The receptive field properties of certain tectal neurons (Figure 15A–D) might be utilized to obtain information from large sections of the visual field (classes T2 and T4) or to localize moving objects of different sizes in the x-y coordinates (T5-type neurons) or on the z-axis (classes T1 and T3).

5.2.2. Responses to moving configural stimuli. Since monocular input is sufficient for prey recognition, we have focused our quantitative investigations on monocularly driven tectal and pretectal “small field” neurons. The relationship between recording sites and the approx-

imately circular excitatory receptive fields (ERF) of these neurons corresponds roughly with retinotopy in the tecum and pretectum, respectively (Ewert et al. 1974). Regarding the sensitivity to configural features of moving visual stimuli, five principal response types can be distinguished: T5(1), T5(2), T5(3), T5(4), and TH3 neurons (for results in toads see: Ewert 1971; 1974; Ewert, Borchers & von Wietersheim 1979; Ewert & von Wietersheim 1974a; Satou & Ewert 1985; von Wietersheim & Ewert 1978; for comparable data in frogs see Schürg-Pfeiffer & Ewert 1981).

Briefly, class TH3 neurons ($ERF \approx 45^\circ$), recorded from Lpd and lateral P, are best activated by large moving square (S) objects. When responses to configural features are tested with stripes of 2° width and varying length, the discharge frequency (R) to the W-configuration averages less than that to the A-configuration; for corresponding edge lengths the following relation is found: $R_S > R_A > R_W$ (Figures 11D and 16A). These neurons are weakly activated by a small 2° square object but respond well to several randomly distributed, simultaneously moving stimuli that fill a large portion of the visual field, such as a moving background structure (Tsai & Ewert, in press). The response properties of tectal class T5(3) neurons, recorded mainly from layer 8, are similar to TH3 neurons, as far as configural stimuli are concerned. Class T5(1) neurons ($ERF \approx 27^\circ$), recorded frequently from layer 8 and sometimes at the border of 6/7, respond strongly to square stimuli in a limited size range; configurationally, however, they are more responsive to the W- than to the A-configuration: $R_S > R_W > R_A$ (Figures 11E and 16B). These neurons cannot be activated by a moving structured background. Tectal class T5(2) neurons ($ERF \approx 27^\circ$), recorded at the border of layers 6/7, exhibit selectivity with respect to the W- and A-configuration of a moving stripe in that $R_W > R_S > R_A$ (Figures 11F and 16C), and they fail to respond to moving background structures (Tsai & Ewert, in press). Class T5(4) neurons are selective for large, compact moving objects such as squares or circular shapes bigger than 4° ; they are unresponsive to small wormlike or antiwormlike stripes: $R_S > R_W \approx R_A \approx \text{zero}$.

If the correlation coefficients ($r_{A;W}$) for comparison between neuronal discharge frequency and prey-catching activity in response to wormlike (W) and antiwormlike (A) stripes of varying length are calculated (Borchers & Ewert 1979), class T5(2) neurons show a better correlation ($r_{A;W} = +0.9; +0.7$) than class T5(1) neurons ($r_{A;W} = 0.0; +0.8$) or class TH3 neurons ($r_{A;W} = -0.9; +0.9$). These evaluations agree with comparisons of the discrimination values for $D(W,A) = f(x)$ (Figure 12) and support the conclusion that the activity of class T5(2) neurons in response to moving configural stimuli is positively correlated with the probability that a stimulus fits the prey category. In a manner comparable to prey-catching behavior, the $D(W,A)$ values of these neurons are always positive, independent of the direction of movement (Figure 17A) (Ewert, Borchers & von Wietersheim 1979) and angular velocity (Ewert et al. 1978). The latter result has been investigated in detail by Roth and Jordan (1982), who demonstrated that the configural preferences of neurons corresponding to classes T5(1), T5(2), and T5(3) were velocity-invariant in the range tested $2 \leq v \leq 20^\circ/\text{sec}$. Of the entire sample of tectal

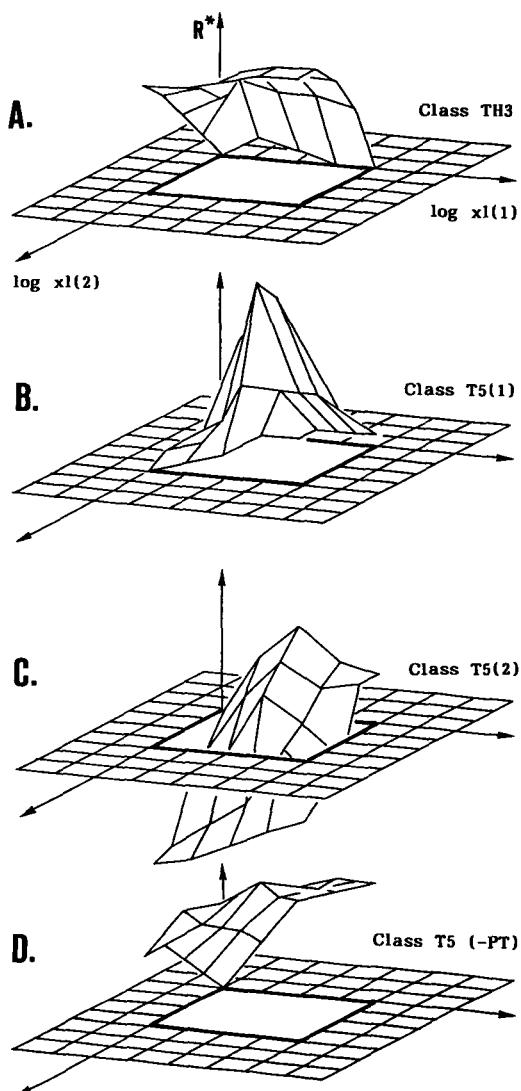


Figure 16. Tuning ranges of common toad's central visual neurons (A–D) across a 5×5 array of the stimulus continuum related to configuration shown in Figure 4 (bottom): class TH3, T5(1), T5(2) neurons, and T5 neurons after ipsilateral pretectal (−PT) lesions; computer-processed data from Ewert & von Wietersheim 1974a;1974b; intermediate values approximated. Ordinate: Average neuronal discharge frequency to stimuli (as shown in Figure 4) minus the response to a $2^\circ \times 2^\circ$ square stimulus serving as reference.

"small-field" neurons examined, only 4% displayed a velocity-dependent preference inversion with worm- and antiwormlike stimuli, and 14% showed a velocity dependence with worm and square stimuli of corresponding edge lengths.

To summarize, among feature-analyzing tectal and pretectal neurons (Figure 16A–C) there are (1) feature-sensitive neurons (classes T5(1), T5(3), TH3) which are optimally tuned to sets of configurational features $xl(1);xl(2)$ assigned to different, partly overlapping ranges in a continuum, and (2) feature-selective neurons which display selective sensitivity to feature combinations, in ei-

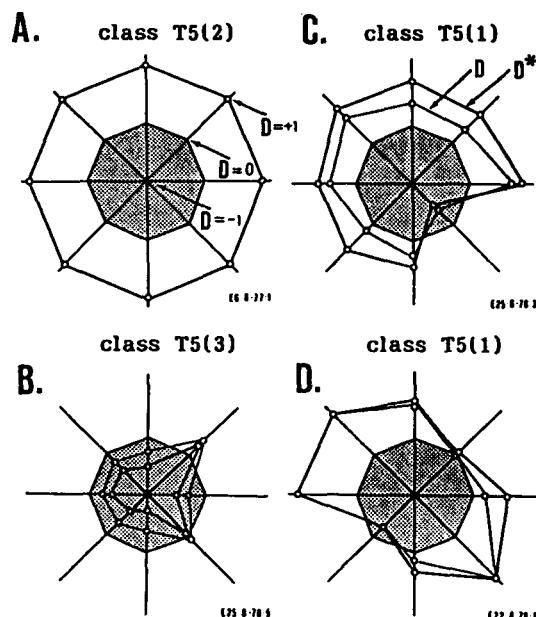


Figure 17. Discrimination values $D(W,A)$ plotted in polar coordinates for wormlike (W) and antiwormlike (A) $2^\circ \times 8^\circ$ stripes that traversed the centers of the approximately radially symmetrical receptive fields of tectal T5-type neurons in different directions of the visual field x-y coordinates at $7.6^\circ/\text{sec}$. Values inside the "zero circle" are negative, indicating anti-worm preference, and those outside are positive, indicating worm preference. D and D^* correspond to different data processing of extracellular records in common toads (from Ewert, Borchers & von Wietersheim 1979).

ther lumping together $xl(1)$ and $xl(2)$ (class T5(4)), or differentiating between $xl(1)$ and $xl(2)$ (class T5(2)).

5.3. Toward determining the circuitry

Experimental results concerning the interaction and behavioral relevance of the tectum and pretectum (Figure 10B,C) in conjunction with the presence of tectal and pretectal feature-sensitive/selective neurons in mutually connected laminated structures (Figures 7 and 13) raise the question of circuitry. There are various specific hints about neuronal connectivity patterns.

5.3.1. Functional considerations. Recent data from intracellular recording and iontophoretic labeling of the grass frog's tectal neurons (Figure 18A) with potassium-citrate/ Co^{3+} -lysine-filled micropipettes confirm the properties of T5-type neurons and further characterize their postsynaptic activities in response to (1) electrical stimulation of the optic tract, (2) moving configural stimuli, and (3) brisk changes of diffuse illumination of the entire visual field (Ewert et al. 1985; Matsumoto et al. 1986). Four main points are of interest here:

First, the responses of T5(1) and T5(2) cells to (1)–(3) are characterized by the occurrence of excitatory and inhibitory potentials (EPSPs, spikes, IPSPs) (Figure 18B), whereas T5(3) cells produce mainly EPSPs and spikes. A further interesting outcome of this approach is the finding that neurons with T5(1) properties are not homogeneous (see also Figure 18Aa,b and sect. 5.3.3), which accords with data from previous extracellular re-

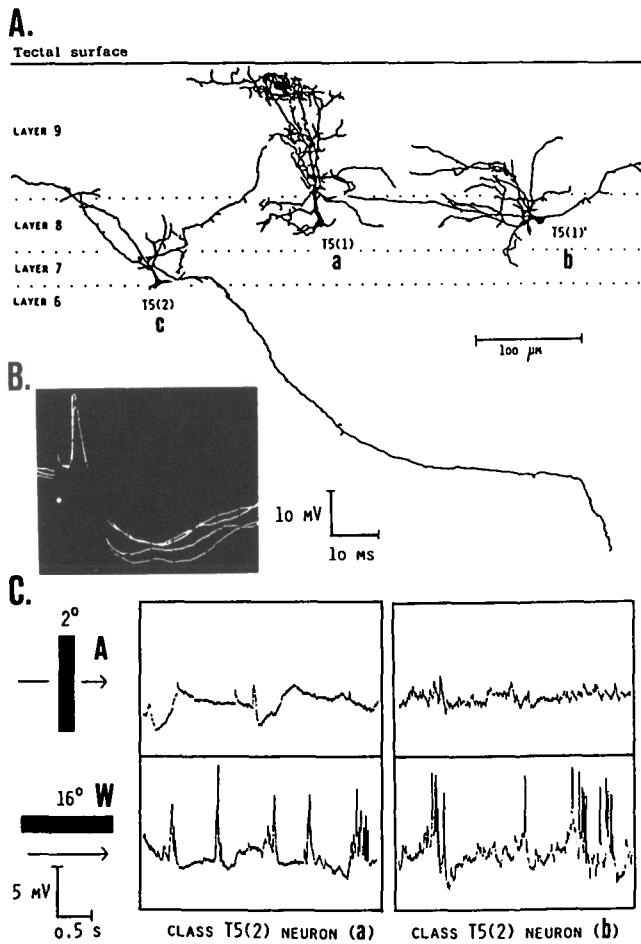


Figure 18. Morphological identification of physiologically classified tectal neurons by intracellular recording and iontophoretic staining with potassium-citrate/ Co^{3+} -lysine filled micropipettes in the grass frog *Rana temporaria*. (A) Camera-lucida reconstructions of a T5(1) pear-shaped neuron (a), a T5(1) large ganglionic neuron (b), and a T5(2) pyramidal neuron (c). (B) EPSP-IPSP responses to a short electrical stimulus (see dot applied to the optic tract, typical for T5(2) and most T5(1) neurons. (C) Records of two class T5(2) neurons (a and b) in response to the antiworm (A) and worm (W) configuration of a moving $2^\circ \times 16^\circ$ stripe (from Ewert et al. 1985; see also Matsumoto et al. 1986).

cording studies (Ewert, Borchers & von Wietersheim 1979).

Second, the various combinations in the occurrence of excitatory (E) and inhibitory (I) postsynaptic potentials in response to brisk changes of diffuse light at onset and offset in tectal T5-type neurons

T5(1): Ion-Ioff, Eon-Eoff, EI_{on}-EI_{off}, or IE_{on}-IE_{off}

T5(2): IE_{on}-IE_{off}

T5(3): Eon-Eoff

in comparison with the on/off spike activities of retinal R-type neurons make it possible to estimate the combination and proportion of direct retinal input and indirect visual input from tectal and pretectal cells (see Matsumoto et al. 1986). For example, the Ion-Ioff response recorded in some T5(1) neurons can be explained by direct excitatory input from retinal R2 neurons and inhibitory input from tectal T5(3) and/or pretectal TH3 neurons driven mainly by class R3. (Retinal class R3 fibers

discharge short bursts of spikes at onset and offset, whereas class R1 and R2 show no spike responses to brisk changes in diffuse light. Class R4 fibers are characterized by a pronounced off response; see Grüsser & Grüsser-Cornehls 1976; Schürg-Pfeiffer 1979.) An assumption of direct inhibitory inputs from retinal R3 fibers to tectal neurons in the present example would be in conflict with other data, such as those showing that, after optic tract stimulation, in no tectal cell of the 314 tested was an EPSP preceded by an IPSP. (Note that the conduction velocity in R2 fibers is less than in R3.)

Third, postsynaptic reverberatory activities in some T5(1) cells indicate mutual excitatory intratectal connections.

Fourth, the fact that altering the configuration of a moving stripe from W to A is responded to by a T5(2) cell with a change from EPSPs to IPSPs (Figure 18Ca), or a strong decrease of any PSPs (Figure 18Cb), provides evidence of "configuration selective" excitatory and inhibitory inputs to this neuron. The inhibitory inputs to this cell may come from neurons (TH3 and/or T5(3)) that respond well to the A-configuration.

5.3.2. Pharmacological considerations. The lack of "flat vesicles" in retinotectal axon terminals (Lázár, personal communication to N. Matsumoto; see Matsumoto et al. 1986) in conjunction with the notion that retinotectal transmission in anurans is mainly nicotinic cholinergic (Freeman & Norden 1984) suggests that the IPSPs recorded from tectal neurons arise primarily from intrinsic tectal and/or extrinsic (e.g., pretectal) connections. Milson and Mitchell (1977) have reported that GABA in the frog's tectum exerts a widespread inhibitory influence on field potentials which is antagonized by picrotoxin. We have observed that topical application of picrotoxin to the tectal surface of toads leads to visual disinhibition of prey-catching, which resembles the "agnostic" phenomena observed with pretectal thalamic lesions (Schürg-Pfeiffer & Ewert, unpublished data). Similar results have been reported for the application of strychnine to the toad's tectum (Ewert et al. 1974).

Pretectal inhibitory influences on the tectum might be concerned with at least two types of action: One depends on visual input and exerts brief influences by "conventional" transmission in determining the configural response properties of certain tectal neurons, and the other depends on motivational states and induces long-term adjustments by peptidergic neuroregulators. The latter idea arises from results of immunocytochemical investigations (Reiner, personal communication; see also Reiner et al. 1983; Kuljis & Karten 1982).

5.3.3. Cytological considerations. Intracellular recording and iontophoretic labeling techniques (Ewert et al. 1985; Matsumoto et al. 1986) have identified tectal cells with T5(1) properties as pear-shaped (Figure 18Aa) and large ganglionic neurons (Figure 18Ab) whose somata are located in layer 8 or near the border of layers 6/7. As so far investigated, class T5(2) are pyramidal cells at the border of 6/7 (Figure 18Ac; see also Antal et al. 1986; Matsumoto & Antal 1984). Class T5(3) can be attributed to large ganglionic neurons whose somata are found in layer 8. If we consider both the site of the somata and the extent of the dendritic trees, the pear-shaped T5(1) neurons in

layer 8 (Figure 18Aa) appear to be suitable for integrating retinal input, whereas large ganglionic T5(1) and T5(3) neurons of the same layer may be particularly appropriate for mediating local interactions. Pyramidal T5(2) cells, whose long axon could be followed up in one case to the rostral medulla oblongata (Figure 18Ac), are projective neurons. T5(1) pear-shaped and large ganglionic cells at the border of 6/7 may be tectobulbar/spinal projective neurons (Satou & Ewert 1985) and/or tectothalamic connecting neurons (Antal et al. 1986).

5.3.4. The proposed circuitry. Given the strong inhibitory prepectotectal influences (sect. 4.3.), I suggest that the prey selectivity of T5(2) neurons is determined both by excitatory input from T5(1) neurons (sensitive to extension $xl(1)$ and area) and by direct and/or indirect inhibitory input from TH3 neurons (sensitive to $xl(2)$ and area) which in turn receive different combinations of retinal input (Figure 19Aa and B). By its firing rate a class T5(2) neuron would thus encode the outcome of information processing that takes place in a "functional unit" (assembly) of connected cells (Figure 19Aa) inherent in a network (Figure 19Ab). Since a prey stimulus activates several adjacent assemblies of the same type, it is reasonable to suggest that prey-related information is transmitted to bulbar/spinal systems by a small population of T5(2) neurons (Figure 19Ac). The proposed network (Figure 19A,B) is characterized mainly by: (1) combinations of certain retinal inputs to pear-shaped T5(1) cells in layer 8 and to TH3 cells; (2) lateral excitation presumably via large ganglionic T5(1) cells of layer 8; and (3) lateral inhibition probably mediated by TH3 and T5(3) neurons (Ewert 1974; 1981; Ewert & von Seelen 1974; Matsumoto et al. 1986).

This feature-analyzing system forms the neuronal basis of the "interaction hypothesis" introduced earlier: If small retinal images are aligned (or a corresponding compact image is extended) parallel to the direction of movement ($xl(1) > xl(2)$), the T5(1) neurons are strongly activated due to mutual excitatory connections, whereas TH3 cells respond only weakly, so that T5(2) neurons convey prey-related activity to the motor systems. If the same images are aligned (or an appropriate compact image is extended) perpendicular to the direction of movement ($xl(2) > xl(1)$), the TH3 neurons will fire more strongly than T5(1), so that T5(2) neurons are inhibited; in response to overall extended images ($xl(1) = xl(2)$) the respective excitatory T5(1) inputs and inhibitory TH3 inputs to T5(2) neurons will interact accordingly.

The basic properties of this recognition system can be tested. If the responses of the same T5(2) neuron are recorded extracellularly before (Figure 20A) and after a direct-current- (Figure 20Ba) or kainic-acid-induced (Figure 20Bb) ipsilateral prepectal lesion in a paralyzed animal, a dramatic change in the response characteristics of the T5(2) neuron occurs, comparable to the "disinhibited prey-catching behavior" (sect. 4.2.2.): (1) impairment of configural selectivity, yielding $D(W,A) \approx 0$; (2) increase in discharge rate with the elongation of the edge of a moving square stimulus yielding no optimal size; (3) strong decrease of surround inhibition (i.e., responses to a moving structured background); (4) enlargement of the functional excitatory receptive field; (5) lack of neuronal adaptation in response to repetitive visual stimulation; (6)

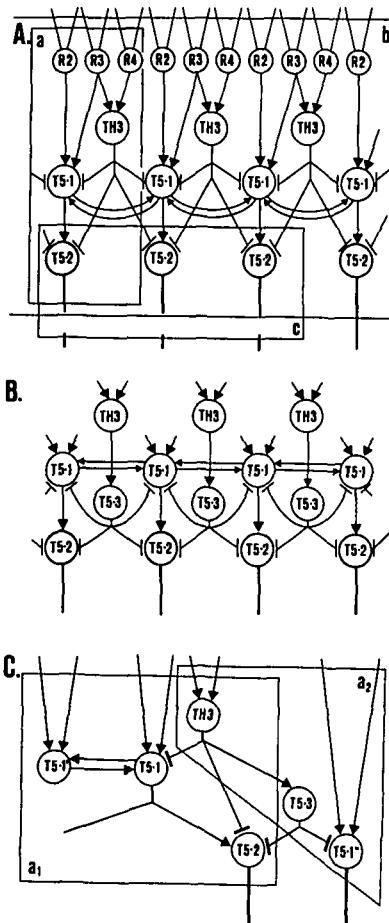


Figure 19. Neuronal correlates of the "interaction concept" for configural prey-selection in anurans. The network pieces shown in (A) and (B) are hypothesized to be parts of an integrated whole. (a) A functional unit of neurons (an assembly) as proposed by Ewert (1974) that broadly corresponds to the "column concept" described anatomically by Székely and Lázár (1976) and analyzed mathematically by Lara et al. (1982); (b) neuronal network; (c) neuronal population. Arrows indicate excitatory inputs and lines with cross bars inhibitory inputs; the lateral excitatory and inhibitory connections are not restricted to immediately adjacent neurons (see also Figure 10C). (C) Concept of "goal-related assemblies" (a_1, a_2). (For explanations see text.)

increased probability of excessive self-sustained activities and after-discharges (Ewert 1985; Laming & Ewert 1983; Schürg-Pfeiffer et al., submitted). Comparable deficits in stimulus discrimination (Ewert & von Wietersheim 1974b) and habituation (Ingle 1973) of T5 neurons have been obtained in toads and frogs whose lesion-induced "disinhibited" prey-catching behaviors were determined before recording (see also Figure 16D). The finding that prepectal lesion-induced changes – particularly with respect to (2) and (6) – also occur in T5(1) neurons supports the idea that inhibitory prepectal influences arrive at different tectal layers (Figure 19A,B) to attenuate mutually excitatory intratectal processes. Thus, the "original" properties of T5(1) neurons – arising from retinal input and intrinsic tectal connectivity – may actually emerge after prepectal lesions (see Figure 16D).

Complementary studies in different amphibians, *Rana temporaria*, *Salamandra salamandra*, and *Hydromantes*

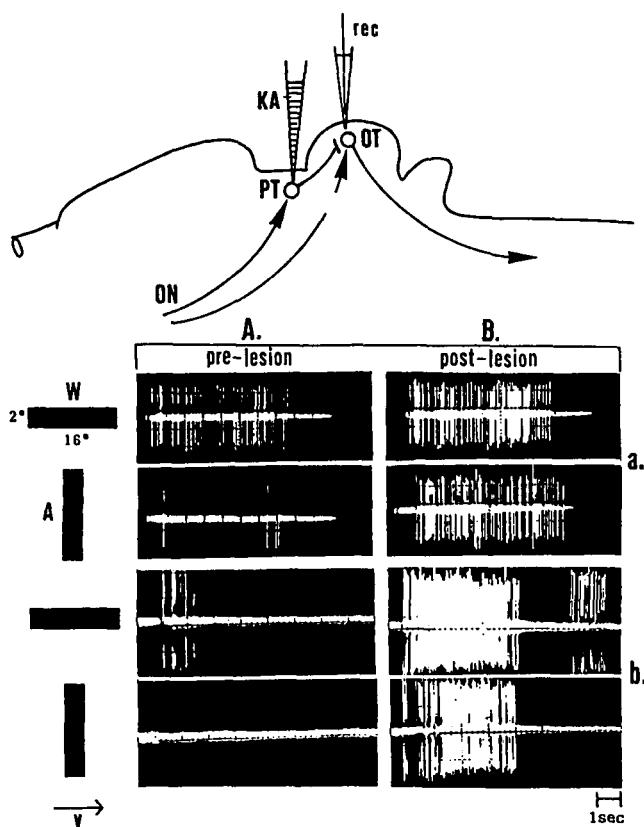


Figure 20. Evidence of pretectotectal inhibitory connections. (A) Examples of extracellular records from single class T5(2) neurons in a paralyzed common toad (a) and a grass frog (b) in response to a $2^\circ \times 16^\circ$ stripe traversing the center of the excitatory receptive field in a wormlike (W) or an antiwormlike (A) fashion at $7.6^\circ/\text{sec}$. (B) Changes of the response of the same T5(2) neuron following an ipsilateral pretectal lesion induced by direct current delivered by means of an electrode (a), or by a kainic acid (KA) solution applied through a micropipette (b); ON, optic nerve; OT: optic tectum; PT: pretectal Lpd/P region; rec: recording electrode (from Schürg-Pfeiffer et al., submitted).

italicus, show that the behavioral preferences for moving configural prey stimuli are reflected in the response properties of prey-selective tectal neurons basically comparable to the toad's T5(2) (cf. Finkenstädt 1981; Hünstedt 1982; Roth 1982; Schürg-Pfeiffer 1979). The species-specific differences can be explained by weightings for tectal and pretectal filter operations. After anterior thalamic or pretectal lesions in the fire salamander, changes in the configural prey selectivity of tectal neurons and prey-catching behavior were comparable to those seen in pretectally lesioned toads and frogs (Finkenstädt & Ewert 1983b).

5.4. How are perceptual categories represented in the anuran's visual system?

From a historical point of view, there have been two extreme positions: The "retina concept" and the "motor concept." The retina concept, initiated by Barlow (1953) and put forward by Lettvin et al. (1959), restricted the filter functions essential for categorization (e.g., detection of prey) to a class of retinal ganglion cells. Thus,

Barlow (1953) favored the frog's R3 neurons when he said: "In fact, 'on-off' units [class R3] seem to possess the whole of the discriminatory mechanism needed to account for this rather simple behaviour [prey capture], . . . and it is difficult to avoid the conclusion that the 'on-off' units are matched to this stimulus (image of a fly at 2 in. distance) and act as 'fly detectors'" (p. 86). Lettvin et al. (1959) preferred R2 neurons: "We have been tempted, for example, to call the convexity detectors [class R2] 'bug perceiver' . . . Could one better describe a system for detecting an accessible bug? . . . The operations found in the frog [retina] make unlikely later processes in his system . . ." (pp. 1950–51).

Such processes were not excluded in the discussion by Maturana et al. (1960):

The [retinal] ganglion cells can be considered as emitting parcels of information about particular useful aspects of the visual image, which aspects depend on the class to which the cell belongs. . . . In a system like this, a unique combination of the four qualitative contexts [provided by the operations mediated by four retinal ganglion cell classes] in a certain spatial relation may define a class of objects. . . . We do not yet know how the recognition of such unique combinations of contexts is made at the tectum, but this can be studied experimentally. (pp. 161, 164)

Although there is no specific retinal prey detector like the one originally suggested, the classes of retinal ganglion cells continue to have the fascinating property that they do say something perceptually important to the central visual system (see also Barlow 1985a).

The motor concept was developed by Grüsser and Grüsser-Cornehls (1970; 1976; see also Grüsser-Cornehls 1984). Both authors claimed that the motor acts (i.e., the accomplishments of the prey-catching action patterns) are essential for prey recognition, emphasizing that: "The construction of the invariants for predators, prey, hiding places, etc. apparently does not precede the motor response; instead, the entire neuronal reaction chain that leads to the observable behavioral sequence *in toto* constitutes the invariant" (Grüsser & Grüsser-Cornehls 1970, p. 215, translated).

This hypothesis, deriving from the problem of how one can know what one sees before one responds, was both attractive and wrong. The argument that prey recognition does not precede a prey-catching response – that the frog or toad must instead run through the behavioral sequence starting with orienting and terminating with snapping in order to recognize prey – was invalidated by the animal's behavior; orienting toward prey presupposes prey recognition (Figures 4A,B and 5A; see also sect. 2.3). To evaluate the "motor concept" it is important to know that in their own investigations Grüsser and Grüsser-Cornehls (1970; 1976) did not distinguish neurons with T5(1), T5(2), T5(3), and T5(4) configural response characteristics. Both authors even disputed the existence and significance of tectal neurons displaying prey-selective T5(2) properties (Ewert et al. 1978; von Wietersheim & Ewert 1978) that were discovered by Ewert (1974) as "small field Type II neuron" responses, quantitatively described by Ewert and von Wietersheim (1974a), and confirmed by Roth and Jordan (1982).

Our neuroethological investigations have led to the

"interaction hypothesis" of configural stimulus selection introduced earlier (Ewert 1968; 1974; Ewert et al. 1970; for systems theoretical analyses and computer simulations see Arbib 1982; Ewert & von Seelen 1974; Lara et al. 1982). The underlying neural interaction principles correspond in some respect to the idea of a "multiple-input, metastable feedback loop" (Bullock 1961). The main components of our hypothesis are the following:

1. The analysis of configural features of a moving visual stimulus ($x(1)$, $x(2)$) is carried out by functional units (assemblies) (Figure 19Aa) of connected feature-analyzing neurons (T5(1), T5(2), T5(3), TH3) inherent in pretectal/tectal networks (Figure 19A,B) related to retinal projection fields (Figure 7). The idea is that an extensive continuous network (Figure 19Ab) is subdivided into "integrative interacting units" (Szentágothai 1967) of minimal size (Figure 19Aa) capable of the same basic information processing as the corresponding network (consisting of these units). The retinal input to such an assembly is mediated by particular combinations of ganglion cells (e.g., R2, R3, R4). Feature-analyzing tectal and pretectal neurons are distinguished by their degree and quality of integration and interaction. Neurons of adjacent assemblies are partially coupled through mutual excitation and lateral inhibition. Outputs of these assemblies are mediated by T5(2) prey-selective tectobulbar/spinal projective neurons (Figure 19Ac).

2. Configural stimulus selection is determined by the properties of feature-sensitive neurons (e.g., T5(1), T5(3), TH3), which are tuned to various sets of configural features assigned to particular, partly overlapping ranges in a stimulus continuum (Figure 16A,B). Moving visual objects that are different in their configural characteristics thus elicit corresponding patterns of activity in these neurons. Specific neuronal interactions determine the range in the stimulus continuum that defines the prey category. In other words, this connectivity provides the "prey schema" with which visual input is compared: Configural cues are extracted by T5(2) prey-selective cells through specific excitatory and inhibitory synaptic contacts with feature-sensitive neurons. Class T5(2) neurons are hence optimally tuned to the sets of configural features that characterize prey (cf. Figures 16C and 4). The result of this analysis in adjacent assemblies, expressed in the spike frequency of adjacent T5(2) neurons, is transmitted to the appropriate bulbar/spinal motor systems. Spatial and temporal summation of their output in the corresponding motor pattern generating network, upon reaching threshold, determines the latency of an action pattern such as orienting to or snapping at prey.

3. Feature-sensitive neurons of classes T5(1), T5(3), T5(4), and TH3 are probably not monopolized for a specific behavioral goal. Certain classes of neurons of cell assemblies related to prey-feature analysis (Figure 19C,a₁) may take part in other goal-related assemblies (Figure 19C,a₂), contributing in that case to the analysis of other objects coded by different tectobulbar/spinal projective neurons. The extension of the idea described in (1) is that different types of functional units (goal-related assemblies) inherent in the same network are defined by the specific integrative properties of particular bulbar/spinal projective neurons (e.g., see T5(2) and T5(1)" in Figure 19C).

4. The feature-analyzing system is relatively stable, given constant inputs from the internal state of the organism related to circadian determinants, nutrition, hormonal balance, and so on.

5. The established feature-analyzing system is to some extent modifiable through modulatory prosencephalic influences depending on internal and external signals that may change the properties of either the whole network or parts of it (see sect. 6.4.).

Finally, some remarks are in order concerning the function of T5(2) neurons. These can be judged from different points of view. (1) If one focuses on the selectivity of T5(2) neurons in worm/antiworm discrimination arising from convergent excitatory and inhibitory inputs by neurons that are sensitive to worm- and antiwormlike stimuli, respectively, one can refer to a "worm detector," in accordance with the wiring principle illustrated in Figure 2A. (2) If we consider that the prey category is determined by sets of configural stimulus features assigned to a range in a stimulus continuum (Figure 4), we can regard (small) populations of T5(2) neurons whose activities are positively correlated with changes in these features (Figure 16C) as feature detectors operating as "prey filters." Such a filter compares information related to configural (spatiotemporal) features of visual stimuli with stored information provided by specific neuronal connectivity. The filter picks out the invariant information that is sufficient to categorize prey. (3) Since feature analysis is concerned with certain neuronal activity patterns in a network of feature-analyzing neurons, we can speak of a "feature-analyzing network," in accordance with the principle illustrated in Figure 2B. The mutually interacting feature-analyzing neurons are distinguished by the degree and quality of converging inputs and diverging outputs. Goal-related information (e.g., regarding prey category) is "read" (weighted) through the specific integrative contacts of feature-selective projection neurons (e.g., class T5(2)). A difference from (2) here would be that excitatory properties of T5(2) neurons are not only derived by input from T5(1) but also result from intrinsic processes in response to direct retinal input. Information related to other behaviorally relevant objects (e.g., predator or mate), or to the location of a stimulus in the visual field, is expressed by distinct types of specialized projective neurons in (partly) the same network.

Pattern recognition in the toad's visual system is thus not a question of either "hierarchical" or "parallel" information processing. Visual recognition systems obviously take advantage of both convergent and divergent organization. A corresponding concept of "parallel-hierarchical information processing" has been put forward for the bat's auditory system by Suga (1984).

6. Sensorimotor interfacing: The command system approach

The prey-catching action patterns o, a, f , and s are activated by different RMs which use comparable feature-analyzing processes but are distinguishable by mechanisms that locate the visual stimulus in space. The various stimulus situations can be monitored by particular combinations of "specialized" feature- and space-selective

neurons that are connected to the corresponding motor systems, thus representing a "sensorimotor interface" (see Appendix). Modulatory inputs – related to attentional factors, motivation, and learning – make such releasing systems adaptive to changes in internal and external conditions.

The experimental approach involves neuronal recording from and electrical stimulation of behaving and paralyzed toads as well as retrograde filling and antidromic firing of tectal cells via axons travelling to bulbar/spinal systems.

6.1. Specialized neurons

Compared to other tectal neurons, class T5(2) neurons display a kind of specialization for extracting configural features characteristic of prey (Ewert 1974; von Wietersheim & Ewert 1978). When in the following description of neurons the adjective "specialized" is used, this refers to a specific selectional property (not necessarily excluding other properties).

Class T2, T4, and TH4 neurons are specialized to obtain visual information from large distinctly organized receptive fields (Figure 15A) suitable for arousing or selectively sensitizing an RM (Brown & Ingle 1973; Ewert 1971; Ewert & Borchers 1971; Gaillard & Galand 1979; Grüsser & Grüsser-Cornehls 1970; Lettvin et al. 1961). The locus of a stimulus in the x-y coordinates of the visual field can be determined by information from a number of T5(2) or T5(1) neurons with relatively small, partly overlapping, receptive fields (Figure 15B). Depth estimation along the z-axis may involve binocular class T1(3) neurons specialized to receive inputs from relevant ("disparate") areas of both retinae simultaneously (Figure 15C) (e.g., see Grüsser & Grüsser-Cornehls 1976), a property resulting from special neuronal circuitry (e.g., see Grubberg & Lettvin 1980; Grubberg & Udin 1978; cf. also Collett & Udin 1983). The monocular class T3 neurons (Figure 15D) are specialized in that the approach of a small object along the z-axis is required to drive the cell maximally, a characteristic that can be used in judging object distance (Grüsser & Grüsser-Cornehls 1976).

6.2. Tectobulbar/spinal output

6.2.1. Physiological and anatomical evidence. Questions related to the access of these "specialized neurons" to motor systems have been investigated in paralyzed toads by extracellularly recording their antidromic activation in response to an electrical stimulus applied to the tectospinal/bulbar tracts in the medulla oblongata (Satou & Ewert 1985). We have recorded class T1(3), T2(1), T3, T4, T5(1), T5(2), and T5(4) neurons that were activated antidromically by contralateral bulbar stimulation (e.g., see Figure 21A). Among type T2(1), T4, and T5(1), however, not all recorded neurons could be backfired, suggesting that there is a distinction within a class (response type) between "locally interacting" (processing) and tectobulbar/spinal projecting (processing and transmitting) neurons. In this context, it is important to note that all investigated T5(2) neurons from frontal and extrafrontal sites of the tectal visual map could be backfired (Satou & Ewert 1985; Buxbaum-Conradi & Ewert, unpublished data). This indicates that the results of prey feature

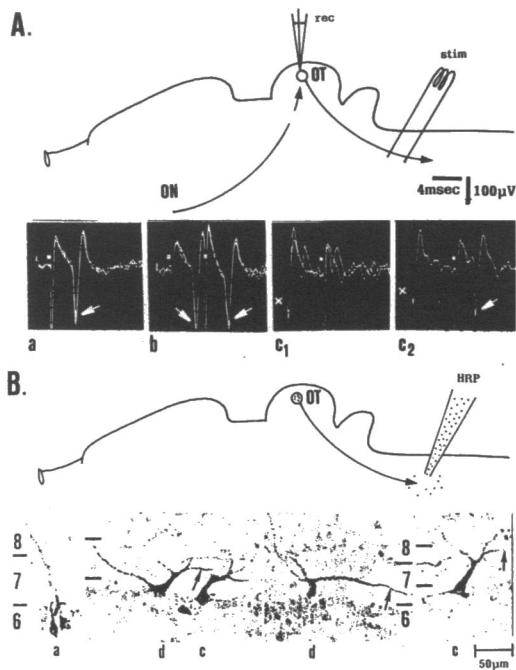


Figure 21. Neurophysiological and anatomical specification of tectobulbar/spinal output in paralyzed toads. (A) Antidromic activation ("backfiring") of a physiologically identified tectal class T5(2) projective neuron in response to a 0.1 ms electrical stimulus applied to the contralateral caudal medulla oblongata through bipolar electrodes; (a) constant latency response (several superimposed traces); the onset of electrical stimulation is marked by a small spot (followed by the stimulus artifact) and the antidromic spike is indicated by an arrow; (b) following ability with electrical double stimuli at intervals down to less than 4 ms; (c) collision between a visual spike (indicated by a cross) and an electrically evoked antidromic spike at a critical spike-stimulus delay of 5.1 ms (c₁); no collision (see arrow) at 5.9 ms (c₂). Extracellular records (Satou & Ewert 1985). (B) Retrograde labeling ("backfilling") of tectobulbar/spinal projective cells following application of horseradish peroxidase (HRP) rostral to the hypoglossal nucleus in the contralateral medulla oblongata. The backfilled cells in tectal layers 6/7 correspond to pear-shaped (a), large ganglionic (d), and pyramidal neurons (c); see also Figure 13Ab (from Weerasuriya & Ewert 1981).

analysis in various parts of the visual field are transmitted by T5(2) neurons to bulbar/spinal motor systems.

The morphological types of tectobulbar/spinal projective neurons have been investigated by injecting horseradish peroxidase (HRP) unilaterally into the medulla oblongata (Weerasuriya & Ewert 1981; for results in frogs see Ingle 1983). In toads, retrogradely filled cells (ganglionic, pyramidal, and pear-shaped neurons) are found on top of layer 6 or at the border of layers 6/7 in both tecta (Figure 21B) – particularly dense in the contralateral tectal hemisphere and especially in the lateral corner – from which neurons with prey-selective and localization properties can be recorded (for complementary investigations in frogs using cobalt labeling, see Lázár et al. 1983; Tóth et al. 1985). Furthermore, retrograde tracing studies with HRP and cobalt techniques have provided evidence of pretectobulbar/spinal projective neurons (Ingle 1983; Tóth et al. 1985; Weerasuriya & Ewert 1981).

6.2.2. Brain stimulation and recording in behaving toads.

Telemetric single cell recordings, electrical stimulation,

and marking via the same microelectrode in freely moving preparations show that orienting and snapping are elicited from appropriate retinal central projection fields in the tectum (Pinkwart & Borchers, unpublished data; see also Ewert 1967b; 1967c; and Figure 9A,B). For example, teletimulation close to a previously recorded T5(2) neuron elicits orienting movements approximately in register with the position of the center of the neuron's receptive field as measured before the animal starts to turn. Stimulation at sites representing the lateral visual field triggers successive turning responses of about the same amplitude; increasing the current or the impulse frequency leads to a decrease in response latency and an increase in turning frequency.

Correlations between visual stimulation, T5(2) neuron firing, and prey-catching activity have been obtained during chronic extracellular recordings in the freely moving toad before and after a DC-induced ipsilateral pretectal lesion applied with a separate electrode. Strong activity of a T5(2) neuron in response to prey precedes the orienting and the snapping response, respectively (Borchers et al. 1983; Megela et al. 1983; Schürg-Pfeiffer & Ewert, submitted). Pretectal lesion-induced "disinhibition" of the same T5(2) neuron was reflected in the toad's disinhibited prey-catching behavior.

6.3. The "command releasing system" concept

It must be borne in mind that (1) the release of each prey-catching action pattern (o, a, f, s) requires basically the same prey feature analyzing processes but different localization mechanisms, that (2) specialized neurons with feature-analyzing and space-monitoring properties project directly to bulbar/spinal motor systems, and that (3) electrical stimulation in the close vicinity of these neurons elicits prey-catching. It is reasonable to suggest that the activation of the corresponding motor pattern generators – in a manner similar to an AND-gate – requires simultaneous activation of appropriate combinations of specialized neurons. Generalizing Kupfermann and Weiss's (1978) definition of "command systems," we call such a combination a "command releasing system" (Figure 22). Its components (specialized neurons), the "command elements," operate between sensory and motor systems and are thus part of a sensorimotor interface (see Appendix). Their simultaneous activation represents "prey" and its "location in space," and this produces the command to activate the related behavioral response. The idea is that different stimulus situations related to an object can be monitored by activity in certain combinations of different types of neurons specialized for feature analysis (class T5(2)) and localization (e.g., T1(3)), and probably for arousal (e.g., T4), and that T5(2) neurons with feature-selecting properties are shared in each combination (Ewert 1980), for example:

$$\{(T5 \cdot 2')(T4)\} \quad \{(T5 \cdot 2')(T2 \cdot 1)(T1 \cdot 1)\}$$

ORIENT APPROACH

o a

$$\{(T5 \cdot 2')(T1 \cdot 2)\} \quad \{(T5 \cdot 2'')(T1 \cdot 3)(T3)\}$$

FIXATE SNAP

f s

() command element

{ } command releasing system (CRS)

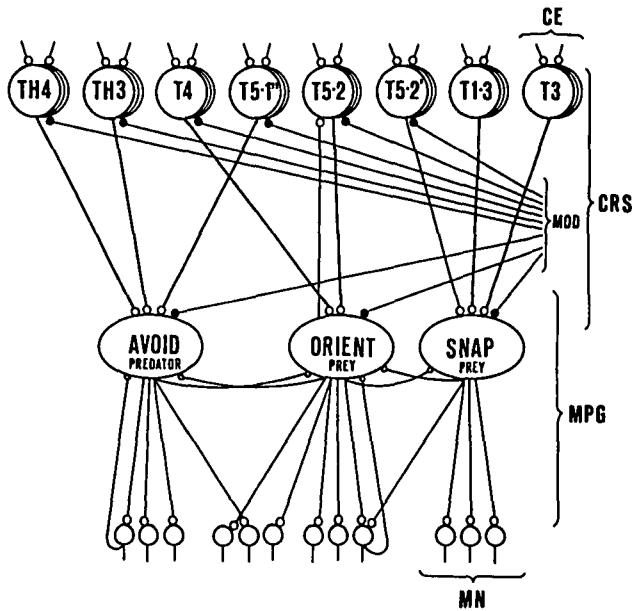


Figure 22. Command releasing systems. Triggering a motor pattern generating circuit (MPG) for an action pattern requires inputs of a certain combination of specialized neurons functioning as command elements (CE). Such a combination is called a command releasing system (CRS). Modulatory influences (MOD) may enter a CRS at the level of particular command elements. Upon activation by the CRS, a specific "routine" is called into play in the appropriate MPG to produce a spatiotemporal pattern of excitation and inhibition to coordinate the activities in the corresponding motoneuronal pools (MN). Among the various CRSs, and MPGs, respectively, certain neurons may be shared. A circle stands for a set of neurons belonging to the same class; an oval symbol stands for a circuit; small circles indicate excitatory or inhibitory inputs (after Ewert 1980, 1985).

According to this hypothesis, CRSs provide "sensorimotor codes" and are neuronal correlates of RMs. Command elements may be compared to a key-board (to use an analogy of Hoyle's, 1984) on which certain combinations elicit specific responses (see also Figure 1): "stimulus moving somewhere in the visual field (class T4)" and "stimulus recognized as prey, n degrees outside the fixation area (class T5·2)" yield the command to orient (o); "stimulus moving in the frontal visual field (class T2·1)" and "stimulus recognized as prey" (class T5·2') and "stimulus far afield (class T1·1)" yield the command to approach (a); "stimulus recognized as prey near the fixation area (class T5·2") and "stimulus close to the toad (class T1·2)" yield the command to fixate (f); "stimulus recognized as prey inside the fixation area (class T5·2'"') and "both retinae adequately stimulated (class T1·3)" and "stimulus within snapping distance (class T3)" yield the command to snap (s).

In these systems, prey-selective neurons of the type T5(2) are essential and decisive for prey-catching. If they are not appropriately activated, no prey-catching command by any CRS can be executed; if these neurons lose their prey-selective properties (after pretectal lesions), any moving visual stimulus sufficiently activates the prey-catching CRSs (for modulatory processes see sect. 6.4.4).

Additional or alternative elements of CRSs remain to be discovered. As an example of additional command

elements, the CRS for orienting toward prey may include prey-selective T5(2) and "minifield" T7 neurons whose tiny ERFs of 4 to 6° in diameter would, according to Ingle (1983a), be particularly suitable for accurate stimulus localization in x-y coordinates. In such a case, Schneider's (1969) "two visual system concept" for functions related to stimulus recognition and localization might be traced back to two classes of neurons (functional units) operating in a CRS. Unfortunately, it has not yet been possible to backfire any of these minifield neurons by bulbar or spinal electrical stimulation (Satou & Ewert 1985) – which of course does not definitively exclude the possibility of T7-mediated tectobulbar/spinal projections. We are currently inclined to interpret T7 responses as dendritic spikes (e.g., from T5 neurons) after a suggestion by Grüsser and Grüsser-Cornehl (1976). As an example of alternative (or substitute) command elements, it is suggested by Grobstein et al. (1983) that following bilateral tectal ablation, neurons of the lateral torus semicircularis mediate snapping in response to tactile stimulation.

I conjecture that other types of behavior require different sensorimotor codes and are thus released by distinct combinations of command elements, in which certain elements of prey-catching CRSs may be shared. For example, a predator traversing the visual field might yield the command $\{(TH3)(T5\cdot1)(TH4)\}$ to avoid; a startle response to a looming large object could be triggered by $\{(T5\cdot4)(TH4)\}$ or $\{(T5\cdot4)(T4)\}$. Whereas orienting toward "prey" may be released by $\{(T5\cdot2)(T4)\}$, the orienting command for a different goal – for example, toward "mate" during springtime – could be issued by $\{(T5\cdot1)(T4)\}$, which involves modulatory inputs from motivational systems.

6.4. Modulatory influences

Prey-catching behavior in toads is influenced by (1) motivation (changes attributable to an alteration in the internal homeostatic state of the animal), (2) attention (changes attributable to processes responsible for alertness, arousal, and selective attention), and (3) learning (changes attributable to the history of previous exposure to stimuli). Modulation of stimulus-response relationships in prey-catching could be brought about through modulatory circuits acting on the stimulus-response mediating CRS. [See also Toates: "Homeostasis and Drinking" *BBS* 2(1) 1979; Johnston: "Contrasting Approaches to a Theory of Learning" *BBS* 4(1) 1981; Vanderwolf & Robinson: "Reticulocortical Activity and Behavior" *BBS* 4(3) 1981]

6.4.1. Motivation. Prey-catching commands cannot be executed if the toad's motivation is not appropriate. Modulatory inputs may be acting on the CRS by influencing the T5(2) prey-selective command elements (Figure 22). In summer, during the hunting season, responses of T5(2) neurons to prey cues are very weak in satiated animals, suggesting inputs related to the nutritional state. In winter, during the hibernation period, both prey-catching motivation and the activity of class T5(2) neurons are extremely low in laboratory animals (Ewert 1984a), suggesting hypothalamo-hypophysial influences (Diericky 1969; Hanke 1976) known to project to deep tectal layers (Wilczynski & Northcutt 1977). In spring, during the mating season, the threshold for visually released escape is high and prey-catching appears to be turned off,

whereas visually guided appetitive orientation and approach behavior by the mating-motivated male toward the female are turned on (Heusser 1959; Kondrashev 1976). Presumably, the T5(2) prey-selective command elements in the CRSs for prey-related orienting and approaching are functionally replaced by T5(1) projective neurons of layer 6/7, specialized in this context for partner detection. It has not yet been possible to identify responses of class T5(2) neurons in male or female toads during the mating period (Ewert 1984a), which suggests that there is inhibitory input to these neurons from changes in the balance of sex hormones (Guha et al. 1980; Heusser 1959).

6.4.2. Attention. Whereas the above-mentioned modulatory effects refer to long-term adjustments, prey-catching is also subject to short-term attentional shifts. Chronic extracellular recordings from T5(2) prey-selective neurons in freely moving preparations within an experimental observation period of about 20 minutes show that at the times when toads are not behaviorally responsive to prey, the discharge frequency elicited by an optimal prey object averages markedly less than at the times when the animal is prepared to attack (Schürg-Pfeiffer & Ewert, submitted).

The toad's readiness to respond seems to be reflected, or monitored, by spontaneously active class T8 neurons frequently recorded from deep tectal and from tegmental areas (Borchers 1982; Borchers & Pinkwart 1983; Ewert 1980). The mildly fluctuating discharge frequency of these neurons averages around 6 impulses/sec when the toad is sitting still; and increase in the frequency to a certain level (about 40 impulses/sec) – comparable to a kind of "warming-up" (Hinde 1954) – then literally predicts a subsequent spontaneous movement of its head or legs. Such a T8 "movement cell" cannot be activated directly by sensory stimuli, but during periods of spontaneously increasing spike frequency a visually driven behavioral response is elicited more frequently. Each action pattern in response to prey, for example, is introduced by a short strong burst of the "movement cell." A mechanism accounting for this modulation might be excitatory input from T8 "movement cells" of deep tectal layers to T5(1) feature-sensitive cells of layer 8, so that the response of T5(2) prey-selective command elements of the output layer 6/7 would be enhanced if activity in T8 overlapped in time with the response to the visual stimulus. A similar explanation has been suggested by Wurtz (1979) for enhancement effects in collicularly controlled eye movements in monkeys.

6.4.3. Visual habituation. Long-term repetitive presentation of the same visual prey object leads to stimulus-specific aftereffects (Ewert 1967a; Finkenstädt & Ewert, submitted). These are presumably associated with a "negative value" by telencephalic "habituation neurons" and translated into a buildup of inhibition on tectal T5(2) command elements, which is mediated via thalamic relay neurons. Computer simulations of model networks suggest that in the course of such a hypothesized process, an "image" of stimulus cues may be stored in prosencephalic structures that is then compared with the present stimulus (Lara & Arbib 1985). Mapping of cerebral glucose utilization has shown that visual habituation in response

to prey is accompanied by strong 2DG-uptake in the posteroventral medial pallium (vMP), whereas central and ventral layers in the optic tectum display a dramatic decrease of 2DG-uptake. Bilateral lesions to the vMP impair habituation or "wipe out" the aftereffects in previously habituated toads (for details see Finkenstädt & Ewert, submitted).

6.4.4. Associative conditioning. Prey-selective properties can be modified or extended through learning (cf. sect. 3.4.2.). There are different ways of explaining these behavioral changes in terms of circuit modulations: (1) As a result of "visual/visual" (worm/hand) conditioning during hand feeding (Figure 23A) there could be long-term modifications of the properties of T5(2) prey-selective command elements if hypothetical "associative As neurons," receiving repeated concurrent inputs from T5(2) and TH3, developed a sensitivity to TH3 input and then, by recurrent inhibition, attenuated the inhibitory influence of TH3 on T5(2). This could explain why D(W,A) values are decreased and why large nonprey stimuli elicit prey-catching. It is interesting to note that in the posterior vMP there is a learning-dependent 2DG uptake and that bilateral lesions to this structure in conditioned toads abolish the effects of hand feeding, whereas in naive animals comparable lesions prevent this sort of associative conditioning (see Finkenstädt & Ewert, submitted). (2) The properties of T5(2) neurons might be changed temporarily by hypothetical "associative As' neurons" (e.g., receiving excitatory visual T5(2) and olfactory input) if, and only if, the conditioned stimulus (prey odor) were present (Figure 23B). This would explain why configural prey discrimination is impaired in the presence of a familiar prey odor. (3) The existing prey recognition properties could be extended by an "associative

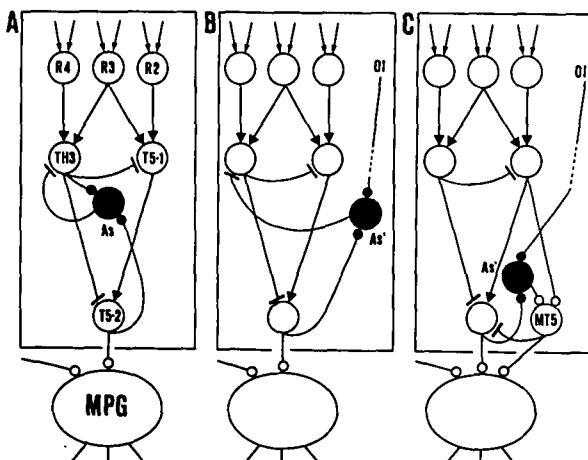


Figure 23. Speculative approach to the dynamic aspects of feature-selective properties in CRSs. Modulation by associative conditioning might act on a CRS either by influencing the property of T5(2) command elements in changing the network characteristics of the corresponding prey feature analyzing neuronal assembly (A,B) (cf. Figures 19Aa and 22) or by functionally replacing T5(2) in activating substitute modulatory command elements mT5(C). As and As': hypothetical associative neurons; OI: olfactory input; mT5: hypothetical command element mediating "associative" messages; arrows: excitatory inputs; small open circles: excitatory inputs to an AND-gate; small solid circles: associative concurrent excitatory inputs; lines with cross bars: inhibitory inputs. (For explanations see text.)

As'/mT5 unit," whose hypothetical modulatory mT5 command elements would be activated only in the presence of the associated (e.g., olfactory) stimulus and, while inhibiting T5(2) neurons, mT5 might take over T5(2) function (Figure 23C).

6.4.5. Internal loop operations. What are the potential routes through which modulatory signals could reach the tectum? Various diencephalic structures are involved in circuits (Figure 24A) by which striatal and pallial telencephalic influences could determine or modulate feature-selective properties of tectal CRSs (Ewert 1967a; 1980; 1987; Kicliter & Ebbesson 1976; Neary & Northcutt 1983; Northcutt & Kicliter 1980; Reiner et al. 1984; Wilczynski & Northcutt 1977; 1983a; 1983b). One such internal loop (1) is concerned with the striatum ("paleostriatum") and involves the lateral forebrain bundles; the retina projects via the optic tectum (OT) to the lateral anterior thalamic nucleus (La) and from there to the striatum (STR), which

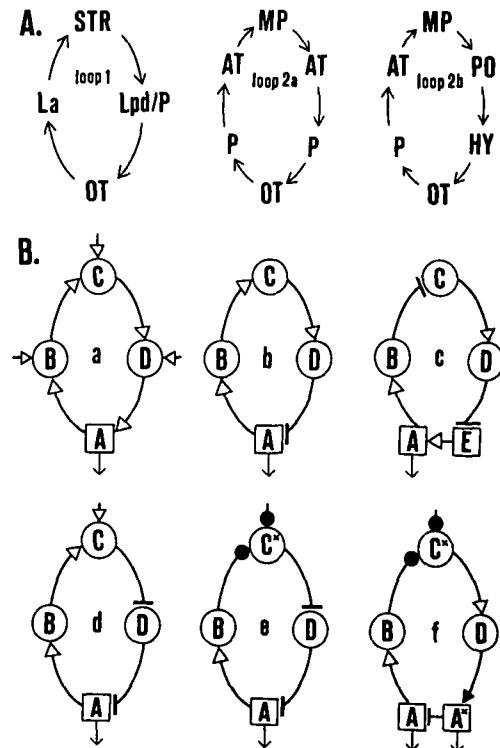


Figure 24. Concept of "internal loops" by which prosencephalic structures might determine the properties of tectal neurons and modulate their respective activities. (A) Anatomical substrates (according to data by Neary & Northcutt 1983; Wilczynski & Northcutt 1977; 1983a; 1983b). HY: hypothalamus; PO: preoptic area; for other abbreviations see Figure 8. Arrows indicate projecting pathways. (B) Simple diagrams illustrating several possible loop operations in hypothetic neural structures A,B,C,D exerting effects on A: (a) integration ("priming"), (b) buildup of inhibition ("screening"), (c) polysynaptic disinhibition ("arousing"), (d) disynaptic disinhibition ("gating"), (e) associative disinhibition ("modifying"), or (f) associative inhibition ("replacing/extending"). Arrows: excitatory influences; small solid circles: associative concurrent excitatory influences; lines with cross bars: inhibitory influences. A stands here for tectal T5(2) command elements and A* for a substitute command element; C refers to telencephalic, B and D to diencephalic, and E to tegmental reticular structures; retinal inputs are not shown.

in turn feeds back to the optic tectum via the pretectal Lpd/P nuclei or tegmental cell groups. Another loop (2) is concerned with the medial pallium ("primordium hippocampi" of Herrick 1933) involving the medial forebrain bundles; the retina projects directly (or via the optic tectum and the pretectal P nucleus) to the anterior thalamus (AT) and from there to the medial pallium (MP), which in turn feeds back to the tectum, either in the same way (loop 2a), or via the preoptic area (PO) and the hypothalamus (HY), sending axons to deep tectal layers (loop 2b).

Loop operations might be concerned with: (1) the integration of external and internal excitatory inputs (e.g., "priming" or "warming up" a CRS, Figure 24Ba), (2) the buildup of stimulus-specific inhibition (e.g., "screening" a CRS, Figure 24Bb), (3) polysynaptic disinhibition (e.g., "arousing" a CRS, Figure 24Bc), (4) disynaptic disinhibition (e.g., "gating" a CRS, Figure 24Bd), (5) associative disinhibition (e.g., "modifying" a CRS, Figure 24Be), and (6) associative inhibition (e.g., "extending" a CRS by replacing an innate feature-selective command element, Figure 24Bf). I suggest that the innate prey-selective properties are mediated by loop 1 (as illustrated in the wiring shown in Figure 24Bd), whereas the modulating influences are integrated through loops 2a and b (e.g., according to Figure 24Bb,c,e, or f). Needless to say, the diagrams shown in Figure 24B are rather simplistic representations of complex processes, but I think they are nevertheless useful conceptual guides for experimental approaches (e.g., see Ewert 1987; Finkenstädt et al. 1986; Finkenstädt & Ewert 1985).

6.5. Premotor networks

There is to date no evidence that tectobulbar/spinal output mediated by command elements impinges directly on tongue, neck- or limb-muscle motoneurons (Grobstein et al. 1983; Satou et al. 1984; Székely & Czéh 1976; Weerasuriya & Ewert 1981). A motor pattern generating internuncial network with the following properties thus appears to exist (see also Doty 1976): (1) The integration of sensory input provided by command elements of the corresponding CRS activates the network if, and only if, a specific (combination of) input occurs; (2) an intrinsic pattern of neuronal connectivity between tectal output and motoneurons assures the generation of a consistent spatiotemporal distribution of excitation and inhibition; (3) the output of the network, mediated by premotor neurons, has privileged access to the requisite motoneuronal pools; (4) particular command elements, through positive feedback from the network they excite, can take part in the temporal program of a motor pattern; (5) motoneuronal and proprioceptive feedback can play a role in the coordination and maintenance of a motor pattern.

General assessments of motor pattern generation and its comparative aspects have been discussed elsewhere (e.g., by Massion et al. 1983; Roberts & Roberts 1983; Russel & Hartline 1978; Selverston 1980; Sjölund & Björklund 1982; Székely & Czéh 1976). Little is known about related functional processes in visually guided behaviors of amphibians. In the present context I will focus on two issues.

6.5.1. Behavior-related efferent channels. The backfiring studies (sect. 6.2.1) in conjunction with the data presented in Figures 4A,B and 16C show that the results of prey-feature analysis for different parts of the visual field are transmitted by T5(2) neurons to bulbar/spinal motor systems (see also Figure 18Ac). So far, it has been possible to "backfire" all recorded T5(2) neurons by contralateral bulbar stimulation electrode positions (except for one case in which an ipsilateral stimulation site was effective). None of these results support Ingle's (1983a) suggestion that T5(2) efferents project exclusively ipsilaterally and are "monopolized" for snapping:

As J.-P. Ewert proposes, T5-2 neurons are of critical importance in initiating feeding responses, and they may be the source of ipsilateral projections which control the lunge-and-snap response. But, I propose that T5-2 neurons are not the source of efferents [contralateral projections] which activate the motor mechanism for turning. However, T5-cells might provide facilitatory input necessary to activate the turn-generating system. (Ingle 1983a, p. 210)

Putting aside the question of whether we can really distinguish as yet between T5(2)-mediated efferents that on the one hand "activate" a motor pattern generating system and on the other hand "provide facilitative input necessary to activate," I suggest that both turning and snapping motor systems receive prey feature-related command signals from T5(2) neurons of the corresponding tectal map in layers 6/7 via crossed and uncrossed descending axons. It seems likely that fibers running in the crossed tectospinal pathway are essential for turning, whereas those in the uncrossed tectobulbar tract are critically involved in snapping. Ingle (1983a) has shown that selective transection of the crossing tectospinal projecting fibers impairs turning toward prey but not snapping for appropriate stimulus positions.

6.5.2. Search for the sites of sensorimotor integration. The tongue in amphibians is an effector specific to feeding. The motoneurons controlling the toad's tongue flip are situated in the hypoglossal nucleus of the caudal medulla oblongata. Their topography has been investigated by retrograde cell labeling using HRP (Weerasuriya & Ewert 1981). Results from intracellular recordings of these motoneurons in response to unilateral or bilateral electrical stimulation of tectal output fibers near the "snap evoking area" (Figure 9B,C) provide evidence of di- or polysynaptic tectohypoglossal connectivity and bilateral convergence (Satou et al. 1984). Regarding the search for interneurons it is interesting to note from previous neuroanatomical degeneration studies that there are tectofugal projections to the medial reticular formation of the medulla (Lázár 1969; Rubinson 1968). This accords with results from antidromic stimulation (Buxbaum-Conradi & Ewert, unpublished data; see also Satou & Ewert 1985) and retrograde labeling studies using HRP (Figure 21B) (Weerasuriya & Ewert 1981).

The medial-ventral part of the central gray of the medial reticular formation has long been proposed to be involved in motor pattern generation for various action patterns (see Ebbesson 1976 and Nieuwenhuys & Opdam 1976 for reviews). Functional explorations of this region by extracellular single cell recording (Ewert et al. 1984; Ewert et al., submitted) and intracellular recording and

labeling (Schwippert & Ewert, submitted) in lightly paralyzed toads have revealed various types of neurons displaying the following properties: (1) configural stimulus sensitivity or selectivity similar to that of T5(1), T5(2), T5(4) and TH3 neurons; (2) selectivity for direction of movement in visual neurons with wide receptive fields; (3) binocularity similar to that of T1(3) neurons; (4) wide receptive fields like those of T2, T4, and TH4 neurons; (5) integration of visual and cutaneous input by wide-field neurons; (6) spontaneous activity; (7) "warming up" and reverberation; (8) cyclic activities consisting of several short equidistant spike bursts occurring either spontaneously or, sometimes, after visual or tactile stimulation; (9) premotor characteristics, since some of these cells could be "backfired" by electrical stimulation in the hypoglossal or spinal motor areas, suggesting ipsi- and contralateral descending axons. The recording sites of these neurons overlap with the location of cells that were "backfilled" after iontophoretic injection of HRP into the caudal medulla oblongata (Weerasuriya & Ewert, submitted).

Tonic discharges, cyclic bursting, and reverberatory activities, in conjunction with the integration of sensory input, appear to be characteristic general features of motor pattern generating circuits responsible for fixed action patterns (e.g., snapping, gulping, yawning, calling), optokinetic movements (e.g., eye and head nystagmus), and autonomic functions (e.g., respiratory movements). At present, however, nothing can be said with confidence about correlations between the responses of the recorded medial reticular neurons and prey-catching behavior. It seems probable that certain neurons are components of different pattern generating circuits. For example, the program for the snapping swallowing action involving rhythmic eyeball retractions accompanied by buccal cavity movements for gulping prey could take advantage of the properties of cyclic bursting neurons which may also be involved in respiratory and calling movements. Multiple single cell recordings in the behaving toad are presently being carried out in our laboratory to examine coincidence properties, phase-locked activities, and premotor functions.

6.6. What are the general properties of command releasing systems (CRSs)?

Command releasing systems (CRSs) are the neurophysiological equivalents of releasing mechanisms (RMs). They are the means by which animals categorize and localize objects (when attention and motivation are appropriate). In a broad sense, they link sensory processes and motor functions and can be described as a sensorimotor interface in that (1) they combine stimulus feature analysis and localization; (2) they link sensory analysis and command functions by activating the motor pattern generating system in response to specific sensory input; (3) they may participate in the temporal sequence of certain motor patterns through feedback of the motor pattern generating network; and (4) they integrate the input of modulatory circuits. Properties (2)-(4) in particular have been analyzed in great detail for command functions related to motor pattern generation in invertebrates (e.g., see Davis & Gillette 1978; Davis & Kovac 1981; Gillette et al. 1978).

The concept of "command neuron," originally developed in invertebrate neuroethology (Wiersma & Ikeda 1964), has received its main support from experiments showing that intracellular electrical stimulation of a single physiologically characterized and morphologically identified cell triggers the motor program of a fixed action pattern (Davis & Kovac 1981; Eaton 1983; Hoyle 1977). Kupfermann and Weiss (1978) proposed the concept of a "command system" for the release of those action patterns in which it was not the activity of a single command neuron but the concurrent activation of several neurons of the same type (command elements) that was necessary and sufficient to activate the motor pattern generating circuit. There are problems with the experimental usefulness of this concept because it is not yet technically possible to depolarize, hyperpolarize, or eliminate all the appropriate cells of a command system simultaneously in order to check its conformity with the "necessity/sufficiency" criteria. The present concept of "command releasing system" (Ewert 1980) involves "sensorimotor codes" and is thus a system comprised of differently specified command elements each corresponding to a small population of neurons. The CRS concept does not rely rigorously on the necessity/sufficiency definition in that it includes the possibility of alternatives (co-existing circuits) and modifications (plastic mechanisms). CRSs have several important features:

1. CRSs are economical, since certain command elements can be shared by different systems (Figure 22). Feature-selective command elements (such as T5(2) neurons) participate in the different CRSs of goal-related (e.g., prey-catching) action patterns and are thus essential and decisive for a behavioral sequence. State-dependent inputs to these neurons would be powerful tools to switch a behavior (e.g., prey-catching) on or off, whereas orienting toward and approaching other goals (e.g., a sexual partner) can be released by the same space-monitoring neurons in combination with other appropriate feature-selecting command elements.

2. A command element does not necessarily correspond to a single neuron; it can be a small population of adjacent neurons of the same class which have similar thresholds and whose receptive fields partly overlap. This assumption has two desirable features: First, it is extremely unlikely that a prey object activates just one T5(2) neuron; second, stimulus localization by a T5-type neuron with an ERF of 20–30° would be inaccurate compared with the information provided by cooperating adjacent T5-type neurons whose receptive fields included a small common area.

3. Command elements may have disproportionate distributions in visual maps. The frontal visual field requires more discrete perceptual operations than the extrafrontal field. This may explain why the frontal visual field in central tectal layers displays a greater density and variety of tectobulbar/spinal projective neurons (Satou & Ewert 1985; Weerasuriya & Ewert 1981); this would also agree with the idea of a "central fovea" (sect. 4.3).

4. The outputs of a distinct combination of command elements "converging" to meet the criterion for a CRS need not impinge on one cell, but may do so on different cells of the motor pattern generating network. Convergence of appropriate activities in a CRS is required to bring the central pattern generator into action.

5. Estimating absolute object size is an important function of the CRS, involving different depth cues in the visual field. This information comes from the lens accommodation mechanism (for orienting, as shown by Collett 1977) and/or binocular cues (for snapping, as discussed by Collett & Udin 1983). The latter assumption agrees with the evidence that, in snapping, one-eyed toads judge objects on the basis of visual angular size and prefer square or disc-shaped objects of 8° diameter independently of the distance between stimulus and eyes within a range of 15 to 170 mm (Ewert & Gebauer 1973). This could account for an involvement of T1(3) neurons in the CRS for snapping. (For models of depth perception in anurans see House 1984.) The situation becomes complex if toads have to reach the prey by making detours around stationary obstacles, a problem that has been investigated in detail by Ingle (1971; 1977; 1980; 1983) and Collett (1983).

6. CRSs are to some extent plastic. Alternative or substitute command elements – mediating the output of coexisting circuits (functional units) – will make a system resistant to disturbances.

7. CRSs are dynamic. Influences from modulatory circuits involving diencephalic and telencephalic structures make a CRS, which mediates between stimulus and response, adaptive to internal and external signals. Modulatory inputs, for example, may act directly on feature-selective command elements or on certain neurons of the circuitry of the corresponding functional units that determine the feature-selective property. It is likely that certain modulatory influences (e.g., those related to circadian rhythms) also act on the premotor network and/or the motor neurons themselves (e.g., see Parent 1973).

Finally, some remarks on the link between "sensory space" and "motor space" and the corresponding "motor routines": The networks responsible for motor pattern generation are situated in the medial reticular formation of the medulla and the central gray of the spinal cord, both operating in connection with rostral brainstem structures (Comer et al. 1985; Masino & Grobstein 1985; Nieuwenhuys & Opdam 1976; Székely & Czéh 1976; Weerasuriya 1983). The different programs for appropriate spatiotemporal coordination of the motoneurons are partly built into these networks (Székely & Czéh 1976). If adequate signals from a CRS concurrently hit certain elements of the corresponding circuitry, a specific motor routine is called into play. Problems arise with the question of how sensory space (e.g., the x-y positions of a prey object) is translated into appropriate motor space (the turning amplitude of the orienting movements). A plausible mechanism would take advantage of topographical correspondence between retinal x-y positions and "turning routines," mediated by the tectal visual map as an interface. This concept has been critically discussed by Grobstein et al. (1983). Other problems are concerned with the question of how object distance is translated into appropriate "locomotion routines" (e.g., approaching, stalking, leaping), or how "snapping subroutines" (tongue flipping or jaw grasping) are triggered in conjunction with successful or unsuccessful trials depending on the size of the prey object. There are still many open questions about "coordinating principles" (von Holst 1939) in premotor networks that can serve (1) to link different motor pattern generating circuits (MPG) by

mutually influencing each other's response thresholds (e.g., activating the orienting MPG or reducing the threshold of the MPG for snapping), or (2) to establish and to time the complex motor routines required for orienting/jumping, or jumping/snapping (see Weerasuriya 1983 for a discussion).

7. Concluding remarks

Reflecting on the lessons to be gained from the analysis of RMs, I would like to stress three points:

1. *Feature extraction.* The experimental analysis of innate releasing mechanisms has the advantage of exploring the problems of pattern recognition and sensorimotor coordination in "dedicated" systems whose basic properties emerged during evolution. In the toad's environment an object usually has to move before it can be visually classified as "edible" (prey) or "threatening" (predator). Moving objects can be evaluated by a neuronal network that examines their spatial dimensions (the size of their area) in relation to their direction of movement (Figure 4A,B) – a property that is invariant under changes of direction of movement. The neuroanatomical substrates are mutually connected central visual maps (Figure 7) and related structures (Figure 13A,B). The neurophysiological correlate is inherent in specific neuronal integrative functions and interactions (Figure 19) which allow feature-analyzing cells (T5(1), T5(2), T5(3), T5(4), TH3) to extract different spatiotemporal features of moving visual objects (e.g., see Figure 16). These neurons are not "feature detectors" – if we take that term to mean that each neuron or class of neurons is unequivocally responsive to one (and only one) specific feature of a moving stimulus object (in the sense of "one neuron for one feature"). Each type of neuron is tuned to a feature range within a stimulus continuum and displays certain preferences (Figure 16A–C). Distinct neuronal interactions determine space-monitoring properties of T1-, T3-, and T5-type neurons.

Agonistic behaviors such as approach and avoidance are "separated" by sensory filters. The T5(2) prey-filters compare information about spatiotemporal aspects of visual stimuli with stored information provided by specific neuronal circuitry (Figure 19). Their response is hence positively correlated with the probability that sets of configural features fit the prey category. The selective filtering property of T5(2) neurons results from inhibitory thalamic/pretectotectal connectivity, using what Barlow (1985b) would call "veto logic"; the pretectal TH3 neurons (and possibly T5(3)) are likely candidates for exercising a "veto" over the activity of T5(2) cells in response to T5(1) input when the spatial dimensions of a visual object perpendicular to its direction of movement (and/or its overall area) exceed a certain range. The inhibitory thalamic/pretectotectal connectivity determines (1) configural prey recognition, (2) prey/predator discrimination, (3) discrimination of prey from background structures, and (4) discrimination of object motion from self-induced motion.

Prey categorization is approximate, which implies that the category boundaries can be influenced by motivation and learning. Modulatory influences acting either on TH3 or on the T5(2) prey-selective neurons could make

RM's recognition adaptive to internal and external signals so that, under extreme conditions, a toad might even snap at a swarm of prey, a predator, or a moving background structure, if its motivation is sufficient (e.g., see "associative disinhibiton," Figures 23A and 24Be). With the thalamic/pretectal region ablated, T5(2) neurons lose their selective function while displaying excessive excitatory reverberatory activity in response to visual input (Figure 16D), a phenomenon which resembles the "lesion-induced disinhibition" of prey-catching behavior (Figure 5B). Recovery of function, which occurs at a variable rate depending on the site and extent of the ablated area, could take advantage of "self-organizing" intrinsic inhibitory mechanisms in the tectum (Ewert et al. 1983).

2. Comparative aspects. Comparable principles of feature extraction, sharpening of tuning through neuronal interaction, and integration of modulatory inputs have emerged in different sensory systems, ranging from fish to monkey. For example: (1) local interactions of higher-order electrosensory neurons for sign selection of jamming-related signals in electric fish (Heiligenberg 1983; Rose et al. 1986); (2) AND-gate properties of neurons that detect mating calls in the tree frog (Capranica & Moffat 1983); (3) parallel-hierarchical processing of biosonar information in determining the properties of specialized neurons tuned to particular information-bearing parameters or parameter combinations in the mustached bat (Suga 1984); (4) template-matching processes in song learning involving song-specific neurons in the white-crowned sparrow (Konishi 1985); and (5) tuning of face-sensitive and selective neurons in monkey to specific feature combinations (Perrett & Rolls 1983).

Visual RMs discussed in this article involve functions of prosencephalotectal circuits in which "striatal" basal ganglionic and "limbic" medial pallial structures, together with associated thalamic nuclei, are responsible for "innate properties" (striato-pretecto-tectal pathway) and "modifications" (medialpallio-preoptic/hypothalamotectal pathways). In all vertebrates so far investigated, the optic tectum (or superior colliculus, respectively), includes a substrate for sensory integration. This, like the ancient image of Janus's head looking in two directions, constitutes a correlational system for afferent messages and efferent commands in that it links sensory processing and motor functions related to orientational behavior. This system processes information by intrinsic circuitry and is subject to extrinsic shaping, gating, and modulatory influences which arrive from striatal (basal ganglionic) and limbic (medial pallial, hippocampal) structures operating via di- or polysynaptic pathways.

Experimental results from different methodological approaches in anurans and mammals imply that certain structures of the basal ganglia are involved in property-shaping and response-gating effects on tectobulbar/spinal output neurons in the determination of whether or not a behaviorally meaningful stimulus can be taken as a target for an orienting movement (e.g., see Chevalier et al. 1984; Ewert 1967a; 1984a; 1987; Finkenstädt et al. 1986). In anurans, the putative anatomic substrate is provided by a "striato-pretecto-tectal" and a small "striato-tegmento-tectal" pathway (Neary & Northcutt 1983; Wilczynski & Northcutt 1983a; 1983b). In reptiles and birds, the former pathway (striato/pallido-pretecto-tectal) is promi-

nent, whereas another takes the form of a small "striato-nigro-tectal" route (Reiner et al. 1984). According to Wilczynski and Northcutt (1983a), such a "dual-route" system is the ancestral tetrapod condition (see also Reiner et al. 1984). In mammals, the comparable pathway mediated by the substantia nigra is a prominent circuit in this context (besides the main basalganglio-ventrothalamic-motocortical pathway), whereas the one via the pretectum may have been "lost" (Wilczynski & Northcutt 1983a). Despite the absence of homology between the anuran "striato-pretecto-tectal" pathway and the mammalian "striato-nigro-tectal" pathway, the disinhibitory properties of both (as illustrated in the wiring shown in Figure 24Bd) exhibit some interesting similarities which suggest comparable operational principles in subserving the animal's specific behavioral requirements (see Ewert 1987 for a review).

The mammalian hippocampus, together with its limbic connections, obviously influences (modifies) stimulus-response mediation at the collicular level, suggesting that the

hippocampus is not concerned with the initial stages of involuntary orienting to particular spatial locations, but rather with more subtle aspects of stimulus selection and scanning involving much preprocessed information . . . probably relating to subtle stimulus characteristics – stimulus ambiguity, reward significance, and perhaps spatial position. . . [The hippocampus also functions] to detect novelty and, as appropriate, to "block" or "deblock" the arousal system and so to alter motor behaviour. (Foreman & Stevens 1987, p. 108–9)

The amphibian ventral medial pallium too is significantly involved in arousal, stimulus-specific habituation, and associative conditioning (e.g., see sect. 6.4.3., 6.4.4., and Figure 24Bb,e; cf. also Ewert & Finkenstädt 1987; Finkenstädt et al. 1986; Finkenstädt & Ewert 1983b; 1985; submitted). Thus Herrick's (1933) term "primordium hippocampi" for this brain structure is justified not only from anatomical homology but also with respect to functional properties.

3. Sensorimotor codes. The fact that many of the tectal neurons analyzing feature- and space-related cues project to the motor systems supports the hypothesis that particular combinations of their outputs determine the properties of goal-oriented command releasing systems (CRSs) (Figures 22 and 25) – the neurophysiological equivalent of releasing mechanisms RMs (Figure 1). These systems are responsive to a complex of necessary conditions, including alternatives and modifications. CRSs encode the diverse stimulus situations through distinct combinations of specialized neurons involving those with recognition properties – hence providing specific "sensorimotor codes." An action pattern is released according to such a code.

This picture is of course incomplete, given the indirect nature of much of the evidence, the speculativeness of conclusions, probable oversights concerning not yet identified neurons, and the omission of certain stimulus parameters. Relative completeness, however, is not the primary objective here, but the crystallization of principles whereby a brain can derive universals from the visual environment to activate goal-directed behavior. The operations between sensory analysis and motor response – represented by sensorimotor codes – are of general

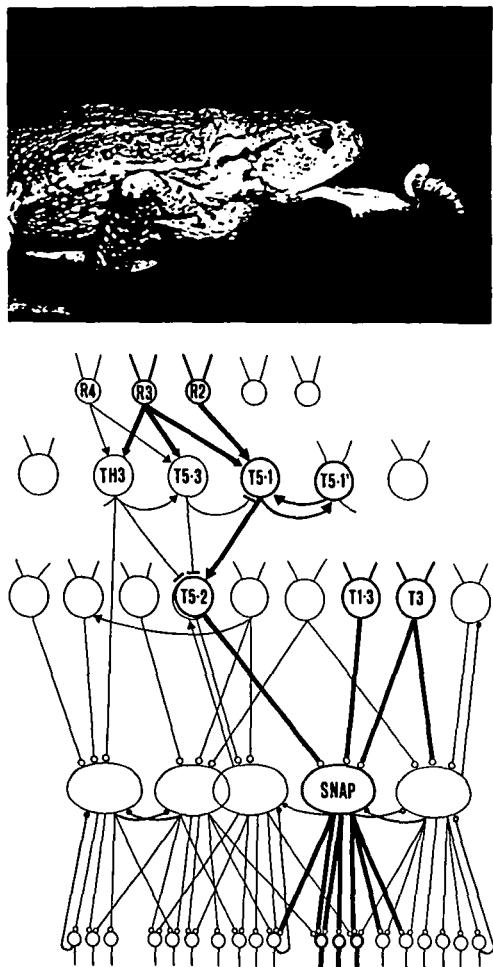


Figure 25. Upper, photo: Toad snapping at prey (photo by H.-C. Meyer). Lower, diagram: Neuronal correlate of the RM for prey-snapping (see thick "labeled lines") inherent in a neuronal network that subserves different feature-analyzing and stimulus-localizing tasks. Each circle symbolizes a set of neurons which belong to the same class; oval symbols stand for neuronal circuits.

importance, since these are in a broad sense related to what we call cognition. The sensorimotor codes of innate RMs can be interpreted as "species-specific cognition," in terms of predetermined categories. "Individual cognition" requires the situation- and context-dependent formation, modification, and recombination of such codes and is in its highest performance manifestations (in primates) not necessarily related to motor behavior. There may not be a fundamental difference between innate and acquired properties in the principles of the neuronal interactions that determine perceptual categories and the formation of sensorimotor codes. One of the critical questions still to be answered concerns how "associative" feature-selective processes become tuned; that is, how novel recognition lines in a feature-analyzing network are "labeled" and acquire access to evaluating and executing systems – connections which have emerged in innate releasing mechanisms (Figure 25) under selection pressure during evolution.

APPENDIX

The following definitions and explanations are formulated for the purposes of this BBS target article and do not necessarily lay

claim to being lapidary. They are presented for the sake of communicative clarity across specialities and to prevent misunderstandings in this peer interaction.

Sign stimulus (synonymous with "key stimulus") refers to a stimulus that represents a behaviorally relevant object by a few characteristic *features* adequate to elicit a fixed action pattern through the activation of an (innate) releasing mechanism (RM). Sign stimuli often have *configural* properties (Tinbergen 1951).

Configuration (in the sense of the German word *Gestalt*) refers to the arrangement (or combination) of the characteristic parts (or features) of an object, whereas "shape" refers more to the form of the object's contour. (Two distinct configurations could, in principle, have identical shapes.) According to Tinbergen (1951), configural properties of a visual sign stimulus are determined by particular inherent relationships (e.g., spatial or spatiotemporal ones) between specific features. The recognition of such a holistic stimulus configuration (a "configural stimulus") is *invariant* under changes of certain stimulus parameters. Depending on the way features are related to each other, we can distinguish between a "static configuration" (disregarding motion) and a "dynamic configuration" (including motion).

Static configuration; an example is shown in Figure 26A: The sign stimulus for the gaping response of blackbird nestlings can be represented by a simple head(*h*)-rump(*r*) model of the parent bird, consisting of two adjacent solid discs of different diameters (Tinbergen & Kuenen 1939). Here *r* and *h* are features; their combination (spatial arrangement) yields the configuration. A characteristic property of a configuration is the nonadditive nature of its parts (features): The algebraic sum of the nestling's responses (*R*) to either feature alone ($R_h + R_r$) is much less than the response to the combination of both features: $R_{(h,r)} > (R_h + R_r) \approx 0$. $R_{(h,r)}$ is maximal if the relationship between the diameters of *h* and *r* is 1 : 3 (Figure 26A, left); this can be best demonstrated by a rump/two-head model (Figure 26A, right). The recognition is invariant under changes of other stimulus parameters such as size (within limits) provided the 1 : 3 ratio is maintained.

Dynamic configurations involve movement and therefore take into account the spatiotemporal relationships between features. An impressive example is provided by the "goose/hawk" phenomenon (Tinbergen 1951) (see Figure 26B): The shape of the model of an airborne bird will be recognized by domestic fowls (or ducks) as a harmless goose if the long neck, oriented parallel to the direction of movement, is in front; but the same model will be recognized as a predatory hawk if the wings, oriented perpendicular to the direction of movement, are in front. A comparable example of dynamic configural properties is provided by the "worm/antiworm" phenomenon (Ewert 1968) (see Figure 26Ca): In toads, the sign stimulus for prey is determined by the spatiotemporal relationships between two features, namely, the area of extension of an object parallel to ($xl(1)$) and perpendicular to ($xl(2)$) the direction of movement. Thus, a stripe will be recognized as prey if its longer axis is in a wormlike orientation (*W*), parallel to the direction of movement ($xl(1) > xl(2)$), but the same stripe will be disregarded as prey or associated with threat if the longer axis is oriented in an "anti-wormlike" (*A*) way, perpendicular to the direction of movement ($xl(2) > xl(1)$). The *W*- and *A*-configurations are defined by the ratio $xl(1):xl(2)$. The *W* versus *A* preference in prey-catching is invariant under changes of other stimulus parameters, such as speed and direction of movement in the *x-y* coordinates of the visual field. The nonadditive character of the various features of a configural stimulus can be shown by another example (see Figure 26Cb), in which a very small black square (*S*) – itself subliminal for the prey-catching response (*R*) – presented in a certain spatiotemporal relation to a wormlike moving stripe (*W*) yields a configuration associated with nonprey or threat (Ewert et al. 1970; see also Ewert & Traud 1979): $R_W > R_{(W,S)} \approx R_S \approx 0$.

Stimulus continuum denotes a spectrum of stimuli resulting

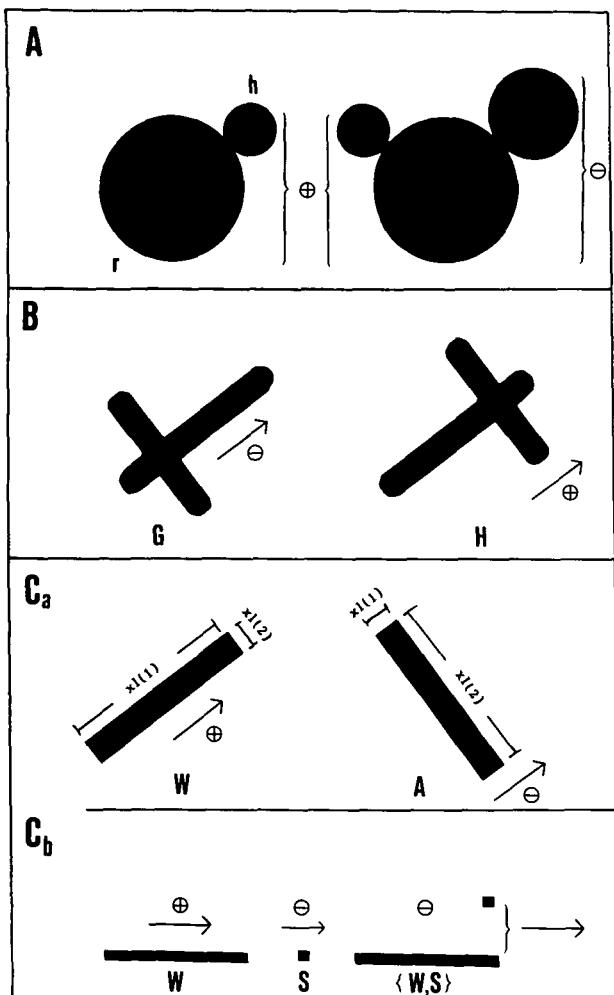


Figure 26. Examples of "static" (A) and "dynamic" (B,C) configurational properties of sign stimuli. (A) The head (*h*)-rump(*r*) model of a parent bird elicits gaping responses (+) in blackbird nestlings if the ratio of head to rump length is 1:3, but the model fails to elicit a response (-) if the difference in size between *h* and *r* is less (cf. "rump/two-head" model) (Tinbergen & Kuenen 1939). (B) The "goose(G)/hawk(H)" phenomenon in domestic fowls (see Tinbergen 1951): With fowls the model of an airborne bird elicits no escape (-) if the long neck leads in the direction of movement (indicated by an arrow), but the same model releases escape (+) if the perpendicularly oriented wings lead. (Ca) The "worm(*W*)/antiworm(*A*)" phenomenon in common toads (see Ewert 1968): A stripe moving in the direction of its longer axis elicits prey-catching (+); but the same stripe remains unresponsive to or is associated with threat (-) if its longer axis is oriented perpendicular to the direction of movement; *xl*(1) is the stimulus side oriented parallel to the direction of movement and *xl*(2) the side perpendicular to the direction of movement (see arrow). (Cb) Illustration of the nonadditive nature of features in a configurational stimulus: Optimal wormlike prey stimulus (*W*); small square stimulus subliminal for prey-catching (*S*); stimulus configuration (*W,S*) associated with threat (Ewert et al. 1970; Ewert & Traud 1979).

from a continuous variation in feature relationships as shown in Figure 27A and B. Various stimulus configurations with different meanings (e.g., *W*- and *A*-configuration, Figure 27A) often pertain to particular points (e.g., the "extremes") of such a stimulus continuum. A certain range within this continuum sets the boundaries of a category; this is a class of behaviorally significant objects that share a set of defining invariant features (see Harnad 1987a; 1987b).

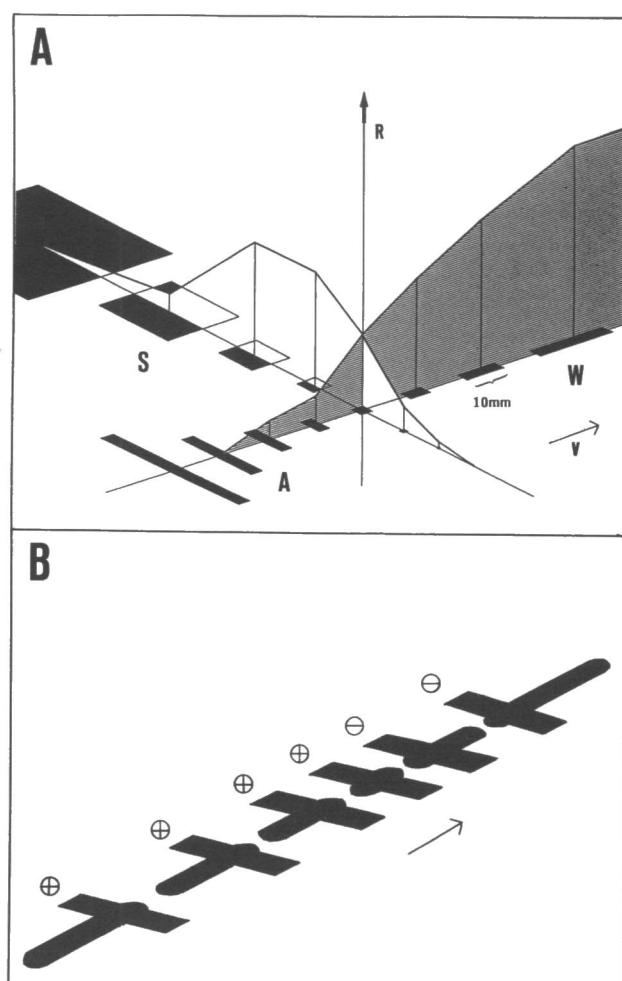


Figure 27. Stimulus continua: Variation of moving stimulus objects in their configurational (spatiotemporal) properties. (A) Stimulus continuum corresponding to changes in black two-dimensional forms in the side parallel (*xl*(1)) and/or perpendicular to (*xl*(2)) the direction of movement for *v* = 23°/sec (see arrow): wormlike (*W*), antiwormlike (*A*), and square (*S*) objects. In this continuum the prey category for toads is described by the corresponding prey-catching orienting activity (*R*) in response to a single object (according to data from Ewert 1969a). (B) Stimulus continuum corresponding to changes of configurational features in models of airborne birds that release escape (+) or remain unresponsive to (-) by domestic fowls; arrow indicates the direction of movement of a single object (according to data from Tinbergen 1951; for a discussion see also Schleidt 1961).

Sensorimotor functions involve neural mechanisms that link afferent sensory processes to motor pattern generation: *Sensorimotor transformation* (or coordination) refers to the operations that translate a specific pattern of sensory input into an appropriate spatiotemporal pattern of excitation and inhibition in motoneurons (the motor pattern), necessary to activate and coordinate the muscle contractions for the corresponding action pattern. (The term *sensorimotor coordination* has a broader applicability in that it also encompasses motosensory coordinating feedback loops.) The "specialized" neurons which encode the outcome of feature/space-related sensory information processing and transmit the resulting information to the "motor pattern generating circuits" (MPGs) are part of the *sensorimotor interface* (see also Scheich 1983). *Sensorimotor integration* refers to the modes by which processed sensory information – mediated by specialized (projective) neurons – is transferred to

and integrated by neurons of the MPG (e.g., AND-gate, OR-gate properties). An MPG is triggered (in much the way a safe is unlocked) according to a sensorimotor code, requiring concurrent activities of specialized neurons in a specific combination. With respect to their efferent effects, the specialized neurons of such a combination are acting as "command elements" and together form a "command releasing system" (CRS), the central core of the "releasing mechanism" (RM). The prefix "command" points to the initiating, primarily ballistic function of the system and "releasing" refers to its coded property (see "sensorimotor code").

ACKNOWLEDGMENTS

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NOTE

1. German text of Grüsser and Grüsser-Cornehls, 1970, p. 215: "die Invariantenbildung Feind, Beute, Versteck usw. vor der motorischen Reaktion nicht erfolgt, sondern die gesamte neuronale Reaktionsfolge, die zu der beobachtbaren Verhaltensfolge führt, *in toto* die Invariantenbildung darstellt."

retina, tectum, and pretectum in prey recognition in toads; moreover, he has from the first been concerned with another level of interaction – that between theory and experiment. In particular, he has been a generous critic of models developed by Rolando Lara, myself, and our students (some of which are reviewed in my accompanying target article). In his present target article, Ewert not only presents his classical pattern-recognition studies but also introduces new data vital for the further development of models of visuomotor coordination. However, there are many data needed for modelling that are not yet available. Let me, then, focus on several such issues to develop the theme of the fruitfulness of interaction between theory and experiment in neuroscience.

Reexpressing Ewert's concepts in the language of perceptual and motor schemas (see my accompanying target article), we may say that, in Figure 1, Ewert introduces four motor schemas: orient, approach, fixate, and snap. In Sections 2.2 and 2.3, he shows that these need not occur in this generic order – rather, each proceeds to completion (but this appears to be completion of the control program rather than of the motor activity it normally elicits) to be followed by the execution of perceptual schemas that will determine which motor schema is to be executed next. However, motor schemas may take the form of "compound motor coordinations" (such as the programmed route to its prey observed by Collett 1983, or the snap-gulp-mouthwipe sequence) which comprise a set that will proceed to completion without intervening perceptual tests. This seems to accord some measure of reality to perceptual and motor schemas, but it also raises quite crucially the experimental question: Having determined the patterns of neural activity which embody two schemas, determine what it is about such ensembles that corresponds to the statements (a) schema A proceeds to completion; (b) completion of schema A triggers initiation of schema B; or (c) schema A passes parameter x to schema B.

To use the language of Ewert's Figure 22, we may pose the related question: What is the pattern of neural activity in a CRS (command releasing system) which serves to trigger an MPG (motor pattern generator)? In the toad studies, a schema and its instantiation usually appear to be coextensive – instantiation of a schema appears to be identifiable with "appropriate" activity in fixed portions of the toad's brain. However, as Figure 22 emphasizes, each schema may involve several cell types/brain regions, while a given cell type/brain region may be involved in several schemas. An intriguing question for future experiments is: How could one detect that schema A had been instantiated in network N when schema A can have multiple instantiations? However, a CRS embodies a perceptual schema that exists for only one purpose – to determine the conditions for the activation of a specific MPG (embodiment of a motor schema) – but the story is more complex than Figure 22 suggests, because the CRS must not only trigger the MPG, but must ensure that, in this case, the resultant movement is directed toward the prey. Each cell of Figure 22 corresponds to an array of cells in the toad's brain. Since cells in each array have overlapping receptive fields, we may pose the experimental question: Can a weak distributed pattern of activity prove as effective a trigger as a stronger localized pulse? What are the necessary conditions for a spatiotemporal pattern of activity (and note from Figure 22 that it may be distributed over several cell types) to serve as trigger? This leads to the technical question: What is the smallest microelectrode array (in terms of both density and number of electrodes) that can let us adequately estimate such spatiotemporal questions?

Until recently, the modelling of amphibian tectal-pretectal interactions was done by informed conflation of data from anatomy and physiology – when the augmented tectal column model of Figure 16(b) of my target article was formulated, no data were available as to the anatomical correlates of such physiologically defined units as the T5(2) cells. Encouraging

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Advantages of experimentation in neuroscience

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More than 10 years ago, at a conference in Portland, Oregon, Curt Boylis presented his model of how the cerebellum might adjust parameters of locomotor synergies (see Szenthágothai & Arbib 1974, Chapter 5, for an exposition). Although the development of the model had involved an exhaustive analysis of the pertinent experimental literature, one neurophysiologist immediately objected to the model: "Your model is based on the data of so-and-so which we have demonstrated in our lab to be mistaken. This just confirms my opinion that modelling is premature." Whereupon I replied, "If anything, your evidence suggests that experimentation is premature!" My point was, of course, simply to emphasize that both modelling and experimentation are incomplete without the other.

Professor Ewert has long analyzed the interactions between

progress has been made with the data of Ewert et al. (1985) and Matsumoto et al. (1986) reported in Ewert's Section 5.3.1. However, we are challenged to further research by the gaps that remain between the augmented tectal column model and the circuits shown in Ewert's Figure 19. The model leads the data in that it postulates connections which have not yet been verified experimentally; moreover, it posits synaptic weights which enable the circuit (or an array of such circuits) to subserve observed behaviors. The important point is that the same anatomical circuit can be shown to exhibit *qualitatively* different behaviors depending on these weights. Thus the experimenter is challenged to better estimate what these weight might be. But in fact the matter is more delicate: In our model and in Ewert's Figure 19 we show a typical cell of each class, with a small set of well-defined synapses whose weights are entered into the model equations. However, a glance at the morphology of the cells in Ewert's Figure 18 makes it clear that each synapse of the model must "lump" a complex aggregate of synaptic interactions in the toad's brain. This calls for intense collaboration between theorist and experimenter to determine what it is that must be measured in the real brain and how it must be transformed to provide testable parameters for the model.

To close this commentary, I want to address a conceptual problem that recurs in Ewert's target article. In Section 3.5.2 we read that "[a naive] animal responds preferentially to particular visual stimuli with motor patterns related to prey-catching; we hence [sic] infer that this is based on comparing the incoming signal with a 'prey image' . . . established . . . during its evolutionary history. . . . More generally, visual pattern recognition is defined here as the assignment of space time-dependent contrast distributions (features) from the visual environment to innate or learned categories that have behavioral significance ('invariants' or 'universals')." Section 5.4 tells us that "Specific neuronal interactions determine the range in the stimulus continuum that defines the prey category. In other words, this connectivity provides the 'prey schema with which visual input is compared.' What is to be noted is that 'comparison with a template-image' is a very special case of 'the assignment of space time-dependent contrast distributions (features) from the visual environment to innate or learned categories.'" In the theory of pattern recognition (e.g., Sklansky & Wassel 1981), one definition of a classifier for a set of patterns $\{p_1, p_2, \dots, p_n\}$ as against a set of nonexamples $\{q_1, q_2, \dots, q_m\}$ within some universe X of patterns is any function $g: X \rightarrow R$ such that $g(p_i) > g(q_j)$ for each i and j . There is nothing that requires that g be based on comparison with a template p_0 so that, for example, $g(x) = k(|x - p_0|)$ for some monotone decreasing function k . Whatever the form of g , we can categorize all patterns by choosing any β such that $g(p_i) \geq \theta > g(q_j)$ for all i and j – and then set $h(x) = 1$ if $g(x) \geq \theta$ and $h(x) = 0$ if $g(x) < \theta$. However, we must note that there are many g 's for which $g(p_i) \geq \theta > g(q_j)$ for all i and j , and thus many dichotomies compatible with the original training sets $\{p_1, p_2, \dots, p_n\}$ and $\{q_1, q_2, \dots, q_m\}$. In particular, it is not clear that there exists a universal "prey." The experimenter can chart the relative efficacy of different patterns in releasing prey-catching behavior, but even for a given animal this can vary under the influence of many factors; there is no guarantee that the releaser of such a behavior meets other criteria for being prey, such as being something the animal can eat to gain nourishment.

It should also be noted that Ewert's own experimental methodology goes beyond assignment to categories. In his Figures 4 and 16, for example, we see that differing patterns yield different response rates, rather than being assigned a 0 or 1 as they do or do not match the concept "prey." We have, as it were, a g but no h . Figure 27 exhibits not an invariant dichotomy but rather a structure of relationships, whose shape can be modulated by many factors, including motivation. In coming to understand the networks that undergird such structures of relationships –

and these are certainly far from template comparison – we may do well to consider (whether on the time scale of evolution, development, or learning) the Markov chain training models for nonseparable classes of patterns given in Chapter 6 of Sklansky and Wassel.

In summary, with its data on behavioral sequences and releasing mechanisms, its morphological and physiological analysis of neurons, its contributions to the study of sensorimotor interfacing, its review of experimental techniques, and its analysis of major conceptual issues in neuroethology, Ewert's target article provides a major stimulus to the interaction of theory and experiment in neuroscience.

Ethology and physiology: A happy marriage

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I have read this survey of the work carried out by Ewert and his group with great admiration, enjoying the design as well as the ingenious experimental techniques. As an ethologist, I was pleased to see how the physiological penetration into the hardware subserving the snapping response was built upon an ethological analysis of its innate releasing mechanism (IRM), a type of work now in danger of being considered outdated.

The IRM concept resulted from one of the first questions raised when ethology began its development as a separate discipline among the behavioral sciences. It concerns the problem of how animals are able to recognize those stimulus situations in their environment that are of functional importance for survival and reproduction. This issue particularly crops up when an animal is observed to respond fully adequately to situations it has never before experienced. It is much less obvious with respect to human behavior, where learning and teaching are likely to be involved. Early experiments on the nature of this responsiveness suggested that the perception of a set of only a few (but very characteristic) elements of the adequate situation (the key- or sign- stimuli) were effective for the triggering of each innate response.

Lorenz proposed that this stimulus selection would be mediated by IRMs in the responding animal, one for each activity. The perceptual processes detected in these experiments were originally thought to be essentially different from recognition processes in humans. This inspired further experiments to explore the IRM, investigating different responses of various kinds of animals. In a black box approach the responses of intact animals to different stimulus situations (dummies) were studied, often in the field. The experiments substantiated the IRM construct and produced further interesting information on the software underlying response release. They showed that sign stimuli can have a configurational character, and that different sign stimuli of the same situation interact according to the principle of heterogeneous summation. At least two different types of internal factors were found to influence the sensitivity of the IRM: the motivational state of the animal and the time elapsed since the previous exposure to the same stimulus (habituation, sensory adaptation, response waning).

Although the results obtained warranted the extension of this software analysis – not in the least to prevent a premature generalization of findings from particular cases – the interest in this work died down in the seventies. One reason was that for its further development greater sophistication of experimental ethological techniques was required; in particular, a rigorous standardization of the test situations. That demand was difficult to fulfill in the field, and in the laboratory it could often only be reached at the cost of the subject's responsiveness. Another

reason was that ethological studies on function, especially those along sociobiological lines, had become fashionable and attracted most of the field workers. As a result, students of animal behavior nowadays tend either to take the classic IRM concept and its derivatives for granted, or reject them as amateurish physiology. Both attitudes are unfortunate since they impede further research. The concepts were never meant to have an explanatory value in themselves and suggestions concerning the underlying physiological mechanisms were only intended to stimulate their investigation and, it was hoped, to guide it. It is therefore gratifying to see that the monumental work of Ewert and his collaborators has indeed developed along this line. Ethological analysis, amounting to an unravelling of the software principles of the programming involved, preceded the meticulous neurophysiological study of the hardware. This demonstrates how the marriage between ethological (software) and physiological (hardware) analysis leads to an increase of our insight into the processes involved. (The advantages of this liaison have become even easier to explain now that we can use the terminology borrowed from the computer!)

Although ethological analysis of the software will serve a further analysis of the hardware best when it proceeds independently of physiological assumptions, in a more advanced stage of the study a careful use of the evidence produced on the hardware can back up the software analysis or help to set priorities among alternative hypotheses to be tested. Correspondingly, the work of the Ewert team can be said to justify the ethological black box approach. For most of the phenomena attributed to IRMs by ethologists, it has indeed turned out to be possible to trace the hardware structures involved. This is true, for example, of the sensitivity to "Gestalts" (sect. 5.2.2). Furthermore, Ewert's work has opened the possibility of understanding on the physiological level how the motivational state of the animal could influence the effectiveness of sign stimuli and how response-decrements may be brought about (sect. 6.4). In the case of the snapping toad, concrete suggestions can be made for circuit modulations inducing changes in the effectiveness of stimuli through learning, which correspond well with modern views in ethology about the interaction of innate and learned information. Although Lorenz never denied that an IRM could become extended by learning processes, his statements strongly suggested that recognition by means of an IRM and by means of knowledge acquired through experience with the adequate situation would proceed through separate channels. Work on egg recognition in herring gulls, however, indicated that heterogeneous summation between learned and unlearned features of the egg does take place; the relative impact of each category is determined by the modulating effect of the motivational state present at the time of response performance. The impact of learned egg features was found to increase when the strength of an escape tendency in the bird rose relative to that of the tendency to incubate. These findings led to the design of a model for the releasing mechanism in which combination of innate with learned knowledge is proposed and the two-channel hypothesis abandoned (Baerends & Drent 1982). I have even suggested that when time and the capacity for learning are available to an animal it is in general not likely to react to unlearned cues only, but to an IRM extended through conditioning (Baerends 1985). The IRM would primarily function to guide this learning process.

Since the snapping response is a relatively simple activity, the software analysis on which the neurophysiological research is based could be carried out under highly controlled laboratory conditions, mostly already in combination with physiological measurements. However, extension of this work to more complicated behaviors is highly desirable. It will accordingly often be necessary to allow the experimental subject a more varied environment. This will make the demands on the ethological analysis heavier and it is therefore to be hoped that the interest in the black box analysis and in improving and extending the

methods to be used will revive. As demonstrated in the present target article, the study of the software forms an essential part of the causal analysis of behavior and should not be forsaken as out of date.

After the sensory analysers: Problems with concepts and terminology

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The mechanisms involved in visual pattern recognition have been investigated in a comprehensive way by Ewert and his collaborators. I regard their studies of feature analysis in toads as being of sufficient importance to form the central example of sensory analysis mechanisms for students of behaviour (Broom 1981, pp. 42–48). The work summarised in the target article provides additional information about the link between sensory analysers and motor responses; but there would seem to be much still to be discovered about this link, and Ewert's explanations and terminology are sometimes confusing.

So long as the results are explained in a descriptive way, they are interesting and uncontroversial; as soon as terms like innate, fixed action pattern, and command releasing system are used, however, there will be differences in the meanings ascribed to each by readers. Ewert (1980) stated that the word innate "does not mean that the environment is totally irrelevant in the development of fixed action patterns and releasing mechanisms as well" (p. 58). Many readers, however, will interpret innate as meaning genetically determined and independent of environmental effects. In the target article (sect. 3.5.3) Ewert chooses "something that is phylogenetically adapted" as a meaning of innateness and he mentions that "genes alone may not be sufficient for the expression of a property." These explanations devalue the word innate to the point of being largely useless, since embryological and other developmental studies indicate that the expression of all genes involves interactions with environmental factors and that every characteristic of an organism is, to some extent, phylogenetically adapted. Hence it would make explanation clearer if the word innate were not used at all. A more descriptive statement is always possible; for example, in Section 3.3.3. it would be better to state that the worm/anti-worm preference is present even after a wide variety of early rearing conditions (Traud 1983). Work like that of Burghagen (1979) has shown that, given appropriate previous experience, prey-catching behaviour may be directed at large black square objects, so Ewert does not call the avoidance response innate. There is little value in calling the worm/antiworm preference innate.

The persistence of some confusion about terminology concerning sensory analysis and motor output is exemplified by Ewert's explanation of sign stimulus (Appendix). There is no necessity to refer to fixed action patterns when explaining the term sign stimulus. Ewert (1980) uses fixed to mean genetically determined when he speaks of fixed action patterns. This usage is uncommon now, and indeed the word fixed seems quite redundant. It is better to refer only to "action patterns," for only very brief sequences of movements (generally < 1 second) are immutable once initiated (Broom 1981, p. 62 ff.).

The factors affecting prey-catching behaviour in toads are discussed by Ewert in Section 6.4. Motivation is not, as Ewert states, solely concerned with homeostasis, but prey-catching is clearly influenced by motivational state, attentional mechanisms, and learning. Having said this, it is difficult to see why Ewert is willing to present a rather simple diagram of his command releasing system in Figure 22. There is an implication that the output circuits, such as "orient prey," are merely

released, but much more is in fact involved than just triggering. The data presented do go some way toward explaining how the sensory-motor links are made in the toad's brain, but the models are, as yet, too simple and there are still many unknowns in the process.

How is a toad not like a bug?

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Ewert's work, carried out over 20 years' time, has provided us with one of the most completely analyzed behaviors in the vertebrate world. As a good neuroethologist, Ewert selected for study an animal having a limited repertoire of rather fixed behavioral responses to sign stimuli. Following a detailed ethological analysis of the releasing value of differently shaped moving stimuli, he has been searching out, from retina through motor circuits, the neural elements responsible for the behavior.

This strategy of selecting a simple, fixed behavior and then examining from input through output the underlying neural circuit is a tradition well established among invertebrate neuroethologists. Vertebrate workers more rarely focus on the full circuit for a single behavior. It may be instructive, then, to compare the toad's prey-catching system to some invertebrate systems studied by a similar sensory-to-motor approach. The list would include, among others, the gill withdrawal response of *Aplysia* (Kandel 1979) escape behaviors of crayfish and cockroach (Camhi 1984, Ritzmann & Pollack 1986; Wine & Krasne 1982), and swimming in the leech (Brodfueher & Friesen 1986).

It seems immediately clear that prey-catching by toads is a more complex behavior than any of the invertebrate examples mentioned above. The toad's sensory discrimination of worm versus antiworm, the invariance, and the gestalt perception are not even approached in any of the invertebrate systems mentioned. True, there are invertebrate behaviors even far richer than the toad's prey-capture, a case in point being honeybee orientation (Gould & Marler 1987). But an input-output circuit for, say, a bee's navigation by celestial polarization maps is currently far beyond technical feasibility. Of those systems for which partial circuits are known, perhaps cricket phonotaxis (Huber & Thorson 1985) more closely approaches the intricacy of toad prey-capture. Indeed, anyone who has seen these two behaviors is struck by their general similarity.

The neural complexity of the toad's prey-capture system also seems well beyond that of most invertebrate circuits so far known. The toad circuit, though by no means fully worked out as yet, contains at least 8 to 10 sequential neuronal types from receptor cell to motoneuron. This is two to three times as many processing stations as in most known invertebrate circuits. (The count for cricket phonotaxis is not yet available.) Moreover, there seems to be a great difference in the number of cells at each station, perhaps up to tens for the invertebrate circuits mentioned, and thousands for the toad. It is as yet difficult to compare the degree of lateral interaction, or either internal or proprioceptive feedback in these systems, for want of sufficient information. Nevertheless, it already seems clear that much more neuronal processing is going on when a toad strikes at a cockroach than when the cockroach executes its escape.

Even when comparing the toad to the seemingly similar cricket phonotaxis, however, striking differences appear. In the cricket, there is an apparently limited number of neurons that are excellent candidates for song recognition cells (Huber & Thorson 1985; Schildberger 1984) – far fewer than the number of T5(2) worm-recognizing cells in the toad. Moreover, the destruction of single interneurons in the cricket phonotaxis system produces substantial errors in orientation direction

(Aikin et al. 1984). Although I doubt it's been tried, it seems unlikely that killing one cell in a toad would produce any behavioral deficit at all.

It thus appears that there are very major differences between the known invertebrate circuits, even including cricket phonotaxis, and toad prey-capture. It is not at all clear why this should be. That is, why does the toad need all those cells to catch its prey? Here are some possible reasons: (1) Perhaps the invertebrate systems are all dedicated to single behaviors whereas the toad circuit is multifunctional; (2) perhaps, although the toad's circuitry is more intricate, its individual neurons are more simple than in invertebrates; (3) perhaps vertebrates feature redundancy as a failsafe, providing a backup in case of damage or death to some cells; (4) perhaps the toad's prey-capture behavior only appears to be simple but is really complicated; and (5) perhaps a radical step occurred in the evolution of vertebrate nervous systems, whereby neural processing is carried out according to different, more complicated, principles.

None of these explanations is fully satisfying. The first suggestion, differences in neural dedication, appears simply to be wrong, since several invertebrates share this property. For example, neurons of the command system for leech swimming are also involved in producing other behaviors (W. Kristan, personal communication). Likewise, circuit elements with multifunctional properties are found among the giant interneurons of the cockroach escape circuit (Ritzmann et al. 1980) and the cells of the *Tritonia* escape system (Getting & Dekin 1985).

As regards the second idea (simpler cells in the toad), there is insufficient direct information for comparison, in spite of ongoing intracellular studies on amphibian tectal neurons (Matsumoto et al. 1986). However, it is worth noting that some of the physiologically most complicated neurons known come from the vertebrate world (Llinas & Yarom 1986).

Concerning the third, failsafe idea, this often-mentioned notion has always seemed to me nonsensical. The likelihood of an individual animal's suffering a loss of part of its brain and surviving seems so remote as to provide no evolutionary pressure for multiplying the number of its brain cells as a failsafe.

As for the fourth idea – that toad prey-capture is really substantially more complex than even cricket phonotaxis – well, it just doesn't look that way. True, as Ewert points out, the toad's behavior includes several sequential acts, from the initial orientation to the final swallowing and wiping; and there are powerful motivational factors controlling sensitivity. Moreover, barrier avoidance can be incorporated into prey orientation (Ingle 1973b), and there is the problem of translating sensory space into motor space in spite of head-to-body movements. However, crickets in the field must also circumvent barriers, presumably using antennal and other inputs, and the problem of compensating for the toad's head-to-body angle does not seem any greater than compensating for the movement of the cricket's ears, located on its legs. Finally, a great many invertebrate behaviors, presumably including cricket phonotaxis, are under strong modulatory and motivational control.

The fifth and final suggestion, that vertebrate and invertebrate behaviors operate by different organizational principles, makes many people uncomfortable, especially us invertebrate neuroethologists whose bread and butter is the idea that invertebrates are good model systems for studying vertebrates. Nevertheless, it is important to be open to the possibility of radical differences. So let us examine this possibility briefly. On the one hand, evidence against this idea is not hard to find. For example, the escape circuitry of fish, admittedly low on the vertebrate evolutionary scale, looks more like the crayfish escape circuitry than like any other known vertebrate circuit (Eaton & Hackett 1984), and though honeybee navigational circuits are not yet known, one must imagine that they would be quite complex, perhaps rivalling many vertebrate circuits. On the other hand, a fish is only a fish, and maybe the Mauthner

circuit is the last evolutionary vestige of the simple life. Invertebrate ganglia probably just don't have sufficient numbers of cells to approach the complexity of the toad tectum.

There seems to be no firm explanation as yet for the much greater apparent complexity of the toad prey-capture circuit when compared to invertebrate circuits such as that for cricket phonotaxis. I will close with the suggestion that perhaps the behavior by which toads capture prey is just *slightly* more intricate, and perhaps this slightly increased complexity, together with newly evolving vertebrate ways of organizing circuits, led to the development of a higher order of neuronal complexity. If so, there are two lessons. First, behavior itself must be examined very carefully, to reveal subtle differences. Second, one must search for commonalities between possibly simpler invertebrate, and more complex vertebrate, forms of organization, in order to discern the general laws of neurobehavioral organization.

Sensorimotor functions: What is a command, that a code may yield it?

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The optic tectum of the vertebrate brain is often described as a site of sensorimotor integration or sensorimotor translation. This presumably means that sensory signals enter the tectum, and then tectal cells issue motor commands for appropriate behavioral responses. These commands would produce orienting movements toward visual targets or, if one is mindful of the polysensory nature of the optic tectum in most vertebrates, they may also direct movements with respect to acoustic, tactile, or other sensory stimuli in the environment (see Grobstein et al. 1983 for an alternative view).

Research by Professor Ewert and his colleagues has had much to say about the organization of tectal cells in the toad and their possible role in orienting responses to prey items. This research is now progressing to the cellular analysis of some of the "post-tectal" circuitry (Ewert et al. 1984; Satou & Ewert 1984), and it appears to me that the findings challenge a simple sensory-to-motor model of tectal function as sketched out briefly above. This might not be apparent, however, given the terminology used to describe tectal efferents in the toad.

The target article indicates that "many of the tectal neurons analyzing feature- and space-related cues project to the motor systems." The hypothesis is that action patterns are released according to "sensorimotor codes" carried by distinct combinations of tectal efferent neurons. I find this an appealing notion. The terminology of command systems, however, is used to describe the tectal efferents and their relation to brainstem circuitry. This forces tectal integration into a framework that just doesn't fit. The elements of a command system were envisioned as a group of "homogeneous neurons" (see Kupfermann & Weiss 1978), whereas the tectal efferents represent a diverse population of feature-analyzing neurons. Perhaps most important, the concept of a command neuron or unit is compelling in those few instances where it describes a funneling of information through one or a few cells which control the occurrence of a coordinated motor act. Thus at the heart of the concept is a sense of what Roeder referred to as "neural parsimony" (e.g., Roeder 1959). That the toad's tectomotor processing may not fit under such a rubric is actually what makes Ewert's model interesting: It gives a possible cellular explanation for a not-so-simple system.

If tectal efferents are referred to as "command elements," then by applying the logic of the command neuron (or command

system) concept, we might assume that the firing of a given type of neural element signifies a decision to produce a specific action pattern (see Eaton 1983; Kupfermann & Weiss 1978). However, many different efferents, and even classes of efferents, would apparently be activated by a visual stimulus, and the resulting action pattern (approach, snap, etc.) is assumed to depend upon the particular combination of efferents activated in a given stimulus situation. No one class of efferents appears to uniquely specify a given type of action pattern. This would seem to be a rather elegant example of ensemble coding. If the combinatorial code emanating from the tectum "yields" a command for a particular act, then presumably the command is more a property of brainstem circuitry which decodes tectal efferent activity than of tectal circuitry itself.

The challenge of understanding sensorimotor functions is at the heart of the neurobiological analysis of behavior. Research by Ewert and his colleagues on the neuroethology of the toad's visual system has produced an amazing volume of information by any standards. The problem of "sensorimotor interfacing" is the particular area of Ewert's work which I think is producing, and will continue to produce, the most significant new information of general relevance to neuroscience. It is also, I would suggest, an area where the language describing neural organization needs to be most carefully considered.

Eliminate the middletoad!

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Philosophical controversy about the mind has flourished in the thin air of our ignorance about the brain. The humble toad, it now seems, may provide our first instance of a creature whose whole brain is within the reach of our scientific understanding. What will happen to the traditional philosophical issues as our theoretical and factual ignorance recedes? Discussion of the issues explored in the target article is, as Ewert says, "often too theoretical, sometimes philosophical and even [as if that weren't bad enough?] emotion-laden." The research reported by Ewert has interesting philosophical implications, as he probably recognizes, but he wisely leaves the philosophy to the philosophers. Being one, I would like to draw some of the conclusions he eschews.

First, just to keep enthusiasm in check, we should remind ourselves that although toads are "smart" enough, or "psychological" enough – unlike *Aplysia*, for instance – to raise (at least for discussion, prior to dismissal) the fascinating questions, they are still remarkably stupid, and the research program depends critically on their stupidity. Insofar as the experimental results are unequivocal, it is thanks to the *limits* of plasticity and discrimination that have been uncovered. Toads, we learn, are born with hard-wired prey-capture routines with only modest degrees of plasticity. They will go on striking at dummy targets indefinitely, and their standards for prey recognition, though serviceable in their niches, are gratifyingly crude. Imagine how we would react to the discovery that some human beings were so oblivious that we could substitute cardboard silhouettes on wheels for real people in their environment without seriously disrupting their behavior. "Social" psychology would be a lot easier using these people as subjects, but we would no doubt have the same feeling with regard to them that we now have – thanks to the researches of Ewert and his colleagues – with regard to toads: When you look closely, you find that there's nobody home.

I take it that most readers, after digesting the details of the target article, are ready to relinquish whatever remaining convictions they may have had that residing behind the toad's

bulging eyes, watching and waiting and deciding when to strike, was a middletoad, a conscious self, the something that must be there if it is to be like something to be a toad (Nagel 1974). Why? What is it about Ewert's model, and (more important) its supporting research, that promotes this opinion of the toad as a "mere" automaton, a zombie in spite of its biological commonality with us?

Dualists may be tempted to say that the mere fact that Ewert can explain the toad's behavior without ever advertiring to any transactions between the toad's brain and some nonphysical mind would be sufficient (if confirmed) to establish that toads are mere automata, however "clever" they appear to the uninitiated. The objections to this view do not need rehearsing here. Modern-day materialists, who have no doubt that in principle there can be a purely physical, mechanistic account of even a self-conscious, human mind, may still feel that if Ewert's account is right in outline, toads lack something crucial for consciousness. I would like to draw attention to a confusion that may affect even subtle materialists in their attempts to say what is missing in Ewert's toads.

Ewert does not claim that his model is complete. Note that he attempts to account for only one of the four F's, feeding, alluding only in passing to the interfaces still to be described with the others: fleeing, fighting, and reproduction. What is important is that within one quarter of the toad's control agenda, the model claims to show us *how the corner is turned* at what Ewert calls the "sensorimotor interface": how afferents are eventually "interpreted" to the point where (normally) appropriate efferents are generated.

Tradition would interpose the Mind or the Self at that sensorimotor interface, contemplating and comprehending the input, and figuring out the wisest output, given that input. But that particularly wise homunculus – or bufunculus – has been brusquely dismissed in Ewert's model, replaced by nothing but a few generally hard-wired AND-gates. Even though there are neural messages with meanings passing through the sensorimotor interface – Ewert speaks somewhat misleadingly of a "sensorimotor code" – they are not *decoded* by any salient intervening entity; they have their apposite effects by being already wired up by Mother Nature to trigger the appropriate "commands."

For instance, the convergence of a T5(2) firing, meaning "stimulus recognized as prey, n degrees outside the fixation area," with activity in T4, meaning "stimulus moving somewhere in the visual field," yields the command to orient; T5(2'), meaning "stimulus recognized as prey," firing concurrently with T1(2), meaning "stimulus close to toad," yields the command to fixate, and so forth.

Consider the grounds offered for these renderings of the meanings of types of neuronal firing. The particular form of words chosen by Ewert is dictated not by any isolation of "syntactic" features of some neuronal "language of thought" as candidates for word-for-word translation into English, but rather by an appreciation of the "semantic" contribution of those events to the ongoing control problem of the toad, expressed (roughly) from the toad's narcissistic point of view (Akins 1986). As Ewert notes, "prey categorization is approximate" and moreover, his decision to elevate the semantics of an event type such as T5(2') to "stimulus recognized as prey" (italics added) is governed by pragmatic considerations (Dennett 1987). As opposed to what? As opposed to presumably objective, information-theoretic criteria of the sort envisaged by Dretske (1981) [see also multiple book review, *BBS* 6(1) 1983], Fodor (1980), and others. The objective informational parameters (e.g., reliable covariation with shape and motion properties of the sort distinguished in Ewert's Figure 4) set outside limits, at best, of the *potential* narcissistic-information-bearing properties Ewert is prepared to assign to the events. The support he offers for going beyond the (Dretskean) information given when fixing his renderings of meaning includes his recognition of the appropri-

ateness (under normal conditions) of the normal continuations of those events, as modulated by "goal-related information . . . result[ing] from intrinsic processes." But these continuations are normal precisely because *that's the way toads are wired*, not because something in the toad "recognizes" or "analyzes" the meaning of those neuronal events as the result of some sort of perception-and-parsing process.

In other words, the "decision-making" relating those messages to those commands does not occur in real time in the toad, but occurred eons ago in the course of the design process that created the wiring diagram that now implements those policies. Their rough wisdom is endorsed, probabilistically, by the very existence of the toad as a surviving descendant, but, it seems, the toad itself has no intelligent contribution to make to its own survival. (Here is where the mistaken line of thought begins.) The toad, one gathers, is *none the wiser* for having messages with these meanings zapping around in its brain. It doesn't appreciate or comprehend or figure out what the observing neuroethologist does. It can get through life reasonably well without benefit of comprehension, thanks to its felicitously arranged inner wiring – and that, it seems, is what makes toads zombies.

It is this line of thought that makes the idea of a language of thought (Fodor 1975) so treacherous. There is a strong temptation to suppose that in a truly intelligent, intentional, conscious creature (unlike the poor toad), the meaning-bearing events streaming in from the sense organs would have to be couched in some parseable, comprehensible language, so that the middletoad (or middleman or self-module) would have some way of recognizing and appreciating their meanings. But this just postpones the problem of meaning, and makes it even more mysterious by setting an impossible task of comprehension and inference for the inner module (Dennett 1978). The mistake lies in confusing the toad itself (the whole toad, from whose self-centered perspective all content-ascription must proceed) with some imagined inner middletoad, which, indeed, as a proper part of the toad's nervous system, would be none the wiser for having events coursing through it with various meanings. But the whole toad is the wiser; its capacity to pick its way through its world with some adroitness is *explained by* the presence of events in its brain having the sort of significance Ewert assigns to them.

This conclusion is hard to accept if one is still enthralled with the common vision of meaning being *present* in items (in the mind or in the brain) as if it were candy in a box, to be sent from A to B, there to be unpacked and enjoyed (comprehended) by the (intelligent) receiver. The mistake is to concentrate all the intelligence in the imagined middletoad, instead of spreading it through the whole system. This involves offloading inexpressible portions of meaning into the appropriate hard-wiring, and into the acquired interactive effects entrained by experience, in the manner Ewert's model illustrates very well. Once the intelligence is seen as distributed, no inner thing remains to be a candidate for the Mind or Self, but this does not in itself rule out consciousness.

The real reason, finally, why we may be inclined to give up on the toad's inner life is not because when we look closely at the inside, we find nothing but wise wiring – that's all we are ever going to find in us, too – but because of what we find on the outside, in the ethology: Toads don't catch on to very much. If toads were much harder to fool, and learned more, and in particular if they could learn that they were being manipulated, and come to take evasive or counteractive steps of some kind, we would find that our sense that "somebody was home" would survive. Such cognitive prowess as this would take much more internal machinery than the toad has, but other creatures have it, and we can know in advance that when we look closely at its details (if we can master them at all), we will find no concentration of insight in an inner module, but just much more wise wiring.

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Toward a reformulation of the command concept

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In his engaging review, Professor Ewert expresses concern that his conceptual treatment of command might be controversial. However, the lively debate surrounding command has not prevented its use. In a computer search for the years 1981–1986, we found well over 200 papers related to various neurobehavioral usages of the command concept. This activity reflects the importance of command as an explanation linking neural action to behavioral effects, and therefore justifies its discussion and analysis.

A reigning concept of command has been what we call the "command neuron experiment," the CNE, of Kupfermann and Weiss (1978). The CNE idea of "command system" has been found to be experimentally untestable, and the "command neuron" concept is theoretically oversimplified, resulting in contradictions depending on how experiments are performed (Eaton & DiDomenico 1985). In one test case using the Mauthner neuron, results from the CNE concluded that this cell was a command neuron (Hackett & Greenfield 1986); in other experiments, the CNE concluded it was not (Eaton et al. 1986).

In addition, the CNE and other command concepts are ultimately inadequate to explain the neural mechanisms underlying the behavioral complexities that many neurobehaviorists find important. Even a "simple" escape response of a fish involves decision and localization processes, and also mechanisms permitting one system to temporarily take over and coordinate the entire activity of the animal. These processes activate the subsystems mediating the response and inhibit expression of conflicting actions and input signals (DiDomenico & Eaton, in press; Nissanov & Eaton, in press). Thus, we agree with Ewert that previous notions of command have been theoretically inapplicable to the numerous experimental results revealing the complexity of neural networks and behavioral processes. Because of these difficulties, we have recently proposed a restructuring of the concept of command (DiDomenico & Eaton, in press).

Our approach consists of an ensemble of principles in which command is a dynamic neural process reflecting the selection and direction of specific sequences of behavioral action (DiDomenico & Eaton, in press). As outlined below, we define command by using neuroethological, systems theory precepts that are independent of any single structure, causal paradigm, or method.

1. The neuroethology of command. In many usages, "command" is a name for the neural events (of some type) leading to a temporary change of behavior, from one activity or state to the next. Thus, command, like learning, is a larger-scale concept than the neurophysiological events leading to its expression. In the context of natural behavioral conditions for which animals have evolved, command becomes a neuroethological concept requiring explicit behavioral definition and quantification. This contrasts with the previous idea that command can be defined only in neurophysiological terms, *regardless* of the behavioral conception (Eaton & DiDomenico 1985).

A behavioral shaping of command is consistent with many other successful neurobehavioral approaches. For example, the behavioral description of habituation by Thompson and Spencer

(1966) helped to determine the design of experiments leading to the discovery of its neurophysiological basis (Kupfermann et al. 1970). The same applies to studies on learning (Carew et al. 1981; McCormick & Thompson 1984). In these examples, neurophysiology is guided by behavioral concepts rather than the reverse, because arbitrary behavioral definitions are not ascribable to the types of concise neural mechanisms that neurobiology seeks to discover.

2. The causal basis of command. We have defined command *independently* of any single causal paradigm, such as the previous "necessity and sufficiency" definitions. This separation is essential (Eaton & DiDomenico 1985). Ewert argues the same point on experimental grounds; ours is based on both empirical and general scientific grounds.

There is no scientific reason to tie command to preconceived and explicit causal schemes – various scientific fields acknowledge that no one causal explanation has precedence in all experimental contexts. Many scientific laws, principles and theories are not derived from preconceived causal paradigms; rather, the mechanistic explanations *are* the causal explanations (Eaton & DiDomenico 1985). Likewise, the purpose of neurobehavioral explanation is to *discover* the causal neural mechanisms of behavior. This alternative to explicit causal schemes enables the discovery of new causal explanations which will become the basis of neurobehavioral theories.

3. Methodology for command. The liberation of command from preconceived causation opens the concept to enrichment by diverse methodological approaches. This is in concert with Ewert and in contrast to previous ideas that the meaning of command was exhausted by tests for "necessity and sufficiency."

Tests for "necessity and sufficiency" can seem unequivocal while at the same time hiding extant alternative mechanisms which are revealed only through different methods (Eaton & DiDomenico 1985). Like Ewert, we call for a multidisciplinary approach that directs a variety of questions at the same subject, thereby verifying that the emerging principles are consistent with different experimental paradigms and techniques. This concept acknowledges the very real complexity of neural networks.

One of the complexities, as pointed out by Ewert, is functional plasticity. Here, we do not mean compensatory regrowth, but extant mechanisms that automatically regulate the output of the network (Eaton et al. 1984). One candidate mechanism utilizes central feedback loops (Nissanov & Eaton, in press). Because of compensatory feedback, a behavioral effect may continue to be expressed following a lesion or other inactivation procedure. The attempt to confine the definition of command to tests for "necessity and sufficiency" therefore, overlooks important underlying neural mechanisms.

4. Command as a function. In our view, command is a functional process resulting in the expression of a behavioral act. Command describes what a neural network *does*, and is not limited to any particular part of the nervous system. As a behavioral concept, command is analogous to learning. Both command and learning are processes resulting in a change in behavior. Ewert's presentation is consistent with this functional approach since he considers command releasing systems (CRSs) to be neurophysiological equivalents of behavioral releasing mechanisms. They're shared between different systems and are not restricted to single cells or particular structures.

Many others have assumed that command is confined to specific structures – individually identifiable command neurons, or elements. There are several problems with this type of assumption. First, to literally explain the behavioral inference of command by saying that the command process is mediated by command neurons is equivalent to explaining motion by saying that the moving body is made up of moving particles. Second, the assumption that command is necessarily embedded in a particular structure contradicts recent experimental findings.

Cells from sensory to motor seem to serve commandlike functions. For example, in the cricket, a sensory cell Int-1 has commandlike properties in triggering turning flight movement (Nolen & Hoy 1984).

Separating command from an anatomical specification is consistent with how complex processes of various types are usually defined. For example, writing is not defined by the instrument but by the recording of words or other coded information in some medium (unspecified) by some instrument (unspecified). It is not that processes cannot be specified by various media, but the meaning of the process cannot be exhausted by a particular medium.

5. Command as a dynamic process. If command is to account for temporal properties of behavior, then it must incorporate dynamic processes of the neural tissue. Both Ewert and ourselves have described command systems as dynamic. Ewert emphasizes the dynamic potential of neuromodulatory effects. In addition, we refer to the dynamic neural changes that are inferred to be occurring as animals switch from one behavior pattern to another.

In this context, we envision a command system as being created from a seminal decision that may arise in one or a few prominent trigger cells and that grows to include various neural circuits for its execution. In this way the command system changes in time as it recruits its appropriate subsystems and then abandons them when a new behavior pattern is executed.

In conclusion, command is both attractive and elusive because it is a conceptual bridge between neural activities and behavior. Because of its intermediate position, command cannot be completely incorporated by existing neurophysiological or behavioral concepts, and this has contributed to the ongoing confusion and debate. We are encouraged by the similarity between Ewert's conception of command and our own: They are based on complementary theoretical views and are strengthened by their emergence from different experimental preparations.

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Has the greedy toad lost its soul; and if so, what was it?

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This is the 350th anniversary of the publication of Descartes's *Discours de la Méthode* (Gilson 1962). Furthermore, with his *Meditations* (Haldane & Ross 1967), Descartes provided the earliest and perhaps most famous example of the style now followed by BBS: an extensive exposition by one author which is then subjected to commentaries by other authorities in the field, with ensuing response thereto by the author. It is thus doubly fitting that Ewert's target article, which with such elegant and convincing thoroughness delineates the mechanism of a Cartesian machine, the toad, should also be treated in the Cartesian style of "objections" and "response."

Descartes's most critical commentator was Gassendi, who vigorously attacked the principle that the human mind/soul is uniquely different from the neural processes of animals:

You [Descartes] say that in the brutes everything takes place through blind impulsion of the (animal) spirits and the other organs, just in the same way as motion is achieved in a clock or any other machine. But however true is the case of the other functions, like nutrition, the pulsation of the arteries, and so forth, which functions take place in man in precisely the same way as in brutes, can it be said that either the operations of sense, or what are called the emotions [passions] of the soul are affected in brutes by means of blind

impulses, and not in our case also? A morsel of food discharges a semblance of itself into the eye of a dog, and this being transferred to the brain, attaches itself to the soul, as it were, by means of hooks; and the soul itself thenceforth and the whole body, which coheres with it, is haled to that food, as it were, by chains of the most delicate contriving. (Haldane & Ross 1967, p. 145)

The nature of those "chains" is now largely revealed by Ewert's work! Yet in the subtlety of their operation these neuronal chains are more closely allied to the vagaries of human mentation than to the ineluctability of clocks. For the intact toad the decision to attack is conditioned not only by the machinelike evaluation of appropriate size, shape, and distance of the moving object, but also by attentive state, satiety, or even past experience with bees. It is only following loss or perturbation of pretectal circuitry that the toad displays an unbridled greed, and attacks all moving objects with the consistency expected of a true Cartesian machine.

What, then, is the neuronal nature of this soul which in normal circumstance instructs the toad's decision to attack? Ewert's data clearly define the processes whereby the retinal messages are decoded; but they are far from satisfactory regarding the manner in which the system is restrained by satiety, past experience, or simple inattention. True, the T8 neurons in their rate of discharge, much like the omnipause neurons of cats and monkeys (Fuchs et al. 1985), reflect the attentive state of the animal, and may thus provide a facilitatory background. Yet the gross facilitation achieved by pretectal lesions does not seem to be accompanied by any increase in background discharge of the tectal T5(2) neurons (Figure 20). Of course, the latter fact might be explained by a loss of feedback inhibition from the pretectal area; but what of satiety? How are its enduring effects produced? One might hypothesize the quieting of arousing input from the gut, once the gut is full, and thereby lessening of the facilitation from the T8 neurons, and so on.

Two observations, however, suggest that there may be a more subtle, but as yet mysterious, means of obtaining long-term suppression of "erroneous" or unnecessary responses, without the cost of continuous inhibitory discharge. The first is with learned suppression, for example avoidance of bees, where it seems most unlikely that a specific and continuing pattern of inhibitory discharge persists continuously following the acquisition of the learned suppression. The other instance is the lifelong suppression of brainstem reflex patterns achieved by adult mammals, including man. Such suppression is not achieved by loss of the brainstem organization, for it can subsequently be "released" by loss of relevant forebrain systems (e.g., Doty 1976; Pilleri 1984); yet it is difficult to imagine the forebrain as sending a steady stream of suppressive messages to the brainstem, decade after decade. Rather, it would seem that in both these instances, of learning and of developed organization, the suppression must be achieved by some enduring alteration of the capability of the relevant synapses. One might perhaps distinguish between the two possibilities – constant and continuing availability of inhibitory impulses versus long-term down regulation of synaptic excitability – by the time course of the "release" achieved by destruction of the putative controlling system.

Prey-catching in toads: An exceptional neuroethological model

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Prey-catching in toads is one of the best vertebrate models for correlating neuronal circuitry and related functions because the behaviors and associated neural structures are exceptionally

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 in toads 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 (postero-lateral 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., Meredith & 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

cockroaches walk, their perceived "fixed" action patterns involve different combinations of flexor and extensor activity. The actions remain reasonably stereotyped due to invariances in the product of individually variable flexor and extensor activation (Hoyle 1964). Flexor and extensor action "boxes" may be individually variable while still producing coherent coproduction, in a reasonably "invariant total form."

Another problem with boxes is that they are often generalized beyond their appropriate contexts. Thus, Pearson (1985) has recently shown that "central motor program" concepts (boxes) derived from analyses of partial systems may be misleading when applied to behavior in intact organisms. There are many cases of this type of contextual sensitivity. Berridge and Fentress (1986), for example, recently found that the effects of trigeminal deafferentation on the form of ingestive and grooming movements in laboratory rats changed systematically with the motivational and sequential contexts in which these movements were embedded. There were, in a sense, invariances, but these were dynamic and context dependent.

Even at a descriptive level invariance is often relative and relational. Baby mice may often show increased invariance (precision) in contact pathways between their forepaws and face during grooming development, while at the same time they show more flexibility in the kinematic details and individual limb segment trajectories that in combination make these paw to face contacts possible (Golani & Fentress 1985). Are their actions becoming more or less fixed? Similar issues have been addressed in the recent target article by Berkinblit et al. (1986).

When descriptions are generalized across criteria and in absolute terms many problems can arise. These problems can be extended beyond reach when mechanisms are inferred. Thus, in early ethology, "fixed," as a descriptor of action, was taken to imply "centrally programmed," which was in turn taken to imply "innate."

In the present target article Professor Ewert has not only provided an elegant survey of much present day neuroethology, but he has also argued convincingly for a position that relates individual properties to "dynamic properties of their interaction." In addition, he has shown how such dynamic and distributed approaches can yield precise data in the integration of previously established activities. The work of Ewert and his colleagues is exemplary in this regard. It serves as a liberating guide to potential future connections between neuroethology and the growing interest in "parallel distributed process" models of human cognitive neuroscience (Rumelhart et al. 1986). Finally, I applaud Ewert's awareness of the pervasive problems of categorization that affect our own search for invariances in nature (e.g., in reference to Harnad 1987a). It is this combination of breadth in perspective with detailed focus in experiment that will bring present-day neuroethology into its potential for mature contribution.

It is important that problems of categorization that we study in animals remind us of our own too frequent categorical (box-like) conceptual predispositions. Thus, although Ewert does express some uneasiness with terms such as "innate," and "release" and unitary "mechanism" (*the three foundations of IRMs in ethology!*), "innate releasing mechanisms" do invade his manuscript (e.g., sect. 7, para. 1), along with "commands" and other traditional box trappings. Perhaps these terms are used as a convenient shorthand, but they can imply clarity where there is at present mystery (cf. previous target article by Berkinblit et al. 1986).

There is, for example, no doubt that Ewert's toads reared in educational deprivation still do remarkable things. But these critters continue to have a complex developmental history in which experiential events and phylogenetic predispositions are intimately entangled. Removing one source of experience does not in itself clarify the processes underlying behavioral differentiation. This point has been emphasized recently for invertebrates by Murphrey (1986), who reviews compelling evidence

that changes in afferent activity can have important effects on the detailed construction of neural networks. The extent to which particular behavioral products are changed or buffered under particular expressive contexts (Berridge & Fentress 1986) is of course a matter for detailed study (Fentress & McLeod 1986).

We do not yet have an appropriate framework for evaluating the diverse effects of experience during behavioral development, nor the effects of the contextual factors that may exist external to the organism (or, at least, "external" to the particular system under investigation). A number of related questions remain. Here I am restricted to a few of the most obvious ones.

What are the rules over which the consequences of a given experiential manipulation generalize, for example? These rules may or may not be modality-specific, may or may not be constrained by actions similar in form, may or may not follow more broadly defined principles of integrated function. Reasonable distortions of experience might facilitate normal behavior in comparison to omissions of experience, whereas more severe distortions may be more likely to respecify developmental trajectories (Fentress, in press; Horn 1985).

Full evaluation will necessitate a very careful documentation of qualitative, quantitative, and temporal variables, separately and together. The very concept of differentiation implies predispositions operating within the context of developmental experience, and it is my guess that one of the most potent areas for future neuroethology will involve the painstaking dissection of these interlocking events during development.

This dissection will almost certainly spell the end of the very boxes on which classical ethology was based. Developmental "invariants" are as relative, relational, and dynamic as are the integrative "invariants" that occupy the core of this impressive survey. Indeed, one might speculate that a framework similar to the dynamic center-surround and distributed processes approach Ewert has applied successfully to integrative systems will have direct and important developmental analogues (e.g., in the changing balances among interactive and self-organizing networks of ontogenetic processes; Fentress 1986). I look forward to Ewert's next review, as he and his colleagues are forced to abandon the last vestiges of the very (box + arrow [e.g., innate "versus" learned]) framework that has, to date, served them so well!

More than meets the eye

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Neuroethologists know that the systems most likely to be understood at a neuronal level will be those responsible for eating, reproducing, or fleeing, because natural selection sees to it that these behavioral patterns suit the animal particularly well. For the past several years, most experimental effort has been focused on invertebrate or "lower" vertebrate systems where the prospects for experimental manipulations are particularly good. The target article by Ewert provides elegant experimental evidence of how the toad manages to detect worms and reject "antiworms" using a reasonably tractable experimental system. I would like to comment on two details of the experimental analysis and then on the generality of the results for visual pattern recognition per se.

1. The orienting response of the toad appears to be important in most of the naturally occurring cases observed. It is likely that the animal brings the prey into the frontal visual field because more optimal optics or a more advantageous photoreceptor distribution may be utilized from that perspective. Although Ewert reports the failure to find a foveal pit or other

obvious retinal specialization, there is a clear predominance of cones in the temporal retina in other toads (*Bufo marinus*, personal observation). This suggests that there could be specialization of the feature perception pathways in localized anatomical structures. If there are such differences in specialized processing networks within a single animal, it could prove useful to compare processing strategies. Ewert discusses the possibility that there might be a computational "central fovea" achieved dynamically which would enhance any directly "wired" differences.

2. In describing the velocity invariance of the worm versus antiworm preference (Figure 6), Ewert's figure suggests that the toad could be easily confounded by a fast moving worm! It seems curious that there is no threshold of stimulus angular velocity. Since the other data suggest that the toad is making most of its decisions based on the size of the stimulus, the velocity data suggest that such decisions can be quick indeed for the optimal "worm" stimulus. Could it be that with less optimal stimuli there would be an optimal velocity, leading to an estimate of processing time?

One of the most important questions is whether the toad's methods for sorting its visual world will turn up in other animals. Put another way, are there general principles to be had from the analysis of this system? First, it seems certain that the dependence of prey-catching commands on motivation will be general. One might postulate very strong circadian rhythms influencing the motivational states of the toads. It is particularly interesting that toads in the mating period suppress responses to worm stimuli. I suspect that the cellular basis of this inhibition will provide some powerful insights into the neural basis of decision making in the animal, particularly when the choice is between sex and something else.

Second, the modification of prey selection through learning offers an opportunity to understand generally the circuitry of such phenomena but no quick access to its neuronal basis. The number of possible sites and the coordination of processes involved make it unlikely that this will be easily solved.

Third, the discovery that such a highly specific detection process is based on symmetrically organized "nonfeature detecting" neurons is extremely interesting. Retinal ganglion cells do have higher firing rates for particular stimulus edge lengths (Ewert's Figure 11), but these can be understood from general principles of the receptive field construction. Whereas these cells deliver information used directly in the detection process, feature-analyzing neurons first appear in the pretectum and tectum. Although it is not entirely surprising that this is so, the axes along which the toad sorts information are different from what one might first imagine. Rather than continued refinement of the required parameters, the toad constructs a truth table from reported properties of the stimulus.

Fourth, Ewert's conceptualization of the "command releasing system" offers a solution to the difficulties in finding a one-to-one correspondence between behavioral patterns and elements of the CNS. I would be interested in a comparison between young and old toads to see whether the postulated dynamic and plastic features persist as the animal gains in age and experience. It seems likely that much older toads would no longer exhibit the dynamic changes found in younger ones, and that such a command system would be the site of change during a critical period in the animal's development.

Finally, it seems clear that the analysis of the toad prey-catching neuroethology demands the development of a new collection of terms which will allow less restrictive metaphors for the description of the central phenomena. To some extent, we constrict our imagination by the terms we use to describe how things work. Useful concepts like the "command neuron" dominate how we describe and even think about problems in neuroethology. The distributed, modulated, dynamic, plastic control centers also need descriptions which help in thinking about them.

The compleat visual system: From input to output

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Ewert's beautifully detailed exposition of the neural circuitry subserving visually guided behavior in the toad is an object lesson on how to study the relationship between brain and behavior. Workers in the field of mammalian visual systems would do well to follow his example.

Ewert begins with a natural category of behavior – visually guided prey-catching – and attempts to work out the neurobiology of the different components of that behavior. This approach, though not an unfamiliar one in neuroethology, is radically different from that used by most investigators in physiological psychology. Rather than testing animals in the familiar discrimination paradigms of the psychological laboratory, Ewert instead looks directly at the visually guided movements made by the toad as it catches its prey, avoids obstacles, and escapes from predators. Thus, in addition to working out the way in which particular features of prey and predator are extracted from the retinal array, Ewert pays close attention to the interface between particular combinations of stimulus features and particular motor outputs. Indeed, the approach is explicitly visuomotor rather than visual. As such, it concentrates on both the selectivity of the sensory inputs to the different visuomotor networks and the characteristics of the different motor outputs they elicit or control.

In sharp contrast to this explicitly visuomotor approach, most workers in the field of mammalian vision treat the visual system as a piece of perceptual machinery, in which the different visual channels are seen as contributing to a rich and complex, but largely monolithic, representation of the external world. Thus, great emphasis is put on the way in which different features of the visual world are extracted and analyzed, but almost no attention is paid to the way in which visual information is used to produce different kinds of visual behavior. Indeed, it is this theoretical commitment to vision *qua* perception that has shaped the methodology used in most laboratories that study the functional architecture of the visual system in mammals. By using paradigms such as the visual discrimination task, the investigator studying mammalian vision hopes to discover how normal animals (and perhaps animals with specific brain lesions) extract information from the stimulus array and how they code and store that information. From their point of view then, it makes little sense to look at the large range of different visually guided movements or responses that animals make, since, except for a few visual reflexes, the behavior the animal generates is always in relation to the perceptual representation the visual system provides. Thus, the argument appears to go, the organization of the visual system can be studied quite independently of motor output. It does not matter what the actual motor behavior is that the animal produces in a visual discrimination task. The animal could be pressing a lever, jumping from one platform to another, running down an alleyway, pulling a string, knocking aside the cover of a foodwell, or picking up an object. What matters is that the animal discriminates (or does not). It is the *decision*, not the motor act, that interests most of these investigators. The organization of the different motor outputs, when considered at all, is seen as being largely independent of the organization of the sensory inputs and as being the province of motor physiology or of the psychology of motor skills. In fact, with the notable exception of eye movements, the visual system of mammals has been studied almost entirely on the input side, with no attention being paid to the way the control of different motor acts might influence either the specificity or the organization of those inputs.

It is true that there have been attempts within the mammalian

literature to fractionate the monolithic visual system into separate functional entities. The "two-visual systems hypothesis" of Gerald Schneider (1969) was one of these. But, as I have argued elsewhere (Goodale 1983 a; 1983b; Goodale & Milner 1982), the functional categories put forward by Schneider and his many followers were never well-defined in terms of actual behavior. The emphasis was always on psychological abstractions such as "recognition" and "localization" rather than on observable behaviors such as reaching, jumping, walking, or grasping. Whereas I would not deny that visual input can influence the cognitive functions of mammals quite independently of its contribution to particular motor outputs, I believe that the visual system will never be fully understood unless we are prepared to study the motor outputs controlled by that system with the same rigor and attention to detail that we apply to the inputs. To do this properly means that we have to study the spatial and temporal organization of behavior in relation to the spatial and temporal characteristics of the visual stimuli controlling that behavior. The power of such an approach has been demonstrated time and time again in the study of eye movements and is demonstrated here by the work of Ewert and his colleagues who have provided for us what must be the best-understood visual system in the whole vertebrate line.

Ewert has also made a brave attempt to deal with the fundamental difficulty encountered by any account of the neural substrates of vision that invokes independent visuomotor channels – the problem of integrating the different outputs into a well-organized sequence of behavior. I found that his "command system approach," although highly speculative in many respects, was a very useful way of grappling with the problem. As one might guess, any discussion of this problem is seldom encountered in the mammalian visual literature (outside of the study of eye movements). Again, it is the emphasis on the input side that obviates the necessity of dealing with this issue. It is nevertheless an issue that must eventually be faced in the monkey (and in the human for that matter) as much as in the toad. Indeed, until we are prepared to study the outputs of the mammalian visual system as carefully as we study its inputs our understanding of its underlying neural architecture and organization will remain quite incomplete.

The nervous system/behavior interface: Levels of organization and levels of approach

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For decades, the neuron has been the centerpiece of neuroscience, with efforts to account for neuronal properties in terms of subcellular and molecular phenomena on one side and efforts to account for behavior in terms of interconnected nets of neurons on the other. In recent years, there has come to be some doubt as to whether the center can hold. The explosion of information in cellular and molecular neuroscience has distracted many investigators from any interest in behavior, and left others with an uncomfortable feeling that with so much to learn about neurons the immediate prospects of relating them to behavior are limited at best. Over the same period, the so-called cognitive revolution has provided a perspective and methodology for exploring at least some aspects of behavior which would seem to make direct studies of the nervous system at least unnecessary, and perhaps irrelevant. In this context, a retrospective review by one of the small number of senior investigators who has maintained a persistent focus on the nervous system/behavior interface is a welcome reminder that there continues to be an interface discipline. Ewert's target article should serve to assure younger investigators not only that one

can have a foot in both camps without severe bodily damage but that one can work productively in this posture. Having myself wrestled with both orienting amphibians and disoriented colleagues skeptical of the value of interface research, I cannot but be pleased to have Ewert's article available. At the same time and for the same reasons, I want to be sure that readers do not take from the article inaccurate impressions about the nature of the circuitry underlying orienting, or about the character of interface research itself. Both are more complex and rich than the article makes clear.

Ewert's work reflects a particular approach to the nervous system/behavior interface, one which begins with a set of descriptors for behavior and presumes the task to be to find neurons and neuronal networks which correspond to them. Though demonstrably productive, this is not the only approach available, and it has some noteworthy limitations. The most obvious is that the behavioral descriptors one begins with tend to constrain what one looks for in the nervous system and to influence whether one regards particular observations as interpretable. How serious this is depends on the richness of the descriptors with which one begins, and on the investigator's ability to be both skeptical of observations that "fit" and alert for relevant observations that don't. Ewert's behavioral base is in ethology, and his research took its origins from the appealing parallel between the ethological concept of an innate releasing mechanism and the neurophysiological concept of a trigger feature. That he has looked beyond ethology for behavioral descriptors, and allowed his observations to challenge a straightforward interpretation of the relation between behavior and the nervous system is a mark of good interface science. These advances are, however, not inevitable given the starting conditions. It is not in practice possible to establish that there does not exist somewhere a neuron having a particular set of trigger features. It is only possible, having observed a large number of relevant neurons, to begin to doubt that looking for such a neuron is a useful approach to characterizing the nervous system.

A more fundamental limitation of the approach Ewert exemplifies reflects the assumption that, whatever behavioral descriptors prove appropriate, there must exist neurons or neuronal networks whose properties bear a close relation to them. This assumption is by no means unique to Ewert; it has become so embedded in modern neuroscience that most forget it is not actually an essential starting point but rather a hypothesis to be explored (Lashley 1951). Regularities in behavior represent properties of a complex organized system, whereas regularities in circuitry or neuronal response characteristics are properties of elements of the more complex system. The two sets of regularities need not in principle be isomorphic, and there are an increasing number of reasons to doubt that they are so in practice (Grobstein, in press a). Ewert has proven himself mindful of this problem as well. His discussion of feature-analyzing networks, of interaction, and of command systems clearly reflects a recognition that what appears simple in behavior may be complex in the nervous system. Again, however, it is worth noting that it's not actually logically possible to get here from there. Given a starting assumption of a simple relation between behavioral and neural properties, persistent failure to find certain properties might ultimately persuade one that they don't exist, but it's a long and never definitive path.

My final concern is that Ewert's target article may leave an impression that the business of research at the nervous system/behavior interface is necessarily reductionist, that its sole mission is to find the neural correlates of previously established behavioral realities. This characterization of interface research is a common one, which seems to endow the enterprise with a logical justification as well as a certain pride of place as a particularly rigorous form of behavioral science. My own sense is that the characterization is not only misleading, for reasons described above, but also impoverishing, and on both counts

enhances rather than reduces the risk that the center will fall apart. Neither behavioral scientists nor neuroscientists will really be convinced of the worth of interface research unless it is established that "there can be a much more dynamic and two-way interaction between the two fields than is suggested by thinking of one as exploring what the other will ultimately explain mechanistically" (Grobstein 1983, p. 622).

That interface science can contribute simultaneously to understanding the nervous system and to understanding behavior is obvious. Such fundamental neurobiological concepts as mapping, central pattern generation, and corollary discharge were established by studies of normal behavior and behavior after nervous system lesions. The latter have also produced fundamental changes in the way one thinks about behavior. Split-brain phenomena provide a recent dramatic example, but many others could be mentioned (see Jeannerod 1985 and a review of it by Grobstein 1986). The advantage of such studies is not only that they can contribute simultaneously to neural and behavioral sciences but also that they avoid some of the disadvantages of the more cellular approach exemplified by Ewert's work. One need not begin with particular behavioral descriptors and wait to be disabused of their relevance for studying the nervous system; the behavioral abnormalities resulting from brain lesions suggest natural descriptors relevant to both. Similarly, the issue of whether there are simple correspondences between behavioral and neural descriptors can be directly and quickly approached by lesion studies (Comer & Grobstein 1981; Grobstein, in press a; in press b; Kostyk & Grobstein, in press b; Lashley 1951).

These matters are relevant in a specific as well as in a general context. Whereas Ewert's characterization of the sensory side of the circuitry underlying orienting has clearly moved beyond limitations inherent in the initial approach, this is less obviously so for his characterization of subsequent circuitry. Our recent lesion studies (Grobstein, in press b; Grobstein et al. 1983; Grobstein & Masino 1986; Kostyk & Grobstein, in press a,b,c) strongly suggest that between the tectum and the motor pattern generating circuits underlying orienting there are more neural structures and information-processing steps than is obvious, or likely to become so, from single unit observations. Among these is one in which a critical behavioral variable, stimulus location in space, is synthesized and coded in a rather complex and unexpected way. The lesion findings make it highly unlikely that the entire sensorimotor interface consists of a set of tectal neurons which simultaneously categorize, localize, and activate pattern generating circuitry in an appropriate fashion. Ewert's hypothesis of a straightforward neural correlate for the behavioral concept of a releasing mechanism is appealing but almost certainly an oversimplification.

In short, the sensorimotor interface and the nervous system/behavior interface are both broader than they might appear in Ewert's article. The latter is at least large enough to usefully accommodate a variety of approaches, with the more cellular, exemplified by the target article, toward one end of the spectrum and the more molar, briefly outlined here, toward the other. Significantly, what is common to productive studies of the behavior/nervous system interface is an interest in the relation not between neurons and behavior but between nervous system organization and behavior. I have argued elsewhere that for these sorts of studies it is often not the neuron and its connections that is the appropriate level of analysis but larger information-processing blocks, consisting of meaningful neuronal ensembles such as maps and pattern generators, and the interactions among such blocks (Grobstein, in press b). The notion of the neuron as the centerpiece of neuroscience has served the field well for an extended period, but the time may have come when it is necessary to acknowledge openly that the complexity of the nervous system in general precludes linking neuron and behavior without new attention to intermediate level concepts and methods. The latter, rather than the neuron,

may be the most stable center for the behavior/nervous system interface. [See also Anderson: "Methodologies for Studying Human Knowledge" *BBS* 10 (3) 1987.]

Sampling and information processing

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Dr. Ewert presents a large and impressive body of work which has illuminated the field. I would like to comment on a few issues that are thorny and difficult for me.

Sampling. One component of the neurophysiological work under discussion is an attempt to relate single unit activity in the thalamus and tectum to toad prey-catching. Implicit in such an approach is the assumption that one has a representative sample of the neural elements involved. The deeper layers of the tectum (layer 6 and below) contain the bulk of tectal cells. From Golgi-stained material it is known that most cells in the deeper layers have dendritic processes that extend into the superficial layers. For many of these neurons, the axon originates not at the cell body but at a dendrite (an example is cell c of Ewert's Figure 13Ac). My colleagues and I have found, much to our dismay, that in recording extracellularly in the deeper layers of the frog tectum there are relatively few cell bodies that are electrically responsive. In addition, where cell bodies are electrically active there is uncertainty whether that activity is an accurate rendition of what passes down the axon. We have argued elsewhere that axonal output of at least some tectal cells may be different from what is seen from monitoring their cell bodies (Gruberg & Lettvin 1980).

Nonetheless, Ewert finds good correlation, between the response of a certain type of tectal neuron, the T5(2) and prey-catching. Under conditions when these cells fire selectively to prey, the animal is in turn selective in prey-catching. When these cells do not selectively fire for prey the animal is less selective in its snapping. Ewert describes the cells as "essential and decisive for prey-catching." Are they? How compelling is the suggestion if there are inherent limits in knowing what other cells are doing? If in the future we were technically advanced enough to ablate just T5(2) cells, how probable is it that visually guided prey-catching would be eliminated? Even if visually guided prey-catching were eliminated after such an ablation, does that make T5(2) cells essential and decisive? The Sprague Effect is a reminder of the limits of such claims (Sprague 1966).

Another part of the system? Ewert has focused primarily on thalamic and tectal interactions. However, a related area that appears to contribute to tectal function is the midbrain structure, the nucleus isthmi. In frogs, the n. isthmi receives a topographic visual input from the ipsilateral tectum and the nucleus projects topographically and bilaterally back to the tectum. In addition, n. isthmi and retinal fibers terminate in the same superficial layers of the tectum; they are intimately related. Other extrinsic inputs (including from posterior thalamic areas) project primarily to deeper layers. Unilateral ablation of the n. isthmi leads to a scotoma to visually presented prey in the contralateral monocular field (Caine & Gruberg 1985). We have found that up to 11 months after ablation the scotoma remains. These results are surprising if the tectum and thalamic areas are the principal areas that one concentrates on and other areas are presumed to have modulatory effects. Can the results obtained from n. isthmi ablation be integrated with what Ewert has discovered about cells of the tectum and thalamus?

Information and energetics. What is the relationship between spike activity and stimulus? Ewert goes to some lengths to demonstrate that discharges of T5(2) neurons are well correlated with prey-catching activity and better correlated than other types of units (particularly T5(1) and TH3). In his computation the underlying assumption is that the cells that read the output

of tectal and thalamic cells are responding to the rate of discharge alone. Is that necessarily true? Can we rule out that the target neurons are sensitive to other changes in firing patterns? Average neuronal discharge can be much the same and yet the interspike interval patterns can be very different. This is not just a theoretical issue. It was shown in frog optic nerve fibers that an observer viewing the axons' interspike interval patterns could make a good assessment of a variety of conditions simultaneously prevailing in the visual field (Chung et al. 1970). If one had access to just the average discharge rate of these fibers, information would be lost. Presumably some of those types of optic nerve fibers project to the tectum. Do the tectal cells discard the information embedded in the patterns of interspike intervals? Do the neurons that read the output of tectal cells in turn only measure average rate or are they more sophisticated readers? A whispered sentence and a shouted sentence generally require different power outputs, but they can transmit the same amount of information. T5(2) cells may be at the heart of the matter, but that presumes we know what is signal, what is noise, and what is to be filtered out.

Presumptions based on keyhole peeping

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One bewildering feature of this work is the great volume of words said about the neural explanation of the toad's response to preylike objects in comparison to the relatively small number of recording sites that have yielded interesting neurons. From the toad's point of view a lot of papers have resulted from the exposure of relatively few neurons. The electrode, in fact, behaves like a keyhole, but the resulting gossip is enormous.

What is the general relation between neuronal properties, models, and behavior? To date, most workers have assumed that either models or neuronal features explain behavior. The opposite turns out to be a more faithful approximation to the truth. Neurons are the only components we know. When we uncover their previously unknown features, we explain neurons by reference to the known behavior. Model building with known or imagined features of neurons is a quantitative confirmation. This conclusion is the fundamental driving force behind the mechanistic analysis based on recording.

Ewert's target article will interest me in 20 years' time as a historical document that shows clearly the limitations of our present concepts, which are in turn determined by the limits of our techniques and revealed by the limited range of technical terms we have available. Whether the animal is a toad, an insect, or a leech is largely irrelevant to the methodological problems of analyzing behavior in terms of parallel neurons recorded in the nervous system. The basic problem is that a complex story of detection has to be inferred from a few peeps through a keyhole (the electrode), but there are many other problems.

First, dozens of sentences in Ewert's review are circular in the sense that they postulate a cause in terms of the effect, not in terms of the mechanism, because the mechanism is unknown. Even the type of mechanism is unknown. The first sentence of the abstract begins: "Sign stimuli elicit specific patterns of behavior. . ." Of course they do, because in this sentence the object and the subject define each other, in that a sign stimulus is that which generates specific behavior. There are many such imaginary bridges of fancy over the swamps of ignorance. Second, quite a separate matter, the terms describing and attempting to explain the behavior are derived from observations of the behavior. Most of the keywords – such as "action patterns, releasing mechanisms, sign stimuli, command sys-

tems, neuromodulation, feature analysis" – are hypothetical components of a verbal model that has not progressed beyond the level of the simple observations of behavior that inspired them. That is, they have not yet been revised into the language of even the imagined mechanistic explanations, let alone the vast as yet unknown real neuronal interactions.

Third, neurons are discussed as if they were known. The question, "whether the perceptual operations . . . are performed by a 'feature detector' [neuron] . . . or by a 'feature-analyzing network,'" as outlined in Figure 2, is treated as if the neuronal networks were real. But we already know that this question cannot be answered unless exactly the right combinations of identified neurons are simultaneously recorded. That itself would be an improbable feat in recording. Unfortunately, the toad's neurons are not identifiable, so no experiment can be duplicated; and in any case we know from the anatomy that the mechanism is both parallel and hierarchical. Also, having said that, we have said very little, because the whole circuit – even its components – have yet to be discovered. Numerous examples illustrate this naive idea of causality. For example, "several small moving images aligned at small distances parallel to the direction of movement are interpreted as prey *because of excitatory interactions*" (italics mine); but in fact no such interactions have been observed inside the toad. All we have is the primary observed fact.

Also, the data that could be used to build up a neuronal model are so limited that no satisfactory model is possible, or alternatively, *any* satisfactory model is possible. The problem is compounded by the fact that neurons can be distinguished only into classes, and the definition of the boundaries of the classes is circular (being based on the occurrence of distributions that look like classes).

Now look at this quotation: "Human beings, facing complex phenomena, exhibit an almost obsessive urge to conceptually mold these phenomena into structures of cause-and-effect relationships. This tendency is, in fact, so compulsive that it sometimes comes at the expense of precision and often requires the invention of hypothetical, unobservable entities . . . to make theories fit the mold of a causal scheme" (Pearl & Tarsi 1986). The first danger of this method of explaining behavior is to fall into the error of a spurious correlation; but a greater danger is to be so aware of the uncertainties of this method of analysis by neuronal recording, or by analysis of behavior, that the springs of action dry up. The third danger is Whitehead's "misplaced concreteness" – that we or others actually believe in the reality of the postulated model, or even in the reality of the nouns invented as parts of explanations. But we are perpetually in a dilemma, because scientific knowledge can increase only as the postulated causes are tested, and replaced by better approximations. It is not sufficient to discard them (in Popper's sense) if nothing else is put in their place. Refining the models by building into them the data from real neurons is the only way that the analysis of behavior will approximate more and more the analysis of neuronal activity.

Of course, the model is frequently not tested but is simply presented. For example, toads learn to approach and snap at visual stimuli that are not innately effective, but the neurons on the visual pathway have not been examined in these educated toads.

Twenty years ago I published a book (Horridge 1968) which rapidly went out of print, and which has been stolen from many libraries. In it I pointed out some of the difficulties in the study of interneurons because (1) they operate in parallel, (2) the nervous system is open-ended and (3) yet-to-be-discovered interneurons operate in clusters but are recorded singly, and (4) the message in the nervous system is that recorded by the cluster of next neurons down the line, not the signal recorded by the electrode. Given these difficulties, and numerous others in continuations of the same theme (Horridge 1983), it is amazing that neurons exist with properties that match any aspect of

behavior at all. Almost all vertebrate neurons operate in clusters. Have we been misled by a few fortunate discoveries into believing that all neurons will turn out to have clearly self-revealing functions?

My own view is that we know so little about primitive or stripped down nervous systems of moderate complexity that there are many more simple neurons to be found with properties that fit into models of the behavior. Already, however, researchers are wondering about the next stage, how the message can be identified in the neuron cluster. The answers will come only by recording simultaneously downstream, to track the information flow, and upstream to find the source. Perhaps the toad is a good animal through which to track that flow. The importance of these very general questions is realized as soon as a new look at the primary data and especially a new discovery or a better technique overturn a nicely constructed model.

The progressive introduction of new techniques introduces a new question. Each technique new to science (e.g., de-oxyglucose, lucifer yellow, kainic acid, lesions, or immunofluorescence) gives us access to a new range of observations on old preparations such as the toad. The real advances in science, however, come from ideas, discoveries of new principles, and new techniques. It is a serious question whether this analysis of toad visual behavior has yielded anything really new to science.

Ewert's model: Some discoveries and some difficulties

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There are (in my opinion) two main achievements of Ewert and his collaborators. First, they have provided a large variety of data to document the specificity of the prey schema (favoring "wormlike" stimuli) in various species and at different ages, further localizing key elements of the so-called IRM (innate releasing mechanism) in the optic tectum (T5(2) cells) and lateral medulla near the final motor output to the tongue (snapping) muscles. Second, they have shown that the pretectum plays a major role in the IRM (in addition to retinal afferents) by supplying inhibition to the T5(2) cells. This mechanism, which achieves specificity by a "subtractive" interaction between two afferents to a visual neuron, should be considered by students of mammalian vision, who mainly consider additive mechanisms in the hierarchical arrangement of feature detectors. Ewert's model does resemble that postulated for wide-field motion detectors in cortex, where ERFs and IRFs (excitatory/inhibitory receptive fields) have opposite directional selectivities (Aliman et al. 1985).

Configurational perception by toads. Unfortunately, Ewert appears to misconstrue the idea of "perceptual invariance" in shape recognition as derived from studies of human and mammalian vision. In one paper, he begins by quoting the standard example that the letter "A" can be recognized despite changes in size, location, orientation, or script. But his so-called worm configuration is dependent upon the object's moving along its major axis. Properly speaking, it is not the *configuration* (rectangle) that is identified with prey, but a particular relationship between shape and motion. The concept of invariance as applied to higher mammals (and perhaps birds as well) specifies that stimulus motion (compatible with useful acuity) is irrelevant to shape recognition! Furthermore, Ewert's own experiments (Ewert 1968) indicate that the preference for a worm over a square is not shown by toads when somewhat larger stimuli are used (stimuli fitting within the ERFs of T5(2) cells). The salience of an 8° square is equal to that of an 8 × 16° or a 8 × 32° "worm." The striking data for "worm preference" are obtained (in several articles) with long 2° high worms as compared to 2° squares.

Ewert does not always make it clear that his strong statements concerning invariance of "worm sensitivity" involve worm/anti-worm comparisons. This is a somewhat trivial observation, since this discrimination simply reflects the well-known function of IRFs in providing some size selectivity. Indeed, it is well known that many tectal cells in the cat respond best to moving objects much smaller than the ERF size and that these would also show a worm/antiworm discrimination for a wide range of object sizes, although one would not venture the suggestion that worms are of much interest to a hungry cat. What is of greater interest (but little studied by Ewert) is the summation mechanism in the tectum which makes the T5(2) cell more sensitive to worms than to squares of equal height. That discrimination is not made by retinal cells, whereas the worm/antiworm discrimination is seen at that level. Surprisingly, Ewert does not mention the nice demonstration by Roth (1986) that frogs (unlike toads) fail to show preference for worms over squares. This fact fits nicely with the experiments of Schürg-Pfeiffer and Ewert (1981) in which the frog tectum harbors few T5(2) cells compared with their plenitude in toad tectum, and it supports his contention that T5(2) cells are a major component of the filter for "prey." This facet of the prey schema has been of particular interest to me, since we have observed a distinctive difference between frogs & toads in the dendritic morphology of those tectal "ganglionic" cells which project to the lateral medulla (Ingle & Arango 1986).

Ewert several times implies that toads are sensitive to "configuration" per se in their worm-preference behavior. Not only would I disagree with use of the term "configuration" (as argued above), but it would seem that Ewert has ignored his own arguments (Burghagen & Ewert 1982) against my earlier attempt to demonstrate configurational recognition in toads (Ingle 1968). In that initial study, pilot film records indicated that *Bufo americanus* turned to snap at the head (rather than the tail end) of actual mealworms or of either black or white dummy worms. We have confirmed this with large amounts of film data from both American and marine toads; I will rely however, upon a published account of worm preference in *B. marinus* (Ingle & McKinley 1977), to make my point. In that paper we measured the locus of tongue strikes toward double stimuli, made from two cylindrical yellow stimuli (mounted on a black wire like a shishkabob) moved along a dark floor. When stimuli were only 7° apart, 85% of the strikes were aimed at the "head" stimulus, but when the separation was increased to 15°, toads struck equally at head and tail. Burghagen and Ewert (1982) criticized our claim on the basis of his observation that toads would strike at the *tail* end of a long white "worm" (a 2° × 32° stripe) but at the *head* end of a black worm: an anticonfigurational result. However, he ignored our earlier finding that the "configurational" mechanism breaks down for such long stimuli. It seems likely that most prey taken by toads (insect larvae) are not nearly so long as Ewert's experimental stripes and would better match stimulus configurations used in our experiments.

Efferent outputs of the tectum. A second point of disagreement concerns Ewert's hypothesis that T5(2) cells are the chief elements of command systems for both *orienting* and *snapping* at prey. I have shown (Ingle 1983a) that severing the crossed tectal projections at the level of the ansulite commissure of the tegmentum abolished turning toward prey (but not snapping) while cuts of the ipsilateral tectal projections to the medulla produced a loss of snapping at prey in the opposite monocular field, with retention of accurate orientation in the same directions. Backfilling of tectal cells via the ansulite commissure by horse-radish peroxidase implants in the medial medulla (the so-called tectospinal tract) labels a homogeneous population of neurons with dendrites ramifying only in the uppermost tectum (Ingle 1983a; Lázár et al. 1983) where the class-2 retinal fibers terminate. Because the studies of Ewert and von Wietersheim (1974b) show that T5(2) cells have a major input from class-3 fibers, I proposed (but did not demonstrate) that T5(2) cells do

not provide input to the tectospinal projection (Ingle 1983a). Ewert misquotes my hypothesis as denying that some contralateral projections of T5(2) cells can be found (Sect. 6.5.1, para. 1). In my chapter (Ingle 1983a) in the volume Ewert edited, I explicitly stated that the ipsilateral tectobulbar tract has a strong commissural component at the medulla level by which the initially ipsilateral tectal efferents can cross over to influence the contralateral medulla (p. 203). The issue as I have stated it is whether the *tectospinal* tract contains T5(2) cells as part of a "localization" mechanism (which I doubt) or whether T5(2) cells, some of which are known to project ipsilaterally, contribute via the medullary decussation to "priming" the orientation mechanism (as I suggest).

In this same chapter (Ingle 1983a) I did suggest that small field tectal cells would be more appropriate than T5(2) cells for a fine-grained localization role. However, McIlwain (1975) has presented a telling argument in favor of the efficiency of population encoding by wide-field cells in the mammalian tectum directing eye and head movements. Now converted to the "population encoding" model, I can offer a better alternative to Ewert's supposition regarding tectospinal cell identity. There is a class of cells in the frog tectum recorded in my lab, but scarcely mentioned since the pioneering observations of Lettvin et al. (1961), which fits my expectations for a tectospinal cell: very large spikes, selectivity for small stimuli (implying dependence on class-2 input), and fields of 40–90° in diameter. These cells escalate their response to successive movements of a 1° or 2° spot, much as Lettvin described for his so-called sameness cells. The fact that these wide-field cells do not respond immediately to the first "prey" incursion (as do T5(2) cells) makes them candidates for efferent cells that require priming from intratectal circuitry (see discussion in the accompanying target article by Arbib, this issue). Important future experiments with these prey-sensitive cells include attempts to produce antidromic stimulation from the ipsilateral and contralateral medulla (are they tectospinal cells?) and possible changes in size-selectivity following pretectal lesions. If these cells do *not* change their size-selectivity (as I would hypothesize) they cannot depend on major input from T5(2) cells, which become "large object detectors" after a pretectal lesion.

Roles of tectum and pretectum in visually elicited avoidance behaviors. In the same review chapter (Ingle 1983a) I argued that the tectum, not the pretectum, is critical for eliciting and directing avoidance jumps in the frog (e.g., *Rana pipiens*). This contradicts Ewert's original suggestion that the pretectum mediates avoidance behavior by a mechanism parallel to the food-pursuit role of the tectum. First, Ewert's finding that electrical stimulation of the pretectum elicits crouching or side-stepping is not conclusive evidence, since these responses are also components of barrier-avoidance behavior (crawling under or stepping around) which I have demonstrated to depend upon the pretectum (Ingle 1980) and not the optic tectum (Ingle 1977). Second, I agree with Ewert's observation that pretectal lesions impair or abolish the avoidance of visual threat within a few days of surgery, but I have reported (Ingle 1980) that normal avoidance jump directions are recovered within 1–2 weeks by frogs with complete ablation of the pretectum. On the other hand, rewiring of retinal inputs to the (wrong) ipsilateral tectum results in avoidance jumps *toward* an approaching black disk instead of fleeing into the opposite field, as occurs with normal frogs (Ingle 1976). Despite these findings, Ewert has preferred to characterize this behavior as a mere "startle response" (section 4.3, para. 1).

One way to resolve our differences as to pretectal/tectal control of avoidance behavior may be to change the terminology. I do not regard the main responses of toads elicited by overhead disks as avoidance maneuvers – rather, ducking, backing, crouching, or sidestepping are better called "protective" responses. On the other hand, leaping many inches into space to avoid a potential collision is clearly a successful avoid-

ance of capture. It may be that the first class of responses does depend upon pretectal function, whereas the second class does not. The circumstances biasing toads to one or the other alternative response should be studied in conjunction with new lesion experiments.

Tectal modulation. Finally, I wish to reinforce and add to Ewert's list of experiments indicating that the tectum is under strong control of tegmental or diencephalic modulatory influences, since this "contextual" discussion of avoidance or feeding behaviors has been largely omitted by students of the mammalian tectum who frequently lack familiarity with the ethological literature. Ewert has made a notable discovery in showing that familiar prey odor is a powerful facilitator of feeding behavior in toads: That is, it compels them to pursue even large objects that they would normally avoid. Ewert has made a significant step toward understanding the link between olfaction and visuomotor circuitry by finding that medial pallial lesions disrupt this association. However, he is on shaky ground in comparing this aspect of learning to functions of the mammalian hippocampus. Although there is good evidence that the hippocampus participates in spatial memory among rodents, one must recall that the integrity of simple associative memory is a standard control observation in rats or monkeys with hippocampal damage. [See also Foreman & Stevens: "Relationships Between the Superior Colliculus and Hippocampus" 10 (1) 1987.]

Under the rubric of "attention" Ewert describes tectal cells whose discharge frequency correlates with "response readiness." I have noted that frogs with consistently short response latencies prefer larger prey than frogs with longer latencies (Ingle 1973a). Because size preference is itself presumably under the control of the pretectal-tectal afferents, it seems possible that the activity of deep tectal cells is reciprocally related to the activity of modulatory cells of the pretectum. Ewert (1971) has described in toads an interesting class of pretectal cell that gives a long discharge (typically 15–20 sec.) following brief incursion of a visual stimulus. Such cells also exist in the frog's pretectum (my unpublished studies) and may be linked to my behavioral observation that following 5 sec. of "intimidating" a frog with a large black object, there is a 15 sec. interval during which the frog is inhibited from attacking prey on the same side of the midline (Ingle 1983b).

A class of modulation not mentioned by Ewert concerns my demonstration that pretectal lesions abolish the ability of frogs to make detours around obstacles to approach prey seen through a semitransparent barrier. I have shown (Ingle 1983a) that the overshooting of the barrier depends upon the integrity of the isthmus level decussations, but these split-isthmus frogs are still inhibited from snapping at occluded prey, whereas the pretectal-lesioned animals jump into the barrier in a feeding attempt. These data suggest that pretectal projections to the tectum modulate the decision whether to snap at or merely to fixate prey. This decision, in the absence of a barrier, is guided by prey distance (Ingle 1976), which in turn is a determinant of the optimal angular size of prey (the size-distance constancy effect, described in the target article). Since animals with pretectal damage lose this constancy behavior, it seems that the pretectum is associated with the discrimination of object distance as one factor controlling the size preference. Thus, the snap/fixate decision may come under pretectal control in two different ways: influenced both by the presence of barriers and by the perception of distance. Our unpublished finding is that anterograde horse-radish peroxidase (HRP) transport from medial pretectum is mainly to deep laminae, and from lateral pretectum it is mainly to superficial layers; this may be relevant to the functional dichotomy in question.

In summary, a good deal of the complexity of tectal functions in frogs and toads may reflect the multiplicity of modulating inputs. Unravelling the details of these systems will be critical for understanding the variability and subtlety of natural behav-

ior and will have considerable significance for studies of homologous systems in the mammal. Ewert's suggestion that pretectal-to-tectal connections have dropped out in mammals is incorrect: Each of the three major pretectal nuclei in various mammals projects to the tectum, although we remain ignorant of their functions. It is to be hoped that Ewert's pioneering approach to toad pretectal functions will prove heuristic for mammalian studies as well.

Neuroethology and color vision in amphibians

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About 10 years ago we conducted experiments on common frogs with lesions of the dorsal thalamus (Kondrashev & Dimentman 1978) and succeeded in reproducing many effects described by Dr. Ewert. Our evidence, which was obtained both in the breeding season and in the winter hibernation period when no prey-catching reactions can normally be seen, convinced us that visually guided behavior of amphibians really results from complex interactions of different brain centers. The role of central mechanisms was also confirmed in our control electrophysiological experiments by the fact that the characteristics of retinal detectors (ganglion cells) remained unchanged even in the breeding season.

The results of Ewert's data and our own (Gnyubkin & Kondrashev 1978) have suggested that the caudal dorsal thalamus may determine some sort of hierarchy in the toad's motivation, and consequently its choice of behavior on the basis of analysis of external and internal stimuli. Ewert's target article justly attributes a special significance to the motivation that modulates the prey-catching activity in toads (sect. 6.4.1); the role of motivation, however, has been poorly studied and needs further research.

It seems to me that applying a broad neurobiological approach to the study of other types of visually guided behavior could help us understand the role of motivational factors. Mating behavior of anuran amphibians, which has been found to be controlled to a great extent by visual stimuli (Kondrashev et al. 1976) is of particular interest. Most noteworthy is the similarity of many parameters of visual stimuli eliciting approach and clasping responses in mating behavior and some elements of prey-catching behavior in toads (similar to avoidance behavior in both cases; Gnyubkin & Kondrashev 1978). Moreover, as the motivation to mate fades, the same "prey"-sized visual stimulus (a ball of 1 cm in diameter) can alternatively elicit prey-catching and sexual responses in the same male individual of *Rana temporaria*. This evidence seems to corroborate Ewert's suggestion that there is a functional similarity between command elements of these different types of behavior.

There is one visual stimulus parameter, however, that Ewert excludes from his discussion (sect. 3.1): the color of the object. Color plays a key role in the breeding behavior of frogs and toads: Male common frogs prefer red objects and male common toads prefer blue objects (Kondrashev et al. 1976). This turns out to be a "true" case of color discrimination, including the property of perceptual constancy (Gnyubkin et al. 1975); the discrimination is pronounced even at very low illumination (about 0.01 lux, Kondrashev 1985). Blue color attracts the animals so strongly that male common toads even preferred motionless flat discs presented together with living female toads (Gnyubkin & Kondrashev 1978).

If we adhere to the hypothesis of "interaction" (sect. 5.4) we should suggest the existence of command elements of a "color type." But how is the color information transmitted through

neural circuits? I believe we have here an interaction of neural information from a tectal projection and from a projection into the rostral dorsal thalamus (the neuropil of Bellonci). It has been convincingly shown that these two projections differ significantly in color-coding properties (Maximov et al. 1985, Orlov & Kondrashev 1978) and that only the thalamic projection containing blue-sensitive "on"-elements of an opponent color type provides a reliable signal about the color of an object. It is interesting that some color preference was also observed in the prey-catching behavior of *Bufo bufo* and *Bufo viridis* (Orlov & Maximov 1982). However, the question of the site of convergence of different information on a colored prey-stimulus object remains open in this case as well, as tectal type-2 units are completely devoid of the ability to discriminate color, whereas the elements from the neuropil of Bellonci, which discriminate colors perfectly well, respond very feebly to objects of prey size.

A study of the color stimulus as a key parameter in some types of behavior can also be very useful in elucidating onto- and phylogenetic aspects of the problem under discussion (sect. 3.3.3). In fact, the difference in organization of the command neurons in male toads preferring blue objects and in male frogs preferring red ones is quite obscure. Another problem: What is the difference between these mechanisms in male and female individuals of the same species, as active visual search for and sexual approach toward "mates" in the breeding period is observed in males only?

Worm detector replaced by network model – but still a bit worm-infested

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J.-P. Ewert was among the very first to bring together quantitative work on unrestrained behavior and studies of the properties of neuronal networks. Ewert's multidisciplinary approach, using ethological, neurophysiological, neuroanatomical, and theoretical methods, has served as a paradigm for the whole field of neuroethology. This is his most important contribution to biology, which stands above any of the details of his work. Furthermore, through his own experiments, as well as the suggestions of others, he has transcended the concept of feature detectors that has dominated the field of neuroethology for some time. This concept has been replaced by the insight that object recognition is a function of a network consisting of several types of neurons with overlapping preferences for certain features, rather than discrete prey detectors.

A few observations are in order, however.

1. Despite much modification relative to earlier versions, Ewert's model remains too restricted in the sense that it applies almost exclusively to the prey-catching behavior of one species (the common toad, *Bufo bufo*) under laboratory conditions. The key stimuli that most strongly release a particular behavior pattern are regularly observed to be highly abnormal. For example, the stimulus that is the strongest releaser of the snapping response in *Salamandra salamandra* is a square that is far too large to be eaten (Roth in press). Thus, there is no necessary association between the strength of a releasing stimulus and its relevance to natural behavior. Furthermore, general statements by Ewert concerning prey preferences in anurans are inaccurate. By far the most common dietary specialization found among anurans in general, and bufonids in particular, is a preference for small compact prey such as ants, not for wormlike objects (Emerson 1985). Considering only *Bufo bufo*, the preference for wormlike objects over compact prey is not as strong as it would appear from Ewert's arguments. In the range of edible

prey sizes, there is no significant preference for wormlike over compact prey. Only well above the range of edible sizes of the square, which represents compact prey, is the wormlike stimulus preferred.

2. In Ewert's network model, although based on the idea of interaction between different types of tectal and pretectal neurons, the role of the T5(2) type, which responds preferentially to wormlike objects as a second order processing neuron, is exaggerated. It has been shown by several investigators, including Ewert and coworkers, that in other anurans (e.g., ranids) characteristics of T5(2) tectal cells are not as clearly expressed as they are in toads. The same is true for most species of salamanders, which prefer very small, compact prey (Roth 1982; in press). Ewert's network model should be formulated in more general terms, in the sense that the minimal prey recognition network is composed of a number of response types, some of which are universal (e.g., T5(1), T5(3), T1, T3 etc.) and some of which are characteristic of only certain species with preferences for certain types of prey (e.g., T5(2)). It has been shown in a network model by an der Heiden and Roth (1983) that small changes in inhibitory coupling among tectal/pretectal neurons may change response characteristics dramatically.

Related to this point is the question of tectal output elements. Ewert assumes that T5(2) cells are the main output elements with regard to prey recognition from the tectum to brainstem premotor centers. However, as we argue above, the relative importance of cell types as output elements should vary among species with different prey preferences. Furthermore, the data of Ewert and coworkers, as well as others, show that more than one type of tectal cell sends efferent fibers to the premotor centers. There is insufficient experimental evidence and no conceptual necessity for assuming that the tectum is the final stage in the prey recognition process, the result of which is summed up by one output element. It could well be that the activity of different cell types involved in prey recognition is only summated at premotor levels.

3. Precise distance estimation and recognition of absolute size are necessary prerequisites not only for prey localization but also for prey recognition, especially for distinguishing between predator and prey. However, all tectal cell types studied so far respond only to the angular, rather than the absolute, size of prey objects. This means that they cannot distinguish reliably between large but distant objects (e.g., enemy) and small nearby objects (e.g., prey). To date there is no known mechanism in the tectum by which size constancy can be explained on the basis of tectal response types. Ewert does not give enough consideration to this very important problem. It appears that those tectal cell types usually regarded as being involved in prey recognition only provide information about shape, relative size, and relative velocity; distance information (most probably based on disparity cues; Collett 1977) is processed separately by tectal and/or pretectal/thalamic networks. Only together do these pieces of information form the percept "prey" or "predator." If these independent pieces of data are not summed in the tectum, but converge on motor centers separately, then there is no true prey recognition center in the tectum and, in a strict sense, there may not be such a center in the brain at all.

We emphasize that these comments are suggestions for enlargement of Ewert's model, and not alternative views.

Sensorimotor maps in the tectum

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Ewert stresses the tight linkage that may exist between sensory input and motor output in prey-catching and, more particularly,

the orienting behavior of toads. He postulates that the translation between sensory and motor space, that is, the transformation of the spatial coordinates of the target into the appropriate motor coordinates of the different segments involved, is realized thanks to a fixed correspondence between the sensory map, in retinal coordinates, and the motor map, which is in turn connected with circuits controlling "fixed action patterns." In our opinion, this hypothesis of a relatively rigid sensorimotor interface raises important problems of adaptability that the author leaves open. We would like to argue that a strict topographical sensorimotor correspondence at the tectal level is unable to explain how the movements of all the segments involved in orienting behavior are individually programmed. Indeed, if the sensory transducer (the eye in this case) is mobile with respect to the segment to be oriented, the sensory (retinal) and motor (head or trunk) coordinate systems may differ. This misalignment of the two sets of coordinates is proportional to the rotation of the eye in the orbit or the head on the trunk.

What is the mobility of these different segments in anurans? According to Dieringer and Precht (1982), the head-immobilized frog has vestibular and optokinetic reflexes of the eye, composed mainly of slow compensatory drifts, the amplitude of which is typically more or less 4 deg. There are no data, to our knowledge, about the presence of these reflexes during spontaneous or visually triggered head rotations in the free animal. Moreover, spontaneous eye saccades seem to be absent when the head does not move. The head movements, on the other hand, are of quite a large amplitude. Toads do make exploratory movements of the head in a stationary visual environment (Ewert 1984a). Dieringer et al. (1982) have measured frog optokinetic and vestibular head movements extending about 45 deg. As a consequence, the anuran eye, despite its small intrinsic mobility, may be oriented, with the help of the head, through quite a large range with respect to the body axis. It could thus happen that a toad detects a prey object when its head is not aligned on the trunk. In this case, a rigid visuomotor connection would perhaps yield a good head movement but certainly not an adequate trunk rotation: A correct alignment of head and trunk on the target would not be possible. The orienting behavior must be modulated not only by selective attention, motivation, and so on, but it must also be guided by positional information about the mobile segments.

In man, fixating a visual target usually requires a coordinated eye and head movement. The amplitude of the head rotation depends on the initial eye position: It is encoded in a craniocentric set of coordinates (Roucoux & Crommelinck, unpublished observations). We have explored this problem more extensively in alert cats by microstimulation of the superior colliculus (SC) (Guitton et al. 1980; Roucoux et al. 1980). From this study, it appears that the SC of the cat is directly involved in visual orientation of eye, head, and trunk. It can be divided functionally into three regions. The central visual field (25 to 30 deg. around the area centralis) projects in topographical order onto the superficial layers of approximately the rostral half of the structure (zone 1). Microstimulation of the deep layers in this area yields eye saccades, the amplitude and direction of which are independent of initial eye position (retinocentric coding). In this zone, the visual and motor maps seem to be rigidly connected, something that would be expected in a structure implicated in eye orientation only. The visual field extending from 30 to 60 deg. is projected onto the medial region of the SC (zone 2). Microstimulation in this zone evokes a combination of eye and head movements such that gaze is displaced according to the overlaying visual map. Here, when initial eye position changes, the amplitude and direction of the ocular saccade varies; the head saccade, on the contrary, remains constant. This suggests that zone 2 output layers encode eye as well as head movements in the frame of reference of the head (craniocentrically) and that a coordinate transformation occurs somewhere in the functional path between collicular input and output. It is as if the sensory

map could "move" as a function of eye position, with respect to the motor map. There is still a third zone in cat's SC which is caudally situated. This zone receives projections from the periphery of the visual field. Stimulation there produces head saccades that, are not constant for a given site. They change in amplitude and direction with initial head position and tend to bring the head to a given position on the trunk. The deep layers of this zone thus appear to be coded in the frame of reference of the trunk (somatocentrically). This observation suggests that in this zone the sensory map "moves" with respect to the motor map as the head turns on the trunk.

In a large part of the SC of the cat, there is thus no rigid topographic link between input and output. The existence of zone 1 seems to be tied to the ability of the cat to execute an ocular saccade without simultaneously turning the head or trunk. This ability is characteristic of all foveate animals and is particularly well developed in man and monkey. In the latter species, the whole SC appears to be devoted exclusively to controlling eye movements; in parallel, these saccades attain 45 to 50 deg. from the primary position, twice the oculomotor range of the cat. One might speculate that collicular zone 1 develops progressively along the phylogenetic scale in parallel with the fovea and the foveate type of eye saccade to the point of completely "invading" the SC. Zone 1 could be considered a "neo-colliculus." The cat's zones 2 and 3 might represent the state of evolution of the SC at the anuran level; a structure mainly devoted to orienting the oral pole and the visual receptors toward prey by rotation of the neck and the rest of the body, as well as to triggering the motor sequence necessary to consummate. As a consequence, it is highly improbable that there is a fixed topographic correspondence between input and output in the anuran's SC. A head position signal must be integrated in the orienting sequence.

Before continuing, I hasten to add that my characterization of the functional organization is necessarily a simplification, but not an oversimplification, I believe. For example, the substantial sustained response exhibited by R2 neurons and the relative latencies and timing of the interneurons all provide important (but not, I suspect, critical) contributions to the overall W-configuration detection scheme.

As a first approximation, consider the algebraic combination $(R2 - R3)$. The optimal stimulus for $(R2 - R3)$ would be a moving circle that just fills the ERF of R2, since it would be optimal for R2 but suboptimal for R3. Any larger stimulus would produce a net negative—that is, R3 acts as inhibitory evidence. The computation $(R3 - R4)$ would operate similarly over correspondingly larger stimuli (optimal for 8°). Computing $((R2 + R3) - (R3 + R4))$ extends over the entire range of scales from R2 to R4, and would "pass" bars moving in W-configuration and squares, with optimal response for widths that fill the R3 ERF.

To perform this computation, first compute the inhibitory sum $(R3 + R4)$ by the interneuron TH3. Then, at T5(1), add R2 + R3 and subtract TH3. The function computed by T5(1) is far too dependent on stimulus area (Figure 11). Better specificity for elongation is achieved at the level of T5(2) by sharpening the inhibition from TH3. Thus far we have a purely feed-forward, hierarchical computation, on the order of the "feature detector" in Figure 2. Mutual facilitation across neighboring T5(1) cells and mutual inhibition of TH3 neurons on adjacent T5(2) cells (Figure 19) would allow correlation of the W and A evidence across space and time as the target moves across the visual field. One can thus view the repeating elements of the network in Figure 19 as encoding, by analogical circuitry, a *truth table*, whereupon only those signals that would arise from a stimulus moving in W-configuration are passed through to T5(2). One finds that the combinations of responses of R2, R3, and R4 in Figure 11 to different stimuli are highly predictive of the TH3 and T5(1) intermediate results and of T5(2) responses.

Reflecting on this computation, I was quite struck by how the toad has so completely sidestepped the need for explicit processing of orientation and of elongation (the defining spatial properties of the W-configuration). Evolution discovered an alternative spatiotemporal relationship that permits the T5(2) neuron to be tuned to the W-configuration "directly." I take from this the lesson not to trust intuitions as to what would constitute the most natural or direct technique for implementing some function neurally.

Note that if the functional components resembled Hubel and Wiesel's (1962) simple cells, as might have been expected, it would have taken considerable redundancy to achieve isotropic behavior. With the toad's scheme, one starts with and ends with circularly symmetric operators.

Ewert proposes that prey is represented in terms of schemas defined by shared spatiotemporal features. The toad has evolved a schema/antischema pair that seems both elegant and economical. The worm/antiworm distinction permits one neural substrate to compute a quantity that subserves both prey pursuit and predator avoidance, all within one bounded continuum of spatiotemporal features. But is the notion of paired antagonistic schemata a principle that is extensible? Or is it serendipitous that the defining features of prey and predator happen to lie at opposite ends of the same continuum? I suspect the latter.

At various points (e.g., sect. 3.5.2, para. 3) Ewert remarks that the explicit assertion "worm" does not appear to exist in the toad's visual world. The worm-antiworm schema is intimately tied to the motor processes. But if toads had a larger repertoire of behavior regarding worms than merely eating them, wouldn't one expect to find neurons that more obviously asserted the existence of a worm? Even then it would probably be difficult to argue that any given neuron or cluster of neurons served the sole purpose of representing "worm." Another lesson from the toad, I suggest, is to lead us to expect functional assemblies rather

Implicit versus explicit computation

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Suppose you were asked to design a detector that is selective for moving elongated shapes traveling in the orientation in which they are elongated (W configuration). To make things challenging, could you construct such a detector using only radially symmetric operators, and could you devise a scheme that would not require the intermediate computation of either the orientation of elongation or the motion? Since the detection task for W configuration is formulated in terms of elongation and orientation, and yet the restrictions placed on the solution prohibit the use of oriented, elongated, motion-selective receptive fields, some "trick," or at least some elegant method seems necessary. Just such a method was adopted by the toad, it seems.

Here is approximately the scheme, as I infer it. The basic operator is a spatiotemporal differentiator, a receptive field that resembles a difference of Gaussians, which delivers a signal approximately proportional to the time rate of change of the spatial convolution, roughly comparable to a transient "Y-cell." There are three such operators of increasing size: R2, R3, and R4 (ERF diameters of 4°, 8°, and 12–15°). The optimal stimulus is a moving spot that just fills the ERF—referring to Figure 11 of the target article, note where the peak response occurs in *a-c*. The substantial independence of the response of these operators with respect to bar length when the bar is moving in W-configuration can be understood largely in terms of spatial integration of the balanced center-surround organization. One can construct a remarkably clever detector, or filter, specific to W configuration just by combining their relative responses.

than representational maps. That is, the cytoarchitecture will give evidence for the *functional* architecture of the processors, and only very indirect evidence for the internal representations operated upon by those processors. In that regard, the notion of a releasing mechanism (RM) might well carry over to higher organisms – but it will be hard to demonstrate. Rather than an RM leading to an external response, it would result in an assertion within an internal representation, which would then constitute a potential stimulus for a subsequent level of RMs. Studying such internal processes is of course much more difficult than studying those that give rise to external behavior.

Are the toad's basic strategies for representing and manipulating stimulus features extensible much beyond the task domain of the toad? In human vision there would seem to be a need for substantially different methods for describing visual events and for constructing higher-order descriptions of the visual world which might or might not yield overt behavior. The central difference, perhaps, concerns the richness of the intermediate representations, and the flexibility required of these representations to support the astronomically complex mapping between the set of stimulus features and potential behavioral responses one might make.

Let us consider, for the moment, the various patterns of tetrapod locomotion over land. The salamander is only capable of performing a single pattern: the diagonal coordination of the four limbs, in phase with the sinusoidal undulating movement of the whole body. (Concavity is associated with protraction, convexity with retraction, of the limb.) Several lines of evidence (Székely 1963; Székely & Czéh 1971; 1976; Brändle & Székely 1973) suggest that a predetermined structure in the medullospinal neuraxis controls this movement pattern. If the spinal cord is transected at the midthoracic level, the diagonal coordination of the four limbs is destroyed, while the alternating coordination of the forelimbs and hind limbs is maintained. If the transsection is made at the rostral border of the hind limb moving spinal cord segments, the alternating coordination is destroyed and the limbs paddle synchronously on the two sides. The same happens to the forelimb pair if the spinal cord is separated from the medulla. However, thoracic spinal cord segments and the medulla are interchangeable in this respect, since thoracic segments grafted in front of forelimb moving segments, and the medulla in front of the hind limb segments, are able to control the alternating coordination of limb pairs. The limbs receive their innervation from three spinal cord segments; if one of them is removed, the paddling coordination is destroyed while the limb-like coordination in the movement of the single limb is maintained.

As we have surveyed the different levels of coordination, it seems that they are associated with the different lengths of the neuraxis involved in the control rather than with the presence of hypothetical intelligent neurons that command the timing of different motor activities. In other words, the capacity to control the different levels of coordination is very probably distributed in the medullo-spinal neuraxis. We may also ask whether the capacity of the frog spinal cord to control walking or jumping is a distributed property, or else associated with the action of intelligent neurons that can gauge the situation and command the appropriate motor pattern. I do not think that anyone would vote for the second alternative.

What have all these to do with vision? We have learned that prey-catching is composed of a series of sequentially released acts: orienting, approaching, fixating, and snapping. Although it is emphasized in Ewert's article that these actions may occur in variable order, Ewert still suggests that prey-catching behavior is controlled by serial information processing. The toad is a very sluggish creature; this makes possible the clear distinction of these sequences. A salamander larva, which is a predator, snaps at the moment it sees a moving object in its visual field without any distinguishable sequences. The same applies to the tree frog, which may jump even if the prey is not in the frontal visual field. Sequences, therefore, appear at the output channel, like the regular sequence of muscle contractions in the act of walking; they do not necessarily refer to corresponding serial processing in the center. If the forebrain is removed, the animal loses its spontaneity in feeding, but I would question the notion that this inertia is the consequence of the removal of an inhibitory effect of the forebrain on the pretectum which inhibits catching, as suggested in the target article. The effect suggests that prey recognition, localization, and snapping may be controlled by wide areas of the brain in which parallel processing looks more plausible. At this point I would like to introduce into the picture some elements of the concepts of the Grüssers (1976) that the ever-moving, orienting, approaching animal receives important feedback signals whose contribution to the establishment of the visual universal cannot be overlooked.

Throughout Ewert's article a special emphasis is placed on the T5(2) neuron, which plays a key role in visual behavior. I cannot help noticing a similarity between this and the classical concept of somatosensation in which, after the discovery of modality-specific sensory spots in the skin by von Frey (1910), morphologically defined receptors are assigned to each modality

Intelligent neurons

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I do not think that anyone else would know better what the frog's brain understands of the story the eye tells than Jörg-Peter Ewert. His target article indeed provides enjoyable reading in which he explains to us the complex series of neural events that occur between prey recognition and snapping. The article and the large body of fascinating work by the author are all the more interesting because the problem of neural control mechanisms he so effectively tackles in connection with the visual system has a more general applicability to the behavior of a living creature. The basic idea is that there are a few types of key neurons which are selectively sensitive to certain sign stimuli and decide on the release of the appropriate motor behavior. This suggestion touches one of the fundamental questions about neural control mechanisms, namely, whether they process information serially or in parallel. This question has a strong bearing on the main topic of the target article and is also raised in the introduction. The serial processing mechanism requires as a prerequisite – I would say creates – intelligent neurons capable of making decisions somewhere along the line in a neural net of well-defined connectivity blueprints. Parallel processing is much more difficult to define; it involves networks of dynamic structural organization and the decision-making property is a distributed, I would say, an emergent, property of the network. The question is a great deal more difficult than it may seem at first sight, because the end result of processing, either serial or parallel, is almost always a regular sequence of events appearing serially at the output channel. The simplest way to circumvent this problem is to pose the question of whether the two processing mechanisms are mutually exclusive, or the brain can make use of both principles. Unfortunately, this cannot be demonstrated or disproved, in our present state of knowledge about central mechanisms. I will therefore make a brief conjecture about this problem and then propose that we investigate, by making comparisons with other neural mechanisms, the model featuring the T5(2) neuron as the neural mechanism underlying visually guided behavior.

despite almost a century of futile effort to correlate receptor types with specific sensory areas. Just as the free nerve endings in the epidermis complain of pain when irritated, the TH3 cells tell the T5(2) cells that they must not snap, whereas the T5(1) cells encourage them to do so. The complicated visual behavior is drastically reduced to a switchboard in which the decision is made by the intercommunication of three or four types of intelligent neurons in a process of unidirectional information flow.

The T5(2) master cell is supposedly an efferent neuron, but its identification is apparently not an easy task. In their recent intracellular recording experiments Ewert and his colleagues (see target article) injected cobalt into a physiologically identified T5(2) neuron and described it as a pyramidal cell. In Figure 18A this neuron resembles a partially labelled ganglion cell more than a pyramidal neuron and the presumed axon takes a rather unusual pathway for an efferent neuron. I can well imagine that difficulties in physiological and morphological identification are enormous with 10 classes of pretectal neurons and 9 classes of tectal ones. These large numbers (supplemented by subclasses) suggest that the cell-types may represent a continuum rather than discrete classes, and transition from one class into another may not always be obvious. I wonder whether it ever happens that a neuron in a certain class changes its physiological properties under changing experimental conditions (e.g., varying background illumination). Toward the end of the article Ewert makes a compromise and composes a "feature-analyzing network" of "feature-analyzing neurons." This does not alter the principle of information processing, since instead of just one or a few, a group of intelligent neurons play the leading role in the same cast.

It only remains to show how I envisage a "feature-analyzing network" with the eye of a neuroanatomist. As mentioned above, it is very difficult to define a structure without subtle knowledge about its component elements and its dynamic functional properties. One physiological parameter is known, namely, there are neurons which display distinct sensitivity to some well-defined stimuli. One histological parameter is also known: There are a variety of neurons arranged in a number of layers in the optic tectum. Looking at this structure one cannot fail to realize that single neurons cannot perform an operation independently of each other; but ought to form – as Ewert also proposes – some kind of functional unit. This may assume a columnar form or any other form. If the microelectrode picked out a neuron from one of these assemblies its response properties would depend on direct and indirect retinal input, non-visual input, and on intra- and interassembly interactions within the excited area. I would think it a plausible supposition that the response properties of a neuron are determined by the actual excitatory state of that assembly rather than by a series of predetermined interconnections among intelligent neurons within the structure. An apparent "commanding" neuron in one state of excitation may change to a "subordinate" neuron in another state. Prey perception, recognition, and all the other computation that occurs until the worm is caught require the operation of a number of interacting assemblies. There is therefore a large gap between the specific sensitivity of a neuron and prey recognition. The latter is a distributed property of the visual system, and the mesencephalic and diencephalic (probably also prosencephalic) centers may be equally involved in feature detection, analysis, recognition, and so forth – activities not of the single cell, but of the frog.

Author's Response

Toad's prey-catching: A complex system with heuristic value

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First I should like to thank all twenty-two commentators for preparing such an exciting array of commentaries which tackle the subject in depth from so many points of view (see Table 1). The following main topics turned out to be of particular interest.

Table 1. *Outline of author's response*

Topic	Commentators
1. The usefulness of ethological concepts in neuroethology	Baerends; DiDomenico & Eaton; Fentress
2. Problems with conceptual boxes	Broom; Fentress
3. The analysis of behaviorally relevant stimulus features	Fernald; Ingle; Kondrashev; Roth & Nishikawa
4. The principle of feature extraction	Arbib; Fernald; Stevens
5. The modes of neuronal coding	Gruberg
6. The question of serial and parallel processing	Fentress; Székely
7. The evaluation of behavior-specific efferents	Ingle
8. The concept of command releasing systems	Comer; DiDomenico & Eaton; Kondrashev
9. The idea of interacting neural assemblies	Arbib; Székely
10. The linkage between sensory- and motor-spaces	Comer; Goodale; Grobstein; Roucoux & Crommelinck
11. The modulation of neural function	Baerends; Doty; DiDomenico & Eaton; Ebbesson; Ehret; Fentress; Fernald; Ingle; Kondrashev
12. The onto- and phylogenetic aspects	Baerends; Camhi; Ebbesson; Ehret; Fernald; Fentress; Goodale; Roucoux & Crommelinck; Stevens
13. The question of a "self-module"	Dennett; Doty
14. The heuristic value of the analysis of toad's visual behavior	DiDomenico & Eaton; Doty; Ebbesson; Ehret; Fentress; Fernald; Goodale; Ingle; Stevens
15. The limitations of our view	Grobstein; Horridge

Concepts and terms. On the occasion of a neuroethology workshop at Airlie House (Maryland) in 1985 there was a discussion of why we lack concepts original to neuroethology, comparable to the ones that stimulated advances in ethology (e.g., sign stimulus, heterogeneous summation, innate releasing mechanisms (IRMs), fixed action patterns (FAP), command function). Do we really need new concepts in advancing neuroethology, which receives its impulses from ethology? According to Baerends, the IRM concept and its derivatives "were never meant to have an explanatory value in themselves and suggestions concerning the underlying physiological mechanisms were only intended to stimulate their investigation and, it was hoped, to guide it" (see also Tinbergen 1951). Through an interdisciplinary approach, neuroethology allows us to elucidate these historical concepts in terms of evolving concepts (e.g., see Eaton 1983). DiDomenico & Eaton point out that in many instances neurophysiology is guided by behavioral concepts rather than the reverse. Hoyle (1984) was one of the first to explicitly stress this aspect, although perhaps in too restrictive a manner.

As Fernald suggests, in certain cases neuroethology may call for a new collection of terms. I believe, however, that we can, proceed with the three classic terms *innate* (Baerends), *command release* (Comer, DiDomenico & Eaton), and *mechanism* (Doty), if these are appropriately redefined and if we are aware of the problems of conceptual boxes and their reciprocal actions, to which Fentress draws attention. For example, I see in the dynamic parallel-hierarchical processing of feature combination-related information expressed by an ensemble of specialized neurons, an "evolving detector concept of the sign stimulus" (see commentaries by Fentress, Fernald, and Stevens). The "evolving concept of command functions" allows us to envision a command releasing system (CRS) created from a critical decision that arises in an ensemble of several types of trigger cells, and that grows to include various neural circuits for its execution (see DiDomenico & Eaton). The concept of the releasing mechanism is not obsolete, since it offers neuroethology the advantage of studying softwired operations in connection with hardwired processes, so that an analysis of IRMs may actually guide the functional approach to learning (see Baerends and Fernald). As suggested by Fentress, an "evolving concept of IRM" refers to the predispositions operating in the context of developmental experience. In this approach, we take the advice of Fentress and Fernald as a challenge to test CRSs as the putative sites of the changing balances among interactive and self-organizing networks of ontogenetic processes (Fentress 1986).

I cannot share Broom's view that the notion of the interaction of genes with other factors (for the sake of perceptual sharpening) would devalue the term *innate*. Gene products depend upon developmental contexts (see Fentress) and are subject to modification which may have effects on sensorimotor codes of the respective CRSs (see Broom's question concerning learning). The problem of a fixed action pattern has been extensively debated ever since Lorenz and Tinbergen (see Fentress's commentary). Despite the redefinitions by Barlow (1977) and Schleidt (1974), the uncertainty of the adjective *fixed* is still manifest in vague descriptions; "indeed the word *fixed* seems quite redundant" (see Broom's commentary)

or "the term 'fixed action pattern' does not seem very relevant or useful" (see Broom 1981, p. 63). Hoyle (1984, p. 376) in his *BBS* article defines the primary target in neuroethology as "the study of the cellular events underlying fixed action patterns" and recommends against giving a different name to the numerous examples of behaviors that in part resemble FAP.

I agree with Broom and Fernald that motivation is not just a matter of homeostasis, although the latter as the dominant concept in regulatory biology has loomed large in theoretical concepts of animal motivation (e.g., see Stellar 1954; Zucker 1983). Following Fentress and Kondrashev in an operationally guided analysis of behavioral networks, motivation (1) allows animals to link physically different classes of actions into functionally coherent ensembles, (2) integrates the same class of actions into different functional contexts, and thus (3) frees animals from the enslavements of simple stimulus responses (Fentress 1983).

Control of the "Cartesian machine." It is argued by Doty that the toad's visuomotor system operates in the manner of a "Cartesian machine" if it is released from inhibitory control: The "greedy toad" has then "lost its soul." Here I am reminded of an analogy of Jung's (1953), who said that without inhibition, excitation in response to any external stimulus accumulates in the brain like an avalanche, thus, so to speak, driving the synaptic engine-powder magazine to explosion. Our intracellular recordings from 330 neurons of the grass frog's tectum have shown that 74% receive postsynaptic inhibitory inputs (Schwippert, Matsumoto & Ewert, unpublished). Hence Doty's question about the sources and time courses of inhibitory influences is particularly important. There are at least four main extratectal structures involved: (1) Certain pretectal neurons responsible for the visual RM's prey recognition exert their inhibitory influence on tectal neurons in response to visual stimulation. (2) The posterior ventral medial pallium (vMP) via an inhibitory preoptic-hypothalamic relay probably adapts the retino-pretectal/tectal circuit to past experience with a stimulus, for example, decisions about novelty (Finkenstädt & Ewert 1987). There is indirect evidence that inhibition of tectal output does not persist continuously upon habituation (Ewert 1984a; Finkenstädt 1987). (3) Preoptic-hypothalamic influences related to homeostasis and circadian rhythms may inhibit tectal neurons by long-term down-regulation of synaptic excitability. Additional targets of modulation are bulbar/spinal premotor and motor neurons (Parent 1973; Székely et al. 1983.). Prey-catching may also be influenced by modulatory inputs to pretectal neurons (see Kondrashev). (4) Reticular tegmental structures – probably modulated in an inhibitory manner by hypothalamic input – may be involved in short-term sensitization of tectal neurons depending on attentional state (Finkenstädt & Ewert 1985; 1987).

The question of whether toads have a "self-module," providing the animal with a conscious self, is discussed by Dennett. If we take consciousness as the "recognition of cognition," our experimental data yield no evidence for this property in toads. However, this is no reason to call toads "automata" (see Doty). Although their behaviors are partially mediated by a preprogrammed repertoire of sensorimotor codes designed for predictable stimulus

situations, these are also to some extent adaptable to unpredictable situations (see also Ewert's commentary on Anderson's target article, this issue). I see a general difficulty in treating the question of "conscious self" in different domains of inquiry – philosophy and physiology – with a concept from the former domain being investigated in the latter. This produces problems because the algorithms underlying logical thinking are probably different from the algorithms applied by neuronal networks for information processing (for a discussion see Creutzfeldt 1983, pp. 422–26).

Stimulus features and tectal efferents. As indicated by Tinbergen (1951), the dynamic configural properties of a moving visual object are determined by the spatiotemporal relationships between certain features. In the present analysis of prey features (Ewert 1968; 1969a) these are the areas of extension in $(xl(1))$ and perpendicular to $(xl(2))$ the direction of an object's movement – within certain behaviorally relevant limits of the total area – which explains Ingle's question about why elongating of $xl(1)$ for $xl(2) = 16\text{mm}$ ($\Delta 8^\circ$) leads to no further increase of its efficacy as prey (see Figure 4). Ingle obviously uses different definitions for "configuration" (vs. "shape") and does not seem to distinguish between static and dynamic configuration (see Appendix to target article). I disagree with Ingle's general statement that stimulus motion is irrelevant to object recognition. (For example, see the relevance of the direction of movement in the goose/hawk phenomenon in domestic fowls, Figure 26B, or the relevance of motion in the recognition of a configural stimulus if this is masked by noise, e.g., Figure 3B.)

There is a point in Ingle's as well as in Roth & Nishikawa's comments which needs clarification. It is not sufficient to investigate some releasing features of a stimulus; rather, it is also important to consider parameters that extinguish releasing values. We can correctly evaluate configural features by their variation along a stimulus continuum (Figure 4, bottom). Studying the effects of their changes on prey-catching allows us to describe the boundary of the prey category within this stimulus continuum (cf. Figure 4 and Figure 27A) and to understand the algorithm of configural pattern discrimination. In this context, as emphasized in the target article, the universal is not represented by a specific feature but by an invariant structure of feature relationships. The configural contrast is greatest between W- and A-stimuli at the opposite ends of this continuum. Ingle is wrong in concluding that "this discrimination simply reflects the well-known function of IRFs" if he compares $D(W,A)$ in the range of $2 \leq x \leq 10$ for retinal ERF/IRF-neurons (Figure 12, R2 and R3) and for tectal prey-selective neurons (Figure 12, T5(2)) (cf. Fernald and Stevens).

Velocity invariance in dynamic configural discrimination refers to the fact that $D(W,A)$ values never become negative for changes of the direction or the speed of stimulus movement and that these values remain constant if the configuration-defining features are sufficient, which – contrary to Ingle's assumption – is not a trivial result (see Ewert's commentary on Arbib's target article, this issue). In response to Fernald, we have found that with very small, black worm- and antiwormlike $2.5\text{ mm} \times 5.0\text{ mm}$ stripes of a weak configural contrast the acuity of discrimination in prey-catching is best ($D(W,A) = 0.7$

around an optimal speed, whereas for $2.5\text{ mm} \times 10.0\text{ mm}$ stripes constant values of $D(W,A) = 0.9$ were obtained with variable speed (Ewert et al. 1983).

The above data call Roth & Nishikawa's arguments about supernormal releasers into question (see also Figure 5Aa for $xl = 5$ or 10 mm). Many small invertebrates – such as ants or wood lice – have elongated shapes in the aforementioned size range moving wormlike in the direction of their longer axes. I am also puzzled by Roth's new observations suggesting that fire salamanders presented with square dummy objects prefer those that are far too large to be eaten. If we take this mismatch as a general rule, it would be in contradiction to Roth's findings with square prey dummies in cave-dwelling salamanders, emphasizing that "the size interval from 1 to 5 mm^2 , which is the optimum, corresponds fairly well to the sizes of *Drosophila* and *Musca domestica* which in captivity are the preferred prey animals" (Roth 1976, p. 52). Burghagen (1979) has measured in seven investigated anuran species (*Bufo bufo*, *Rana temporaria*, *R. esculenta*, *Hyla arborea*, *H. cinerea*, *Alytes obstetricans*, *Bombina variegata*) a positive correlation between the width (j) of an animal's jaw and the edge length (xl) of the preferred square prey dummy, yielding $xl = 0.43j$.

For the evaluation of species differences, it is again necessary to compare discriminative features between objects across the stimulus continuum (Figure 4, bottom). Our comparative results in T5(2) neurons of common toads (Ewert & von Wietersheim 1974a) and grass frogs (Schürg-Pfeiffer & Ewert 1981) have shown that (1) a fundamental algorithm for configural discrimination is implemented by both species; (2) species differences in configural selection refer to different ranges of the stimulus continuum. These results (Figure 28A and B) suggest that Ingle's general statement that "frogs (unlike toads) fail to show preference for worms over squares" is not correct.

Ingle reviews our data on the toad's preference toward the leading (head) or trailing (tail) edge of a wormlike moving stripe (of $2.5 \times 40\text{ mm}^2$ or $2.5 \times 80\text{ mm}^2$ size), depending on the contrast direction between stripe and background, that is, black versus white or vice versa (Burghagen & Ewert 1982). These results are not in conflict with the concept of configuration (Gestalt) that refers to the visual analysis of the figure in relation to its background (see also Figure 3B). Our comparative neurophysiological recording studies (Tsai & Ewert, 1987) have shown that the behavioral head/tail phenomenon is resembled by retinal off-dominated R3 neurons (but not by R2) and by tectal T7 and T5(2) neurons in response to a stripe's off-producing moving edge. What can we learn from these data? First, the toad's prey-catching system is most sensitive to off-effects, hence allowing sharp configural discrimination for dark objects against a bright background; for objects with reversed contrast, however, this leads to some confusion between figure and ground resulting in a less sharp discrimination (e.g., expressed by smaller $D(W,A)$ values; see also Burghagen & Ewert 1983). Second, since the contrast-direction-dependent head or tail preference is implemented in both orienting and snapping, it can be concluded that the respective tectal efferents involved in triggering these action patterns take advantage of tectal information processing which receives substantial inputs from retinal R3 (class-3)

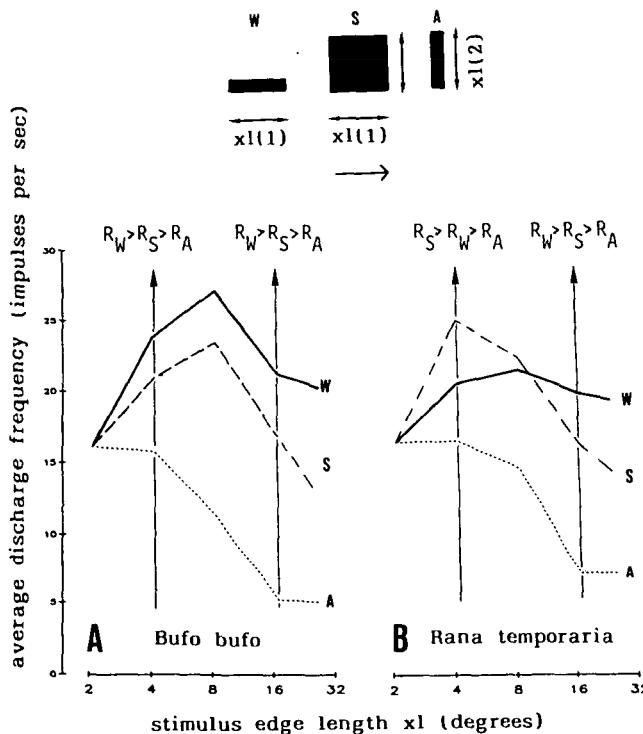


Figure 28. Species differences in prey-selective T5(2) neurons. Comparisons between toad (A) and frog (B) class T5(2) neuron responses across three segments of a stimulus continuum: Extracellularly recorded spike activity (R) in response to W-, S-, and A-stimuli of varying edge length (xl) moving at 7.6°/sec. Note that in toad T5(2) neurons the relation $R_W > R_S > R_A$ is valid for $2^\circ < xl \leq 32^\circ$; in frog T5(2) neurons the relation $R_S > R_W > R_A$ is valid for $2^\circ < xl \leq 8^\circ$ and $R_W > R_S > R_A$ for $8^\circ < xl \leq 32^\circ$. (From Ewert & von Wietersheim 1974a (A); Schürg-Pfeiffer & Ewert 1981 (B).)

neurons, besides inputs from R2 (class-2) (see also Matsumoto et al. 1986).

The above result does not support **Ingle's** hypothesis that tectal efferent neurons responsible for prey-orienting, and descending in the tractus tectospinalis cruciatus (tr.ts.c.), should be driven almost exclusively by retinal R2 ganglion cells whose weights Ingle determines from the extent of dendritic arborizations labeled after backfilling with HRP (horseradish peroxidase) implants to the tr.ts.c.: "most (if not all) of the retinal input to cells projecting into the tectospinal tract receive input from class-2 fiber terminals" (Ingle 1983a, p.207); "efferent cells which participate in orienting to prey have heavy (if not exclusive) inputs from the class-2 ('bug detecting') retinal fibers" (Ingle & Quinn 1982, p. 406). There are various other problems with Ingle's hypothesis: (1) We have found that of a total of 103 intracellularly recorded neurons in the grass frog's tectum 94% showed off- and on-responses to changes of diffuse light, indicating a strong contribution of R3 input (Matsumoto et al. 1986). (2) If the tectal efferents projecting in the tr.ts.c. were responsible for prey-catching orientation and were activated (almost) only by retinal R2 (so-called bug-detecting) input, it is difficult to explain that, disconnected from pretectal influences, these efferents mediate prey-catching orientation toward very large objects. (3) If the tectospinal efferents projecting in the tr.ts.c. were monopolized for prey-orienting, then we must ask for the tectal

efferents that activate orienting movements toward other goals, such as a sexual partner, hardly attractive to "bug detectors." (For a comprehensive treatment of tectofugal pathways involved in frog's prey-orienting, see Kostyk & Grobstein, in press a,b,c).

Feature extraction. A specification of the terms *category* (class) and *comparison* (classification) is called for by **Arbib**. According to von Seelen (1970; 1973), pattern recognition is defined as the assignment of two-dimensional, space-time dependent contrast distributions from the environment to classes with functional significance. This operation proceeds in two steps: First, the extraction of significant features v_x from the patterns to be perceived; second, the separation of the feature vectors x by means of a discriminating function U_D in such a way that upon presentation of a pattern of the v th class of significance: $U_D(v_x) > U_D(\mu_x)$ for $v, \mu = 1, 2, \dots, M$ and $v \neq \mu$, where M is the number of possible classes to be discriminated (in the present study $M = 2$, referring to prey or nonprey). This separation procedure involving weighted neuronal threshold-value operations is called *classification*. The strength of the output depends on the number of times the threshold is crossed with a latency depending on the neuronal impulse frequency. If $y(r,s,t)$ is the space(r,s)- and time(t)-dependent input signal, $H(r,s,t)$ the coupling function of neurons involving lateral inhibition and lateral excitation, and $z(r,s,t)$ the system's output, then

$$z(r,s,t) = \int_0^t \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} H(r - r', s - s', t - \tau) y(r', s', \tau) dr' ds' d\tau$$

With the aid of Fourier-transformations the convolution integral according to the above equation becomes

$$F[z(r,s,t)] = F[H(r,s,t)] \{F[y(r,s,t)]\}, F = F_{r,s,t}$$

Given that the operations of feature extraction are implemented by a retinotectal filter described by H_1 and a retinopretectal filter described by H_2 , the space-dependent course of their subtractive interaction, $\{H_1^*; H_2^*\}$, reproduces the function of U_D (Ewert & von Seelen 1974) and

$$F[z(r,s,t)] = F[y(r,s,t)] \{F[H_1(r,s,t)] F[H_1^*(r,s,t)] \\ - F[H_2(r,s,t)] F[H_2^*(r,s,t)]\}$$

According to this model, the configural prey schema refers to stored information provided by neuronal circuitry (interacting functional units) whose output is mediated by prey-selective neurons acting as filters. Prey recognition is implemented in such a way that these filters *compare* – cross-correlate – the incoming visual information with their filter property (for details see Ewert & von Seelen 1974; for a different model see Arbib's target article, this issue). I certainly agree with **Arbib** and with **Ebbesson** that Figures 18 and 19 challenge the experimenter to verify the postulated neuronal connections and synaptic weights for which we have as yet mainly indirect evidence (e.g., from intracellular recordings and extracellular tectal recording before and after pretectal lesion).

Fentress and **Stevens** stress the proposed parallel-hierarchical organization in the feature-analyzing circuit. Furthermore, Stevens draws our attention to the principle of implicit processing that (unlike the principle ap-

plied by so-called simple cells of mammalian visual cortex) allows radially symmetrical processors to discriminate moving configurational stimuli, a method which an engineer might not have thought of by intuition; that is, according to Fernald, the axes along which toads sort information are different from those one might first imagine (see also Ewert's commentary on Arbib's target article, this issue). An engineer's solution of the problem would have taken considerable redundancy to achieve this behavior. As indicated by Stevens, the toad's visual system carries out this analysis by means of economically working functional assemblies (in contrast to feature representational maps) which are integrated in a macronetwork with dynamic properties (see also commentaries by DiDomenico & Eaton, Ehret, Fentress, Fernald and Kondrashev).

Roth & Nishikawa confirm our model, suggesting that species-specific differences in configurational prey selection (Figure 28A, B) can be explained by variations in coupling functions H_1 and H_2 of retinotectal and retinopretectal circuits, respectively, and by the weights of their interaction $\{H_1^*; H_2^*\}$ as mentioned in Section 5.3.4. In this context, however, I cannot follow Roth & Nishikawa's arguments that the role of T5(2) neurons is "exaggerated." The size-constancy effect may be achieved by appropriate tuning of $\{H_1^*; H_2^*\}$ according to depth information (Collett 1977) provided by the lens accommodation mechanism (see also Ingle). The presence of different classes of tectobulbar/spinal projective neurons (Figure 22) can be explained with their participation in different goal-related sensorimotor codes involving feature- and space-related messages.

The important data reported by Kondrashev on different color sensitivities of mating male frogs and toads raise the question of where this information is encoded and whether sex and species differences exist. I learn from his commentary that color cues may provide us with new landmarks in the investigation of feature-coding neurons, which also should not be overlooked in the context of a central fovea (see also Fernald).

Referring to the Sprague effect, Gruberg correctly criticizes the notion of "essential" and "decisive" neurons. However, I am using these adjectives with respect to a given functional structure F . If an integral component f_j of this structure were eliminated, we would not necessarily be dealing with $(F - f_j)$, but rather with some different self-organizing structure. Given the multiconnectivity in the pretectal/tectal network – of which in Figure 19A, B only the putative main connections are emphasized in connection with the function under investigation – I would not be surprised if the role of T5(2) neurons (after their selective elimination) were executed by other cells, for example, modified T5(1) projective neurons. Long-term "functional recovery" of prey selection after pretectal lesions is an example of compensation in the inhibitory framework (Figure 10C; see also Ewert et al. 1983).

In response to Gruberg's question about sampling, there is a correlation between state-dependent behavioral visual responsiveness and electrical activity of tectal neurons. The fickle frogs were therefore particularly problematical under laboratory conditions. In non-responsive toads or frogs, spikes were extracellularly recorded frequently in the optic tectum only from retinal

fiber terminals and from somatosensory afferents in sub-tectal structures; however, we found almost no visual activity in tectal neurons. Intracellular recordings showed inhibitory and/or excitatory slow postsynaptic potentials also from pear-shaped cells in deep tectal layers, probably electrically coupled with more superficial neurons, as suggested from multiple labeling (Matsumoto et al. 1986). Taking all our information together, I doubt that recordings with one method, in one species, at a given period of time will allow us to obtain a representative spectrum of neuronal classes (see also Ewert 1980).

Gruberg's discussion of coding by spike patterns is welcome, since I see here important evaluational criteria for future investigations. We have compared neuronal output determined by the average spike frequency i/t and by i^2/t (taking into account the total numbers of spikes i) and have found that neuronal selective properties emerge sharper by the latter method (Schürg-Pfeiffer & Ewert 1981; von Wietersheim & Ewert 1978). I was confronted with the question of temporal discharge patterns while recording from thalamic TH9 memory neurons (Ewert 1971, unpublished) whose bursting afterdischarges were correlated with the configuration of a moving object. Here I was reminded of Chung et al.'s (1970) demonstration that the frog's retinal R4 dimming fibers transmit messages about various stimulus characteristics through their spike temporal patterns, which can be resolved by the axonal trees into a spatial pattern arising from different probabilities of invasion for spikes into the various axonal arborizations. Transferred to our problem, the physicogeometry of a neuron might be used to select, store, and compare finer-tuned differences of features within the broad prey schema in the context of previous experience. Although I doubt that tectobulbar/spinal projective neurons use temporal discharge patterns for stimulus-specific codes, the involvement of short bursts may be interpreted in terms of their trigger properties. In a recent computer analysis of tectal visual neurons recorded from the freely moving toad, my coworker Dr. Schürg-Pfeiffer has discovered in spike interval histograms consistently intermingled double-spikes whose occurrence was correlated with the stimulus efficacy, the toad's motivation, the neuron's average discharge frequency, and the probability of prey-catching (Schürg-Pfeiffer & Ewert, submitted). Schürg-Pfeiffer could show that electrical stimulation of the optic tectum with pulse patterns derived from T5(2) spike patterns (in contrast to regular pulse trains) were more effective triggers of prey-catching in that they released finer-tuned action patterns.

"Parallel" and "hierarchical" processing. Székely seems to be gently pushing our concepts of configurational discrimination and sensorimotor function toward an extreme position through qualifying notions such as "the intelligent neuron," "a switchboard," and "the commanding neuron," in order to invalidate such a version and to replace it by a concept basically not much different from our original one. By using the term "intelligent neuron," Székely shifts the weight toward serial processing as the underlying mechanism of prey-catching behavior and entirely away from parallel processing, which is not justified by the model presented in the target article (see Dennett, DiDomenico & Eaton, Fentress, and Fernald). The network piece shown in Figure 19A, with its

prosencephalic modulatory inputs (Figures 23,24), does not apply to a simple "switchboard" (see also Doty, Ehret, and Fernald). In our concept of CRS there is no room for a single "command neuron" (see Comer and DiDomenico & Eaton). Nevertheless, I acknowledge the strategy of the criticism since this allows us to make our position more clear.

First of all, we must accept the guidance from quantitative behavioral data showing that configural stimulus selection precedes the toad's ballistic orientational turning movement toward the prey (see Figures 4A,5A). There is no experimental evidence that the common toad receives from subsequent action patterns (orienting, approaching, snapping) "important feedback signals whose contribution to the establishment of the visual universal cannot be overlooked" as claimed by Székely. For example, in a special double-choice procedure (Ewert & Institut für den Wissenschaftlichen Film 1982) toads always orient toward the stripe presented in W-configuration rather than the one in A-configuration (see also Goodale's commentary, which mentions that visual information processing in mammals influences cognitive functions in terms of recognition independent of motor output). Since Székely's assumption is not valid, the attractive example introducing his commentary is not adequate in our context. The study of the neuronal basis of the toad's prey recognition can be focused on the analysis of processes that translate visual input into target-oriented motor output, the orienting response toward prey. Keeping this in mind, I should like to reply to Székely with some indirect questions and some comments:

1. Given the presence of T5(2) tectobulbar/spinal projective neurons, whose responses are correlated with the probability that the dynamic configuration of a stimulus resembles prey, how can their property be explained by strict parallel processing? The fact that T5(2) neurons are activated antidromically (criterion: the collision test; see Figure 21A; c₁, c₂) is evidence of their tectobulbar/spinal projective character. The T5(2) neuron of Figure 18Ac is indeed a pyramidal neuron of the morphological type shown in Figure 21Bc, identified according to the morphological criteria by Székely and Lázár (1976, p. 411): "The axon arises from the shaft dendrite, ascends to layer 7 where it turns laterally . . . and leaves the tectum." The axon – whose pathway is distorted in the pictorial representation of Figure 18Ac – could be followed in sequential brain sections down to the rostral medulla oblongata. We do not generally claim that prey-selective neurons are pyramidal cells (Matsumoto et al. 1986).

2. Is the network of interacting assemblies for the release of orienting toward prey that Székely would envisage essentially different from the one we are suggesting? Even if the monocular T2(1), T2(2), T3, T4, T5(1), T5(2), T5(3), T5(4) neurons (and others) might – according to Székely – represent a continuum (whatever this means with regard to distribution over tectal layers) we cannot deny that neurons with distinctive response characteristics exist, that these mediate the outputs of interacting assemblies (functional units), that they project to bulbar/spinal motor systems, and that the message they convey (probably as assembly codes, Bullock & Perkel 1968) must be read by respective premotor networks (see Comer). For example, if the motor pattern generating circuit (MPG) for snapping would also receive

input from T5(4) neurons, we must then explain why strong activity of T5(4) in response to a predator does not activate this MPG; for example, because adequate releasing conditions (size, configuration, localization, state, etc.) to which the snapping-MPG is adapted are not fulfilled (see the concept of sensorimotor codes), and because the escape-MPG tuned to T5(4) input inhibits snapping-MPG (see the concept of interacting MPGs).

3. Is Székely's view of "distributed property" different from our concept of parallel/hierarchical processing in a macronetwork emphasized in various places in the target article? Parallel, distributed processing allows a different evaluation of visual information in terms of (1) configural features (involving optic tectum and pretectum, respectively; Ewert 1974), (2) novelty (e.g., involving the medial pallium; Ewert & Finkenstädt 1987), (3) past experience (e.g., involving lateral amygdala and medial pallium; Finkenstädt & Ewert 1987), (4) attention (e.g., involving tegmental reticular structures; Finkenstädt & Ewert 1985), and (5) motivation (e.g., involving preoptic-hypothalamic structures; Dierickx 1969); the results of this information processing partly converge in the optic tectum and in the bulbar/spinal premotor and motor structures, respectively. (See also the commentaries of DiDomenico & Eaton, Doty, Ehret, Fentress, Fernald, and Kondrashev.)

Coded commands. Our concept of coded commands is stressed by Comer: Firing of various classes of efferent neurons (command elements) in certain combination characterizes objects in space and selects the appropriate goal-directed motor pattern. Comer focuses on the advantage of the combinatorial nature of codes, which provides a relatively high potential of information content with "neural parsimony." I agree with Kondrashev that the proper description of sensorimotor codes will become an important issue for future neuroethological research. His experimental data call for color-coding command elements in CRSs of clasping-oriented behaviors in frogs and toads. Following Comer and Grobstein, we suggest that in the performance of goal-oriented action patterns further structures are undoubtedly involved (e.g., see Grobstein & Masino 1986; Masino & Grobstein 1985).

Arbib's concept of schemas extends the usage from classic ethology (Lorenz 1943; von Uexküll 1909) in that it allows us to study the interpretation of the environment in terms of the interaction of perceptual schemas (interacting functional units) yielding appropriate coordinated control programs (sensorimotor codes) for motor and compound motor schemas (see Ewert's commentary on Arbib's target article, this issue). Regarding "multiple instantiations" of perceptual schemas, "interacting motor schemas," and "target orientation," Arbib addresses a variety of significant questions which require further experiments and can ultimately only be answered in a dialogue between experimentation and modeling.

Roucoux & Crommelinck draw our attention to the problem that the retinotectal map alone does not explain the programming of the various body segments involved in orienting. Here we may also have to distinguish between *Bufo bufo* and *Rana esculenta*, the latter having a stiff neck so that head and trunk are always aligned on target before and after the ballistic orientational turn of the body. Electric microstimulation of the frog's and

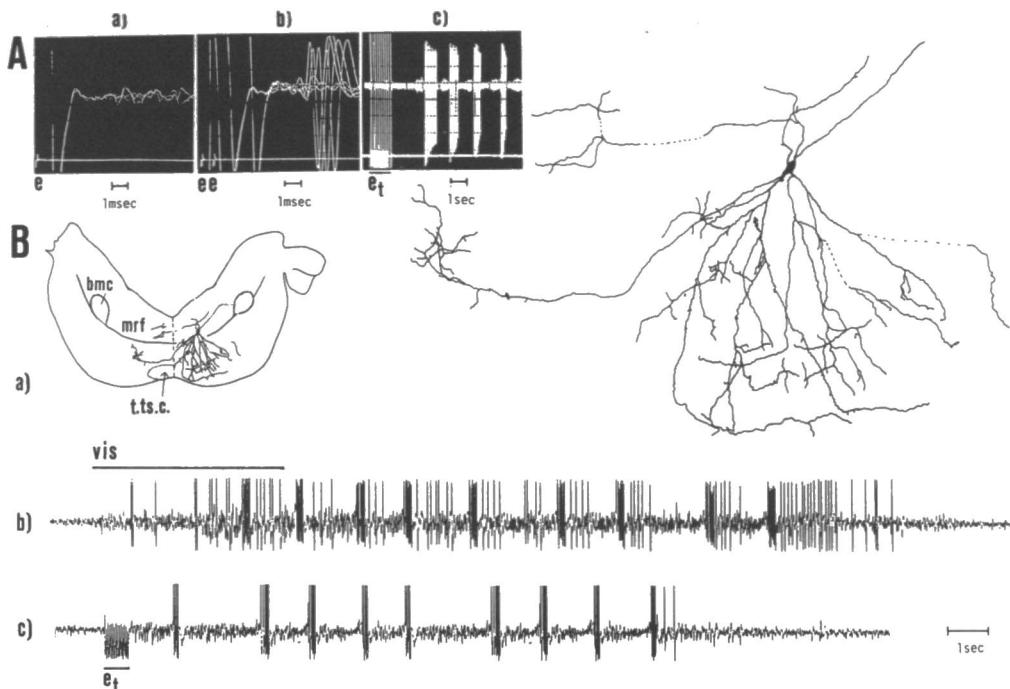


Figure 29. Putative premotor neurons of the common toad's rostral medulla oblongata. (A) Extracellular records from a bursting neuron of the brachiomotor column *bmc*. The neuron was silent in response to electric stimulation with a negative square wave pulse *e* of 0.1 msec duration and 50 μ A applied to the medial reticular formation *mrf* (a); the neuron discharged one spike of varying latency in response to an electric double stimulus *ee* (b), and upon electric stimulation *e*, with a short train of double pulses responded with a sequence of cyclic spike bursts as a poststimulus event. (From Ewert et al., submitted.) (B) Identification of a neuron in the *mrf* after intracellular labeling with Co^{3+} -lysine (a); note that most dendrites extend ventrally to the tractus tectospinalis cruciatus *t.ts.c.*, some reach *bmc* and *mrf*, and some cross the midline. Intracellular records from this neuron show poststimulus burst activity in response to a large looming visual stimulus *vis* (b), or to electric stimulation *e_t* of the optic tectum with a short train of spikes (c). (From Schwippert & Ewert, submitted.)

toad's optic tectum may allow us to study the integration of head position signals.

Comer is right when he admits that "commanding according to a code" must also be a property of the decoding premotor circuitry. Grobstein and Comer were among the first to show that the one-to-one correspondence between eye and optic tectum is not precisely correlated with the required target-oriented movement, suggesting that the retinal local sign is combined with the additional information necessary to specify the appropriate motor output according to a population code (Grobstein et al. 1983; Grobstein, in press b). Since small partial lesions to the respective tectal output pathways in frogs caused inaccuracy in orienting rather than in producing a scotoma, Grobstein and coworkers concluded that these lesions had not disturbed motor commands but had modified their interpretation in terms of spatial localization. These results suggest distributed population-coded motor command signals that are read by a decoding premotor network. Our recent intracellular recording and labeling studies from bulbar putative premotor neurons (Schwippert & Ewert submitted) show bewildering dendritic trees (Figure 29B), suggesting a highly integrative capability for various inputs (e.g., from tectal, pretectal, solitary, raphe, reticular, and contralateral bulbar structures). All this accords with DiDomenico & Eaton's view of a command system as a "multibody system" with dynamic properties.

DiDomenico & Eaton emphasize that describing releasing mechanisms as CRSs operating in terms of sen-

sorimotor codes acknowledges "the very real complexity of neural networks." We thus realize important common features in our thinking about the release of behavior (cf. Eaton & DiDomenico 1985; Ewert et al. 1983). DiDomenico & Eaton (in press) define "command function" as the process by which the operation of the nervous system is channeled to select and direct specific patterns of behavioral action, and they discuss various principles for its approach. Their command concept is formulated in functional rather than structural terms, which implies that a command is not necessarily signified by particular cell types or structures. This is in agreement with our CRS concept according to which the release of action patterns can result from the activity of cells located in various structures (see also Kondrashev). Here the same class of command elements in different combinations with other command elements may take part in CRSs for different action patterns; the same action pattern can be triggered by CRSs distinguished by the combination of their command elements (see also Arbib's commentary referring to "multiple instantiations of perceptual schemas"). Associative, compensatory, alternative, and other dynamic properties in command functions may involve recombinations of sensorimotor codes (see also response to Gruberg's commentary on this subject). DiDomenico & Eaton emphasize that their concept

does not eliminate the search for specific functional roles, but realizes that the command neurons, or other cell types, may interact in different manners: some will be highly coupled and act as a group, others are capable

of acting individually, and some will form aggregations. . . . Arrays of different neurons are activated by different combinations of inputs and consequently turn on appropriate portions of related motor response. Some command neurons might be responsible for only a single part of a complex sequence that defines a behavioral act. A constellation of command neurons would be required for some if not most complex acts. (DiDomenico & Eaton, in press)

Evolutionary perspectives. A fundamental question is introduced by Camhi: Why do toads "need" a relatively complex brain involving so many neurons for relatively easy sensorimotor tasks? This touches on differences in the organization of vertebrate and invertebrate nervous systems (Bullock 1977, p. 435). Although, for example, the visual system of a fly cannot be called simple (e.g., Kirschfeld 1973; Wehner 1973), we must consider that articulata and vertebrata have a *Bauplan* (archetype), that has evolved differently.

When comparing insects with vertebrates the most dramatic difference seems to be the shift from a rather invariant to a highly flexible behavior including an apparently much more complex 'drive or motivational background.' . . . Insects exhibit barely features comparable to the organization of cortical columns; there is no clear evidence of overrepresentation of neurons and fields solving specific behavioral tasks, nor do we find comparable geometrical arrangements and topological features, which evolved to handle specific analytical tasks on the sensory and motor side. . . . This enhanced capacity of the vertebrate nervous system undoubtedly depends on the increased number of neurons and connections. (Huber 1983, p. 127)

Ebbesson's parcellation theory of vertebrate brain evolution shows a possibility of differentiation of neural circuits involving an inherent capacity for overproduction of neurons out of which specialized subcircuits with finer tuning properties (selectivity filters) are formed through an increase of connections and selective loss (Ebbesson 1984, p.321). The prediction is that a larger number of higher-quality filters would result in a better adaptation of behavior. It is unknown how selective pressures ultimately affect the changes that result in a genetically programmed parcellation, so that, in a species, primordial structures may also be installed whose potential is not entirely used. As indicated by Camhi, this means that slightly increased complexity in behavior might be concerned with the development of a higher order of neuronal complexity, including the possibility of newly evolved vertebrate ways of organizing circuits. Hence, although the toad's brain is designed to control and regulate behavioral functions in an environment that challenges the animal to survive as a toad, its brain is interesting over and above what it can tell us about the brain of higher vertebrates (see also Ewert's commentary on Anderson's target article, this issue).

Ebbesson brings into focus the fact that an annuran's visual discrimination based on pretectal/tectal interaction can be improved through pretectal parcellation in the course of ontogeny and phylogeny, yielding "better quality filters." He accordingly recommends ontogenetic studies related to (1) pretectal/tectal synaptic organization, (2) the identification of pretectal/tectal connecting

neurons, and (3) the identification of neurotransmitters – investigations which are now in progress. From a phylogenetic point of view the comparative immunocytochemical studies of pretectal nuclei by Reiner (personal communication, 1984; see also Reiner et al. 1980; 1982; Karten et al. 1982) are also promising since they show that the bird's lateral spiriform nucleus SpL and the reptile's dorsal nucleus of the posterior commissure nDCP (equivalent to the anuran's pretectal P nucleus, also called PC) harbor enkephalin (ENK)-containing neurons terminating in deep tectal layers close to the tectobulbar/spinal projective neurons. The bird's nucleus pretectalis PT and the reptile's dorsal pretectal nucleus NPd (equivalent to the anuran's pretectal Lpd nucleus, also called PL), on the other hand, harbor neurons that produce an avian pancreatic polypeptide (AAP)-like substance giving rise to scattered APPergic terminals in more superficial retinorecipient tectal layers. Presumably the frog's pretectal Lpd is the source of APPergic terminals which have been identified by Kuljis and Karten (1982) in the frog's superficial tectal layers, whereas pretectal P is the source of the ENKergic terminals found in the frog's deep tectal layers.

Ingle correctly mentions that pretectal nuclei and their tectal projections are also present in mammals, so that a comparative approach to pretectal functions is challenging. Reiner et al. (1984), however, hypothesize that the pretectal SpL/nDCP system was greatly de-emphasized in the line of evolution leading to modern mammals. As pointed out in the target article, mammals – in contrast to anurans and sauropsids – seem to lack basal ganglionic input to pretectal nuclei: "Reptiles and birds possess two disynaptic pathways from the basal ganglia to the tectum [a striato-pretecto-tectal and a striato-nigro-tectal circuit]. . . . The pretectal leg of this system may have been lost in mammals or may not yet have been found" (Wilczynski & Northcutt 1983b, p. 342).

Ehret adds depth to the discussion of the evolutionary potential of the anuran's macronetwork in terms of a sensory/motivational/associative interface mediated by tecto-prosencephalo-tectal circuits (Ewert 1987; Finkenstädt & Ewert, submitted), one that is to some extent comparable to mammal's cortico-limbo-cortical circuits (Perrett & Rolls 1983; see also Rolls in Changeux & Konishi 1986; Feigenbaum et al. 1986; Rolls 1987). From this point of view Ehret's question regarding a telencephalic origin of the toad's T5(2) properties is reasonable. It must be answered negatively, however: (1) Lesions to the posterior medial pallium ("primordium hippocampi" of Herrick 1933) impair stimulus-specific habituation and associative conditioning but leave configural prey selection unchanged (Finkenstädt & Ewert, submitted); (2) no prey-selective properties have been obtained in neurons of the striatum that project via pretectal Lpd/P nuclei to the optic tectum, suggesting that tectal T5(2) prey-selectivity does not arise from but is determined by strial/pretectal inputs. Ehret's notion that cerebral structures do "not contribute" to prey-catching obviously refers to the observation that the action patterns can be released in telencephalon-ablated, pretectally-lesioned toads (Ewert 1984a; for modulatory telencephalic influences see Ewert 1967a; 1987; Patton & Grobstein 1986; Finkenstädt 1987). Wilczynski and Northcutt (1983b) speculate that a portion of the striatum may also be involved in the organization of multimodal

sensory information into meaningful attentional behavior, in which tectal/subtectal structures play a prominent role through all vertebrate species.

Ehret recognizes another important similarity between anurans and mammals in circuits mediating messages related to arousal. We have found that arousing electrical stimulation of the tegmental reticular formation in toads leads to enhanced metabolic activity (measured by 2DG uptake) in structures of the visual pathway, especially the optic tectum and the anterior thalamic nucleus (Finkenstädt & Ewert 1985; Finkenstädt 1987), comparable to what has been reported by Gonzalez-Lima and Scheich (1984) for the acoustic pathway. Based on studies using 2DG, electrostimulation, extracellular recording, and lesion techniques in toads, Finkenstädt (1987) proposes a circuit involving the medial pallium, the preoptic-hypothalamic area, and the tegmental reticular formation that affects the retino-pretectal/tectal stimulus-response pathway due to attentional states and past experience.

Recent lesion studies reported by **Gruberg** indicate that the mesencephalic nucleus isthmi, as part of a system of centrally projecting cholinergic neurons (Caine & Gruberg 1985; Desan et al. 1986), provides internal sensory feedback in tectal processes (see also Grobstein & Comer 1983). This has not yet been sufficiently considered in the discussion of visual behavioral (e.g., attentional) functions. The corresponding parabigeminal nucleus of mammals is regarded as a "satellite system" of the superior colliculus (e.g., see Graybiel 1978; Mufson et al. 1985).

The results reported by **Roucoux & Crommelinck** suggest that a conservative phylogenetic structure for the mediation of target-oriented responses such as the optic tectum "progressively includes" functions that fulfill the appropriate species-specific requirements. Some of these can be studied in the cat's superior colliculus where a "zone 1" displays properties of foveate animals with movable heads and eyes (particularly well developed in primates), whereas "zones 2 and 3" correspond to afoveate animals (such as amphibians) in which "zone 2" might exhibit the features of toads with movable heads and "zone 3" those of frogs with stiff necks.

Goodale stresses the value of the present approach "from input - to output" for students of the mammalian visual system, in which the concept of CRSs provides a useful tool for grappling with the problem of integrating various inputs for the activation of behavior patterns. Although in the analysis of mammalian vision the emphasis was always on "psychological abstractions" (recognition, localization), Goodale (1983a) himself has shown in his work that functional categories of the "monolithic visual system" of mammals can be separately investigated through the requisite observable behaviors.

Fernald summarizes the heuristic value of the analysis of the toad's visual RMs as follows: (1) A new principle of feature extraction can be studied (see also **Stevens**), (2) a circuitry underlying sensory decision making can be investigated under the influence of motivational inputs (see also **Doty** and **Kondrashev**), (3) a circuitry underlying the modification of pattern recognition can be approached (see also **Baerends**, **Ebbesson**, **Fentress**, **Ehret**, and **Ingle**), and (4) the concept of CRSs offers an advantage in describing the release of behavior in terms of distributed information processing and cooperative

functions (see also **Arbib**, **Comer**, **DiDomenico** & **Eaton**, **Fentress**, and **Kondrashev**).

Limitations of our view. A famous neuroethologist – whose research I admire – once told me that he sometimes has the same bad dream: His experimental subject, a cricket, sits in front of his bed telling him that the several decades of his life the neuroethologist has dedicated to the analysis of the cricket's behavior have been in vain, since the actual story is entirely different than he believes. The cricket then smiles and disappears. I sometimes have similar dreams involving toads. Permanent skepticism and external constructive criticism help us remain aware of problems.

To illustrate the limitations of our view of the world, Mao Tse Tung (1935) used the analogy of a frog sitting in a well. The frog says that the sky does not extend beyond the brim of the well. The frog's conclusion is wrong; however, the animal has the chance to extend its view by climbing up to a higher level inside the well. To suggest the limitations of our view arising from our technical instruments in neuroethological research **Horridge** uses the analogy of "keyhole peeping," the peephole being represented by the recording electrode. He does not, however, stress the advantage of "multiple hole peeping" by means of different experimental techniques that allow the experimenter to describe a subject from various points of view (e.g., morphological, distributed functional, cellular, connectional, synaptic, dynamic, metabolic), techniques that acknowledge the complexity of the neuronal network under investigation (e.g., see **Ebbesson**, **Fentress**, and **DiDomenico** & **Eaton**).

Whereas **Horridge** argues that "neurons are the only components we know" and "when we uncover their previously unknown features, we explain neurons by reference to the known behavior," I appreciate **Grobstein's** commentary, which points out that single-cell analysis is not the only approach available and that it has noteworthy limitations. It constrains what one looks for in the nervous system, which leads to the impression of reductionism and oversimplification. I agree with Grobstein that it is often not only "the neuron and its connections that is the appropriate level of analysis but larger information-processing blocks, consisting of meaningful neuronal ensembles such as maps and pattern generators, and the interactions among such blocks." Yet how are we to determine the morphological and physiological properties of these conceptual boxes (see **Fentress**) if not by a multimethodological neurobiological approach involving the analysis of cellular properties? The more we learn about the distributed, interactive, and dynamic natures of these interwoven "blocks" and the bewildering morphological (dendritic and axonal) features of the neuronal elements (including their neuropharmacological potential), the more I hesitate to guess functions on the basis of lesion studies alone. I know that Grobstein shares this opinion.

Horridge's criticism of the subject matter of the target article does not seem constructive because it does not take all the data, strategies, and concepts sufficiently into account. Picking out just the initial seven words of the target article's abstract, he sees "imaginary bridges of fancy over the swamps of ignorance"; still sampling the abstract, he finds that key words such as "releasing

mechanisms" and "command systems" have "not progressed beyond the level of the simple observations of behavior that inspired them" and that there is no reference to neurons and their interactions. Referring to Figures 2A and B of the target article's introduction, he suggests that I am discussing recognition concepts as if the neurons were known. These cells are of course not known, but various types of retinal, tectal, and pretectal neurons in toads are known in terms of (1) certain response characteristics to critical features of test stimuli (e.g., Figure 16), (2) their stratification, (3) their morphological geometry (e.g., Figure 18), or (4) their interactions with other brain structures (e.g., Figures 20, 21) from which parallel recordings of studies in progress in our laboratory are yielding further information. The structure of the networks in which these neurons are undoubtedly integrated is not known. However, various experimental approaches allow us to suggest and discuss certain modes of wiring. In this context, the presence of specialized neurons addresses a variety of conceptual questions (see Section 5.4). Figure 19A illustrates not the wiring of a part of the brain but a putative wiring underlying the function under investigation, involving this part of the brain: "This picture is of course incomplete" (see Section 7).

With Horridge's criticism in mind we might ask how one should proceed in the neurobiological analysis of behavior:

To find out what goes on . . . you have to use the inspired guess where to look [target article; Figure 7], then the hunt [Figures 8–10], the tedious trial and error, the right stimulus as bait [Figures 4–6], and the critical recording of the evidence at the moment of the crucial activity in a simplified situation where an interpretation can be made [Figures 14–17]. . . In analysing nervous systems, we find ourselves opening up ways of observing the neurons in action so that we can then guess further what is happening in that part of the system. We rarely have excluded all possible interpretations [Section 5.4]. The resulting theories [Figures 19, 25] always have a little extrapolation beyond the direct evidence and a little generalization to make a more attractive picture. (Horridge 1983, p. 379)

As we connect neurons in a manner similar to the way an engineer works with components having known specifications, we are aware that these neurons

. . . are in fact connected in as yet undiscovered ways: their individual properties such as fields [Figures 14, 15], responsiveness and temporal characters [Figures 16, 17], are the very details that we must necessarily uncover by exploration. We are still at the stage of listing the components, finding how they are connected together [Figures 10, 20, 21] and how they interact dynamically. We use every bit of information from anatomy and behaviour [Figures 6–10] to try to interpret the responses of the individual neurons that we find [Figures 16–18, 20]. So we slowly elucidate. Then we make a tentative picture of how parts of the nervous system actually work [Figure 19A]. Naturally, if we use a part of the behaviour [Figures 4A, 5A] to find the function of a neuron, the properties of the neuron that we discover [Figures 11F, 16C] are going to explain partially that bit of behaviour. [This behavior] is

part of the evidence relating to the elucidation of how the neurons interact. (Horridge 1983, pp. 380–381)

Needless to say, we are far from a complete picture of the neuronal circuitry underlying a behavior. However, I think that the present multidisciplinary approach to the toad's prey-catching in concert with this peer interchange offer a conceptual framework providing us with ideas and guides for neuroethological research in which principles of distributed properties and interaction in neural function (Ewert 1974) – as general themes – will be of fundamental interest.

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