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Adapted and Adaptive Properties in Neural Networks for Visual Pattern Discrimination: A Neurobiological Analysis Toward Neural Engineering

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A topic of interdisciplinary research in neurobiology and neuroinformatics concerns visual pattern recognition by neuronal networks. Drawing on quantitative studies of visual releasers of prey catching in toads, it can be shown that moving objects are classified based on an evaluation of certain configurational features. The information regarding these features is provided in the manner of parallel distributed processing within a retino-pretectal-tectal interacting network. This processing structure is, to a considerable extent, modifiable and adaptive. Associative and nonassociative learning processes take advantage of loop operations involving various forebrain structures. An artificial neuronal net, applying some principles of the toad's visual system, is tested to promote the dialogue between neurobiology and engineering.

Key words: Visual pattern recognition; parallel distributed processing; implicit computation; sensorimotor codes; modulation; learning; gating; prey catching; toad

Neurobiology and Neuroinformatics

Exploration of the principles of brain function involves two main research disciplines, *neurobiology* and *neuroinformatics*. The former asks how sensorimotor systems, in interacting with their environments, are *adapted* to predictable behaviorally relevant stimuli and how *adaptive* they are in response to certain conditions. The experimental investigation is addressed to task-oriented neuroarchitectures (Ewert, Capranica, and Ingle, 1983; Guthrie, 1987). The interplay between experimentation and modeling, an important goal of neuroinformatics, is crucial for understanding brain functions.

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Neural models interpret experimental data and are predictive, hence making the theory testable. Models may also help us to develop perceptual robots, the domain of neural engineering. The objective here is to figure out task-oriented principles in terms of their “philosophies” which, having emerged in the course of evolution, are often more efficient and economical than those an engineer, faced with solving a comparable problem, might devise (Stevens, 1987; Mallot and von Seelen, 1989; Arbib, 1989). One famous example is parallel integrative processing which, tracing back to H. K. Hartline’s and F. Ratliff’s (1957) discovery of “lateral inhibition” in the compound eye of the arthropod *Limulus*, stimulated developments in neurocomputing. Another principle on loan from brain research is parallel distributed processing (PDP), whereby the same information can be processed in different structures and the same structure may be involved in the processing of different information (Rumelhart and McClelland, 1986). A branch of neuroinformatics investigates information processing by means of artificial neuronal nets (ANNs) that take advantage of brain network topologies (Eckmiller, Hartmann, and Hauske, 1990).

2 A Case Study: Discrimination of Moving Visual Objects

A theme of this interdisciplinary domain is pattern recognition. There are organisms whose visual systems are adapted to the discrimination of moving objects. This is the case for the release of prey catching and predator avoidance commands in amphibians. These behaviors are phylogenetically adapted to certain kinds of objects, and they are adaptive to a considerable extent, to internal and external conditions. In toads we show that (1) configurational features of moving visual objects are discriminated for the release of prey catching; (2) feature-related information is evaluated in different brain structures under different aspects according to a PDP paradigm; (3) the principle of feature discrimination can be explained by means of a conceptual brain network model; (4) the network is modifiable; and (5) some characteristics of (3) can be simulated by means of an ANN to establish an experimental platform for neural engineering (for reviews of our previous data, see Ewert, 1984, 1987).

2.1 Releasing Mechanisms

The toad’s catching behavior in response to prey consists of different action patterns: [o] *orienting* toward a moving object after identifying it as prey (visually grasping the prey into the binocular field); [a] *approaching* prey (depth estimation and reducing the distance between animal and prey); [f] *fixating* prey (distance estimation and corrections suitable for snapping); and [s] *snapping* prey (mechanically grasping the prey with the tongue). In ethological terminology, the responses [o], [a], and [f] are “directed appetitive behaviors,” whereas [s] is the “consummatory act.” All are

activated by *command-releasing systems* (Ewert, 1987) that draw on comparable prey recognition processes but are distinguishable by the operations that locate the visual object in space. Consequently, in a prey-motivated toad (1) the probability of the occurrence of an object-oriented response [o], [a], [f], or [s]—the prey-catching activity *R*—is correlated with the resemblance of this object to prey, and (2) the selection of these responses and their sequence depend on the prey's locomotive behavior.

2.2 Object-Defining Features

Toads do not display voluntary or involuntary eye movements comparable to mammals. Hence they respond to certain *moving* objects with prey catching. In search of releasing features, it is thus reasonable to test stimulus parameters that are related to the movement, so-called dynamic configurational features. Derived from a black cube of $2.5 \times 2.5 \times 2.5 \text{ mm}^3$ moving at constant velocity v against a white background (Fig. 1a–c), the efficacy of three different classes of objects can be investigated: (1) bars of different lengths oriented parallel to the direction of movement, (2) bars of different lengths oriented perpendicular to the direction of movement, and (3) cubes of different sizes. Comparably, the two-dimensional silhouettes of such objects can be tested (Fig. 2A,a–c) if, from a two-dimensional black square ($l_1 \times l_2 = 2.5 \times 2.5 \text{ mm}^2$), the edge of which is parallel to (xl_1) or perpendicular to (xl_2), the direction of movement is varied (for $x = 1, 2, 4, 8,$ and 16). Different procedures were used in which the stimulus was either moved around the toad (sitting in a glass vessel) or attached to a white belt that traversed the toad's visual field in the vertical plane (Ewert, 1984) or was computer-generated on the screen of a video monitor (Dinges and Ewert, in press). In principle, the same results were obtained. Toward three-dimensional objects, the prey-catching activity *R* shows the same dependences on xl_1 and xl_2 as for their two-dimensional silhouettes (see Figs. 1a–c and 2A,a–c), approximated by

$$R = \begin{cases} \beta_1 \log(xl_1) + k_1, & \text{valid for } xl_1 < 30 \text{ mm}; xl_2 = 2.5 \text{ mm} = \text{constant} & (1a) \\ \beta_2 \log(xl_2) + k_2, & \text{valid for } xl_2 > 2.5 \text{ mm}; xl_1 = 2.5 \text{ mm} = \text{constant} & (1b) \end{cases}$$

[orienting responses per time interval]

The configurational selectivity is given by $\beta_1 > 0 > \beta_2$. This is valid for a behaviorally relevant range of size. If cube or square objects of different edge length xl ($= xl_1 = xl_2$) are moved at constant v , then the xl_1 -depending and xl_2 -depending effects interact, so that approximately

$$R = \beta_3 \left| \log\left[\frac{(xl)}{(xl^*)}\right] \right| + k_3 \quad \text{[orienting responses per time interval]} \quad (2)$$

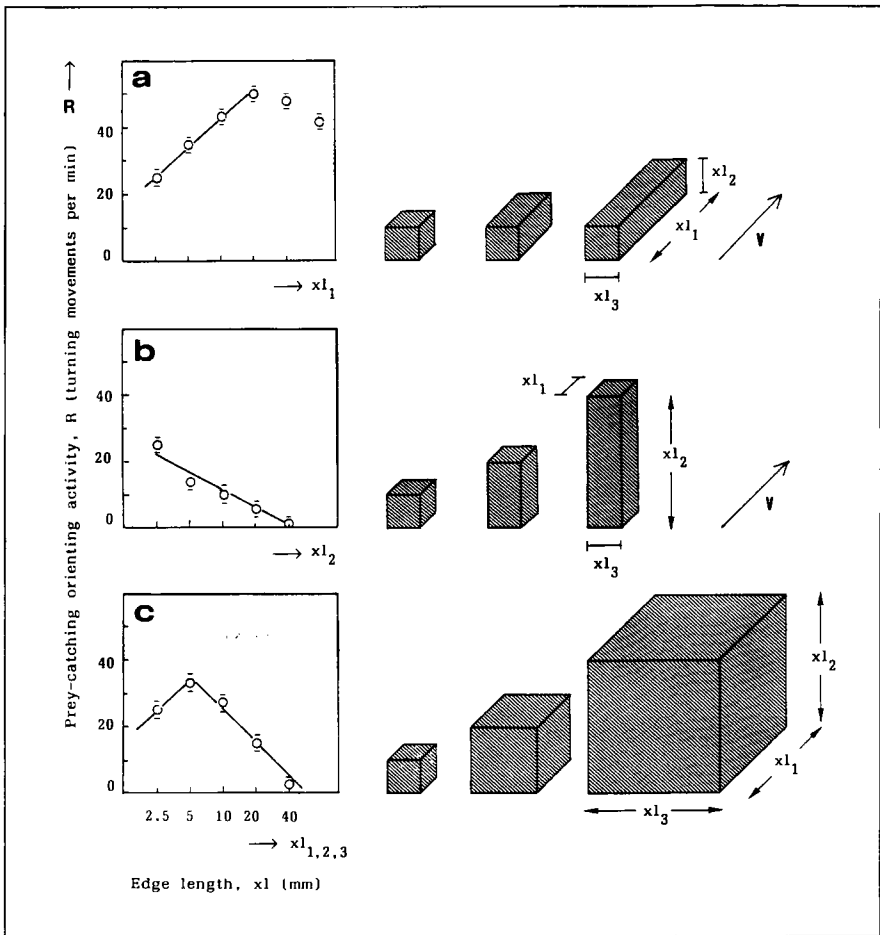


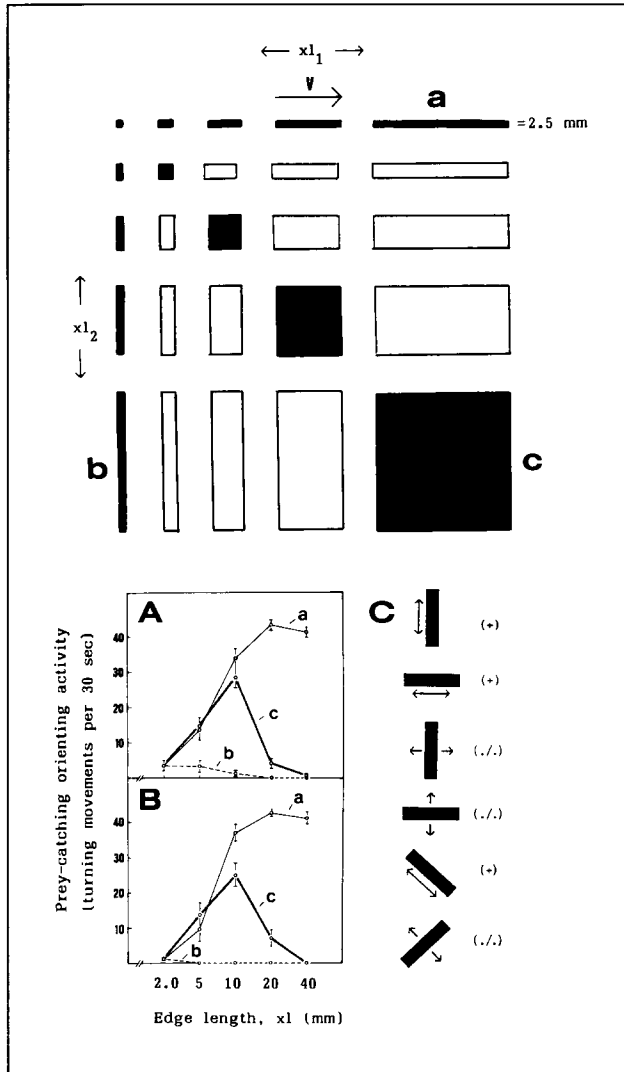
Figure 1

Influence of configurational features—(a) $x_{1,1}$, (b) $x_{1,2}$, and (c) $x_{1,1,2,3}$ —of three-dimensional black objects (moving at $v = 20^\circ/\text{sec}$ against a white background) on the *Bufo bufo* toad's prey-catching activity. Averages of 20 animals. (Courtesy of Ewert and Ganthner, unpublished report.)

with $\beta_3 < 0$, meaning that R is maximal for an optimal size $x_{1,1}^*$, approximately 8 mm. Interestingly, the value of $x_{1,1}^*$ remains constant if the object's distance (d) to the animal is varied between 20 and 200 mm. This *size constancy phenomenon* is displayed both by monocular and binocular toads (Ewert and Gebauer, 1975; cited in Ewert, 1984; Ingle, 1976). A comparison across different anuran species shows a correlation between the width j of the animal's jaw and $x_{1,1}^*$ ($= 0.43j$ [mm]). In the same species, however, $x_{1,1}^*$ is largely constant (e.g., if the big females and the small males of *Bufo bufo* are compared). The constants k_1 , k_2 , and k_3 are depending

Figure 2

Influence of the features—(a) x_{l1} , (b) x_{l2} , and (c) $x_{l1,2}$ —of two-dimensional moving objects (selected [black] from the stimulus continuum shown above) on the toad's prey-catching activity. (A) Each object was moved around the toad at $\nu = 10^\circ/\text{sec}$. (B) The toad, sitting on a rotating platform, was faced with a stationary object that produced retinal images according to Aa–c. (C) Invariance of prey selection under the direction of movement. ($\nu = \text{constant}$ [see double arrow]; (+) = prey-catching; (./.) = no motor response.) (After Ewert, 1969; Ewert, Arend, Becker, and Borchers, 1979; Burghagen and Ewert, 1983, as cited in 1984.)



on other stimulus parameters, such as ν and d , but also on the toad's prey-catching motivation. Various constants of Equations 1 and 2 depend on the direction of the stimulus/background contrast (Ewert, 1984) (i.e., black objects moving against a white background [b/w] or vice versa [w/b], whereby $\beta_1(b/w) > \beta_1(w/b)$ and $k_{1,2,3}(b/w) < k_{1,2,3}(w/b)$). This means that off-effects of moving contrast borders obviously play an important role in configurational object discrimination (Wang and

Ewert, 1992). The fact that $xI^*(b/w) > xI^*(w/b)$ suggests an optical *irradiation phenomenon*.

2.3 Directional Invariance

Regarding the stimulus continuum shown in Figure 2 (top), it is of interest that a stripe (e.g., $2.5 \times 30 \text{ mm}^2$ in size) elicits prey catching if it travels in the direction of its longer axis but stimulates no response if this axis is oriented perpendicular to the direction of movement (see Fig. 2C). In the former case, we speak of W[orm]-configuration, being aware that W refers to elongated prey in general (e.g., also woodlice and millipedes) and, in the latter, of A[ntiworm]-configuration. The discrimination value

$$D_{W,A} = (R_W - R_A)(R_W + R_A)^{-1} \quad (3)$$

describes the *configurational contrast*, whereby $D_{W,A} = f(x)$ approaches 1 for an increasing edge magnification factor x . Furthermore, it is important to note that $D_{W,A} > 0$ is independent of the velocity and the direction of the stripe's movement in all toad and frog species investigated. There is another important point to consider, namely that the R -determining effects of xI_1 and xI_2 are related to the moving retinal image and thus are maintained independently of whether the object moves in front of the toad (see Fig. 2A) or the toad is moved (see Fig. 2B) in front of an appropriate stationary object (Burghagen and Ewert, 1983, cited in Ewert, 1984). Obviously, toads do not apply a mechanism according to the reafference principle to distinguish object motion from self-induced motion.

2.4 Segmental Patterns

The toad's natural environment includes things such as leaves, stones, and branches among those objects of prey size (Fig. 3A). Thus, prey recognition requires figure-ground discrimination. In this scene, a motionless prey object cannot be identified, and it is masked when the toad moves its head due to the many shifting retinal images. However, the toad readily responds with prey catching if the object moves across the stationary background texture. This situation can be abstracted and investigated in more detail by means of a randomly textured background. Given a toad sitting in front of the stationary texture shown in Figure 3B, how could a signal with prey features emerge? It must differ from the rest in certain spatiotemporal properties: If just one $3 \times 3 \text{ mm}^2$ pixel P1 moves, the prey-motivated toad responds with prey catching, and the response activity increases, within limits, with the number of adjacent pixels, moving at the same speed, aligned in the direction of movement: P1–P2–P3–P4–P5. But if one pixel, P6, is added to this pattern in a position perpendicular to the direction of movement, the prey value is remarkably reduced, depending on

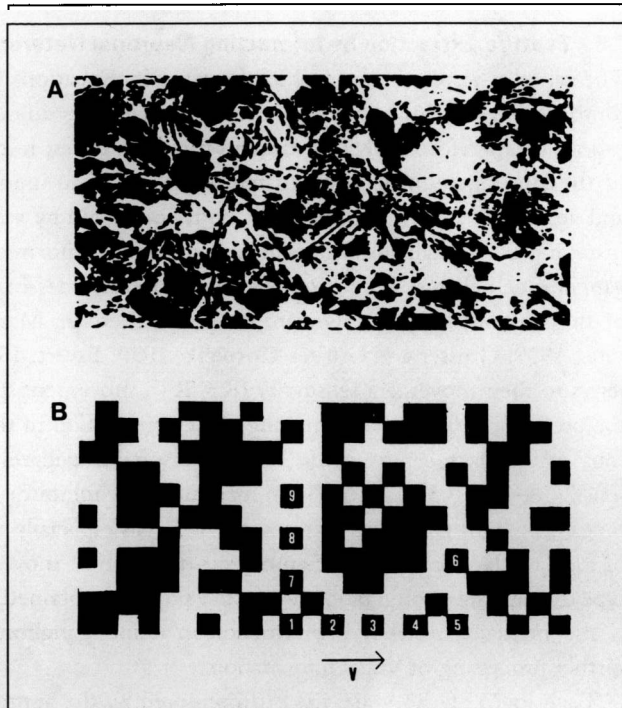


Figure 3
 Figure-ground relationships. (A) Ground in a forest. (B) Artificial texture. The velocity arrow refers to numbered pixels. For explanations, see text (After Ewert 1987).

the distance of P6. When two pixels, P1 and P7, moving at the same speed, are aligned perpendicular to the direction of movement, prey catching averages less than to either P1 or P7, and it decreases further the greater the extent of such a segmental pattern perpendicular to the direction of movement: P1–P7–P8–P9. Note that all these patterns are discriminated adequately if they traverse the stationary textured background.

In summary, we emphasize that the behavioral relevance of a stimulus pattern can hardly be determined by testing only this pattern; rather, we must conduct comparisons with patterns in which certain features are changed and others are held constant. It is the effect of these changes (see Equations 1–3) that allows one to evaluate the efficacy of features for the release of a behavior. This involves an analysis of features in relation to each other, the *configuration*. The configurational object discrimination corresponding to Figures 1 and 2A is species-universal—that is, it can be obtained in toads just collected from the field as well as in those kept for years in the laboratory.

2.5 Feature Extraction by Interacting Neuronal Networks

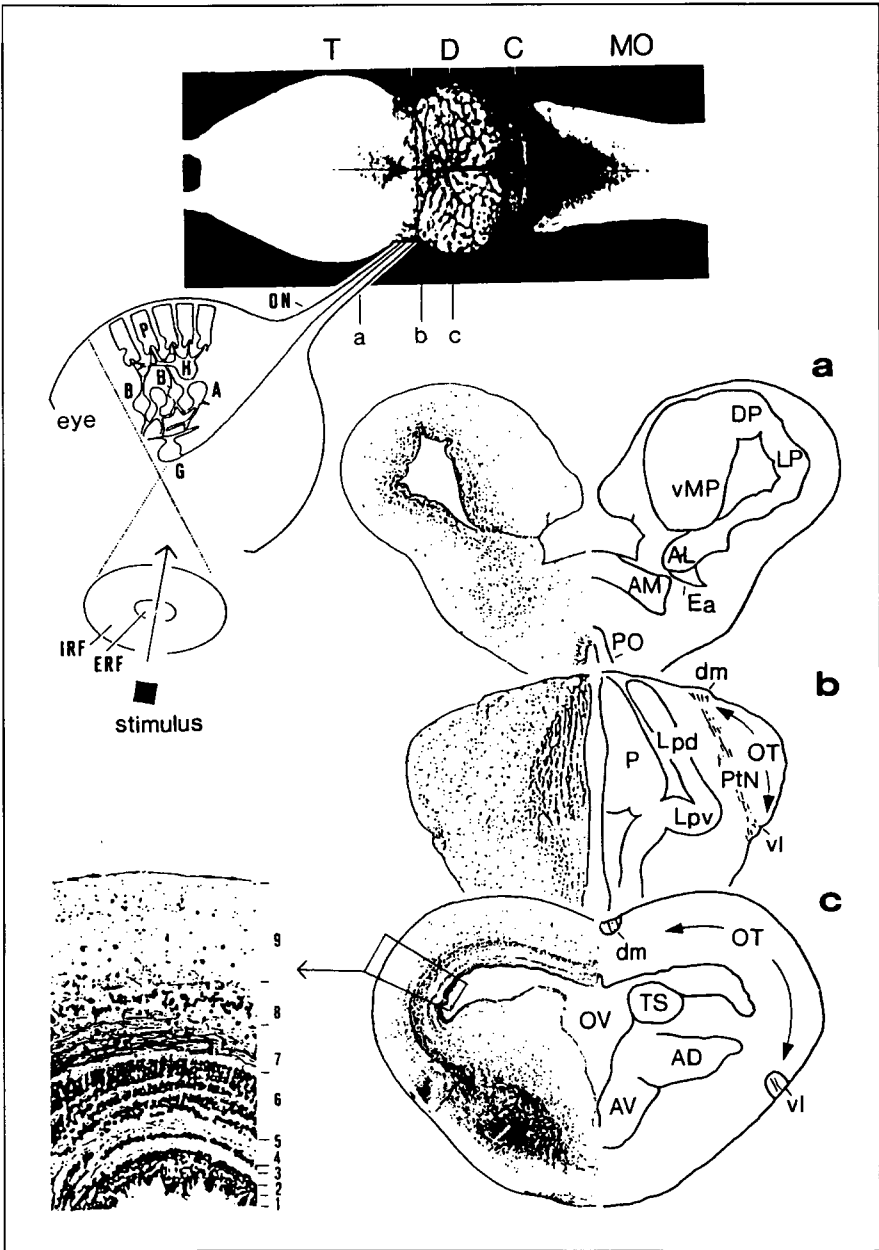
The stimulus-response relationships described by Equations 1 through 3 are obtained for toads' prey catching only. In search of the neurophysiological basis of prey recognition, we therefore apply this stimulus paradigm to test responses of single neurons of the visual system. The anuran retina consists of an input layer (photoreceptors) and an output layer (ganglion cells), both connected by an interneuronal network involving horizontal, amacrine, bipolar, and interplexiform cells (Fig. 4). Different ganglion cell classes, R1 to R4, express various modes of information processing of the network in which they are integrated (Lettvin, Maturana, McCulloch, and Pitts, 1959; Grüsser and Grüsser-Cornehls, 1970; Ewert, 1984). This, for example, refers to their movement sensitivity (R3, R4), movement specificity (R1, R2), and the preferences for compact moving objects in relation to the diameter of the neurons' excitatory receptive fields (ERFs) measured in degrees of visual angle ($= 4-6^\circ$ [R1,2], $8-10^\circ$ [R3], $12-16^\circ$ [R4]) surrounded by inhibitory receptive fields (IRFs). Regarding configurational features, the R3 cells especially are sensitive to variation of xl_2 , largely independent of an object's direction of movement. However, no cell type displays the configurational-selective property obtained in prey catching. There is also no size constancy phenomenon in retinal ganglion cells. All this suggests further processing of visual information.

Each locus of the visual field is monitored by the approximately circular ERFs of the different ganglion cell classes. Retinal information is subject to PDP (Fig. 5). The retinal (R) output is fed topographically to various structures of the contralateral brain hemisphere, mainly to the optic tectum (OT), the pretectal thalamus (lateral posterodorsal [Lpd]), and the anterior thalamus (AT) (Fite and Scalia, 1976). The tectum is a laminated network (see Fig. 4c) with retinal inputs arriving in the laminae A through C of layer 9, pretectal inputs in layers 8 and 9, and hypothalamic input in the deep layer 6. The tectal output to thalamic structures arises from layer 8, and to tegmental and medullary structures from layer 7 and the top of layer 6.

Since toads can recognize prey monocularly, our neurophysiological recordings focus on movement-sensitive cells with monocular contralateral input (Ewert, 1984, 1987). In the tectum, T-neurons of type T5.1 are responsive to the area ($xl_1 \cdot xl_2$)

Figure 4

Facing page. The toad's brain. (T = telencephalon; D = diencephalon; OT = optic tectum; C = cerebellum; MO = medulla oblongata; G = retinal ganglion cell; A = amacrine; B = bipolar; H = horizontal; P = receptor cells; ERF, IRF = excitatory, inhibitory receptive field; ON = optic nerve.) (a) Section through the caudal telencephalon. (DP, LP = dorsal, lateral pallium; vMP = ventromedial pallium; AL, AM = lateral, medial nucleus amygdalae; Ea = anterior nucleus entopedunculus; PO = preoptic area.) (b) Section through the caudal diencephalon. (Lpd, Lpv = pretectal lateral posterodorsal and posteroventral thalamic nucleus; P = pretectal posterocentral thalamic nucleus; PtN = pretectal neuropil.) (c) Section through the medial mesencephalon. (AD, AV = dorsal, ventral anterior segmental nucleus; TS = torus semicircularis; OV = optic ventricle; dm, vl = dorsomedial, ventrolateral optic tract.) On left is a cutout of OT showing layers 1 through 9.



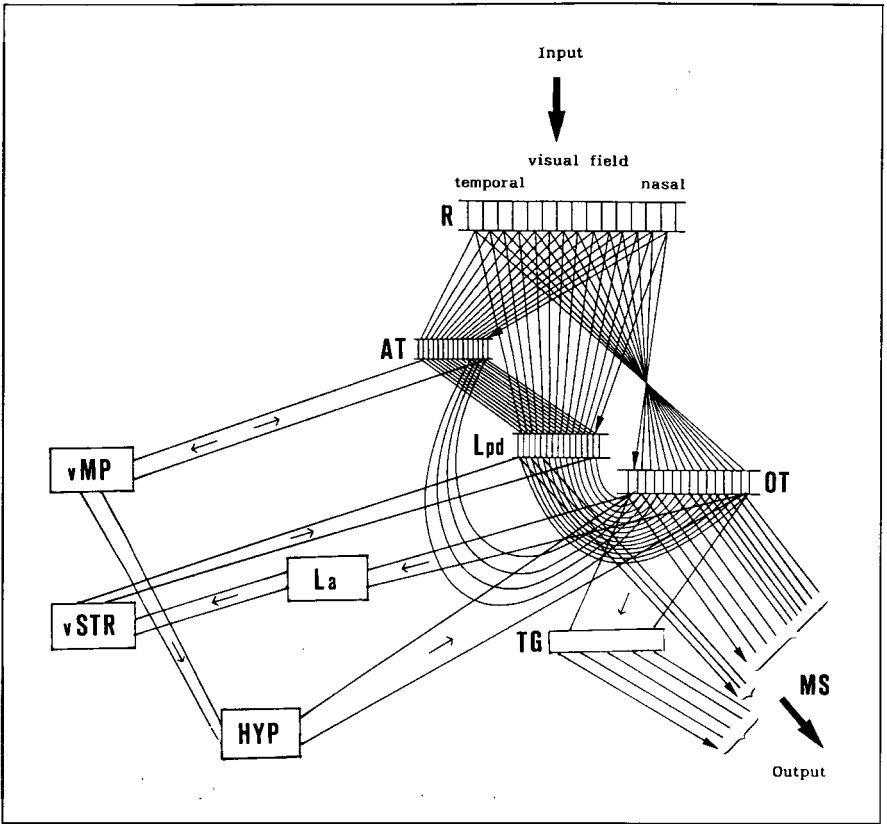


Figure 5 Neural macronetwork in anuran amphibians *mediating* between visual input to the retina (*R*) and output to the medullary-spinal (*MS*) motor systems and *modulating* this transfer. (Mesencephalic: *OT* = optic tectum; *TG* = tegmentum. Diencephalic: *AT* = anterior thalamus; *La* = lateral anterior thalamic nucleus; *Lpd* = pretectal lateral posterodorsal thalamic nucleus; *HYP* = hypothalamus. Telencephalic: *vMP* = posterior ventromedial pallium; *vSTR* = posterior ventral striatum.) Arrows indicate monosynaptic information flow. (Anatomical pathway tracings by Ebbesson, Fite, Kicliter, Lázár, Northcutt, and Scalia, as cited in Ewert, 1987.)

of a moving object and configure better to variation of x_{l_1} than x_{l_2} , whereby

$$\beta_1 > 0 = \beta_2$$

given R in Equation 1 describes the average neuronal discharge frequency, and $h_{1,2} = 2.5$ mm corresponds to 2° visual angle, valid for $x_{l_1} < 16^\circ$ and $x_{l_2} > 2^\circ$. In the pretectal thalamus, TH-neurons of a type TH3 are—opposite to T5.1—more sensitive to variation of x_{l_2} than x_{l_1} , so that

$$\beta_1 = 0 > \beta_2$$

valid for $x_{l_1}, x_{l_2} > 2^\circ$. These neurons are particularly responsive to large moving areas and to a moving textured background. Tectal T5.3 neurons are resembling properties of TH3, and there are T5.4 neurons responding selectively to large moving objects suitable to elicit avoidance behaviors in toads. Furthermore, the tectum contains a type we call T5.2, the discharge activities of which (Fig. 6A) resemble the probability with which a moving object, regarding its configurational features $\{x_{l_1}; x_{l_2}\}$, fits the prey schema

$$\beta_1 > 0 > \beta_2$$

valid for $x_{l_1} < 16^\circ$ and $x_{l_2} > 2^\circ$. In freely moving toads, strong activity of T5.2 in response to prey precedes and predicts prey catching (Schürg-Pfeiffer, 1989). Opposite to TH3 and T5.3, both T5.1 and T5.2 neurons do not respond to large moving textured patterns (Tsai and Ewert, 1988).

The approximately radially symmetrical ERFs of all these neurons are distributed over the visual field of the contralateral eye in a retinotopic fashion, so that different types of neurons may obtain information from the same region of the visual field (Fig. 7 top). The ERF diameters are 25 to 35° [T5.1, T5.2, T5.3] and approximately 45° [TH3]. In T5.1 and T5.2 neurons—unlike R-type neurons—the optimal object size x_{l^*} (after Equation 2) does not accord with their ERF diameter. Even tectal T4.1 neurons whose ERFs encompass the entire visual field of the contralateral eye respond best—like T5.1 cells—to compact objects of 8° diameter. These are important hints suggesting that the configurational response properties of tectal neurons cannot be explained in terms of classical concepts drawing on ERF/IRF interactions. There is another point to consider: Whereas in retinal and tectal monocular neurons recorded in succinylcholine-immobilized toads the optimal object size x_{l^*} for variable d is determined in degrees of visual angle ($x_{l^*} = 6^\circ$ [R2], 8° [R3], approximately 8° [T5.1, T5.2]), in freely movable toads the T5.1 and T5.2 neurons—but no R-type neurons—are responsive to the real object size (Schürg-Pfeiffer, Spreckelsen, and Ewert, 1990). Presumably, depth information from the lens accommodation mechanism (Collett, 1977) is provided only in the latter situation.

2.6 Concept of Feature-Related Processing

In summary, there are tectal and pretectal neurons that are displaying different sensitivities to variation of x_{l_1} and x_{l_2} ; furthermore, certain tectal neurons, by their response, express the degree of the configurational resemblance of objects to prey. This discovery led to the development of various network models (Ewert and von Seelen, 1974; Ewert, 1987; Arbib, 1989). The basic concept deals with a retinotopically organized retino-pretectal-tectal network in which TH3, T5.1, T5.2, and T5.3 neurons are integrated (Figs. 7, 8). It is suggested that T5 neurons at two levels are

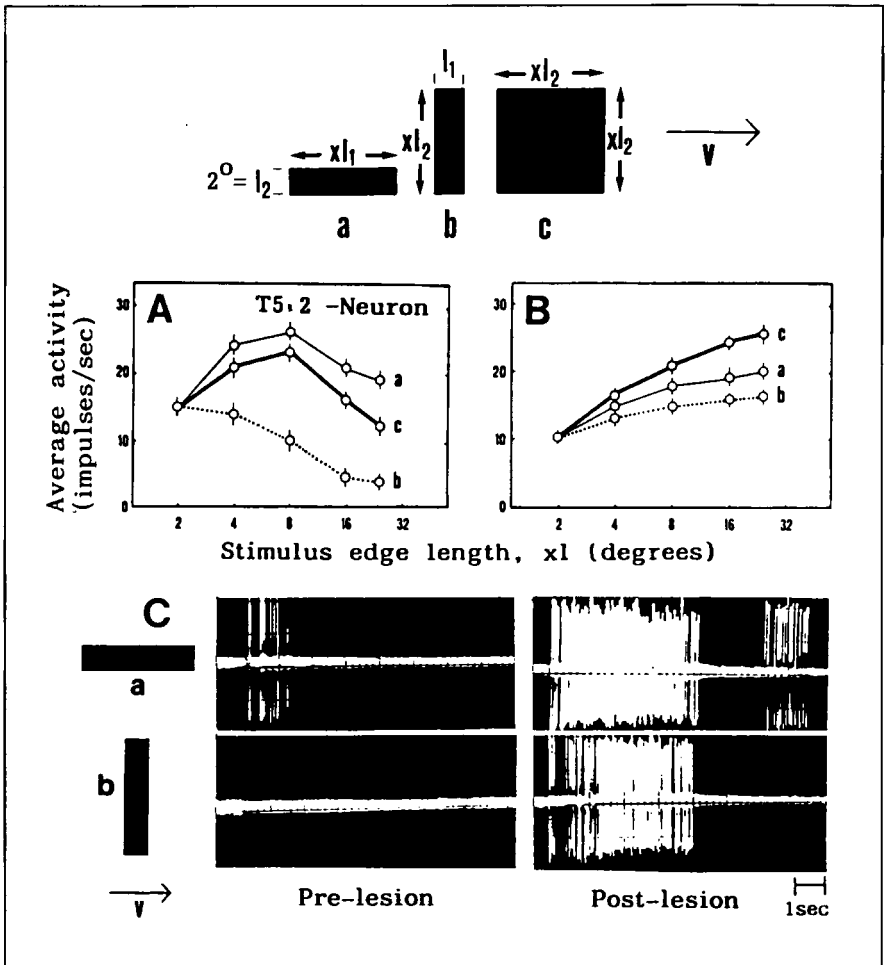


Figure 6

(A) Activity of tectal T5.2 neurons recorded extracellularly in the immobilized common toad in response to black moving visual objects of different configurations (a-c) according to Fig. 2 (top). (B) Responses of neurons of the same tectal layer recorded in toads whose configurational prey-selection behavior was impaired after pre-tectal lateral posterodorsal (Lpd) lesion. Averages of 20 neurons (A,B); $\nu = 7.6^\circ/\text{sec}$ (Ewert and von Wietersheim, 1974, as cited in Ewert, 1984). (C) Response of a grass frog's T5.2 neuron to different configurational moving stimuli (a,b) before and after a pre-tectal (Lpd) lesion applied with the neurotoxin kainic acid delivered with a glass micropipette. (Courtesy of Schürig-Pfeiffer and Ewert, unpublished report.)

inhibited by TH3 neurons, either directly (see Fig. 7b) or via tectal T5.3 interneurons (Fig. 7b'), to determine the feature-sensitive T5.1 [$\beta_1 > 0 = \beta_2$] and selective T5.2 [$\beta_1 > 0 > \beta_2$] properties.

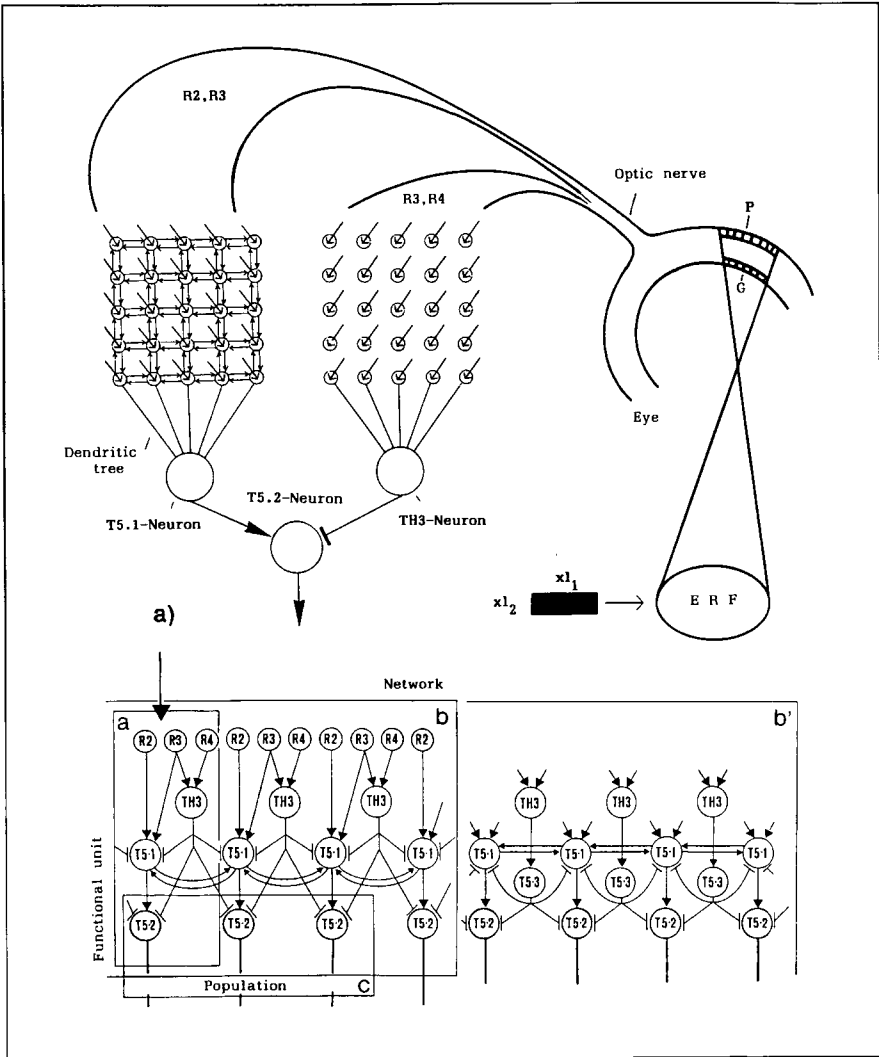


Figure 7

Parallel distributed interactive processing of visual information in a neuronal network. (Top) Functional unit (a). (Bottom) Networks involving direct (b) and indirect (b') pretecto-tectal two-level inhibition. Arrows indicate excitatory influences; lines with bars indicate inhibitory influences. (ERF = excitatory receptive field; P = photoreceptors; G = retinal ganglion cells.)

In accordance with this model, TH3 cells—but no spontaneously active pretectal cells—project to the tectum, evidenced by the antidromic stimulation-recording technique (Fig. 9). After pretectal lesions, the tectal mutual excitatory activity

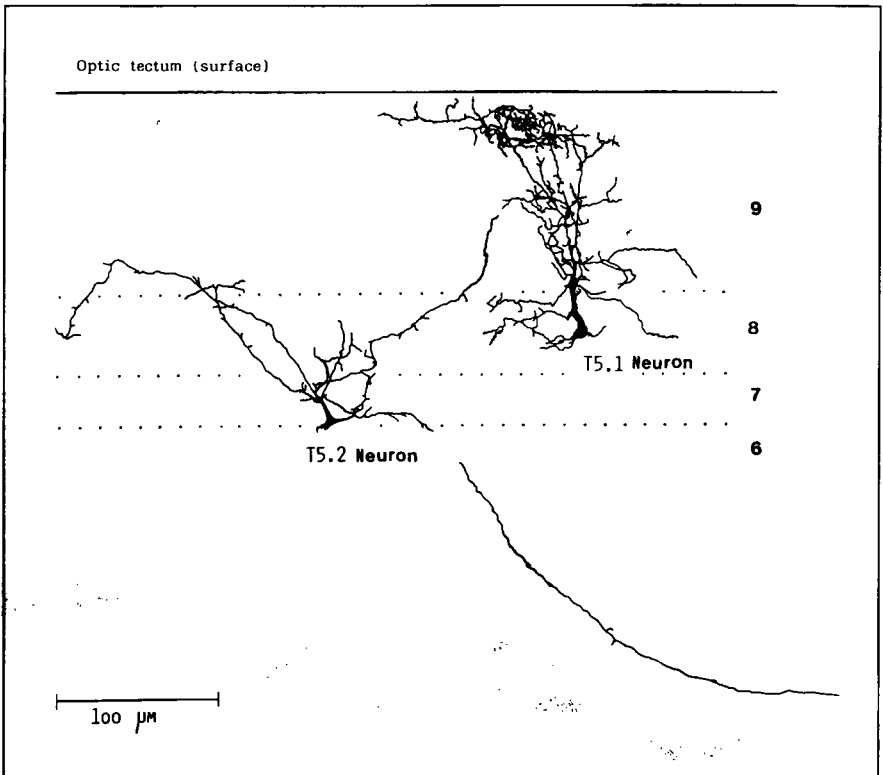


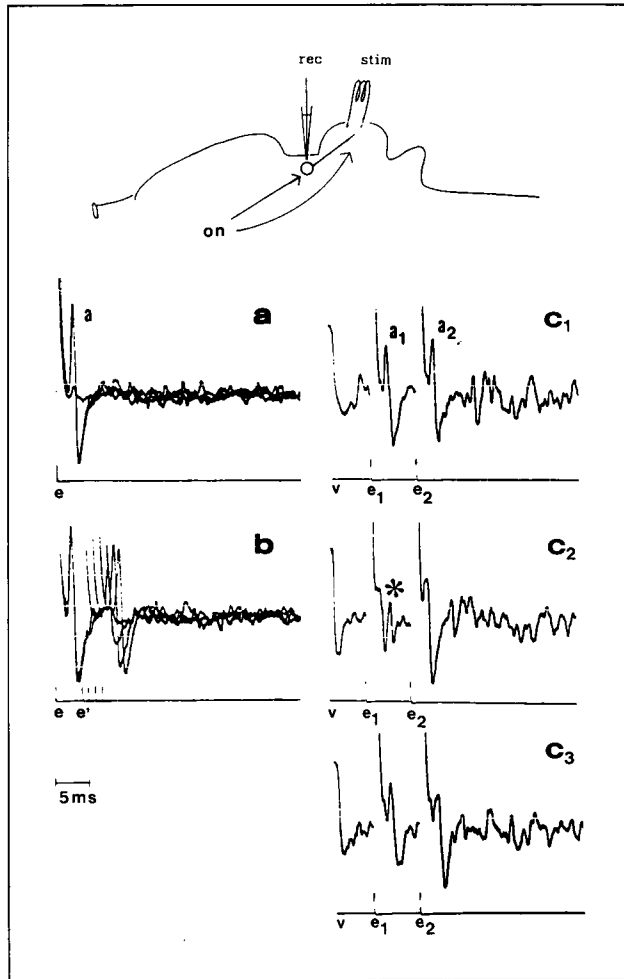
Figure 8

Morphology of a pear T5.1 and a pyramidal T5.2 neuron in the grass frog. Camera-lucida reconstructions after intracellular recording and iontophoretic Co^{3+} -lysine labeling. Tectal layers: compare Figure 4c. (After Matsumoto et al., 1986.)

to any visual input accumulates, thus reducing the configurational selectivity in T5.2 neurons and prey catching. This was shown by neurophysiological studies (see Fig. 6B,C), chronic T5.2 recording (Schürg-Pfeiffer, 1989), and ethological experiments, whereby $\beta_1 > \beta_2 > 0$ and xI^* approaching 20° , so that even predator objects were treated as prey. Pretecto-tectal influences are consistent with the observation that tectal field potentials evoked by electrical stimulation of the contralateral optic nerve are reduced in their amplitude (initial negative deflection) shortly after ipsilateral electrical pretectal stimulation (Fig. 10b). Intracellular records from T5.2 cells display sequential excitatory postsynaptic potentials (EPSPs) and inhibitory postsynaptic potentials (IPSPs) in response to electro-stimulation of the optic nerve but mainly IPSPs in response to electrical pretectal stimulation (Schwippert, Beneke, and Ewert, unpublished report).

Figure 9

Identification of a TH3 neuron projecting ipsilaterally to the toad's tectum by means of the antidromic stimulation (*stim*)-recording (*rec*) technique. (*on* = optic nerve; *e* = electrical impulse of 0.1 ms applied bipolarly to the tectum; *a* = antidromic spike in response to *e* recorded from a TH3 cell; *a*_{1,2} = two antidromic spikes elicited by double impulses *e*₁ - *e*₂ triggered by a visually elicited spike *v* recorded from the TH3 cell.) (a) Constant latency response of *a* and all-or-nothing property (superimposed traces) for *e* around threshold intensities. (b) Refractory period measured with four electrical double-impulse *e* - *e'* of variable interval (superimposed traces). (c₁) Collision test: no collision between *v* and *a*₁ for a delay of 6 ms between *v* and *e*₁; (c₂) Collision of *a*₁ (see asterisk) for a critical delay *d* = 5.5 ms. (c₃) Control: no collision for *d* = 5.8 ms. (After Buxbaum-Conradi and Ewert, in press.)



Antidromic stimulation-recording studies have shown that the output of the network regarded here, mediated by integrated T5.2 neurons (Figs. 7, 8, 11), feeds to the motor systems of the medulla oblongata (Satou and Ewert, 1985; Ewert, Framing, Schürg-Pfeiffer, Weerasuriya, 1990). We infer that for the evaluation of other moving objects (mate, predator), the same network with different connectional properties partly takes advantage of the information processing provided by T5.1, T5.3, and TH3 neurons, which is expressed by other output neurons. For example, predator-sensitive T5.4 cells, known to project to the medulla oblongata, may compute threshold-operated coincident excitatory inputs of T5.1, TH3, and

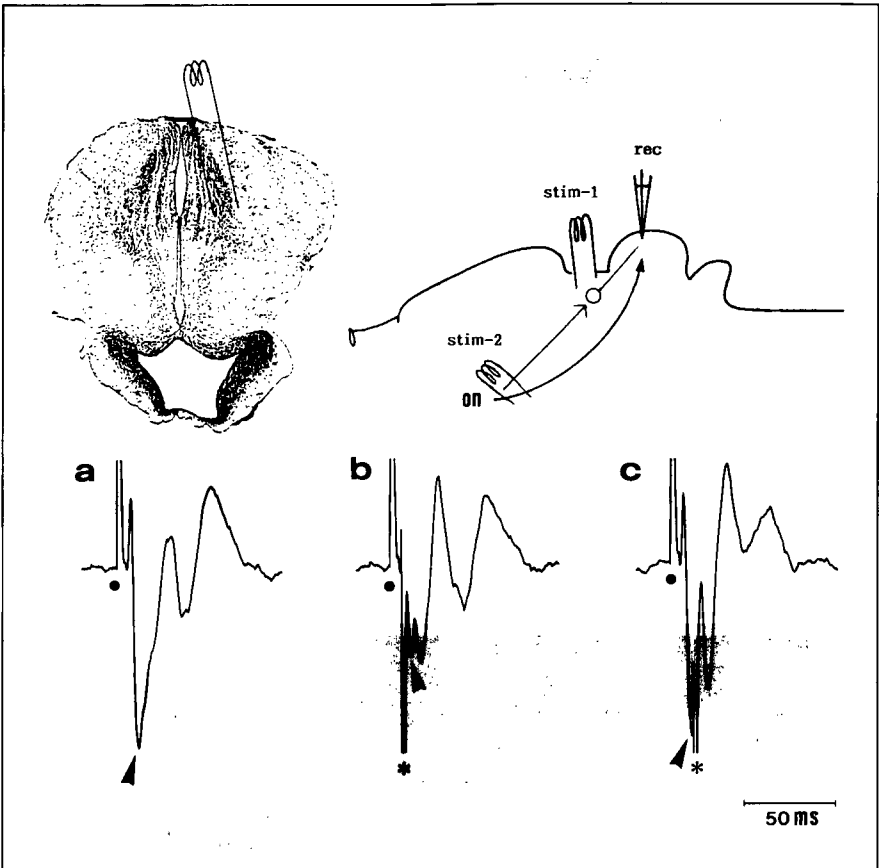


Figure 10

Ipsilateral pretecto-tectal influences. (a) Field potential recorded from the toad's optic tectum (FPT), evoked by a 0.1-ms electrical impulse (black circle) applied bipolarly to the contralateral optic nerve (*on*). (b) FPT in response to optic nerve stimulation (*stim*) and, at a delay of $t = 8$ ms, to ipsilateral electrostimulation (asterisk) in the pretectal lateral posterodorsal-posterocentral region. (c) Experiment as in (b) for $t = 16$ ms. The initial negative deflection of the FPT is reduced in (b) but not in (c); compare vertical arrows. (After Beneke, Schwippert, and Ewert, 1992.)

T5.3 neurons. After large pretectal or tectal lesions, predator avoidance behavior fails to occur.

3 The Principle of Implicit Computation

Important properties emerging from this network are (1) the preference of a stripe traveling in the direction of its longer axis (*W*-configuration) versus the same one

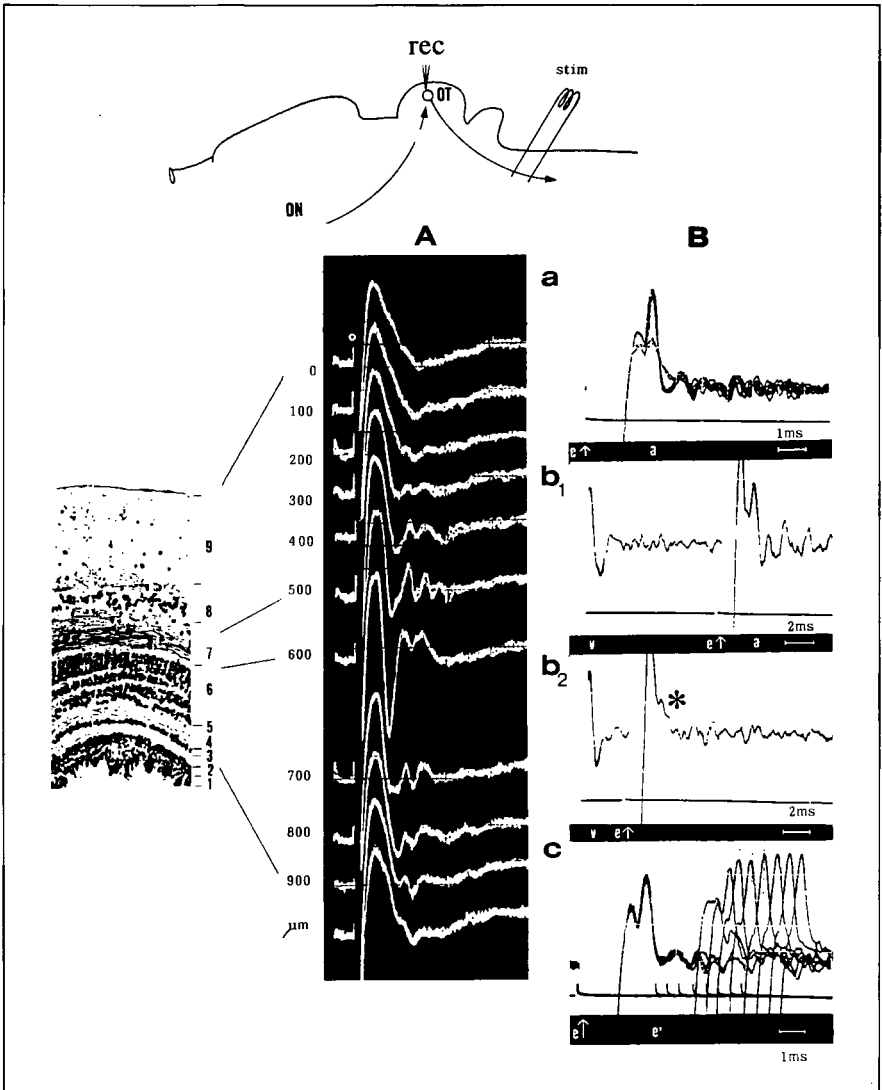


Figure 11

Evidence of the tectubular-spinal projection of T5.2 neurons in toads. (*OT* = optic tectum; *ON* = optic nerve; *stim* = stimulation) (A) Antidromic field potentials recorded from OT, evoked by a 0.1-ms impulse *e* applied bipolarly to the contralateral tectubular-spinal tract in the medulla oblongata. Note the strong negative deflection at a depth of approximately 600 μm corresponding to tectal layers 7 and the top of 6. (B,a) Antidromic spikes *a* of a T5.2 cell in response to *e*, displaying constant latency at 2.3 ms (superimposed traces), and all-or-nothing property around threshold intensities. (*b*₂) Collision of *a* (see asterisk) by a visually elicited spike *v* for a critical delay between *v* and *e* of 3.3 ms. (*b*₁) No collision for 9.5 ms. (c) Refractory period measured with double impulses *e* - *e'* of variable interval; superimposed traces. (From Ewert, Framing, Schürg-Pfeiffer, and Weerasuriya, 1990; Ewert, unpublished report.)

whose long axis is oriented perpendicular to the direction of movement (A-configuration) and (2) the invariance of the W versus A preference under the movement direction. In the mammalian visual cortex, such discrimination can be achieved by *explicit computation* based on asymmetrical ERF/IRF interactions of elongated, differently oriented receptive fields. This requires a huge number of appropriate detectors for any locus of the visual field. In the toad's brain, the above problem is obviously solved in a different manner, more economically. The invariant discriminatory property emerges from *implicit computation* (Stevens, 1987) involving largely symmetrical receptive fields. This means that even T5.2 neurons with slightly oval ERFs discriminate between W- and A-configurations of a stripe not with reference to this ERF asymmetry. In fact, the W/A preference is perfect for stripes that are much shorter than the ERF diameter.

The principle of implicit computation can be explained by multilateral excitation in connection with weighted lateral inhibition in the retino-pretectal-tectal system. Given retinotopic input from R2 and R3 neurons to the T5 neuronal network and supposing a topographical lateral excitation mediated by dendrodendritic synapses (of which only some are illustrated in Figure 7 [top, left]), then (1) the resulting mutual excitatory processes (between the input structures of the T5 neuron and across laterally coupled neurons) will be somewhat stronger for a stripe moving in W-configuration than for the same one moving in A-configuration [$\beta_1 > \beta_2 > 0$], and (2) the excitation in response to W would increase with its extension x_{l1} . (The spread of dendritic arborizations of certain tectal neurons toward layer 9 [Fig. 8; T5.1] and the presence of dendrodendritic synapses [described by Székely and Lázár, 1976] is consistent with this hypothesis.) The W versus A preference hence considers the different spatiotemporal properties of the stimulus patterns. Symmetrical lateral couplings make this discrimination independent of the direction of movement.

The detection problem, however, is not solved satisfactorily in this way for two main reasons: First, the tectal self-excitatory processes in response to visual input must be kept within biologically suitable limits. Second, an enhancement of configurational discrimination is required. Both can be achieved by inhibitory influences from pretectal TH3 neurons (see Fig. 7, top right), which receive many retinal R3 and R4 converging inputs. Provided that the topographical input structures of these pretectal neurons are not excitatorily coupled, they would take advantage of the R3-mediated responsiveness to changes of x_{l2} , hence yielding an A versus W preference for a wider ERF. (The sensitivity to large moving surfaces is enhanced by R4 inputs.) Given that the retinopretectal system acts topographically on the retinotectal system in an inhibitory manner (see Fig. 7, top) at two levels (see Fig. 7, bottom), then an increase of the W versus A sensitivity [$\beta_1 > \beta_2 = 0$ for T5.1 neurons] and selectivity [$\beta_1 > 0 > \beta_2$ for T5.2 neurons] will emerge. We suggest that the pretecto-tectal

inhibitory influences also account for the velocity invariance found in the W versus A preference of T5.2 neurons.

4 Feature Detection and Sensorimotor Codes

What does *prey selectivity* mean in terms of neuronal responses? The role of single neurons for perception is still controversial, although there is no doubt that vertebrates' brains contain highly integrative feature-selective cells that express complex information processing. Examples are the Df-sign-selective neurons in jamming-avoidance behavior of electric fish, song-selective neurons in song birds, biosonar information-bearing neurons in mustached bats, face-selective neurons in monkeys and, as this article shows, prey-selective neurons in common toads (for reviews, see Ewert et al., 1983). We suggest that one of the properties of the network in which T5.2 cells are integrated is that of a *prey feature filter*. By cross-correlation, this filter compares input information y regarding configurational cues of a moving object with stored information inherent in a property H of the network to yield an output z : if $y(r, s, t)$ is the space (r, s) - and time (t) -dependent input signal, $H(r, s, t)$ is the coupling function of neurons involving lateral excitation and lateral inhibition, and $z(r, s, t)$ is the network's output expressed by T5.2 neurons, then

$$\mathbf{F}[z(r, s, t)] = \mathbf{F}[H(r, s, t)]\{\mathbf{F}[y(r, s, t)]\} \quad (4)$$

describes the Fourier transform of the convolution integral of the cross-correlation function. Given that an operation H_1 characterizes the x_{l_1} -extraction in the retinotectal network and H_2 the x_{l_2} -extraction in the retinopretectal network, feature discrimination results from pretecto-tectal subtractive interaction (Ewert and von Seelen, 1974). If this interaction is tuned to depth information from the lens accommodation mechanism arriving in pretectal structures, a size constancy phenomenon will emerge.

The network in which T5.2 cells are integrated determines the toad's prey schema that allows a category of objects to fit. The approximateness of the boundary of this category can be regarded as an advantage rather than a handicap, because it suggests a considerable freedom for adaptive modifications. An argument that information provided by T5.2 cells is not sufficient for the release of prey catching is refuted by the concept of *command-releasing systems* whose sensorimotor codes (Ewert, 1987) take advantage of certain combinations of different types of neurons, including those with recognition and localization properties (Ewert et al., 1990; Schwippert, Beneke, and Ewert, 1990).

5 Plastic Network Properties

Many questions arise from this model, concerning such issues as evolutionary aspects of pretectal-tectal circuits, self-organization after pretectal lesions, pharmacological modulation, self-control of inhibition, and adaptive modification.

5.1 Developmental Aspects

Since pretectal thalamic visual structures seem to play an important role for visual perception in amphibians, it is interesting to explore species at stages in which these structures are differently developed. Ontogenetic neuroanatomical studies in anurans show that the dorsal thalamus begins to parcellate before metamorphosis and is completely differentiated after 6 months to 1 year of terrestrial life. The dorsal-thalamic parcellation into a posterocentral (P) and a lateral posterodorsal (Lpd) nucleus proceeds with the elaboration of connections between Lpd/P and optic tectum (Clairambault, 1976). In accordance with Ebbesson's (1984) *parcellation theory*, this anatomical differentiation is paralleled by an improvement of configurational selection ($\beta_2 < 0$), size constancy, and depth estimation (Ewert, 1984). Note that these visual properties are strongly impaired if in adult toads or frogs the Lpd/P is surgically disconnected from the tectum.

5.2 Self-Organization

The observation that small lesions in the pretectal network lead to perceptual deficits in circumscribed regions of the visual field is consistent with the notion that retino-pretectal and retinotectal maps are topographically connected. Interestingly, both the size of this visual region and the perceptual recovery time depend on the lesion's extent. In particular, the recovery time—ranging from minutes (very small lesions) to several days (larger lesions) or even several months (extended ablation)—suggests a capacity for functional self-organization that leads to a rough repair (Fig. 12, 30 days) but not to a perfect restoration (Schürg-Pfeiffer, Burghagen, Weerasuriya, and Ewert, unpublished report). Multilateral pretecto-tectal connections, rather than distinct point-to-point projections, might play a role, probably in addition to tectal intrinsic processes.

5.3 Pharmacological Modulation

It is known that the dopamine agonist apomorphine strongly facilitates pecking in pigeons and other species of birds (Dhawan, Saxena, and Gupta, 1961). In common toads we have found that 5 minutes after lymphatic injection of apomorphine (4 mg/100 g body weight), the visual response field for prey catching shrinks toward a narrow frontal region, whereby snapping is facilitated and orienting (turning) inhibited. Whereas in normal toads snapping behavior displays a variability at the expense of accuracy, after apomorphine application snapping is stereotypical but well-aimed

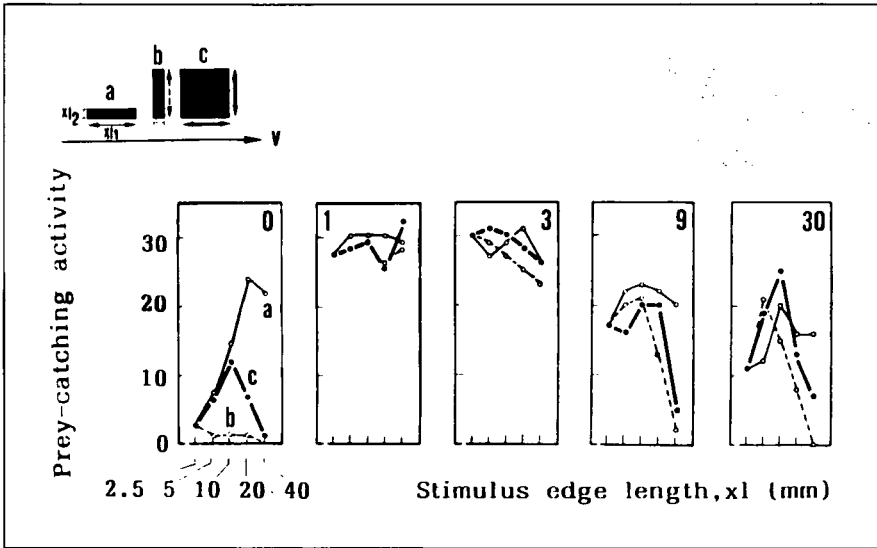


Figure 12
 Functional recovery. Configurational stimulus response relationships of a toad before (0) and 30 days after (1–30) pretectal lesion. Representative example.

(Schürg-Pfeiffer, Spreckelsen, and Ewert, unpublished report). There is a correlation between the apomorphine-induced shrinking of the response field, topographical disproportionalities of visually evoked potentials in the tectum, and metabolic activity evaluated by means of the [14 C]-2-deoxyglucose(2DG)-method (Schwippert, Beneke, and Glasgow, unpublished report). The configurational discrimination was not impaired (no decrease in the value of β_2 and no increase of xl^* in Equation 2; however, $k_{1,2,3}$ significantly increased under apomorphine (Fig. 13A). Since it is accepted that retinal R2 and R3 neurons feed into the network responsible for prey recognition, the dose-dependent influence of apomorphine on their visual responses is an interesting neuronal phenomenon: Both the ERF diameter and the discharge frequency significantly increased (Fig. 13B). Dopamine plays a role as a neurotransmitter in vertebrate retinal interplexiform cells and as a modulator of spatial summation in horizontal cells (Bodis-Wollner, 1990). The influence of apomorphine on other visual (and nonvisual) neurons is being investigated (Glasgow and Ewert, unpublished report).

5.4 Forebrain-Mediated Modulation in the Macronetwork

Neuroanatomical studies in anurans revealed a wealth of connections between the telencephalon and the optic tectum, mediated via diencephalic structures (see Fig. 5),

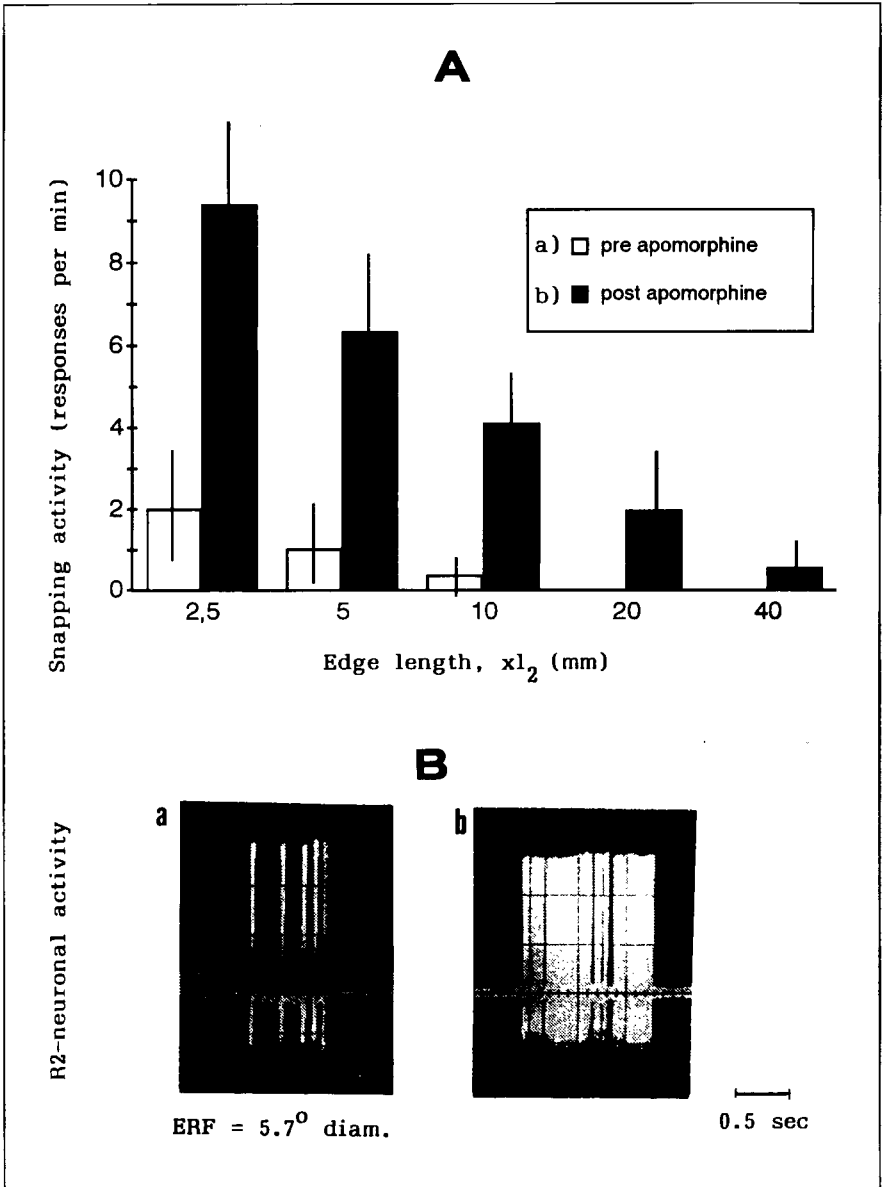
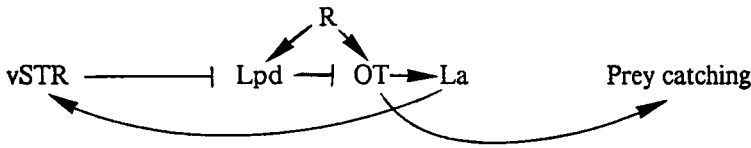


Figure 13

Influence of apomorphine on prey catching. (A) Snapping activity of toads in response to black antiwormlike moving black stripes ($v = 7.6^\circ/\text{sec}$) of 2.5 mm width and variable length $x l_2$, before (a) and after (b) intralymphatic injection of apomorphine. (B) Activity of a retinal R2 neuron in response to a black $2^\circ \times 16^\circ$ antiwormlike stripe ($v = 7.6^\circ/\text{sec}$) before (a) and after (b) systemic injection of apomorphine. (ERF = excitatory receptive field.) (After Glasgow and Ewert, 1992.)

which suggests loop operations (Ewert, 1987). Based on the quantitative data obtained from behavioral investigations, [¹⁴C]-2DG studies, single-neuron recordings, and lesion experiments, in the following we hypothesize various loops with different properties that make the sensorimotor codes of command-releasing systems (Ewert, 1987) adaptive to internal and external conditions (see Fig. 5):

5.4.1 Gating a Visual Response to Prey We suggest that the reaction to prey is gated by a disinhibitory process. In response to retinal (R) input, the tectal (OT) prey-catching releasing system is initially inhibited by the pretectal Lpd nucleus (arrows indicating excitatory influences and lines with cross-bars inhibitory influences):



The toad safely hesitates. In a toad not ready to catch prey, T5.2 neurons discharge moderately to a prey object (Schürg-Pfeiffer, 1989). Prey catching could be gated through inhibition of Lpd from the telencephalic ventral striatum (vSTR), thus disinhibiting the tectal prey-catching system to retinal visual input (vSTR may respond to internal and to tectal information mediated via the thalamic La nucleus). In fact, a strong increase in the T5.2 firing rate precedes prey catching (Schürg-Pfeiffer, 1989). The following evidence of a disinhibitory pathway is found: Mainly IPSPs (Fig. 14B,c) and combined EPSPs/IPSPs are intracellularly recorded from Lpd/P to electrical stimulation of the ipsilateral vSTR. With bilateral vSTR lesions, there is visual prey neglect (Patton and Grobstein, 1986). With bilateral Lpd lesions, there is binocular disinhibition of visual prey catching. With a unilateral Lpd lesion, there is disinhibition of prey catching toward objects moving in the visual field of the contralateral eye. Finally, in the face of telencephalic ablation involving Lpd, there is disinhibition of prey catching, comparable to the behavior after an Lpd lesion only (Ewert, 1984). The lack of prey catching after vSTR lesions thus can be interpreted as a permanent hesitating and the behavior after Lpd lesions as a permanent gating of prey catching. The suggested disinhibitory striato-pretecto-tectal projection in anurans with arousing-gating functions seems, to some extent, to be analogous to the basalganglio-nigro-collicular projection in mammals (Chevalier and Deniau, 1990).

5.4.2 Prey Specification by Habituation For prey-selective habituation, the following loop is suggestive: With the repetitive presentation of the same prey stimulus, the telencephalic posterior ventromedial pallium vMP (response to visual informa-

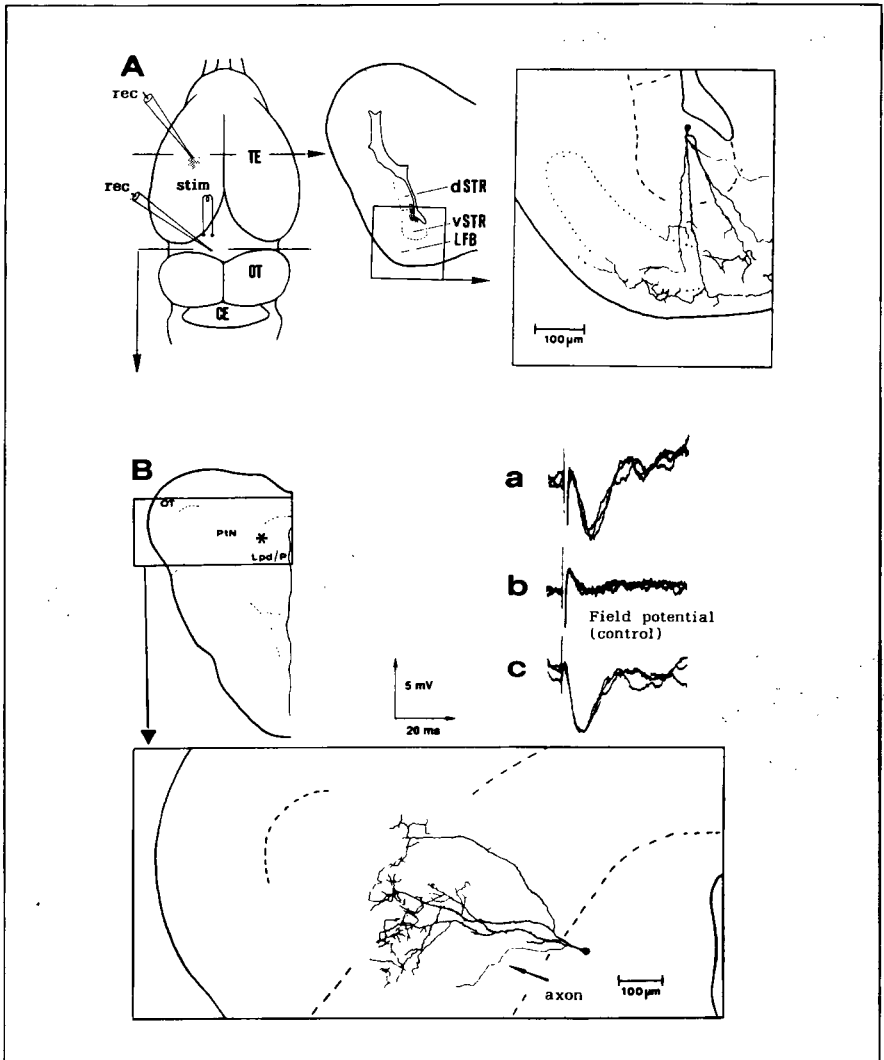
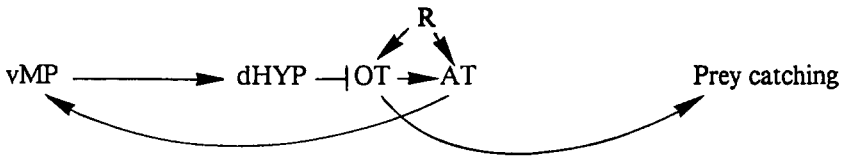


Figure 14

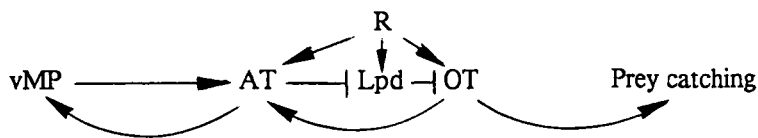
Striatopretectal connections in toads. (A) Camera-lucida reconstruction of a T5.1 property displaying wide-field neuron in the posterior ventral striatum (*vSTR*, top right). (B) Short-latency inhibitory postsynaptic potential (IPSP) activity of a reconstructed prepectal TH3 property-displaying neuron (a) in response to electrical stimulation of the ipsilateral forebrain bundle (*LFB*), which contains axons of striatal cells; (b) field potential for *LFB* stimulation; (c) IPSP activity of another TH3 cell in response to electrostimulation of *vSTR*. (*TE* = telencephalon; *OT* = optic tectum; *CE* = cerebellum; *rec* = micropipette for intracellular recording and iontophoretic labeling with Co^{3+} -lysine; *stim* = stimulation site in *LFB*; *d, vSTR* = dorsal striatum; *PtN* = prepectal neuropil; *Lpd/P* = prepectal thalamic nuclei.) (After Matsumoto, Schwippert, Beneke, and Ewert, 1991.)

tion mediated via anterior thalamus [AT]) decides about the novel character of the stimulus by comparing its cues with previously stored ones. In case of repetitive sameness, vMP is excited and, via dorsal hypothalamus (dHYP), inhibits the tectal prey-catching releasing system:



If certain configurational cues of a prey stimulus within the prey schema are altered, vMP is not activated and prey catching proceeds. This hypothesis is consistent with [¹⁴C]-2DG studies and lesion tests. In habituated toads compared to nonhabituated animals, the vMP and dHYP show stronger uptake, whereas OT reveals much less [¹⁴C]-2DG uptake in response to prey. With bilateral vMP lesions, there is weak prey habituation in naive toads and dishabituation in prelesion habituated ones. With bilateral AT lesions, there is weak prey habituation in naive animals (Finkenstädt and Ewert, 1988a; Ewert, 1984). For a model of prey discrimination responsible for stimulus-specific habituation, see Wang and Ewert (1992).

5.4.3 Prey Generalization by Prey-Predator Association We suggest that the prey schema can be generalized by a conditioned disinhibitory pathway. In the course of feeding a toad with a mealworm (prey) presented with the experimenter's moving hand (predator), vMP—informed by OT via AT—takes part in prey-predator conditioning. On the combined stimulus presentation, vMP finally becomes sensitive to the hand alone or to other large moving objects and facilitates prey catching by an inhibitory influence on Lpd:



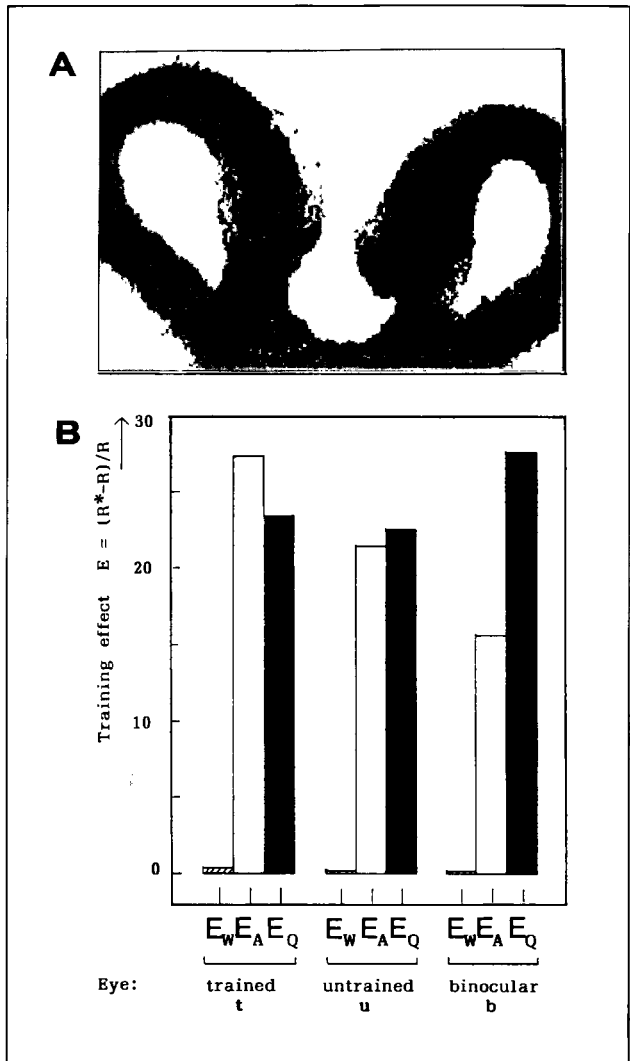
The configurational pattern discrimination of these prey-predator-conditioned toads is largely impaired, comparable to Lpd-lesioned animals. In conditioned toads compared to unconditioned animals, vMP and OT show stronger uptake, but Lpd reveals less [¹⁴C]-2DG uptake toward a large moving object. Bilateral vMP lesions prevent the associative learning in naive toads and restore the species-universal pattern discrimination in previously prey-predator-conditioned toads (Finkenstädt and Ewert, 1988b; Finkenstädt, 1989). Monocularly trained toads, whose contralateral vMP exhibits much stronger [¹⁴C]-2DG uptake than the ipsilateral one (Fig. 15A), display memory transfer (Fig. 15B) that calls for an investigation of vMP and OT neuronal

Figure 15

Prey-predator conditioning.

(A) Increased uptake of [¹⁴C]-2DG in the right ventromedial pallium of a monocularly (left) prey-predator-conditioned toad in response to a large predatorlike moving square object (for anatomy, see Figure 4a) (Finkenstädt and Ewert, 1988b).

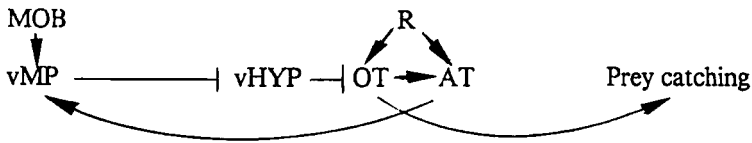
(B) Interhemispherical memory transfer of monocularly conditioned toads. For black wormlike (*W*) or antiwormlike (*A*) moving stripes of 5 × 30 mm² and for a 30 × 30 mm² moving square (*Q*), the relative training effect [$E = (R^* - R)/R$] is calculated from the prey-catching responses (per minute) of 16 animals before [*R*] and after [*R**] conditioning. The *E_W*, *E_A*, and *E_Q* values refer to the trained (*t*) eye (other eye covered), the untrained (*u*) eye (trained eye covered), and binocular (*b*) vision. Training effects emerging for nonprey *A* and *Q* are similar for *t* and *u*. (After Dinges and Ewert, in press.)



responses and commissural (telencephalic?) connections (Dinges and Ewert, in press). This differs from stimulus habituation, which is specific for the retinal locus and the eye stimulated (Ewert, 1984).

5.4.4 Visual Prey Generalization in the Presence of Known Prey Odor For associating visual and olfactory stimuli, loop operations different from the one for prey-predator conditioning are probable, suggesting a concept of conditioned prey

motivation (Merkel-Harff and Ewert, 1991). During feeding, toads associate unknown odor (e.g., cineole) with prey, due to inputs from the main olfactory bulb (MOB) and the OT-AT connection. On the combined stimulus presentation, vMP develops a sensitivity to this odor, so that in the presence of visual input *and* known prey odor, almost any moving visual object, largely irrespective of size and configuration, elicits prey catching. This is consistent with increased glucose utilization both in vMP and OT. The decrease of [¹⁴C]-2DG uptake obtained in the ventral hypothalamus (vHYP) suggests vMP-induced inhibition of certain hypothalamo-tectal connections that normally may have a suppressive influence on the tectal prey-catching releasing system:



In the absence of prey-associated odor, the prey odor-conditioned toads discriminate moving configurational objects according to the species-universal schema.

Regarding comparative aspects in learning, we note that the vMP is homologous to the mammalian hippocampus, which is involved in spatial cognitive maps (Thinus-Blanc, 1987) and the significance of which, for long-term potentiations (McNaughton and Morris, 1988), is discussed for memory in the cerebral cortex (Artola, Bröcher, and Singer, 1989; Schmajuk, 1990).

6 Edge Detection by Artificial Neuronal Nets

Artificial neuronal nets are composed of highly connected computing elements that copy some functions of the nervous system. An ANN displays a certain topology (input layer, hidden layer, and output layer). The input patterns and output patterns are known. The network's task is to discern the corresponding functional relationship through adjustments of the computing elements' input weights and sensitivity thresholds by means of a backpropagating algorithm (or some other learning technique).

In collaboration with mathematicians, a backpropagation network—applying some principles of the toad's visual system—was computer-simulated. This preliminary ANN consists of a 4 × 4 input neuronal matrix (referring to properties of retinal R3 neurons), connected to two clusters composed of a total of nine hidden neurons (referring to the pretectal-tectal network), and converging onto two output neurons that indicate the degree to which a stimulus is preylike or threatlike, respectively (Klöppel, 1991).

Toward a further development, the BACKPROP-net is replaced by a net that better takes advantage of neurobiological principles corresponding to Fig. 7. This MOD-net involves various modules: one in which retina-like input regarding an object's dimension x_{l2} is evaluated by an integrator, and another module consisting of a lateral excitatorily coupled network that in response to parallel retina-like input yields a signal correlated to x_{l1} . A third module provides a classification based on the signals related to x_{l1} and x_{l2} (Ewert, Beneke, Buxbaum-Conradi, Fingerling, Glasgow and Schwippert, 1992).

The following advantages characterize the MOD-net: (i) The objects to be discriminated—moving on a belt such as illustrated in Fig. 16—are not trained; (ii) the evaluations of x_{l1} and x_{l2} —both invariant under object's direction of movement—are inherent in the properties of the network modules; (iii) the lengths discriminations

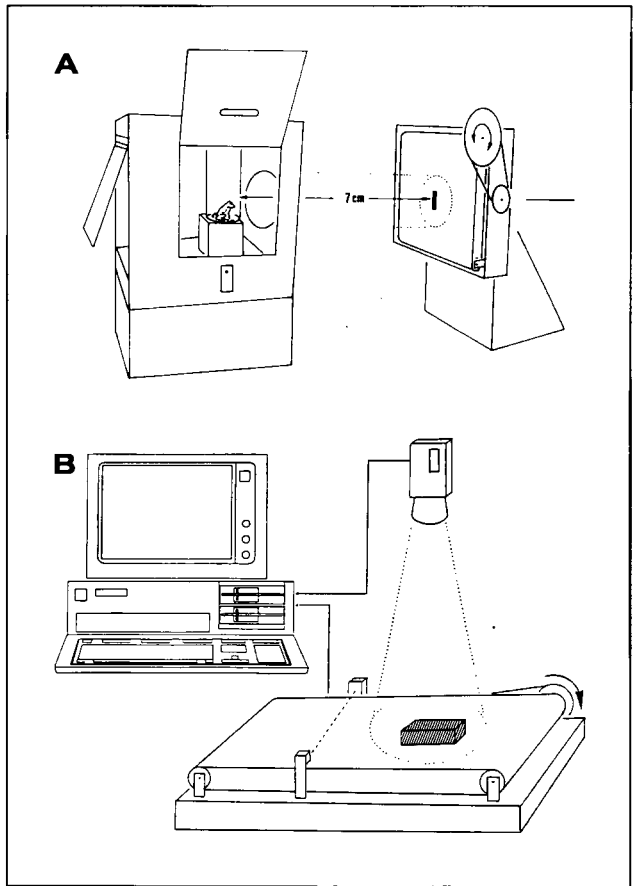


Figure 16
 Experimental procedures in which (A) a toad by its prey-catching activity distinguishes between stimulus patterns moved on a belt and (B) a computer-simulated artificial neuronal net discriminates belt-moved objects after passing an infrared gate that releases a CCD video camera whose signals (of two subsequent pictures) are XOR-preprocessed in a bit map. (From Fingerling and Ewert, BMFT Report, 1992.)

of xl_1 and xl_2 , respectively, are implicit in the network's properties; (iv) the input matrix to the MOD-net is largely extended; (v) the following objects were classified in a toadlike manner as nonprey: a bar whose axis was oriented obliquely (e.g., at 45°) to the direction of movement; two simultaneously moving wormlike bars arranged in parallel; a wormlike bar moving together with a small cube beside it; overall distributed small cubes.

7 Comments

An experimental platform was established to promote dialogue between specialists in the fields of neurobiology and neuroinformatics (Department of Neurobiology, University of Kassel) and engineering (Institute of Mechanics, Technical University of München). For the pilot study, the MOD-net was implemented in a perceptual robotic device to select three-dimensional objects (shown in Fig. 1a–c) moving on an assembly line. Our goal is to develop a neuronal net that, considering neurobiological principles (implicit computation, sensorimotor codes), is adaptive to task-oriented operations.

Acknowledgments

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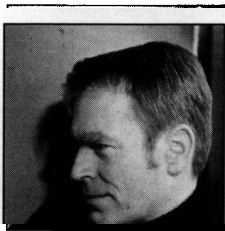
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