

# The Neural Basis of Visually Guided Behavior

*Techniques from ethology and neurophysiology are combined to show how an animal localizes a visual object, discriminates its significance and then makes the appropriate motor response*

by Jörg-Peter Ewert

Animals see things and then act on the basis of what they see. What chain of events connects some key stimulus with a specific fixed pattern of responses? In recent years workers in several laboratories have sought by many different means to analyze the nerve mechanisms by which animals interpret sensory signals and select the most appropriate response. The most effective way to understand the neural basis of behavior appears to be to apply a broad spectrum of experimental techniques: to combine ethological studies of an animal's behavior with experiments involving brain anatomy and brain-cell stimulation and the recording of individual nerve-cell activity.

For the past six years, in my laboratory first at the Technical University of Darmstadt and then at the University of Kassel, we have been taking this broad approach to learn about two kinds of visually controlled behavior in the toad: orienting (prey-catching) behavior and avoidance (escape) behavior. There are several good reasons for working with the toad. Amphibians are vertebrates, so that what we learn at their relatively low level of behavioral integration contributes to our understanding of more complex vertebrate functioning. Toads in particular have a limited and easily surveyed behavioral repertory. In response to specific stimuli one can repeatedly elicit predictable reactions, such as snapping at prey, fleeing from an enemy, clasping during courtship and making particular wiping motions after tactile stimulation. (The fickle European frog, in contrast, undergoes short-term changes in motivation and is not suitable for behavioral experiments.) Finally, the toad is not easily conditioned, so that its

innate behavioral functions can be measured in successive experiments for some time without being significantly affected by accumulated experience.

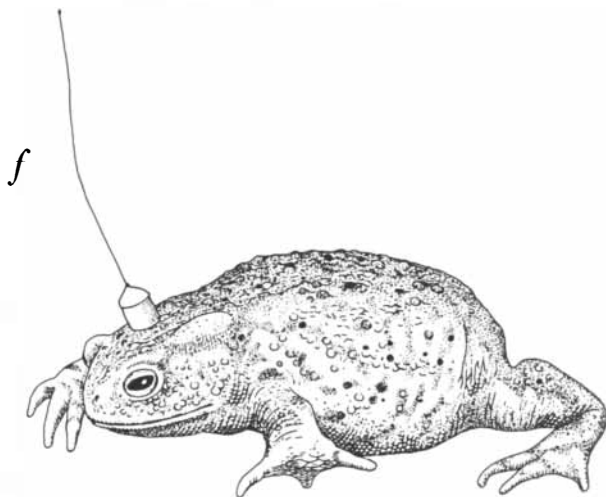
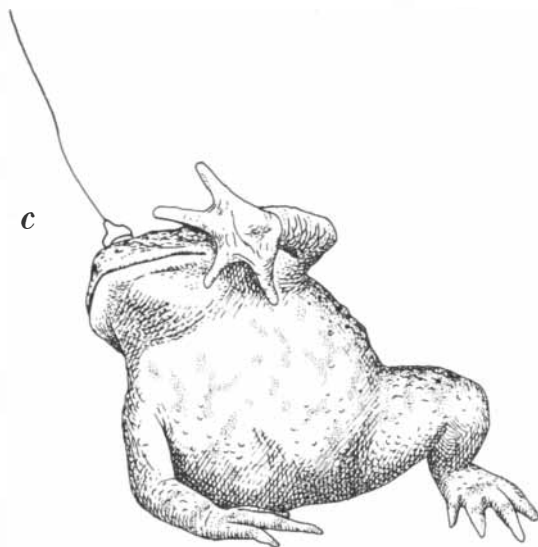
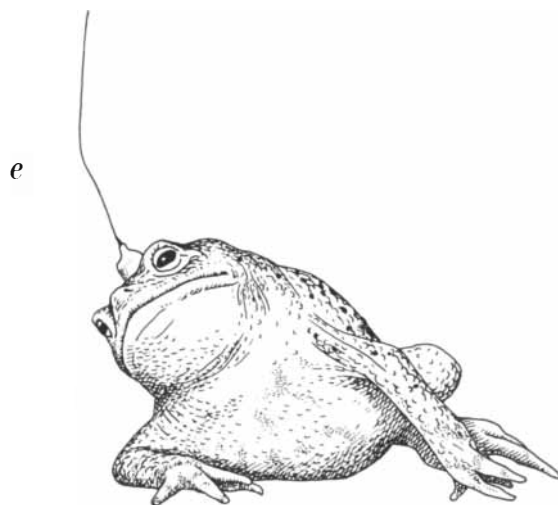
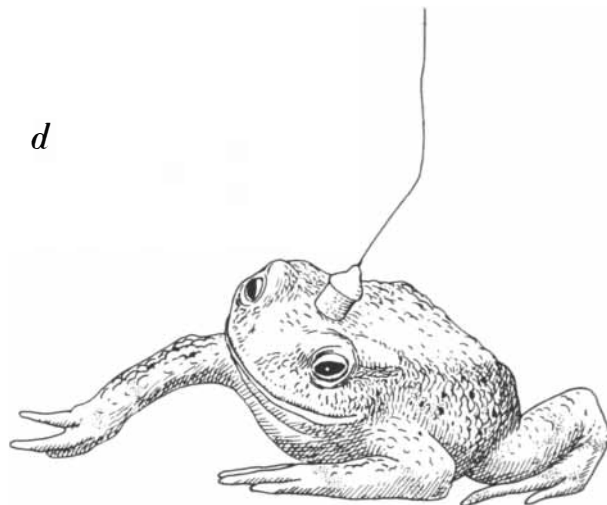
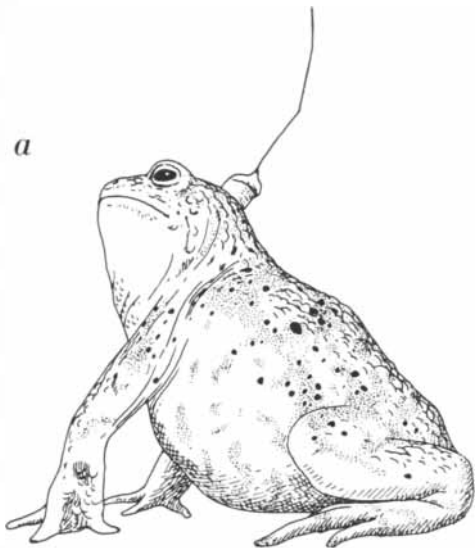
Toads respond to small objects, such as a piece of white cardboard moved over a black background, with a series of prey-catching reactions. First there is orientation toward the prey, then binocular fixation, then snapping, gulping and mouth-cleaning. Two basic processes are required to produce the overall orienting reaction: the identification of a stimulus and the location of it in space. The identification process determines the type of behavior. It is dependent on specific features of the stimulus such as its angular size, the orientation of the boundaries between light and dark, its angular velocity, its contrast with the background and so on. A detection process then localizes the stimulus and, together with the result of the identification process, determines the motor response, which can be either to turn toward the stimulus if it is identified as prey or to avoid it if it appears to be an enemy. In what follows I shall attempt to analyze the neurophysiological basis of signal identification, localization and the triggering of the associated instinctive actions.

To begin one must analyze quantitatively the key stimuli for orienting and avoidance behavior. This is done by changing various characteristics of a visual stimulus in an ordered way. The toad is placed in a cylindrical glass compartment where it observes a small square of black cardboard moving against a white background at a constant angular velocity, describing a circle around the animal at a distance of seven centimeters. The toad interprets such a stimulus as prey

and tries, through successive turning movements, to keep the object fixated in the center of its visual field. The degree of orienting activity is measured by counting the number of turning responses per minute.

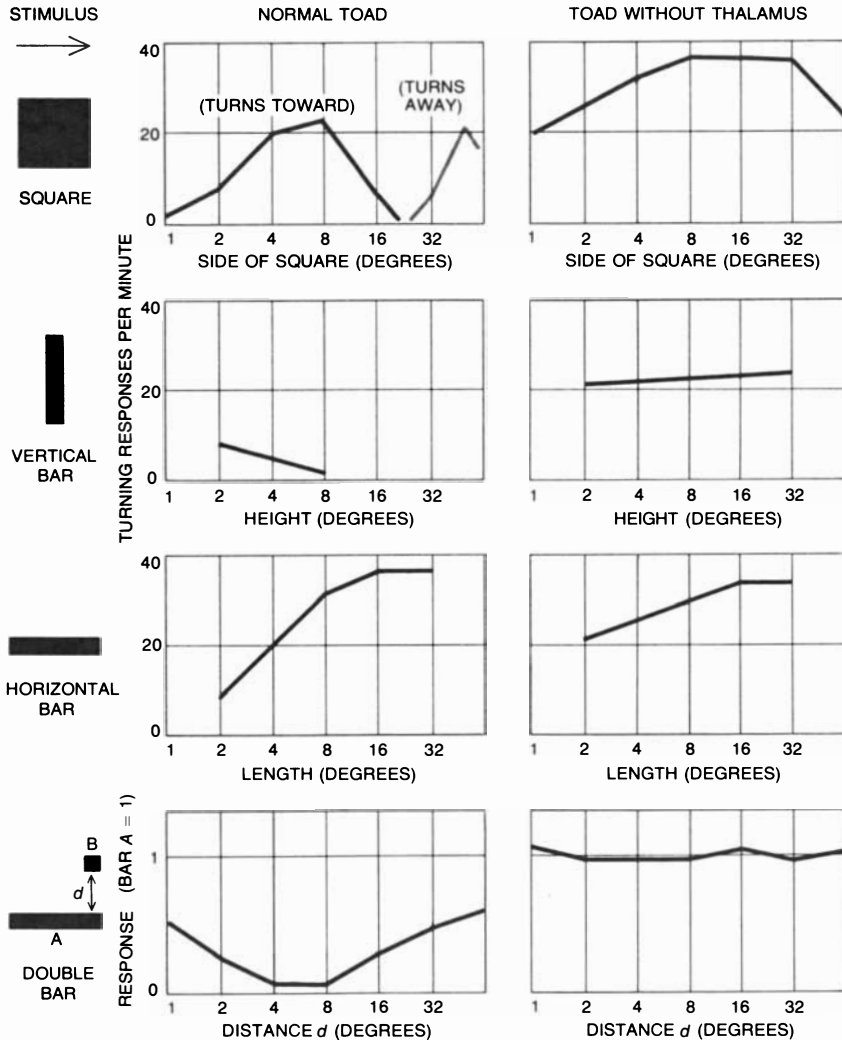
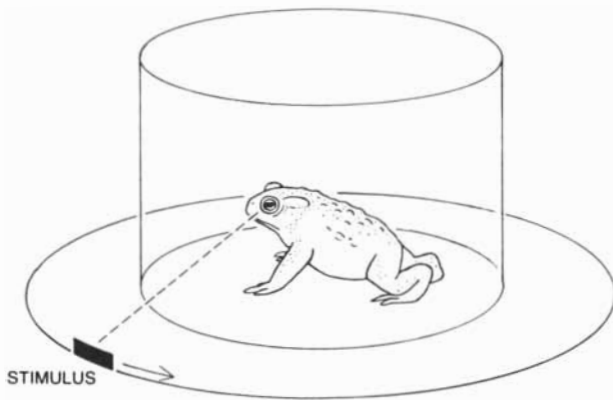
The angular size of the stimulus—the angle it subtends—influences the orienting activity [see illustration on page 36]. Of a variety of square objects toads prefer those with an edge length of four to eight degrees. (The absolute size of such stimuli is five to 10 millimeters. Experiments where the distance between animal and stimulus is varied show that it is the absolute—not the angular—size that counts; in prey-catching behavior toads display “size constancy.”) The toads turn away from objects larger than 30 degrees on a side, exhibiting the avoidance response. More particular information is obtained by substituting bars of various lengths for the square stimuli. As a two-by-two-degree stimulus is elongated along the horizontal axis the orienting activity increases until a saturation level is reached; wormlike objects turn out to be particularly attractive to toads. In contrast, the response decreases as a small stimulus is extended vertically, or perpendicularly to the direction of movement.

Other experiments indicate that toads discriminate prey from enemy objects through analysis of the visual stimulus in terms of point or edge configurations, also taking into consideration the direction of movement. A horizontal chain consisting of several two-by-two-degree units moving along the same path signifies prey. One such unit moving alone constitutes a prey stimulus just above the response threshold. When the horizontal chain is supplied with a separate vertical



**BEHAVIORAL PATTERNS** characteristic of the toad *Bufo bufo* are illustrated. The actions are commonly elicited in the animal by the sight of visual objects. These drawings, however, are based on photographs of toads whose brains were being stimulated electrically as part of the author's investigation of the neural bases of visually guided behavior. The electrode on the toad's head penetrates

to the brain. An electric current applied to the optic tectum, a visual center in the brain, elicits a prey-catching sequence: orienting, or turning (*a*), snapping (*b*) and mouth-cleaning (*c*). Electrical stimulation, instead, of a site in the left or right thalamus brings a "planting-down" defensive posture (*d, e*) and stimulation of another part of the thalamus brings a crouching avoidance response (*f*).



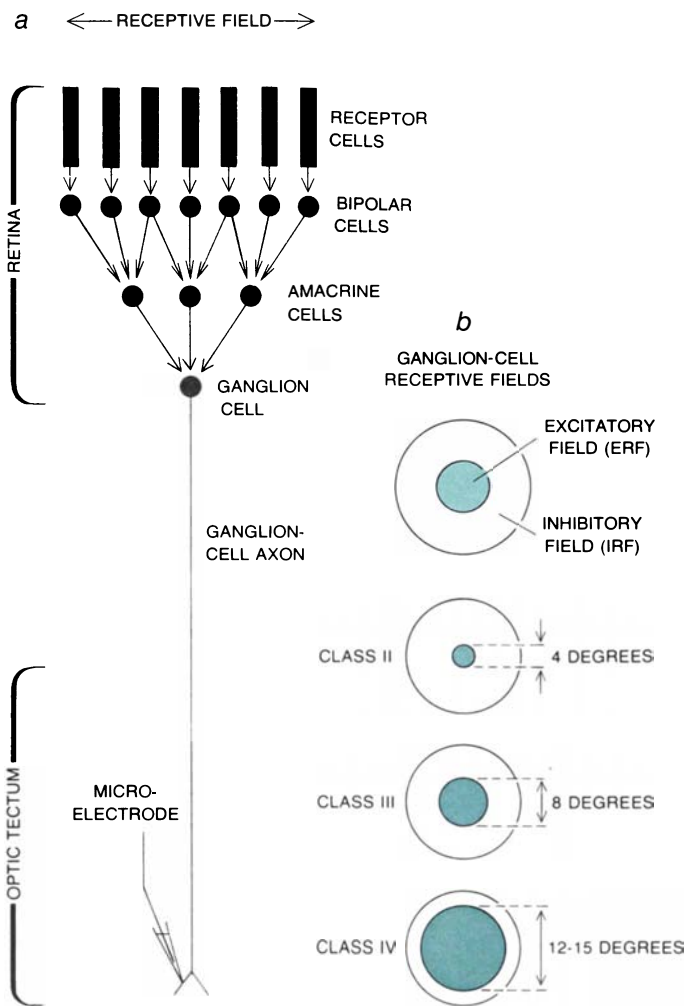
**BEHAVIORAL RESPONSES** of the toad to objects of various shapes and sizes were quantified. Small black objects were moved across the visual field at seven centimeters' distance and the orienting response was determined for normal toads (*left*) and those whose thalamus had been removed (*right*). Prey-catching responses (turning toward the object) were elicited most effectively in normal toads by squares with sides subtending four to eight degrees; the toads turned away from larger squares. Vertical bars were ineffective as prey objects—and increasingly ineffective with increasing height. Horizontal (wormlike) bars were increasingly effective as prey objects with increasing length, up to a limit. Double bars (a horizontal bar plus a vertical extension) were less attractive, the effect varying with distance between bars; the ratio of their effect to that of a single bar is shown (*bottom*). In toads lacking the thalamus the orienting response becomes “disinhibited.” The animal tends to orient toward a target without discrimination, even if the target normally signals “danger.”

extension (making it in effect an L-shaped structure moving on its long side), it loses efficiency as a prey-catching stimulus. The inhibitory effect of the vertical extension depends on its distance from the horizontal element. If a second vertical extension is introduced, in effect making the stimulus a shallow U-shaped structure, the total configuration signifies “enemy.” The ethological interpretation is that it symbolizes a “swarm,” and in the toad’s brain inhibitory interactions first restrain prey-catching behavior and then induce escape behavior.

For constant form and angular velocity the behavioral activity generally increases as the amount of contrast between stimulus and background increases. White objects moving against a black background are normally more attractive as prey than black objects on white; the latter, on the other hand, are more effective in eliciting avoidance behavior. When the size and contrast are held constant, behavioral activity increases with increasing angular velocity, reaching a maximum at between 20 and 30 degrees per second. Stationary objects usually elicit no prey-catching or avoidance response. The common critical feature for key stimuli representing both prey and enemy is movement, and the two kinds of stimulus are differentiated primarily on the basis of their form: extension of the object in the horizontal direction of the movement generally means prey, whereas extension perpendicular to the direction of the movement signifies “not prey” or “enemy.”

What does the toad’s eye tell the toad’s brain? This question was first formulated for the frog and dealt with in the fascinating research of Jerome Y. Lettvin and his colleagues at the Massachusetts Institute of Technology, and was later investigated quantitatively by O.-J. Grüsser and his co-workers at the Free University of Berlin. To ask the question is to open the “black box” of the toad’s brain, or at least to examine the brain functions that participate in transforming input from visual stimuli into relevant behavioral patterns. At this point I shall describe neurophysiological findings concerning whether it is in the retina of the toad’s eye that the key stimuli “prey” and “enemy” are encoded.

In the toad retina there are three types of ganglion cells that send their fibers by way of the optic nerve to the structure called the optic tectum in the midbrain. One can record the action potentials, or nerve signals, from the ends of these fibers by introducing a microelectrode into the tectum. John E. Dowling, then at



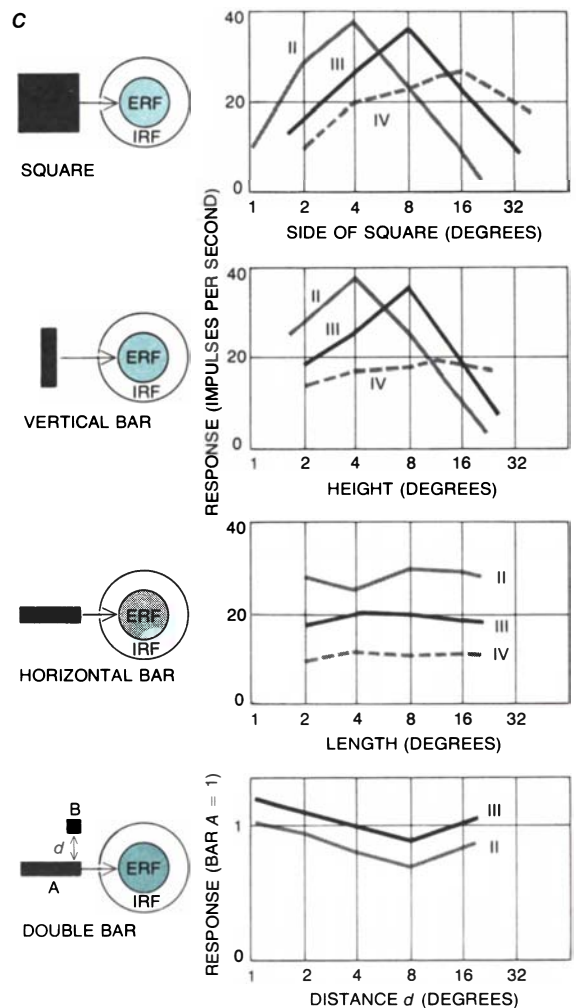
NEURAL RESPONSES of the toad to the same objects were measured with recording electrodes. The electrodes recorded impulses at the terminals in the optic tectum of fibers from individual ganglion cells, the cells in the retina of the eye on which signals from the receptor cells converge via intermediate cells (a). Each ganglion cell has an excitatory receptive field surrounded by an inhibitory receptive field. The diameter of the excitatory fields and

the Johns Hopkins University School of Medicine, showed through electron micrography that in the frog (or toad) retina each ganglion cell is connected to a number of receptor cells by bipolar and amacrine cells. Each ganglion cell is thus fed information from a particular part of the animal's visual field. Lateral connections established by horizontal and amacrine cells play a role in determining the properties of this receptive field. In toads as well as frogs the field consists of a central circular excitatory receptive field immediately surrounded by an inhibitory receptive field. The movement of an object through the excitatory field elicits a ganglion-cell discharge, which is inhibited if another object is simultaneously moving through the inhibitory field. The three ganglion-cell types in the toad (as in the frog) differ in several character-

istics, including in particular the diameter of their excitatory receptive fields: about four degrees for the so-called Class II ganglion cells, about eight degrees for Class III cells and from 12 to 15 degrees for Class IV cells. (Class I cells have been identified in frogs but not in toads.)

With microelectrodes we measure the rate of ganglion-cell discharge to see how it changes when objects (corresponding to those in the behavioral experiments described above) are moved through the receptive field of the cell. The impulse frequency increases with the length of the side of a square object until the length about equals the diameter of the excitatory field; then it decreases as the object becomes large enough to stimulate part of the surrounding inhibitory field. In accordance with the different sizes of the excitatory fields the maximum activa-

the strength of the inhibitory surrounds are different for each of three classes of ganglion cells (b). For the square object and the vertical bar (which the ganglion cell "confuses"), maximum activity is elicited when the size of the object matches the excitatory-field size of each type of ganglion cell (c). Horizontal length does not much affect these cells' response. Vertical extension of a horizontal bar has less effect on these cells than on behavior (*opposite page*).



tion of each cell type is therefore elicited by objects of different sizes [see illustration above]. Extending a small square horizontally (making it a "worm") does not bring about any change in nerve-cell activation; this is in sharp contrast to the previously noted effect of extension on the behavioral response. The dependence of neuronal activation on the size of the stimulus is instead primarily a function of extension perpendicular to the direction of movement. Indeed, the discharge frequency is almost exactly the same in response to a narrow vertical bar as it is to a square with the same height as the bar. A retinal ganglion cell "confuses" the two stimuli—but the toad does not: the square excites behavioral activity and the bar inhibits it. When the object size is held constant, however, the dependence of the discharge rate on con-

trast between stimulus and background and on angular velocity is the same as it is in the behavioral experiments.

In summary, it is clear that the first important operations on the visual input from a prey stimulus or a threatening one are performed by the toad retina. For any particular prey or enemy stimulus the behavioral response to velocity and background contrast seems to depend on information processing in the retina. The size-dependent excitatory and inhibitory processes, however, which were noted in the behavioral experiments and which play an essential role in pattern discrimination, cannot be traced to the influence of the excitatory and inhibitory fields of retinal ganglion cells. There are no retinal "worm-detectors" as distinct from "enemy-detectors." The differential analysis, and thus the behaviorally relevant interpretation of the stimulus, must be achieved in nerve-cell populations beyond the retinal level.

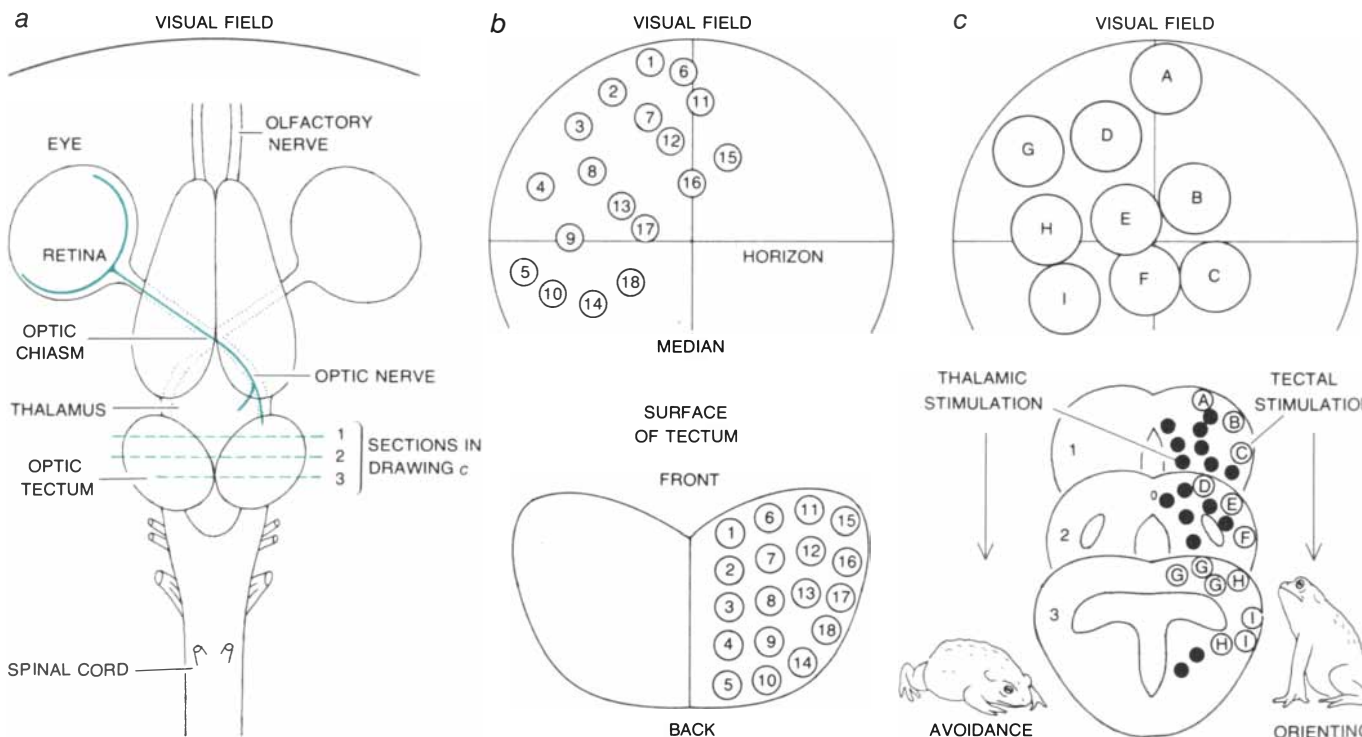
Since different characteristics are coded by any one type of ganglion cell the question becomes: Where is that coding interpreted? What tells the central nervous system whether an increased rate of ganglion-cell firing stems, for example, from an increase in stimulus-

background contrast or from larger size? The differentiation can be made only if separate groups of cells receive different inputs from different optic-nerve fibers. In fact they do. The fibers of the optic nerve pass from each eye through the optic chiasm to the opposite side of the brain, ending in various parts of the forebrain and midbrain. Two of these destinations are of particular interest in our work. One, to which most optic-nerve fibers project, is in the surface layers of the optic tectum in the midbrain. The other is in the thalamus and the pretectal region of the diencephalon.

The optic tectum constitutes a localization system. In the tectum there is an exact topographical mapping of the retina and hence of the entire visual field. Movement of an object in a particular part of the visual field excites a corresponding region of the tectum, where the appropriate optic-nerve fibers terminate [see illustration on these two pages]. Recording from individual tectal neurons, or nerve cells, tells one how the individual retinal ganglion cells that excite them are reacting. In certain layers, for example, there are tectal neurons with excitatory receptive fields of about 10 to

27 degrees that are activated exclusively by moving objects. These neurons probably represent a localization system. This supposition is reinforced by experiments in which we stimulate the tectum of freely moving toads with trains of impulses delivered by means of an implanted electrode. Stimulation of a given region of the tectum always causes toads to turn toward a particular part of the visual field. Presumably the neurons we are thus activating have a direct connection with the animal's motor system, since (in contrast to the natural orienting movements made in response to a prey object) the electrically induced orienting is not disrupted by simultaneous presentation of a threatening object.

If the recording electrode is driven deeper into the tectum, it encounters neurons with larger receptive fields. Some of these cover the entire visual field on the opposite side, some the entire lower part of the field and some the entire field directly in front of the animal. Interestingly enough, all three types include the fixation point: the point of maximum visual acuity near the center of the visual field. The degree of activation of these three types of neurons could provide the toad with information about the



**NEUROPHYSIOLOGICAL EXPERIMENTS** yield data on the functions of different parts of the toad's visual system. Fibers of the retinal ganglion cells project primarily to the optic tectum and to the thalamus (a). The visual field of each eye is mapped (b), on a one-to-one basis (numbers), on the dorsal surface of the opposite side of the tectum. By the same token experimental electrical stim-

ulation (c) of various parts of the tectum (letters) causes the toad to turn to corresponding parts of the visual field. On the other hand stimulation (black disks) of the thalamus, which partially underlies the tectum, causes the opposite action: avoidance, or turning away. As a recording electrode penetrates below the surface of the tectum it encounters successive populations of cells with differ-



location of a large object, since whenever the three types are excited simultaneously the object must be at the fixation point.

In natural situations the behavior of toads can be influenced by sensory modalities other than vision. If, for example, a beetle crosses the field of vision, the toad's orienting reaction can be either accelerated or retarded by simultaneous vibratory and tactile stimuli. Such results can be obtained in experiments if prey models are presented together with acoustic or tactile stimuli. The area for producing such changes in behavioral activity seems to be in the subtectal region, where multisensory integration is achieved. In the area below the third ventricle of the midbrain there are large-field neurons with fields similar to those of the large-field tectal cells. These subtectal neurons receive additional inputs from neurons excited by tactile and vibratory stimuli. The "mechanoreceptive" field of one of these bimodal neurons is always localized on the same side as the visual receptive field. The additional inputs from nonvisual neurons could serve to lower the threshold of a part of the visual field in which a visual stimulus is anticipated and thus

in effect to raise the level of visual alertness.

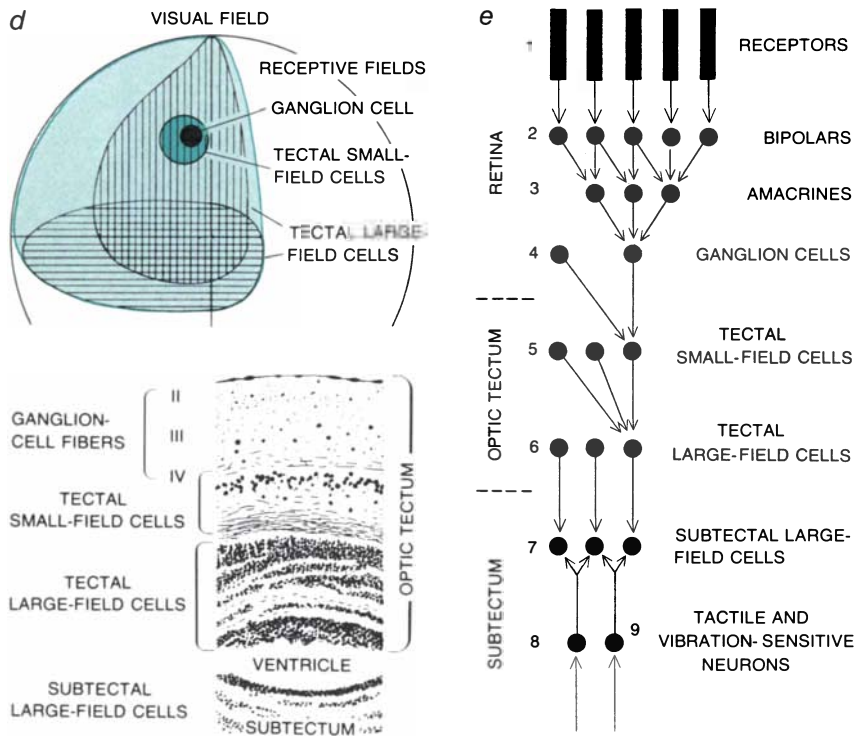
The optic tectum also comprises a neuronal system that processes behaviorally relevant aspects of moving stimuli [see illustrations on next page]. The cells have excitatory receptive fields about 27 degrees in diameter. Those designated Type I tectal neurons are activated mainly if the stimulus surface of an object moved through the receptive field is extended in the direction of movement; extension perpendicular to direction of movement does not have the same effect. Other cells, the Type II tectal neurons, differ from Type I neurons in that their discharge rate actually diminishes with surface extension perpendicular to direction of movement. The response of these neurons constitutes the key stimulus "prey." That is, they can presumably be considered the trigger system for the prey-catching response.

The thalamic-pretectal region, the second major destination of fibers from the retina, apparently provides what can be called a "caution" system. I have recently identified four main types of visually sensitive neurons in the toad's thalamus by means of single-cell recordings.

They are activated respectively by four distinct stimulus situations: (1) movement of enemy objects extended perpendicularly to the direction of motion, excitatory receptive field of about 46 degrees; (2) movement of an object toward the toad, field about 90 degrees; (3) large stationary objects, field about 45 degrees; (4) stimulation of the balance sensors in the toad's ear by tilting. In general these thalamic neurons are activated principally in situations that tend to call for evasive movements—turning away from an enemy, sidestepping or compensating for tilting of the body. Brain-stimulation experiments support our feeling that the thalamic-pretectal region is one in which reactions can be assembled that lead to protective movements. Electrical stimulation of various sites in the region elicits the following reactions: closing of the eyelids, ducking, turning away, panicky springing away or tilting of the body.

We constructed a working hypothesis involving connections between the optic tectum and the thalamic-pretectal region: Electrical triggers in the tectum mainly elicit orienting, and triggers in the thalamic-pretectal region elicit avoidance. In a natural situation trigger impulses in particular layers of the tectum are evoked by small wormlike prey. Large objects extended perpendicularly to the direction of movement stimulate particular neurons in the thalamic-pretectal region, both directly through retinal inputs and indirectly by way of the optic tectum. These thalamic-pretectal neurons in turn inhibit the tectum and can also activate avoidance behavior [see illustration on page 41].

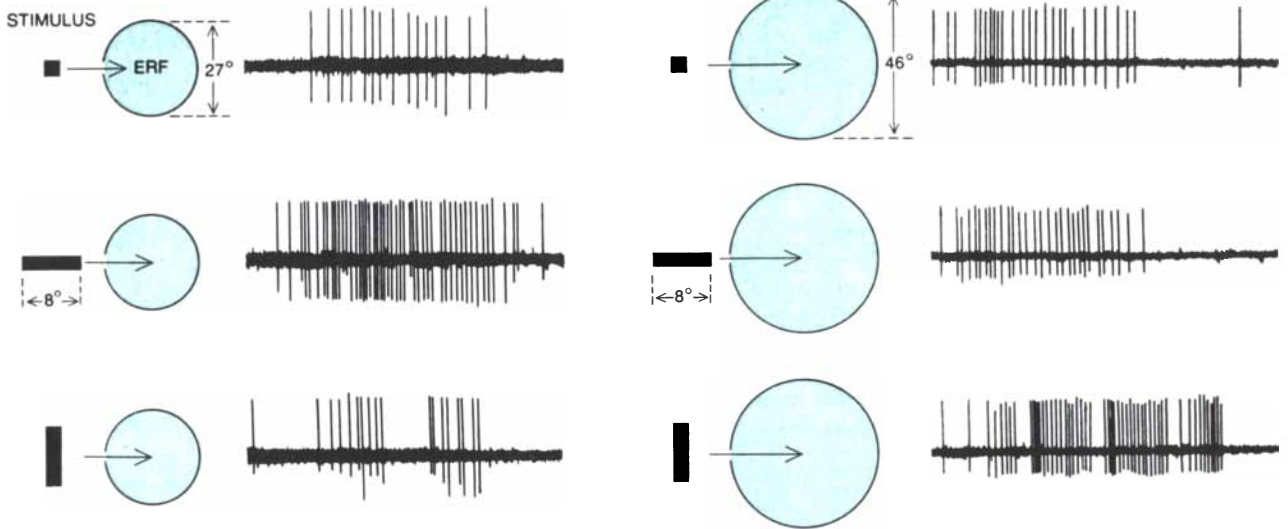
The existence of the postulated connections between the structures in the midbrain and the diencephalon has been demonstrated physiologically in two ways. One way is by direct electrical stimulation. Thalamic neurons that are sensitive to movement can also be activated by stimulation of points in the optic tectum. When the stimulating and recording electrodes are interchanged, the response of Type II neurons in the tectum to moving objects can be inhibited by the stimulation of cells in the thalamus. The other way is by surgical operation: if the optic tectum is removed, orienting movements are lost—and so are avoidance reactions, which is evidence for pathways from the tectum to the thalamus. If the thalamic-pretectal region is removed without damage to the tectum, then avoidance behavior is lost—and the orienting response is dramatically freed from inhibition even in the presence of enemy objects; this may be



ent receptive fields (d). There are small-field cells with fields a little larger than those of ganglion cells and, lower down, three kinds of large-field cells, each with different coverage (color, horizontal hatching and vertical hatching). A drawing based on a stained brain section indicates the layers at which each of these is found. The final drawing (e) relates the various cell populations and shows another layer of large-field cells that receive inputs from visual cells above them and also from cells that respond to tactile or vibratory stimuli.

TYPE I TECTAL NEURON

THALAMIC NEURON



FEATURE DETECTION beyond the retinal level is accomplished by cells in the tectum and the thalamus. Recordings from individual cells indicate that tectal Type I neurons (*left*) are most activated

if the object moving through the field is extended in the direction of movement. The cells in the thalamic area (*right*) respond most to an object extended perpendicularly to direction of movement.

evidence for the existence of inhibitory pathways from the thalamus to the optic tectum. In toads lacking the thalamic-pretectal region every moving stimulus elicits the orienting movements; the cautionary thalamic-pretectal system, which ordinarily allows orientation toward the stimulus only in behaviorally appropriate situations, is missing. If one lateral half of the thalamic-pretectal region is re-

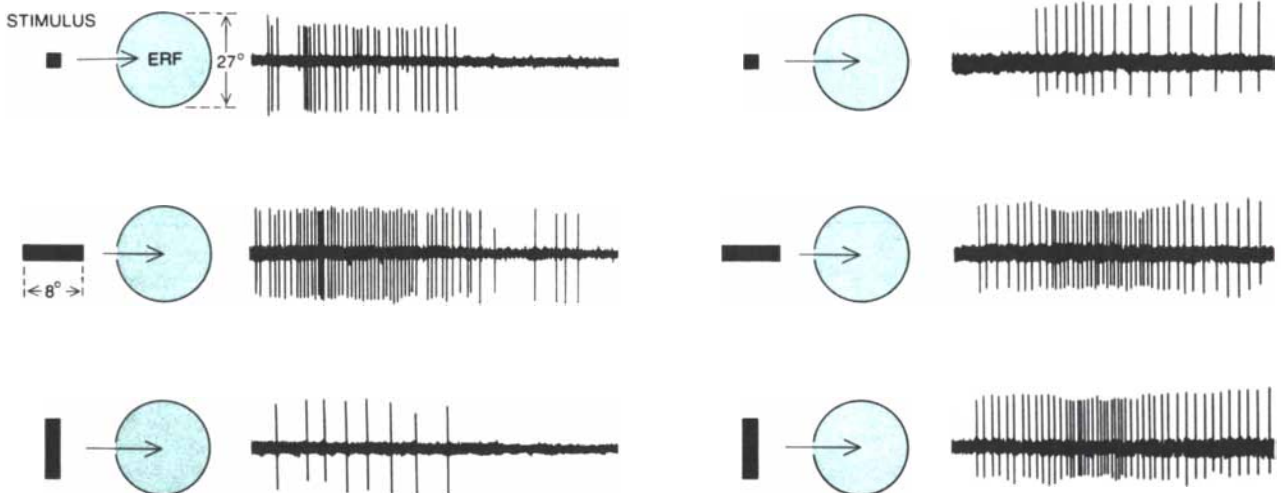
moved, the disinhibition extends to the entire visual field on the opposite side; small lesions in the thalamic-pretectal region affect only local small parts of the visual field. Quantitative experiments with toads lacking the thalamic-pretectal region make it clear that these animals cannot discriminate between stimuli that are behaviorally relevant and those that are irrelevant. The response of the Type

II tectal cells to moving stimuli shows a similar "disinhibition" effect after thalamic-pretectal removal [see illustrations on page 36 and below].

The findings I have described so far suggest the following sequence of events: On the basis of retinal ganglion-cell input, the optic tectum tells the toad where in the visual field a stimulus is

TYPE II TECTAL NEURON (NORMAL TOAD)

TYPE II TECTAL NEURON (TOAD WITHOUT THALAMUS)



TRIGGER UNITS for the entire prey-catching response seem to be the Type II tectal neurons. In the normal toad (*left*) the cells are most activated by wormlike objects (*horizontal bar*). They are less activated (and the decrease is greater than in the case of Type I

tectal neurons) by stimuli that in behavioral experiments are irrelevant for prey-catching (*vertical bar*). After removal of the thalamus, however (*right*), their response to those irrelevant stimuli is greatly increased, suggesting that the thalamic signal is inhibitory.

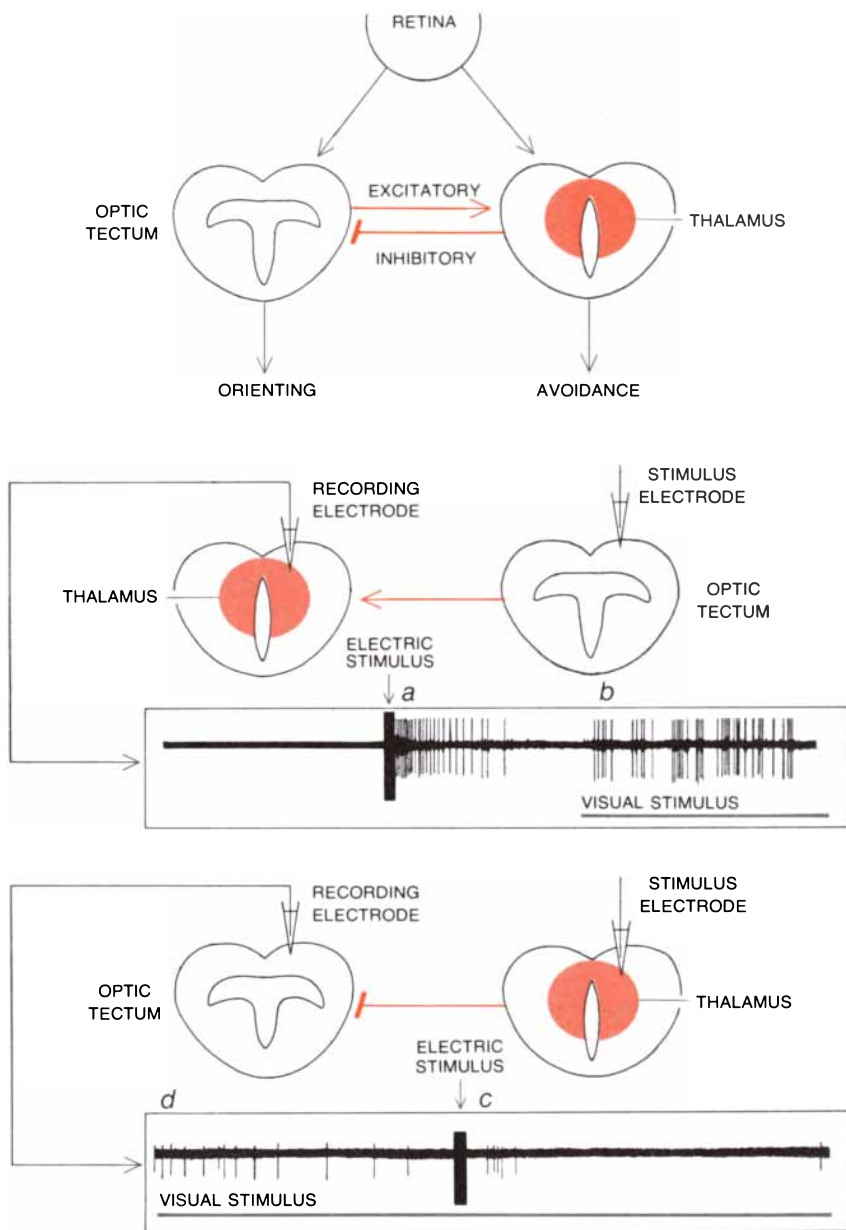
situated, how large it is, how strongly it contrasts with the background and how fast it is moving. The connections from the tectum to structures in the thalamic-pretectal region enable the toad to discern the significance to its behavior of the visual signals. The basic filtering process for the prey-enemy differentiation can be conceived of as passage through a series of "window discriminators" [see illustration on next page], each stage of which analyzes a particular aspect of the object in question. Each retinal ganglion cell acts as a vertical window that codes extension perpendicular to the direction of movement. The retinal analysis is repeated and amplified in the thalamic-pretectal region, where a neuron pool acts as another vertical window, this one with a certain minimum-response threshold. Extension in a horizontal direction is coded primarily by Type I tectal cells, which constitute a horizontal window. Type II tectal cells perform a summation, with signals arriving from the thalamic-pretectal region having an inhibitory effect and those from the Type I cells having an excitatory effect. The resultant signal acts as the trigger stimulus for the orienting movement. The triggering of avoidance behavior is probably achieved through the activation of still another pool of thalamic-pretectal neurons, the activation being proportional to an additive function of inputs from two of the window-discriminator pools.

One of the remarkable aspects of this system is a degree of plasticity, or changeability. During the summer months white prey objects moved against black backgrounds elicit orienting behavior much more effectively than do black objects against white. In fall and winter the situation is reversed, and at the same time the overall prey-catching activity of the toads decreases. Recently our recording electrodes revealed that the activation of single Class II ganglion cells in the retina exhibits this seasonal shift in white-black preference. In winter neurons with receptive fields in the lower part of the visual field are more strongly activated by black objects than by white ones; in the upper field the situation is reversed. In summer, however, the neurons whose receptive field is in the upper half of the visual field are activated primarily by black stimuli, whereas neurons receptive to the lower half of the visual field become more strongly activated by white stimuli and remain so until in the fall black stimuli again become dominant.

What is the biological significance of

these observations? One can speculate that for toads, which are active at twilight, biologically important prey stimuli that appear in the lower half of the visual field are paler than their background; those in the upper part of the field, however, are for the most part relatively dark, or at least just as often dark as pale. Each of these contrast relations could be reflected in the sensitivity characteristics of the Class II retinal ganglion

cells. With the approach of winter and the period of hibernation, toads stop catching prey. What makes them stop? One mechanism may be an inversion of ganglion-cell response characteristics, brought about by signals from the brain to the retina, such that the stimulus-background contrast relation is out of phase with the real world, making prey objects less visible. For the toad, in other words, identical objects appear to be dif-



**CONNECTIONS** between the optic tectum and the thalamus were indicated by preceding experiments: signals from the retina excite both tectum and thalamus; subsequent impulses from Type I tectal neurons further excite cells in the thalamus, whereas signals from the thalamus inhibit activity in Type II tectal neurons. Two different kinds of motor activity are thereupon initiated by the two structures (top). Confirmatory evidence was obtained by electrical stimulation. Stimulation of the tectum (middle) elicits impulses (a) from cells in the thalamus that ordinarily respond to visual stimuli (b). Stimulation of the thalamus (bottom) inhibits (c) impulses normally elicited (d) in Type II neurons by moving objects.



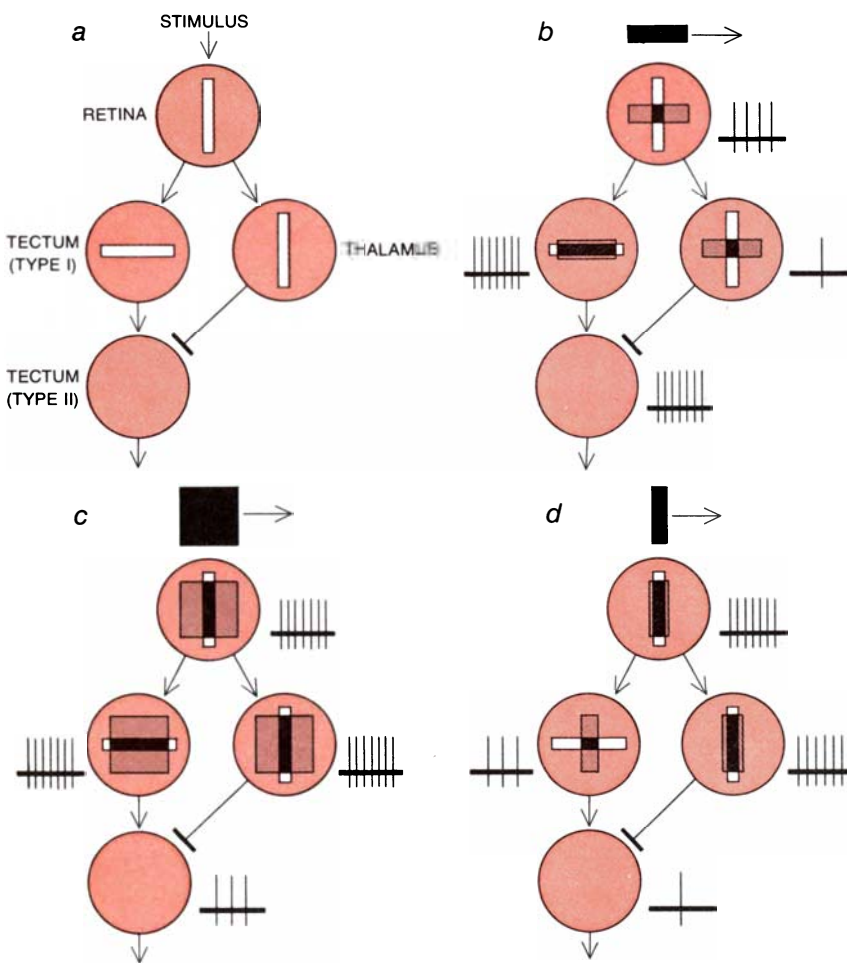
ferent when they are seen in winter than when they are seen in summer, a reminder that an organism's picture of the environment is a product of its brain.

In contrast to the plasticity of the systems for the filtering and storage of information and for pattern recognition, brain mechanisms involved in instinctive actions are quite inflexible and do not adapt easily to changes in the stimulus situation. For each instinctive action in the behavioral repertory there is a pre-programmed "printed" neuronal circuit that coordinates the appropriate motor act—even if it becomes inappropriate! If such a circuit is triggered (either naturally or by electrode stimulation), the innate reaction proceeds automatically. Pre-catching behavior is a good example. On the basis of brain-stimulation experi-

ments we believe the sequence of events controlling a natural orientation response is about as follows: A pattern is formed by a natural stimulus on a portion of the retina that is outside the fixation region; the retinal locus has a corresponding projection locus in the optic tectum. If the filtering process described above has identified the object as prey, then the appropriate neuronal system is activated. A value corresponding to the distance between the prey's locus on the retina and the fixation point is transferred to the toad's motor system. The result is orientation: a turning movement such that the retinal representation of the prey is brought to the fixation point. That triggers a locus in the optic tectum that corresponds to the fixation point. As soon as this triggering reaches a threshold value

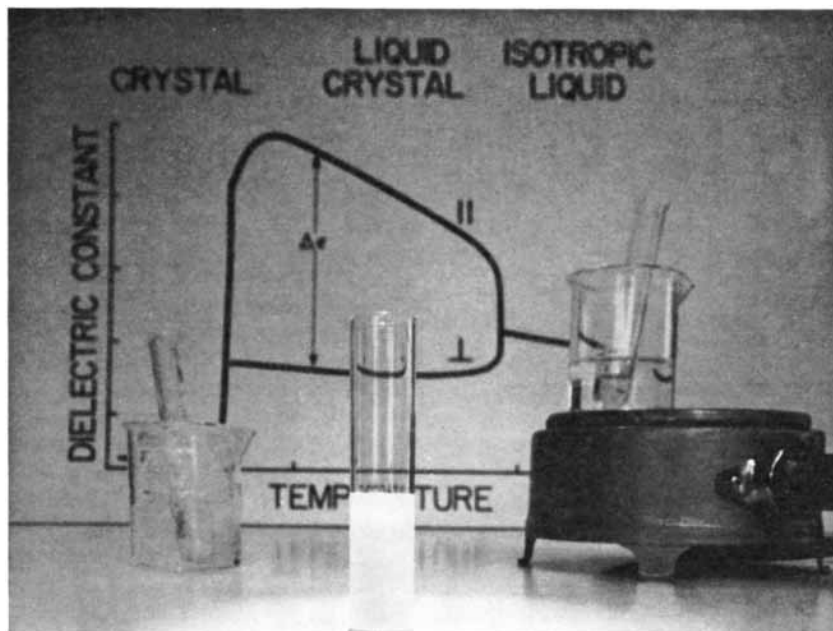
the rest of the prey-catching sequence is activated, quite independently of the result, or even of the short-term benefit to the animal, of such activation. For example, if an experimental prey object is removed at the instant when it is fixated by the toad, the entire normal prey-catching routine nevertheless proceeds. The toad snaps, gulps and wipes its mouth in spite of the "situational vacuum." The sequence is similar in its inevitability to what happens when the triggering region of the tectum is stimulated with an electrode.

As for avoidance behavior, the results of thalamic stimulation indicate that it is controlled by a single master program. The response consists in a firm planting of the extremities on one side of the toad's body and a gathering together of the limbs on the opposite side. With the toad in this stationary, poised position the additional behavior patterns for correcting tilting of the body or making the various evasive movements can be readily incorporated.



**IDENTIFICATION OF AN OBJECT AS PREY OR ENEMY** is symbolized as a series of operations by "window discriminators" (a). A ganglion cell in the retina codes vertical extension (perpendicular to direction of movement), in effect responding to as much of a visual object as appears in a vertical window; extension beyond the window has an inhibitory effect. Cells in the thalamus do the same thing. In the tectum Type I cells code horizontal extension (in the direction of movement). Type II tectal cells sum the excitatory signal from Type I cells and the inhibitory signal from the thalamus, and the resultant signal triggers an orienting movement. At each stage the cell discharge depends on the relation between the object and the window that senses its extension either in or perpendicular to the direction of movement (b, c, d). (The cell-discharge patterns shown here are schematic.)

The evidence I have reviewed shows that in a lower vertebrate the neuronal processes for localization and identification of a visual signal and for releasing the associated instinctive motor responses are separated topographically but are intimately connected with one another. In the course of evolution the centers for two of these processes, visual localization and instinctive action, have apparently remained in about their original positions. They occupy the same areas of the brain, the tectum and the thalamus, in monkeys and cats as they do in toads. The organization of these parts of the brain, to which both neurophysiological and ethological methods have provided investigative access, shows remarkable constancy in all classes of vertebrates. That is not the case, however, for stimulus identification. In toads this process takes place primarily in the thalamic-pretectal region and also in the retina and the tectum. Mammals, however, underwent further evolution, corresponding to the importance of pattern recognition in the evolution of their behavior. A new substrate developed for two associated but highly specialized processes, filtering and storage of information: the visual cortex. From the investigations of Gerald E. Schneider at M.I.T. we learn that in this case ontogeny reflects phylogeny. In newborn hamsters subcortical pathways between the tectum and the thalamus are implicated in pattern discrimination. In adult animals, on the other hand, pattern discrimination takes place in the cortex.



## Glamorous, mysterious liquid crystals.

### We make them.

**Behind the mystery and glamour:** Those who could reasonably be expected to phone Mr. Grau are probably interested in making display devices ranging from mass-marketed consumer goods to some of the more ambitious reaches of the engineering imagination.

Liquid-crystal technology has blazed up after smoldering quietly for most of the time since 1888. Organic chemists get to collaborate with electronic engineers through the medium of the marketplace, if not personally. For now, Kodak has set up its booth on the chemical side of the street.

The present generation of electronic engineers catch on fast to subjects they didn't necessarily concentrate on in school. In liquid-crystal work, one deals with the different forms and degrees of orderedness among molecules, ranging between the randomness of an ordinary isotropic liquid and the periodic architecture when it freezes to a crystal. Only certain compounds assume this mesomorphic state. Molecules of such compounds have a generally elongated shape.

The most highly ordered kind of liquid crystal, called smectic, where the molecules tier up in layers and the layers can only slide against each other, can be seen

when water sits in contact with a bar of soap. In a nematic liquid crystal there are no tiers, but the molecules stay parallel. Possibilities exist for controlling their alignment. And this alignment controls what they do to light passing through. And that's what the action is mostly about in industry circles.

*Field effect*, one approach used to create a visible pattern in a thin layer of nematic material between patterned, transparent electrodes, amounts to electrically tuned birefringence. (We hope you didn't cut the lecture on birefringence in Physics 1.) Contrast between "on" and "off" is attained through various arrangements of light polarizers and quarter-wave retardation plates. Where and when the field is off, the molecules must line up parallel to each other and to the cell walls. This is called "homogeneous" alignment. Surface treatment to make it happen is protected by patents or trade secrecy.

*Dynamic scattering* is the other approach. Here, in the "off" state, the alignment can be either homogeneous or perpendicular to cell walls. The latter is "homeotropic" in the lingo of the art. Either way, light passes straight through, and the layer looks clear. Where field is applied, then regardless of previous orien-

**News:** For field-effect devices, EASTMAN 14080 is now ready to ship. At 18  $\mu\text{m}$  spacing, a typical lot shows a threshold of only 1.5 volts rms for 60-Hz sine wave (or 2 volts dc), an *operating* temperature range of 0 to 75°C, and a dielectric anisotropy of +11.9 at 25°C. At 5 V rms, turn-on time at room temperature is about 100 ms; turn-off time, about 350 ms; contrast ratio, about 50:1.

For dynamic scattering devices, EASTMAN 14099 is equally ready, with the same 0 to 75°C operating temperature range. It aligns itself homeotropically on clean electrodes without additional magic—an important advantage. Typical threshold is 4 volts rms, 5 volts dc.

More details from George Grau at Organic Chemical Sales, Kodak, Rochester, N.Y. 14650 (716-325-2000, ext. 57288).

tation, all the molecules strive for parallelism to the wall. But ions that have been incorporated in the mixture migrate, colliding with them to knock them every which way. The resulting optical inhomogeneity scatters light. These turbid areas can be made to look either darker or lighter than the clear areas, depending on directions of illumination and viewing. Appearance of the pattern is more sensitive to angle of view than with field effect. Power drain is more, because of the turbulence to be maintained. But you don't have to find (or license from somebody) a way to align the molecules. You just use EASTMAN 14099.

*Say, if you've read this far you are probably interested enough to ask Dept. 412-L, Kodak, Rochester, N.Y. 14650 for Eastman Organic Chemical Bulletin, Vol. 45, No. 2 (1973), where four scientists of the Kodak Research Laboratories, who write more like scientists than engineers, will take you farther into this than you'd want to go for just recreation. It has a 76-item bibliography. For our 3,281-item Liquid Crystal Bibliography (Kodak Publication JJ-193) on microfiche, make that Dept. 454 and send \$25\* (plus applicable state and local taxes).*

*\*Price subject to change without notice.*

