A NEURAL MODEL OF THE INTERACTION OF TECTAL COLUMNS IN PREY-CATCHING BEHAVIOR

Michael A. Arbib
and
Rolando Lara

COINS Technical Report 81-3

(February 1981)

A NEURAL MODEL OF THE INTERACTION OF TECTAL COLUMNS IN PREY-CATCHING BEHAVIOR[1]

Michael A. Arbib and Rolando Lara[2]
Computer and Information Science Department
University of Massachusetts
Amherst, MA 01003, USA

ABSTRACT

Building on an earlier model of a tectal column as the unit of processing in the amphibian tectum, we conduct a computer analysis of the interaction of a linear array of such columns. The model suggests that the inhibitory and excitatory activity in the tectum may have three functions: 1) spatio-temporal facilitation of column activity to a moving stimulus; 2) preference for the head of the stimulus, probably to avoid possible defensive reactions of the prey; and 3) modulating the state of excitation of the column once it has produced a response. The model also shows that the spatio-temporal effects of excitation and inhibition increases the acuity of the animal to the direction of the prey, through processes similar to lateral inhibition.

---

[1] The research reported in this paper was supported in part by NIH grant NS14971-02. Our thanks to Peter Ewert and David Ingle for valuable discussions of the experimental data; and to Andrew Cromarty and Donald House for their help with the computer implementation.

[2] Present address: Universidad Nacional Autonoma de Mexico, Centro de Investigaciones en Fisiologia Celular, A.P. 70-600, Mexico 20, D.F., Mexico.

1. Introduction

Prey orienting behavior in amphibia depends on the form, speed, size, configuration, and contrast of the prey stimulus (Ewert, 1970, 1976; Ingle, 1971, 1976a and b; Ingle and Mckinley, 1978; Grusser and Grusser-Cornehls, 1976). Ewert (1970, 1976) found that elongation of a 2 degree high black rectangle to a length of 8 degrees in the direction of motion greatly facilitated the toad's rate of pursuit; if the elongation was perpendicular to the direction of motion, prey orienting behavior was greatly inhibited. Ewert also found that prey orienting activity is proportional both to the angular velocity of the stimulus and to the contrast of the object with respect to the environment. Using a double stimulus aligned in the direction of motion, he found that this configuration is a somewhat weaker stimulus than a single object; if the two stimuli are aligned perpendicular to the direction of motion, the orienting response is greatly inhibited, but when the distance between objects is increased this inhibitory effect disappears. Ingle (1971, 1976a and b; Ingle and McKinley, 1978) studied further the effects of a double stimulus aligned in the direction of motion in prey orienting behavior. He found that the animal has the tendency to snap at the leading (head) object when the two stimuli are moving toward the animal, while they snap between the stimuli if they move away from the animal. Using stimuli of 2 degrees square and an interstimulus distance of 4 degrees, he observed a facilitatory effect in prey catching activity, suggesting that the animal considers the two objects as a single prey, similarly to facilitation of prey orienting behavior when the stimulus is elongated along the direction of motion. If the interstimulus distance is increased to 8 up to 16 degrees, the animal starts to react independently to each stimulus. In this case, the animal will snap independently at the leading (head) or the second (tail) object. When the size of the stimulus is enlarged to 15 degrees, an inhibitory effect is observed in the orienting response, similarly to the inhibition in prey pursuit studied by Ewert (1970).

These authors have tried to correlate the observed behavior with the function of the brain regions related to visuomotor coordination of prey-orienting behavior. Ewert (1976) and Grusser and Grusser-Cornehls (1976) found that the rate of response of retinal ganglion cells is proportional to the speed and contrast of the stimulus, in close correlation with the observed behavioral results. These neurons, however, were not sensitive to the elongation of the stimulus along the direction of motion; while they were sensitive in a certain range (depending on their respective receptive fields) to elongation perpendicular to the axis of movement. Based on this, Ewert concluded that retinal processing of information could not explain the effects of size, form, and configuration of several stimuli in prey orienting behavior; but that a close correlation exists between the sensitivity of retinal ganglion cells to speed and contrast and the animal's conduct.

Ewert (1976) found that some tectal cells increase their rate of response when the stimulus was elongated in the direction of motion; while other neurons were sensitive both to horizontal and vertical elongation. He found that the sensitivity of the tectal cells to elongation perpendicular to the axis of motion was mediated by the pre-tectum, because pretectum ablation impairs this sensitivity; moreover, he found (Ewert, 1971) a pretectal cell whose sensitivity to vertical elongation is closely related to the observed behavior. This evidence, added to the fact that electrical stimulation of the tectum elicits specifically-directed orienting behavior, and that tectum ablation impairs prey catching activity, indicates that the tectum integrates the information coming from the retina and the pretectum to give the proper orienting response. This region itself, however, seems to be mostly sensitive to the elongation of the object along the direction of motion. For this reason, the processing of information of this region may also account for the configuration effects on prey orienting behavior, such as: 1) the animal's preference to snap at the head of the prey (leading object); 2) facilitation of prey orienting activity when the interstimulus distance is small; and 3) inhibition of prey pursuit when the size of the stimulus is large. Although there is no direct physiological evidence, Ingle and McKinley (1978) suggest that these effects could be the result of facilitatory and inhibitory interactions within the tectum, without excluding possible intertectal effects. They postulate that the inhibitory effect is the result of lateral inhibition among tectal cells and the facilitatory action is the result of overlapping receptive fields.

In the present paper, we propose a neural model of the tectum that studies the possible role that this region may play in the sensitivity of the animal to the elongation of the stimulus along the axis of motion, the sensitivity to double prey stimuli aligned in a single axis, and the sensitivity to the speed of the object. The structure of the model is based on the anatomical studies of Szekely and Lazar (1976) and its function is based on the behavioral and physiological studies of facilitation of prey catching behavior when two stimuli are serially presented (Ingle, 1971, 1973a and b, 1976a). The basic unit of the tectum is the tectal column, whose model has been described in detail elsewhere (Lara, Arbib and Cromarty, to appear). In the present model we do not consider the role that the retinal ganglion cells play in the tectal processing of information; we define the optic input as an external excitation to the different tectal regions, without considering the actual processing within the retina. We defer the study of the interaction between tectum and pretectum to another paper (Lara and Arbib, to appear).

2. <u>The Model</u>

2.1 One-dimensional structure of the tectum.

The architecture and the type of cells considered in the one dimensional model of the tectum are based on the minimal model of a tectal column (summarized in Appendix 2 of Lara, Arbib and

Cromarty, to appear). We here simulate eight columns (see Fig 1), where each functional unit consists of 1 glomerulus (GL), 1 large pear shaped cells (LP), 1 stellate neuron (SN), 1 small pear shaped cell (SP), and one pyramidal neuron (PY). Each unit column is affected by both its right and left neighbors through the GL and the LP cells. The PY receives as input the activity from 2 LP and 1 SP neurons. Briefly, the interaction among cells in the tectum is as follows: the glomerulus comprises optic afferents, the dendrites and recurrent axons of both large and small pear-shaped cells (in this model we have not considered the diencephalic input). Each large pear cell (LP) is activated by the optic fibres, type 1 and 2 (types 3 and 4 are not considered in this model), both through the glomerulus and through interglomerular dendrites; it activates neighboring stellate neurons (SN), the one of its own and neighboring columns, and sends recurrent axons to both its glomerulus and neighboring ones, spreading in this way the facilitation among columns, and finally this neuron excites the pyramidal cell (PY) of its column. The small pear shaped cell (SP) is excited both through the glomerulus and interglomerular dendrites by the optic fibres, it sends recurrent axons to neighboring glomeruli and excites both neighboring LP cells and the PY cell of its column, recruiting in this way the activity of all cells within the column. The stellate neuron (SN) is activated by the neighboring LP cells, and it inhibits SP and LP cells, of its column as well as neighboring columns, spreading in this way the inhibitory effect. Finally, the pyramidal cell, which is the efferent neuron of the column, is excited by the optic fibres, two

LP neurons and one SP neuron, integrating the general state of excitation of its column.

2.2 Spatio-temporal hypothesis of the role of the tectum in motor prey catching activity.

With the one dimensional model of the tectum we want to simulate behavior related to prey-orienting and prey-catching activity; thus a hypothesis of the spatio-temporal relation of the proposed structure with the actual behavior is needed. The basis of this hypothesis relies on preliminary physiological and behavioral evidence.

We propose that each glomerulus has a receptive field of 15 degrees, with 5 'focal' degrees, and with a 10 degree overlap with each of its neighbors. This assumption is based on the fact that retinotectal axons project to a receptive field no larger than 15 degrees (Ingle, 1973b). Each SP cell receive input from two neighboring glomeruli covering a receptive field of 20 degrees (see Fig 1). This hypothesis is based on physiological evidence that superficial tectal cells have a receptive field ranging between 15 and 20 degrees (Ingle, 1973a, 1975; Lettvin et al., 1959). Each LP cell has a direct receptive field of 15 degrees, but it receives the excitatory activity of two SP cells in an indirect way, expanding its receptive field to approximately 25 degrees, which is also the observed receptive field of some cells in layer 6 in the tectum. The PY receives excitation from one SP cell and 2 LP neurons expanding its receptive field also within a range from 20 to 40 degrees. We postulate, however, that the strongest effect produced by a given stimulus lies within 5 degrees around (2.5 degrees either side of) its spatial location. This assumption allows us to propose that the tectum is sending information to subsequent regions for the location and importance of the stimulus, as we discuss below.

Based on the above assumptions, the model of 8 tectal columns (Fig 1) covers focally a range of approximately 40 degrees of the visual field of the animal. As we will see later, this range is also in accordance with the phenomena we have simulated.

2.2.1 Hypothesis of the possible role of the tectum in prey-orienting and prey-catching activity:

It is well known (Ewert, 1976) that electrical stimulation of the optic tectum in the free moving toad elicits natural orienting or snapping movements toward a part of the visual field represented by the visual retinotopic projection to the same region of the tectum. Moreover, unilateral tectal ablation in frogs impairs visual orienting or snapping responses via the contralateral eye within one year postoperatively (Ingle, 1971). This evidence indicates that the tectum plays a determinant role in visual prey-orienting and prey-catching behavior. On the other hand, it has been shown by Comer and Grobstein (1978) that atectal frogs snap and orient when a tactile stimulus is presented. The torus seems implicated, and they postulate that a third region receives input from both tectum (visual) and torus (tactile) to control the motor response. A good candidate may be the reticular formation.

The optic tectum sends efferents to the cervical spinal cord but only a few degenerated fibers can be followed in the anterior funiculus to the lumbosacral segments, showing that this tecto-spinal projection is limited. Optic tectum also send fibres to the reticular formation, the tegmentum and the thalamus. There is also evidence (Szekely and Czeh, 1976) that the neurons in the spinal cord receive afferents from the vestibulo-spinal tract and terminate in the vicinity of the medioventral motoneuron column; the effects on motor behavior from these afferents is still poorly understood.

Based on the above discussion, we postulate that the tectum regulates visually-directed orienting and snapping behavior in two ways: first locating the direction of the spatial object; and second, regulating the speed and number of the orienting repsonses. We postulate that the tectum codes this information through the state of activity of the efferent cells of one or several columns. Spatial location is given by the column that produces the first and longest response; the activity of other columns increases the state of excitation of the region controlling the motor response, thus reducing the threshold for behavior. We still lack adequate analysis (both theoretical and experimental) of the motor expression of general patterns of columnar activation. An alternative explanation, that we will study with our model in our next paper (Lara and Arbib, to appear) is that the activity of a column suppresses the response of other units via pretectal interactions. When two columns are simultaneously active with the same frequency, we propose that the brain region controlling the orienting response "waits" until one of them is suppressed. A second alternative is that one of them is chosen randomly (see discussion in the next paper for these alternatives).

In the next section we will study the response of the model to different stimuli; first we consider the animal to be immobilized; but later we explore the possible effects of recently activated columns when the orienting repsonse occurs.

2.3 General Behavior of the Model.

When a moving stimulus is sequentially presented in several glomeruli of the tectum, a wave of spatio-temporal facilitatory-inhibitory effects is observed. The facilitation is mainly produced by the recurrent activity of large and small pear-shaped cells to their own and neighboring glomeruli in combination with the glomerular receptive field; while the inhibitory effect is the result of the stellate neuron inhibition, as a consequence of LP excitation, in both its own and neighboring columns. In this way a combined effect of excitation and inhibition is spread within the column and toward neighboring columns. In more detail, the way the spatio-temporal excitatory-inhibitory effect is produced is as follows: If the state of excitation of a given column is strong enough for the SP cell to fire, a recruitment of the cells within the column is produced, facilitating the response of the PY, which may represent a motor response. This increased state of activity of the column is followed by a strong inhibitory effect produced by the SN, silencing its own as well as neighboring columns. In these conditions, columns neighboring the column previously excited do not respond as strongly as the previous column to the passing stimulus, but as a consequence of this the inhibitory effect on its neighbor will be less intense. For this reason, when the moving stimulus passes through a column that is weakly inhibited by its neighbor but facilitated by the LP cell recurrent axons as well as through the effect of its receptive field, the cells in the column are greatly activated. In this way, a spatial alternation of facilitatory and inhibitory columns is created. From a temporal point of view, when the inhibition of the stellate neuron is no longer present within the column, the long lasting depolarization of the glomerulus produces a rebounding excitation of the column activity, which facilitates subsequent firing if the stimulus is presented again. This facilitatory effect has been described in detail elsewhere (Lara, Arbib and Cromarty, to appear).

3. Computer Simulation

3.1 General Considerations.

The model was simulated on a digital computer CDC Cyber 175 and the graphics were obtained from a Grinnell Systems color graphic display system (GMR-27) attached to a DEC VAX 11/780.

To simulate the excitation of a moving stimulus in the tectum, we introduce a pulse of unit intensity that activates a column for a certain period. The larger the stimulus, the more glomeruli are activated simultaneously, and the longer is the period of presentation of the stimulus in each glomerulus. Simulation of different velocities of stimulation was obtained with the period of presentation of the stimulus in each glomerulus and the overlapping of excitation between neighboring glomeruli inversely proportional to the speed of the object, i.e. the faster the object moves, the shorter the period of presentation in each glomerulus and the shorter the simultaneous activation of glomeruli. As a simple representation of the overlap of receptive fields, we model the receptive field of each glomerulus as sensitive to stimuli presented in its closest neighbors, i.e. the one to the right and to the left, but with half of the intensity of the stimulus. In all cases the stimulus was serially presented from glomerulus 0 to glomerulus 7 (see Fig 1).

The results of the simulation are shown in two ways: via the display of the simulated physiological behavior of the 8 pyramidal cells, because each integrates the general activity of its column and is the tectal efferent; and secondly, through graphs showing the relationship between different stimuli and both the general state of excitation of the tectum, measured as the total number of spikes (which in this formal model is simply proportional to the period of above threshold membrane potential) produced by the 8 PY, as well as the latency of response, measured as the period required for the first tectal response, i.e., PY activity. In following sections, we will study the behavior of the tectal columns when a moving stimulus is presented, changing different parameters such as the size and speed, and studying different configurations when double stimuli are used. We will also compare the general activity of the tectum for the different cases and relate this to the observed behavioral and, when available, physiological results.

3.2 Tectal Response to a Moving Stimulus Elongated along the Direction of Motion.

As we have mentioned above, elongation of a stimulus along the axis of motion facilitates prey orienting behavior and increases the rate of firing of some tectal cells (Ewert, 1976).

Figs 2-4 show the behavior of the 8 tectal columns to a moving stimulus of different sizes. In Fig 2 the size of the stimulus is such that it only activates one glomerulus focally, and is thus of approximately 5 degrees according to our hypothesis, and no overlapping occurs between neighboring glomeruli, except the effect produced by the receptive field of each glomerulus (see table of Fig 2 to see the period of presentation of the stimulus in each column). This figure shows that the moving stimulus builds up a wave of excitation-inhibition, starting from column 0 and moving to column 7; when the stimulus is in column 3, it produces a response (two spikes), subsequent columns respond in an alternating way to the moving stimulus. This alternation of excitation and inhibition in the unit columns may represent a means for increasing the acuity of the motor response, because as we have postulated, the tectum codes the location of the stimulus. It is important to stress that these results could only be obtained from an experimental point of view if the animal is immobilized. We will explore below a second interpretation of this alternating behavior in terms of the preference of the animal to orient and snap to the leading of two objects. Fig 3 shows the effects of elongation of the stimulus in the response of the tectal columns; this experiment studied the effect of the stimulus 10 degrees in size, simultaneously exciting two glomeruli focally. This figure shows that the latency of the first response (in column 2) is shorter than in the above case, and the state of excitation in all columns has been greatly increased by the elongation of the stimulus along the axis of motion. In this case the spatial alternation of excitation-inhibition and the rebounding excitation are more evident. If we elongate still further the size of the prey dummy (focally activating simultaneously three glomeruli, 15 degrees in size) the facilitatory effect both in the latency of response as well as in the number of times the pyramidal cell of each column responds is more evident (see Fig 4). The curves showing the relationship between size of the stimulus and both latency of response and state of excitation of the column can be seen in Fig 5 A and B, where it can be seen that the activity of the tectum is increased and the latency of response is decreased with elongation of the stimulus. Notice also that in figures 2-4 a particular tectal cell fires more strongly with the elongation of the stimulus; this can be seen not only in the PY firing but in the subthreshold potential of this neuron which manifests the activity of LP and SP neurons. If we consider the activity of the tectum to represent the rate of pursuit of the animal toward the prey, then the results presented above reproduce the observed behavior; moreover, we also reproduce the increase in the rate of firing of tectal cells when the stimulus is elongated.

In the next paper (Lara and Arbib, to appear), we study the effects of the interaction between pretectum and tectum on prey orienting behavior when the stimulus is elongated, showing that the response of the unit columns is now more precise and simultaneity of activity of several columns does not happen as often as in the above case. This indicates that possibly the tectum when influenced by pretectum inhibits weaker responses so that its activity converges toward the more strongly activated unit column.

3.3 Tectal Behavior when the Orienting Response is Present.

We now want to see the effects on tectal behavior when a moving stimulus activates a unit column producing an orienting response that will bring the stimulus back to a region already activated. In the case studied in Fig. 6, the activation of unit column 3 enables the stimulus to be present again in column 0; because this column was already activated it now produces a response. This result may indicate that presenting the stimulus for a second time will produce a stronger response so that, instead of simply exhibiting an orienting response, the animal will now snap at the prey.

3.4 Tectal Behavior with a Double Stimulus.

Ingle (1971, 1973b, 1976a, and b, 1978) in his studies of the effects of stimulus configuration on elicited prey catching behavior found the following results: 1) animals have the tendency to snap at the head of the stimulus; 2) prey catching behavior is greatly facilitated when two stimuli move on the same axis with a short interstimulus distance, 4 degrees, and the response is mostly directed to the leading (head) object; in these conditions the animal always prefers the double to a single stimulus of the same size; 3) when the interstimulus distance increases, to 8 to 16 degrees, the animal responds randomly to either the head or the tail and there is no preference between the single and double stimulus; 4) when the size of the two stimuli is large, an inhibitory effect in prey pursuit is manifested, because animals prefer single rather than double stimuli.

In Fig 7 we show the behavior of the tectal columns when a double stimulus is presented with a short (one glomerulus, 5 degrees) interstimulus distance. It can be seen that the onset of the stimulation in column 0 and column 2 makes the latter column respond first to the leading edge; subsequent columns also respond first to the leading stimulus, giving a weak response when the second stimulus is presented. If we compare the state of excitation of the tectum when a double stimulus is applied in contrast to a single stimulus (see Fig 2 for the tectal behavior when a single stimulus, with the same parameters used in the above case, is applied, and Fig 5 I for the comparative graphs) we can see that the tectum reacts more strongly and faster to the double stimulus, indicating that a facilitatory effect is present. If we increase the distance between stimuli (two glomeruli, 10 degrees, see Fig 8), we still see that the columns respond to the leading object (column 4) but the subsequent response to the tail has also increased; notice the strong inhibitory effect over columns 0 to 2. Increasing the interstimulus distance further (three glomeruli, 15 degrees, see Fig 9) we now see that the columns respond first to the tail (column 2) but this is followed by a response to the head (column 5 and 6). Notice that the tail is still inhibited when it passes through columns 3 and 4 (see the response to a single stimulus in Fig. 2), but the head is now behaving as an independent stimulus. From these results it is evident that increasing the interstimulus distance reduces the facilitatory effect and the animal has the tendency to dissociate the two stimuli (see Fig 5 I). In these conditions it is obvious that the animal will snap randomly to any of them because both are equally strong. Figs 5 C and D show the graphs relating the level of facilitation against interstimulus distance. All these results are in agreement with experimental results.

Due to the restriction to a one dimensional array of columns, we could not test the inhibitory effect produced by the presentation of two large objects aligned in the axis of motion. This property, however, has been related (Ewert, 1976) to intertectal interaction as a result of prey competition. Ingle (1978), on the other hand, has found inhibition of prey orienting behavior in monocular frogs in these circumstances, which indicates that other inhibitory processes, perhaps through the pretectum, are also present.

3.5 Tectal Behavior with Changes in Prey's Speed.

Ewert (1976) and other authors (Grusser and Grusser Cornehls, 1976) have shown that orienting behavior is dependent on the angular speed of the prey; moreover, this effect has been closely correlated with the sensitivity to speed in the retinal ganglion cells. It is, however, interesting to study the effects in column behavior when an object is presented at different speeds to see if this structure by itself produces a facilitation or inhibition depending on the velocity of the stimulus.

Figs 10-12 show the tectal behavior when an object is presented at different speeds. When an object is moving fast (see our definition of fast and slow in "general considerations") the tectal response is low and the latency is large (see Fig 10); lowering the speed of the object (see Fig 11 and 12) increases the state of excitation of the columns and reduces the latency of response (see Fig 5 E and F for the above relations). This indicates that either the sensitivity of the retinal ganglion cells to speed must compensate for this slowing down effect, or the tectal cells are also sensitive to this parameter. Trying to study in a crude way the interaction of retinal ganglion cells sensitive to speed and tectal neurons, waiting for a more precise and sophisticated model of the retina, we changed the intensity of the stimulus in proportion to the velocity of the object, i.e., the faster the object, the more intense would be the excitatory input.

Figs 13-14 show the results of this simulation, with the state of excitation of the tectal column stronger to faster stimuli and the latency of response shorter (see also Fig 5 G and H). These reults indicate that the sensitivity of the retinal ganglion neurons to speed may counteract the inhibitory effect observed in the tectum to this parameter.

4. Discussion

With the present model of the tectum we have been able to study the effects of size, speed, and configuration of the stimulus on a linear array of its functional units, the tectal columns. The structure proposed for the column (Lara, Arbib and Cromarty, Appendix 2), based on anatomical, behavioral, and preliminary physiological results allows us to reproduce the observed behavioral and physiological results in prey orienting behavior to a moving stimulus. The next step in studying the behavior of our model are the following: 1) expansion of the one dimensional model to two dimensions; 2) introduction of the processing of the optic input by the retina; 3) the interaction of tectum and pretectum. With these new factors we will be able to simulate the following processes that have been studied both behaviorally and physiologically: 1) competition among different prey stimuli; 2) prey-predator recognition; and 3) invariance of prey stimuli independent of the direction of movement.

We have observed that the general behavior of the tectum is the result of spatio-temporal facilitatory-inhibitory interactions that depend on the size, speed, and configuration of the stimulus. It is interesting that this wave of excitatory and inhibitory activity has been described in the thalamus and hippocampus and has been related with the EEG. Moreover, Purpura (1970) has suggested that these waves of excitation and inhibition could be used as filters of incoming information. Based on our results, it seems that the inhibitory and excitatory activity in the tectum may have three functions: 1) spatio-temporal facilitation of column activity to a moving stimulus; 2) preference for the head of the stimulus, probably to avoid possible defensive reactions of the prey; and 3) modulating the state of excitation of the column once it has produced a response. The model also shows that the spatio-temporal effects of excitation and inhibition increases the acuity of the animal to the direction of the prey, through processes similar to lateral inhibition.

The present model postulates the following hypotheses:

1. The tectum codes the location and speed of the orienting response.
2. The interaction between tectal columns to a moving stimulus generates a wave of excitation and inhibition of tectal unit columns.
3. The preference for the leading edge of two stimuli moving along the same axis is the result of this excitatory and inhibitory effect.
4. The tectum response decreases with increasing speed of the

object; retinal sensitivity to speed counteracts this effect in the behavioral response.

5. The orienting response brings the stimulus back to the site recently activated, thus increasing the probability of a stronger response.

REFERENCES

1. Comer, C., and Grobstein, P.: Prey acquisition in atectal frogs. Brain Research 153 (1978).

2. Ewert, J.P.: Neural mechanisms of prey-catching behavior and avoidance in the toad (Bufo bufo L). Brain Behav. Evol. 3, 35-56(1970).

3. Ewert, J.P.: Single unit response of the toad's caudal thalamus to visual objects. Verg. Physiologie 74, 81-102(1971).

4. Ewert, J.P.: The visual system of the toad: behavioral and physiological studies in a pattern recognition system. In: The Amphibian Visual System. Fite, K. ed. Academic Press, 1976, pp. 142-202.

5. Grusser, O.J., and Grusser-Cornehls, V.: Neurophysiology of the anurans visual system. In: Frog Neurobiology. Llinas, R., and Precht, W. eds. Springer Verlag, New York, 1976, pp 297-385.

6. Ingle, D.: Prey catching behavior of anurans toward Moving and stationary Objects. Vision Res. Supp. 3, 447-456(1971).

7. Ingle, D.: Disinhibitlon of tectal neurons by pretectal lesions in the frog. Science, N.Y. 180, 422-424(1973a).

8. Ingle, D.: Selective choice between double prey objects by frogs. Brain Behav. Evol. 7, 127-144(1973b).

9. Ingle, D.: Focal attention in the frog: behavioral and physiological correlates. Science 188, 1033-1035(1975).

10. Ingle, D.: Spatial visions in anurans. In: The Amphibian Visual System. Fite, K. ed. Academic Press, New York, 1976a,

pp. 119-140.

11. Ingle, D.: Central visual mechanisms in Anurans. In: Neurobiology of the Frog. Llinas, R., and Precht, W. eds. Springer Verlag, New York, 1976b, pp. 435-451.

12. Ingle, D., and McKinley, D.: Effect of stimulus configuration on elicited prey catching by the marine toad. Anim. Behav. 26, 885-891(1978).

13. Lara, R., and Arbib, M.A.: A neural model of interaction between pretectum and tectum in prey selection (to appear).

14. Lara, R., Arbib, M.A., and Cromarty, A.S.: The role of the tectal column in facilitation of amphibian prey-catching behavior: a neural model. (To appear)

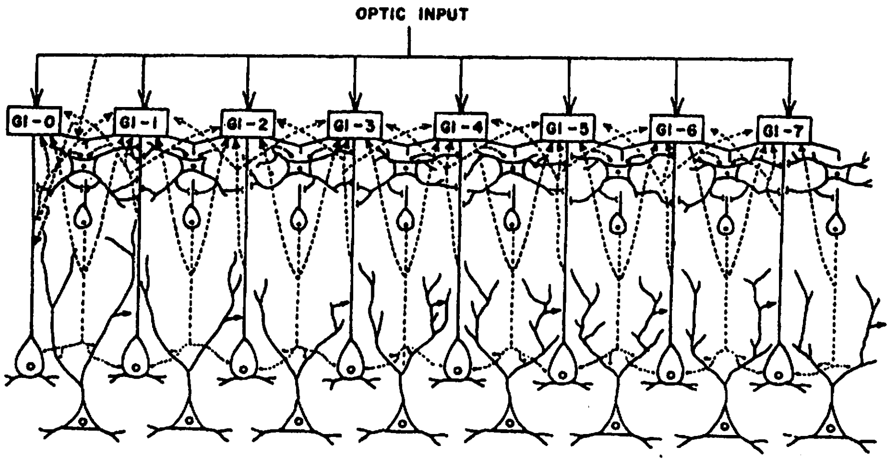
15. Lettvin, J.Y., Maturana, H., McCulloch, W.S. and Pitts, W.H.: What the frog's eye tells the frog's brain. Proc. IRE. 1940-1951 (1959).

16. Purpura, P. D.: Operations and processes in thalamic and synaptically related neural subsystems. In: The Neurosciences Second Study Program. Schmit, F.O. ed. The Rockefeller University Press, New York, 1970, pp. 458-471.

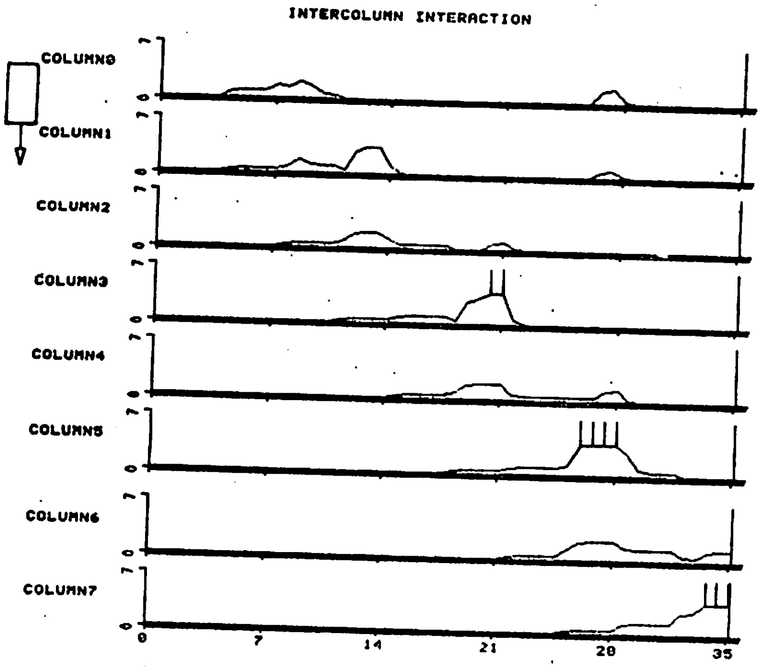
17. Székely, G., and Lazar, E.: Cellular and synaptic architecture of the optic tectum. In: Frog Neurobiology. Llinas, R., and Precht, W. eds. Springer Verlag, New York, 1976.

18. Székely, G. and Czeh, G.: Organization of locomotion. In: Frog Neurobiology. Llinas, R., and Precht, W. eds. Springer-Verlag, New York, 1976, pp. 765-792.

FIGURES

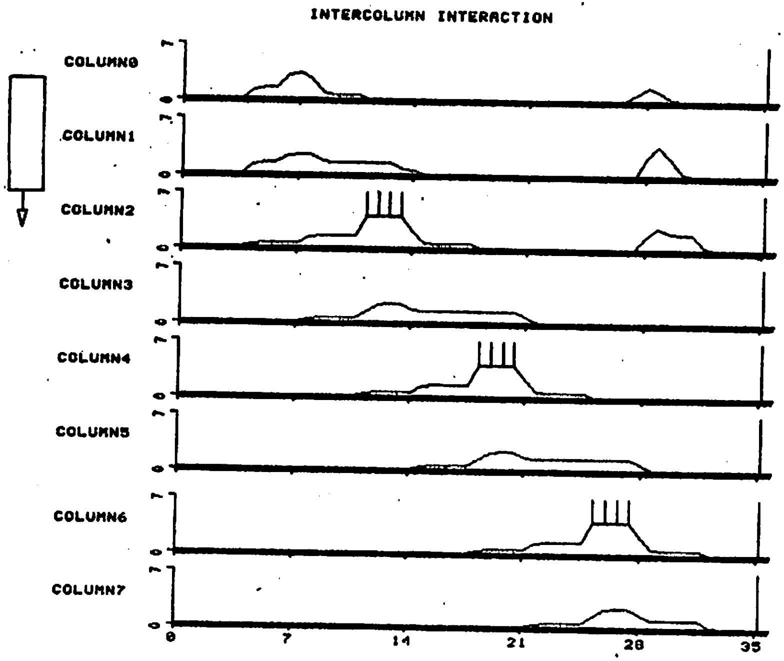


1. Architecture of the model of the tectum. Each column is constituted by one GL (glomerulus), one LP (large pear-shaped) cell, one SP (small pear-shaped) neuron, one SN (stellate neuron), and one PY (pyramidal cell). The afferents are the optic fibres that arrive at the GL, LP, SP, and PY cells, and the efferents are the PY axons. LP cells are activated by the GL and the optic input and they send recurrent axons to their own as well as neighboring glomeruli. The SN neurons are activated by the LP cells and they inhibit LP and SP neurons of their own as well as neighboring columns. The SP receive excitation from GL and are inhibited by SN; finally PY receives afferents from the retina, the LP and SP neurons.



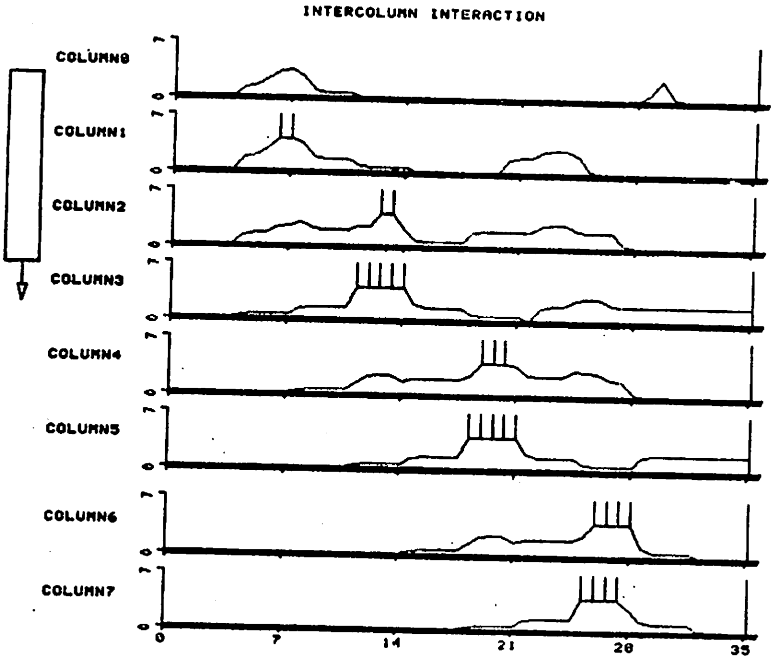
GL-0	GL-1	GL-2	GL-3	GL 4	GL-5	GL-6	GL-7
0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-4.0	4.0-4.5	4.5-5.0

2. Figures 2, 3 and 4 present a computer simulation of tectal response to a moving stimulus of different sizes. The table shows the period of presentation of the stimulus in each glomerulus, and the graphs show the behavior of the 8 PY neurons of the tectum to a moving stimulus. Notice that in this case an alternate response is given in columns 3, 5, and 7 when the stimulus size only covers one glomerulus.



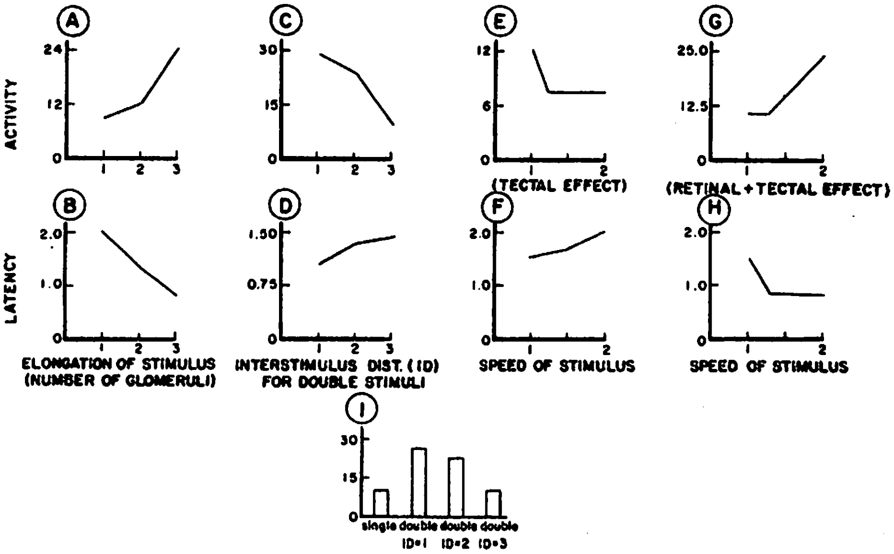
GL-0	GL-1	GL-2	GL-3	GL-4	GL-5	GL-6	GL-7
0.5-1.0	0.5-1.5	1.0-2.0	1.5-2.5	2.0-3.0	2.5-3.5	3.0-4.0	3.5-4.5

3. Here the stimulus covers 2 glomeruli simultaneously. The results show that the strength of activation increases when the size of the object is elongated. The latency of response is also shorter (column 2).

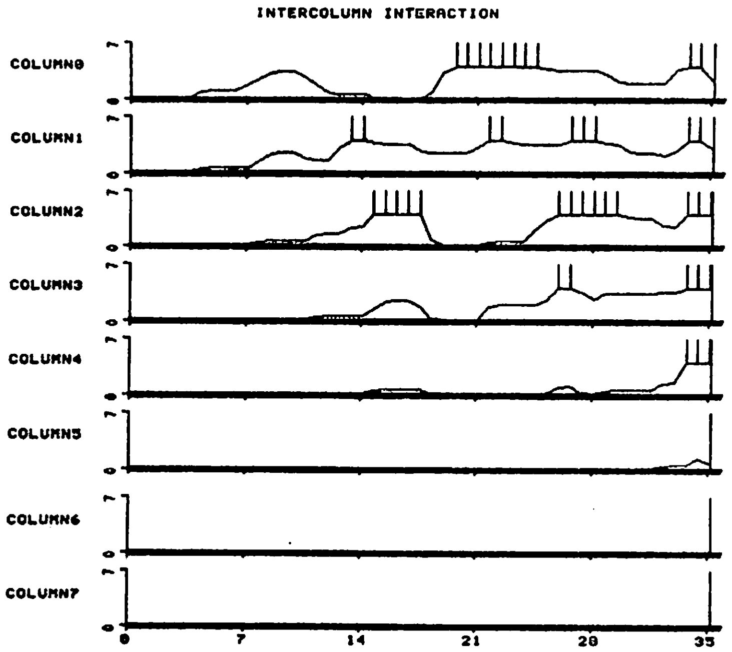


GL-0	GL-1	GL-2	GL-3	GL-4	GL-5	GL-6	GL-7
0.5-1.0	0.5-1.5	0.5-2.0	1.0-2.5	1.5-3.0	2.0-3.5	2.5-4.0	3.0-4.5

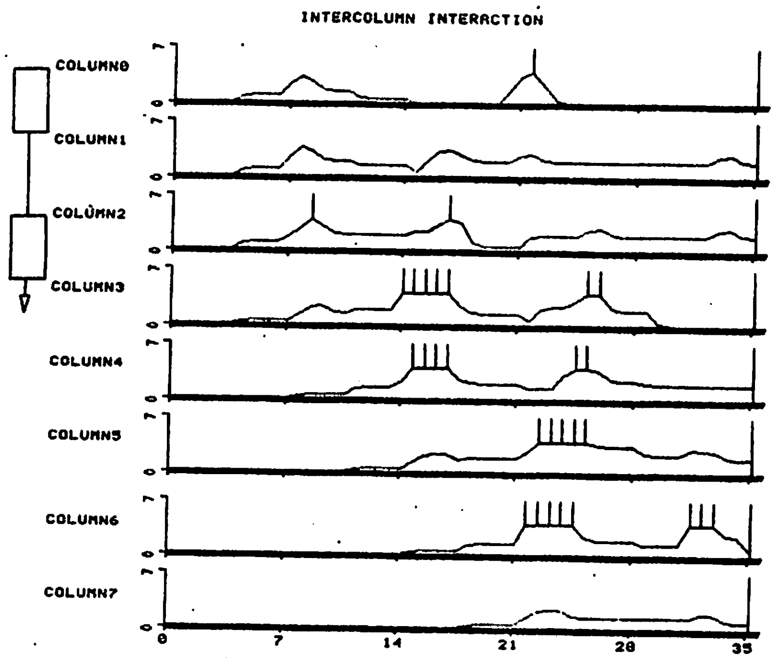
4. Computer simulation of the behavior of the tectum to different sizes of stimulus. In this figure the stimulus covers 3 GL simultaneously. It can be seen that the latency of response is shorter and the total activity is greater than in Fig 2 and 3. Notice that all columns fire with this stimulus.



5. Graphs showing the relationship of the level of activity of the tectum and the latency of repsonse to different parameters of the stimulus, such as size, speed, and configuration. The total activity of the tectum increases (A) and the latency of response decreases (B) with elongation of the stimulus. The tectal activity is also increased (C), with shorter latencies of response (D), when the interstimulus distance between two objects is small. In E, F, G, and H we show the dependency of the tectal behavior on the speed of the object. E and F show that the faster the stimulus moves, the weaker the tectal response and the larger its latency; and G and H show the combined effect of retinal and tectal sensitivity to speed of the moving object, showing that the above effect is reversed. Finally, (I) shows the different state of activation of the tectum when double or single stimuli are presented. It can be seen that when the interstimulus distance is small, the double stimulus produces a larger response than the single stimulus, but this effect is reduced when the distance is increased.

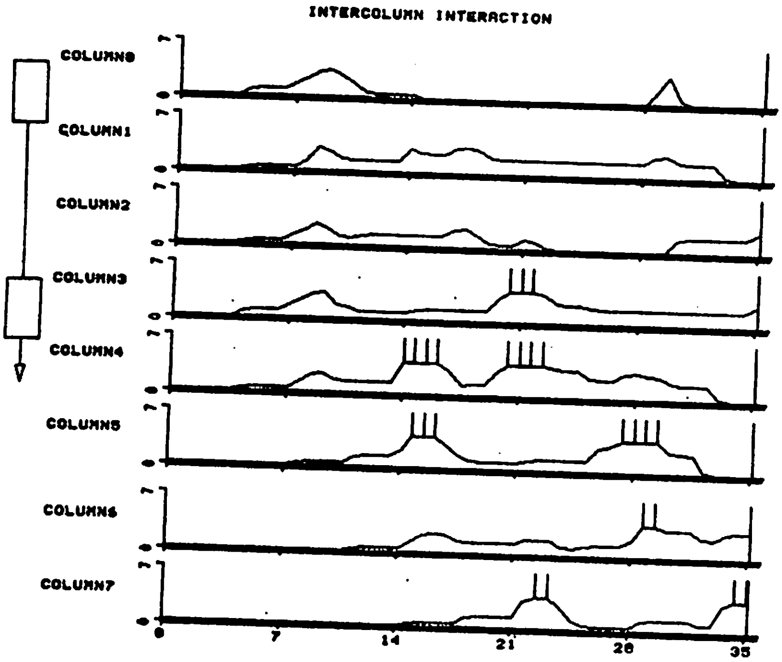


6. Computer simulation of tectal response to a moving stimulus taking into account the effect of the orienting response. This figure shows that when the stimulus is presented for a second time in the same region, due to the orienting response, the second activation of the unit column is stronger that the first time.



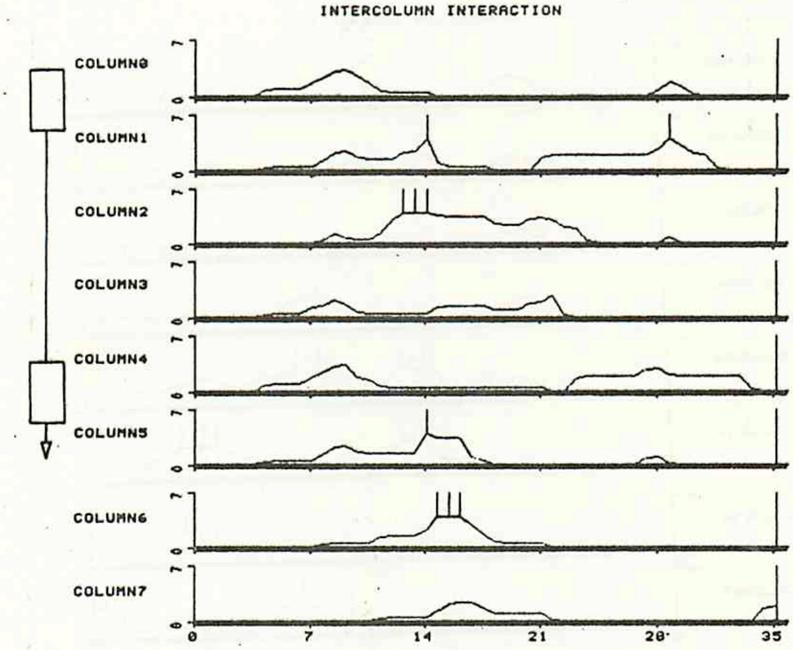
	GL-0	GL-1	GL-2	GL-3	GL-4	GL-5	GL-6	GL-7
Tail	0.5-1.5	1.0-2.0	1.5-2.5	2.0-3.0	2.5-3.5	3.0-4.0	3.5-4.5	4.0-5.0
Head			0.5-1.5	1.0-2.0	1.5-2.5	2.0-3.0	2.5-3.5	3.0-4.0

7. Computer simulation of tectal behavior when double stimuli are presented. The graphs show that when the 2 stimuli are separated by a short distance (1 GL) the level of activity is increased (see Fig 11 for comparison with the effects of a single stimulus) and there is a clear preference to fire at the leading edge (head) (notice the weak activity of columns 0-2).



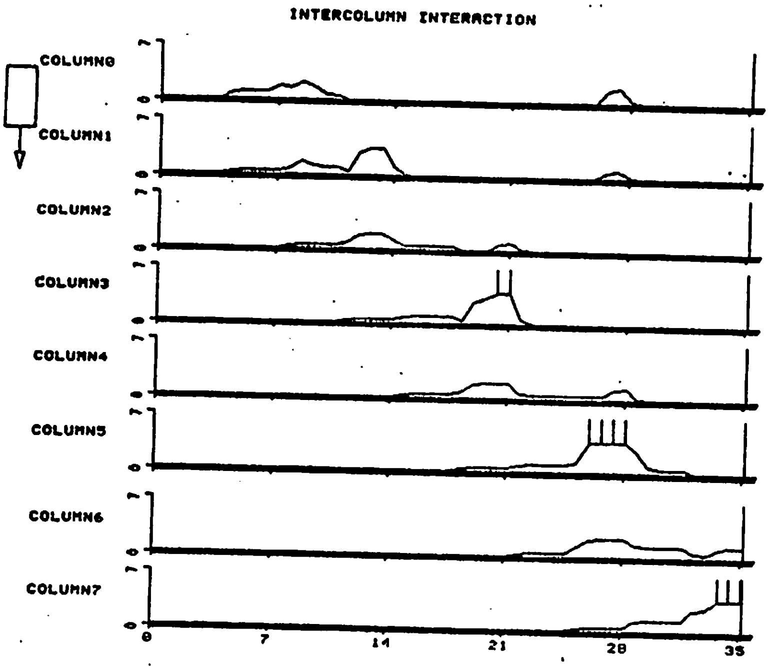
	GL-0	GL-1	GL-2	GL-3	GL-4	GL-5	GL-6	GL-7
Tail	0.5-1.5	1.0-2.0	1.5-2.5	2.0-3.0	2.5-3.5	3.0-4.0	3.5-4.5	4.0-5.0
Head				0.5-1.5	1.0-2.0	1.5-2.5	2.0-3.0	2.5-3.5

8. Computer simulation of tectal behavior when double stimuli are applied. The interstimulus distance in this case is 2 GL. The inhibitory effect over the tail of this stimulus is still more evident than in Fig 7 (see columns 0-3 and Fig 11 for the effects of a single stimulus). A preference for the leading edge is evident.



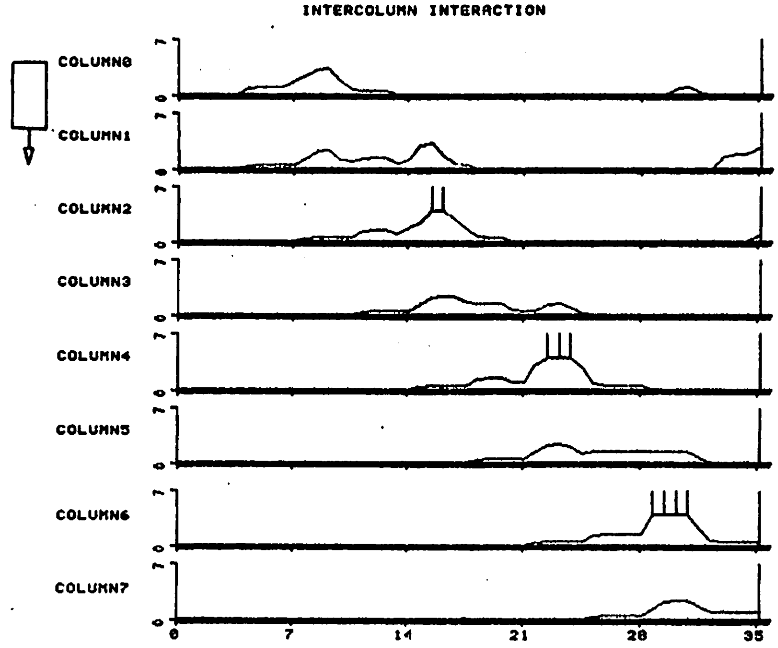
	GL-0	GL-1	GL-2	GL-3	GL-4	GL-5	GL-6	GL-7
Tail	0.5-1.5	1.0-2.0	1.5-2.5	2.0-3.0	2.5-3.5	3.0-4.0	3.5-4.5	4.0-5.0
Head					0.5-1.5	1.0-2.0	1.5-2.5	2.0-3.0

9. Computer simulation of tectal behavior when double stimuli are applied. In this experiment the interstimulus distance is 3 GL. In these conditions the first response is given toward the tail (column 2), but the inhibitory effect over subsequent columns is still present. Notice also that the response to the head (columns 5 and 6) is identical to that produced by the single stimulus on column 1 and 2 in Fig 11, indicating that it starts to behave as an independent stimulus.



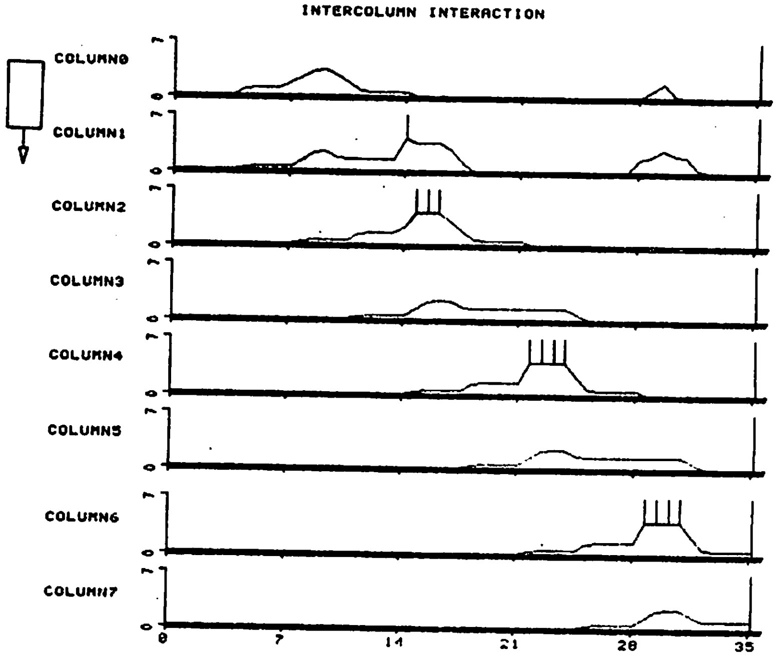
u	GL-0	GL-1	GL-2	GL-3	GL-4	GL-5	GL-6	GL-7
1.0	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-4.0	4.0-4.5	4.5-5.0

10. Figures 10 through 14 exhibit computer simulations of tectal behavior to stimuli moving at different speeds. When the stimulus moves fast along the tectum, the response is rather weak.



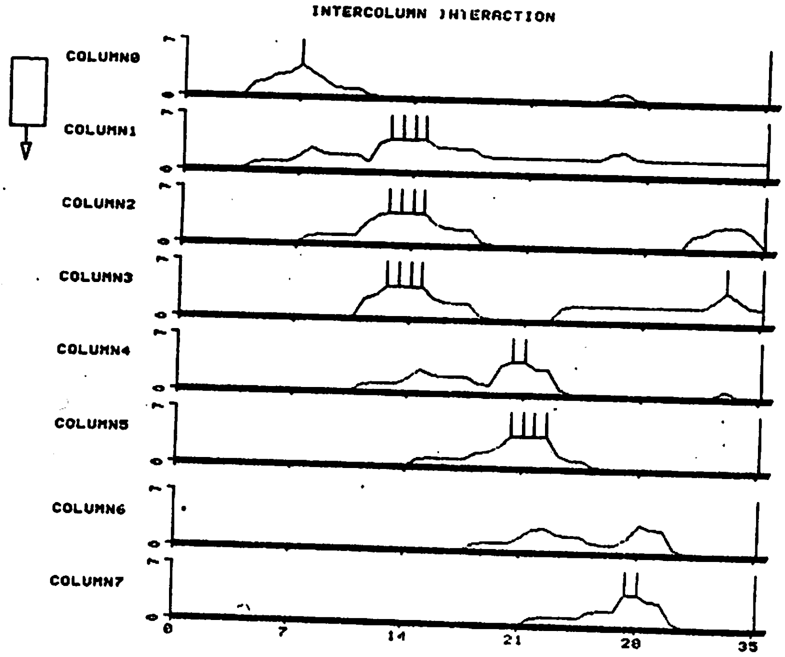
u	GL-0	GL-1	GL-2	GL-3	GL-4	GL-5	GL-6	GL-7
1.0	0.5-1.25	1.0-1.75	1.5-2.25	2.0-2.75	2.5-3.25	3.0-3.75	3.5-4.25	4.0-4.75

11. Computer simulation of tectal behavior to stimuli moving at different speeds (continued). In this case, the speed of the moving object is reduced, in comparison with Fig 10, with a concomitant increase in tectal activity as well as a shortening of the latency of response.



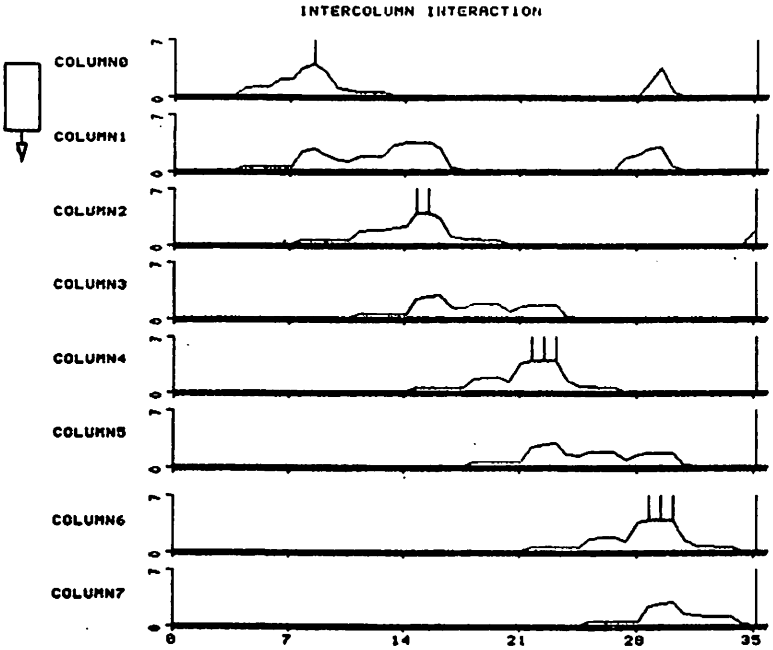
u	GL-0	GL-1	GL-2	GL-3	GL-4	GL-5	GL-6	GL-7
1.0	0.5-1.5	1.0-2.0	1.5-2.5	2.0-3.0	2.5-3.5	3.0-4.0	3.5-4.5	4.0-5.0

12. Computer simulation of tectal behavior to stimuli stimuli at different speeds (continued). Now the stimulus is moving even more slowly than in the above cases, with an increase in tectal activity and a reduced latency of response.



u	GL-0	GL-1	GL-2	GL-3	GL-4	GL-5	GL-6	GL-7
2.0	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5	3.5-4.0	4.0-4.5

13. Simulation of the same conditions of Fig 10 but considering the speed sensitivity of the ganglion retinal cells. Notice that the state of excitation is greatly increased and the latency of response is reduced, even more strongly than in Fig 12.



u	GL-0	GL-1	GL-2	GL-3	GL-4	GL-5	GL-6	GL-7
1.25	0.5-1.25	1.0-1.75	1.5.2.25	2.0-2.75	2.5-3.25	3.0-3.75	3.5-4.25	4.0-4.75

14. Simulation of the same conditions as in Fig 11, but adding the speed sensitivity of ganglion retinal cells. Again, the state of excitation is increased and the latency of response is reduced.