# Two-Dimensional Model of Retinal-Tectal-Pretectal Interactions for the Control of Prey-Predator Recognition and Size Preference in Amphibia[1]

Rolando Lara,
Francisco Cervantes, and
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# Two-Dimensional Model of Retinal-Tectal-Pretectal Interactions for the Control of Prey-Predator Recognition and Size Preference in Amphibia

Rolando Lara, Francisco Cervantes and Michael Arbib*
Centro de Investigaciones en Fisiología Celular
Universidad Nacional Autónoma de México
Apartado Postal 70-600
04510 México, D.F.
*Center for Systems Neuroscience, and Department of
Computer and Information Science
University of Massachusetts
Amherst, MA 01003/USA
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## I. Introduction

In the present paper, we propose a model of the interactions among retina, tectum and pretectum in the amphibian brain which simulates prey-predator recognition, direction invariance of prey-predator recognition as a consequence of tectal architecture, size preference and latency of response of the animal depending on its motivational state. The model is an extension of the one dimensional model of the tectum, described elsewhere, [1-3] which takes into consideration the anatomical, physiological and behavioral studies of the tectum. With this model we have been able to study the different experimental hypotheses described below with the aim that a single model could explain the observed results, reproduce the experimental observations, and predict new experiments for future research.

Amphibia (and we emphasize frog and toad) have been considered a good biological model for the study of visuomotor coordination because much of their behavior is guided by visual stimuli, they are almost static animals, their nervous system is not as complex as those of higher vertebrates, although some of the complexity of their behavior and processing of information is present in these animals, and they have been extensively studied from anatomical, physiological, behavioral and theoretical points of view.

Ethological studies [4,5,6] have shown that these animals have innate mechanisms to recognize different stimuli in their environment to elicit the proper response. It has been shown that the geometry of the visual stimulus in relation to the direction of motion plays a prominent role in the orienting response of the animal: objects whose longest axis moves in the direction of motion are considered as prey, while objects whose longest axis moves perpendicular to the direction of motion are considered as predators, because they do not elicit prey orienting behavior or they give an avoidance response [4] (see Fig. 1). It has also been shown that this prey/non-prey recognition is invariant to both the direction and speed of the stimulus.[7]

Ingle[8,9] has shown that the size, color preference and latency of response to prey stimuli can change depending on the motivational state of the animal. He showed

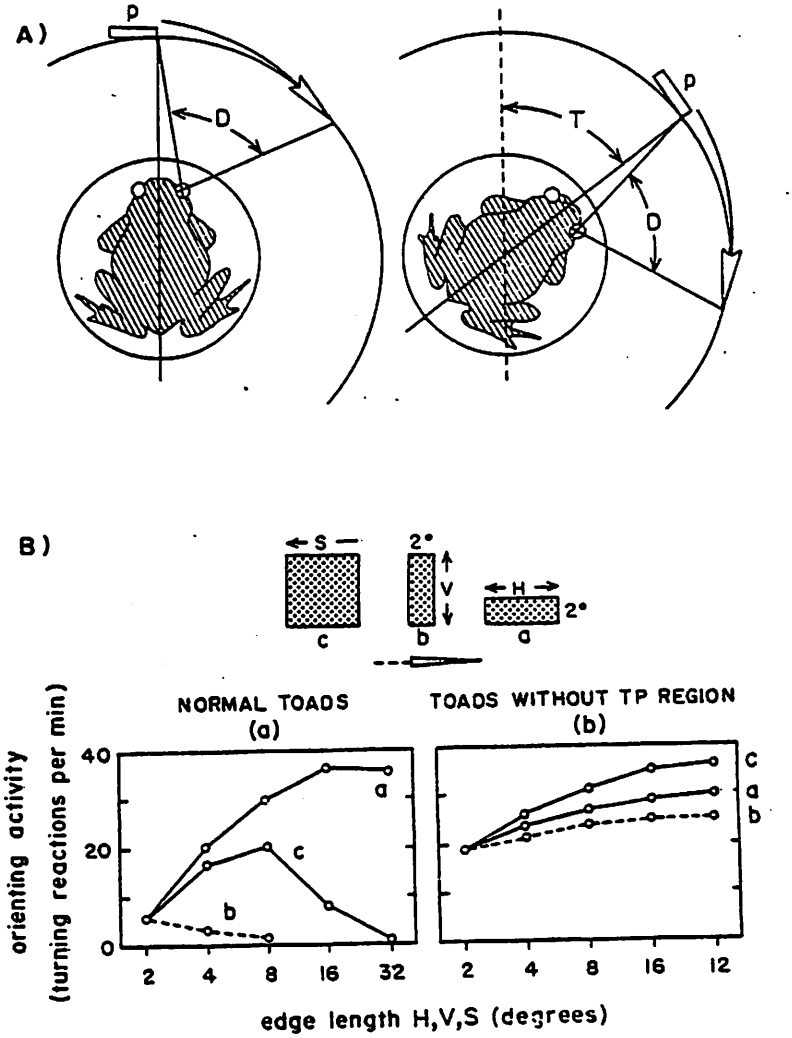



Fig. 1. Prey orienting behavior to different configurations of the stimulus. A) Turning reaction to the stimulus presentation. B) Orienting activity to three configuration (a,b,c): facilitation to stimulus a, inhibition to stimulus b, and an initial facilitation and then an inhibition to stimulus c. When pretectum ablation occurs this discrimination disappears. (From Ewert, 1976)

that animals which were good feeders had low response thresholds and preferred 16° long worms to worms of 6° length, while slow feeders had the opposite preference; thus response readiness is correlated with size preference. Ingle suggests that these mechanisms of prey preference may be associated with the known size constancy capacity that amphibia have for a limited distance.

A great deal of research has been aimed at trying to find the neuronal mechanisms responsible for these processes. Ewert has shown[4] that prey-orienting behavior is disrupted when the tectum is destroyed. Moreover, the tectum receives information from the retina in a retinotopic way and electrical stimulation of a specific tectal region

elicits the orienting response to the corresponding retinal projection. This suggests that the tectum plays a prominent role in prey orienting behavior. Ewert has also shown that lesions of the pretectum, another brain region which receives retinotopic information from the retina and establishes closed loop interactions with the tectum,[10,11] disrupts the recognition abilities of the animal to the different configurations of the stimuli.[4] (see Fig. 1b) Furthermore, he observed that toads with pretectum ablation snap indiscriminately to any object, they switched their preference from black to white stimuli, and they lost size selectivity. This suggests that the interaction among retina, tectum and pretectum may be responsible for the processes of prey-predator recognition, size preference and size constancy.

Trying to establish the role that each one of these brain regions may play in the control of these behaviors, Ewert studied the neuronal responses in the retina, tectum and pretectum to the different configurations of the stimulus.[4,12-14] He showed that in toads and frogs ganglion retinal cells of types II, III and IV do not change considerably their rate of response when a worm-like stimulus of different sizes was presented; whereas when an anti-worm-like stimulus whose longest axis moves perpendicularly to the direction of motion was presented, ganglion cells of types II and III initially increased their rate of response up to the size of their respective excitatory receptive field and then the rate of response decreased when the object was larger than the excitatory receptive field (ERF). The inhibitory effect is stronger in ganglion type II cells than ganglion type III cells. Class IV ganglion cells increase their rate of response depending on the size of the object. (see Fig. 2) Ganglion cells of types II, III and IV increase their rate of response depending on the speed of the object, but they respond independently of the direction of motion.[12,13]

From the above results, Ewert concluded that the observed behavioral responses could not be explained simply by the retinal responses; thus he continued studying the response of tectal and pretectal cells to the different configurations of the stimuli. He found that some tectal cells responded in a strikingly similar way to the behavior of the animal when the different stimuli were presented: facilitation of the rate of firing when the stimulus was elongated along the direction of motion, inhibition when the stimulus was elongated perpendicularly to the direction of motion, and an initial facilitation and then an inhibition when the stimulus was expanded in both directions (Fig. 3). Moreover when pretectal ablation occurs this tectal cell responds similarly to the behavioral response when the different stimuli are presented. Ewert also showed that some of the tectal cells could discriminate between prey and non-prey stimuli independently of the direction of motion while other tectal neurons were directionally selective or responded more strongly to a predator-like stimulus.[7] For the above reasons, Ewert suggests that this neuron, tectal type T5(2), may be responsible both for the discrimination between prey and non-prey stimuli and for indicating the position to which the animal should orient. The tectal neuron performs this through combined activity with pretectal cells, possibly through an inhibitory effect. Studies of the

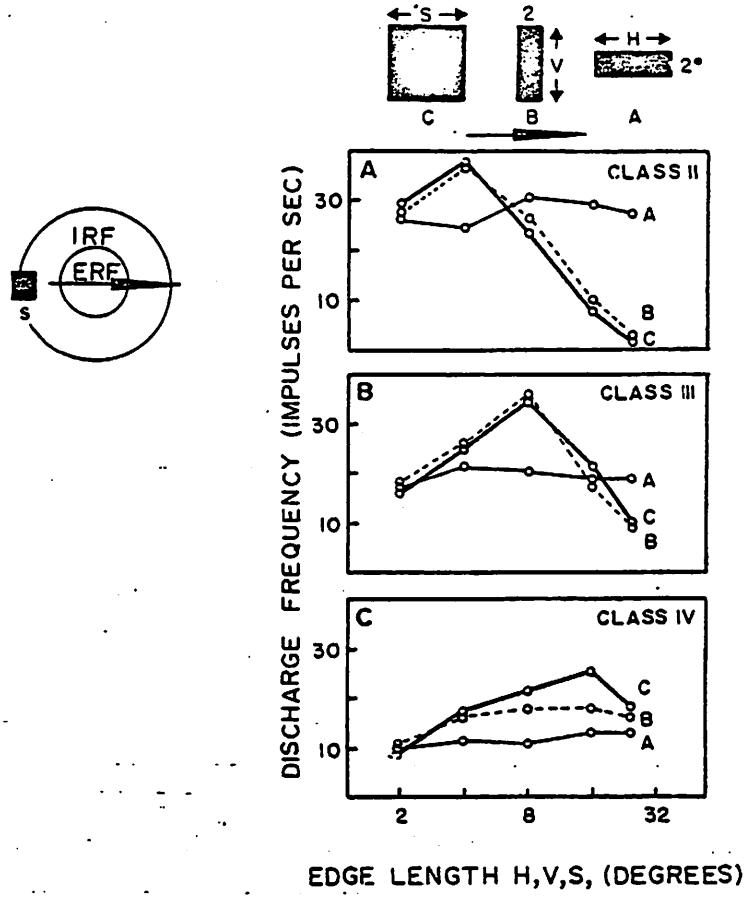



Fig. 2. Retinal ganglion cell response (II, III, IV) to different configurations of the stimulus (a,b,c). For stimulus type a the response of the three ganglion neurons is almost invariant for the different sizes of the stimulus. For stimulus type b and c, ganglion type II and III increase their rate of response up to their respective receptive field and then the response is reduced. For type IV ganglion cells the rate of response is proportional to the size of the stimulus. (From Ewert, 1976)

response of the pretectal cells[14] showed that most of these neurons had large receptive fields and that they were more sensitive to a predator-like stimulus (see Fig. 3). One of these pretectal cells TH5 with a relatively small receptive field responded mostly to non-prey like stimuli; for this reason, Ewert postulates that this cell inhibits the activity of tectal cells when a predator-like stimulus is present, thus allowing the animal to orient to the proper prey stimulus. In this way, Ewert suggests that the combined activity of retina-tectum and pretectum may control prey-predator recognition. With respect to the direction invariance recognition, Ewert simply says that it must be a consequence of the tectal architecture rather than of a sophisticated "software"-like processing of information.

In relation to size preference, Ingle, following Ewert's hypothesis of pretectal inhibition over tectal activity, suggests that the changes in size, color and latency of response could also be modulated by the pretectum.[6,8,9] He postulates that in normal

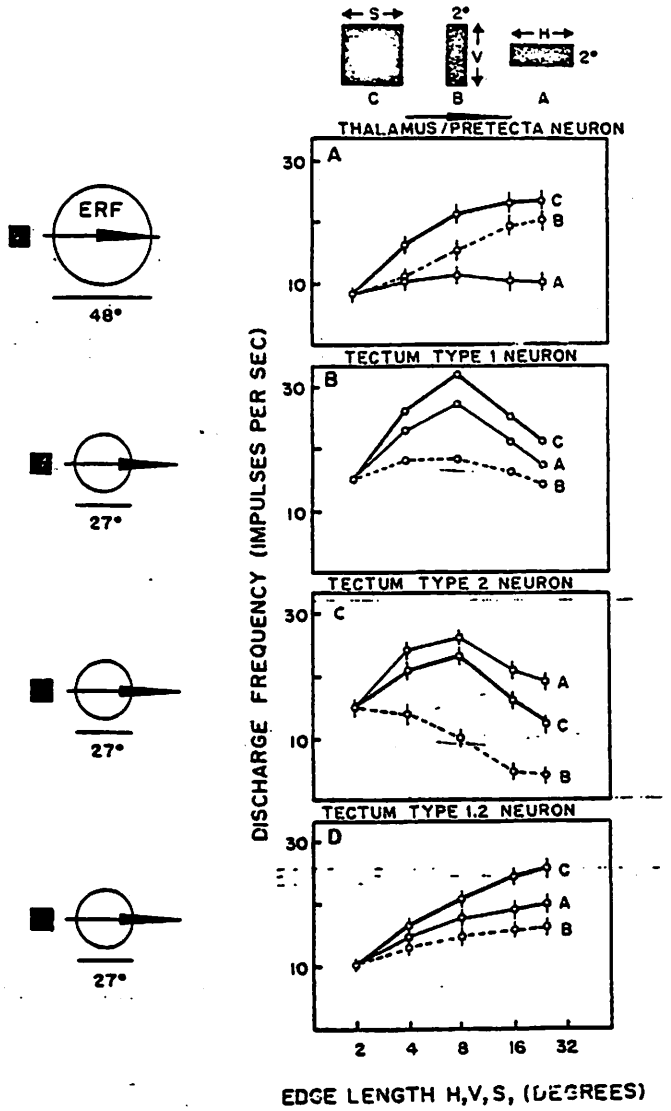



Fig. 3. Tectal and pretectal cell activity to different configurations of the stimulus (a,b,c). A) Response of a pretectal neuron which is mostly sensitive to stimulus b and c. B and C show the response of two tectal cells to the three types of stimuli. Neuron C response is mostly sensitive to stimuli type a and c and its response is greatly reduced for stimulus type b. This response is similar to the observed behavioral response. D shows the response of both tectal cells (B and C) without pretectum and how the discriminative abilities of these cells are lost. (From Ewert, 1976)

conditions tectal cells are mostly guided by type II ganglion neurons, and the afferents from ganglion type III and IV cells are normally inhibited by the pretectum. Ingle suggests that retinal-type II cells can overcome the pretectal inhibition through a facilitatory effect as a consequence of recurrent excitatory activity but the response has a long latency. In this way he explains why animals normally prefer small size stimuli. Whenever the pretectal inhibition is decreased, either by an increased

motivational state or by a lesion, the tectal response is now controlled by tectal ganglion type III cells, thus changing the receptive field, color size preference, and reducing the latency of response, because these neurons arrive closer to the soma of tectal neurons.

## II. The Model

The description of the model will be divided in four parts; a brief description of the black box model of the retina, waiting for a more realistic retinal model, the description of the different pretectal cells, the proposed architecture for the two-dimensional model of the tectum and, finally, the proposed interaction among retina, tectum and pretectum.

### II.1 Black box model of the retina

As we have seen, retinal ganglion cells are sensitive to geometry in relation to the direction of motion, to contrast, and to the speed of the stimulus.[4,15]

Our black box model of the different ganglion cells (types II, III and IV) is based on the curves obtained by Ewert for the response of these cells to prey and non-prey like stimuli (see Fig. 2) and the speed function obtained by Grüsser and Grüsser-Cornehls[15] and Ewert.[4]

The model simply defines the rate of response of type II, III and IV ganglion cells depending on the size and speed of motion: the first with Ewert's graphs and the second with the following equation.

$R = kv^{\delta}$; where $k$ and $\delta$ are constants and $v$ is the speed of the object. $R$ is the frequency response of the retinal cell.

Each type of ganglion cell projects point to point to each tectal and pretectal column. In the present model we have not considered the spatial representation of the different retinal receptive fields; we have only considered that the center of each type of retinal cell projects to the corresponding point either in the tectum or pretectum. Each retinal ganglion axon projects to a specific column, and excites the surrounding neighbors with less intensity.

Each time a stimulus arrives at the receptive field of a group of ganglion cells, they will generate a response frequency R depending on the size, speed, and direction of motion of the object. The parameters of the stimulus are specified by the modeller. We simulated the presence of a stimulus simply by a variable which defines when the stimulus should be present in a given zone and for how long it should rest there, depending on the speed and size of the object.

### II.2 Pretectal cells

Because of the limited data about the anatomy of the pretectal region, in this model we simply considered single units to simulate the postulated behavior of pretectal cells. We proposed two types of pretectal neurons: The first which represents the pretectal TH-3 cell of Ewert which is mostly sensitive to predator-like stimuli

and which Ewert postulates to play a very important role, through its inhibitory action, for prey-predator recognition of tectal neurons. This neuron receives retinal afferents from ganglion cells of types III and IV. The second pretectal neuron is related to prey selection and has already been described elsewhere.[3] Briefly, this neuron is called a sameness cell, and receives the excitatory effects of all tectal pyramidal cells except the one or the ones of its blind spot. These cells in their turn inhibit retinotopically the corresponding tectal column. (see Fig. 6)

II.3 Two-dimensional model of the tectum

The two-dimensional model of the tectum is shown in Fig. 4 and is an expansion of the one-dimensional model of the tectum described elsewhere.[2,3] The model is now constituted of 64 columns. For the two-dimensional model the number of cells and their

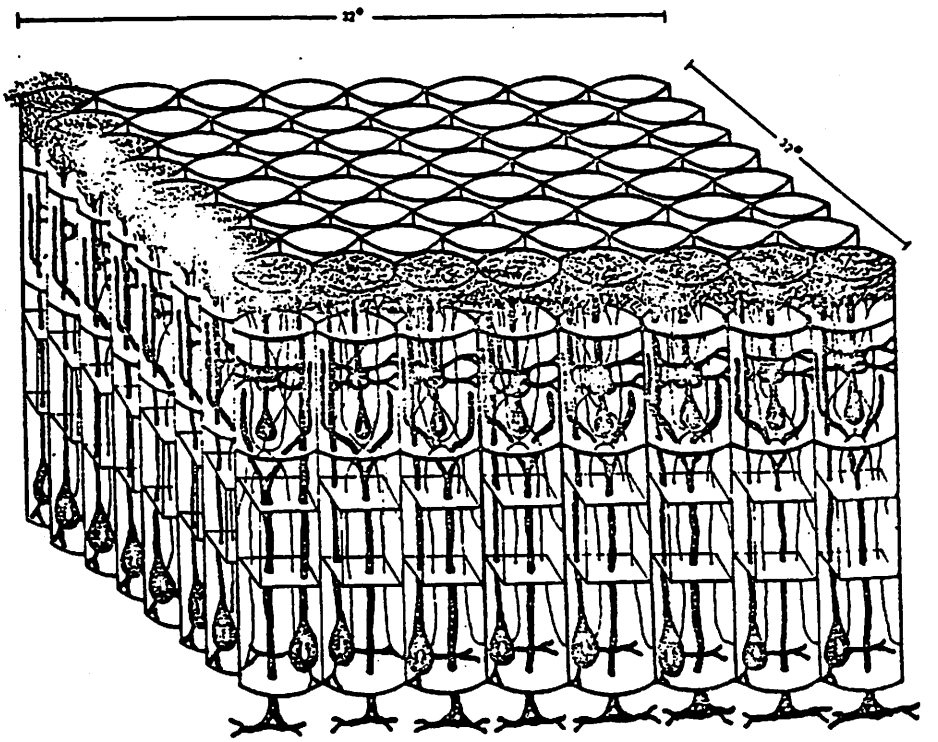


Fig. 4. Representation of the two-dimensional model of the tectum constituted of 64 columns.

interactions is greatly increased. We will give a brief description of the most important considerations. We have elsewhere[2,3] modelled the tectum as constituted of tectal columns. Briefly, each column is constituted of one large (LP) and one small (SP) pear shaped cell, one stellate neuron (SN), one pyramidal (PY) cell (the efferent cell of the column) and one glomerulus (GL) where the optic fibres arrive. The connections are indicated in Figure 5:

a) The glomerulus is constituted of the dendrites of LP and SP cells of its own column, the afferent optic fibres from ganglion type II cells, and the recurrent

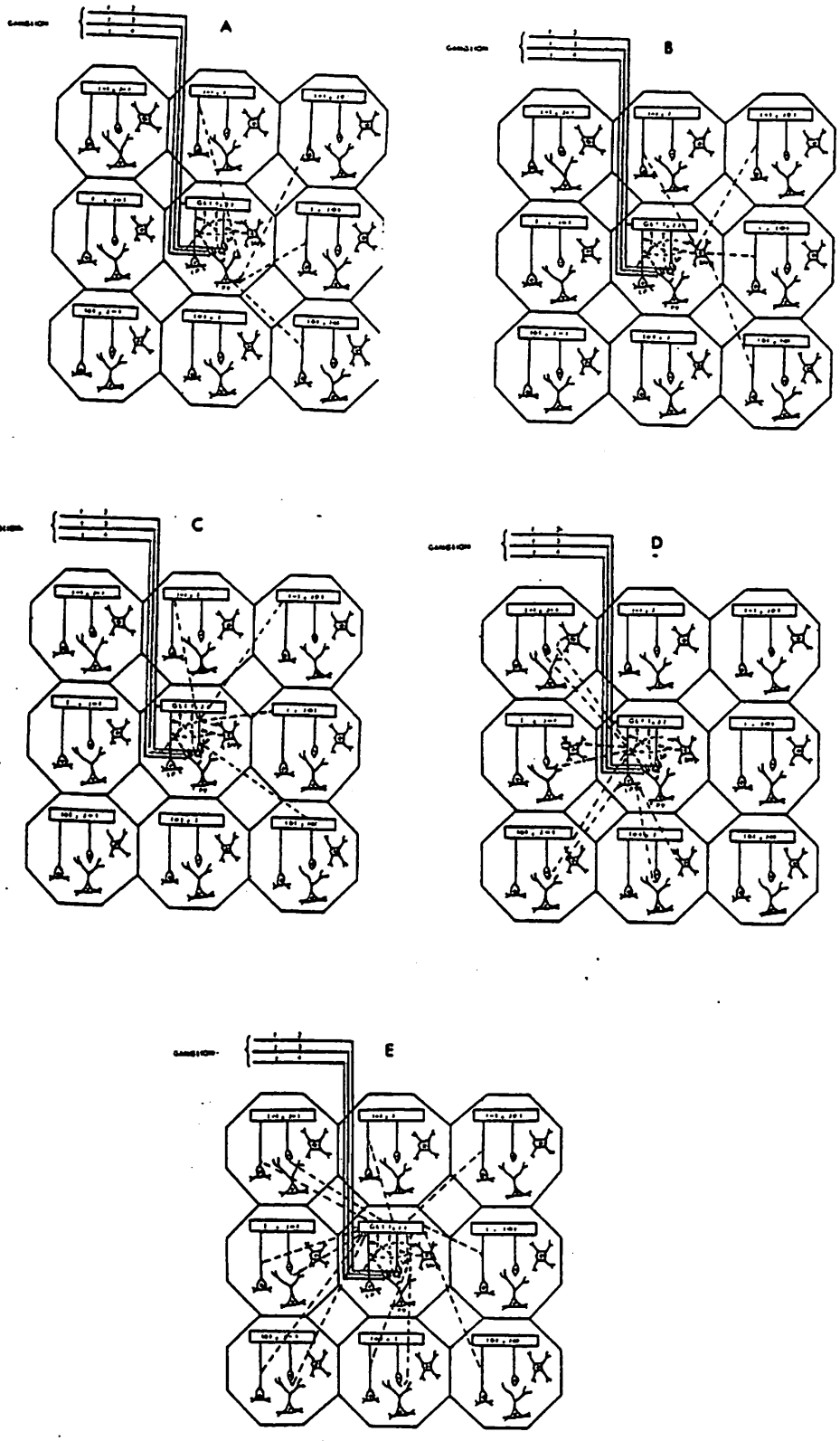



Fig. 5. Interactions among the tectal columns in the two-dimensional model of the tectum. (caption continued, next page)

A) Cellular afferents to PY cells. This cell is activated by LP, SP of its own column and by LP's of neighboring columns and it also receives afferents from retinal ganglion cells type II, III and IV. B) Cellular afferents to the SN neuron. This cell is excited both by LP's of its own and neighboring columns. C) Cellular afferents to SP. This cell receives excitatory afferents from the ganglion cells type II and from neighboring glomerulus and it is inhibited by SN of its column. D) Cellular afferents to LP. This neuron is excited by both retinal ganglion type II cells and by SP cells both from neighboring and its own column and it is inhibited by SN cells both from neighboring as well as its own column. E) Cellular afferents to the glomerulus. It receives afferents from retinal ganglion cells type II and is excited by recurrent axons from LP and SP cells both from its column and neighboring columns.

axons of LP and SP cells both from its own column as well as from neighbor ones (see Fig. 5e).

b) Each LP cell receives afferents from retinal ganglion type II cells both through the glomerulus and through its dendrites along the length between glomerulus and cell body, from SP cells from its own as well as from neighboring columns, and they are inhibited by the SN of its own column as well as by neighboring ones (see Fig. 5d).

c) Each SP neuron is also activated by retinal ganglion type II cells through the glomerulus and interglomerular dendrites both from its own column and from right neighboring columns; this cell is inhibited by SN neurons from its own column (see Fig. 5c).

d) The SN receives afferents from LP cells both from its column and from right neighboring columns (see Fig. 5b).

e) The PY cell, the efferent cell of the column, receives afferents from optic fibres of type II, III and IV, from LP and SP cells of its own column and from LP cells of neighboring columns (see Fig. 5a).

II.4 Interactions among retina, tectum and pretectum

The diagram that shows the interactions among retina, tectum and pretectum is shown in Fig. 6. This figure shows that the retina sends retinotopically its fibres to both tectum (II, III and IV) and pretectum (III and IV). The two pretectal cells inhibit the activity of LP, SP and PY neurons of its corresponding column (see inset Fig. 6). One of these pretectal cells receives its afferents from ganglion retinal cells type III and IV, while the other receives its afferents from all the PY tectal neurons except from those of their blind spot. Finally the PY cell activity defines the direction of the orienting response and the discriminative abilities of tectal neurons.

The mathematical description of the two-dimensional model of the interactions among retina, tectum and pretectum can be seen in the appendix.

It is important to notice that the final architecture proposed for the interactions among retina, tectum and pretectum is the result of testing several alternatives from which this architecture is the one that best reproduces the physiological and behavioral results. For a detailed analysis of the architecture proposed for the tectum

see Lara et al.[1-3]

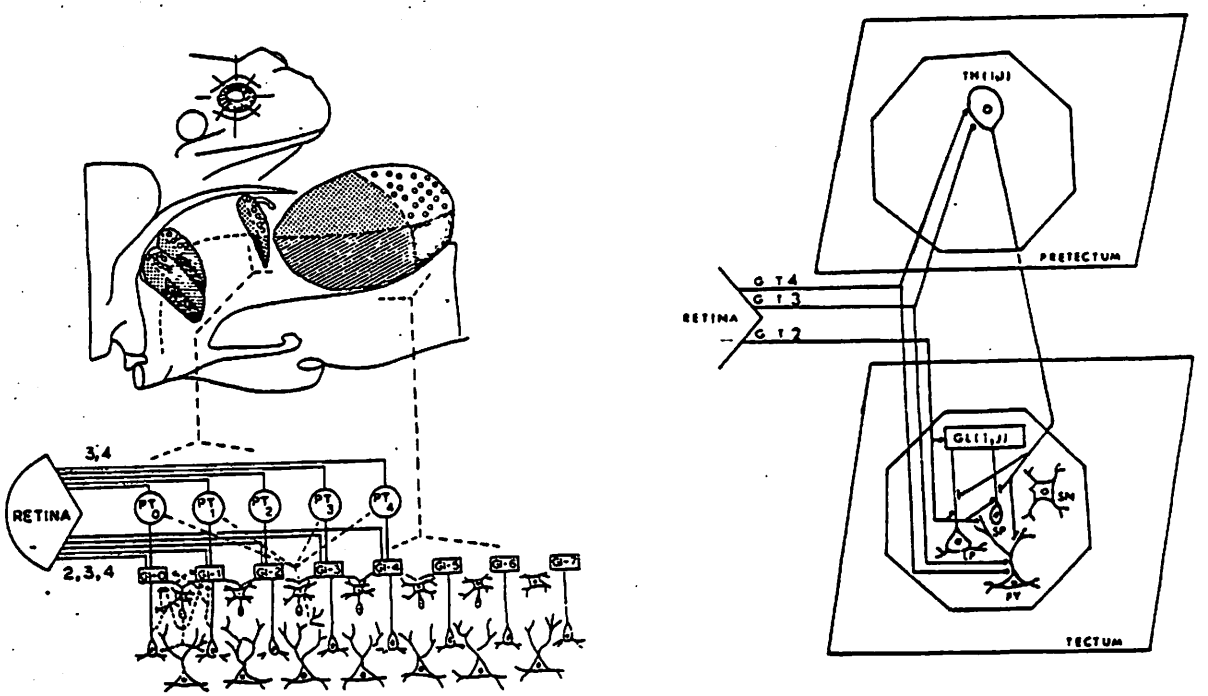



Fig. 6. Interactions among retina, tectum and pretectum. The retina sends fibres in a retinotopical way to both tectum (2, 3, and 4) and pretectum, TH3 (3, 4). The tectum PY cell excites all sameness cells (shown as PT for simplicity) except the one of its own column. Both pretectal neurons inhibit LP, SP and PY of the tectal column (right section).

## III. Computer Simulation

As mentioned above, the aim of the present model is to test the hypothesis both of prey-predator recognition independent of the direction of motion and size preference through a model based on anatomical and physiological grounds. We will present the results of the computer simulation in two ways: pyramidal tectal response of each of the 64 columns of the two-dimensional model of the tectum and through graphs that show several computer experiments that could be directly compared with experimental results. In the first case we divided the tectum in 64 sections each one representing in the horizontal axis the period of simulation and the vertical axis the PY activity. The PY activity is shown through its membrane potential and whenever the membrane potential reaches the threshold value we indicate it by an action potential. We did not simulate the generation of the action potential in our neurons but it is simply a way of showing the results that could be easily compared with experimental results. Both ways of showing the actual behavior of the model allow us to make analogies and comparisons with experimental observations.

For the different simulations we used three types of stimuli: rectangles whose longest axis moves in the direction of motion (type a); rectangles whose longest axis moves perpendicular to the direction of motion (type b); and squares of different sizes (type c).

III.1 Behavior of pretectal cell TH3

Our purpose in the simulation of the behavior of this neuron to the different types of stimuli is to show how the interaction of ganglion type cells III and IV could generate their properties. Trying different weights (see table for the final values) the behavior of this cell to the different types of stimuli is shown in Fig. 7A. As can be seen in this figure, the response of this cell to the different types of stimuli is very similar to the behavior of the pretectal cell that Ewert suggests is related to prey-predator recognition: see Fig. 3 for comparison. This neuron responds more strongly to stimuli of type c, then to those of type b, while the response to stimuli type a does not change very much for different sizes of the object presented.

III.2 Behavior of tectal cells to different configurations of the stimulus without the inhibitory effect of pretectal cells

It has been shown that tectal neurons without the inhibitory effect of pretectal cells respond better to stimuli of type c, then to stimuli of type a, while they give a slow response to stimuli of type b.[4] (see Fig. 3)

It is also known that ganglion retinal cells of types II, III and IV arrive at the tectum. It has been suggested that the facilitation effect for prey-catching activity is mainly controlled by type II ganglion neurons[4,6] but anatomical studies and changes in the receptive field of the animal, latency of response etc. also suggest that tectal cells controlling prey-orienting behavior are also stimulated by ganglion cells of types III and IV.

For the above reasons, we tested different configurations in our model and the configuration that best fitted the physiological results is shown in Fig. 5. This figure shows that ganglion type II cells arrive at the GL, LP, SP and PY, as already described in detail elsewhere,[1,2,3] while neurons of type III and IV only arrive at the PY neuron. Thus the column activity is mainly controlled by type II ganglion afferents while the PY response is the combination of all three ganglion cell types.

The response of this neuron to the different types of stimuli is shown in Fig. 7D where it can be seen that it responds best to stimuli type c, then to those of type a, and lowest to those of type b. This behavior reproduces in general the experimentally observed behavior of tectal cells without pretectum (see Fig. 3D for comparison).

III.3 Model of the interaction among retina, tectum and pretectum for prey-predator recognition

As we mentioned above, there is a tectal neuron whose behavior closely matches the behavioral response of the animal[4]: its response is facilitated for stimulus

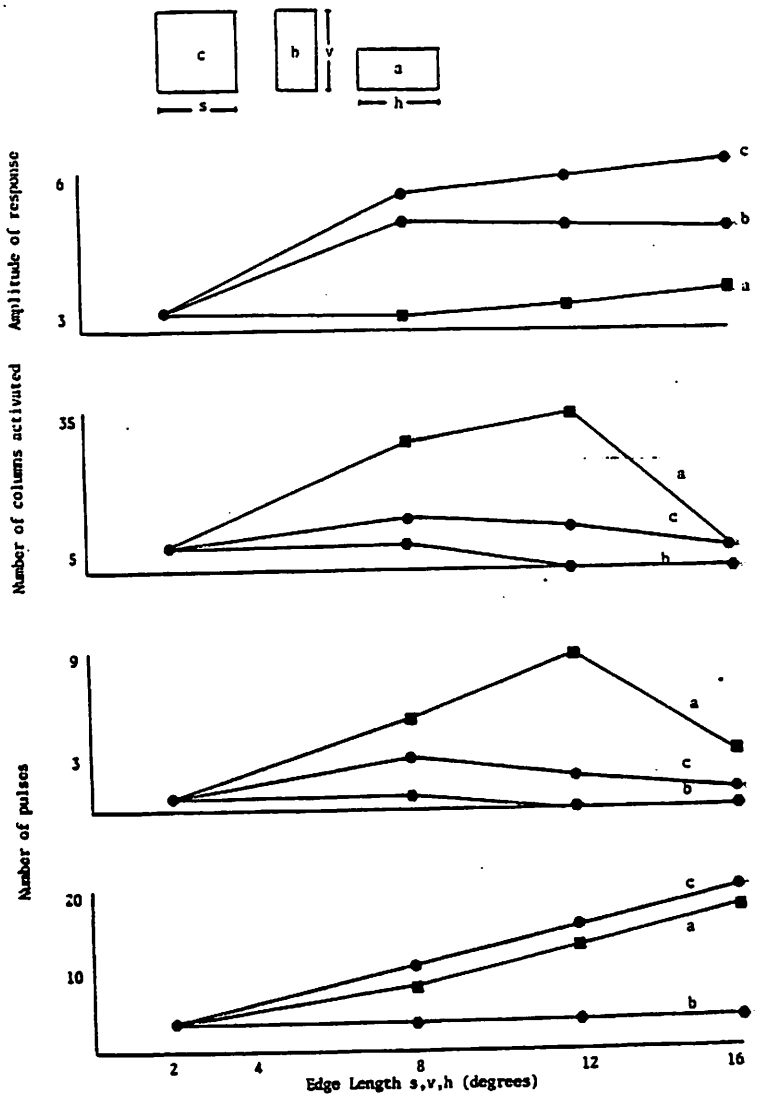



Fig. 7. Computer simulation of the response of pretectal and tectal cells to the different configurations of the stimulus (a,b,c). A) Pretectal cell response: it is mostly sensitive to stimulus type b and c. B) Response of the 64 PY cells to the three types of stimuli (a,b,c): the tectum is mostly sensitive to stimulus type a and it is inhibited by stimulus type b. C) PY response to the three configurations of the stimulus type a. D) PY response when pretectum ablation occurs: PY cells are mostly sensitive to stimulus type c, then to those of type a.

type a, inhibited by stimulus type b, while a combination of an initial facilitation and then an inhibition is observed for stimuli type c.

The interaction among retinal cells, pretectum and tectum in our model, is shown in Fig. 6. In this figure it can be seen that retinal ganglion cells arrive both at the pretectum and to the pyramidal cell of the tectum. The pretectal cell then inhibits LP, SP and PY in the tectal column (see Lara & Arbib[1-3] for this configuration between tectum and pretectum).

In Fig. 7C we show the response of the tectal columns through the activity of

the pyramidal neuron to the three types of stimuli. It can be seen that the PY greatly increases its response for stimulus type a, while for stimulus type b the response is greatly inhibited and for stimulus type c there is an initial facilitation and then an inhibition. These results reproduce in a general way the observed physiological and behavioral observations (see Fig. 2 for comparison). Fig. 7B shows a graph of the number of times the tectum is activated when a stimulus is presented, thus it is a better measure of the possible control by the tectum of the orienting response. This figure is equivalent to Fig. 7C.

In Fig. 8 we show the response of the 64 columns of the tectum to the three types of stimuli. It can be seen that the tectal activity is stronger for stimulus type a (Fig. 8a), then type c (Fig. 8b) and the lowest activity is for stimulus type b (Fig. 8c).

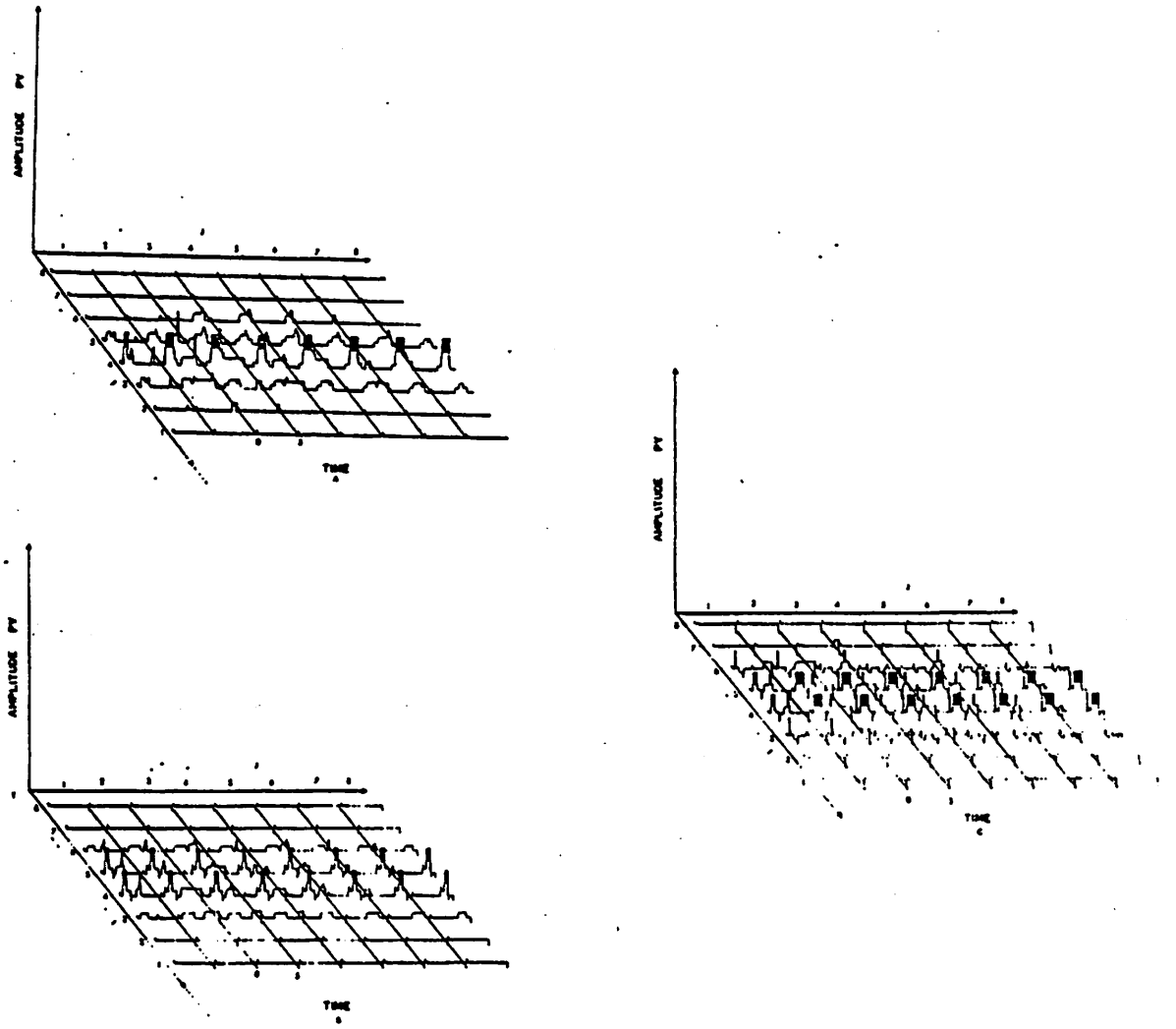



Fig. 8. Computer simulation of the PY response of the 64 columns of the tectum to the different configurations of the stimulus: (A = type a, B = type b, C = type C). The horizontal axis shows the temporal response of each of the 64 columns, while the vertical axis shows the PY cell response. Dark parts of the trace show the action potentials of PY cells. The response of the PY cells is stronger for stimulus type c, then to type a, and finally to type b.

III.4 Directional invariance for prey-predator recognition

It has been shown both behaviorally and physiologically[7] that prey-predator recognition is independent of the direction of motion of the stimulus, the only relevant factor being the relationship between geometry and direction of motion. We test the behavior of our model for prey-predator recognition in eight different directions. We used a 12 x 2° stimulus which we know produces a very weak (almost no response in most tectal cells) response as a stimulus of type b and a strong response as a stimulus of type a. We represent the results of this simulation in the same way that Ewert represented his experimental observations. We used the contrast formula:

$$D_{wa} = \frac{R_w - R_a}{R_w + R_a}$$

where $D_{wa}$ is a measure of the discrimination between worm (w) and antiworm (a) stimuli. $R_w$ is the response to worm-like stimuli and $R_a$ is the response to antiworm-like stimuli. We then formed a circle divided by eight lines each one representing a given direction of the stimulus and the values of $D_{wa}$ ranges between -1 (the origin) and +1 (the outer circle). The inner circle is when $D_{wa}$ is equal to 0.

In Fig. 9 we show the response of tectal columns for prey and non-prey like stimuli showing that the discrimination is independent to the direction of motion.

Fig. 10 and 11 show the actual tectal response of the 64 columns to the presentation of prey (Fig. 10) and non-prey stimuli (Fig. 11) in different directions. It can be seen that the response to prey or non-prey stimuli is invariant to the direction of motion.

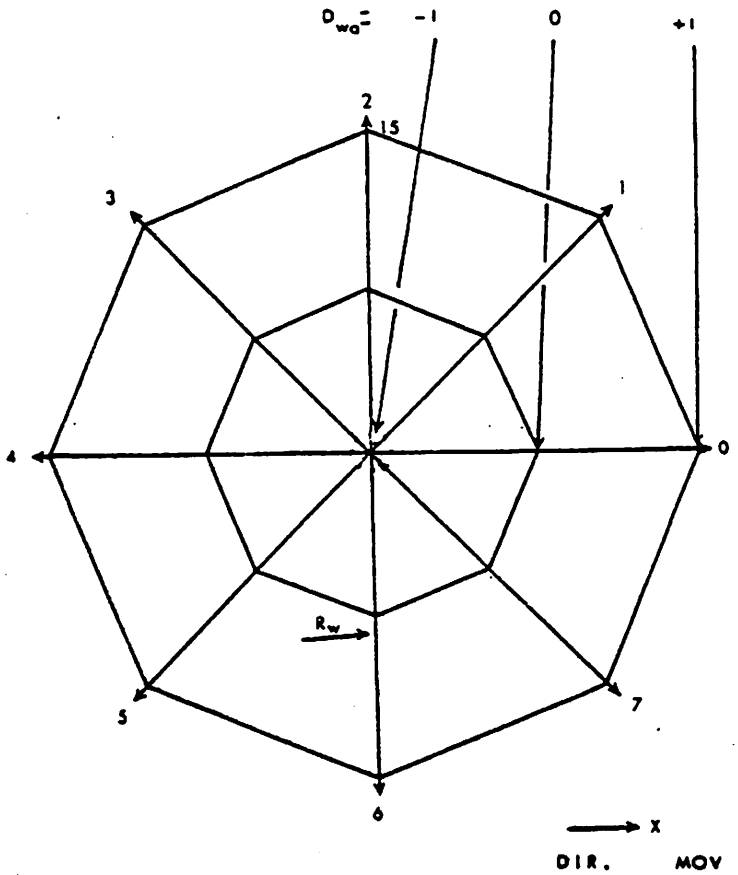
III.5 Size preference as a result of the interaction between tectum and pretectum

It has been observed that prey selection and latency of response can be modulated depending on the motivational state of the animal.[9] Ingle has suggested that these changes are the result of a reduced inhibitory effect from pretectal neurons to tectal activity.

In order to test this hypothesis we used our model of prey selection described elsewhere,[2,3] where pretectal cells receive afferents from all tectal PY neurons except those of a given region which constitute their blind spot. In our present version of this model we postulate that the blind spot can be changed according to the motivational state of the animal simply by an inhibitory effect of the pretectal neurons, possibly from the telencephalon, increasing or reducing the size of the blind spot according to the motivational state of the animal. Thus we postulate that when the animal is greatly motivated for prey catching behavior the following phenomena occur:

The inhibitory effect of pretectal cells of type 2 is greatly reduced (possibly increasing the threshold value of this neuron), and the blind spot of the sameness cells is increased.

Based on the above postulates we studied prey selection of the animal in the normal and motivated state. We represent our results in the same way that Ingle and




W – WORM

a – ANTIWORM

$$D_{wa} = \frac{R_w - R_a}{R_w + R_a}$$

Fig. 9. Computer simulation of PY cell response of the two-dimensional model of retina-tectum-pretectum for prey-predator recognition in eight different directions. The graph shows that the PY response is direction invariant. The formula shows how it has been quantified for the invariance of prey-predator recognition: $R_w$ is the number of responses when a worm-like stimulus is presented and $R_a$ is the response when an antiworm-like stimulus is shown. The outer circle is the value of $D_{wa}$ of the PY cell response.

Ewert did in their experimental observations[8]: we used a stimulus of a given size as a point of comparison; we then used stimuli of different sizes and studied which one of them was chosen when the animal was both in a normal or in motivated state. We also studied the latency of response in both cases.

Fig. 12 shows that a normal animal prefers smaller stimuli of 4° while the motivated animal always preferred larger stimuli. This figure also shows that the latency of response is greatly reduced in the motivated animal. These results reproduce

in general terms the observed experimental results (see inset for comparison).

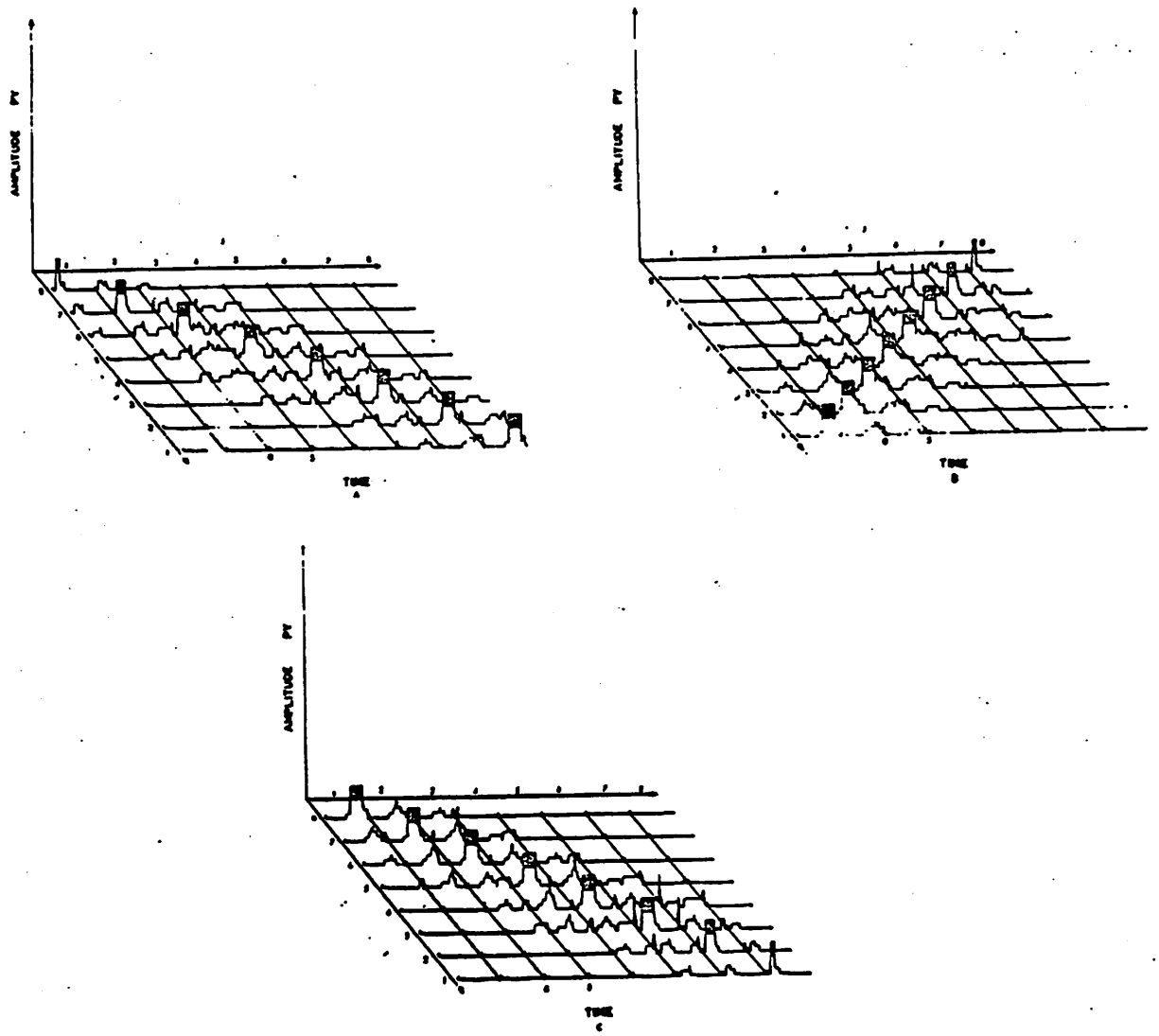


Fig. 10. Computer simulation of the 64 columns for prey-like stimulus in three different directions. The response is direction invariant.

## IV. Discussion

With the present model we have been able to simulate a great range of physiological, anatomical and behavioral observations. When we simulated a tectal column we reproduced the behavioral and physiological results obtained for prey-catching facilitation.[1] This model was based on the anatomical and physiological studies of this region. We then expanded our model of the tectal column to a one dimensional model of the tectum where we reproduced the facilitation of tectal response when the stimulus is elongated along the direction of motion as well as the facilitation to double stimuli moved along the direction of motion, with the preference of the animal being

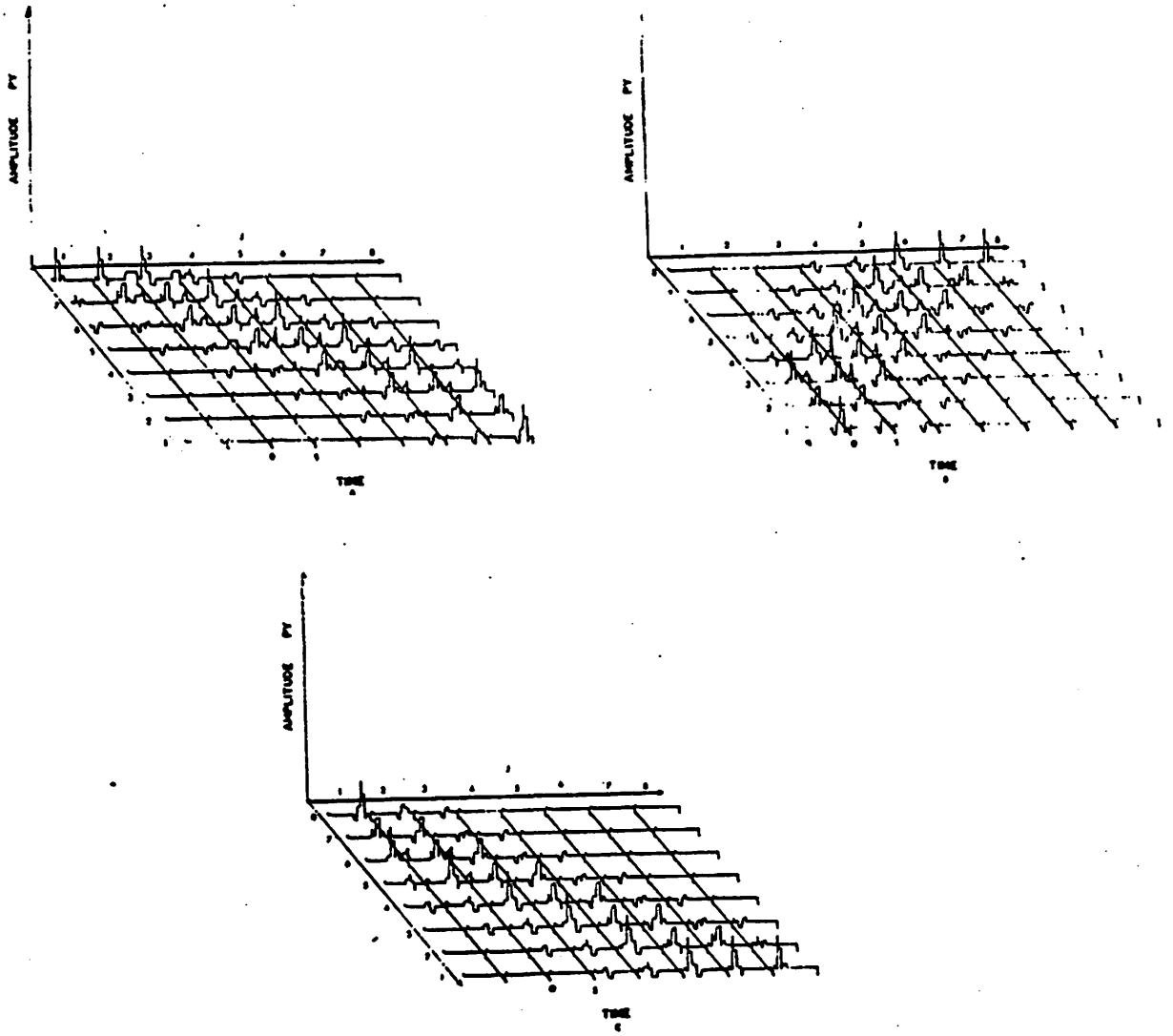


Fig. 11. Computer simulation of the 64 columns for predator-like stimulus in three different directions showing that it is direction invariant.

to orient to the leading of the two objects.[2] We then proposed a one-dimensional model of the interactions among retina, tectum and pretectum for prey selection.[3] With the expansion to two dimensions we have here been able to reproduce prey-predator recognition independently of the direction of motion, and size preference depending on the motivational state of the animal. With this method we thus have been able to integrate step by step, modelling with an increased hierarchical complexity, a theory of how the processing of information performed by the different brain regions of amphibia may control their behavior.

Our modelling studies in combination with the experimental evidence we have used suggest that the behavior of amphibia is controlled by the cooperative activity among

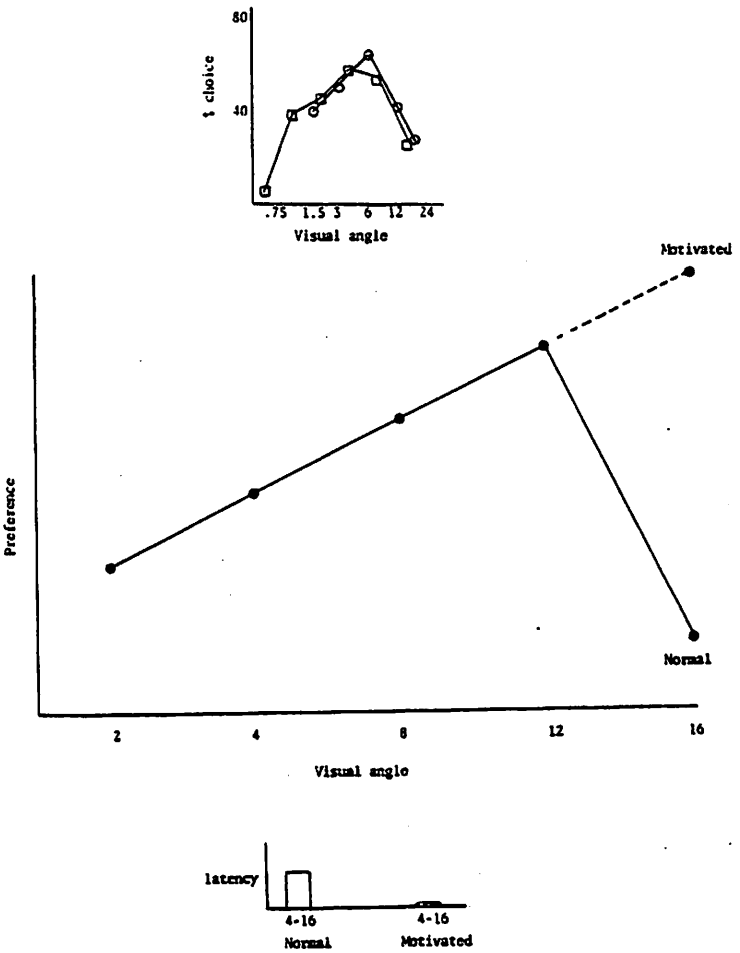



Fig. 12. Computer simulation of the response of the two-dimensional model of retina-tectum-pretectum to two stimuli of different sizes. The graph shows the hierarchy of preference in a normal and a motivated animal. In a normal animal the animal prefers the 4° high stimulus to the 16° high stimulus, while this preference is inverted in the motivated animal. In the lower part of the figure it is shown that the latency of response is also reduced in the motivated animal. See inset for comparison with experimental results. (From Ingle, 1977)

different brain regions. Each region itself has functional units for the processing of information of specific properties of the stimulus. In this way the retina has different features of the stimulus. Then the pretectal neurons, or maybe other thalamic cells, process features of the stimuli related to predator-like stimuli or static objects.[6,15] We know that in the tectum there are cells which seem to be very sensitive to prey-like stimuli; however, there is also evidence of cells which are mostly sensitive to predators as well as to other variables such as distance of the object, position in the visual field, etc.[5,7] This suggests that each region has different functional groups processing different properties of the stimulus whose integrative activity give the desired response. Our present modelling has thus neglected the

existence of other functional units with specific processing of information which will generate the proper response of the animal. Our simulation has only considered a part of the integrative activity of the tectum which controls the size, orientation and the recognition of prey stimuli. Further modelling should integrate other functional units in the tectum and in other regions so we may have a clearer idea of how these functional units interact among each other to produce the proper response. Similar ideas of the type of processing of information that the nervous system is doing has been mentioned by Ewert[5,7] and Pellionisz.[16]

The specific hypotheses of the present model can be listed as follows:

1) The tectal columns controlling prey orienting behavior receive afferents from retinal ganglion cells of type II, III and IV. The tectal column facilitates the response to retinal type II afferents; while retinal ganglion cells of type III and IV control prey orienting behavior when the animal is in a motivated state or for the regulation of size constancy in the animal in combination with pretectal cells.

2) The inhibitory effect of pretectal cells gives tectal neurons the capacity for prey-predator recognition. The inhibitory effect of pretectal cells is mainly directed to the PY cell although a small effect can also be seen either on LP and SP or in the SN.

3) The directional invariance of prey-predator recognition is the result of tectal architecture.

4) Size preference is the result of a combined effect of a reduced pretectal inhibition of pretectal cell TH3 over the tectum and an increased blind spot of the sameness cell for prey selection. The change in the latency of response is also the result of this interaction. Both effects may be controlled by the telencephalon.

The present model can be considered as a different way of simulating the ideas of Ewert and von Seelen for the relations among retina, tectum and pretectum for prey-predator recognition. Ewert and von Seelen[17] proposed a model of prey-predator recognition in which the retina, tectum and pretectum acted as filters for specific configurations of the stimulus. Specifically, they proposed that the tectum was mostly sensitive to predator stimuli. The inhibitory effect of the pretectum to the tectum enabled the latter to discriminate between prey and predator. The limits of this model are: 1) they do not show how the architecture of the different brain regions will give rise to the properties of their postulated filters; 2) they only simulate prey-predator recognition with neither the possibility to reproduce other phenomena nor the capacity for expansion; 3) because of the linear nature of the model, it is only restricted to a given range of values; and 4) because the model is lumped both in space and time, it cannot be tested against the time course of response of specific cell types with specific retinotopic coordinates.

Our model, on the other hand, because of its anatomical and physiological bases can be tested against such experiments.

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## Appendix

We provide the mathematical definition of the two-dimensional model of the interactions between tectum and pretectum which complements the description of the one dimensional model of the interaction between tectum and pretectum given in Lara and Arbib.[3]

The specifications of threshold functions, membrane constants and weights is given in Tables 1, 2 and 3 respectively.

Glomerulus:

The equation defining the behavior of the glomerulus of the ith, jth unit column is given as follows:

$$\tau_{gl}\, \dot{gl}_{ij}(t) = -kl\, gl_{ij}(t) + U2_{ij}(t) + I_{ij}(t)$$

where $\tau_{gl}$ and kl are constants, U2 is the optic input from retinal ganglion cells type II, and $I_{ij}$ are the recurrent inputs from LP and SP cells of the unit as well as those of neighboring columns, and are defined as:

$$I1(t)=w_{gl.sp}(SP_{i-1,\ j-1}(t)+SP_{i,\ j-1}(t)+SP_{ij}(t)+SP_{i+1,\ j-1}(t)+SP_{i+1,\ j}(t))$$

$$I2(t)=w_{gl.lp}(LP_{l-1,j-1}(t)+LP_{i-1,j}(t)+LP_{i-1,j+1}(t)+LP_{i,j-1}(t)+LP_{ij}(t)+LP_{i.j+1}(t))$$

$$I_{ij}(t)=I1(t)+I2(t)+LP_{i+1,j-1}(t)+LP_{i+1,j}(t)+LP_{i+1,j+1}(t)$$

where the values of w are given in Table 3.

Stellate Neurons: (SN)

The ith jth stellate neuron can be defined as follows:

$$A = LP_{i-1,j}(t)+LP_{i-1,j+1}(t)+LP_{ij}(t)+LP_{i,j+1}(t)+LP_{it1,j+1}(t)$$

$$\tau_{sn}\dot{sn}_{ij}(t)=-K2\ sn_{ij}(t)+w_{sn-lp}A$$

where $\tau_{sn}$ is the membrane constant of these neurons, K2 and $w_{sn.lp}$ are constants and can be seen in Tables 2 and 3 respectively.

Large pear shaped cells: (LP)

The behavior of the ith jth LP neuron can be defined as follows:

$$A1 = SN_{i-1,\ j-1}(t)+SN_{i,\ j-1}(t)+SN_{i\ j}(t)+SN_{i+1,\ j-1}(t)+SN_{i+1,\ j}(t)$$

$$A2 = SP_{i-1,\ j-1}(t)+SP_{i,\ j-1}(t)+SP_{i\ j}(t)+SP_{i+1,\ j-1}(t)+SP_{i+1,\ j}(t)$$

$$\tau_{lp}\dot{lp}_{ij}(t) = -lp_{ij}(t)-w_{lp.sn}A1+w_{lp.th}TH_{ij}(t)+w_{lp.sp}A2+gl_{ij}(t)+U2_{ij}(t)$$

where $\tau_{lp}$ is the membrane constant of these neurons; gl is the glomerulus input; U2 is the optic input from retinal ganglion type II cells; TH is the thalamic input; and w's are the weight factors shown in Table 3.

Small pear shaped cells: (SP)

The behavior of the ith jth SP neuron is defined as follows:

$$A3=gl_{i-1,j}(t)+gl_{i-1\ j+1}(t)+gl_{i,j+1}(t)+gl_{i+1,j+1}(t)$$

$$\tau_{sp}\dot{sp}_{ij}(t)=sp_{ij}(t)-w_{sp.sn}sn_{ij}+A3\ w_{sp.th}(IH_{ij}(t))+U2_{ij}(t)$$

where $\tau_{sp}$ is the membrane constant of these neurons; SN is the inhibitory effect of the stellate cells; TH is the inhibitory effect from thalamic neurons; and U2 is the optic input from fibres type II from the retina; w's are the weighting factors that can be seen in Table 3.

Pyramidal Neurons: (PY)

The ith jth PY cell is defined as follows:

$$A4=LP_{i-1,\ j}(t)+LP_{i-1,\ j+1}(t)+LP_{ij}(t)+LP_{i,j+1}(t)+LP_{i+1,j+1}(t)$$

$$A5=w_{py.u2}U2_{ij}(t)+w_{py.u3}U3_{ij}(t)+w_{py.u4}U4_{ij}(t)$$

$$\tau_{py}\dot{py}_{ij}(t)=-py_{ij}(t)+w_{py.sp}.SP_{ij}(t)+w_{py.lp}A4-w_{py.th}TH_{ij}(t)+A5$$

where $\tau_{py}$ is the membrane constant of these neurons; SP is the excitatory effect of small pear cells; TH is the inhibitory effect of both pretectal neurons; and U2, U3 and U4 is the optic input from retinal ganglion cells type II, III and IV respectively.

The w's are the different weight factors shown in Table 3.

Table 1

Threshold Functions

LP = f ( lp - 1.0 )
SP = f ( sp - 2.0 )
SN = h ( sn - 0.2 )
PY = h ( py - 5.559 )
TH = g ( th - 3.7 )

Table 2

Membrane Constants

$\tau_{gl}$ = 0.35, k1 = 0.15
$\tau_{sn}$ = 0.65, k2 = 0.4
$\tau_{lp}$ = 0.3
$\tau_{sp}$ = 0.9
$\tau_{py}$ = 0.12
$\tau_{th}$ = 1, k3 = 7

Table 3

Weights

| | | |
|---|---|---|
| $w_{gl.lp}$ | = 1.0 | LP to GL |
| $w_{gl.sp}$ | = 0.1 | SP to GL |
| $w_{lp.sp}$ | = 0.8 | SP to LP |
| $w_{lp.sn}$ | = 8.0 | SN to LP |
| $w_{lp.th,s}$ | = 0.1, 0.4 | TH to LP |
| $w_{lp.s}$ | = 0.2 | S to LP |
| $w_{sp.sn}$ | = 20.0 | SN to SP |
| $w_{sp.th,s}$ | = .1, 0.4 | TH to SP |
| $w_{sn.lp}$ | = 2.1 | LP to SN |
| $w_{sp.s}$ | = 0.2 | S to SP |
| $w_{py.lp}$ | = 0.8 | LP to PY |

Table 3: Weights (continued)

| | | |
|---|---|---|
| $w_{py.sp}$ | = 1.0 | SP to PY |
| $w_{py.th,s}$ | = 0.9 | TH to PY |
| $w_{py.u3}$ | = 0.3 | U3 to PY |
| $w_{py.u4}$ | = 6.0 | U4 to PY |
| $w_{py.u2}$ | = 4.5 | U2 to PY |
| $w_{th.u3}$ | = 0.3 | U3 to TH |
| $w_{th.u4}$ | = 5.0 | U4 to TH |
| $w_{py.s}$ | = 0.4 | S to PY |