81-4

A NEURAL MODEL OF INTERACTION BETWEEN PRETECTUM AND TECTUM IN PREY SELECTION[1]

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

ABSTRACT

Didday has suggested that closed loop interactions in the tectum could explain prey-selection behavior in amphibia. The present model exhibits this behavior as resulting from closed loop interaction between tectum and pretectum. The work builds on our earlier modelling of the role of tectal columns in prey-catching facilitation. The main components of the model are a model of the tectum as a one-dimensional array of columns, a layer of pretectal sameness cells, and a layer of newness neurons.

---

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

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

Several brain regions in amphibia receive visual information (Fite and Scalia, 1976; Scalia, 1976) and can interact to give the proper motor response by their integrated activity. It has been shown (Ewert, 1970, 1976; Ewert and Ingle, 1971; Ingle, 1973, 1975) that the pretectum exerts a modulatory effect on the tectum in prey-orienting behavior, controlling prey-predator discrimination, habituation of prey-orienting behavior, preference of size of the stimulus, etc. The tectum in turn sends fibres to the pretectum, which seem to play a role in avoidance behavior. These hypotheses of tectal-pretectal interactions, however, have not considered the possibility of feedback systems that may integrate tectal and pretectal regions into a single functional unit to perform a given behavior.

Consider prey selection when several stimuli are present in the visual field of amphibia. It has been shown (Ingle, 1971, 1973; 1976a and b, 1978; Ewert, 1976) that animals always prefer the closer stimulus; the stimulus whose shape is elongated in the direction of motion; or new objects appearing in the visual field. It is not known, however, how this selection is obtained by the different brain regions in amphibia. Didday (1970, 1976) suggested that closed loop interactions in the tectum between different hypothetical layers could explain this behavior from a neural point of view. Present evidence of the anatomy (Szekely and Lazar, 1976) and physiology (Ingle, 1973, 1975) of the tectum indicates that

this structure is arranged in columns with a reduced lateral spread of information. This suggests that lateral processing of information among tectal cells must be done in conjunction with other brain regions. For this reason, we here redefine Didday's model and, instead of considering prey selection to be primarily a consequence of tectal processing, we postulate that is the result of a closed loop interaction between tectum and pretectum. We build on our earlier modelling of the role of tectal columns in prey-catching facilitation (Lara, Arbib and Cromarty, to appear; Arbib and Lara, to appear). The main components of our model of prey selection are: 1) A model of the tectum as a one-dimensional array of columns; 2) a layer of pretectal sameness cells; and 3) a layer of newness neurons that can be located either in the tectum or pretectum (see Fig 1).

2. PHYSIOLOGICAL BASES

Lettvin et al. (1959) defined two categories that must be considered as two extremes of several types of tectal cells. These categories were the newness and sameness cells, and are described as follows:

Newness cell:

1. Its receptive field is approximately 30 degrees in diameter, with considerable overlap with those of other newness cells.
2. It yields small responses to sharp changes in illumination.

3. Its response frequency increases if the motion of an object is irregular. Its response also depends on the velocity and size of the object and on the direction of motion.
4. It habituates very quickly.
5. Habituation is erased with a step of darkness.

Sameness cell:

1. Its receptive field includes most of the visual field, but includes a null region.
2. It does not respond to changes in illumination.
3. It responds to the presence of an object in its field by generating a low frequency pulse train. Response is maximum to objects about 3 degrees in diameter.
4. It notices with a burst of pulses all motion discontinuities. It discriminates among objects, fixing its "attention" on the one with the most irregular movement.

Subsequently, Grusser and Grusser-Cornehls (1976) and Ingle (1975) have reported tectal cells with similar behavior. Ewert (1971), on the other hand, found thalamic cells that presented almost all the properties mentioned for the sameness cells, and others not described by the above authors. He showed that the size of the blind spot could change with time in a range from 10 to 60 degrees.

We have described elsewhere (Lara, Arbib and Cromarty, to appear; Arbib and Lara, to appear) a model of the tectum composed

of columns processing information mostly in a vertical manner. Each column (see especially Appendix 2 of the former paper) has 1 glomerulus (GL), 1 large pear-shaped neuron (LP), 1 small pear-shaped cell (SP), 1 stellate neuron (SN), and 1 Pyramidal cell (PY). The afferents to the tectum are optic fibres arriving at GL, LP, SP, and PY, and diencephalic terminals arriving at GL, LP, SP, PY, and SN; the tectal efferents are the PY axons that can go to the reticular formation, spinal cord and toward diencephalic centers (Rubinson, 1968).

3. THE MODEL

The posited interaction between tectum and pretectum is shown in Fig 1, where we have represented tectal columns and pretectum cells in a schematic way. We posit, as Didday did in his model of the frog's tectum (1970), a competitive role for the sameness cells in the selection of the strongest stimulus, but we now locate these cells in the pretectum rather than in the tectum. The sameness cells, following the definition given above, have a large receptive field with a blind spot (approximately 30 degrees). These cells inhibit the tectum cells that are sensitive to the retinal area corresponding to the blind spot of the sameness cells. We propose that the tectal cell responsible for the localization of the orienting response is the PY neuron of the column, which may be correlated with the tectal cell (type 1) described by Ewert. These cells excite all the sameness cells located outside the blind spot, providing in this way an inhibitory effect on all tectal cells

outside the blind spot.

We study two alternatives for the specific inputs of the sameness cells:

1.- The sameness cells receive inputs only from the tectum, and are sensitive to the whole receptive field except for the blind spot;

2.- The sameness cells receive direct input both from the tectum and from optic fibers that makes them sensitive to the entire receptive field save for a specific blind area.

As we have mentioned above, diencephalic terminals can arrive at the glomerulus, at the LP, SP, and PY cells, and at the SN neurons. For this reason we will study the effects of tectal-pretectal interactions in prey-selection when the pretectal fibres arrive at different sites in the tectum.

An alternative, although functionally identical, architecture would be that the tectal neurons excite only retinotopically matched pretectal cells, and that these pretectal neurons in turn inhibit all tectal cells except those which correspond to it (see Fig 2).

3.1 Behavior of the Model

Whenever a stimulus is presented in a given region of the tectum, the tectal column affected will give a short initial response, through the PY, and then a delayed continuous activity; the delay is produced by the inhibitory effect of SN and diencephalic terminals (TH). When this inhibition is released, then a rebounding excitation in the column occurs as a result of

the long lasting depolarization of the glomerulus. The pyramidal cell activity will then excite the sameness neurons in the pretectal layer, except the one that is in its blind spot and that inhibits its column (located in parallel to the tectal column in Fig 1). This inhibitory effect of TH prevents other tectal columns from giving a response. In the case where simultaneous stimuli are present in the visual field of the animal, the activity of the pyramidal cell in each column will set the strength of inhibition in other columns, each one in proportion to the intensity of its stimulus; after an initial response of all the activated columns, a competitive interaction is established among them until the one that is receiving the strongest excitation suppresses the activity of the others. Following Didday, we propose that the newness neuron is activated when a new stimulus is presented in a specific location of the visual field, thus eliminating the hysteresis of the system to the already established inhibition. We have also simulated habituation effects when a stimulus is continuously present in the receptive field of the animal. For the mathematical definition of the model see the Appendix.

4. COMPUTER SIMULATION

The simulation of selection among different stimuli was studied by stimulation with step functions of different intensities to the appropriate glomeruli. We have chosen (Arbib and Lara, to appear) to simulate the overlap of receptive fields of tectal cells by having the receptive field of each glomerulus of the model

receive afferent fibres focal for its neighbors (from the right and from the left) with half intensity. We show the results of our simulation in two ways: through the PY response of each of the eight columns simulated, because these neurons represent the state of activation of each column and possibly a motor response; and second through graphs indicating the sensitivity to different parameters of the simulation for the convergence to the strongest stimulus. We have considered convergence to occur when a continuous activity of a given column is present for a considerable time.

As in (Arbib and Lara, to appear), the 8 columns of the tectum, now in combination with the 8 pretectal cells, represent a simulated space of 40 degrees. Each column has a receptive field of 15 degrees, with stronger intensity within a central range of 5 degrees. The response of PY cells will represent the orienting reaction of the animal; the location of which is determined by the PY cell that responds first and with the strongest intensity. We have considered different cases where this hypothesis can be slightly changed, waiting for experimental research to better determine the cellular correlates of a spatially-tuned response. We have simulated cases in which the stimuli stay for comparatively long periods in a given location. A more realistic simulation would have to consider multiple moving stimuli.

4.1 Competition among Stimuli of Different Intensities when TH excite SN cells.

Fig 3 shows the behavior of the 8 columns when a stimulus of intensity 2 is applied to column 1, one of intensity 3 to column 4, and one of intensity 1 in column 6. Notice that after a brief initial response in columns 1, 4, and 5, the rebounded excitation yields to convergence of response in column 4. It is interesting that column 5 gave a response even though it was not directly excited, as a result of the overlapping receptive fields of its neighbors. This figure also shows that TH activation of SN suppresses all the activity of the LP and SP neurons within the column, so that the only effect seen in the PY membrane potential is that of the stimulus.

4.2 Competition among Stimuli of Different Intensities when TH inhibit GL.

Fig 4 shows the results of using the same stimulation of the above experiment but with TH now inhibiting the GL. The behavior of the cells is very similar to that in the last experiment, but the PY response is silenced by some periods of inhibition, possibly as a result of the SN inhibitory effect. In this case, however, the state of excitation of the column is suppressed because the long lasting depolarization of the GL has been inhibited (cf. Fig 8 of Lara, Arbib and Cromarty, to appear).

4.3 Competition among Stimuli of Different Intensities when TH inhibits LP, SP, and PY neurons.

Using the same stimulation as above, Fig 5 shows the response of the 8 columns when TH inhibits LP, SP, and PY cells. In this case, the PY response is a combination of the general state of excitation of the column, and inhibitory actions from TH fibres. For this reason, some PY cells produce a brief response, i.e., column 1. It is also interesting that in this case the initial response of the columns excited by a weaker stimulus is delayed.

With these experiments we have shown that TH effects on the tectum in prey selection behavior are similar whenever it arrives at GL, at LP, SP, and PY cells, or (with reversed sign) at SN neurons. The tectal response is, however, more sensitive to the effects of TH fibres when they arrive at the SN neurons (see Fig 6). We will see below, however, that this sensitivity is not very useful for the animal when a new stimulus is presented in the visual field or when a stimulus disappears.

In the following subsections we will only show the behavior of the model to the different sites of destination of pretectal fibres when interesting differences exist among them. Otherwise we will only show the effects when TH excites SN.

4.4 Competition among Stimuli of Different Intensities when the Optic Input also Excites Pretectal Cells.

We have mentioned that pretectum receive optic afferents; and we know that sameness cells are sensitive to small objects. For this reason, it is interesting to study the effects on prey selection in our model when the sameness cells are activated by the visual input. Fig 7 shows the results. The initial response to the weaker stimulus is inhibited, but the rebounding excitation is delayed, thus the latency of convergence is reduced. The latter effect occurs because the inhibitory effect of the SN lasts longer. The general results are identical to those without thalamic optic input, but the suppression of competitive columns is faster, although the latency of convergence is reduced because of the extra inhibition.

4.5 Competition among Two Equally Intense Stimuli.

Fig 8 shows the behavior of the tectum-pretectum interactions when two stimuli of equal intensity are present in the visual field, columns 2 and 5. The PY response of these columns shows an alternation of excitation and inhibition, without convergence to the response. If in these conditions we introduce a third stimulus that by itself does not produce a column response, we can see that it polarizes the tectal excitation in the direction where it is applied (Fig 9 A and B), thus making the system converge to one of the two equally intense stimuli. It is important to notice that this result is not simply the effect of the stimulus upon the

glomerular receptive field, because the new stimulus does not affect it in a direct way, but is the result of tectal-pretectal interactions. In this way it seems that convergence of response is the result of a gradient of excitation rather than a pointwise competition.

4.6 Competition between Two Stimuli with the Response given in the Interstimulus Space.

Ingle (1971, 1976a) has shown that if he presents in the frontal field a pair of stimuli separated by 30 degrees, the animal responds between the stimuli. In Fig 10 we show the conditions needed for this phenomenon to occur in our model. When we present two nearby stimuli (one GL interstimulus distance) with almost equal intensity (3 for one column and 2.5 for the other) the convergence occurs in the column between the two stimuli. We see again in this case that the response is not a pointwise effect but the result of a gradient of excitation.

4.7 Effects on Competition between two Stimuli when One of them Disappears.

In this experiment we found different hysteresis effects following withdrawal of an object from the receptive field, depending on where TH fibres reach the tectum. Fig 11 A shows the effect of competition between two stimuli of different intensity, 2 for column 2 and 3 for column 5. Here the stimulus of the stronger one, column 5, disappears. In this figure TH arrive at the SN and

the recovery from this inhibition is very long, because no response appears in column 2 for the period of simulation. The same thing happened when TH arrive at the GL (see Fig 11 B). In contrast, when the TH arrive at the LP, SP, and PY neurons, the recovery is immediate (see Fig 11 C). This effect is produced because the general state of excitation of the column is still very strong, because the long-lasting depolarization in the glomerulus is still present, and the SN inhibition has not been increased by external means, as is the case for the first experiment. This result suggests a tractable neurophysiological experiment that could illuminate the mechanisms underlying prey competition.

4.8 Behavior of Newness Neurons when New Stimuli are Introduced in the Visual Field of The animal.

We have seen that the hysteresis of the inhibitory effect in tectal-pretectal interactions delays a response to other objects in the visual field of the tectum. It has been observed neurophysiologically that some cells react to the presentation of new stimuli (see Section 2, "Physiological Bases") and they habituate very fast, suggesting that these cells are sensitive to a novel stimulus. We have simulated the effect of introducing a new stimulus when convergence to another one has been established. The new stimulus has a stronger intensity than those already present in the visual field. Fig 12 shows the response to a single stimulus applied in column 2 and the effect of introducing a stronger one to column 5, which immediately suppresses the activity of column 2, as a result of the combined excitation produced by the newness neuron and the stimulus.

4.9 Competition and Habituation.

Another interesting case in prey competition among stimuli is to present repetitively a stimulus in a given position of the visual field of the animal and then present two stimuli, one in the same site of stimulation and the other elsewhere. Behavioral experiments show that the animal always responds to the new stimulus, i.e., there is habituation to the one that was repetitively presented (Ewert and Ingle, 1971).

The simulation of the effects of habituation to a repetitively presented stimulus is shown in Fig 13, where we initially present a stimulus for a given interval (column 1), then we withdraw it, and finally we present two stimuli of equal intensity simultaneously (columns 1 and 4). This figure shows that column 4 gives an immediate response, because the input to column 1 is habituated.

4.10 Tectal Response to a Moving Stimulus with Pretectal Inhibition.

In the accompanying paper (Arbib and Lara, to appear) we have studied the tectal response to moving stimuli of different configurations. We showed that stimulus elongation increased the state of activation of several columns, which were simultaneously firing. In our hypotheses of the possible role of the tectum in orienting behavior, we postulated that the column that was first activated with a sustained response was the one defining the location of the orienting response. In this section we show that the interaction between tectum and pretectum produces an increased

acuity of tectal behavior, with the tendency for only the column that is most strongly activated to be the one that is firing. We have simulated Fig 10 of the previous paper, but now with pretectal interaction. Fig 14 A shows the tectal response to a moving stimulus when the pretectal fibres arrive at the thalamus; we can see that the tectal response is constrained to a single column which, because of the long lasting inhibition of the SN prevents the response of other columns. Fig 14 B shows the response to the same stimulus but now the pretectal fibres arrive at LP, SP, and PY neurons. We can see that the unit column has the tendency to respond independently. However, when it stops firing, other tectal columns start responding. Fig 14 C shows the tectal response when the pretectal fibres arrive at the glomerulus, where we again see the tendency to isolate the tectal response to a single column at a time, but with stonger hysteresis effect than the above case.

5. DISCUSSION

The present paper proposes a modification of Didday's model of prey selection behavior in the tectum. The main differences between Didday's model and our model are the following:

1.- The sameness cell behavior of our model is more tied to the physiological results obtained for these cells than that proposed by Didday. We postulate that the blind spot is completely unexcited, while Didday proposed inhibitory effects when this region was stimulated.

2.- The one dimensional model of the tectum is based on anatomical, behavioral and physiological studies.

3.- The lateral modulation of the parallel processing of information is obtained through the interactions between tectum and pretectum; in contrast, Didday proposed a lateral spread of information in the tectum that is not supported by physiological or anatomical studies.

4.- The convergence to the strongest stimulus in our model is obtained through the natural behavior of the proposed equation for the cells; while Didday had to use a convergence function to assure the speed of response.

5.- The equations proposed in our model simulate the physiological changes occurring in the cell; while Didday used algebraic equations with postulates not completely supported by physiological evidence.

6.- In our model we have not simulated the different types of ganglion cells and their effects on the tectum; while this behavior was simulated in Didday's model.

7.- We have briefly considered the possible effects of habituation in prey selection behavior.

8.- We have studied different possible sites of interactions of thalamic fibres on the tectum.

Ingle (1973b) has shown that double stimuli do not in general produce a delay in motor response, with the exception when they are presented in the frontal receptive field with an interstimulus distance of 30 degrees. He suggests that this inhibitory effect is the result of intertectal competition to control the motor

response. Later studies (Ingle and Mckinley, 1978; Ewert, 1976) indicates that there are cases when the presentation of two large stimuli to the visual field of the animal does produce an inhibitory effect on the rate of pursit of the object. Arbib and Lara (to appear) suggested that, for short distances, this may be the consequence of intratectal interactions. When the interstimulus distance is increased we then propose that the effect results from tectal-pretectal interactions. The contradictory evidence indicates the need for experiments with better controls isolating the stimulus and eliminating the possiblity that other, apparently unimportant, stimuli bias the behavior of the animal. This would eliminate the competitive effect shown in Figs 9A and 9B. These results suggests that the animal will have the tendency to snap toward the visual region which presents a more interesting number of stimuli, eliminating the delay in the response.

Ingle (1973b) has also shown that when two close stimuli are moved away from the animal, it has the tendency to snap between them. We have shown that this could be produced when one of them is less strongly excitatory than the other. New experiments with different stimuli and different motions will further clarify this hypothesis.

Our model studies tectal behavior when pretectal fibres arrive at three different sites on the tectum: the SN; LP, SP, and PY cells; and at the GL. The experiments showed that the convergence of the response was more stable when the fibres arrive at the SN. This stability, however, produces a stronger hysteresis effect, which prevents new columns from firing when the stimulus that was attracting the attention of the animal disappears. When the

pretectal fibres arrive at the LP, SP, and PY neurons the initial response of stimuli simultaneously presented converges to the strongest stimulus, but delayed responses to the other objects is also manifested. With this architecture, the hysteresis effect is minimum and the recovery of the response faster. Experiments are needed to study hysteresis effects when stimuli are simultaneously presented and one is then withdrawn. Measuring the response to the remaining stimulus will clarify the time relationships of hysteresis effects, and will allow us to further constrain and interpret the above results. The structure in which pretectal fibers synapse upon LP, SP and PY cells seems also the more appropriate, according to our hypothesis for the role of the tectum in prey orienting behavior, when moving stimuli are presented. This is because the tectal unit response continuously follows the moving stimulus in alternate, exclusive activity. The role of the pretectum in prey-selection is still obscure; and it is thus important to study the effects of pretectum stimulation when different prey stimuli are in the visual field of the animal.

REFERENCES

1. Arbib, M.A., Lara, R.: A neural model of the role of the tectum in prey-catching behavior. (to appear)

2. Didday, R. L. The simulation and modelling of distributed information processing in the frog visual system (Ph. D. Thesis) Stanford, Calif.: Stanford University, 1970.

3. Didday, R. L. A model of visuomotor mechanisms in the frog optic tectum. Mathematical Biosciences. 30: 169-180. 1976.

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

5. Ewert, J. P. and Ingle, D., Excitatory effects following habituation of prey-catching activity in frogs and toads. J. Comp. Physiol. Psychol. 3, 369-374, 1971.

6. Ewert, J. P., The visual system of the toad: behavioral and physiological studies on a pattern recognition system. In: The amphibian visual system (Fite, K.V. ed) Academic Press, 1976.

7. Fite, K. and Scalia, F. Central visual pathways in the frog. In: The amphibian visual system (Fite, K.V. ed) Academic Press, 1976.

8. Grusser, O.J. and Grusser-Cornehls, V. Physiology of the anuran visual system. In: Neurobiology of the frog. (R. Llinas and W. Precht, eds). Springer Verlag, Berlin and New York, 1976.

9. Ingle, D.: Prey catching behavior of anurans toward moving and stationary objects. Vision Res. Supp. 3, 447-456 (1971).

10. Ingle, D. Disinhibition of the tectal neurons by pretectal lesions in the frog. Science 180: 442-444, 1973.

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

12. Ingle, D. Selective visual attention in frogs. Science 188: 1033-1035, 1975.

13. Ingle, D. Behavioral correlates of central visual functions in anurans. In: Frog neurobiology (R. Llinas and Prechts, eds) Springer verlag, Berlin, 1976a.

14. Ingle, D. Spatial vision in anurans. In: The amphibian visual system (Fite, K.V. ed) Academic Press, New York. pp: 119-141, 1976b.

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

16. 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)

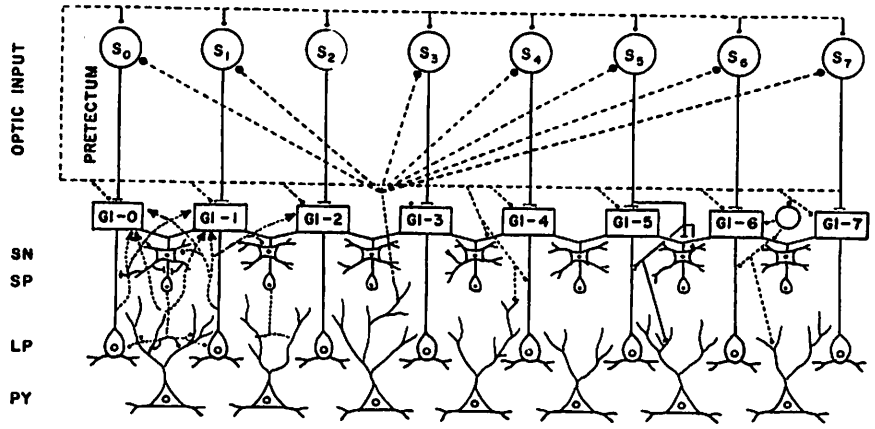
17. Lettvin, J. Y., Maturana, H., McCulloch, W.S. and Pitts, W. H. What the frog's eye tells the frog's brain. Proc. IRE. 1940-1951., 1959.

18. Rubinson, K.: Projections of the tectum opticum of the frog. Brain Behav. Evol. 1, 529-561, 1968.

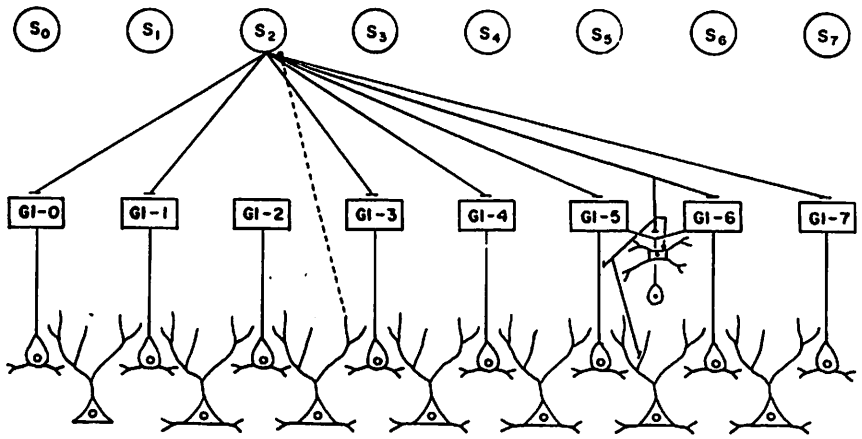
19. Scalia, F.: The optic pathway of the frog: nuclear organization and connections. In: Frog neurobiology. (Llinas, R. and Precht, W. eds), Springer Verlag, Berlin, 1976.

20. Szekely, G. and Lazar, G: Cellular and synaptic architecture of the optic tectum. In: Frog Neurobiology (R. Llinas and W. Precht eds), Springer Verlag, 1976.

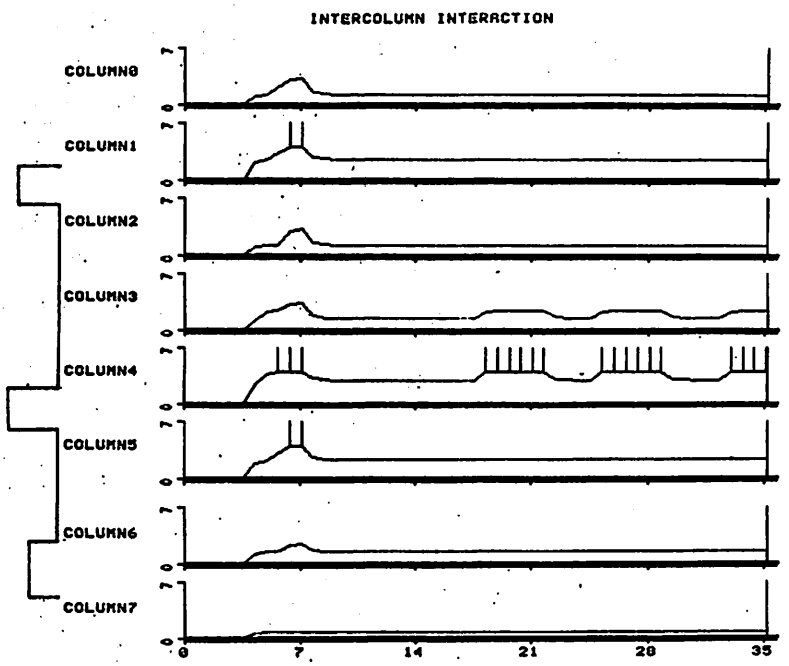
FIGURES



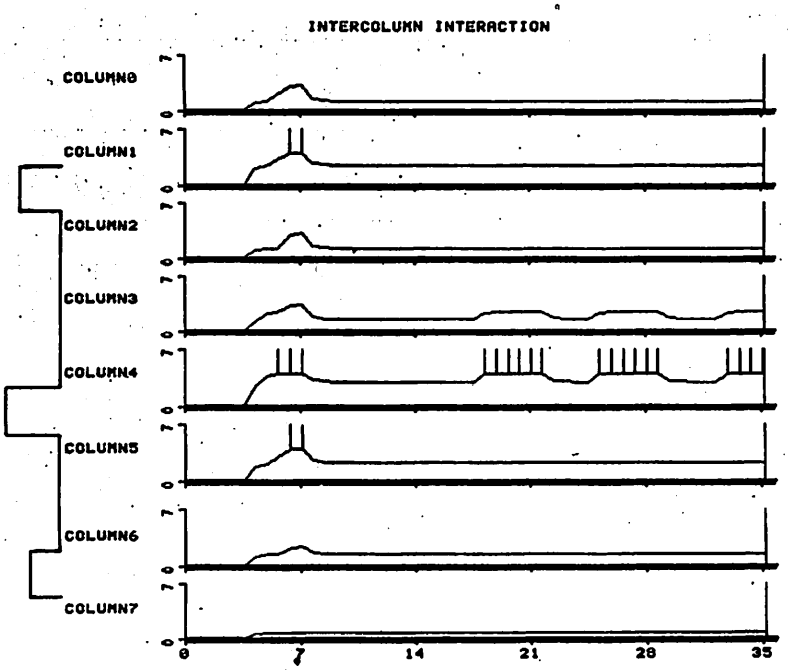
1. Architecture of the model for the interactions between tectum and pretectum in prey selection. Each column receives the afferents from one sameness neuron; each PY (pyramidal) neuron excites all pretectal cells except the one whose blind spot is in its receptive field. The NE (neuroses) neurons arrive at the same site as the corresponding optic fibres.



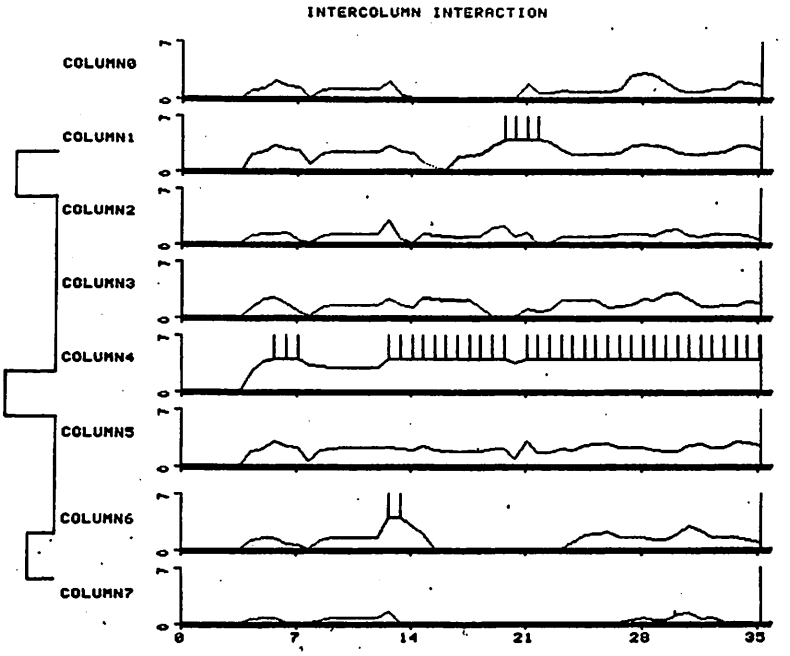
2. Alternative architecture for the model of prey selection. The PY cell excites only the pretectal cell with the same receptive field; and the pretectal cell in turn inhibits all tectal columns except the one with the same receptive field.



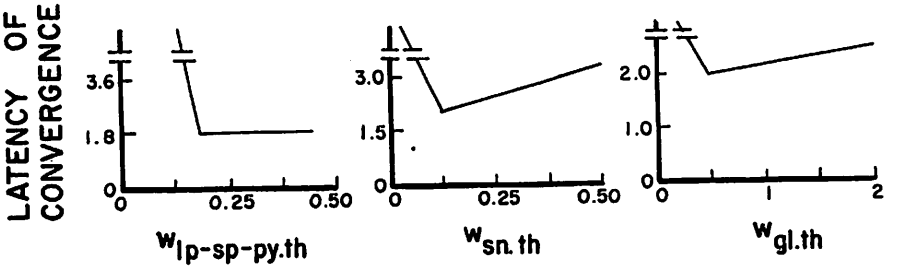
3. Computer simulation of the behavior of prey selection to three stimuli of different intensities when TH excites SN. Column 1 is excited by a stimulus of intensity 2; column 4 by one of intensity 3; and column 6 by one of value 1. After an initial brief response of column 1, 4, and 5 the rebounding excitation converges to column 4.



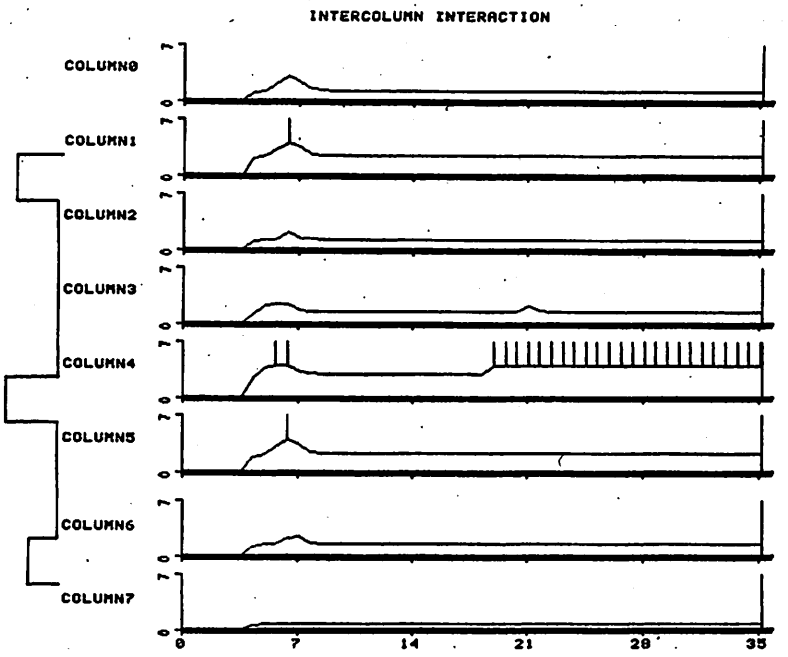
4. Computer simulation of the behavior of 8 PY to 3 stimuli of different intensities in the case that TH arrive at GL. After an initial response of columns 1, 4, and 5, the rebounding activity converges to column 4 with small periods of inhibition.



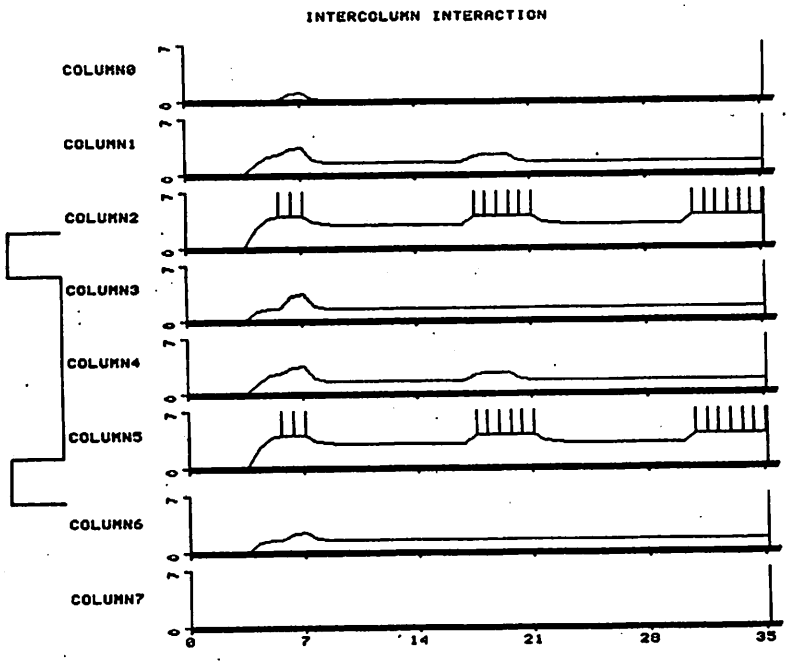
5. Computer simulation of the behavior of 8 PY to 3 stimuli of different intensities in the case that TH arrives at LP, SP, and PY neurons. The initial response is only present in column 4 and the rebounding activity appears faster than in the above cases. Notice the delayed response of column 1 and 6.



6. Graphs showing the relationship between the weighting values and the latency of convergence of the response to the strongest stimuli. Notice that for low values of $w_{sn\cdot th}$ the system still converges, while for $w_{sp\text{-}lp\text{-}py\cdot th}$ and $w_{gl\cdot th}$ it does not, showing that the system is more sensitive to $w_{sn\cdot th}$ than to the others.



7. Computer simulation of the behavior of 8 PY neurons to 3 different stimuli in the case that the optic input arrives both at the tectum and the pretectum. Notice that the initial response in columns 1, 4, and 6 is weaker (see Fig 3), and the rebounding excitation in column 4 is delayed.



8. Computer simulation of the behavior of PY neurons to 2 equally intense stimuli. The stimuli are presented in columns 2 and 5. Notice that an alternation of excitation and inhibition is present without convergence to any of the stimuli.

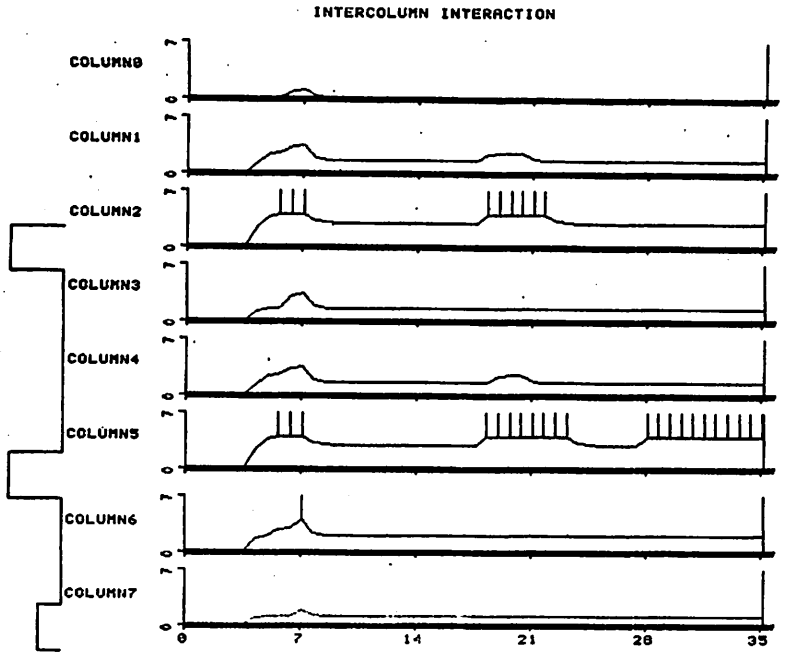


Fig. 9A

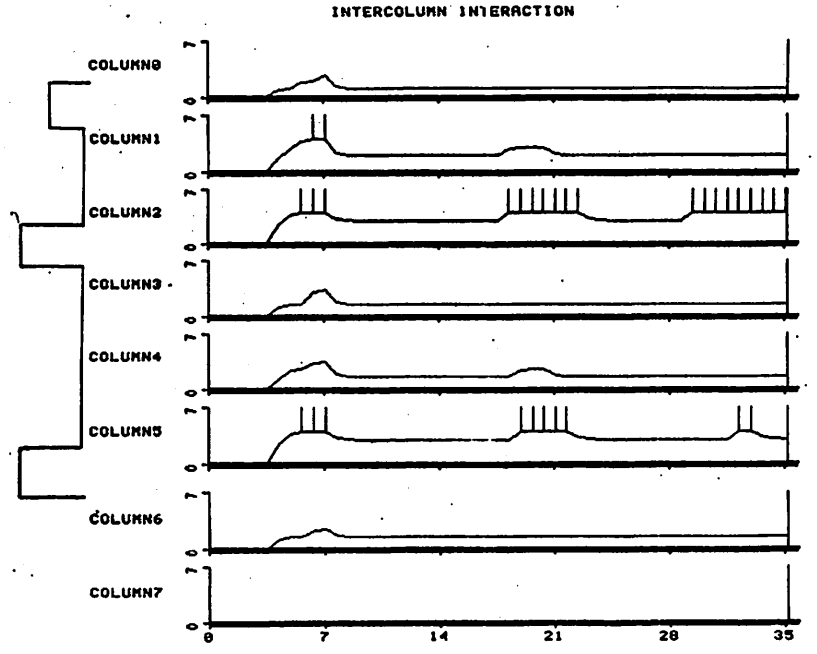
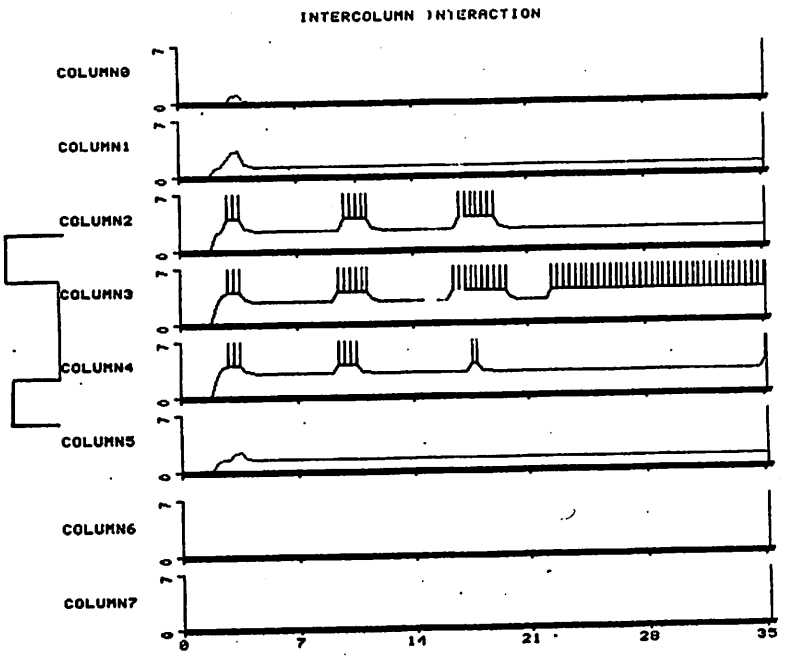


Fig. 9B

9. Computer simulation of the behavior of PY neurons to 2 equally intense stimuli to columns 2 and 5 biased by a third one. When the third stimulus is applied in column 7 (A), then the response converges to the stimulus presented in column 5; while if the third stimulus is presented in column 0 (B), then the response converges to column 2.



10. Computer simulation of response of the 8 PY to the presentation of two nearby stimuli. Here the response converges to a point in between the stimuli. The stimuli are applied in columns 2 and 4 with an intensity of 3 and 2.5 respectively. The response converges to column 3, although this column was not directly excited.

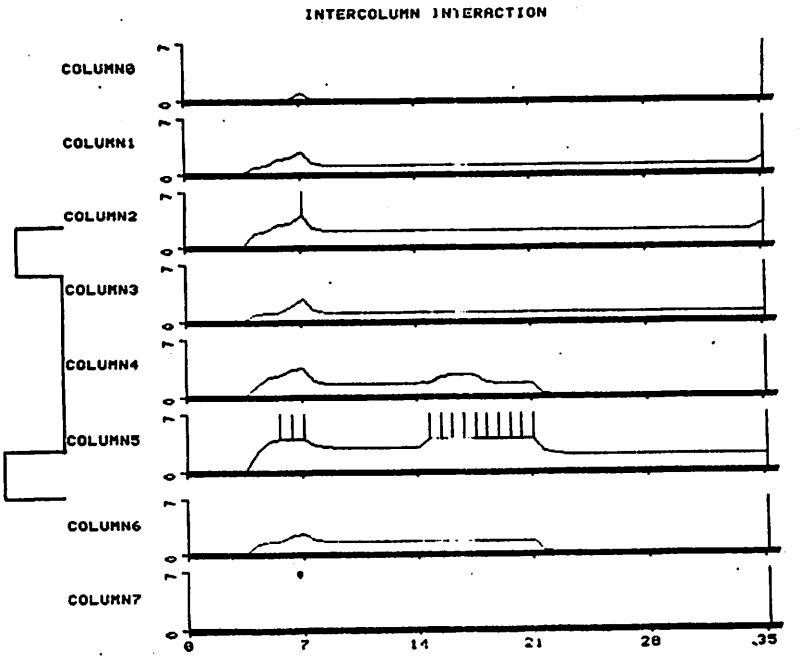


Fig. 11A

(see caption, next page)

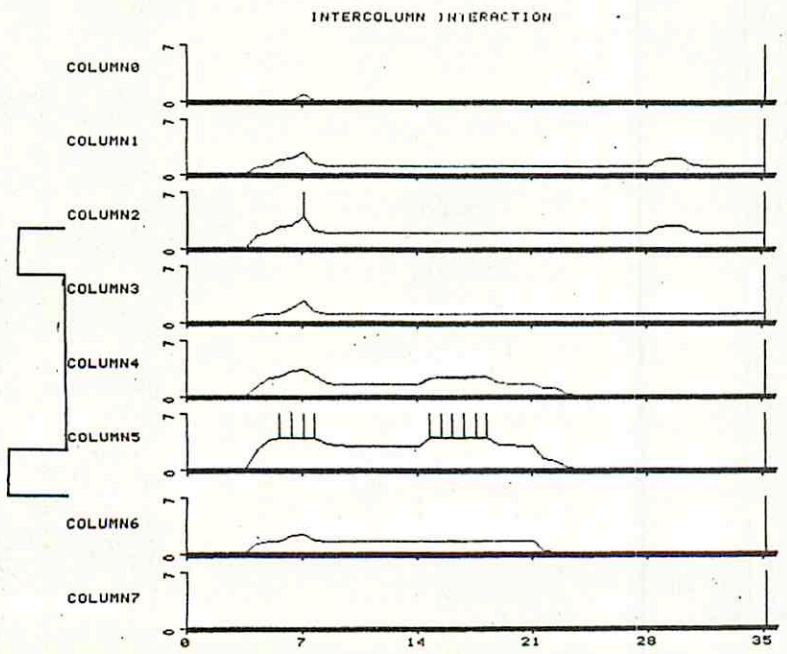


Fig. 11B

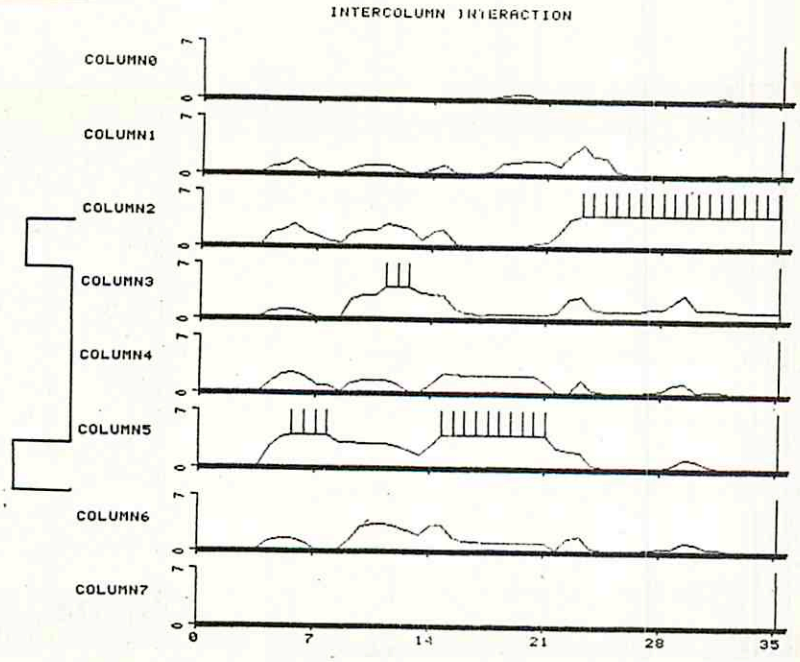
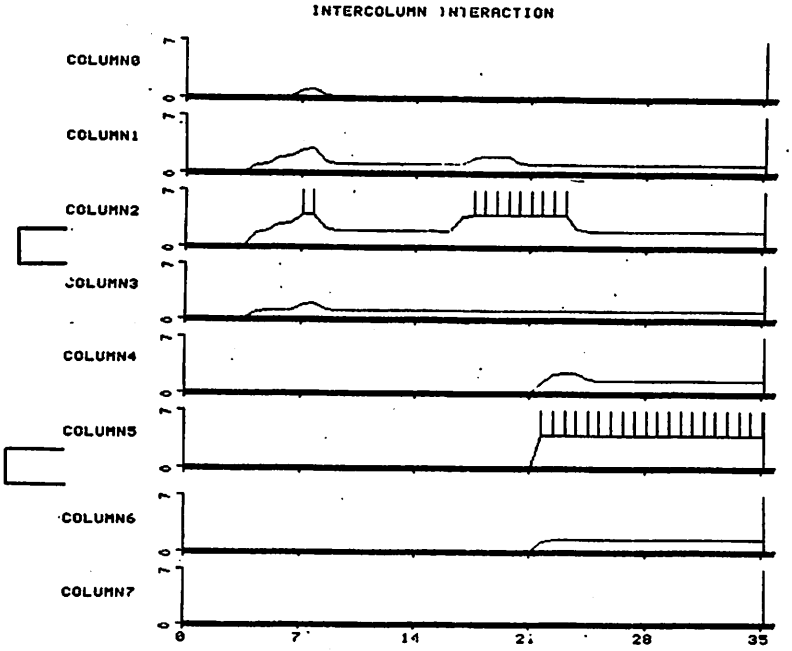
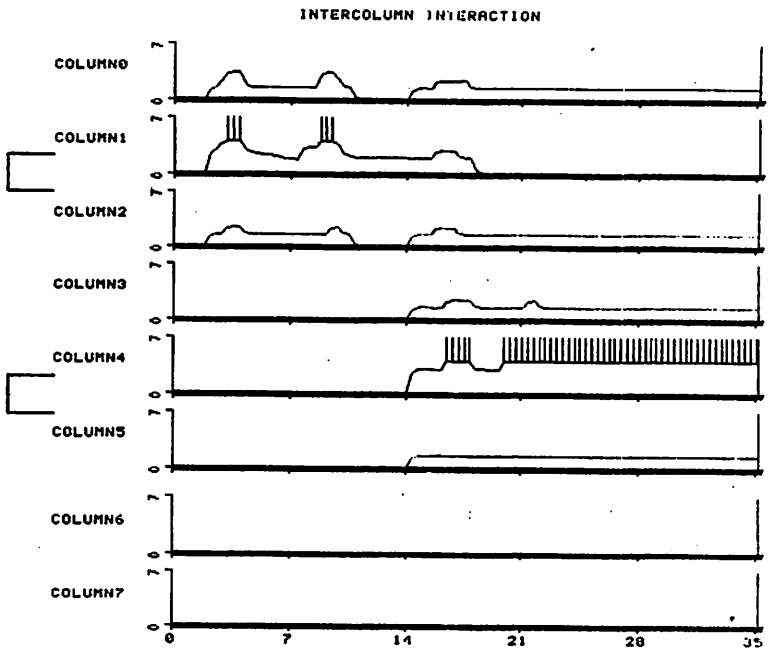


Fig. 11C

11. Computer simulation of the response of 8 PY when, after two stimuli are presented for a short period, one of them is withdrawn from the visual field of the animal. (A) When TH arrives at SN. The stimulus in column 2 has a value of 2 and that of column 5 a value of 3. Initially the response converges to column 5, but then we withdraw its stimulus, thus observing that the response of column 2 only shows a small recovery at the end of the simulation time. In (B) we show that the same behavior of A appears when TH arrive at GL. In C, on the other hand, where TH arrives at SP, LP and PY cells, a recuperation of the response in column 2 is evident.



12. Computer simulation of the effects of NE neurons on PY acitivity. Presenting a new stimulus in column 5 that is bigger than the initial stimulus applied in column 2 produces an increased state of excitation in column 5, thus inhibiting the activity of column 2.



13. Computer simulation of habituation effects on PY activity. We first present a stimulus in column 1. After a period of rest, we present two equally intense stimuli in columns 1 and 4, the response converging to column 4, because the pathway of column 1 is habituated.

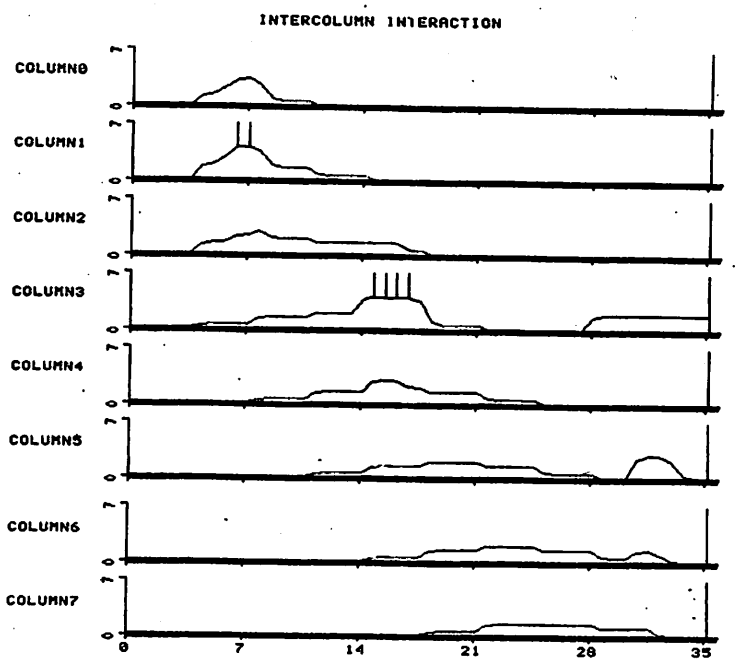


Fig. 14A

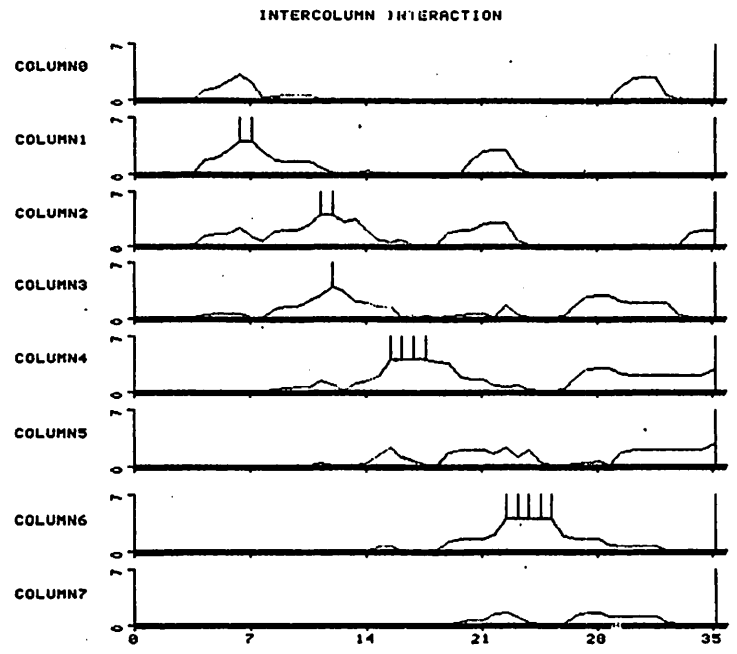


Fig. 14B

Fig. 14C,
next page →

14. Computer simulation of tectal response to a moving stimulus when pretectal inhibition is present. In (A) we show that when the pretectal fibres arrive at the SN there is a strong inhibitory effect to the subsequent response of other tectal columns. In B we show that when pretectal fibres arrive at the LP, SP and PY cells unit columns have the tendency to fire independently. In C we show the same experiment but now the pretectal fibres arrive at the glomerulus showing also the tendency to fire independently but with a strong hysteresis effect.

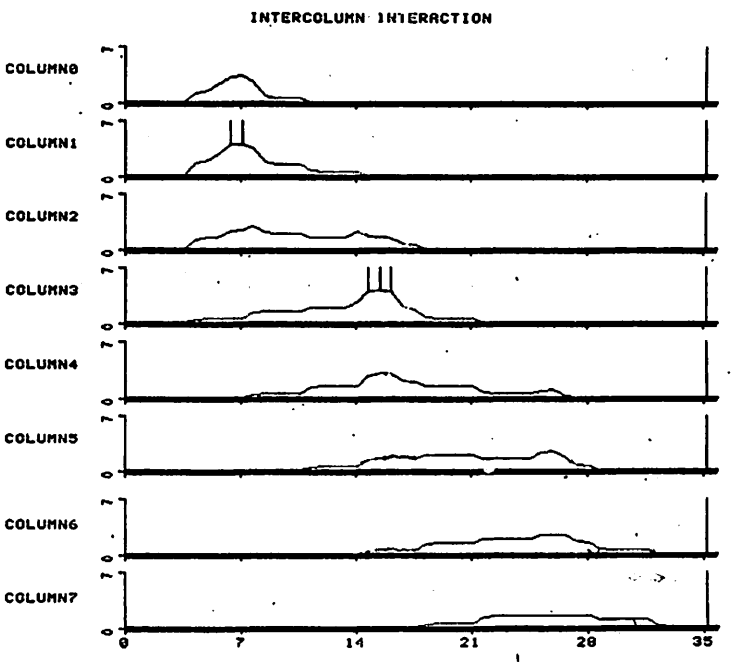

INTERCOLUMN INTERACTION
COLUMN0
COLUMN1
COLUMN2
COLUMN3
COLUMN4
COLUMN5
COLUMN6
COLUMN7
0
7
14
21
28
35

Fig. 14C

APPENDICES

We provide the mathematical material which complements the description of the tectal column given in Appendix 2 of Lara, Arbib and Cromarty (to appear). The specification of threshold function, membrane constants and weights is given in Tables 1, 2, and 3 respectively.

A.1 Glomerulus:

The equation defining the behavior of the glomerulus of the ith unit column is extended to incorporate newness and thalamic input as follows:

$$\tau_{gl}\, gl_i(t) = -k_1 \cdot gl_i(t) + s_i(t) \cdot u_i(t) + I_i(t) + w_{gl \cdot ne} NE_i(t) - w_{gl \cdot th} TH_i(t)$$

where the $I_i(t)$ are the recurrent inputs from LP and SP cells of the unit as well as those of neighboring columns, and are defined as:

$$I_i(t) = w_{gl \cdot lp}(SP_i(t) + SP_{i+1}(t)) + w_{gl \cdot lp}(LP_{i-1}(t) + LP_i(t) + LP_{i+1}(t))$$

and NE_i is the effect of the newness neuron; $s_i(t)$ is the habituation factor defined below; and $TH_i(t)$ is the thalamic effect over GL.

The ith stellate neuron behavior can be defined as follows:

$$\tau_{sn}\, sn_i(t) = -k_2\, sn_i(t) + w_{sn \cdot lp}(LP_i(t) + LP_{i+1}(t)) + w_{sn \cdot th} TH_i(t)$$

receiving inputs from two LP cells, one coming from its own unit column and the other from the right neighbor. The SN also receives

the excitatory effect of the thalamic fibres, $TH_i(t)$.

The behavior of the ith LP neuron is defined as:

$$\tau_{lp}\, lp_i(t) = -lp_i(t) + w_{lp\cdot sp}(SP_{i-1}(t)+SP_i(t)) + gl_i(t) - w_{lp\cdot sn}(SN_{i-1}(t)+SN_i(t)) + u_i(t)\cdot s_i(t) + NE_i(t) \cdot w_{lp\cdot th} TH_i(t)$$

where the LP cell is excited by 2 SP neurons, one coming from its own unit column and the other from the left neighbor. This cell is also activated by the optic input, and is inhibited by 2 SN, one is part of its column unit and the other is the left neighbor. This neuron is also activated by the newness neuron, $NE_i(t)$, and the thalamic input, $TH_i(t)$.

The ith SP neuron is defined as follows:

$$\tau_{sp}\, sp_i(t) = -sp_i(t) + gl_i(t) + gl_{i+1}(t) - w_{sp\cdot sn}(SN_i(t)+SN_{i+1}(t)) + u_i(t)\cdot s_i(t) + NE_i(t) \cdot w_{sp\cdot th} TH_i(t)$$

This neuron receives inputs from the glomerulus of the unit column and the glomerulus from its right neighbor; it is also excited by the optic input; and it receives inhibition from the SN of the unit column. This cell is also excited by $NE_i(t)$ and inhibited by $TH_i(t)$.

The ith PY cell is defined in the following way:

$$\tau_{py}\, py_i(t) = -py_i(t) + w_{py\cdot sp} SP_i(t) + w_{py\cdot lp}(LP_i(t)+LP_{i+1}(t)) + u_i(t)\cdot s_i(t) + NE_i(t) - w_{py\cdot th} TH_i(t)$$

receiving input from the retina, from the SP of the unit column,

and from 2 LP cells, one from the unit column and one from the right neighbor. PY also receives input from $NE_i(t)$ and inhibition from $TH_i(t)$.

A.2 Sameness Neuron:

We have simply required the sameness cells to receive the excitation coming from the PY neurons. Each one of them receives afferents from all tectal PY except the one located in its blind spot; thus this neuron is defined in the folowing way:

$$TH_i(t) = \sum_{j \neq i} PY_j(t)$$

where TH is the sameness neuron activity; and the $PY_j(t)$ are the excitation of all PY outside the ith blind spot.

A.3 Newness Neuron:

The simulation of the newness neuron was obtained through the derivative of a system that acquires the value of its input in a very fast way so that the second presentation of the same input does not produce a response. The mathematical definition of each newness neuron is as follows:

$$NE_i(N) = \dot{DNE}_i = (k_{10})(u_i(t) - DNE_i)$$

where the activity of the newness cell, NE_i, is equal to the derivative, DNE_i, which depends on the value of the input. k_{10} is a large constant which makes DNE quickly reach any maintained value of u_i.

A.4 Mathematical Definition of Habituation:

To simulate habituation, we multiply the input, u, by a factor s whose value decreases according to the number of presentations of the stimulus. This factor is defined as follows:

$$\dot{s}_i(t) = k_3(s_0 - s_i(t)) - k_4 s_i(t)(B \cdot u_i(t)).$$

where s_i is the habituation factor; s_0 is the equilibrium value of s_i; k's are constants; $u_i(t)$ is the stimulus at time t; and B is constant. This expression simulates the fact that the strength of the stimulus will be decreased in relation to the time it has been presented.

TABLE 1

Threshold functions:

LP = f(lp-1.0)

SP = f(sp-2.0)

SN = h(sn-0.?)

TH = h(th)

PY = h(py-0.8)

where

$$f(x) = \begin{cases} 1 \text{ if } x > \text{threshold} \\ 0 \text{ ELSE.} \end{cases}$$

and

$$h(w) = \begin{cases} w \text{ if } w > \text{threshold} \\ 0 \text{ ELSE} \end{cases}$$

TABLE 2

Membrane constants:

$\tau_{gl} = 0.5$, $k_1 = 0.5$

$\tau_{sn} = 0.65$, $k_2 = 0.5$

$\tau_{lp} = 0.3$

$\tau_{sp} = 0.7$

$\tau_{py} = 0.4$

TABLE 3

Weights:

$w_{gl \cdot lp} = 1.0$	LP to GL.
$w_{gl \cdot sp} = 0.1$	SP to GL.
$w_{lp \cdot sp} = 0.8$	SP to LP
$w_{lp \cdot sn} = 8.0$	SN to LP
$w_{lp \cdot th} = 0.4$	TH to LP
$w_{sp \cdot sn} = 15.0$	SN to SP
$w_{sp \cdot th} = 0.4$	TH to SP
$w_{sn \cdot lp} = 1.0$	LP to SN
$w_{sn \cdot th} = 0.2$	TH to SN
$w_{py \cdot lp} = 1.0$	LP to PY
$w_{py \cdot sp} = 1.0$	SP to PY
$w_{py \cdot th} = 0.2$	TH to PY
$w_{gl \cdot th} = 2.0$	TH to GL

A NEURAL MODEL OF INTERACTION BETWEEN PRETECTUM AND TECTUM IN PREY SELECTION

Rolando Lara
and
Michael A. Arbib

COINS Technical Report 81-4

(February 1981)