PROCEEDINGS OF THE SECOND WORKSHOP ON VISUOMOTOR COORDINATION IN FROG AND TOAD: MODELS AND EXPERIMENTS[1]

organized by

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COINS Technical Report 83-19

"Theories pass. The Frog remains."
- Jean Rostand: Notebooks of a Biologist

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This volume provides the proceedings of the Second Workshop. The "Proceedings of the [First] Workshop on Visuomotor Coordination in Frog and Toad: Models and Experiments" are available as COINS Technical Report 82-16 from the Department of Computer and Information Science, University of Massachusetts at Amherst. For ease of reference, the following table of contents is a composite: A (1) after a paper indicates that it appeared in the first proceedings; while a (2) indicates that the paper appears in the present volume.

Chapter 1: An Introduction to Modelling

Chapter 2: Pattern Recognition

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Appendix A: THE TWO WORKSHOPS

Workshop on
VISUOMOTOR COORDINATION IN FROG AND TOAD
MODELS AND EXPERIMENTS

Center for Systems Neuroscience
University of Massachusetts at Amherst
November 16-18, 1981.
(organized by Michael A. Arbib)

Monday, November 16

An Overview of Approaches to Modelling [Arbib]

Detour Behavior and Tectal-Pretectal Interactions [Ingle]

Neurophysiological Basis of Configurational Prey-Selection in the Common Toad. [Ewert]

The Link between Tectum and Prey Capture Motor Output [Grobstein]

Bidimensional Model of the Interactions between Tectum and Pretectum [Cervantes]

Visuomotor Connections in Anuran Mesencephalon [Montgomery and Fite]

Behavior-Correlated Neurons in Freely Moving Animals [Borchers]

Modelling Pattern Recognition [Cromarty]

Tuesday, November 17

Detour Behaviour of *Bufo Viridis* [Collett]

Modelling Detour Behavior [Arbib and House]

The Frog/Toad Depth Perception System -- Cooperative/Competitive Model [House]

Nucleus Isthmi and the Development of binocular Vision [Udin]

Modelling Retino-Tectal Connections [Overton]

Retino-Tectal Connections [George]

Wednesday, November 18

Retino-Tectal Connections [Sharma]

Modelling Cerebellum [Boylls]

The Coordinate System of Visual Climbing Fiber [Simpson]

Configurational Prey-selection by Individual Experience in the Toad [Ewert]

Modelling Habituation [Lara]

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Second Workshop on

VISUOMOTOR COORDINATION IN FROG AND TOAD MODELS AND EXPERIMENTS

Universidad Nacional Autonoma de Mexico
November 17-19, 1982
(organized by Rolando Lara and Michael A. Arbib)

Monday, November 17

The Nucleus Isthmi and the Correspondence Problem [Collet and Udin]

Depth and Detours: Towards Neural Models. [Arbib and House]

A New Notion on Visual Receptive Fields: Multidimensional Opponency. [Martinez]

A Global Model of the Neural Mechanisms of Visuomotor Coordination in Toads. [Lara]

Round Table on Depth Perception. Stereopsis and Detour Behavior

Tuesday, November 18

Outlines of a Network Model for Prey-Predator Recognition in Toads. [Roth]

A Model of the Neural Mechanisms Responsible for Prey-Predator Recognition. [Cervantes, Lara and Arbib]

Habituation: A Two-Dimensional Proposal. [Arbib]

Visuomotor Functions Related to Prey-Predator Recognition in Urodele and Anuran Amphibians. [Ewert]

Single Unit Recording in the Toad's Optic Tectum During Prey-Catching. [Borchers]

The Visual Nuclei Society in Prey-Predator Recognition in Toads. [Negrete and Lara]

Round Table on Neural Mechanisms for Prey-Predator Recognition.

Wednesday, November 19

Possible Neurotransmitters in the Optic Tectum. [Sandoval]

Central Serotoninergic Control of Habituation in Monosynaptic Pathways in the Isolated Spinal Cord. [Rudomin]

Further Thoughts on the Linkage Between Tectum and Prey Capture Motor Output, on that Between Stimulus and Prey Capture Motor Output, and the Relation Between the Two. [Grobstein]

Adaptive Network Representation of Control Surfaces for Motor Systems [Barto and Epstein]

Transformations of Natural Coordinates from Sensory to Motor Frames through Neural Networks. [Pellionisz]

A Concluding Perspective [Ewert]

Round Table on Motor Maps and Motor Schemas.

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Chapter 2: Pattern Recognition

Jorg-Peter Ewert: NEURAL CONTROL OF PREY-CATCHING AND PREDATOR AVOIDANCE BEHAVIORS IN ANURAN AND URODELE AMPHIBIANS: EVOLVING CONCEPTS

Hans-Wilhelm Borchers: SINGLE UNIT RECORDING IN THE TOAD'S OPTIC TECTUM DURING PREY-CATCHING

Uwe an Der Heiden, Gerhard Roth: A MATHEMATICAL NETWORK MODEL FOR RETINO-TECTAL PREY RECOGNITION IN AMPHIBIANS

Rolando Lara, Francisco Cervantes and Michael Arbib: A NEURAL MODEL OF INTERACTIONS SUBSERVING DISCRIMINATION AND SIZE PREFERENCE IN ANURAN AMPHIBIA

Segundo Taller sobre "Coordinacion Visuomotora en Ranas y Sapos, Teoria y Experimentos", Mexico-City 1982

Neural Control of Prey-Catching and Predator Avoidance Behaviors in Anuran and Urodele Amphibians: Evolving Concepts

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During the last decade our working group has comparatively investigated the control of prey-catching and predator avoidance behaviors in anuran and urodele amphibians (e.g., Bufo bufo, Rana temporaria, Salamandra salamandra) through an neuroethological approach. In particular, we have analyzed the question of how neural networks - or rather neuronal assemblies - participate in stimulus recognition and localization and select the appropriate motor response (for detailed reviews see Ewert 1983, Ewert et al. 1983a and b).

A Preliminary Basic Concept

Quantitative ethological experiments using visual moving dummies have shown two things: (1) The prey-catching or predator avoidance activity in amphibians is closely correlated with the stimulus parameters; i.e., if a moving object has neither prey nor predator features the animals do not respond. Hence, the releasing value of a stimulus is expressed by the appropriate behavioral activity. (2) Toads, frogs, and salamanders are able to distinguish configurational features. Prey-selection by Bufo bufo, Rana temporaria, and Salamandra salamandra shows some common basic properties. For example, the investigated species exhibit the "worm/antiworm phenomenon" which is invariant with regard to changes of other stimulus parameters, such as the movement velocity. The main genera- and species-specific differences are concerned with the response to square dummies in comparison with the responsiveness to worm-like and antiworm-like stimuli of comparable edge length.

These and other data lead to the concept that sensory decisions precede motor decisions (for detailed discussions see Ewert et al. 1983a; cf. also Ewert and Inst. Wiss. Film, 1982). Therefore, we postulate a sensory pattern recognition system (SPRS) and a motor pattern generation system (MPGS). Both may be connected by a sensorimotor interface consisting of an interneuronal network acting as command system (CS). In amphibians, the feature extracting characteristics of the SPRS with regard to prey and predator are not determined by the MPGS as claimed by Grüsser and Grüsser-Cornehls (1976; for discussion see Ewert, 1983) - according to a principle: "how can I know what I see, before I am responding". As a result of initial localization and recognition processes, toads (i) program a turn, or (ii) plan a route before they start to move, to name just two examples (Lock and Collett 1979).

In the following, concepts for neuronal correlates of prey/predator recognition will be discussed on the basis of experimental data.

Concept A

The classical concept A (Fig.1A) of prey/predator recognition in frogs has been introduced by Barlow (1953) and Lettvin et al. (1959). Due to the different sizes of excitatory receptive fields of retinal ganglion cells, it is suggested that class R2 neurons (ERF=4-6deg diam.) are specialized for the recognition of prey ("bug detectors") and class R4 neurons (ERF=12-16deg diam.) for the identification of predators ("enemy-detectors"). Ingle (1982, 1983) has adopted this concept and claims that both types of detector feed in separate channels to orienting and avoidance turn command systems which in turn are connected with the MPGS.

This concept is contradicted by quantitative ethological and neurophysiological results obtained in toads and frogs: (1) The configurational prey and predator features are not coded by a single class of retinal ganglion cell. (2) In contrast to the prey-catching behavior, R2 neurons are activated if both prey and a structured background (Julesz-Pattern) are moving simultaneously. (3) Provided that prey/predator recognition would be based on retinal functions and mediated by specialized ganglion cells (Lettvin et al. 1959) that feed in specific separate channels (Ingle, 1982) to the appropriate MPGS, the spectrum of such a pattern recognition system would be a priori extremely limited - which is actually not the case (Ewert and Kehl, 1978).

Concept B

Another concept B (Fig.1B) based on single recordings from neurons of the central visual system of toads, frogs, and salamanders in relation to neuroanatomical studies, brain stimulation and brain lesion experiments overcomes the simple "channel idea": (i) Visual information, passing the retina, is further processed in feature analyzing central neurons; (ii) prey/predator recognition is a result of interactions between those neurons. Hence, retinal class R2, R3, and R4 neurons can be regarded as lower-order neurons acting as primary filters for visual input with respect to processing of different stimulus parameters, such as visual angular size, angular velocity, and stimulus background contrast. Different combinations of outputs of retinal ganglion cell classes feed into higher-order neurons, whose properties are also influenced by intrinsic circuits. Certain combinations of excitatory and inhibitory outputs of these feature analyzing neurons determine the properties of spezialized neurons. In other words, the latter express certain kinds of interactions of neuronal networks.

In toads and frogs, we have identified higher-order neurons as tectal class T5(1), T5(3) and thalamic TH3 neurons, and spezialized neurons, e.g., as tectal class T5(2) prey-selective neurons. Class T5(2) neurons are characterized by the property that their activity in response to a moving stimulus resembles the probability that the stimulus fits the prey-category. In the fire salamander, class T5(2) neurons have not been identified; here, the activity of T5(1) neurons shows best correlation with the prey-catching activity in response to configurational moving stimuli (Finkenstädt and Ewert 1983a).

Concept B has been verified by a variety of neurophysiological tests, and the proposed neuronal connections were confirmed by various neuroanatomical methods in Bufo, Rana, and Salamandra (Ewert 1983, cf. also Weerasuriya cit. in Ewert et al. 1983b). For example, following transsection of the interconnections between thalamic and tectal filters by knife cuts or after micro-injection of the axon-sparing neurotoxin Kainic acid or Ibotenic acid into the caudal dorsal thalamus toads, frogs, and salamanders show a special kind of agnosia: They are unable to identify predators and respond to

anything moving with prey-capture, irrespective of the size and configuration of the stimulus. Recent lesion experiments in toads with Ibotenic acid suggest a topography between the postero-lateral nucleus - were the TH3 neurons are located - and corresponding parts in the visual field were agnosia occurs (Schürg-Pfeiffer, in prep.). Interestingly, there is a correlation between (i) size of the lesion, (ii) field size of agnosia in the visual field, and (iii) repair of prey-recognition - as well as a rudimentary return of escape behavior (Ewert et al. 1983a). With regard to (iii) it must be emphasized that functional recovery of configurational prey-selection resembles only a rough repair; the pre-operative degree of selectivity will post-operatively never be reached.

There is evidence to show that inhibitory effects of neurons from the caudal dorsal thalamic visual map on topographically corresponding neurons of the tectal map provide the basis for at least two important properties of the visual system: (1) configurational stimulus selection, (2) extraction of a stimulus from its background and, along with this, the distinction between object motion and self-induced motion, due to inhibitory surround effects (Burghagen and Ewert 1983). Furthermore, recent lesion studies in toads and salamanders with Kainic acid or Ibotenic acid show that the role of the "inhibitory thalamic network" is twofold in this context: (i) certain networks of the caudal dorsolateral thalamus determine the functions described for the entire visual field of the contralateral eye; (ii) certain networks of the anterior dorsolateral thalamus, in addition, provide an emphasis of these functions for the binocular visual field providing some kind of "central fovea". These functions are subject to modulation through learning which involves the telencephalon, e.g., by combining visual and olfactory cues (Ewert 1983).

In Salamandra salamandra, neurons of the caudal dorsal thalamus appear to determine the properties of prey-sensitive tectal T5(1) neurons. In Bufo and Rana this structure is parcellated into a postero-central (pc) and a postero-lateral (pl) nucleus, the latter obviously determining the prey-selective T5(2) neurons. Genus- and species-specific variations in prey-selection, too, may depend on particular properties of feature detectors and their specific subtractive interactions.

In a recent study by Finkenstädt et al. (in prep.) brain activity of toads was radioactively labelled with (14C)2DG during the toad's behavior in response to a worm-like, an antiworm-like stripe, or a large moving square object. Especially the central layers of the optic tectum of an ipsilaterally enucleated monocular toad showed strong radioactive labelling in response to the worm configuration; but the antiworm configuration was effective too to some extent, presumably as a result of activity in axon terminals from thalamic cells that form inhibitory synapses with tectal neurons. The pl nucleus of the caudal thalamus of an ipsilaterally enucleated monocular toad showed relatively strong (14C)2DG uptake in response to the antiworm configuration of a stripe or to a large square stimulus, but less to the worm-configuration. Following unilateral lesions of the pl nucleus of the thalamus, the tectum ipsilateral to the lesion showed strong radioactive labelling in response to an antiworm-like moving stripe, whereas labelling in the opposite tectum was comparatively weak.

In concept B we suggest that an assembly of T5(2) neurons is involved both in visual pattern recognition and turn commanding. In recent recording experiments from behaving toads it could be shown that activity of T5(2) neurons in response to prey precedes and - so to speak - predicts - the orienting turn, and these neurons are also activated during the turning movement. More specifically, neuronal burst activity is correlated with the movement pattern of the toad. The neurons also discharge during the toad's behavior if the prey stimulus has disappeared (Schürg-Pfeiffer in prep.; cf. also Megela et al. 1983). These results suggest positive feedback from the motor system to T5(2) neurons. Hence, class T5(2) neurons appear to be involved in (i) prey-recognition, (ii) turn commanding, and (iii) motor-pattern generation.

Concept C

According to the results of previous electrical brain stimulation experiments, it seems unlikely that activity of just one T5(2) neuron is sufficient to elicit an orienting turn toward prey (Ewert 1983). We assume that several adjacent T5(2) neurons feed into the corresponding motor system suggesting that adjustment of turns is due to the overlapping nature of their relatively large excitatory receptive fields (ERF=27deg diam.). However, it may also be possible that class T5(2) neurons are mainly involved in prey recognition, whereas tectal class T7 neurons - with their very small receptive fields (ERF=4deg diam.) - provide a substrate of stimulus localization (Ewert et al. 1983a). In extension of concept B the concept C (Fig.1C) suggests class T5(2) and T7 neurons as elements of the command system for the turn toward prey. The motor system, functioning like an AND-gate, may require simultaneous optimal input of different classes of tectal neurons which are serving as command elements according to the definition introduced by Kupfermann and Weiss (1978). Presumably, also tectal class T4 wide-field neurons belong to command elements and fulfill "arousal function" (Ewert et al. 1983a). It is plausible to assume that other combinations of outputs of tectal neuron classes provide command systems for other behavioral components of the prey-catching sequence (Ewert 1983).

The property of class T7 neurons with regard to edge localization has been described in a recent neuroethological study. In response to a black stripe moving worm-like against a white background, toads fixate and snap the leading edge of the stimulus (Ingle and McKinley 1978). If, however, the stimulus background contrast is reversed, the animal clearly prefers the trailing edge and very often snaps

behind the stimulus (Burghagen and Ewert 1982). Hence, for edge localization, a change from white to black is the significant cue. We have recorded class T7 neurons in response to worm-like stripes traversing the center of their ERFs in horizontal direction and have found that toward a black stripe moving against white background a neuronal burst occurs at the leading edge of the stripe, whereas the trailing edge remains unresponded. If the stimulus background contrast is reversed, however, maximal neuronal activity is elicited by the trailing edge of the stimulus; in many cases the leading edge elicits no response at all (Tsai et al. 1983). From a psychophysical point of view, toads may approach to some extent a similar figure/ground problem as we do when we have to decide between a "goblet" or "two silhouetted faces" in the drawing by Edgar Rubin.

The command system for the avoidance turn in response to a predator may consist of combinations of outputs of class TH3 and T5(1), or TH4 and T5(1), or TH4 and T7 neurons. In these cases TH3 (or TH4) neurons would fulfill recognition functions and tectal T5(1) or T7 neurons (with their smaller receptive fields) localization functions. Further combinations of outputs of thalamic and tectal neuron classes may provide command systems for other motor patterns.

Open Questions

Where are the efferent targets of the proposed command elements? We have injected HRP into the tongue muscles of toads - which are specific effectors of the snapping response - and have labelled the hypoglossal motor neurons. By injection of HRP in and arround this nucleus, pyramidal cells, ganglionic cells, and pear-shaped cells could be backfilled in layer 6 of the optic tectum; furthermore, neurons in the caudal dorsal thalamus have been labelled (Weerasuriya and Ewert 1981). The question of correlation between physiologically described neuronal classes and anatomically identified cells is still open and constitutes one of the main research topics of our group.

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Figure Caption

Fig.1A-C. Concepts A-C of sensory pattern recognition and motor pattern generation in the visual control of the prey orienting and predator avoidance response. SPRS = sensory pattern recognition system, CS = command system, MPGS = motor pattern generation system; R = retinal ganglion cells, T = tectal neurons, TH = thalamic neurons. Arrows indicate excitatory connections and dashed lines inhibitory connections. For explanations see text. (From Ewert et al., 1983b)

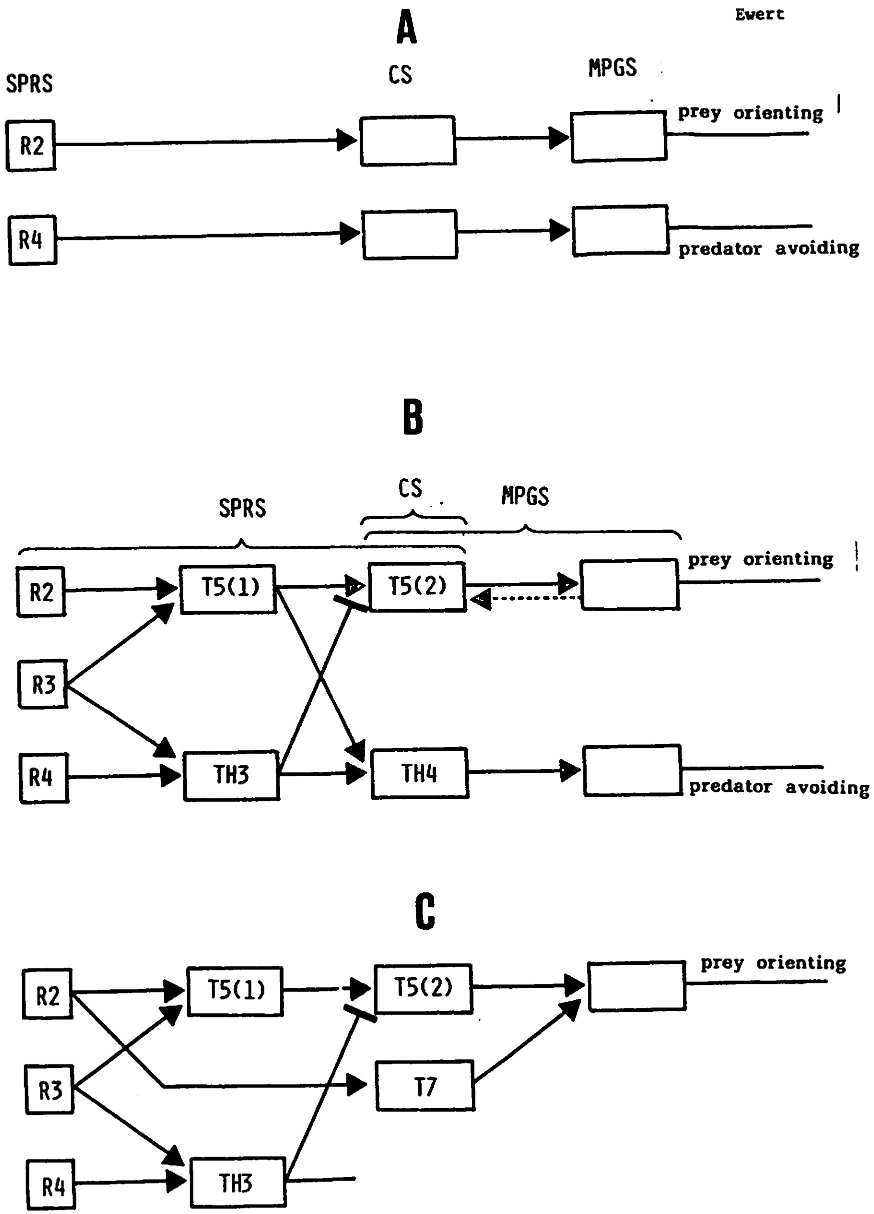

Fig. 1

H.-W. Borchers: SINGLE UNIT RECORDING IN THE TOAD'S OPTIC TECTUM DURING PREY-CATCHING

The optic tectum and the thalamic-pretectal (TP) region of anurans (frogs and toads) are important centers for neuronal processing of visual stimuli that are behaviorally relevant for prey/predator decisions (Ewert, 1983). Tectal neuronal cell types (class T5(2)) show optimal responses to stimuli which signify possible prey over those that represent possible predators. Other tectal cell types (e.g., class T5(1)) show no such configurational selectivity, while some thalamic-pretectal cell types (e.g., class TH3) exhibit sensitivity to predator-like stimuli. Results from recording, brain stimulation, and brain lesion experiments led Ewert (1974, 1983) to propose a model of configurational prey/predator recognition in the toad's visual system, whereby the response characteristic of tectal T5(2) neurons is determined by inhibitory input from the thalamic-pretectal region. It is assumed that T5(2) neurons are "command elements" within a system that releases prey-capture (Ewert et al., 1983).

Most of the neurophysiological work on tectal response properties has been performed on paralyzed animals. A precondition for measurements in each case is a mood of the experimental animal which is adequate to that in the corresponding situation in nature. An immobilized animal cannot indicate its mood as a freely moving animal can. For a behavior program to be activated response thresholds of corresponding neurons must be exceeded. Their level may be influenced by the motivation of the

experimental animal. In an immobilized animal neurons for the release of a behavior mode may have a level of response activity below the threshold for triggering a behavioral response. Certain neurons might be also partly or totally inhibited due to the process of paralysation (Ewert, 1980).

In the last years we developed techniques which allow the simultaneous study of neuronal and behavioral response in freely moving toads. Thus, it is possible to closely investigate the question of coincidence between prey catching behavior and neuronal activity in the visual system (Ewert and Borchers, 1974; Borchers, 1980, 1982).

Recently we recorded neuronal and behavioral responses to moving configurational stimuli in unrestrained behaving toads with lesions of the TP-region (Megela et al., 1983). These animals show extremely short prey-catching response latencies and stereotyped predictable responses to moving visual stimuli. They behave like "input/output" automata (Ewert, 1983). Thus, they provide an excellent opportunity to examine the correspondence between neuronal activity and prey-catching behaviors without habituation effects.

In the experiments the toads were placed in a large cylinder and their responses to moving contrasting behaviorally relevant stimuli of various sizes and shapes were observed.

The responses of retinal neurons located in superficial tectal layers were recorded. The response properties of these neurons were similar to those previously described for both paralyzed and normal freely-moving toads. There was no strict correlation between neuronal activity and visual guided behavior, that is, bursts of activity from these neurons did not necessarily "predict" a subsequent behavioral response.

T2(1) neurons were recorded from deep periventricular tectal layers. As in the intact animals these T2(1) neurons had frontal visual excitatory receptive fields of about 70-90deg diameter, but could show in the TP-lesioned animal varying rates of ongoing spontaneous activity. T2(1) neurons exhibited no configurational selectivity to any of the stimuli presented. These neurons did not respond during spontaneous non-visually-guided movements of the animal. Moreover, there was no relationship between neuronal discharge and prey-catching movements of the toad in response to a visual stimulus, i.e., high neuronal activity did not necessarily coincide with a motor response of the toad (Fig.1). The activity of these neurons seemed to resemble the alertness of the toad which was fluctuating over time.

The activity from tectal class 4 neurons located in the periventricular layers was recorded. The receptive fields of these neurons covered the entire contralateral visual field. Some neurons were spontaneously active. These neurons fired during both active and passive movements of the toad; however, higher rates of neuronal activity were seen when the toad turned in response to a visual stimulus than during spontaneous turning. In either case, neuronal activity did not necessarily precede turning or snapping movements.

TP-neurons were activated both by moving visual stimuli and during the subsequent movements of the animal, suggesting some kind of feedback

which keeps the neuron active during the period of turning behavior. When a stimulus was moved through the receptive field and the toad responded with a prey-catching movement, the frequency of neuronal activity was greater than that observed when the toad did not behaviorally respond to the same stimulus (Fig.2). Thus, relatively high neuronal activity coincided with behavioral responding (Fig.2). The activity preceded and, so to speak, "predicted" a subsequent turning movement. We suggest that these neurons fulfill properties of command elements according to the concept proposed by Kupfermann and Weiss (1978).

Tectal class T8 neurons recorded in the deeper layers were spontaneously active. They showed no direct visual input, although their firing rates seemed to be influenced by visual stimulation. The activity of these neurons coincided with any movements by the toad (e.g., turning, walking, snapping), whether the movement was elicited by a visual stimulus or occured spontaneously (Fig.3). But this kind of "pre-motor" activity showed no specificity with regard to a motor pattern. In any case the neuron continued discharging bursts during the toad's movements, but after the movement the neurons showed clear postexcitatory inhibition (Fig.3).

The basic results of this paper are in accordance with previous investigations of visual neurons in the intact animal (Borchers, 1982; Ewert, 1983). The "TP-preparations" used in this study allowed to more closely study the question of coincidence between prey-catching behavior and neuronal activity. In the activity of retinal ganglion cells there is no correlation between neuronal activity and behavioral response. In tectal class T2(1) and T4 neurons strong neuronal activity not necessarily precedes prey-catching. But their general activation seems to be linked to some extent with the alertness of the toad. Tectal class T5 neurons showed a clear correlation between the frequency of neuronal activation released by a moving visual stimulus and a subsequent orienting (turning) movement. Here, during the traverse of the receptive field, increased activity preceded - and thus predicted - the subsequent behavioral response. These results support the hypothesis that class T5 neurons play an important role in a command system for prey-capture (Ewert et al., 1983). In this context it is interesting to note that these neurons were also activated during the movement suggesting some kind of feedback which keeps the neurons active during the time of turning. This property is resembled by the spontaneously active class T8 neurons: They exhibit premotor activity, are activated during the phase of a movement, and show a period of postexcitatory inhibition with cessation of the movement.

Since the neuronal discharge monitors general motor activity, it may be, that T8 neurons are part of a feedback system. They could receive the information about each movement and then serve to converge the inputs back to an appropriate locus. Since the discharge precedes and, so to speak, predicts the behavioral activity, the question arises if these neurons are related to elements in a feedforward branch of a system in which certain motor patterns are controlled by fixed discharge patterns. We can observe that T8 neurons fire with irregular intervals. The frequency is fluctuating and seems to be modulated by an

overall excitation level of the animal, depending on the stimulus situation. The neuronal discharge passes a maximum before any kind of movement; which points to a threshold function. The enhanced discharge before movements may be related to facilitation of subsequent behavioral patterns (Wurtz and Goldberg, 1972).

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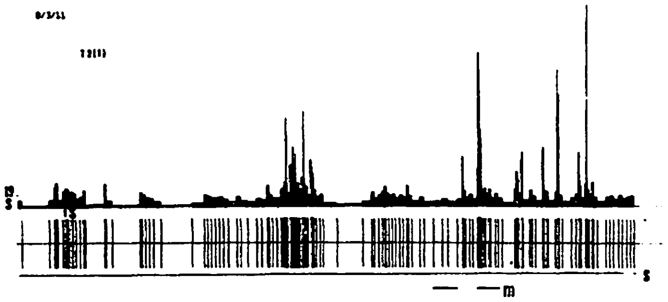

Fig.1. Activity of a class T2(1) neuron during traverse of the ERF with a moving visual stimulus (s); high discharge frequency is not necessarily correlated with a turning movement (m). The computer print-out shows the pattern of action potentials and the corresponding interspike frequency time histogram (Borchers, 1982). The horizontal lines indicate stimulus (s) and behavior events (m) calculated from a frame-by-frame analysis.

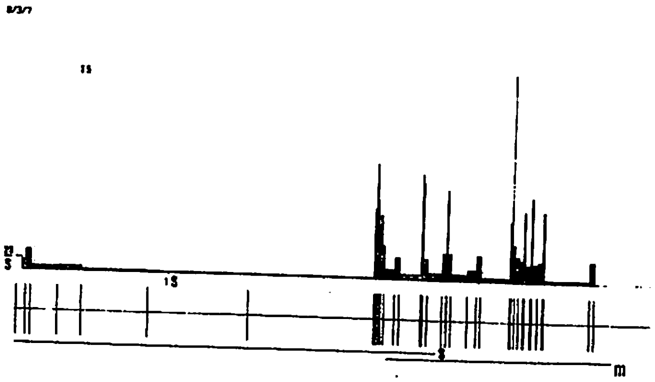

Fig.2. Activity of a class T5 neuron; increased activity during stimulation (s) precedes a turning response (m).

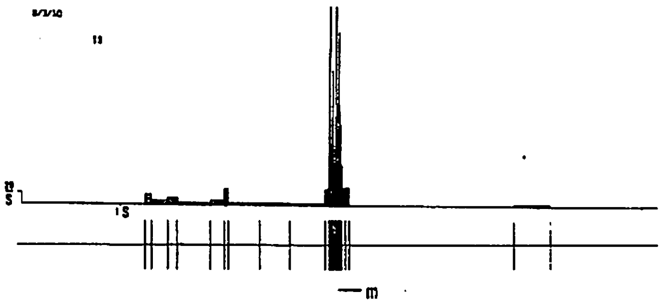

Fig.3. Spontaneously active class T8 neuron; the burst precedes a snapping response (m) toward a moving mealworm; note the subsequent silent period.

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A MATHEMATICAL NETWORK MODEL
FOR RETINO-TECTAL PREY RECOGNITION
IN AMPHIBIANS

1. INTRODUCTION

Within the amphibian brain the optic tectum is usually regarded as the main center for prey recognition. Electrophysiological recordings from this part of the brain have revealed the existence of groups of neurons which show different responses to different types of visual prey dummies. The essential variables of prey dummies are: size, shape, velocity, visual contrast, orientation, direction of movement (see Grüsser and Grüsser-Cornehls, 1976).

In many publications the characteristic differences between responses of tectal cells to rectangular visual stimuli of variable configuration are presented. Fig.1 shows the example of the "T5.1" and "T5.2" cell types in the tectum of Bufo bufo described by Ewert and von Wietersheim (1974). Whereas in both types the rectangle measuring $2^\circ \times 8^\circ$ and oriented perpendicular to the direction of movement (V) elicits the weakest response, T5.1 prefers the square (S) measuring $8^\circ \times 8^\circ$ to a rectangle measuring $8^\circ \times 2^\circ$ and oriented parallel to the direction of movement (H), and T5.2 shows the opposite preference. It is important to notice that neither response type is, by itself, capable to distinguish between, say, S and H on the basis of the impulse frequency. Because, as can be seen in the diagrams, to a given impulse frequency there exist more than one specific stimulus configuration.
From the same laboratory are the data presented in Fig.2 concerning response characteristics of tectum cells of Rana temporaria (Schürg-Pfeiffer and Ewert,1981). It is interisting to see that in the case of Rana more "types" are found and that the variation of the responses within the same type is rather high. If these cells are assumed to be able to distinguish between different stimuli, the question arises whether this is done independent from the stimulus velocity. Fig.3 shows that this is not always the case at least in the T5-tectum cells classified by Grüsser and Grüsser-Cornehls (1976). The neuron presented in Fig. 3b responds equally (with 2 imp./sec) to a $2^\circ \times 2^\circ$-square moving at velocities of $v=0.4^\circ$/sec and $v=20^\circ$/sec and to a square measuring $7^\circ \times 7^\circ$ and moving at 0.18°/sec.
Further investigations have revealed a still larger number of response types both with respect to geometric properties and

velocity of the stimuli presented to the animal. Fig.4 contains responses to three stimulus configurations (S: $8^\circ \times 8^\circ$, H: $8^\circ \times 2^\circ$, V: $2^\circ \times 8^\circ$) at three velocities ($v=2, 6, 20^\circ$/sec) which yields at least 5 different types.

Apart from the difficulty to determine the function of a network responding in such a complex way the question arises which neural processes and connections could produce such a response complexity. Is it necessary to postulate as many mechanisms as response types exist ? How complex should a mechanism be in order to produce the observed behavior ? This question is important because several authors expressed the opinion that - due to the complicated behavior- no "simple" network of tectum cells could exist.

In the following a theoretical neural network is developed in which known neurophysiological properties of the amphibian retina and tectum are incorporated and which generates the observed response properties of tectal cells with a minimal amount of additional assumptions.

The visual stimulation of the optic tectum is mediated by the retinal ganglion-cells (rgc). Three ways of stimulation are conceivable: (i) direct stimulation of a tectum cell (t.c.) by a r.g.c.; (ii) indirect stimulation of a t.c. by another t.c. (stimulated directly or indirectly by a r.g.c.); (iii) indirect stimulation of t.c. by visual brain regions outside the tectum.
In the first step we try to use only the first way of retino-tectal interaction within our model. It will become clear that already under this condition a large number of phenomena can be explained although not all of them. A largely satisfactory solution can be achieved by additional use of the second way of interaction. Extratectal influences are not necessary in order to explain the observed types, though our model does not exclude them (see discussion in Sections 4 and 5).

2. MATHEMATICAL NETWORK MODEL OF THE RETINA

Since visual stimuli never act directly upon tectal cells but always only indirectly via retinal g.c., a model about tectal processes presupposes a model about retinal activities. Within the literature several mathematical models for the frog and toad retina have been developed and analyzed (e.g. by Grüsser (1967), Grüsser and Finkelstein (1967), Ewert and von Seelen (1974), Butenandt and Giebel (1974), Butenandt (1975)).It is important to have at hand a model simulating the output activities of r.g.c of type 2 and 3 (classification following Grüsser and Grüsser-Cornehls) as exactly as possible (as a function of the spatio-temporal stimulus conditions in the visual field). Neurophysiological experiments have shown that the optic tectum is mostly activated by fibers from these two types of r.g.c., the large majority (93 %) of them being of type 2.

In the first part of our modeling we present a mathematical model of the retina generating the responses of r.g.c. types 2 and 3 to rectangular stimuli of different size, configuration and velocity. It contains some elements already used in previous models (cited above) of the retina. In the present state of our model we did not pay too much attention to represent the retinal network in all of its details (e.g. in which way receptors, horizontal, bipolar and amacrine cells really interact with each other), many of which are still unknown, but we were mainly concerned with an exact reproduction of the axonal activity of r.g.c. trying to hold the number of assumed interaction principles essential for the performance as low as possible. This is in line with our purpose to keep the model mathematically perspective.
Fig. 5 shows the assumed retinal connectivity. Accordingly the retina is decomposed into three layers. The light emanating from the external stimulus and its surround excites the receptors in the upper layer. These have excitatory connections to the interneurons in the middle layer. The lower layer consisting of r.g.c. receives both excitatory and inhibitory inputs from the interneuronal layer. This rough partition is well justified physiologically and morphologically. More speculative are the following details.

Since temporally constant light does not elicit a response of real ganglion cells a high pass filter operation is assumed in the network which is here put into the receptor layer (though it may equivalently be represented in the interneuronal layer). The time-dependent output y(t) of a high pass filter (of first order) to a time-dependent input x(t) is described by

$$y(t) = \int_{-\infty}^{t} x(t') \left(\delta(t-t') - T_1^{-1} e^{-(t-t')/T_1}\right) dt' \qquad (1)$$

with a time constant $T_1 > 0$ and a gain factor a_1.
In particular a (temporally) rectangular input

$$x(t) = \begin{cases} 0 & \text{if } t < t_o \text{ and } t > t_1 \qquad (2a) \\ 1 & \text{if } t_o < t < t_1 \qquad (2b) \end{cases}$$

results into

$$y(t) = \begin{cases} 0 & \text{if } t < t_o \qquad (3a) \\ e^{-(t-t_o)/T_1} & \text{if } t_o < t < t_1 \qquad (3b) \\ e^{-t/T_1}\left(e^{t_1/T_1} - e^{-t_o/T_1}\right) & \text{if } t > t_1. \qquad (3c) \end{cases}$$

(3b) describes the ON-reaction to the leading edge, (3c) the OFF-reaction to the succeeding edge of the input. Investigation of spike sequences suggests that the succeeding edge has both excitatory and inhibitory effects to ganglion cells. Also from observations in the fish retina (Levine and Shefner, 1977) it appears possible that the ON- and OFF-components of the high pass filter output are processed in separate channels. Therefore we postulate two types of receptors. The ON-receptors (OFF-receptors) react positively to an increase (decrease) of light intensity. The ON-receptor produces the part (3b) of y, the OFF-receptor the part (3c) (multiplied by a - sign). Generally the operation of these receptors (which may also be conceived as interneurons) consists in transducing the light intensity x(t) into the output signal

$$z_{ON}(t) = a_1 \max(0, y(t)), \qquad (4a)$$

$$z_{OFF}(t) = a_2 \max(0, -y(t)), \qquad (4b)$$

where y is given by equation (1) and a_1, a_2 denote suitably dimensioned positive gain factors. The function max describes the operation of a rectifier

$$\max(a,b) = \begin{cases} a & \text{if } a \geq b \\ b & \text{if } b > a. \end{cases} \tag{5}$$

Identifying points in the retinal surface with points in the two-dimensional visual field by the geometry of light projection a rectangular coordinate system may be introduced in the retinal layers identical with that in the visual field (with ° as unity). Let x(s,t) be the light intensity at location s in the visual field and $z_{ON}(s,t)$, $z_{OFF}(s,t)$ the activity of the receptors at location s of the retina.

Two types of interneurons are distinguished. One of them acts excitatory, the other one inhibitory onto the ganglion cells. Their outputs are denoted by $v_e(s,t)$ and $v_i(s,t)$ respectively. The interneurons receive local, weighted inputs from the receptors and they operate as low pass filters with membrane time constant T_2 (we shall not consider a slightly more complicated model with two different time constants for the two cell types). Mathematically this feature is described by

$$T_2 \frac{d\, v_e(s,t)}{dt} = b_{1e}\, z_{ON}(s,t) + b_{2e}\, z_{OFF}(s,t) - v_e(s,t) \tag{6a}$$

$$T_2 \frac{d\, v_i(s,t)}{dt} = b_{1i}\, z_{ON}(s,t) + b_{2i}\, z_{OFF}(s,t) - v_i(s,t) \tag{6b}$$

with nonnegative coefficients b_{kj}.
A possible threshold or rectifier process in this level is neglected.

Like previous authors we assume in the subsequent layer that the r.g.c. have a farreaching domain of excitation and inhibition by the interneurons. This is concluded from the size of their receptive fields. Since these fields have an excitatory center and an inhibitory periphery, at large distances the influence of the inhibitory interneurons exceeds that of the excitatory interneurons.

Let w(s,t) denote the generator potential of a ganglion cell whose receptive field is centered at location s in the visual field. By a shift of the coordinate system we may assume s=0 and write w(t)=w(0,t) in stead of w(s,t). The influence of an interneuron upon a ganglion cell decays with its distance from the center of the receptive field. As a decay function we choose a bell shaped Gaussian. Then the total influence of the interneurons onto the ganglion at time t amounts to

$$e(t) = \iint \left(E_e v_e(\tilde{s},t)\, e^{-k_e|\tilde{s}|^2} - E_i v_i(\tilde{s},t)\, e^{-k_i|\tilde{s}|^2}\right) d\tilde{s}, \tag{7}$$

where the integration extends over the whole of the visual field. Because of the structure of the receptive field the constants have to satisfy the inequalities

$$E_e > E_i \quad \text{and} \quad k_e > k_i. \tag{8}$$

Supposing a low pass filter property with time constant T_3 the membrane potential w of the r.g.c obeys the differential equation

$$T_3 \frac{d\, w(t)}{dt} = e(t) - w(t). \tag{9}$$

Finally the membrane potential has to be transformed into an axonal impulse frequency. Most simple is the assumption that the impulse frequency is given by

$$w_+(t) = \max(0, w(t)). \tag{10}$$

This relation presupposes that the threshold of the cell is normalized to 0 (say mV).
Equation (10) terminates the description of the retinal network model. It is possible to choose the parameters in this model in a way such that not only the time average of the activities of r.g.c but also their temporal development may be simulated sufficiently close to the experimental data. Fig. 6 shows the average impulse frequencies computed (by a digital computer) on the basis of this model as they are typically observed in r.g.c. of type 2 (Fig.6A) and of type 3 (Fig.6B), parameters being given in the legend. Typical is meant in the sense that data in the literature (Ewert and Hock, 1972, Grüsser-Cornehls, 1976 (rewiew)) and own data have been taken into account. There are some differences

between the laboratories. However, the following characteristics were universally observed and are adequately reproduced by the model (compare Fig.6): At a stimulus velocity of about 7°/sec the retinal class-2 cells respond maximally to squares measuring $4^{\circ} \times 4^{\circ}$ (all stimuli are dark rectangles moving at constant velocity in front of a bright stationary background), class-3 cells respond maximally to $8^{\circ} \times 8^{\circ}$-squares. Horizontal bars (i.e. rectangles oriented in the direction of movement) in both types elicit a response, which is nearly independent of their length. Among the stimuli whose longer edge exceeds 6° the class-2 neurons prefer the horizontal bars. In class-3 cells this holds only for stimuli longer than about 16°.
Fig.6 only shows the temporal mean of the activity. However, the relevant input to the tectum is only given by the actual temporal development and duration of axonal activity. This information is lost by forming the mean. Indeed our model, as will be demonstrated in another publication, is able to produce these details sufficiently precisely. This publication will also contain a discussion of earlier retinal models and also of other not yet explained phenomena in the retina.

3. MATHEMATICAL NETWORK MODEL FOR TECTUM NEURONS

In 1974 Ewert and von Seelen published a model for tectum activity on the basis of which they indeed were able to produce the response characteristics of the two cell types shown in Fig.1, which are classified after Grüsser and Grüsser-Cornehls as T5(1) and T5(2) cells. The first has the preference $S > H > V$, the second $H > S > V$. In fact they explained the first type by a two-dimensional single layer network receiving input directly from the external light distribution (here called $x(s,t)$, in their paper $y(s,t)$). Hence they considered a model, in which the operation of the retina and of the tectum were lumped together. In contrast (not in contradiction !) we propose here a model, where the operations of these two tissues are separated and where, consequently,the problem has to be solved, how the tectum converts the class-2 and class-3 retinal characteristic presented to it into its own characteristics which are many as seen from figures 2-4. For the production of the T5(2)-characteristic Ewert and von Seelen assumed interaction of tectum cells with cells from the thalamus/pretectum region. It is an open question whether such extra-tectal interactions are in fact essential to generate this and other types of tectal response. Recent models by Lara, Cervantes and Arbib also assume such interactions. As an alternative we present here a model which only uses intra-tectal interactions, but nevertheless produces the types shown in the figures. It will be an experimental problem which of the two possibilities or another one is adequate.

A rough draft of the model is contained in Fig.7. The input to the tectal network consists in the axonal activity of the r.g.c. As indicated by the figure the main operations of the tectum cells are spatio-temporal summation and recurrent inhibition. The summation of a tectum cell concerns the output of those r.g.c. which
(i) share their excitatory receptive field with the receptive field of this tectum cell and
(ii)are connected by their axon to this tectum cell.
As mentioned above, 93% of optic fibers projecting to the tectum are estimated to originate from type 2-retinal cells and almost none from types 1,4,5-retinal cells. These last cells may satisfy condition (i), but not condition (ii). Actually in some of our calcu-

lations (see below) we assume that only type 2-r.g.c. project to some tectum cells.

The number of r.g.c. (of a certain type) projecting to a single tectum cell depends on the degree of overlap between the (excitatory) receptive fields of r.g.c. We define the degree of overlap to be the inverse of the average distance (measured in spatial units of the visual field, e.g. °) between the centers of neighbouring receptive fields. Note that this definition is independent of the size of the receptive fields, which is important since this size varies with physiological conditions (in particular in neurons with an excitatory-inhibitory structured receptive field).

The degree of overlap, called Δ, is an important parameter in our model. In particular this feature possibly throws some light on the phenomenon of striated receptive fields (see Grüsser and Grüsser-Cornehls 1976; details will be discussed elsewhere).

Given the number N of r.g.c. of a certain type, projecting to a single tectum cell, and their degree of overlap Δ, the summation process of this tectum cell is defined precisely as following:

The centers of the receptive fields of the N cells are assumed to be distributed in the visual field according to a uniform random distribution such that the degree of overlap equals Δ. Then the excitation e(t) of the tectum cell by the retina is given by

$$e(t) = a_3 \cdot \sum_{i=1}^{N} w_+^i(t)\, e^{-kd_i^2}. \tag{11}$$

Here a_3 is a proportionality factor, w_+^i the output of the i-th r.g.c, and d_i measures the distance (in units of the visual field) of the center of the i-th r.g.c. to the center of the tectum cell. The factor $\exp(-kd_i^2)$ represents the assumption, that the synaptic strength per unit area decays according to a Gaussian distribution with rate k from the center to the periphery of the tectum cell's receptive field. Underlying to equation (11) is the well established hypothesis of a nearly topographic projection from retina to tectum.

Before discussing inhibition between tectum cells it is useful to investigate the output of t.c. under the condition of no inhibition, i.e. in the limiting case of inhibitory coefficients equaling 0. This gives also information on the case of weak inhibitory coupling. Assuming simply the t.c. to act as a low pass filter with a membrane time constant T_4, followed by a transformation of membrane potential (u) to impulse frequency (u_+), the output u_+ is computed from

$$T_4 \frac{d\,u(t)}{dt} = e(t) - u(t), \tag{12}$$

$$u_+(t) = a_4 \max(\Theta, u), \tag{13}$$

Θ = threshold of t.c.

This completes the description of the model tectum cells, if there is no inhibitory interaction between them.

As a thumb rule for the relation between the numbers N,Δ and the diameter d of a t.c. receptive field the approximation

$$N \sim \left(\frac{d}{2\Delta}\right)^2 \tag{14}$$

may be used.

The output behavior of the model tectum cells is shown in Figs. 8A and 9A. In the case of Fig.8A it is assumed that only type2-r.g.c. project to the t.c.(parameters as in the legends of Fig.6A and 8A). It turns out that

(i) the maximal response is obtained to 8° × 8°-squares (in contrast to 4° × 4°-squares with type 2-r.g.c),

(ii)in a broad range of edge lengths the squares are dominant, followed by the horizontal bars, which are preferred to vertical bars.

Thus, in a broad range of angles, the preference type is S > H > V. If, on the other hand, we assume only type 3-retina cells to converge to a tectum cell (with parameters as in Fig.6B and Fig.9A), then the tectal preference type S > V > H is realized, see Fig.9A.

At the moment we have no complete survey which other types may result if the parameters of the t.c. model are varied. It is also not clear which types will be obtained if there is mixed input from both types of retina cells. Here certainly the proportion of the two degrees of overlap plays an important role. However it can be concluded, since in both pure case (input either from type 2- or type 3-r.g.c.) we always found the square to be dominant (for angles not extremely large), the same will hold in the mixed cases. Thus the problem remains how the type evolves where the horizontal bar is dominant. The following section will show that inhibition in the tectum is sufficient to produce this type.

4. THE EFFECT OF RECURRENT INHIBITION WITHIN THE TECTUM OPTICUM

We now extend the previous model by adding inhibitory connections between tectal cells. The inhibition is recurrent (feedback) since the output of the t.c. is considered as inhibitory input to neighbouring t.c. (see Fig.7). For modeling purposes it does not matter very much whether the inhibitory influence is direct (defining lateral inhibition) or mediated by interneurons. Possible candidates for inhibitory interneurons are the stellate neurons (Székely and Lâzâr, 1976). For simplicity we assume the inhibition to be direct and thus may be incorporated into equation (12) for the generator potential u of a t.c. Precisely we assume

$$T_4 \frac{d\,u^i(t)}{dt} = e^i(t) - u^i(t) - a_5 \sum_{j=1}^{L} u_+^j(t),\ i=1,2,\ldots,L. \qquad (12')$$

The indices i and j are used to distinguish between the L tectum cells distributed in a two-dimensional retino-topic surface. The parameter a_5 is a measure of the strength of inhibition. At this stage of modeling we neglect distance-dependence in the summation of inhibition.
The final output u_+^i of the i-th tectal cell is given again by equation (13), index i suitably added.
In order to observe clearly the effect of inhibition we chose the same parameters (for retina and tectum) that led to the output shown in Fig. 8A, only increasing in small steps the inhibitory coefficient a_5 from 0 (no inhibition, (12')<->(12)) to positive values. In fact, for a_5=0.04 the response characteristics shown in Fig. 8B came out showing the t.c. type T5(2) with preference H >S >V, mentioned above. This result is important, since all models investigated so far presupposed interaction with pretectal-thalamic regions in order to produce this type of preference.
The model presented here confirms that this assumption is not necessary, though it does not exclude it as a possibility. The model predicts that the response type H >S >V is due to intratectal interaction alone.
This view is supported by the following observation. Assuming a model tectum cell integrating only inputs from type 3-r.g.c. as shown in Fig.9A (all parameters conserved), increasing the inhibitory coefficient a_5 leads first to the type S > H > V (at least

for stimulus angles not too large , see Fig.9B), and finally for larger values of a_5 the type H> S> V appears again, as shown in Fig.9C. No other types were obtained by further increasing a_5.

5. CONCLUSION AND SUMMARY

We have first presented a mathematical model for the retinae of frogs and toads, that satisfactorily reproduces the response types of retinal ganglion cells to various rectangular stimuli with dimensions of prey dummies. We demonstrated the particular case of the toad, the somewhat different conditions in the frog will be discussed elsewhere. The output of this model serves as input to a model for the optic tectum developed subsequently. The essential features of this tectum model are spatio-temporal summation of retinal ganglion cell activity and recurrent inhibition intrinsic to the tectum.
Several types of experimentally observed tectal cells could be simulated by varying a few of the model paramenters. Hence it is not necessary to postulate different types of mechanisms for the different types of neurons.
T5(1) cells (S > H > V) are obtainable in two ways:
(i) by a summation process with regard to retinal type-2 neurons without any or with little recurrent inhibition;
(ii) by a summation of retinal type-3 neurons with a medium degree of recurrent inhibition in the tectum.
Evidently, T5(1) cells can also be produced by a weighted mixing of the processes (i) and (ii).
T5(2) cells (H > S > V) also result in two ways:
(a) by summation of retinal type-2 output and a sufficiently strong tectal inhibition;
(b) by summation of retinal type-2 output combined with strong recurrent inhibition.
Again, combinations of (a) and (b) also produce this type.
T5(3) cells (S > V > H) result from summation from retinal type-3

cells together with no or little recurrent inhibition.
Our hypothesis, to be tested experimentally, is that the inhibitory coefficient and other parameters (like degree of overlap Δ) vary throughout different regions or columns of the tectum, thus producing most of the cell types observed experimentally. This concept is different from other concepts postulating interactions between tectum and other brain regions (e.g. thalamus/pretectum) as the origin of this variety. This specific role of this diencephalic region is not yet sufficiently confirmed by neuroanatomical studies. Furthermore, it is reasonable to assume an unspecific effect of the pretectal nuclei onto the tectum, e.g. controlling the receptive field size of tectal cells. The increase in receptive field size of tectal cells observed after destruction of the pretectum, can easily be regarded as the basis of the loss of prey recognition capacity of tectal cells.
Clearly, the present model has to be tested further. One aspect not dealt with here is the velocity dependence, since in all computer simulations only one velocity ($v = 7.6^{\circ}$/sec) was assumed. Another aspect concerns the discrepancy between the responses to very extended stimuli (longer edges exceeding 16°) predicted by the model and the actually observed values. In the model the responses to very long horizontal bars are mostly overestimated, those to large squares and vertical bars underestimated. At the moment it is not clear whether this is due to suboptimal choice of parameters or to a pitfall of the model or whether the model gives a hint that large stimuli are in fact processed in a way different from smaller, preylike stimuli. With regard to the known properties of thalamic and pretectal neurons (preference for large stimuli) one can assume an influence of the diencephalon onto the tectum in the presence of large, non-prey objects. In contrast, small prey-like objects would be processed exclusively in the optic tectum.

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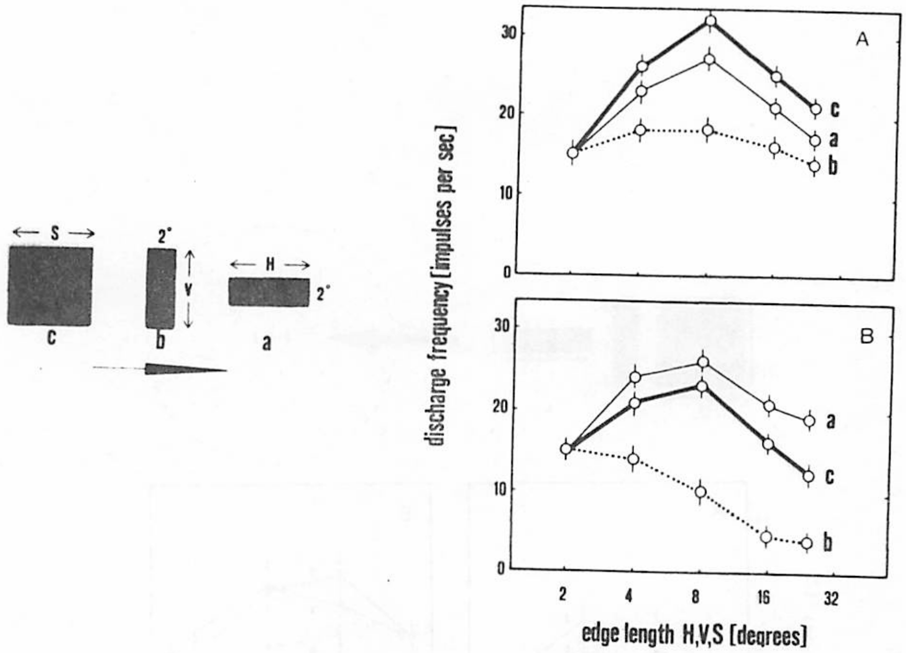

Fig. 1: Responses of two cell types in the optic tectum of the toad Bufo bufo (L.) to moving stimuli ($v = 7.6^{o}$/sec) of different size and orientation with respect to the direction of movement. The curves a-c show responses of 2o cells to stimuli, in which a square measuring 2×2^{o} was extended stepwise either in horizontal direction (curve a) or in vertical direction (curve b) or in both directions (curve c). A: T5.1 - cells; B: T5.2 - cells. The average receptive field (RF) size of both types is 27^{o}. (From: Ewert, J.-P., 1976).

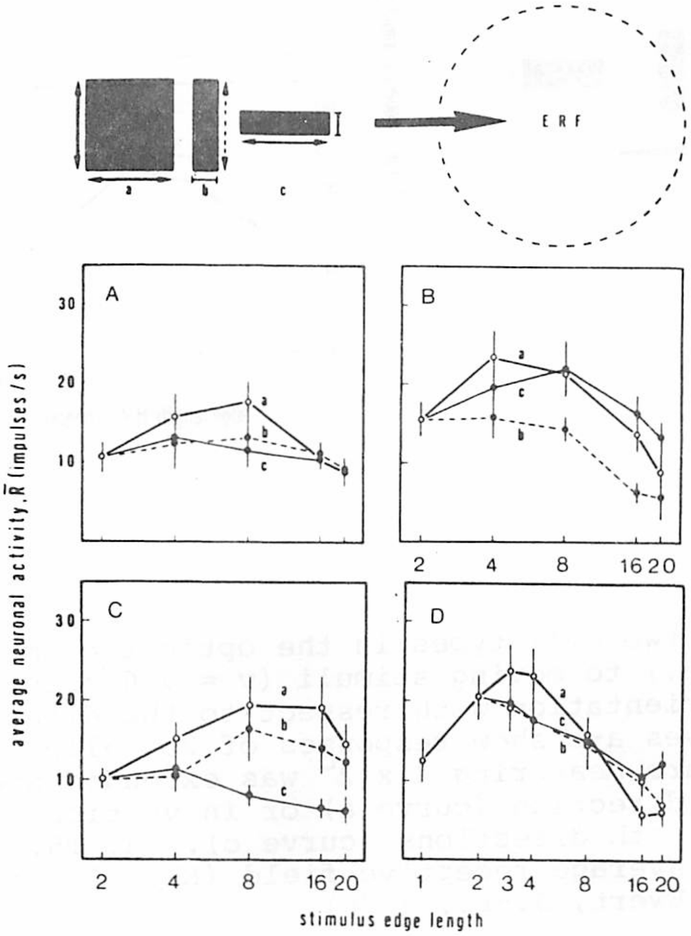

Fig. 2: Responses of four cell types in the optic tectum of the frog Rana temporaria (L.) to moving stimuli. The stimulus presentation is the same as in fig. 1 except that curve a here represents the responses to the squares, curve b that to the vertical bars and curve c that to the horizontal bars.
A: T5.1 - cells, RF-size 21°, n = 9; B: T5.2 - cells, RF-size 17°, n = 8; C: T5.3 - cells, RF-size 24°, n = 6; D: T7 - cells, RF-size 4°, n = 12. (From: Schürg-Pfeiffer, E., Ewert, J.-P., 1981).

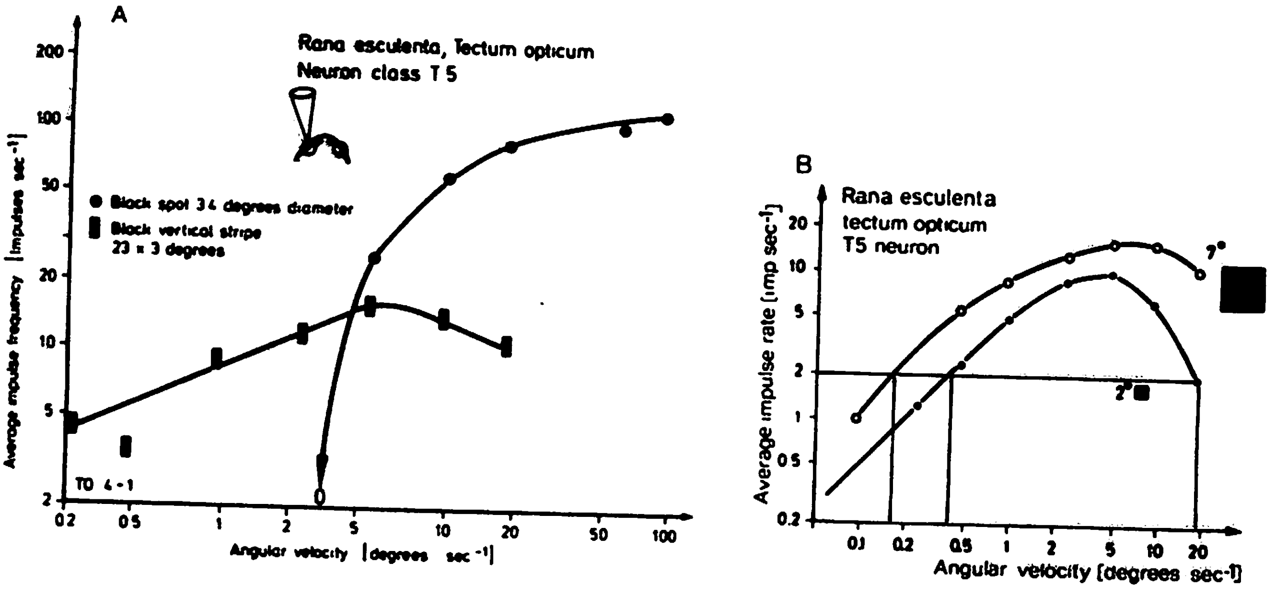

Fig. 3: Velocity function of two class T5 - cells in the optic tectum of the frog Rana esculenta. A: Responses to a vertical bar measuring 23 x 3° moved horizontally, and to a small spot of 3.4° diameter. B: Responses to two square spots of different size (2° and 7°). (From: Grüsser, O.-J., Grüsser-Cornehls, U., 1976).

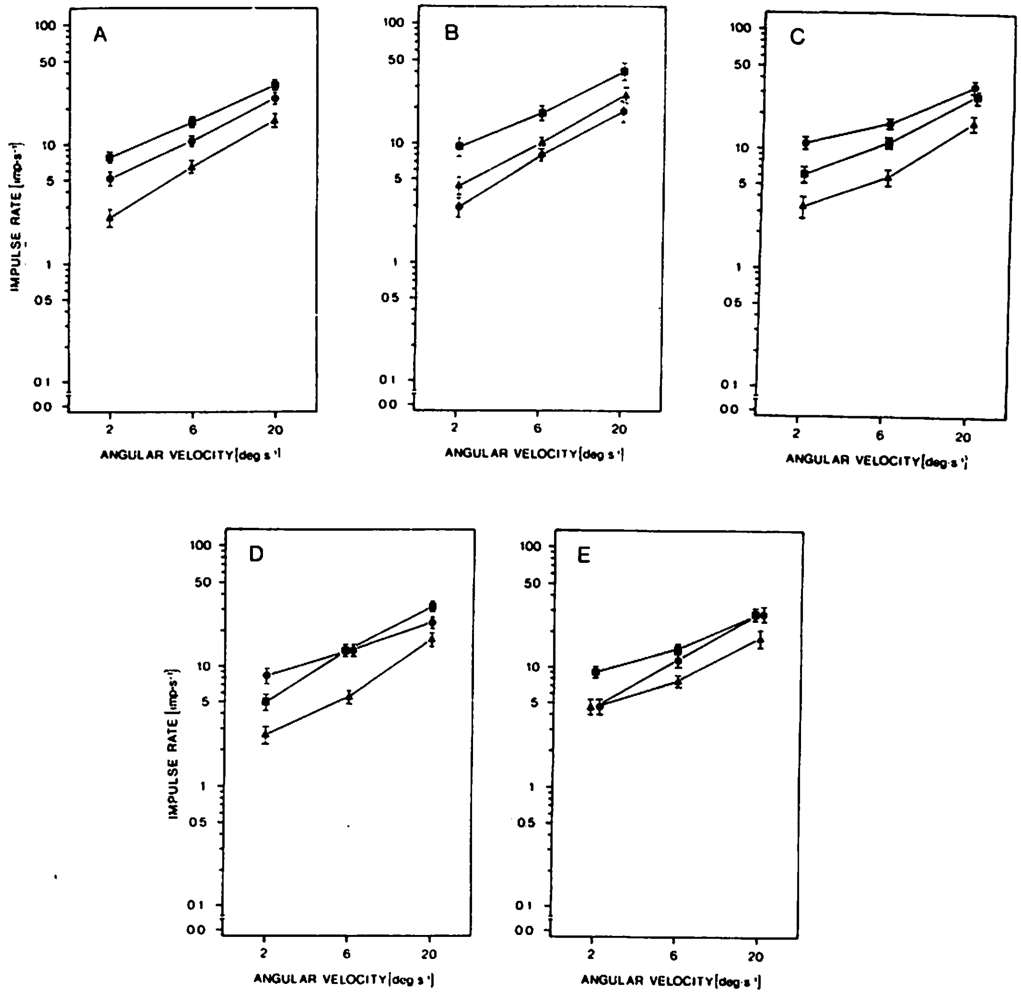

Fig. 4: Responses of five cell types in the optic tectum of the toad Bufo bufo (L.) to stimuli of different configuration and velocity. Stimuli were a square measuring 8 x 8° (S), a horizontal bar measuring 8 x 2° (H) and a vertical bar measuring 2 x 8° (V) which were moved at velocities of 2, 6 and 20°/sec.

A: Neurons (n = 34) with parallel/converging velocity functions preferring S to H and to V. B: Neurons (n = 13) with parallel/converging velocity functions showing a preference S>V>H.

C: Neurons (n = 25) with parallel/converging velocity functions showing a preference H>S>V. D: Neurons (n = 16) with preference inversion between H and S. E: Neurons (n = 22) with a change in preference with respect to H.

Squares ■ , horizontal bars ● , vertical bars ▲ . (From Roth, G., Jordan, M., 1982)

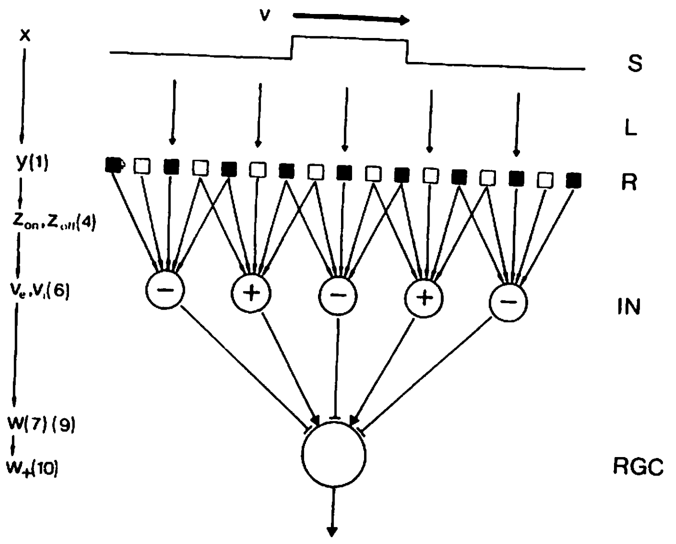

Fig. 5: Hypothetical network of the retina. In the left margin the symbols are listed denoting the activities in the corresponding layers of the network. The numbers in parentheses point to the equations in the text modeling the activities.
v: stimulus velocity, S: stimulus, L: light, R: receptors, IN: interneurons, RGC: retinal ganglion cells, ■ OFF-receptors, □ ON-receptors, ⟶ excitatory connections, ⊣ inhibitory connections, ⊖ inhibitory cells, ⊕ excitatory cells.

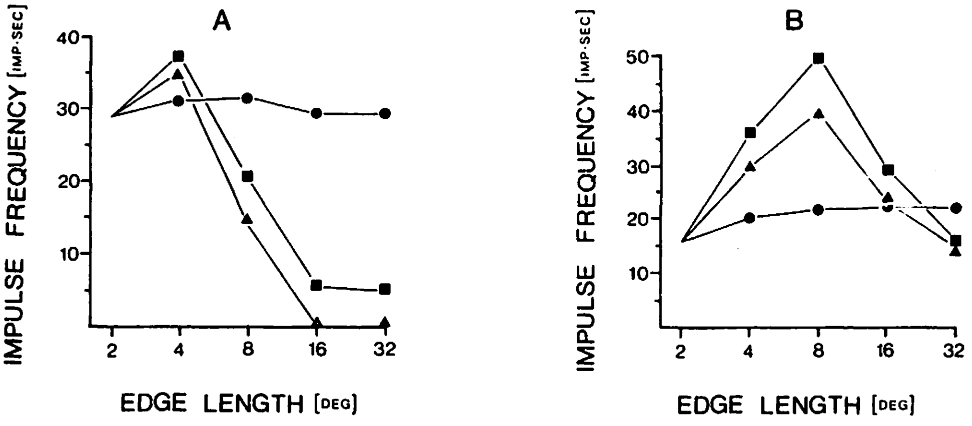

Fig. 6: Average responses of the model retinal ganglion cells to stimuli as in figs. 1 and 2 (squares ■, horizontal ● and vertical bars ▲, v = 7.6°/sec). Parameters of the model:
A: retinal type 2; $a_1=a_2=1$, $T_1= 0.3$ sec, $T_2= 5$msec, $b_{2e}= b_{2i}= 1$, $b_{1e}= 1/6$, $b_{1i}= 0$, $E_e= 50$, $E_i= 14.7$, $k_e=0.37$, $k_i= 0.06$, $T_3= 5$ msec.

B: retinal type 3; same parameters as with A except $E_i= 23.5$, $k_e= 0.07$, $k_i= 0.023$.

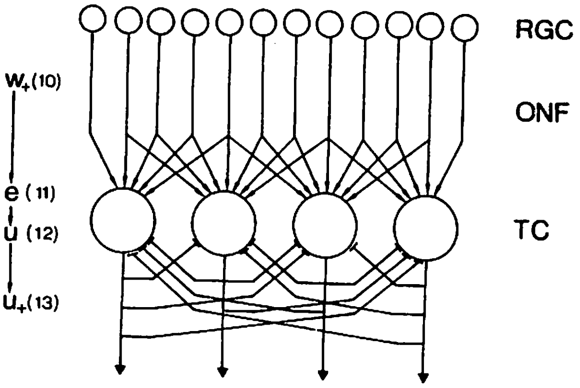

Fig. 7: Hypothetical network for tectum cells. To the left the symbols for the activities in the corresponding level are listed together with the number of the model equations.
ONF: optic nerve fibers, TC: tectum cells.

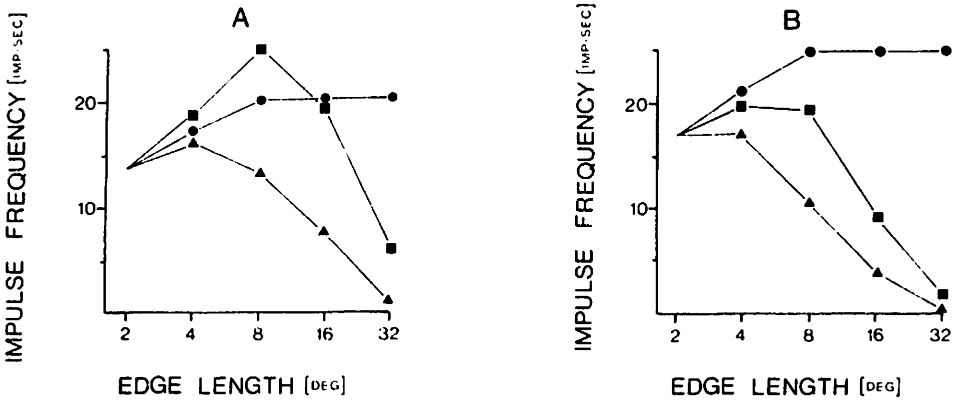

Fig. 8: Output of the tectal cell model, if the input consists only in the axonal activity of type-2 retinal ganglion cells.
A: The case, when no or little inhibition among tectal cells is assumed ($a_5 = o$).
B: The case, when inhibition among tectal cells is sufficiently strong (here a_5=o.o4). Other parameters in A and B are: $a_3=a_4=1$, d = diameter of RF=27°, Δ= 1, T_4= 5 msec.

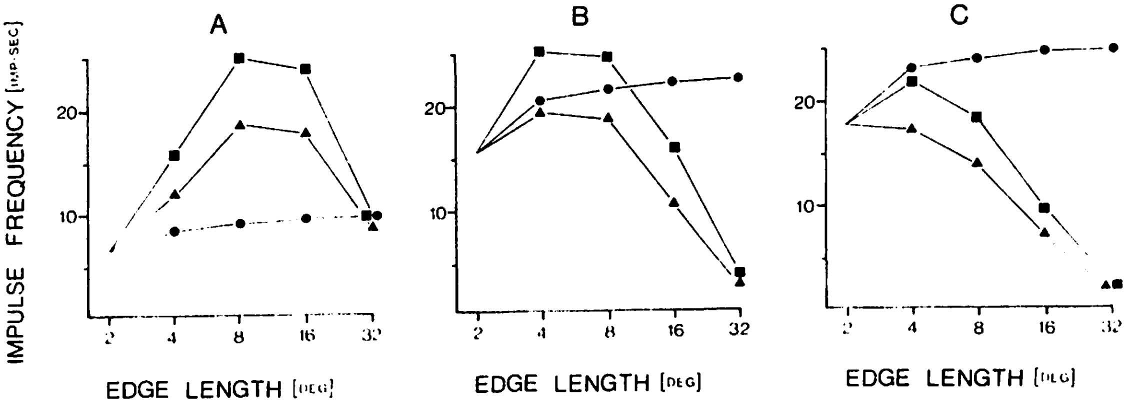

Fig. 9: Output of the tectal cell model, if the input consists only in the activity of type-3 retinal ganglion cells.
A: no or little inhibition (a_5=o).
B: medium inhibition (a_5=o.16).
C: strong inhibition among tectal cells (a_5=2). Other parameters as in fig. 8.

A Neural Model of Interactions Subserving Prey-Predator Discrimination and Size Preference in Anuran Amphibia[*]

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Running title:

Neural Model of Amphibian Prey-Predator Discrimination

Abstract

The model described analyzes how the neural activity distributed accross entire brain regions that interact with each other might lead the animal to yield the proper motor behavior. Computer simulations were conducted to make an analysis of how the interactions among retina, optic tectum and pretectum give the animal the ability to discriminate between prey and predator stimuli. The results of the simulations of the model, which has anatomical, physiological and behavioral grounds, allowed us to suggests new experiments, as well as, to postulate what neural mechanisms might be involved in some phenomena related with the prey-catching orienting behavior, such as prey-predator discrimination, with direction invariance of prey-predator recognition being a consequence of tectal architecture, and size preference and response latency depending on the motivational state of the animal.

1. Introduction

We propose a two-dimensional model of the interactions among retina, optic tectum and pretectum in the anuran amphibian brain. The model analyzes neural processes subserving prey-predator discrimination, with direction invariance of prey-predator recognition being a consequence of tectal architecture, and size selection and latency of response of the animal depending on its motivational state. The model is an extension of the one-dimensional model of the optic tectum, described elsewhere[3,32,33], and takes into consideration anatomical, physiological and behavioral studies in anuran amphibians, as well as earlier modelling efforts (Didday[7], Ewert and Von Seelen [11]).

Neuroethological studies[12,16,28,39] have shown that there are fixed action patterns in frogs and toads released by relatively simple key-stimuli. Innate mechanisms recognize the key-stimuli in the environment to elicit the proper response. It has been shown that both the size of a moving stimulus and its geometry in relation to the direction of motion play a prominent role in the prey-catching behavior of the animal: small objects whose longest axis moves in the direction of motion ("worm-like") are treated as prey; if the same object is moved with its longitudinal axis perpendicular to the direction of movement ("antiworm-like") the animal does not exhibit prey-catching orienting behavior, or may assume a freezing posture, or may exhibit avoidance behavior[12] (see Fig. 1B.a). It has also been shown that, in frogs and toads, worm-antiworm and discrimination is invariant to both the direction of motion[13] and to the velocity function of the stimulus[12,16]. Luthardt and Roth[36] have reported that in Salamandra Salamandra the worm-antiworm discrimination varies with the velocity, the animal preferring "worm-like" to "antiworm-like" stimuli at low velocities, while at high velocities the "antiworm-like" stimulus is more effective. However, Himstedt[22] argues that this phenomenon is not observed in all salamanders, and that it probably depends on the animal's experience with certain types of prey (see

Discussion), and Ewert (personal communication) has not found this change of preference.

Ingle[24,29,30] and Ewert[15,16] have shown that the releasing value of prey stimuli can change depending on the motivational state of the animal. They showed that animals highly motivated (i.e. with hunger or by smelling worms) had low response thresholds and increase the response rate to prey stimuli, even to those normally ineffective. Ingle showed that in these conditions, when a pair of "worm-like" stimuli (cylindrical objects attached to wire holders, moving with their longitudinal axis parallel to the direction of motion) are present in the animal's monocular receptive field, frogs prefer stimuli subtending a visual angle of 16 degrees to the normally preferred stimulus subtending a visual angle of 6 degrees, and present a lower latency in the response. Ingle postulates that the mechanisms subserving response latency do not directly determine size preference, though both processes are the outcome of a reduction in the pretectal inhibitory effect upon the optic tectum (henceforth referred to as "tectum" for short).

Moreover, Ewert[16] showed that prey-catching activity is greatly increased in motivated animals. He argues[15] that the size selection phenomena (determination of the "optimal prey size" to be preferred) remain almost the same for, within certain limits, changes in the motivational state of the animal. In Fig. 13A we can see that highly motivated animals present a smaller response latency than animals under normal conditions or with low motivation.

A great deal of research has been aimed at trying to find the neuronal mechanisms responsible for these processes. Ewert[12,16] has shown that prey-catching orienting behavior is disrupted when the tectum is destroyed. Moreover, as might be expected, since the optic tectum receives information from the retina in a retinotopic way, he has shown that electrical stimulation of a specific region in the tectum, via an implanted microelectrode, elicits the prey-catching orienting response to the corresponding retinal

projection. This suggests that the tectum plays a prominent role in this sort of behavior. Ewert[8] has also shown that lesions of the dorsal pc/pl region within the thalamic-pretectal region (henceforth referred to as "pretectum" for short) disrupts the ability of the animal to discriminate different configurations of the stimulus (see Fig.1B.b). Furthermore, he observed that toads with pretectum ablation snap indiscriminately to any object, they switched their preference from white to black moving visual stimuli, and they lost size selectivity. This suggests that the interaction among retina, tectum and pretectum may be responsible for processes like prey-predator discrimination, response latency, size selection, and size constancy. The hypothesis of Ewert that pretectal neurons modulate tectal activity through an inhibitory effect has been confirmed by Ingle[26,31,41]. He found that there is some recovery after two weeks of the lesion, although the animal never completely recovers its normal discriminatory ability[16], it suggests that there must be other mechanisms, probably inside the tectum itself, which, in addition to the pretectum, exert an inhibitory effect upon the tectum giving the animal the ability to discriminate between worm and antiworm stimuli. Furthermore, these mechanisms somehow increase their participation in the absence of pretectal activity, and so might in this way be responsible for the recovery. Ewert[12,16] reported cells in the optic tectum (T5(3)) that are most sensitive to large stimuli which, through interactions with other tectal cells, might be a good candidate for being such a mechanism. This cell has also been postulated to be involved in avoidance behavior and will be fully discussed in a future report.

Trying to establish the role that each one of these brain regions may play in the control of these behaviors, Ewert[9,10,12,14,16] studied the neuronal response in the retina, tectum and pretectum to different configurations of the stimulus. It has been shown that in toads and frogs retinal ganglion cells of type R2, R3 and R4 each respond with almost the same intensity to a "worm-like" stimulus (type a in Fig. 2); whereas when an "antiworm-like" stimulus or a square stimulus (types b and c respectively in the same figure) was presented, the rate of response of ganglion cells type R2 and R3 initially increased up to the size of their respective excitatory receptive fields (ERF) and then progressively decreased for objects larger than the ERF[6,12,16]. The decreasing effect is stronger in ganglion cells R2 than in R3. On the other hand class R4 ganglion cells increase their frequency of response when the size of stimuli type b or c is extended (see Fig. 2C), giving the strongest response to stimulus of type c. Ganglion cells of type R2, R3 and R4 also increase their rate of response depending on the angular velocity of the object. There are class R2 and R3 ganglion cells exhibiting stronger response for a particular movement direction[10,14]. However, almost no cells have been recorded showing "null-directions". Thus, directional sensitivity at this level may not significantly contribute to the processing of visual signals.

From the above results, Ewert concluded that the observed behavioral responses could not be explained simply by the retinal responses. Ewert[12,16] continued studying the response of tectal and pretectal cells to different configurations of the stimuli. He found that some tectal cells that he called T5(2), which have also been reported by other researchers[18,26,37], responded to moving configurational visual stimuli with an overall firing level that resembled the probability that the stimulus under investigation fitted the prey category. That is, an increased firing rate when the stimulus was elongated along the direction of motion, a decreased firing rate when the stimulus was extended perpendicularly to the direction of motion, and a sort of competition between these two responses when the stimulus was expanded in both directions (see Fig.3C). Moreover, when pretectal ablation occurs, the overall response of this tectal cell (T5(2)) also resembled the behavioral response of the animal to the different stimuli; that is, it responds indiscriminately to any moving object crossing its receptive field. (see Fig. 3D and compare it with Fig 1B.b).

Ewert[13] also showed that tectal T5(2) cells could discriminate between prey and non-prey stimuli independently of the direction of motion while other tectal neurons, which he classified as T5(1), were directionally sensitive. For the above reasons, Ewert suggests that the tectal neuron type T5(2) may be responsible for the discrimination between prey and non-prey stimuli and indicating the position to which the animal should orient. The tectal neurons perform this through combined activity with pretectal cells, both regions receiving retinal input, possibly through an inhibitory effect[11]. One of the pretectal cells, which Ewert classified as TH3, responded mostly to non-prey stimuli (Fig. 3A); 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 of recognition, Ewert argues that it must be a consequence of the tectal architecture rather than of a sophisticated "software-like" processing of information.

Other authors claim to have found different types of neurons in the tectum which process different aspects of the stimuli[21,36,37] (see below). These authors thus suggest that the properties of prey-orienting and prey-catching behaviors are the result of the joint activity of several neurons, rather than the response of a single neuron. In later works, however, Ewert[16,39] postulates a theory of coordination of motor schemas where there are recognition units for prey stimuli, but they need the activity of other neurons or neural units (i.e. group of neurons organized as functional units) to control the prey catching orienting behavior, such as binocularity or depth perception neurons. This is in agreement with the argument that the activity of several neurons is needed to guide the motor response. Moreover, Ewert postulates that the other neurons found in the tectum may be related to those processes (predator recognition, depth perception, binocularity, etc.), and so might play a role in the control of different motor schemas. In our model we have focussed on the behavioral correlates of activity in single cells, but in the Discussion we propose a preliminary hypothesis of how the activity of several neurons, including the prey-recognition units, could control prey-catching orienting behavior. However, further studies should clarify the real nature of these processes.

Ingle[24,28,29,30], following Ewert's hypothesis of pretectal inhibition upon tectal activity, suggests that the changes in size preference and in latency of response could also be modulated by the pretectum. He postulates that when small objects are present, tectal cells are mostly guided by R2 ganglion neurons, and the effects of the ganglion cells type R3 and R4 upon the tectum is normally counteracted by the pretectum through an inhibitory effect. Ingle suggests that retinal R2 cells can overcome the pretectal inhibition through a facilitatory effect, a consequence of recurrent excitatory activity, but that 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 ganglion cells which respond to larger objects (class R3 and R4), i.e., cells with bigger receptive field, then increasing the "response readiness" and reducing the latency of response.

2. Modelling Procedures

The description of the model will be divided into four parts; a brief explanation of the proposed architecture for the two-dimensional model of the tectum, a description of the "black box" model of the retina, which is used to supply the retinal input corresponding to different visual stimuli, the description of the different cells in the pretectal column, and, finally, the proposed interaction among retina, tectum and pretectum subserving prey-predator recognition, size preference and response latency.

2.1 Two-dimensional Model of the Tectum

Previously[32], we analyzed the anatomical data of Székely and Lázár[40], which emphasized the vertical organization of the tectum, with a local "vertical sample" of the tectum being referred to as a "tectal column" — though with no suggestion of the sharp transitions between properties of adjacent columns suggested by some studies of mammalian cortex. We then offered a family of mathematical models of the tectal column (Fig. 4). Each column of the model comprises one glomerulus (GL), one large (LP) and one small (SP) pear shaped cell, one stellate neuron (SN) and one pyramidal (PY) cell (the only efferent cell of the column). In the model we hypothesize that PY corresponds to the neuron classified as T5(2) by Ewert. The present two-dimensional model of the optic tectum (see Fig. 5), composed of an array of 8 by 8 tectal columns receiving retinal input from ganglion cells classes R2, R3 and R4, is an expansion of the one-dimensional model of 8 tectal columns described elsewhere[3,33]. For the two-dimensional model the number of cells and their interactions is greatly increased. We will give a brief description of the most important considerations.

The main retinal input to the tectum is represented by ganglion cells R2 with excitatory receptive field (ERF) ranges of 2-4 degrees (Grusser et al.[18] and Ewert[16]), so we proposed that every column has a "focal" receptive field equal to the maximum ERF of ganglion cells R2 (4 degrees) and a non-focal (8 degrees) overlap with its neighbors' receptive fields. The receptive field of each element of the column is calculated according to their lateral interaction with neurons of other columns (see below). The interconnections among the cells of a column are shown in Fig. 4, while the lateral connections among cells of neighboring columns are all indicated in Table A:

Table A. Lateral interactions among tectal columns. Cells of column (i,j) receive afferents from cells of neighbor columns.

Cells of column (i,j)	Cells of neighboring columns to (i,j) that impinge upon its neurons. GL	LP	SP	SN
GL		+	+	
LP			+	−
SP	+			
SN		+		
PY		+		

a) The glomerulus (GL) is a synaptic complex comprising specific connections among axonal terminals, from retinal ganglion cells, diencephalic regions and recurrent axons (from LP and SP cells), and dendritic arborizations from tectal neurons, both from its own column as well as from neighboring ones. Each glomerulus has a receptive field of 12 degrees, 4 "focal" degrees with 8 degrees of overlap with its neighbors. This assumption is based on the fact that retinotectal axons project to a receptive field no larger than 15 degrees (Ingle[25]).

b) Each small pear-shaped cell (SP) is activated by retinal ganglion cells type R2 through the glomerulus and interglomerular dendrites both from its own and from neighboring columns; this cell is also inhibited by the stellate neuron (SN) from its own column. Thus, each SP cell has a receptive field of 16 degrees, which is in accordance with physiological evidence that says that the receptive field of superficial tectal cells ranges between 15 and 20 degrees (Ingle[26,31]).

c) Each large pear-shaped cell (LP) receives afferents from retinal ganglion cells type R2, both through the glomerulus and through its dendrites along the length between glomerulus and cell body, from the SP cells of its own column as well as of neighboring columns, and it is inhibited by the SN of its own and of neighboring columns. Its lateral connections make its receptive field of approximatly 24 degrees, which is in agreement with the observed receptive field of some cells in layer 6 of the tectum.

d) The stellate neuron (SN) receives afferents from the LP cell, both from its own column and from neighboring columns. This cell is a candidate to produce inhibition (Székely and Lázár[40]), so we propose it as the only inhibitory cell in the model and its function is to control tectal activity.

e) The pyramidal cell (PY) is the only efferent of the model tectal column and receives afferents from ganglion cells of type R2, R3 and R4, from the SP and LP cells of its own column and from the LP cell of neighboring columns, expanding its receptive field to approximately 28 degrees which agrees with physiological findings of Ewert[12,16] for the T5(2) cells.

2.2 Black Box Model of the Retina

As we have seen, retinal ganglion cells are sensitive to several stimulus characteristics, such as the size, the geometry in relation to the direction of motion, the angular velocity function, the contrast[12,16,18], and the chromatic composition of the moving stimulus[19,20]. Until now we only consider black stimuli on a white background, so the last two were treated as constants during the simulations.

Our black box model of the different ganglion cells (types R2, R3, and R4) is based on the curves obtained by Ewert for the response of these cells to "worm-like" and "antiworm-like" stimuli (see Fig. 2) and the angular velocity function obtained by Grusser and Grusser-Cornehls[18] and Ewert[12]. That is, the model simply defines the rate of response of ganglion cells of type R2, R3 and R4 depending on the stimulus geometry and its velocity : the first with Ewert's graphs and the second with the equation

$$R = kv^{\delta}$$

where k and δ are constants and v is the angular velocity function of the object. R is the frequency response of the retinal cell.

Ganglion cells project *retinotopically* to each tectal and pretectal column[16,18,40]. In the present model we have not considered the spatial representation of the different retinal receptive fields; we have only considered that the axon of each type of retinal cell projects to a specific column, and excites the surrounding neighbors with less intensity, either in the tectum or in the pretectum (see Fig. 5).

Each time a group of ganglion cells is stimulated, they will generate a response frequency R depending on the size, angular velocity, and direction of motion of the object. The parameters of the stimulus are specified by the modeler at the beginning of the simulation. 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, size and geometry of the object. Clearly, more refined modelling will also require a more detailed model of the spatiotemporal pattern of retinal activity, rather than the overall firing rates, and such modelling is a target of current research (see also an der Heiden and Roth[1a] for an "intermediate" model of retinal activity).

2.3 Two-dimensional Model of the Pretectum

Because of the limited data about the anatomy of the pretectal region, we simply modelled the pretectum as a two-dimensional array of columns comprised of several types of neurons. The first type of pretectal neuron represents the TH3 cell of Ewert[12,16], which is mostly sensitive to larger stimuli (square and "antiworm-like" stimuli) and which has been postulated to play a very important role for prey-predator recognition through an

inhibitory action on tectal neurons. This neuron integrates the information received from ganglion cells type R3 and R4[16,18,40], in such a way that it gives a stronger response to square stimuli, then to "antiworm-like" stimuli, and a weak response to "worm-like" stimuli (see Fig. 3A). We postulate that this neuron is also responsible, and here we hypothesize, for modulating the changes in the latency of response of PY tectal cells through a mechanism which is the outcome of a tonic inhibitory effect that is a function of the motivational state of the animal. That is, the behavior of these cells is going to depend on two different mechanisms, one, which remains contant during normal conditions and varies according with the animal's motivational state, that is responsible for controlling the response latency, and another one, which depends only on retinal input, that gives the tectal cells the capability of prey-predator recognition. Another type of pretectal neuron (PTN) is postulated to play a role in the prey-selection phenomenon[33]. For this neuron, we posit, as Didday[7] and Lara and Arbib[33] did, a competitive role in the selection of the strongest of several stimuli presented simultaneously in the animal's receptive field. For this competition function we are going to use the cooperation/competition scheme in neural networks as proposed by Amari and Arbib[1].

2.4 Interactions among Retina, Tectum and Pretectum

In Fig. 6A we show the two-dimensional neural model of the interactions among retina, optic tectum and pretectum. For a better understanding of these connections, in this figure we show only three rows of pretectal cells projecting upon the tectal columns. Fig. 6B represents a closer look of the projections from pretectal cells (arranged also in a columnar fashion) to the cells of their corresponding tectal column. This figure shows that the retina projects retinotopically to both tectum (ganglion cells of class R2, R3 and R4) and pretectum (class R3 and R4)[16,18,40]. Every TH3 pretectal cell inhibits the activity of the LP, SP and PY neurons of the tectal column corresponding to its projection. Finally, we propose that the PY cell activity defines the stimulus spatial location, the direction of the prey-catching orienting response and the prey-predator discriminative abilities of the tectum.

The mathematical description of each of the neurons considered in the two-dimensional model of the interactions among retina, optic tectum and pretectum can be seen in the Appendix.

It is important to notice that the final neural architecture proposed for the interactions among these brain regions was built, taking into account the anatomical data now available, with the purpose of obtaining the one that best reproduced the physiological and behavioral results. This model is the fourth stage of *Rana computatrix*[4], an evolving model of neural circuitry subserving, through interactions of neural activity distributed over several brain regions, visually guided behavior in anuran amphibia (see Discussion). Now with the expansion of the model to two dimensions and by including the effect of ganglion cells of class R3 and R4 in the interactions among retina, tectum and pretectum, we want to show the behavior of tectal units that can discriminate among "worm-like", "antiworm-like" and square stimuli, and whose pattern of response is independent of the direction of motion of the stimulus, and for which changes in pretectal inhibition, due to changes in the motivational state of the animal, increase the rate of response and reduce the latency.

For these reasons, we built a symmetric architecture[***] for the tectum. We showed elsewhere[33] that the best configuration for the inhibitory projection from pretectum to tectum, in terms of hysteresis effects and latency of response, was that pretectal fibers project to LP, SP, and PY cells. Finally, in order to simulate the change in the latency of response and the number of pulses discharged by the PY cells, we postulate that this neuron is excited, directly and through LP and SP cells, by ganglion cells R2, R3, and R4 and inhibited by the pretectum (TH3). Thus, our main problem was to adjust the weights from these various neurons to the PY cell. The compromise was that without pretectum the response of the PY cell should be controlled by the activity of ganglion cells with larger receptive fields (classes R3 and R4) in such a way that it emulates the preference for stimulus type c, then to type a and finally to type b (see Fig. 3D); whereas in the presence of pretectal inhibition the PY cell's sensitivity to a "worm-like" stimulus was the outcome of a facilitation of tectal column response through recurrent activity which is completely driven by ganglion cells that respond best to small objects which might represent potential prey (class R2). Furthermore, in this case, the choice had also to include the weight value selection for the inhibitory effect of TH3 upon tectal activity to reproduce the overall behavior presented by PY cells, that is, a preference for a "worm-like" stimulus (type a), then for those of type c, and a poor response to "antiworm-like" stimuli (type b) (see Fig. 3B).

[***] This paper subsumes an earlier study[34], in which we used asymmetric connections. We obtained similar results in both cases, but using symmetric connections simplified the model's architecture, and it made the invariance to the direction of motion of the stimulus an immediate result of simpler lateral interactions among tectal columns. This avoids the postulate of the more complex innate wiring process in the amphibian brain that asymmetric connections presupposed. It seems to be more plausible that asymmetric connections among tectal columns are used by other types of tectal cells to analyze other kinds of information, perhaps by T5(1) to process directional sensitivity (Ewert[13]).

3. Results

We will present the results of the computer simulation in two ways. First, in four dimensional graphs, showing the response of the pyramidal cells of all 64 columns of the model during a specific computer experiment, combined with two-dimensional graphs that offer a closer look of the response of the PY cell of the (ith,jth) tectal column to better appreciate the response rate and latency; and, second, graphs with the same coordinates as those used to express experimental data, that is, graphs that could be directly compared with physiological and behavioral results. In the first case, the two-dimesional plane formed by the x and y axes represents the spatial location of the columns. This plane is divided in 64 sections, with each one representing in the horizontal dimension the time scale of the simulation while the z axis of the graph represents PY cell activity. This activity is shown through the membrane potential of the PY cells and whenever the membrane potential reaches the threshold value we indicate it with spikes. This can be better appreciated in the two-dimensional graphs. We also show the description of the experiment (stimulus type, direction of motion with respect to the stimulus geometry, angular velocity, etc.). We did not simulate the generation of the action potential in our neurons but simply use a "threshold rule" to provide results that could easily be compared with experimental data. 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, rectangles whose longest axis moves perpendicular to the direction of motion, and squares of different sizes, designated as type a, b and c respectively in the figures. We defined the speed of the stimulus as the time required to go from one column to the next, and the velocity used in most of the experiments was 2 columns per unit of time of simulation, which is equivalent to 8 degrees per unit of time

(from above, each column represents 4 "focal" degrees).

3.1 Behavior of Pretectal Cell TH3

Our purpose in simulating the response of TH3 to different stimuli is to show how the combined interaction of ganglion cells R3 and R4 could generate their properties. Trying different weights (see table 3 in the Appendix for the final values) the behavior of this cell to the different types of stimuli is shown in Fig. 7A. Once the membrane potential of this neuron reaches the threshold, its response is modeled to be proportional to its input (see Appendix), otherwise it is equal to a tonic activity. The units of the vertical axis of this figure (Amplitude of Response) represent the overall effect that this cell is going to exert upon tectal activity. As can be seen in this figure, the response of this cell to the different types of stimuli is very similar to that of the pretectal cell that was suggested to be related to prey-predator recognition (see Fig. 3A for comparison). The response of this neuron increases with size most strongly for square stimuli (type c), then for "antiworm-like" (type b), while the response to "worm-like" stimuli (type a) does not change very much.

3.2 Behavior of PY Tectal Cells when we have Pretectal Ablation

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 weak response to stimuli of type b[12] (see Fig. 3D).

It is also known that axons of ganglion retinal cells R2, R3 and R4 project to the tectum[16,18]. It has been suggested that the facilitation effect for prey-catching orienting activity is mainly controlled by type R2 ganglion neurons[12,28], but anatomical studies and changes in the receptive field of the animal, latency of response etc., also suggest that tectal cells (PY) controlling prey-catching orienting behavior are also stimulated by ganglion cells R3 and R4.

As we mentioned earlier, in the final architecture proposed for the tectal column, the column activity is mainly controlled by R2 ganglion afferents while the PY response is the outcome of the combined effect 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 of type c, then to those of type a, and then to those of type b. This behavior reproduces in general the observed behavior of tectal cells (T5(2)) in animals without pretectum (see Fig. 3D for comparison). In Figs. 8 and 9, which present the activity of the 64 tectal columns (Fig. 8) and the response of the PY cell of one column of the tectum (Fig. 9), we can also see the stimulus preference described above. That is, there is a better response to a square of 8x8 degrees (Fig. 8.C and 9.C), then to a rectangle of 8x2 degrees moved as a "worm-like" stimulus (Fig. 8.A and 9.A) and finally to the same rectangle moved as an "antiworm-like" stimulus (Fig. 8.B and 9.B). Here we would like to point out that in Fig. 8 it is clear that the overall tectal response is also stronger to type c stimulus (Fig. 8.C) because it covers a larger area in the animal's receptive field, while in the the case of "worm-like" stimulus the tectal response is lower and concentrated in a narrower area. In these figures the maximal tectal cells response shifts in time as the stimulus moves across the retina, and it coincides with the time in which the stimulus is on its receptive field.

3.3 PY Tectal Cells Behavior with Pretectal Inhibition

As we mentioned above, there is a tectal neuron whose physiological response closely matches the prey-catching orienting behavior of the animal[12], its response is greater the longer the stimulus of type a, decreased by longer stimuli of type b, while a sort of combination of these two responses is observed when we increase the dimensions of stimuli

of type c.

The interaction among retinal cells, pretectum and tectum in our model are shown in Fig. 6. Retinal ganglion cells project both to the pretectum and to the optic tectum. The TH3 pretectal cells in turn inhibit LP, SP and PY neurons in the tectal column.

In Fig.7B and 7C we show tectal activity through the response of the pyramidal cells to the three types of stimuli. We have presented stimuli of different sizes starting with 2x2 degrees and expanding it in three different ways: expanding the dimension in the axis along the direction of motion (type a), expanding the dimension in the axis perpendicular to the direction of motion (type b), and expanding both dimensions (type c). The speed we used was 2 columns per unit of time of simulation which will be equivalent to 8 degrees per unit of time. To build these graphs we counted the number of pulses of a given column (Fig. 7C) and the total activity in the tectum (Fig. 7B) to the presentation of the stimulus. It can be seen that PY cells respond better to stimulus type a, then to type c. In both curves there is an initial increase in the response when we increment the stimulus size followed by a decrease for larger stimuli, whereas they present a very weak response to stimuli of type b. These results reproduce in a general way the physiological and behavioral observations (see Fig. 3C and 1B.a for comparison). Fig 7B shows a graph of the number of times the tectum is activated when a stimulus is present, and is thus a better measure of the possible control of the orienting response exerted by the tectum. This figure is equivalent to Fig. 7C.

Fig. 10 shows the response of the 64 columns of the tectum to the three types of stimuli, whereas Fig. 11 presents the response of the PY cell of the (4th,5th) tectal column. The stimulus is presented from left to right, starting in the column (4th,1th), with a speed of 8 degrees per unit time, and the abscissa time scale represents five units of time, while the vertical axis corresponds to the membrane potential of the 64 PY neurons. Fig. 10

shows that there is a shift of the columnar maximal response as the stimulus moves across the receptive field. The stimulus moves from left to right, so column (4th,1th) is active at the beginning and column (4th,8th) responds at the end of the time scale. We have used in this case a stimulus of 8x2 degrees moved as a "worm-like" (type a) and as an "antiworm-like" (type b) stimulus, and a square of 8x8 degrees (type c). From Fig. 10 it is clear that even though the response to a type c stimulus (Fig. 10.C) is wider spread, it is weaker than that to a "worm-like" stimulus (Fig. 10.A), whereas the weaker response is to an "antiworm-like" stimulus (Fig. 10.B), which also is wider spread than that to type a. At a one cell level, it can be seen that the tectal activity is stronger for stimulus type a (Fig. 11.A) than for type c (Fig. 11.C), and that the lowest activity is for stimulus type b (Fig. 11.B).

3.4 Directional Invariance for Prey-predator Discrimination

It has been shown both behaviorally and physiologically that prey-predator recognition and discrimination are independent of the direction of motion of the stimulus[13]. As a result, we used a symmetric connection scheme in our model. Thus direction invariance is to be expected in the response of the model. We report a simple test of this invariance, monitoring our model for the processes of discrimination and recognition of stimuli moved in eight different directions. We used an 8 x 2 degrees stimulus which we know produces a very weak response (almost no response in most tectal cells) as an "antiworm-like" stimulus (type b) and a strong response as a "worm-like" stimulus (type a). Fig. 12 presents the overall tectal response of the 64 columns to "worm-like" (Fig. 12A) and to "antiworm-like" stimuli (Fig. 12B) in three directions (the results are the same for the other five). It can be seen that the recognition of these stimuli is also invariant to the direction of motion of the stimulus, that is, the tectal activity remains the same regardless the direction of motion.

3.5 Size Preference and Response Latency

It has been observed that prey-catching orienting behavior and latency of response can be modulated depending on the motivational state of the animal[24]. It has been suggested that these changes are the result of a reduced inhibitory effect from pretectal neurons to tectal activity[12,16,24].

In order to test this hypothesis we used our model of the interactions between tectum and pretectum, where changes in the motivational state are represented by modifying the tonic activity of these cells. When the animal is greatly motivated for prey-catching orienting behavior, the inhibitory effect of pretectal cells TH3 upon the tectum changes by reducing their tonic activity.

Based on this we studied the behavior of PY cells, which are postulated to control the prey-catching orienting behavior of the animal, under normal conditions as well as under motivated states. This experiment has not been reported in the experimental literature, but it would not be to hard to design a set-up in which the PY (T5(2) of Ewert) response to "worm-like" stimuli of different sizes is recorded during different motivational states of the animal, that is, highly motivated (with hunger, smelling worms, etc.), or with low motivation (after presenting a threatening stimulus). We used "worm-like" stimuli of different sizes moving from left to right with a visual angular velocity of 8 degrees/sec. We considered the curve obtained in Fig. 7 to type a stimuli to be the behavior of the PY cells under normal conditions, we then used the same stimuli and studied how the response rate and latency behave when we change the level of motivation in the model (through modifying the tonic inhibitory effect exerted by TH3 cells upon the tectal activity). Fig. 13B shows that in normal conditions PY cells response presents a lower response rate (number of spikes) to the stimuli than when it is motivated. This reproduces the behavioral results found by Ewert[12,16] (see Fig. 13A for comparison). To analyze the changes in response latency we chose a stimulus of 8x2 degrees. Fig. 14 displays the response of the PY cell of the (4th,5th) column for different levels of motivation, low (Fig. 14A), normal (Fig. 14B) and high (Fig. 14C). These results clearly show that the latency of response is reduced whereas the number of spikes increases in motivated states. These results are in accordance with the behavioral results reported by Ingle[24,30].

In the case of size preference, we can see that if we present one stimulus at a time, the optimal size preferred by the animal remains the same. In Ingle's case, the experiment he describes is related with the phenomenon of prey-selection and will be completely discussed in another report. It has been shown that when we present simultaneously two prey stimuli in the animal's receptive field, it prefers the one that represents the better prey[7,25,33]. What might be happening in this case is that, in normal animals, a stimulus subtending 6 degrees of visual angle induces a response in the tectal columns it excites which is stronger than the combined response of the tectal columns excited by a stimulus subtending a visual angle of 16 degrees. In this way the smaller stimulus represents a better prey and so it is selected. On the other hand, in motivated animals, as we saw above, tectal response is enhanced. The enhancement produced when we present a 6 degrees stimulus is lower than the overall enhancement produced by a 16 degrees stimulus (it covers more tectal columns at the time). Furthermore, this difference in the increment of the response might be big enough that it makes the larger stimulus become the better prey, and thus be preferred.

4. Discussion

With the present model we have been able to simulate a range of physiological, anatomical and behavioral observations. The present study builds on three earlier papers; in[32], we simulated a single tectal column to reproduce the behavioral and physiological results obtained for prey-catching facilitation. We then[3] analyzed an array of these tectal columns to provide a one-dimensional model of the tectum which 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 to orient to the leading of the two objects. In[33], we incorporated some notions of Didday[7] to form a one-dimensional model of the interactions among retina, optic tectum and pretectum for prey selection. With the expansion to two dimensions in the present paper we have been able to reproduce prey-predator recognition and changes in response latency depending on the motivational state of the animal, all this being independent of the direction of motion of the stimulus. This paper, then, offers the latest stage in the "evolutionary development" of a computational model of increased hierarchical complexity about how different regions of the anuran amphibian brain may interact to control the animal's behavior[4].

Our modelling studies in combination with the experimental evidence we have used suggest that the behavior of anuran amphibia is controlled by the cooperative activity among different brain regions. Each region itself has functional units for the processing of information of specific properties of the stimulus. The retina evaluates different features of the stimulus. Then the pretectal neurons (and no doubt other thalamic cells) process features of the stimuli related to "antiworm-like" stimuli or static objects[18,28]. We know that in the tectum there are cells which seem to be very sensitive to "worm-like" stimuli (T5(2) of Ewert); however, there is also evidence of cells which are mostly sensitive to "antiworm-like" stimuli (T5(3) of Ewert) as well as to other variables such as distance of the object (T1 and T2 of Ewert), its position in the visual field, etc.[13,39]. This suggests that each region has different functional groups of neurons processing different properties of the stimulus whose integrative activity gives the desired response.

These modelling studies present only a qualitative analysis of the functionality of the interactions among several brain regions in prey-predator recognition. Although we know the reality is much more complex, these studies allow us to suggest that some of the brain regions of the visual system of anuran amphibians are organized in functional units (columns) with specific retinotopic configurations where the interactions among several of these regions yield the recognition of the stimulus and consequently the proper motor response. Each of these units, where the input is distributed among all of its elements (neurons), extracts specific features of the stimulus which will then be combined with those from other functional units to yield the motor response. The existence of functional columns has been described in several regions in the brain of higher vertebrates. It has also been shown that retinotopy is also present in the visual system of these animals and that there are different functional columns processing specific features of the stimulus, such as orientation, ocularity, etc. For this reason, the general principles of distributed multifunctional cooperativity postulated in our model could be a general principle for the processing of information for visuomotor behavior in vertebrates in general.

The present modelling has, however, neglected the existence of other functional units which could be used by the animal to define the proper motor response. Our simulation has only considered a part of the integrative, more complex, activity of the tectum which controls the location and recognition of prey-predator stimulus. Further modelling should integrate our tectal column modelling with our studies of other functional systems including depth perception[23], detour behavior[5], and global interactions of motor schemas[35], so that

we may have a clearer idea of how these functional units interact with each other to give the proper motor response. We have elsewhere[3,32] adopted the simplistic hypothesis that the activity of tectal PY cells (equivalent to T5(2) of Ewert) directly controls prey-catching orienting behavior; however, it is important to stress that motor behavior in the animal is really the coordination of several, possibly linked, motor schemas which are activated by a group of neurons which define a specific situation in the world. Therefore we first have to understand how the animal has an internal representation of the world and how he uses it to coordinate its actions. Ewert[13,39] has specifically postulated that motor schemas are activated by a group of cells and the action yields the activation of other neurons which in their turn activate other motor schemas and so on until we get the adequate motor response. This hypothesis, however, does not take into consideration how the firing of neurons could control the animals' behavior nor how planning as a result of linked schemas or competition between schemas may occur. Arbib[2] has outlined how cooperation and competition between schemas may occur, while Lara[35] has specifically postulated how different brain regions could coordinate the activation of motor schemas, in a primitive three-dimensional world, to different situations.

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

1) The tectal columns controlling prey-catching orienting behavior receive afferents from retinal ganglion cells of type R2, R3 and R4. The tectal column facilitates the response to retinal type R2 afferents; while retinal ganglion cells of type R3 and R4 also influence prey orienting behavior in several ways. In this paper we studied how the response of tectal neurons, to retinal input, could be changed by pretectal modulation when the animal is in a motivated state or for the regulation of the size constancy in the animal.

2) The inhibitory effect of pretectal cells gives tectal neurons the capability for prey-predator discrimination. The inhibitory effect of pretectal cells is mainly directed to

the PY cell although a smaller effect can also be seen either on LP and SP cells, with which it inhibits the overall tectal activity when a predator-like stimulus is present.

3) The directional invariance of prey-predator recognition is the result of the tectal architecture, through symmetric interconnections among neighboring columns.

4) Changes in the latency of response are the result of a reduction in the tonic inhibitory effect of pretectal cells TH3 upon the tectal LP, SP and PY cells. This effect may be controlled by other brain regions (possibly by the telencephalon).

The present model can be considered as a way of "unlumping" the ideas of Ewert and von Seelen for the relations among retina, tectum and pretectum for prey-predator recognition. Ewert and von Seelen[11] proposed a model of prey-predator recognition in which the retina, tectum and pretectum acted as filters for specific configurations of the stimulus. The inhibitory effect of the pretectum to the tectum enabled the latter to discriminate between "worm-like" and "antiworm-like" stimuli. As such, their model set forth the basic structure of regional interactions used in our model. However, their model had a number of limitations: 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 simulate only 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. an der Heiden and Roth[1a] have proposed a lateral inhibition model of tectum which can reproduce important properties of worm-antiworm discrimination, but does not address the issues of pretectal inhibition or of intrinsic tectal geometry. These authors postulate that the response of tectal cells is only the outcome of the spatio-temporal summation of retinal input (ganglion cells R2 and R3) combined with inhibitory interactions among the tectal neurons. Because of the linearity of the model, the response of T5(2) cells to large prey objects is not reproduced. The authors mention that an influence, from thalamic or pretectal cells, upon the tectum can be assumed in the presence of non-prey objects. Besides, with this configuration, the model could not explain the disinhibitory effect in the tectum, observed by Ewert[12,16] and Ingle[26], after pretectal lesion.

It has been suggested[18,37] that the motor response is the result not of activity of a single recognition unit but of the spatio-temporal pattern of several neurons acting simultaneously or serially (i.e. when a stimulus is present one or several groups of cells will be activated, then this activity will produce a motor response or will induce the response of other neurons which in their turn will control the motor behavior). This postulate is based on the fact that some workers have described neurons in the tectum which have different sensitivities to the configuration of the stimulus, some of them changing their preference depending on the speed of the stimulus[21,36,37]. Grusser and Grusser-Cornehls[18] and Roth[37] argue that because several neurons are activated in different ways with the same stimulus, prey catching orienting behavior could not be controlled by the activity of a single neuron. Moreover, these authors claim that there is not a correlation between the postulated recognition units and the animal's behavior in the following points: 1) The all-or-nothing character of the different components of prey catching behavior; 2) The cells should respond to the real size of the stimulus and not to its angular size; 3) They should have a long latency of response; 4) They should change their response according to experience; 5) They should monitor the presence of the stimulus and the stationary world in detour behavior; and 6) They should respond to a specific location of space in avoidance behavior.

This criticism is only valid if we identify the response of these units with the actual motor response; but if we consider, as Ewert does (personal communication), that the response of the recognition unit only indicates that a prey or a predator stimulus is present and possibly its location in the visual field, so that the activation of a specific motor schema is the outcome of the joint activity of several neurons, possibly placed in different brain regions[35], these problems can be dealt with as properties of integration of the motor schemas, as we propose below. For example, we could think that the motor center is receiving information from several neurons, some sensitive to specific configurations of the stimulus and others measuring distance to prey objects and their relation to the stationary world. The motor response could then be elicited when the firing of these neurons reaches a certain value as an all-or-none-response (argument 1) with a latency depending on the frequency of response (argument 3), and at the same time, it could use this information in such a way as to give the size constancy effect (argument 2). According with this hypothesis the recognition unit simulated in our model is only an element of a complex interaction of groups of neurons which serve to give the animal the ability to select the next best motor behavior for a specific situation of its world.

Similarly, changes in behavior could be related to the motor center rather than to units in the tectum, although plastic changes have been observed in these neurons (argument 4). Finally, we think that detour behavior is not explained by Ewert's hypothesis nor by the hypothesis of Grusser and Grusser-Cornehls. In Ewert's case, his hypothesis does not show how schemas simultaneously activated could yield the proper sequential response, and Grusser and Grusser-Cornehls postulate a continuous feedback for the control of the behavior which seems not to occur in these animals. In order to deal with these problems we postulate that there should be a group of motor schemas linked together, acting as a single schema, that are activated for a given situation to give the proper sequential motor response[5]. This will allow us to explain detour behavior. However, for the final answer related to these topics, further experimental research is needed.

We have modelled the behavior of cells that we postulate are equivalent to the T5(2) cells of Ewert, which are mostly sensitive to "worm-like" stimuli, then to squares and then to "antiworm-like" stimuli (Ewert[12,16]). So, with respect to the issue of whether the response of these cells is invariant to the stimulus velocity (Ewert[16,17]) or not (Roth and Jordan[37]), we are only able to discuss the cells described by Roth and Jordan that behave as T5(2). These cells represent 39% of the total number of cells these authors recorded (41 out of 115 neurons). They reported 25 neurons that behave exactly as those classified by Ewert as T5(2), preferring horizontal rectangles ("worm-like"), then squares and then vertical rectangles ("antiworm-like") (denoted as the H>S>V cells by Roth and Jordan[37]), and 16 neurons that at low velocities prefer a "worm-like" to a square stimulus, while at high velocities they change their preference between these two types of stimuli (the HxS>V group of cells). In both groups of cells, the "antiworm-like" stimulus is the least effective. It is clear that in toads these cells (T5(2)) do not present any worm-antiworm change of preference as some salamanders do[22,36]. Himstedt[22] postulates that the "inversion phenomenon" reported by Luthardt and Roth[36] perhaps depends on the animal's experience with certain prey. Himstedt bases his argument on the fact that when he conducted the same experiments, with animals that were fed mainly with mealworms, he did not observe any change in the animals' preferences, while in Luthardt and Roth's experiments the animals were fed mainly with crickets. This result is in aggreement with what Ewert[16] says about animal care in different laboratories. First, he says, animals do not always exhibit their natural repertoire of behavior in captivity; second, gross differences in animal maintenance (feeding among them) between different research groups using the same experimental animal may be an unrecognized cause of the criticism that one and the same experiment is not always reproducible in every hand.

As we saw above, Ewert[16] showed that when pretectal ablation occurs the animal's (and T5(2) cells') ability to discriminate among configurational visual patterns is lost, and the phenomenon of habituation of prey catching behavior to specific stimulus is greatly diminished, so pretectal cells can be considered as being involved in some processes that represent experience. Moreover, it can also be seen that T5(2) cells present a change in the preference between "worm-like" and square stimuli, that is, in normal animals a "worm-like" stimulus is preferred to squares (Fig. 3B), whereas in lesioned animals the square stimulus is more effective than the "worm-like" (see Fig. 3D). Besides, Ewert[16] and Ingle[30] have shown that this tectal-pretectal interaction is modulated by the motivational state of the animal (e.g. the kind and the amount of food the animal gets before the experiment, the time the experiment lasts, etc.). Based on these facts, we pose that the mechanisms responsible for the differences between the results obtained by Ewert[17] and Roth and Jordan[36] might be related with parameters that produce changes in the pretectal inhibitory effect upon the tectum.

In our model we followed Ewert's hypothesis for the role played by the retina-tectum-pretectum interactions in the prey catching orienting behavior. We considered two different mechanisms that might be modulating the pretectal inhibitory effect upon the tectum; first, changes in the pretectal tonic activity, which are controlled by the animals' motivational state; and second, modifying the response latency of the pretectal TH3 cells, making it longer, possibly through changes in their membrane constants.

Analyzing Roth's experiment, we find that he presented small stimuli (horizontal rectangles of 8x2 degrees and squares of 8x8 degrees), for which the response of ganglion cells R2 (even at 7.6 degrees/sec) is almost equal to squares and to a "worm-like" stimulus, whereas in R3 and R4 the response is stronger to squares (see Fig. 2). So, following our previous reasoning, if at high velocities in some way (through experience or motivational changes) we reduce or delay the inhibitory pretectal effect over the tectum when we present the square stimulus, the retinal input, before the pretectum start its inhibitory effect, will have the oportunity of building up a strong effect upon the PY cells which is going to cause the change in preference reported by these authors.

In Ewert's case, he presents a rectangle of 32x2 degrees moved as a "worm-like" and as an "antiworm-like" configuration, that is he does not analyze the cells' response to a square. The R2 response is almost null to square of this size, while it is strong to "worm-like" stimulus. The R3 response to these stimuli is stronger to "worm-like" than to squares, whereas R4 is still stronger to squares than to a "worm-like" stimulus (see Fig. 2). We saw above that R2 is responsible for the tectal column activity, through recurrent activity, so it is going to be very difficult for a square of this size to produce a greater activity than the "worm-like" stimulus, even if its effect increases exponentially when we increase its velocity, unless we delay the pretectal activity for a very long period of time or we suppress it completely with a lesion.

To properly address these issues, our model will require a more refined retina model, as well as more detailed modelling of the temporal response of the different types of tectal neurons. Based on the previous argument and on early simulations varying the membrane constant of the TH3 pretectal cell, we conclude that changes in an animal's experience that modify the pretectal inhibitory effect upon the tectal activity could produce changes of the tectal preference between "worm-like" and square stimulus. Both experimental and simulation research addressing this hypothesis is necessary and will clarify the real nature of these processes.

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Appendix

We provide the mathematical description of the elements (neurons) of the two-dimensional model of the interactions among retina, optic tectum and pretectum which updates and complements the description of the one-dimensional version provided in Lara and Arbib[3].

In these models, we have used a simple neuron model, which receives n inputs x_1, $x_2,\ldots, x_n$ and produces one output Y, to represent the behavior of tectal and pretectal neurons. We use differential equations and threshold functions to model the dynamics of such neurons' behavior. According to these equations, the state of a neuron at time t is defined by two quantities, one (shown in lower case) representing its membrane potential and the second (shown in upper case) denoting its firing rate.

The fundamental equation describing the dynamics of each membrane potential m(t) increases in proportion to the algebraic weighted sum S(t) of the excitatory and inhibitory inputs.

The membrane potential decays according to its membrane constant τ towards a resting potential m_0. Thus, its equation will be of the form

$$\tau\, \dot{m}(t) = -\, m(t) + S(t) - m_0$$

In the weighting factors, the first subscript represents the cell that receives afferents from the neuron represented by the second subscript. For example,

$$W_{gl\text{-}sp}$$

represents the effect of a small pear (SP) shaped cell (second subscript) upon the glomerulus (GL) (first subscript).

The output firing rate FR(t) at time t will be determined as a function of the membrane potential m(t) by the formula $F(m(t)-\theta)$, where θ is a suitable threshold value and F may be of the form

$$f(x) = \begin{cases} 1 & \text{if } x \geq 0 \\ 0 & \text{if not} \end{cases}$$

or

$$h(x) = \begin{cases} x & \text{if } x \geq 0 \\ 0 & \text{if not} \end{cases}$$

or

$$g(x, k) = \max(x, k)$$

where k represents a tonic activity.

The specific choices of the threshold functions, as well as the membrane constants, and the weight factors are shown in Tables 1, 2 and 3 respectively. For further discussion about these values refer to[3,32,33].

The (ith,jth) unit column in the optic tectum receives, symmetrically, afferents from all of its neighbor columns and retinotopic projections from ganglion cells of types R2, R3 and R4. The pretectal cell TH3 receives retinotopic projections only from R3 and R4. We are now going to describe the equations that define the behavior of the tectal and pretectal cells considered in this model.

Glomerulus (GL)

The equation defining the behavior of the glomerulus of the (ith,jth) column of the optic tectum is given as follows:

$$\tau_{gl}\,\dot{gl}_{i,j}(t) = -k1 * gl_{i,j}(t) + S_{gl_{i,j}}(t)$$

where

$$S_{gl_{i,j}}(t) = U2_{i,j}(t)+W_{gl\text{-}lp1}LP_{i,j}(t) + \sum_{n=-1}^{+1}\sum_{m=-1}^{+1} W_{gl\text{-}sp}SP_{i+n,j+m}(t) +$$

$$\sum_{n=\pm1}\sum_{m=\pm1} W_{gl\text{-}lp}\, LP_{i+n,j+m}(t)$$

where $U2_{i,j}$ is the retinal input from ganglion cells type R2, and S(t) denotes the recurrent axons (see the text above) from LP and SP cells of its own unit as well as from neighboring columns. The weight factor associated with the LP cell of the same column is larger than those of LP cells of the neighbor columns, ensuring, in this way, a mainly vertical processing of the information which is in accordance with the experimental data[28,40].

Stellate Neuron (SN)

The behavior of the stellate neuron of the (ith, jth) tectal column can be defined as follows:

$$\tau_{sn}\dot{sn}_{i,j}(t) = -k2^{*}sn_{i,j}(t)+S_{sn_{i,j}}(t)$$

where

$$S_{sn_{i,j}}(t) = \sum_{n=-1}^{+1}\sum_{m=-1}^{+1} W_{sn\text{-}lp}LP_{i+n,j+m}(t)$$

where S(t) shows that these neurons receive afferents only from LP cells from its own column as well as from neighboring ones.

Large Pear Shaped Cells (LP)

The behavior of the LP cell of the (ith, jth) unit column can be described as follows:

$$\tau_{lp}\dot{lp}_{i,j}(t) = -lp_{i,j}(t)+S_{lp_{i,j}}(t)$$

where

$$S_{lp_{i,j}}(t) = E_{lp_{i,j}}(t) - I_{lp_{i,j}}(t)$$

where

$$E_{lp_{i,j}}(t) = gl_{i,j}(t)+U2_{i,j}(t)+W_{lp\text{-}sp1}SP_{i,j}(t) + \sum_{n=\pm1}\sum_{m=\pm1} W_{lp\text{-}sp}SP_{i+n,j+m}(t)$$

and

$$I_{lp_{i,j}}(t) = W_{lp\text{-}th3}TH3_{i,j}(t)+W_{lp\text{-}sn1}SN_{i,j}(t) + \sum_{n=\pm1}\sum_{m=\pm1} W_{lp\text{-}sn}SN_{i+n,j+m}(t)$$

where $gl_{i,j}$ represents the afferent from the glomerulus of its own column, $U2_{i,j}$ is the retinal input from ganglion cells type R2, and E(t) and I(t) show that these cells receive afferents from SN and SP cells from its own column as well as from neighbor ones and from its corresponding projection in the pretectum through the $TH3_{i,j}$ cell. Again, to ensure a mainly vertical processing of information, the weight factor of the SP cell from its own unit is larger than those from neighbor columns.

Small Pear Shaped Cells (LP)

The behavior of the small pear shaped cell of the (ith, jth) column can be described as follows:

$$\tau_{sp}\dot{sp}_{i,j}(t) = -sp_{i,j}(t)+S_{sp_{i,j}}(t)$$

where

$$S_{sp_{i,j}}(t) = E_{sp_{i,j}}(t)-I_{sp_{i,j}}(t)$$

where

$$E_{sp_{i,j}}(t) = U2_{i,j}(t)+W_{sp\text{-}gl1}gl_{i,j}(t) + \sum_{n=\pm1}\sum_{m=\pm1} W_{sp\text{-}gl}gl_{i+n,j+m}(t)$$

and

$$I_{sp_{i,j}}(t) = W_{sp\text{-}sn}SN_{i,j}(t)+W_{sp\text{-}th3}TH3_{i,j}(t)$$

where $U2_{i,j}$ is the retinal input from ganglion cells type R2, and E(t) and I(t) show that these cells receive afferents from the glomerulus of its own column as well as of its neighbors, with a larger weight factor associated with the glomerulus of the same column, and from the pretectal neuron $TH3_{i,j}$.

Pyramidal Cell (PY)

The membrane potential of the (ith,jth) Pyramidal cell (PY) is defined as follows:

$$\tau_{py}\,\dot{py}_{i,j}(t) = -py_{i,j}(t)+S_{py_{i,j}}(t)$$

where

$$S_{py_{i,j}}(t) = E_{py_{i,j}}(t)-I_{py_{i,j}}(t)$$

where

$$E_{py_{i,j}}(t) = W_{py\text{-}u2}U2_{i,j}(t)+W_{py\text{-}u3}U3_{i,j}(t)+W_{py\text{-}u4}U4_{i,j}(t) +$$

$$+ W_{py\text{-}sp}SP_{i,j}(t)+W_{py\text{-}lp1}LP_{i,j}(t) +$$

$$+ \sum_{n=\pm 1} \sum_{m=\pm 1} W_{py\text{-}lp}LP_{i+n,j+m}(t)$$

and

$$I_{py_{i,j}}(t) = W_{py\text{-}th3}TH3_{i,j}(t)$$

where $U2_{i,j}$, $U3_{i,j}$ and $U4_{i,j}$ are the retinal input from ganglion cells type R2, R3 and R4 respectively, and $TH3_{i,j}$ is the inhibitory effect from one cell of the corresponding pretectal projection, and, again, the weight factor of the LP cell of the same column is larger than those associated with the cells of the neighbor columns.

Pretectum (TH3)

The behavior of the TH3 neuron of the (ith,jth) pretectal column (there is a retinotopic projection between tectum and pretectum) can be defined as follows:

$$\tau_{th3}\,\dot{th3}_{i,j}(t) = -th3_{i,j}(t)+S_{th3_{i,j}}(t)+ton$$

where

$$S_{th3_{i,j}}(t) = W_{th3\text{-}u3}U3_{i,j}(t)+W_{th3\text{-}u4}U4_{i,j}(t)$$

ton is the tonic inhibition that these neurons exert over the tectal activity (see text above), and $U3_{i,j}$ and $U4_{i,j}$ are the input from retinal ganglion cells type R3 and R4 respectively.

Table 1

Threshold Functions

$LP = f(lp, 1.0)$

$SP = f(sp, 2.0)$

$SN = h(sn, 0.2)$

$PY = h(py, 2.3)$

$TH3 = g(th3, 3.8)$

Table 2

Membrane Constants

$\tau_{gl} = 0.35$ $k1 = 0.15$

$\tau_{lp} = 0.3$

$\tau_{sn} = 0.65$ $k2 = 0.4$

$\tau_{sp} = 0.9$

$\tau_{py} = 0.12$

$\tau_{th3} = 0.02$

Table 3

Weighting Values

$W_{gl\text{-}lp1} = 1.2$ LP to GL (s. c.)

$W_{lp\text{-}sp1} = 0.8$ SP to LP (s. c.)

$W_{lp\text{-}sn1} = 8.0$ SN to LP (s. c.)

$W_{sp\text{-}gl1} = 1.0$ GL to SP (s. c.)

$W_{py\text{-}lp1} = 0.7$ LP to PY (s. c.)

$W_{gl\text{-}sp} = 0.1$ SP to GL

$W_{gl\text{-}lp} = 0.8$ LP to GL

$W_{sn\text{-}lp} = 2.1$ LP to SN

$W_{lp\text{-}sp} = 0.6$ SP to LP

$W_{lp\text{-}sn} = 8.2$ SN to LP

$W_{lp\text{-}th3} = 0.1$ TH3 to LP

$W_{sp\text{-}gl} = 0.5$ GL to SP

$W_{sp\text{-}sn} = 20.0$ SN to SP

$W_{sp\text{-}th3} = 0.1$ TH3 to SP

$W_{py\text{-}sp} = 2.0$ SP to PY

$W_{py\text{-}lp} = 0.56$ LP to PY

$W_{py\text{-}u2} = 3.5$ U2 to PY

$W_{py\text{-}u3} = 0.3$ U3 to PY

$W_{py\text{-}u4} = 7.0$ U4 to PY

$W_{py\text{-}th3} = 0.9$ TH3 to PY

$W_{th3\text{-}u3} = 0.3$ U3 to TH3

$W_{th3\text{-}u4} = 5.0$ U4 to TH3

note : s. c. = from the same column

Figures

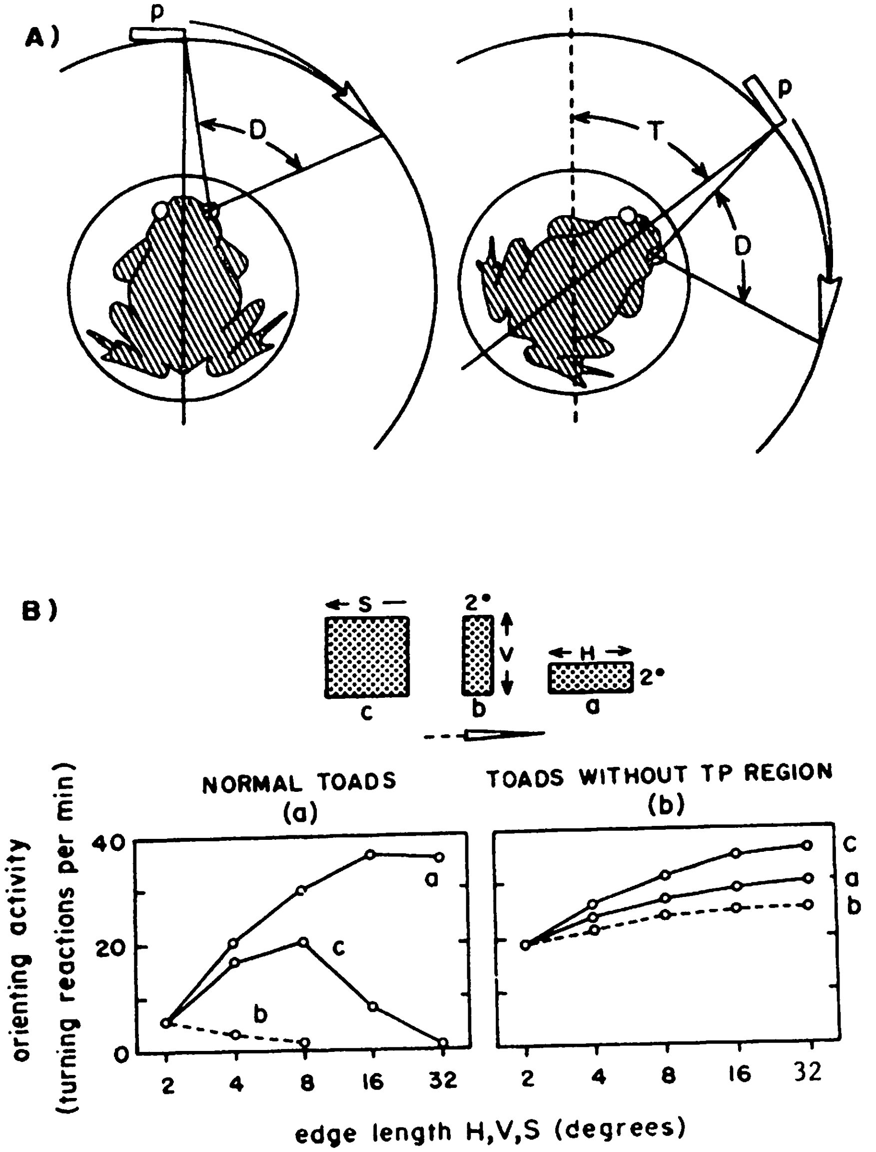

Fig. 1.

Prey-catching orienting behavior to different configurations of the stimulus. A) Turning reaction to the stimulus presentation. D: effective angular displacement of the stimulus (p); T: angle of turning movements. B) Orienting activity to three stimulus configurations, horizontal ("worm": type a) and perpendicular ("anti-worm": type b) rectangles, and squares (type c). B.a) Normal animal's response becomes more frequent when we increase the dimension (H) of a stimulus of type a, whereas response frequency rapidly drops to zero when we increase the dimension (V) of a type b stimulus, and a sort of summation of these two responses is obtained when we increase both dimensions of stimulus type c. B.b) This discrimination is lost in toads with pretectal lesions (From Ewert[12]).

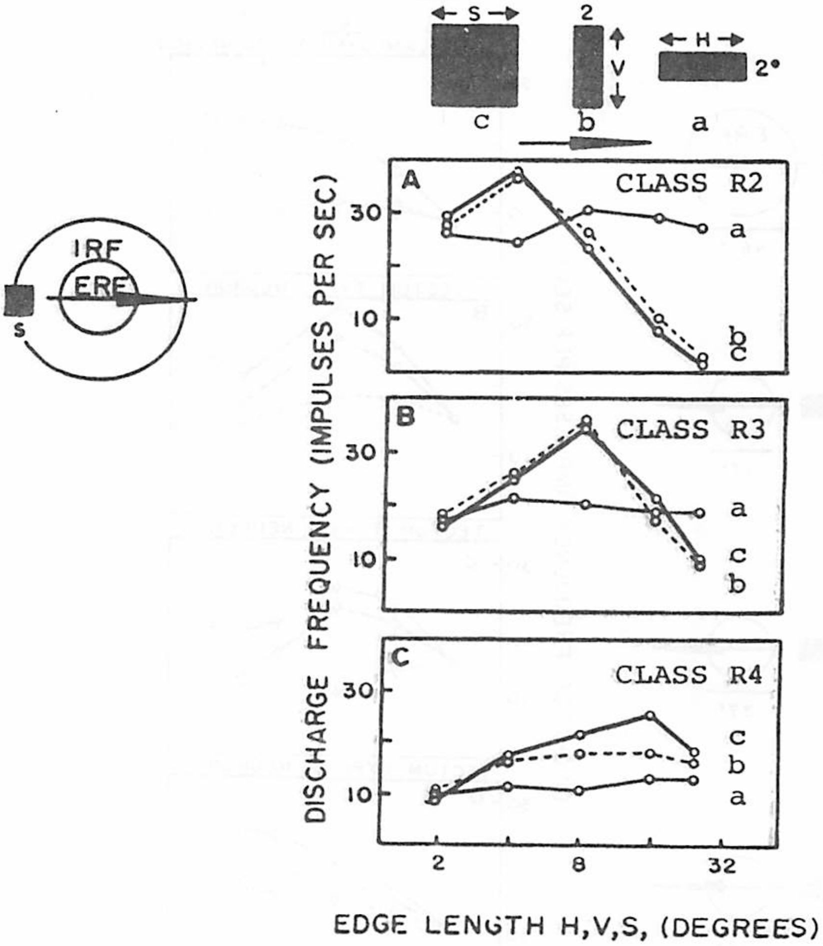

Fig. 2.
Retinal ganglion cells response (classes R2, R3, and R4) to different configurations (type a, b and c) of moving stimuli with a visual angular velocity of 7.6 degrees/sec. Left, they present a receptive field formed by a central excitatory (ERF) and a peripheral inhibitory (IRF) area. The three ganglion neurons respond almost with the same intensity to stimuli type a of different sizes. For stimuli of types b and c, ganglion cells R2 and R3 increase their rate of response up to their respective receptive field sizes and then it drops down, whereas R4 increase their rate of response when the size of the stimulus increases, giving the strongest response to stimuli of type c (From Ewert[12]).

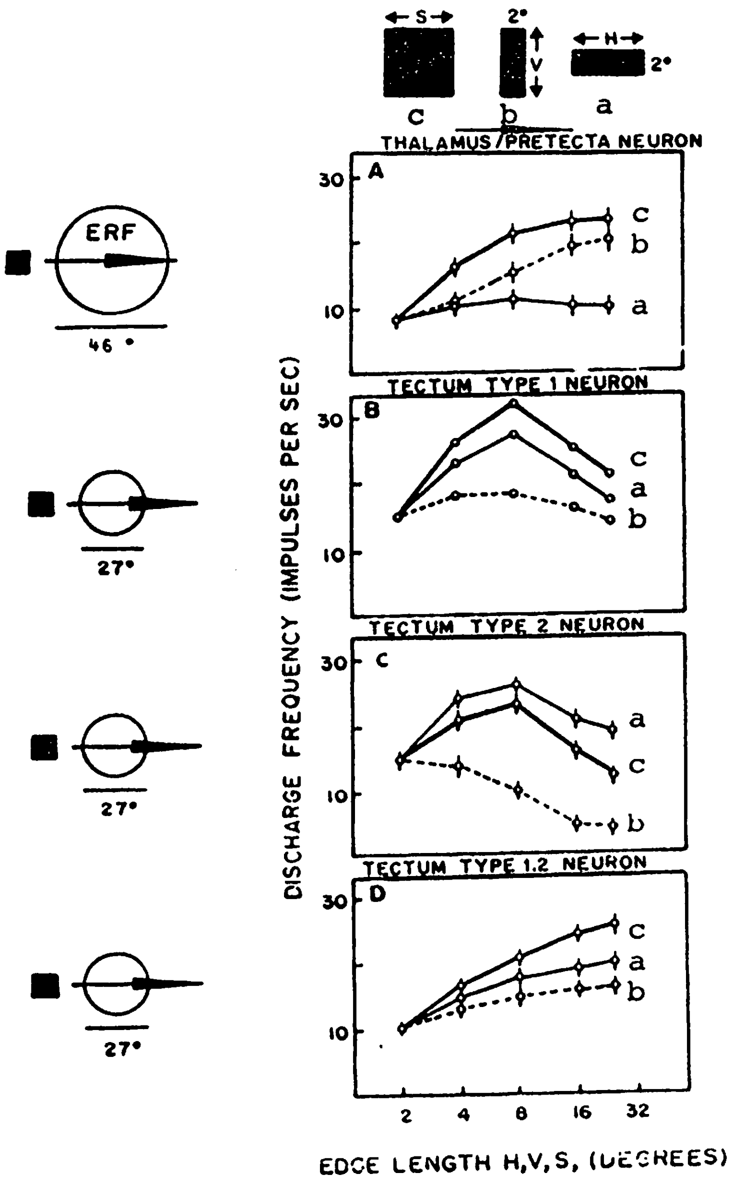

Fig. 3.
Tectal and Pretectal cell response from common toads to different configurations of moving stimuli (see Fig. 1 legend). A) Response of a pretectal neuron TH3 which is mostly sensitive to large (type c) and perpendicular (type b) stimuli. B) Response of a tectal cell T5(1) which is most sensitive to stimuli type c, then type a, and then type b. C) Response of tectal neuron T5(2) which prefers mostly stimuli type a, then type c, and gives a very weak response to type b. This neuron's response resembles the animal's behavior (see Fig. 1.B). D) Response of both tectal cells (T5(1) and T5(2)) after thalamic pretectal lesions. It shows how the discriminative abilities of these cells are lost (From Ewert[12]).

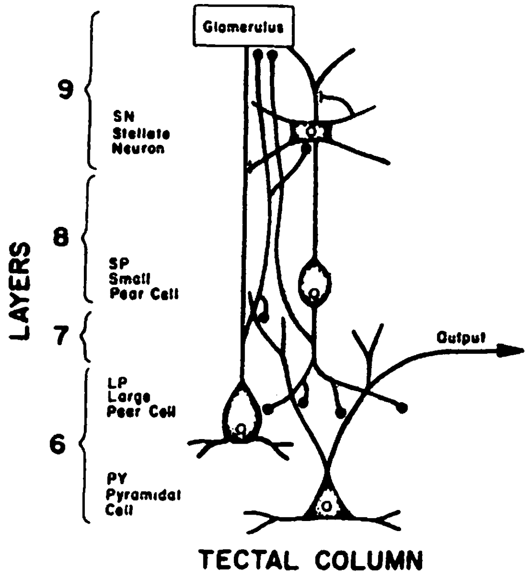

Fig. 4.
Interconnections among the cells of a tectal column. The pyramidal cell (PY) is activated by the large (LP) and the small (SP) pear shaped cells. The stellate neuron (SN) is excited only by the LP cell. The SP cell receives excitatory afferents from the glomerulus (GL), and it is inhibited by the SN neuron. The LP cell is excited by both the SP cell and the GL, and it is also inhibited by the SN neuron. GL receives afferents from recurrent axons of LP and SP cells (from Lara and Arbib[33]). GL, LP and SP also receive afferents from retinal ganglion cells R2, whereas PY receives from R2, R3 and R4 (see Fig. 5 and Fig. 6B).

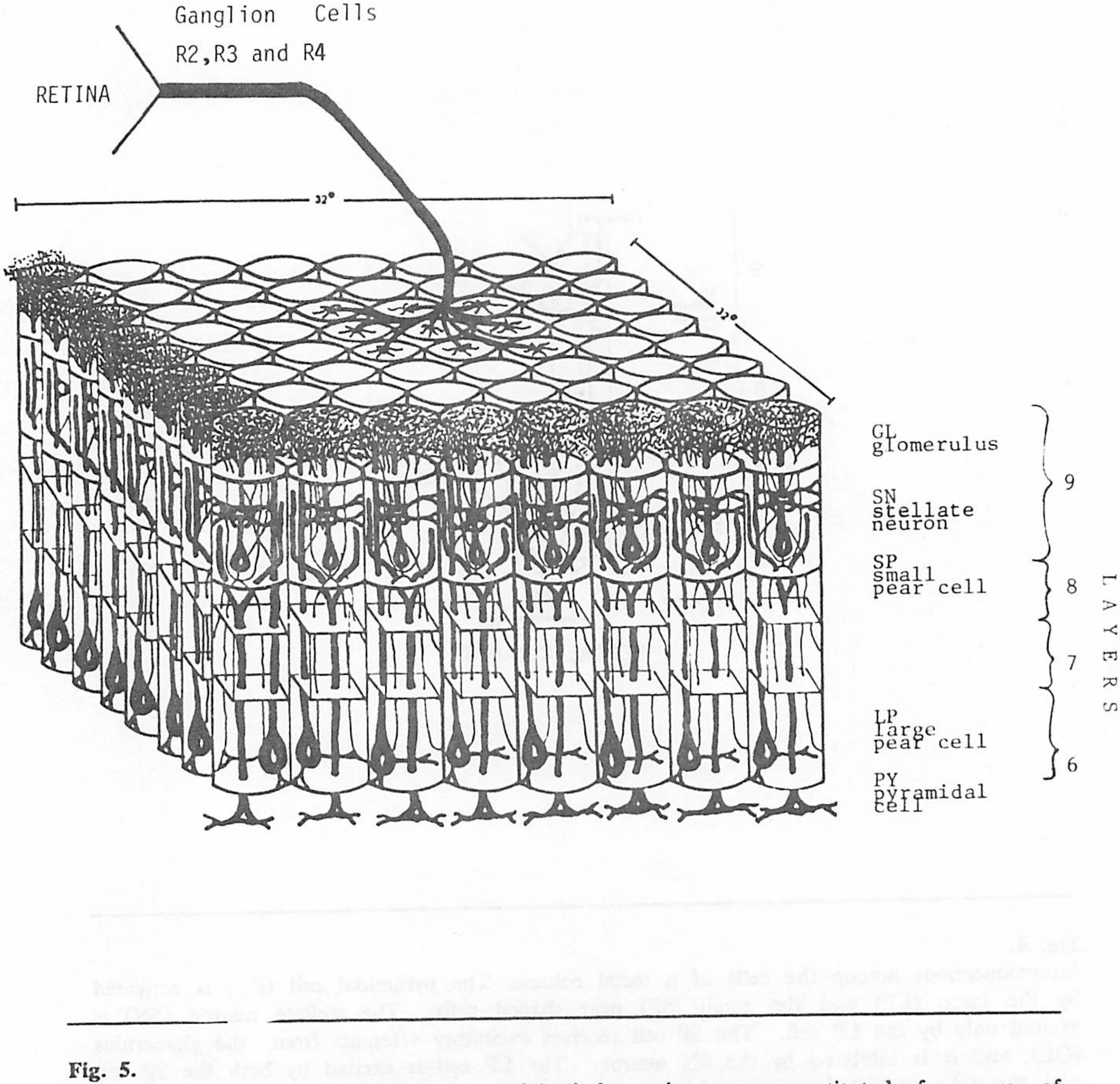

Fig. 5.
Representation of the two-dimensional model of the optic tectum, constituted of an array of 8 by 8 columns that covers a receptive field of approximately 32 by 32 degrees (see text for explanation), and receives "focal" as well as overlapping information from retinal ganglion cells of classes R2, R3 and R4. For simplicity we only show the retinotopic projection to one tectal column and its neighbors.

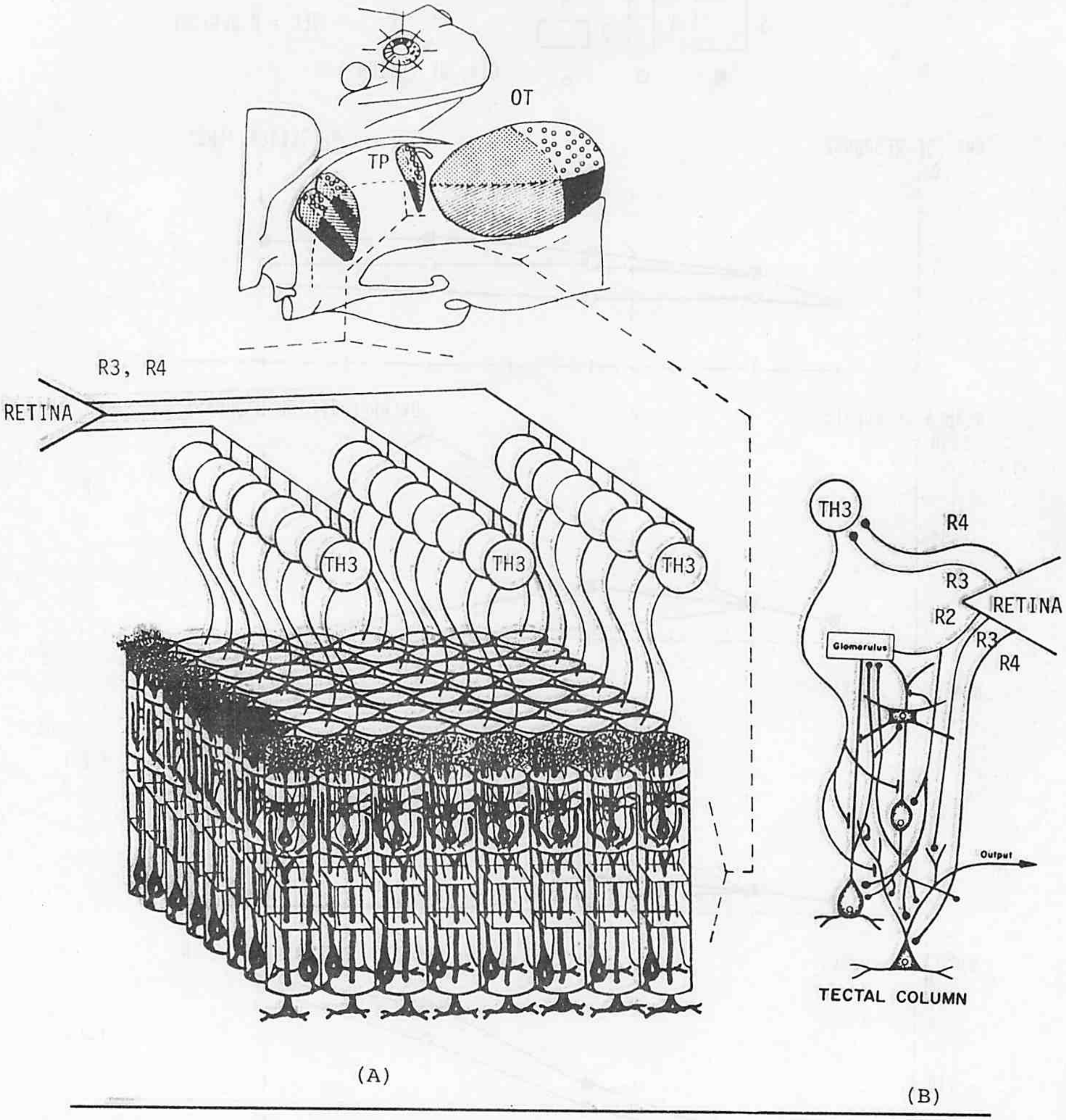

Fig. 6.
Interactions among retina, optic tectum and pretectum. The retina sends fibres in a retinotopical fashion to both optic tectum (class R2,R3 and R4 (see Fig. 5)), and pretectum (class R3 and R4). A) TH3 neurons also project retinotopicaly to the optic tectum. For simplicity we only show the projection of three rows of TH3 cells projecting upon the tectal columns. B) A closer look of the interactions among retinal, tectal and pretectal cells. The TH3 cell of the pretectal column inhibits LP, SP and PY of the tectal column corresponding to its retinotopic projection. .

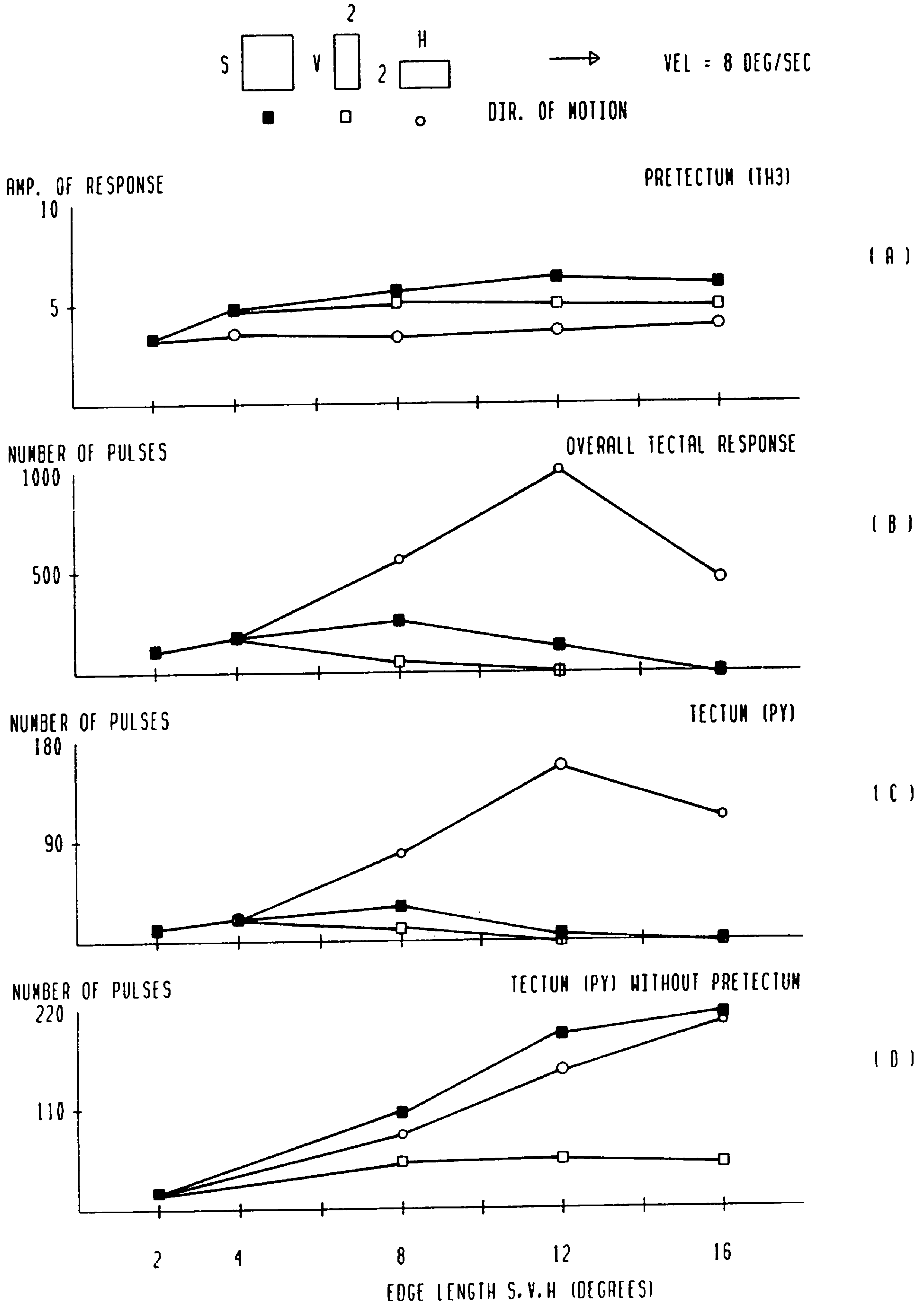
S
V
2
H
2
■
□
○
DIR. OF MOTION
VEL = 8 DEG/SEC
AMP. OF RESPONSE
10
5
PRETECTUM (TH3)
(A)
NUMBER OF PULSES
1000
500
OVERALL TECTAL RESPONSE
(B)
NUMBER OF PULSES
180
90
TECTUM (PY)
(C)
NUMBER OF PULSES
220
110
TECTUM (PY) WITHOUT PRETECTUM
(D)
2
4
8
12
16
EDGE LENGTH S,V,H (DEGREES)

Figure 7

Fig. 7.

Computer simulation of the response of pretectal and tectal cells to different configurations (type a,b and c) of moving stimuli (visual angular velocity of 8 degrees/sec). A) Pretectal TH3 cell response: it is mostly sensitive to stimuli type c and b. B) Overall response of the tectum to the three types of stimulus (a, b and c): tectum response is mostly sensitive to stimulus type a and it is weaker to stimulus type b. C) Response of a PY cell to the three different stimuli : it respond better to stimulus type a, then to type c and it gives a very weak response to a stimulus of type b. This curve is equivalent to B. D) PY response when pretectum ablation occurs: these cells are mostly sensitive to stimuli of type c or a, and less to those of type b.

Fig. 8.

Figures 8 and 9 present a computer simulation of the PY cell response of the 64 columns of the tectum to the different configurations of moving stimuli when pretectal ablation occurs: All stimuli are moved from left to right with a visual angular velocity of 8 degrees/sec. Fig. 8 shows four-dimensional graphs, where the x and y axes are used to represent the spatial localization of the (ith,jth) column. The y axis of this plane is also used to show the time scale for the response of every column's PY cell, while the vertical axis (z axis) represents its local membrane potential. In the graph when the PY local potential is about the threshold, this is indicated by spikes. Figure 9 offers a closer look at the response of the PY cell of column (4th,5th) for the different configurations of the stimuli. In both graphs: A) response to a "worm-like" stimulus (type a) of 8x2 degrees; B) to the same stimulus moved as "antiworm-like" (type b); and C) to a square stimulus (type c) of 8x8 degrees. At the level of one PY cell, the tectal response is stronger for stimulus type c, then to type a, and finally to those of type b. The overall response of the tectum is also stronger to type c stimulus. It is also wider spread, while the response to "worm-like" stimulus, although it is strong too, is concentrated in a narrower area.

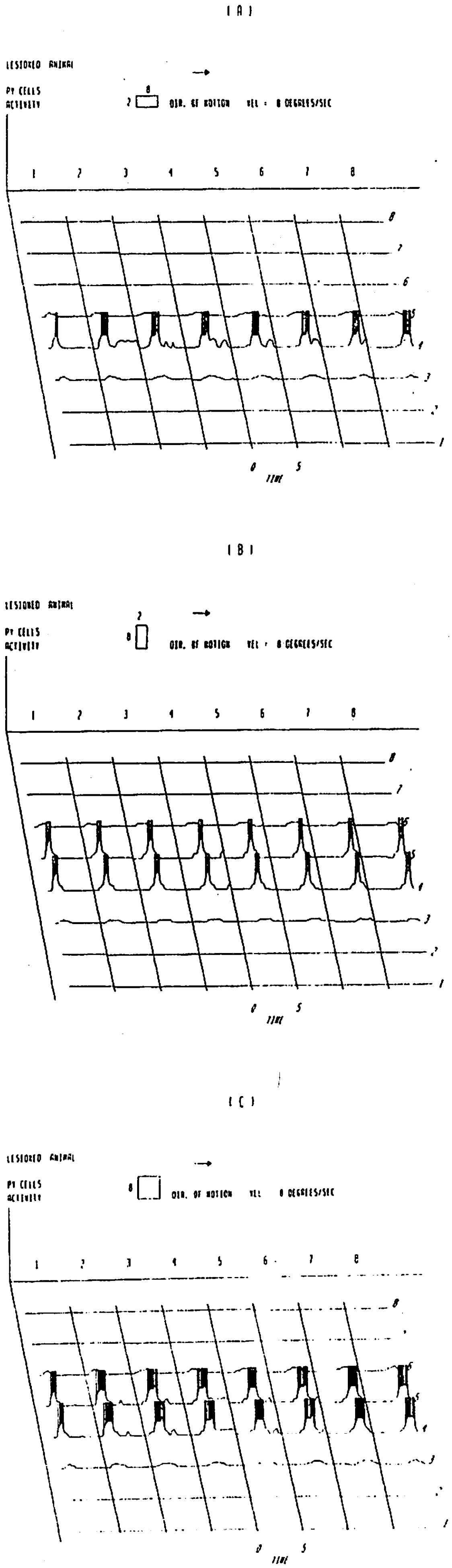
(A)
LESIONED ANIMAL
PY CELLS
ACTIVITY
8
2
DIR. OF MOTION
VEL = 8 DEGREES/SEC
1 2 3 4 5 6 7 8
8 7 6 5 4 3 2 1
0 5
TIME
(B)
LESIONED ANIMAL
PY CELLS
ACTIVITY
2
8
DIR. OF MOTION
VEL = 8 DEGREES/SEC
1 2 3 4 5 6 7 8
8 7 6 5 4 3 2 1
0 5
TIME
(C)
LESIONED ANIMAL
PY CELLS
ACTIVITY
8
DIR. OF MOTION
VEL = 8 DEGREES/SEC
1 2 3 4 5 6 7 8
8 6 5 4 3 2 1
0 5
TIME

Figure 8

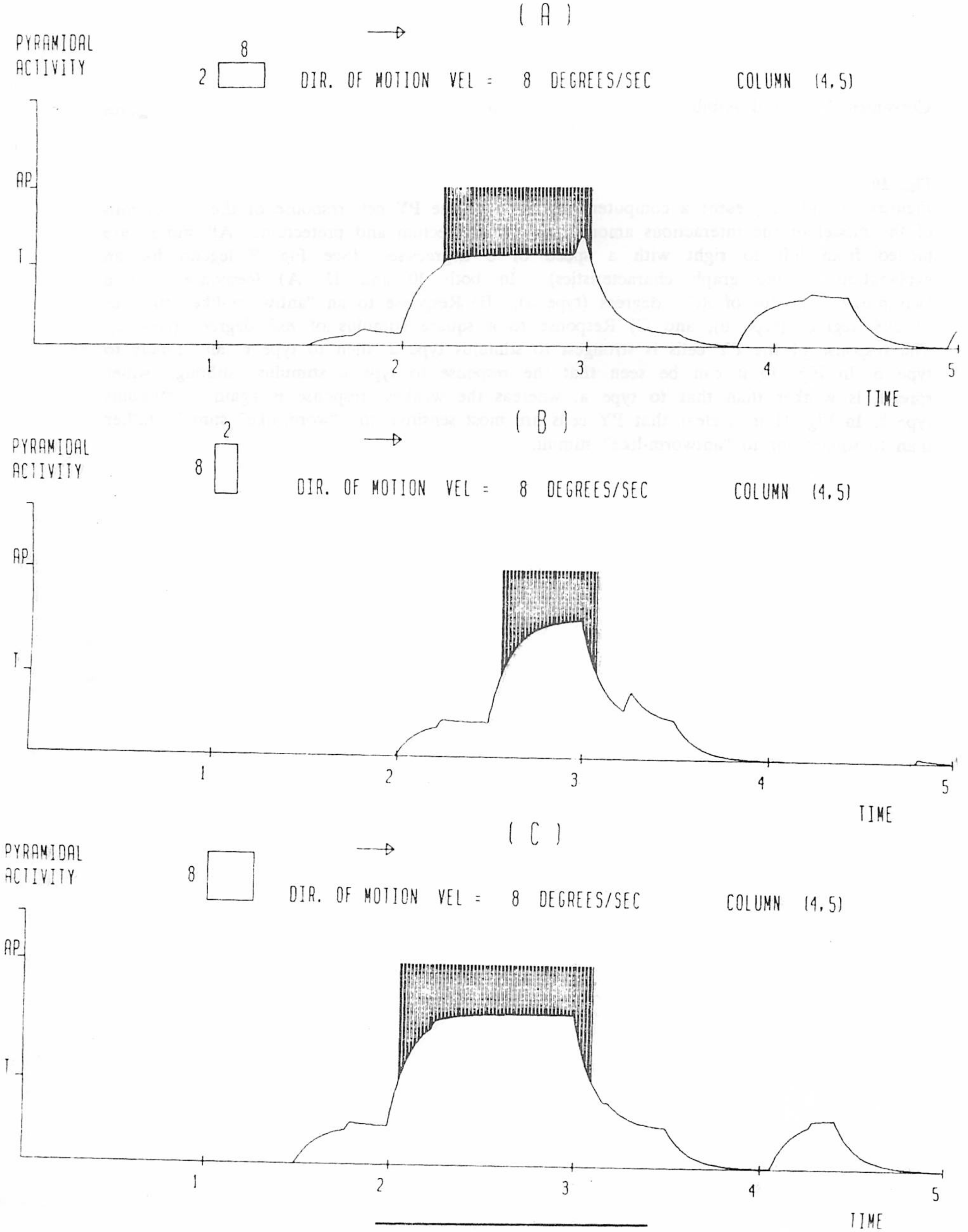

Fig. 9.
See legend for Figure 8.

Fig. 10.
Figures 10 and 11 present a computer simulation of the PY cell response of the 64 columns of the model of the interactions among retina, optic tectum and pretectum. All stimuli are moved from left to right with a speed of 8 degrees/sec. (See Fig. 8 legend for an explanation of the graph characteristics). In both 10 and 11: A) Response to a "worm-like" stimulus of 8x2 degrees (type a); B) Response to an "antiworm-like" stimulus of 2x8 degrees (type b); and C) Response to a square stimulus of 8x8 degrees (type c). The response of the PY cells is strongest to stimulus type a, then to type c, and finally to type b. In Fig. 10 it can be seen that the response to type c stimulus, although wider spread, is weaker than that to type a, whereas the weakest response is again to stimulus type b. In Fig. 11 it is clear that PY cells are most sensitive to "worm-like" stimuli, rather than to squares or to "antworm-like" stimuli.

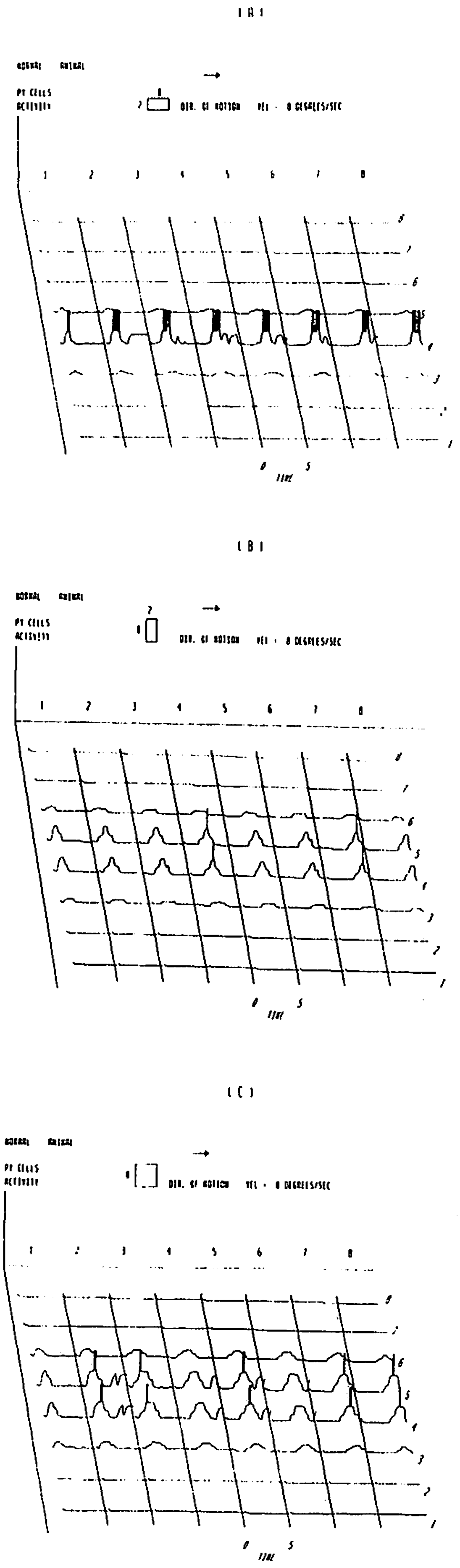
(A)
NORMAL ANIMAL
PT CELLS ACTIVITY
DIR. OF MOTION
VEL = 8 DEGREES/SEC
1 2 3 4 5 6 7 8
8 7 6 5 4 3 2 1
0 5 TIME
(B)
NORMAL ANIMAL
PT CELLS ACTIVITY
DIR. OF MOTION
VEL = 8 DEGREES/SEC
1 2 3 4 5 6 7 8
8 7 6 5 4 3 2 1
0 5 TIME
(C)
NORMAL ANIMAL
PT CELLS ACTIVITY
DIR. OF MOTION
VEL = 8 DEGREES/SEC
1 2 3 4 5 6 7 8
8 7 6 5 4 3 2 1
0 5 TIME

Figure 10

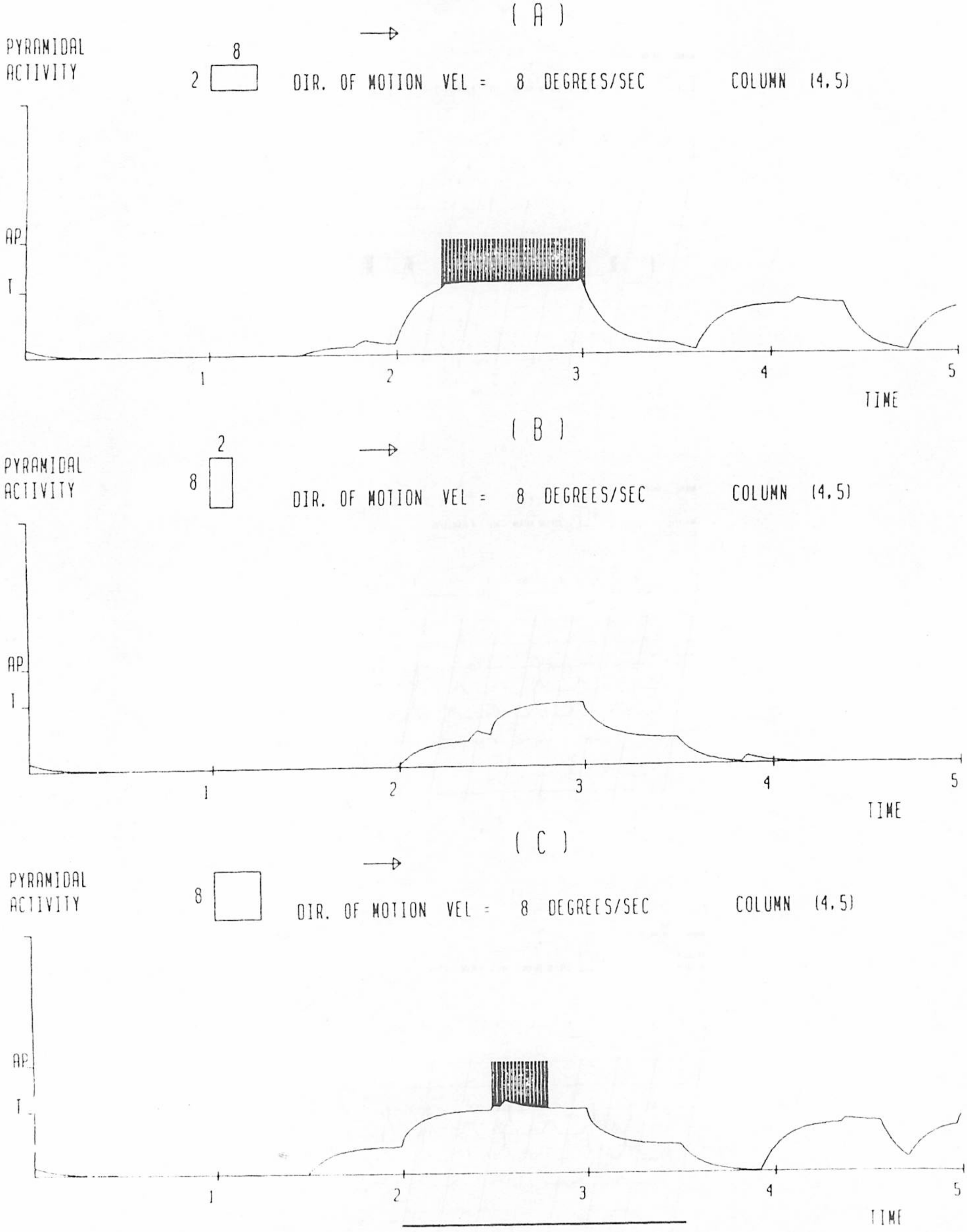

Fig. 11.
See legend for Figure 10.

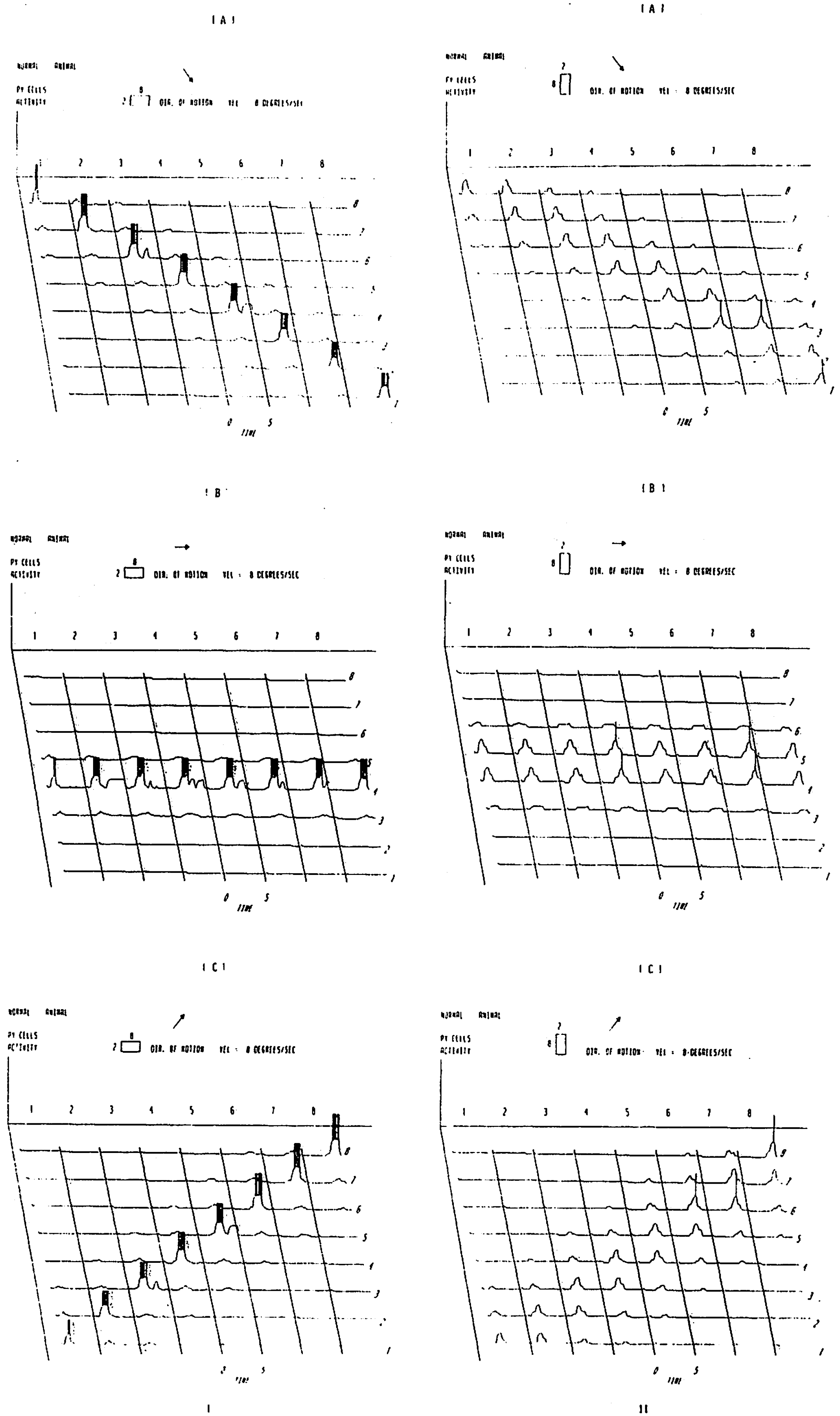
(A)
NORMAL ANIMAL
PY CELLS ACTIVITY
DIR. OF MOTION VEL = 8 DEGREES/SEC
(B)
(C)
1 2 3 4 5 6 7 8
0 5 TIME
I
II

Figure 12

Fig. 12.

Computer simulation of the PY cells response of the 64 columns to a rectangle stimulus, of 8x2 degrees with a speed of 8 degrees/sec. (see Fig. 10 legend). I) The stimulus is moved as a "worm-like" in three different directions. II) The stimulus is moved as an "antiworm-like" in the same directions as in I). In both I) and II): A) moving from the upper left corner of the figure to the lower right; B) from left to right in the middle of the receptive field; and C) from the lower left to the upper right corner of the figure. The response is direction invariant, so the recognition of both stimuli does not depend on the direction of motion.

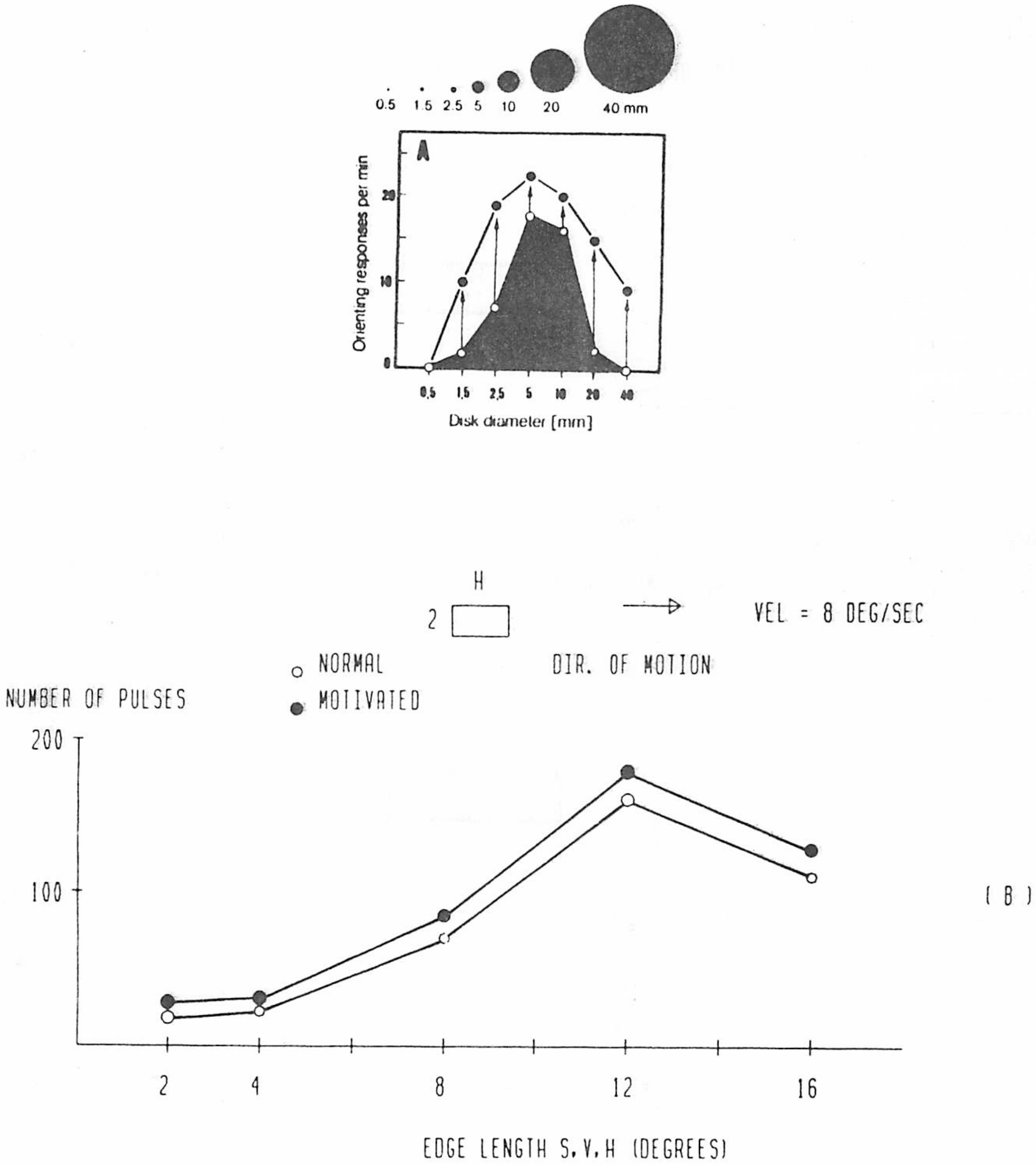

Fig. 13.
Behavior of tectal cells to changes in the motivational state of the animal. A) Behavioral response of common toads to prey dummies (disks) of different sizes with a visual angular velocity of 20 degrees/sec. In the presence of prey odor (motivated animal) the stimulus efficacy is greately enhanced (see arrows) (from Ewert[16]). B) Computer simulation of the PY cells response to changes in the motivational state level. The curves correspond to normal (same as Fig. 7C) and motivated states, when we present "worm-like" stimuli of different sizes with an angular velocity of 8 degrees/sec. The response (number of spikes) increases if the motivated state is increased, although the size selection (selection of the "optimally" preferred prey size) remains the same.

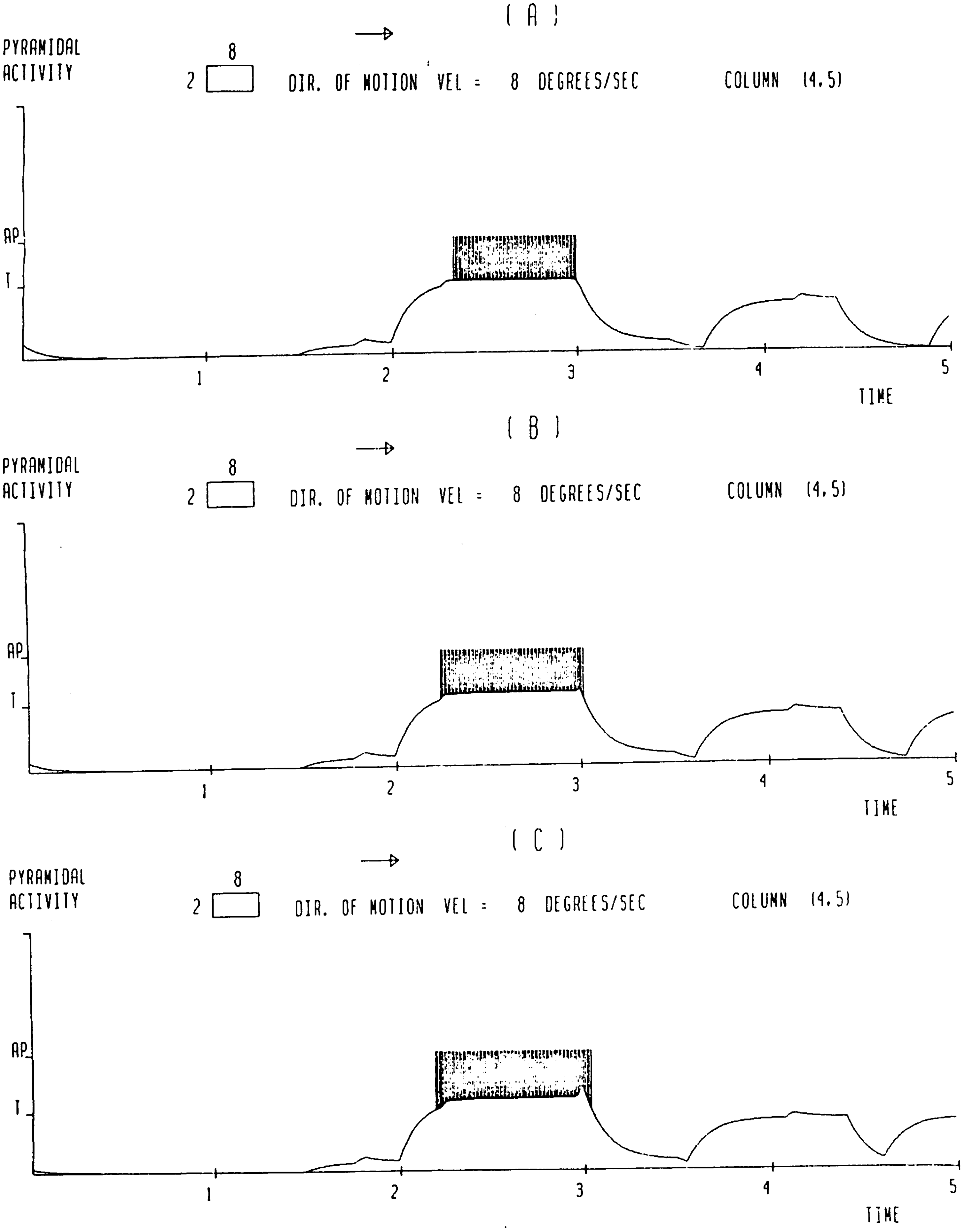
(A)
PYRAMIDAL ACTIVITY
8
2
DIR. OF MOTION VEL = 8 DEGREES/SEC
COLUMN (4,5)
AP
T
1
2
3
4
5
TIME
(B)
PYRAMIDAL ACTIVITY
8
2
DIR. OF MOTION VEL = 8 DEGREES/SEC
COLUMN (4,5)
AP
T
1
2
3
4
5
TIME
(C)
PYRAMIDAL ACTIVITY
8
2
DIR. OF MOTION VEL = 8 DEGREES/SEC
COLUMN (4,5)
AP
T
1
2
3
4
5
TIME

Figure 14

Fig. 14.
Computer simulation of the PY cells latency of response to different motivational levels. We used a "worm-like" stimulus of 8x2 degrees moved with a visual angular velocity of 8 degrees/sec. The curves show the response of the PY cell of the (4th,5th) tectal column with: A) low; B) normal; and C) high motivation level. It is clear that the latency of response reduces and the number of spikes increases when the motivational level increases.

Chapter 3: Motor Control

Paul Grobstein: WORKING NOTES FOR TALK AT THE SECOND WORKSHOP ON VISUOMOTOR COORDINATION IN FROG AND TOAD

Andras Pellionisz: SENSORIMOTOR TRANSFORMATIONS OF NATURAL COORDINATES VIA NEURONAL NETWORKS: CONCEPTUAL AND FORMAL UNIFICATION OF CEREBELLAR AND TECTAL MODELS

Andrew Barto and Steven Epstein: ADAPTIVE NETWORKS AND SENSORIMOTOR CONTROL

Paul Grobstein
Working notes for talk at the Second Workshop on Visuomotor Coordination in Frog and Toad
Universidad Nacional Autonoma de Mexico, November, 1982

Further thoughts on the linkage between tectum and prey capture motor output, on that between stimulus and prey capture motor output, and on the relation between the two.

At the last meeting, I reviewed studies from this laboratory done over the previous five years and concerned with understanding how the nervous system is organized so as to yield the correspondence between stimulus location and the direction of movement which is seen in frog prey capture behavior. These studies led to a working model in which each tectal lobe is linked bilaterally to several different sets of pattern generation circuitry, including one each for leftward and rightward turns and a third for the bilaterally symmetric components of the output, those which vary most obviously with variations in stimulus elevation and distance. I also noted that the model included the assumption of a particular form of relation between tectum and pattern-generating circuitry, one in which each local tectal region was differently connected to the pattern generating circuitry such as to yield a specific and appropriate motor output. At the same time, I discussed both experimental observations and theoretical considerations which were causing us to question the validity of this assumption. The results of lesion studies suggested that the output associated with a given tectal region might be a repertoire of movements rather than a single movement. For several reasons, including a distance/direction ambiguity in the interpretation of the significance of activation of a local tectal region, I suggested that this sort of organization might in fact be expected. At this year's meeting I will discuss studies done in collaboration with Sandra Kostyk, Lee Zwanzigger, and Alex Reyes over the past year and aimed at providing new information about variations in motor output with stimulus distance, at testing several specific aspects of our working model, and at evaluating the possible role of the cerebellum in a spatial coordinate transform which I had suggested was probably required between the tectal retinotopic maps and the output pattern-generating circuitry.

Distance-related variation

Our studies on variations of prey capture motor output with distance proceeded from David Ingle's observation that as stimulus distance increases there is a fairly abrupt switch between two qualitatively different motor output patterns. For nearer stimuli the triggered output involves a directed snap, including a tongue flip. For more distant stimuli it involves a directed body movement, without a tongue flip. The behavioral repertoire suggests that in addition to a measure of absolute distance, some measure corresponding to "within reach" is important in understanding the linkage between stimulus location and motor output. The relationship between the edge of the "snap zone" and the limits of the frog's ability to discriminate distances or to increase snap amplitude has however not been investigated. Nor has the prediction that snap zone size should increase with body size. We have addressed these issues by observing the responses of frogs of various sizes to live mealworms presented at varying distances on the saggital plane. Many frogs snapped with low frequency but reasonable accuracy for stimuli located beyond the point at which orienting movements are the greatly predominant response. This observation indicates that the snap zone border bears no simple relationship either to motor output capability or to the limits of distance discrimination ability. While the size of the snap zone varied significantly among frogs of the same size, snap zone size was nonetheless on the average about twice body size, a result confirming the importance of a "within reach" variable. Unilateral optic nerve section in three of four of the larger frogs significantly reduced snap zone size, without effect on distance discrimination as judged by the accuracy of snaps to stimuli within the snap zone. These observations are of interest from three points of view. First, they raise questions about what kind of information processing is necessary to produce a stable "within each" variable over frogs of different sizes. Secondly, they confirm that an "in reach" variable exists in monocular frogs, that a distance analysis involved in determining snap amplitude does as well, and that the value of the former can be altered without influencing the calculation of the latter. Thirdly, they raise questions about whether the simple assumption that some parts of the tectum project to snap circuitry and others do not is an adequate explanation of the observed switching between the two forms of motor output.

An ipsilateral path for turning

Based on indirect evidence, our working model hypothesized the existence of a crossed descending path linking the part of tectum receiving input from the contralateral visual hemifield with pattern generating circuitry producing turns in the contralateral direction, and of an uncrossed path linking the part of tectum receiving input from the ipsilateral visual hemifield to pattern generating circuitry producing turns in the ipsilateral direction. To test directly for the existence of ipsilateral descending paths we have observed the behavior of frogs subjected to bilateral interruption of the crossed paths by a ventral midline incision at the level of their decussation. Consistent with previous reports of Ingle, nearly all such frogs failed to turn toward stimuli in binocular field during the first weeks after the lesion. This makes uncertain the element of our model which identified the tectal regions representing the ipsilateral visual hemifield as the source of the ipsilateral projection. The animals did however turn in the expected directions for stimuli at more peripheral locations, most within two or three days of the lesion and all within one week. Stimuli at locations more peripheral in one hemifield (the left for example) and hence activating the opposite tectal lobe, triggered turns of progessively greater amplitude toward the side of that tectal lobe (to the right), the direction expected of turns triggered by an ipsilateral descending path. For near stimuli a snap was included in the response. The results confirm the existence of ipsilateral descending paths adequate to trigger prey capture turns. Perhaps more importantly they indicate that tectal regions representing the contralateral hemifield are linked not only to pattern generating circuitry for turns in that direction but to circuitry for ipsilateral turns as well. Finally they raise further doubts about whether the distinction between stimulus locations eliciting snaps as opposed to orienting movements can be accounted for on the basis of tectal regions which do or do not product to snap circuitry. In our experimental animals we observed snapping for near stimuli at positions so caudal as to appear to be well outside the limits of the snap one in normal animals and hence to be causing activity in tectal regions which would be presumed not to be projecting to snap circuitry.

Direct links between tectum and pattern generators?

In our working model, the descending paths were hypothesized to be rather direct links between the tectal lobes and the pattern generating ciruitry. As described last year, hemisected frogs respond to stimuli located ipsilateral to the lesion with forwardly directed movements which do not vary with stimulus angle on the horizontal but do vary with distance. We interpreted this behavior as a consequence of destruction of the paths to turn generating circuitry and survival of paths to circuitry generating distance related output patterns. If this were true, one would expect a normally sized snap zone in the ipsilateral hemifield. We have now tested this prediction and found it not to be the case. The distance to the edge of the snap zone at 90° into the ipsilateral hemifield increased so that in hemisected frogs the snap zone size is the same as that in front of the animal. The observation provides a clear demonstration of snapping as a result of activation of retinal, and presumably tectal, loci which would not be expected to project to snap generating circuitry. It also makes unlikely our previous interpretation of the behavior of hemisected frogs. The outputs triggered by laterally placed stimuli are not in fact equivilent to those expected if one takes the normal outputs and substracts the turning component. They are instead apparently those appropriate for frontally located stimuli. What appears to be disturbed in the hemisected animals is not a direct link to pattern generating circuitry but rather a process by which information about stimulus location coded retinotopically is transformed into information about location in body centered space. This is in accord with our previous suggestion that there may be intermediate circuitry between the tectum and the pattern generators which performs such a transformation. What is cut in the hemisections may be tectal projections to this circuitry.

Cerebellum

The possible role of the cerebellum in prey capture behavior has not been evaluated experimentally. There have been suggestions that it may be involved in pattern generation and there are substantial reasons to believe it may be generally involved in co-ordinate transformations. We have been studying the prey capture behavior of frogs following lesions intended to totally remove the cerebellum. The results are preliminary and the conclusions depend on an histological analysis of the extent of the lesions which is in progress; gross dissection however indicates massive if not total cerebellar removal. All frogs displayed a transient dysmetria for a week or so following the lesion; by two weeks they turned toward stimuli in our standard testing paradigm with the same precision as do normal frogs. At this time they were also tested in ways designed to accentuate the importance of a co-ordinate transform. These included observing turns made from unusual starting postures as well as responses to stimuli at varying distances on the saggital plane and on a line corresponding to 90° into the peripheral field. All frogs displayed slight persistant dysmetrias in turning from abnormal postures to more peripheral stimuli but not to more central ones. With the exception of one frog, there were no gross abnormalities in snap accuracy or snap zone size for stimuli on the saggital plane. Frogs also behaved normally for stimuli on the 90° line except for an increased scatter in turn angle for the most distant stimuli. These observations indicate that the capability to generate the motor programs involved in prey capture behavior survives massive or complete cerebellar removal. They also suggest that the ability to transform retinocentric information about stimulus location into appropriately directed movement is not strongly dependent on the cerebellum. The abnormalities we have obseved are small and do not fall into a pattern which corresponds in any obvious way to what might be expected from the failure of some necessary coordinate transform to occur. They involve principally small dysmetrias and increased variances in situations calling for more substantial body movement. We suspect these result from small disturbances in muscle co-ordination or in the processing of reafferent signals, perhaps from the vestibular system, and are not indicative of an involvement of cerebellum in the spatial co-ordinate transformation.

Summary

In sum, our observations over the last year have resulted in a continuing evolution of our model of the neuronal organization underlying the coupling between input and output in prey capture behavior. We have obtained new supporting evidence for the general picture of bilateral paths from each tectal lobe to at least three distinct sets of

pattern-generating circuitry, one each for turns to right and left and a third for distance related movements. At the same time we have obtained further evidence suggesting that the normal correspondence between input and output can probably not be accounted for by discrete and different projections of various tectal regions. Regions which would be expected to be linked to turn-generating only on the opposite side of the brain are linked to such circuitry on the same side of the brain as well; regions which would be expected to be linked only to circuitry for turns are linked to circuitry for snaps as well. These observations are consistent with our earlier observations which also suggested that there are not a single output but rather a repertoire of outputs associated with individual tectal regions. This interpretation of observations following lesions is paralled by theoretical considerations, as well as behavioral observations over the past year, which suggest that retinal local sign probably provides insufficient information to uniquely specify the location of a stimulus in the coordinate frame used for movement. We suspect that the pattern of tectal activity provides necessary but not sufficient information to account for the normal linkage between input and output. It defines a range of possible outputs from which one is selected using additional information. This we suspect occurs in an intermediate level of neuronal machinery between the tectum and the pattern generating circuitry, machinery which accomplishes the transformation from a retinal coordinate frame to a body coordinate frame which is necessary to uniquely specify stimulus location. Our observations suggest that this circuitry is not located in the cerebellum but probably is caudal to the isthmus region. Our current efforts are directed at determining the origins and targets of fibers passing through this region as well as at trying to characterize the logic of the information processing involved in the transformation using both theoretical considerations and further behavioral observations.

SENSORIMOTOR TRANSFORMATIONS OF NATURAL COORDINATES VIA NEURONAL NETWORKS: CONCEPTUAL AND FORMAL UNIFICATION OF CEREBELLAR AND TECTAL MODELS

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I. INTRODUCTION

In comparing the development of models dealing with the anatomy and physiology of the tectum and cerebellum, their similarities are more striking than their differences. In fact, there is a parallelism between the two lines of research, which is evident at several levels of the analysis. Given their common features and the fact that much more time and effort has been invested in cerebellar than in tectal research, a cross-fertilization initiated from cerebellar modeling and perhaps a merging of these hitherto separate attempts at understanding CNS subsystems may now be mutually beneficial.

In this paper, a brief outline of the parallelism is given from the point of view of a cerebellar modelist. This is followed by some ideas of how the two fields could be merged, if desired, by using both a common conceptual approach and a unified formalism of analysis.

II. DRAWING A PARALLEL BETWEEN CEREBELLAR AND TECTAL MODELING

First Level: Establishing the Structural Basis of Function from Morphology. Fundamental features of the material basis of CNS function, the basic neuronal networks of different subsystems, had been revealed quite early by Ramon y Cajal (1911). However, the explicit goal of deducing a rudimentary structuro-functional scheme, in order to serve as the anatomical basis for modeling of the function of the cerebellum, organized in parallel, had not been set until the so-called lateral inhibition scheme (Szentagothai 1963, 1968). For the tectum, a conceptually and methodologically comparable attempt was made by Scalia et al. (1968), Szekely (1973), Szekely et al. (1973, 1976) and Sprague et al. (1973). Fig. 2. in ref. Szekely et al. (1976) now serves as a generally accepted basic morphological scheme for the structuro-functional interpretation of the tectum.

Second Level: Establishing the Functional Features of the Neuronal Elements. The most important functional properties of single neurons in the cerebellum were revealed chiefly in the papers of Eccles, Llinas and Sasaki (1966a,b,c,d) and Ito & Yoshida (1964). A corresponding set of investigations of the tectum is comprised in the work of Ingle (1973,1975,1976a,b), Ewert (1970,1971, 1976), Ewert & Ingle (1971), Grusser & Grusser (1976). As a result, basic information is available to explain the function of both of these CNS subsystems in terms of the properties of neuronal elements.

Third Level: Synthesis of the Knowledge on Structure and Function: Phenomenological Computer Modeling. In the late sixties, a wealth of data was amassed in *cerebellar research* and was consolidated into a single volume (Eccles, Ito & Szentagothai 1967). The book challenged brain modelists & theorists to synthesize this large array of disparate data into a coherent body of knowledge and then to transform this knowledge into a conceptual understanding of this part of the CNS. Likewise, in the early seventies, a collection of morphological and physiological data from the tectum was also gathered (Ingle & Sprague 1972), posing a similar challenge to brain modelists & theorists.

Fulfilling these goals required several steps. In the case of the cerebellum, attempts were first directed towards developing *single cell models*, capable of encompassing the dynamic temporal characteristics from electrophysiological observations. Using a multicompartmental Hodgkin-Huxley model of Purkinje cells, explanations were offered e.g. for the dynamism of generating simple and complex spikes (Pellionisz & Llinas 1977), and for the plastic characteristics of such firings (Pellionisz 1976). A subsequent major approach in phenomenological modeling was to provide a computer simulation of the neuronal interconnections in a *large network model*. Such studies of the cerebellum were carried out e.g. by Pellionisz & Szentagothai (1973, 1974) and Pellionisz, Llinas & Perkel (1977). (For the general philosophy of phenomenological modeling of the cerebellum see e.g. Pellionisz (1979b).)

As for the tectum, just as any work on morphology can be traced back to Cajal's studies, most models of the superior colliculus have some roots in McCulloch & Pitts' early attempts. Specifically, Pitts & McCulloch (1947) envisioned a scheme of neuronal networks, including that of the colliculus, as controlling eye movements. By tieing the workings of a neuronal network to a physically measurable emergent function, they deviated rather sharply from their previous model of neurons implementing Boolean algebra (McCulloch & Pitts, 1943). Unfortunately, they did not continue to develop their later model into a conceptually and formally explicit treatise of the internal representation of external invariants. Instead of further clarifying the conceptology, Lettvin, Maturana, McCulloch & Pitts (1959) turned this approach towards phenomenology, trying to relate the model more closely to the slowly consolidating data-base.

Lettvin's line was resumed during the upswing of modern modeling (Didday 1970, 1976). At the meeting in 1972 (see Ingle & Sprague), it became clear, however, that an orchestrated effort was needed to bring the experimental data, turned out with increasing speed through the seventies, into harmony; in the form of phenomenological and then, perhaps, of conceptual models. Dr. Arbib set up a framework to encompass such essential team-effort by initiating these two workshops on visuomotor coordination in frog and toad. *Phenomenological models of the tectum*, contained in this frame, are a) single cell computer models (Lara, Arbib & Cromarty 1982), capable of reproducing the dynamism of firings (cf. Ingle 1975); b) computer models of the retinal-pretectal-tectal connectivities (Lara, Cervantes & Arbib 1982, Lara 1982, Lara & Arbib 1982). For insights to the philosophy of these models, see Lara & Sandoval (1982).

Fourth Level: Transformation of Knowledge into Understanding CNS Function: Conceptual Models. The parallelism between cerebellar- and tectal modeling can also be drawn at the most significant level of analysis. This is the conceptual identification of the function of a specific subsystem of the CNS, and the demonstration of how the observed structurofunctional properties enable the neuronal mechanism to perform its function.

As for the evolution of concepts of cerebellar function, motor coordination has long been concluded to be the role of the cerebellum (cf. reviews listed in Dow & Moruzzi 1958, Pellionisz 1979a or Llinas & Simpson 1981). Nevertheless, some early models were restricted only to stating the problems (e.g. Arbib, Franklin & Nilsson 1968) or aimed only at ideas concerning specific subsystems of the total circuitry (e.g. Szentagothai 1963, 1968, Pellionisz 1970). Other models identified the function as being limited only to a facet of what is known as coordination; either in the form of "timing" (Braitenberg & Onesto 1961), or control of "synergies" (sets of parameters) in the Bernsteinian sense (Boylls 1974, 1981, Arbib, Boylls & Dev 1974). Eventually, the realization that the function-identification of the cerebellum as a "learning machine" (Brindley 1964, Grossberg 1964, Smolyaninov 1966, Eccles et al., 1967, Szentagothai 1968, Marr 1969) was both overly narrow and mistaken, led Marr (1982, p.15.) to repudiate his earlier theory that reduced the cerebellum to a pattern-recognizing function. While Ito (1982) still stresses the possibility of plasticity within the cerebellum, it is often pointed out by him and others that the primary role of the cerebellum appears to be coordination, secondary is perhaps timing (prediction) and a tertiary may invoke plasticity. It is emphasized here, that while a degree of plasticity probably cannot be excluded from any subsystem of the CNS (as a general means for the living organism of becoming able to function), it may be a philosophical error to mistake the becoming for the function. For example, in "learning to read" the function is reading, whereas the learning is just the development of the function. We suggest that the cerebellum serves as a space-time coordinator (by acting as a predictive space-time metric; Pellionisz & Llinas 1982b) and the genesis and modification of this metric tensor-like circuitry entails phenomena associated with plasticity (Pellionisz & Llinas 1981).

There is a need for a gradually enlarging view of the function of CNS subsystems. This is clearly pointed out by the evolution of the conceptology of cerebellum, outlined above. Integrative cerebellar theories cannot exclude any specific aspect of the function; in fact, Tensor Theory does consolidate e.g. the elements of timing, plasticity, control of a set of parameters or lateral inhibition. On the other hand, subsystem-theories that are restricted to only one or a couple of such aspects, brilliant as they may be (such as e.g. the Braitenberg' "timing" notion), they serve as transient, too sharply focused flashes on the details. Also, such narrow presentations usually have to be rather considerably reinterpreted when eventually they are fitted into a model with enough power to enlighten a much broader perspective.

A trend towards unification, starting with integrating different aspects of the function of cerebellum into a coherent model cannot stop at the boundaries of the cerebellum. It has long been questioned, for example; "Can we make a real systems approach to cerebellar function without modelling the whole motor system?" (Arbib et al., 1968). The real challenge to a brain theorist & modelist is, therefore, whether one can integrate one's separate models of particular subsystems of the brain. For instance, can one merge models of the motor part of the CNS (cerebellum) with available models of a sensory part (tectum) thereby generating a model of how the sensory transforms into the motor (cf. Grobstein et al., 1982)? The goal of developing entire sensorimotor models is explicit e.g. in Arbib, Boylls & Dev (1974), whereas the disparate models of the cerebellum (Boylls, 1974) and that of the tectum (Arbib, 1982) have yet to be integrated into a meaningful whole.

The goal of theoretical brain research, it seems, is not the modeling of any specific part of the CNS per se. In the process of developing an integrated brain theory, it may only be for technical reasons that research is concentrated first on the simpler, and then on the more complicated parts of the brain. It has already been stressed that, for instance, the cerebellar theory is aimed at finding the unifying conceptual and formal means by which the brain as a whole can be understood (cf. Pellionisz & Llinas 1979b, 1982ab), and this understanding utilized (cf. Pellionisz 1983a).

The evolution of concepts on the function of the tectum, unfortunately, is not as advanced at this time as that of the cerebellum. Indeed, the general underlying theme appears to be the rather vague notion (cf. Ingle & Sprague 1972) that the colliculus serves as a sort of sensory coordinator for visually (and acoustically) guided behavior; examples are the eye-saccade in higher mammals or the body saccade (snap) in lower vertebrates (amphibia). This general description, not unlike the notion that the cerebellum is a motor coordinator, is approached by experimentalists from different conceptual standpoints.

One school of experimentalists works at heuristic behavioral level (pray catching and avoidance in frogs and toads) combined with single cell electrophysiological studies (cf. Ewert & Ingle 1971, Ewert 1976, Ingle 1976). Neuronal modeling & brain theory is already contributing to this approach by filling the gap between the single cell and behavioral levels of phenomenology by computer modeling (Lara & Arbib 1982, Lara, Arbib & Cromarty 1982, Lara, Cervantes & Arbib 1982). Another expected contribution of brain theory would be to fertilize such phenomenological models with concepts that the CNS may utilize to be able to play the role of sensory coordinator.

In another major approach, through the elegant studies of Sparks and colleagues (Sparks 1975, Sparks & Pollack 1977, Sparks & Mays 1981, 1983, Sparks & Porter 1983), the function of the tectum is not only experimentally investigated but the data are also conceptually interpreted, albeit not quite modeled, as representing (not in a retinocentrically but spatially coded form) the saccade-vector of the eye movement. This approach centers neuronal firings of the tectum and the well-measurable physical events (the movement of the eye) around the powerful concept of vectorial representation. It is, indeed, unlikely that coordination can be explained without using coordinates.

In this paper, by introducing a methodology capable of handling natural coordinate systems in which such CNS vectors are expressed, an integration of tectal experimental data and models is proposed, as well as formal-conceptual unification of tectal and cerebellar models into a tensorial sensorimotor scheme is offered. This cerebellar modelist & brain theorist has been asked to put other parts of the brain, e.g. the tectum, into the focus of the conceptual and formal approach already elaborated for other subsystems of the CNS. Thus, this study serves as a precursor to our forthcoming full paper which applies Tensor Network Theory to tectal systems. If what seems conceptually and formally applicable to one part of the brain appears to be applicable to other subsystems as well, then one may claim some general understanding of the brain in a more profound sense than that inherent in phenomenology.

Tensor Network Theory of the Central Nervous System (Pellionisz & Llinas 1978, 1979a,b,c, 1980a,b 1981, 1982 a,b) has already implicated sensorimotor transformations and has proposed a functional role of the tectum (cf. refs. 1982 a,b). The theory itself is not exposed in the scope of this work; the reader is referred to the original papers and the explanations which put them into perspective (cf. Llinas 1981, Llinas & Simpson 1981, Pellionisz 1983a,b). The rest of this paper is limited solely to a further illumination (with the help of the composite diagram of Fig. 10.) of how the conceptual and formal approach of Tensor Network Theory may be applied to general integrated functions of the CNS, as sensorimotor transformations including tectal, cerebellar and other neuronal networks of the brain.

III. APPLICABILITY OF TENSOR NETWORK THEORY TO SENSORIMOTOR MODELING

The fundamental thesis of Tensor Network Theory is that the function of the CNS is to deal with invariants (physical objects) of the external world by means of internal coordinates which are transformed through neuronal networks. For example, the space-time event of a movement (a fly's path, the movement of the frog's head, or of the whole body during a snap) is usually assigned externally with x,y,z,t Cartesian coordinates in a Newtonian space-time reference-frame. However, inside the CNS these movements are both detected and generated by concerted activities of many neurons, which mathematically constitute internal vectorial components assigned to the external invariant. Such sensory and motor vector components are e.g. the firing frequencies of neuronal axons arising from the usually non-orthogonal vestibular semicircular canals, and firing frequencies of motoneurons that innervate a set of hindlimb muscles involved in a snap.

There are major differences, understandably, between CNS vectors (ordered sets of quantitities) that express external invariants in natural coordinate-systems and vectors expressed in the "regular" (man-made, x,y,z Cartesian, three-dimensional, orthogonal) frame of reference. Two of the many differences are self-evident. First, the number of CNS vector-components is potentially much higher than three (even for the quite compact vestibular system, the number of semicircular canals is six, and the skeletal muscles involved e.g. in a snap are obviously more numerous). Second, the coordinate-axes are usually not perpendicular to one another, not even in the vestibulum (c.f. Curthoys et al., 1975). Thus, an analysis of the CNS in terms of dealing with external invariants by means of internal vectors presents both a possibility and a problem.

The promise is that CNS function can be conceptualized in a mathematically precise manner as representing an external invariant in different sensory and motor frames of reference, where the operation is identified as tranformation from one vectorial expression to another. In the composite Fig. 10. of this paper, for example, a four-dimensional oblique optic-auditory frame of reference is shown. Here the axes at 60° may be thought of as reference for audition, while the 120° directions as visual axes. In turn, the vestibular reference frame is represented as a three-axis oblique system. In a much more abstract manner, the motor frames of how a set of neck or forelimb muscles would yaw or roll the head, or how a set of hindlimb muscles would move the whole body in a snap, are symbolized in the figure only by two dimensional non-orthogonal frames. Since tensor operations can be described in a generalized reference-frame without invoking any specific one, the restriction of the pictoral symbolism into 2 and 3-dimensional graphs will in no way invalidate the approach. However, such simple heuristic diagrams will keep the the tensorial blueprint of an amphibian CNS at a not totally unreasonable level of complexity.

The problem that this approach raises is twofold: a) How can vector-transformations be implemented by the CNS so that an object is expressed first in one one and then in another frame so that the two vectors represent the same invariant (e.g. detecting a target in optic-auditory frame, and then moving the body, using another, motor frame of hindlimb muscles and thus achieve a spatio-temporal coincidence of the target and the body). b) How can such vector-representations of invariants be treated by neuroscientists in a conceptually and formally homogeneous abstract manner? Our answer to this double question is the basic tenet that Tensor Network Theory invokes. According to a general conceptual definition, a tensor is a matematical device that expresses the relation among (possibly an infinite number of) different vectorial expressions assigned to the same invariant (cf. Pellionisz & Llinas 1982a).

While tensors are abstract instruments, in a particular frame of reference, a tensor transforming one kind of vectorial expression of an invariant into another may be implemented by a matrix with particular numerical components. Given a network, connecting n input neurons to m output neurons, mathematically representing an nxm matrix, the general function of such a neuronal network can be identified as performing a tensor transformation.

A common problem, which leads to misunderstandings is that the general mathematical tool of tensor analysis is now being used in a novel scientific application. Thus, the usage is, by definition, unconventional. Tensors have been primarily used in engineering, describing tensions in elastic bodies (hence tensors). In ordinary engineering applications, for reasons of convenience, the selected reference-frames are nearly always three-dimensional orthogonal Cartesian systems of coordinates. As a result, the meaning of the word "tensor" to many engineers, is identical to the narrowly defined "Cartesian tensor applied to a linear system and implemented by a 3x3 matrix". A subsequent major application of tensor theory, relativity, stressed the importance of general, unspecified coordinate-systems. Thus, tensors were no longer limited to linear systems (relativity theory is a nonlinear tensor theory), and the reference frames could be multidimensional and non-conventional (e.g. non-orthogonal) systems of coordinates. However, precisely because relativity theory is a highly abstract construction, the tensorial description nearly always remained in the realm of the abstract, using general reference-frames without numerically operating in any particular non-conventional frame of reference.

In Tensor Network Theory of the Central Nervous System it is necessary to deal with both the abstract description (for conceptual understanding) and with the particular expressions in the specific coordinate systems dictated by natural selection. These frames include highly non-conventional, e.g. oblique, overcomplete reference frames. If one desires to trace the actual neuronal implementation of transformations, one has to numerically deal with such natural frames of reference. Therefore, for a neuroscientist to use Tensor Theory it is necessary first to familiarize oneself with peculiarities of vectorial expressions in non-orthogonal frames of reference. Indeed, in every novel application of any mathematical approach, one must always overcome an initial resistance to the non-conventional usage of an abstraction, necessitated by the new scientific application (cf. Dirac-delta, or the notion of imaginary numbers). In the case of tensors expressed in Nature's general non-orthogonal coordinates, this may mean tensors implemented by non-square nxm matrices, where the components may not be constants, and where non-linearities are often implied. It is also quite likely that, as in any new scientific application, the mathematical apparatus itself will need further development by perceptive, able and willing mathematicians.

The single most important feature which reveals the non-conventional character of Tensorial Brain Theory is the utilization of the mathematical distinction between the two kinds of basic forms of vectors in non-orthogonal frames: covariant and contravariant vectors. This distinction is not always necessary in Cartesian frames, e.g. in the theory of elastic tensions. However, relativity theory made profound use of their differences. This author introduced this distinction into neuroscience with Fig. 3. in Pellionisz & Llinas 1980a. Since this distinction is of cardinal importance in Tensor Theory of CNS, the reader must clearly understand it before proceeding. The significance of covariant and contravariant-type vectors in neurobiology lies in the fact that there are two basic operations that the CNS must perform regarding an invariant of the external world. One operation, the covariant-type, starts from the invariant (e.g. presenting a frog with a target), to which the CNS responds (e.g.

by assigning to the target a set of sensations evoked in the form of different sensory modalities of vision, hearing, etc). It is of fundamental importance, that such components of optic-auditory reception are established separately, independently of one another (e.g. vision is possible without hearing, or that even monocular or monochromatic vision is possible). It is also essential to note that such covariant-type components, while they represent the invariant, they do not physically add to generate it.

Another type of CNS operation ends with the invariant, e.g. when the CNS initiates an action by triggering the muscles to move the body to match the invariant (location of the fly). Such motor action is of contravariant type, since, by definition, the components of muscle activities must physically generate the invariant, the displacement. It is also noteworthy that in such contravariant-type expression the components are interdependent. The above features of covariants and contravariants are discussed in more detail in Pellionisz & Llinas (1979c, 1980a,b, 1982a).

Based on the above fundamental tenets of the Tensor Theory, the sensorimotor action of a frog can be conceptualized as the transformation of a covariant sensory reception vector, expressed in the sensory frame, into a contravariant motor execution vector, expressed in a different motor frame of reference. Such general sensorimotor transformations invoke several major problems. First, how can a covariant expression be changed into a contravariant type? Second, how can a vector, expressed in one coordinate system, be transformed into another vector, expressed in a frame in which the directions of the axes are different? Third, how can such a transformation be performed when the number of axes in the sensory and motor frames are different, including the possiblity of an increase of dimensionality from sensory to motor?

IV. TENSORIAL SCHEME OF NEURONAL NETWORKS TRANSFORMING VECTORIAL INFORMATION FROM A SINGLE SENSORY FRAME OF REFERENCE TO A SINGLE MOTOR FRAME

All of the above problems, inherent in sensorimotor transformations, have already been dealt with in the case of a single sensory- and a single motor system (Pellionisz & Llinas 1982 b). As it was shown there, the basic covariant-contravariant transformation can be implemented by a network that performs the role of a contravariant metric tensor. The covariant and contravariant metric describes the relationship of these two kinds of vectors (cf. Fig. 3. in Pellionisz & Llinas 1980a). The matrix of the covariant metric and its inverse or generalized inverse, in case of singularity, (Albert 1972) establish the required transformations between covariant and contravariant type expressions. The change of the direction and the number of axes from one coordinate-system to another can be implemented by a network that performs the so-called covariant-embedding transformation (for details, see Pellionisz & Llinas 1980a, 1982b, and detailed numerical explanation in Pellionisz 1983b).

A "tensorial blueprint" of the amphibian CNS was offered in Figs. 7. and 8. of Pellionisz & Llinas (1982b). In these schemes, the transformation of a sensory covariant reception vector into contravariant sensory perception vector was suggested to be the role of the superior colliculus. The telencephalon ("sensorimotor cortex") was to perform the covariant embedding from sensory to motor frame (independent of the number of axes). Finally, the cerebellum was pictured to serve as the motor metric which transformed the covariant motor intention into contravariant-type motor execution. For detailed description of the network-operations the reader must be referred to Pellionisz & Llinas 1982ab, and to further explanation in Pellionisz 1983b.

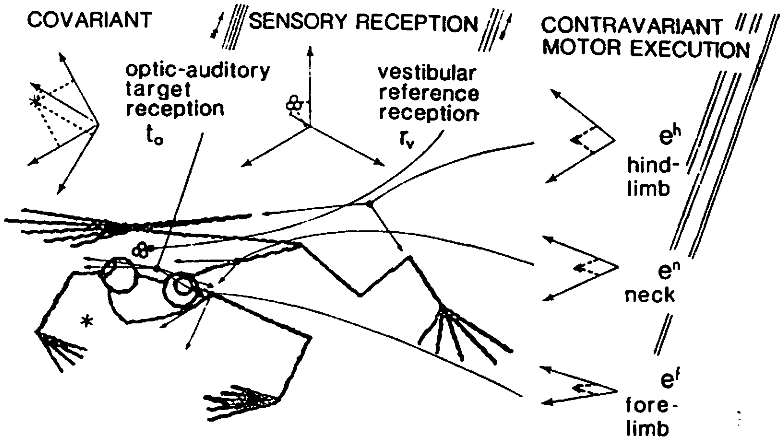

Fig. 1. Symbolic depiction of natural frames of reference in which multisensory-multimotor transformations are expressed by neuronal networks of CNS.

V. TENSORIAL SCHEME OF MULTISENSORY-MULTIMOTOR TRANSFORMATIONS BY NEURON NETS

A more complex, multisensory-multimotor scheme of visuoaditory and vestibular coordination is outlined in the scheme (Fig.10.) provided in this paper. This expands the previous model by one major new consideration: The complexities of sensorimotor transformations in the CNS are better represented by a model in which the CNS draws information from several sensory modalities and transforms the coordinated input into different optional motor responses.

In the particular example of a frog, motor options are such basic survival skills as e.g. stabilizing the horizontal position of the head by forelimb muscles, turning the head by "optokinetic" head nystagmus into central targeting position by neck muscles, and snapping by a whole "body saccade" to a target by hindlimb muscles (Fig.1.). A particularly significant problem is, that the frog must use a coordinated input from different sensory modalities to perform such a delicate act as snapping to a fly from a rolling platform (e.g. a lillypad). The space-time coincidence that is implied in a target interception obviously cannot be achieved without visuoaditory target reception. However, since the snap involves moving the whole body against gravity, a successful implementation must take into consideration the vestibular information about the reference; the initial position, velocity and acceleration of the body. Thus, a sensory coordination of visuoaditory and vestibular information is involved here, as well as the location of the target and a spatiotemporal prediction of its future position. All such transformations from one frame to another are performed by CNS neuronal networks (Fig.2). These functions are known to be executed with the help of the superior colliculus. Visuoaditory-vestibular interaction (cf. Henn, Cohen & Young, 1980), and especially motor coordination are closely related to cerebellar function (cf. Llinas & Simpson, 1981). Thus, a snapping action (or the less complicated head-nystagmus or horizontal head-stabilization) are all CNS operations that most conspicuously involve both tectal and cerebellar actions. Accordingly, such functions must be addressable by Tensor Theory if it is claimed as an approach with a substantial integrative power.

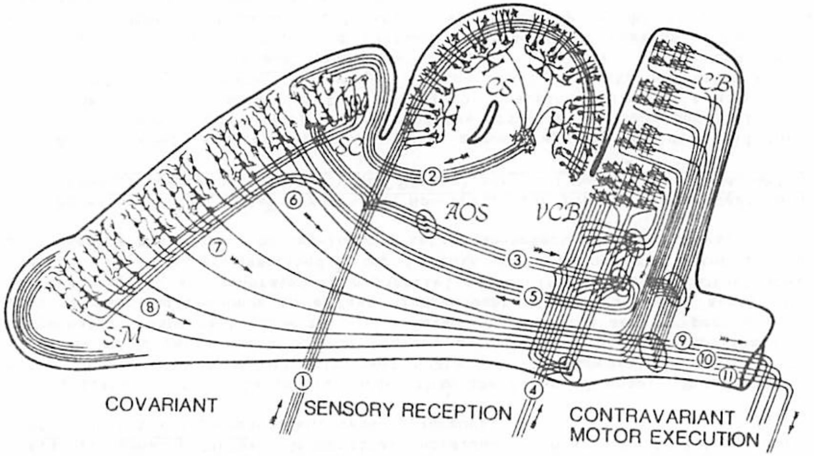

Fig. 2. Tensorial scheme of the CNS neuronal networks of amphibia, performing sensorimotor transformations expressed in frames shown in Fig.1.

Superior Colliculus: Acting as a Sensory Metric

In some sensory systems it is a self-evident physical fact that the primary sensory reception takes the form of a covariant vector expressed in a non-orthogonal frame of reference. This is the case in the semicircular canal system of the vestibular apparatus, where each of the non-orthogonal set of canals (Curthoys et. al., 1975) responds proportionately to the cosine-projection of the acceleration onto the plane of each canal. The method of establishing the separate components independently from one another can also be made obvious by lesioning one canal; the function of the others will not change. The concept of a covariant vestibular vector has been explicitly utilized in developing tensorial models of the vestibulo-ocular reflex system (Pellionisz & Llinas 1980a, 1982b, Ostriker, Pellionisz & Llinas 1982, and Robinson 1982).

The separate and overcomplete covariant measures of invariants by different sensory modalities, (e.g. vision, audition), all have been widely reported to converge in the colliculus superior (cf. Jay & Sparks, 1982). This leads to the concept, stating that the colliculus may serve as a sensory metric; not only in the sense that it converts the covariant reception into contravariant sensory perception (cf. Pellionisz & Llinas 1982b), but also that different sensory modalities can be interpreted as representing different axes in a unified sensory hyperspace. In this manner, just as binocular vision adds a new dimension to target perception, or color reception adds still another, audition may be interpreted as an independent but unifiable component of a multisensory vector. This interpretation describes the colliculus not as an optic tectum, where projections of from different sensory modalities may be separated according to their spatial distribution, but rather, as a multisensory coordinator where the different sensory modalities may be related to one another, yielding a unified (contravariant) sensory percept. Thus, while at the primary sensory reception level a target may be visually or acoustically detected, the perception of a target location, for example, should not (and, in fact, cannot) be dissected to a "seen" and a "heard" position. This feature becames even more evident when the representation of space-time is considered in the CNS (Pellionisz & Llinas 1982a,b). It is well known that auditory, and especially visual reception, are considerably slow types of neuronal information processing. A successful snap at a fast-flying target would not be possible if a) a separate "seen" and a "heard" target-positions would be established by the CNS, since the two would differ by their delays, and b) if the unified target-perception would not temporally predict the would-be target position. Predictor-modules and a neuronal network serving as a metric tensor were demonstrated to be feasible in the cerebellum. The "temporal lookahead module" (Pellionisz & Llinas 1979b, 1982b) is a functional redefinition of the role of stacks of Purkinje cells, albeit it is not incompatible with the morphological lateral-inhibition scheme (Szentagothai 1963, 1968). The possibility is raised here that experimentation may find tectal neurons with firing characteristics that correspond to first- and second-order time-differential of the input. These may serve as the basis of lookahead modules in the tectum similar to those in the cerebellum (c.f. Pellionisz & Llinas 1979b).

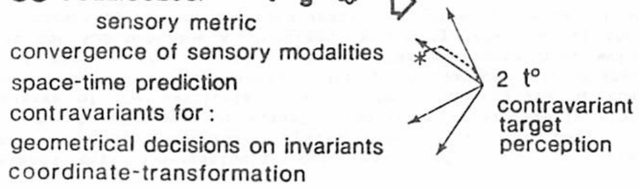

Fig. 3. Superior Colliculus: Transforms covariant target reception (t_o) into contravariant target perception vector (t^o), expressed in orientation (visuoaditory) frame of reference. The notation of vectors throughout this paper is that the symbol stands for the type of information carried by the vector (t: target), the sub- or superscript denotes the frame in which the invariant is expressed (o: optic-type frame), subscripts and superscripts are used to denote covariant and contravariant expressions, respectively. Different vectors are also assigned a number and a verbal expression throughout this paper (e.g. 2; contravariant target perception; t^o), for heuristic reasons and to ease the tracking of the traffic of vectors in Fig. 10.

Two further, higher-level arguments support the view that the tectum may serve as a sensory metric. A technical requirement in the CNS is, arising from the changing of coordinate systems (eg. from sensory to motor), that a contravariant expression of the sensory information, in addition to the covariant sensory reception, must also be available. This enables a covariant embedding procedure (see the explanation of this operation, in Pellionisz 1983b). An even stronger, functional requirement for the contravariant expression is that targeted movements necessitate certain decisions, made within the CNS, on external physical invariants. Size, stereoscopic distance, velocity and direction are all "physical objects", that are represented by covariant vectorial expressions inside the CNS. As pointed out in Pellionisz & Llinas (1982b), availability of both the covariant and contravariant expressions of an invariant, expressed in the same frame of reference, yields a measure of the invariant by the inner product of the two vectorial expressions. Summing the products of the two kinds of components is an operation easily implemented by neuronal networks (see Fig. 7. in Pellionisz & Llinas 1982b).

"Sensory Cortex": Intention Selection on the Basis of Geometric Decisions on Invariants

Given that the tectum makes a contravariant target perception vector t^o available, this vector together with the covariant target reception vector t_o enables geometrical decisions based on properties of the external invariant such as size, distance, velocity, etc. A network, tentatively placed into the telencephalon "sensory cortex", is pictured in Figs. 2. and 10. as implementing the inner product of the covariant optic-auditory target reception vector t_o with the tectum-supplied contravariant target perception vector t^o. The resulting d^2 value, for example, can serve as a basis for sending an inhibitory "block" of a snap intention in the "sensorimotor" area of the cortex, whenever this d distance of the target is larger than the range of snap. Thus, while all motor intentions; an optokinetic head nystagmus (a compensatory response to a slow yaw of a large array of the sensory percept), a horizon-stabilization (a compensatory response to slow roll of a large array of the sensory percept) and a snap (a matching response to a fast displacement of a target-size array of the sensory percept) are generated in a parallel manner in the "sensorimotor" area of the CNS (in a manner described later in this paper), only the motor intention unblocked by the sensory-cortex-induced intention-selection, will prevail.

SC SENSORY CORTEX $d^2 = t^o t_o$
intention selection
neck: optokinetic head nystagmus
forelimb: horizont stabilization
hindlimb : snap (body saccade)

Fig. 4. Sensory Cortex: Geometrical decisions in invariants by inner product of covariant and contravariant sensory vectors.

Accessory Optic System: Expressing Non-vestibular Information in Vestibular Frame of Reference: Necessary for Visuoaditory and Vestibular Coordination

As mentioned earlier, especially those movements that involve rapid actions of a significant proportion of the mass of the body, for obvious physical reasons cannot be properly executed while ignoring the position, velocity & acceleration of the body in reference to gravity. On the other hand, target information is primarily given in the visual (auditory) frame of reference. This necessitates a coordination of visuoaditory and vestibular sensory information. For various aspects of visuo-vestibular coordination, see Llinas & Precht (1969, 1976) and the review by Henn, Cohen & Young (1980).

For the above physical reason, it is postulated that target-oriented actions (especially a snapping) are organized in "vestibular" coordinates, which already carry covariant reception-information about the posture-reference. An important series of experimental findings that corroborate this suggestion, in more ways than one, were made by Maekawa & Simpson (1973), Simpson et. al. (1981) and Lazar (1972). First, it has been found that visual information is projected (through the accessory optic system; AOS) to the vestibulocerebellum. Second, the AOS represents this non-vestibular orientation-information vectorially, in a natural non-orthogonal coordinate system inherent in the CNS. Third, this internal frame of reference for visual orientation is strikingly similar to the coordinate-axes of the vestibular system. While the nature of the vectorial expression in the AOS is currently under investigation (cf. Simpson et. al, 1982), given the sensory character of this CNS subsystem here we tentatively assume that the AOS provides a covariant, secondary reception of the target in vestibular coordinates (hence the term vestibular correception is introduced).

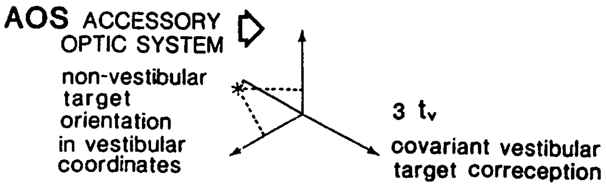

Fig. 5. Accessory Optic System: Yielding information on target orientation, expressed in vestibular coordinates: hence target and reference informations are made compatible.

Vestibulocerebellum: Vestibular and Visuoaditory Coordination

It is known that the vestibulocerebellum receives vestibular sensory information expressed covariantly in vestibular coordinates (cf. Llinas & Precht 1969, 1976). The reference signal r_v and the covariant target correception t_v (expressed also in vestibular coordinates) together present a possibility for a new interpretation of the function of the vestibulocerebellum.

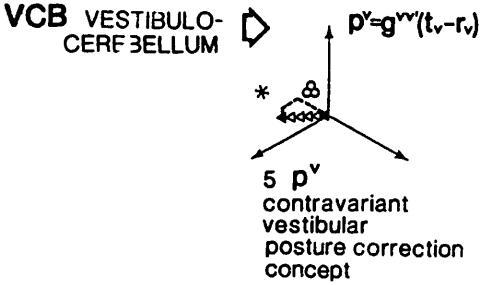

Fig. 6. Vestibulocerebellum: Covariant-contravariant transformation of the posture-correction vector (target-reference).

The present interpretation is both consistent with the earlier suggestion that the cerebellum serves as a covariant-contravariant metric transformer (Pellionisz & Llinas 1980a), and also fits into the extended scheme of multisensory-multimotor system. Further, while it is a complicated digression, it may be briefly outlined in this paper how the cerebellar climbing fiber system would significantly interfere with the visuoaditory-vestibular coordination in cases when there is a mismatch of these two vital subsystems (cf. Llinas & Walton 1979).

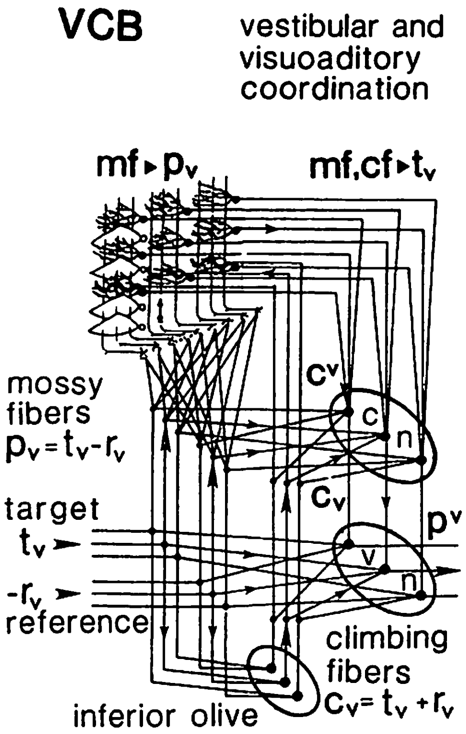

Fig. 7. Vestibulo-cerebellar circuitry: transforming p_v (covariant posture correction vector) into contravariant form p^v. Abbreviations: cn: deep cerebellar nuclei, vn: vestibular nucleus.

Fundamentally, the function of vestibulocerebellum is envisioned as receiving an input that is the difference of the covariant target and covariant reference, and transforming this difference into a contravariant expression. The resulting vector will represent how the posture needs to be corrected (either by head-saccade, body-saccade, or forelimb-roll). While this vector is a contravariant expression (thus it is physically executable to yield the necessary invariant), the medium in which it is expressed is vestibular, different from the actually usable motor frames of reference. Such CNS vectors that do represent needed actions in an executable expression but in a non-executory medium, may be called concept-vectors (a concept being an isomorphic representation of the reality, but one that needs to be carried out in executable media).

Fig. 7. features the mossy fibers as representing the difference of target and reference coordinates ($p_v = t_v - r_v$). The inferior olive is expected to perform a complementary operation; firing according to the sum of these signals, whenever the visuoaditory and vestibular systems conflict ($c_v = t_v + r_v$). If only the mossy fiber system acts, the cerebellar circuitry performs a $p^v = g^{vv'} . p_v$ metric transformation (mf to p^v). Such transformation is explained in detailed, numerical form in Pellionisz (1983b). However, the mossy fibers together with the climbing fiber vector will override the vestibular reference (yielding a posture correction vector that relies exclusively on the visuoaditory system, ignoring the vestibulum: mf,cf -- t_v). This interpretation is in good agreement with the compensatory behavior of rats with vestibular lesion (Llinas and Walton 1979).

An even further implication relates to the collision of the covariant climbing fiber vector c_v in the cerebellar nuclei with its contravariant counterpart c^v (arriving via the Purkinje cells). As suggested in Pellionisz & Llinas (1981) such collision may be the basis of modification of metric connections in the cerebellar nuclei.

"Sensorimotor Cortex": Motor Intention Yielded by Covariant Embedding

The contravariant posture correction vector p^v, expressed in vestibular coordinates, may be transformed into frames of motor execution; either of the hindlimb muscles, of the neck muscles or the forelimb muscles, respectively. The required transformation, called covariant embedding procedure, is similar to such operation elaborated in Pellionisz & Llinas 1982b, Figs. 7,8. Since further, detailed explanation of such operation is given in Pellionisz 1983b, within this paper this transformation is only symbolically represented.

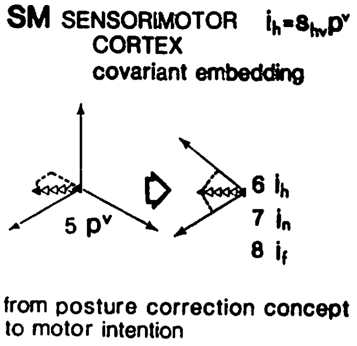

Fig. 8. "Sensorimotor Cortex": Covariant embedding of contravariant posture correction vector (expressed in vestibular coordinates) into executable medium, but not physically executable form (motor intention).

As stressed earlier, this transformation can be implemented even if there is a mismatch of the dimensionality of the vestibular and the motor frames. However, it yields covariant motor intention vectors, which are expressed in an executory medium but in the version that would yield physically incorrect execution. These vectors i_h, i_n, i_f are expressed in the hindlimb-, neck- and forelimb-muscle frame, respectively. As also pointed out already, the release of the behaviorally adequate motor intention vector requires an unblocking by the intention-selection neuronal network.

The contravariant motor execution vectors (expressed in proper motor frames) will generate a compensatory displacement of the body; ideally producing a displacement which matches perfectly the invariant that triggered the tensorial sensorimotor response.

Cerebellum: Covariant Motor Intention Transformed into Contravariant Motor Execution

This last step of the transformation has been suggested to be the role of the cerebellum. Since this function is elaborated elsewhere (cf. Pellionisz & Llinas 1982b, explained in Pellionisz 1983b), it is not discussed here in detail.

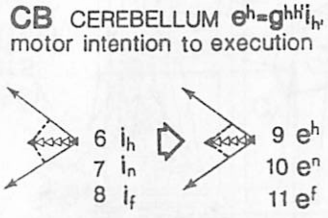

Fig. 9. Cerebellum: metric transformation from intention (i) to execution (e) vectors, expressed in hindlimb-, neck- and forelimb-muscle frames, respectively

*

Finally, the entire scheme of transformations of various vectors through the neuronal circuitries of the CNS is presented in the tableau of Fig. 10. There, the flow and the transformations of the vectorial information can be traced throughout the schematic representation of the CNS of Amphibia.

It is emphasized, that the attempt of this paper at putting forward a coherent conceptual framework for developing a working model of sensorimotor systems (summarized in Fig.10) does not, at all, have the character of a conclusion of existing modeling efforts. Rather, it may be interpreted as an outline for a just unfolding new way of looking at brain function. It might result in a primary understanding of CNS, brought into completion (in the not immediately foreseeable future) as a result of tremendous further investment in effort and time.

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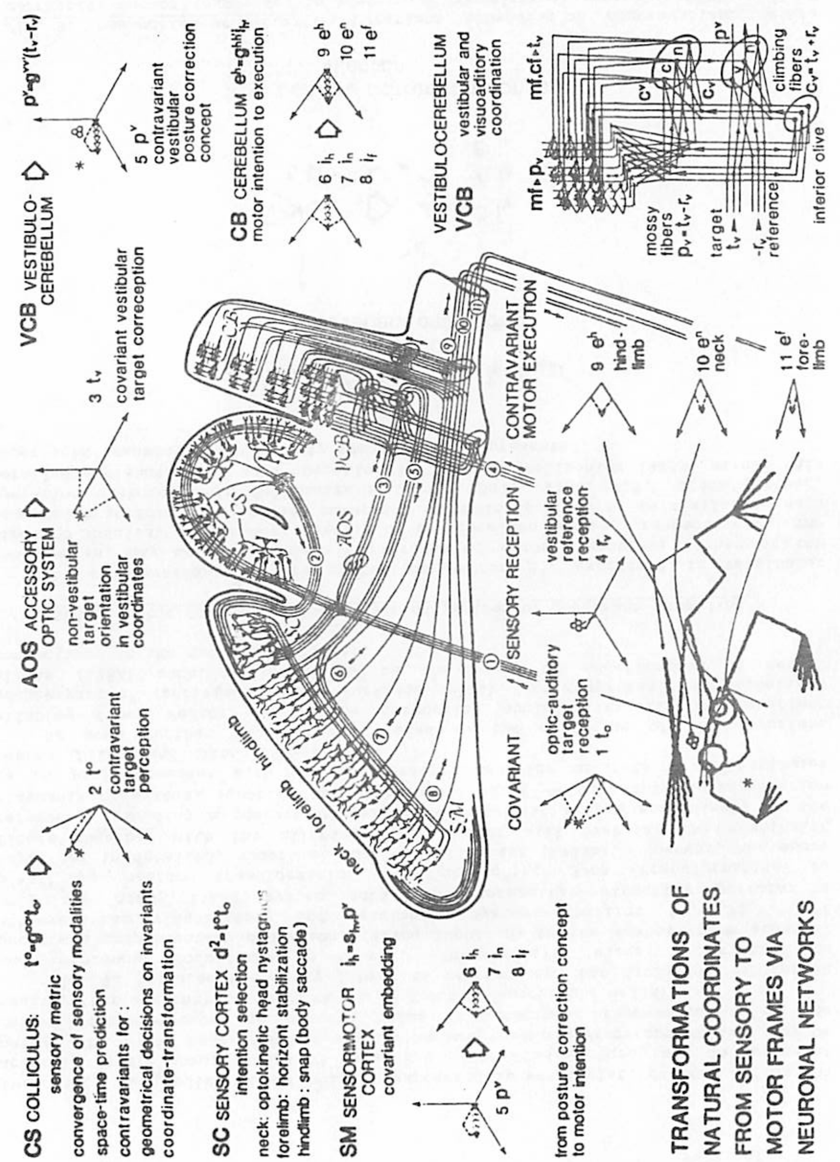

Fig. 10

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ADAPTIVE NETWORKS AND SENSORIMOTOR CONTROL[1]

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1. INTRODUCTION

Over the past two decades most amphibian visuomotor research has been devoted to one aspect or another of visual pattern discrimination. The result has been considerable progress in our understanding of visual perception and behavioral choice, much of it led by the work of participants in this symposium. It is only recently, however, that the motor processes by which pattern discrimination finds expression in behavior have begun to receive comparable attention from experimenters [Grobstein, this volume; Ingle, 1982]. The last few years have also witnessed an upsurge of theoretical interest in motor control, motivated in part by progress in robot manipulation and locomotion and thus pursued by computer scientists and mechanical engineers as well as neurobiologists [Hollerbach, 1982; Hogan, 1982]. Though this work is not specifically concerned with amphibian visuomotor mechanisms, we believe it has much to contribute to their study. In what follows we discuss some basic issues in low level motor control from a computational viewpoint and describe our approach to a kind of adaptive

control that may play an essential role in many kinds of sensorimotor performance.

We begin with an abstract characterization of control tasks, developing the idea of a <u>control surface</u> determined jointly by the requirements of a control task and the abilities of an effector apparatus. We then illustrate some of the computational problems that are posed by the mechanical complexity of musculoskeletal systems, examining the control surface associated with the task of controlling an idealized two-dimensional "limb". In the context of this example, we then discuss how the time and memory demands of a control <u>algorithm</u> (the realization of a control surface as a computational procedure) depend upon the way a control surface is represented. We shall see how a choice of representation is governed both by the structure of the control surface itself and by the repertoire of computational primitives available to the mechanism that must execute the control algorithm. A comparison of alternative representational schemes will lead us to consider in detail control surfaces that are represented as patterns of interconnection in large networks of relatively unsophisticated processing elements. We shall ask how control surfaces represented in such networks could be acquired or modified by experience. It will be shown that certain networks with modifiable connections are capable of altering the control surfaces they represent so as to improve their performance in tasks with uncertain or variable parameters. This is an important capability, as even very simple organisms must have some means of compensating for developmental, pathological, or functional alterations (such as fatigue) in their effector systems [Partridge, 1979]. We shall illustrate how such adaptive networks can be used for acquiring approximations to unknown, partially known, or time-varying control surfaces.

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2. CONTROL SURFACES

Aizerman et al. [1964] define the general problem of automatic control as "the problem of assigning the input situation to one or another class, and [generating] the optimal response as a function of that class." The mapping or function that associates with each possible input situation the (optimal) action for that situation is often called by control theorists a control surface [Mendel, 1970].

It is clear that part of the solution to a control problem involves pattern classification. Input situations must be separated into classes appropriate for the problem at hand. However, in addition to the classification of input patterns, the control system must generate the action or response appropriate to each class. Consequently, the solution to a control problem requires not merely pattern classification, but also, the association of actions (which may themselves be complex patterns of signals) with input situations.

Moreover, the pattern classification aspects of a control problem form a natural hierarchy. At the higher levels, coarse and slowly varying control situations must be identified, whereas at lower levels the appropriate discriminations must be made between more detailed variations of the higher level situations, forming parameterized families of those situations. At still lower levels, estimates of the instantaneous system state must be made. Consider, for example, a pilot controlling a plane. He must first recognize the overall control situation C: the type of plane and the cockpit configuration. This is a high level pattern classification problem. Then he must determine the response characteristics of the plane (determined in part by the mechanical properties of the plane, in part by the setup of the cockpit control devices). This is a parameter identification problem. Finally, he must have a goal (e.g., the desired trajectory of the plane) and an estimate of the state of the plane (e.g., its position and momentum) to determine the appropriate control action to take at that time.

In short, recognition of the overall control situation C gives the pilot access to a parameterized family, f_p, of control surfaces, such that

$$a = f_p(g, s)$$

is the appropriate action to take toward goal g when the system of the class C is characterized by parameters p and is in state s. Note, then, that a control surface f_p is more than just a stimulus/response map, since the input situations (g,s) for f_p need not consist solely of externally supplied signals, but may contain information from within the controlling system itself, providing, for example, state estimates for the controlled system and (goal) states of higher command centers.

Some control systems implement control surfaces that are completely specified from the start. A thermostat, for example, has a built-in control surface which causes it to turn the furnace on if a room is too cold and off if it is too hot. Here the goal g is the desired temperature, the state s is the actual temperature, and the action f(g,s) determined by the control surface is

$$f(g,s) = \begin{cases} \underline{\text{furnace on}} & \text{if } g > s \\ \underline{\text{furnace off}} & \text{otherwise.} \end{cases}$$

These control decisions are wired-in "reflexes" of the thermostat.

Other types of control systems begin with only partial specification of the control surface. They may initially contain no information at all about which control actions are appropriate and operate, at first, randomly; or they may "know" exactly what to do in some situations but have no knowledge at all about what actions are appropriate in others; or, they may initially implement control surfaces which specify actions for every input situation but only in an inaccurate or approximate way. If its performance is to improve, a control system with a partially specified control surface must contain mechanisms for filling in or refining its surface through its experience. Control systems capable of doing this are called *learning control systems* [Mendel and McLaren 1970]. We shall have more to say about such learning systems below, but let us first look in some detail at the structure of a particular control surface.

3. CONTROLLING A SIMPLE LIMB

In order to execute almost any response -- for concreteness, say an orientation turn -- a frog must coordinate the contraction of scores of muscles throughout its body so as to exert just that pattern of forces through its trunk and limbs which will result in the appropriate rotation of the body axis. The pattern of this coordination must be set up within a few hundred milliseconds and executed in half a second or so. Though it looks practically effortless and is over very quickly, this is in fact a prodigiously complex behavior and presents formidable problems of planning and control; it would seem to require that the frog maintain a highly accurate internal model of the dynamics of its musculoskeletal system and use that model, in real time, to compute the appropriate pattern of signals to the muscles. This is no easy matter, as we shall try to illustrate below.

To get a feeling for the computational difficulty of the problem, let us ignore almost all of the frog's motor apparatus and consider just the tiny subproblem of controlling one forelimb. Let it be (grossly) idealized as a two-joint mechanical linkage restricted to movement in a plane. Let us provide this idealized limb with idealized muscles, sidestepping the complexities of the real muscular system by planting an ideal torque generator at each joint. This schematic "limb" is diagrammed in Fig. 1. It consists of two links of equal length and mass, and two revolute joints, a "shoulder" whose pivot is fixed at the origin of a cartesian "world" coordinate system and an "elbow" joining the proximal and distal links. The joint angles Q_1 and Q_2 specify the position of the limb in "proprioceptive" coordinates. Its motion is confined to a horizontal plane and controlled by a torque vector $N = (N_1, N_2)$ whose components are applied at the shoulder and elbow, respectively. Let us also idealize the task -- which in reality involves both free movement and the exertion of controlled forces against the substrate -- as the problem of moving the unloaded free end of the distal link (call it the "tip") along a planar trajectory $X(t)$ given in world coordinates.

This task defines a single control surface. A goal is specified by a desired tip trajectory. The corresponding action is given by a vector-valued function of time $N(t) = (N_1(t), N_2(t))$ comprising the pair of joint torque functions which act together to move the limb along the given trajectory. In vector notation,

$$N(t) = F(X),$$

where X represents the goal, the entire tip trajectory function in "world" coordinates. Fortunately, Newton's laws allow us to characterize X locally, given an initial $X(0)$, by its value and first two derivatives at any instant

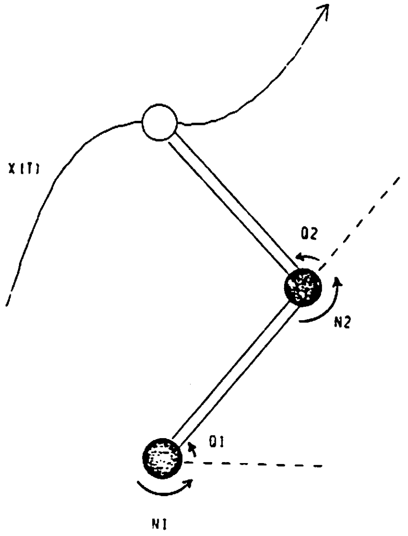

Figure 1

A schematic planar limb with two equal links. The "shoulder" is fixed at the origin of a cartesian coordinate frame. Q1 is the angle of the proximal link, measured with respect to the x-axis; Q2 is the angle of the distal link measured with respect to the proximal link. N1 and N2 are actuating torques about the "shoulder" and "elbow" joints, respectively. X(t) represents a trajectory to be followed by the tip of the distal link.

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t. So we can rewrite the above control surface equation as

$$N(t) = G(X(t), X'(t), X''(t)).$$

The kinematic relations between the tip position X in world coordinates and the vector $Q = (Q_1, Q_2)$ of joint angles allows us to rewrite this as the "inverse dynamic equation"

$$N(t) = H(Q(t), Q'(t), Q''(t)).$$

Here, then, is a prescription for solving the computational problem of trajectory control for our simple case. From the goal trajectory, specified as instantaneous values of joint angles, angular velocities, and angular accelerations we may compute a function H giving the appropriate instantaneous action, the joint torque vector N.

But how is H to be computed? A tedious but straightforward expansion of the inverse dynamic equation in either Lagrange or Newton-Euler form leads to one, rather inefficient, way of computing the components of N. (See [Whitney, 1972] or [Paul, 1981] for an exposition of the mathematical details.) By manipulating the Lagrange or Newton-Euler equations of motion for the limb, it is possible to write the inverse dynamic equations in many other ways. Each formulation leads to a different algorithm for computing H. These algorithms differ in a number of ways. One of the most important, because it bears directly on the *cost* of the computation given a choice of computational primitives, has to do with the number and nature of the intermediate steps required for computing H.

At one extreme, H is not "computed" at all. Instead the input space, consisting of all possible values of (Q, Q', Q''), is partitioned into small regions and an appropriate value of H is simply stored for each one. This is the pure *table-lookup* approach discussed in the next section. The control surface is represented by the values of the table entries. There are many variants of this method that take advantage of redundancies in H to reduce the enormous size of the tables required for accurate function representation. Some of these are discussed below.

At the other extreme are pure computational methods, which calculate H by combining or composing the results of intermediate computational steps. Here, the control surface is represented in the structure of the algorithm. For systems, like our idealized limb, that admit a straightforward analytic formulation, highly efficient recursive algorithms of this type have recently been developed and are now widely used in robotics [Hollerbach, 1980; Luh, Walker and Paul, 1979].

Between these extremes are various schemes that employ computation and table lookup in combination. An example is the so-called "state space method" of Raibert [1978], in which H is expressed as

$$H = J(Q)Q'' + K(Q, Q'),$$

where $J(Q)$ is a configuration-indexed table of inertial coefficients and K is a table of configuration and velocity dependent terms. The only computation required at each time step is to multiply $Q''(t)$ by the tabulated value of $J(Q(t))$ and add the result to the tabulated value of $K(Q, Q')$. Here, part of the control surface is represented in the table and part in the structure of the equation. Raibert [1977] discusses tradeoffs involved in designing representation schemes that combine computation and table lookup in this manner.

It should be emphasized that this trajectory control example was introduced only to illustrate the control surface concept and to show that even a radical simplification of the sort of motor task animals perform routinely can demand considerable computational effort. Though it is probably safe to say that a control strategy that could not handle it easily is unlikely to be useful in controlling more realistic motor systems, the example is seriously inadequate as a paradigm for the low level motor problems faced by animals. Our idealizations depart in at least two important respects from biological reality. In the first place, we have represented the goal of a movement as a precise trajectory specification X(t) in "world" coordinates. But even the free movements of animal limbs are probably not planned in such terms. Natural motor tasks do not usually require high precision trajectory-following. Secondly, we have modelled muscles as pure torque generators, partly to emphasize the analogy with robot manipulators, but mostly to keep the equations manageable. This is a gross misrepresentation of the real properties of muscle. Muscles behave much more like spring-dashpot systems of controllable stiffness and damping than like DC motors (see [Partridge and Denton, 1981] for a review). Thus it is likely that nervous systems do not manipulate joint torques directly, but instead control variables more like stiffness and viscosity. This greatly alters the problem of movement control, though whether it makes things harder or easier seems to depend on the nature of the task. The implications of muscle mechanical properties for motor control are the subject of much current research, both experimental (e.g. [Bizzi and Abend, 1982], [Polit and Bizzi, 1979], [Morasso, 1981]) and theoretical (e.g. [Feldman, 1981], [Hogan, 1980], [Delatizky, 1982]), but fall outside the scope of our discussion.

It is worth noting here, however, that the apparent difficulty of the problem may or may not be reduced by invoking task-specific constraints or "synergies" [Bernstein 1967] that link numerous muscle groups into a smaller number of functional units specialized for a given class of movements. Although such synergies certainly exist, and do indeed reduce the number of degrees of freedom to be controlled at the lowest level, the computational difficulty can reappear in the problem of selecting and tuning appropriate synergies to accomodate muscular output to the highly variable mechanical conditions of particular movements.

Before we go on to consider control surface representations in a more general context, we wish to outline briefly how a "synergy" approach to the trajectory control problem might be expressed in terms of control surfaces. Roughly, the idea is to replace the single and perhaps unnecessarily general control surface H by an organized collection of smaller, more specialized ones.

In our example, a complete trajectory specification (the vector of joint positions in "world" coordinates as a function of time) is mapped into the appropriate actuator control function by a control surface that calculates the joint torque vector using a complete, accurate model — tabular, analytical, or both — of the inverse kinematics and dynamics of the limb. If the limb's mechanical properties can be represented precisely enough, such a control surface will be able to form any trajectory of which the limb is physically capable. However, it attains its generality at the cost of considerable storage or computational complexity.

An alternative strategy is possible when the task has a natural decomposition into a parameterized family of subtasks, each of which approximates the original task in some control situation, i.e., over some region of the input space. One can then map each trajectory plan X in the input space into a small subset of elements $C(X) = \{c_i\}$ drawn from a space K of control situations, and replace the original control surface, say F, with a battery of simpler control surfaces $f_c(p_c(X))$, one for each control situation c in K, where $p_c(X)$ is a small parameter vector, dependent on X, representing the information about X that is relevant in control situation c. This is a slight generalization of the approach discussed in connection with the airplane pilot example above, since it permits the map from input space to the set of control situations to be one-to-many as well as many-to-one. Thus a given control surface f_c can be selected or "activated" by any of a class of "similar" trajectory plans, and several control surfaces f_{c_i} can be activated by the same plan X. The function $p_c(X)$ compiles attributes of the trajectory plan X into the values of a few control parameters which comprise the input space of f_c. Thus each f_c can be viewed as a parameterized "pattern generator" specific to the control situation c. The combined output to the limb's actuators of all the control surfaces activated by a trajectory plan generates the desired trajectory. In this approach, knowledge about limb dynamics is partly spread out among the control surfaces f_c and partly embedded in the mappings C(X) and $p_c(X)$. In this respect it resembles Arbib's [1972, 1981] "schema" approach, but is less general, since there is no explicit provision for interaction among simultaneously active control surfaces.

Is such an approach really feasible? We don't know, because it has not yet received adequate study. The answer depends in part on how many little control surfaces f_c are necessary for generating all the movements potentially required by the tasks the limb is called upon to perform. This number need not be astronomical; a trajectory formation algorithm is not obliged to be able to form all possible trajectories because no practical repertoire of motor tasks calls for more than a limited set of them. And this subset may itself be well enough approximated by "piecewise" combinations of an even more limited subset. Moreover, because each f_c uses no more than a small amount of special-purpose dynamic knowledge, trajectory formation algorithms based on this approach would not need to maintain an explicit, global model of limb mechanics. It therefore seems possible that this shallow, distributed approach to trajectory control could offer significant advantages of modularity and speed over single-control-surface approaches.

4. REPRESENTING CONTROL SURFACES

4.1 Computation and Table-Lookup

As we indicated above, there are many methods which can be used to represent the control surface F, ranging from pure *computational* schemes, in which F is described in terms of equations which can be evaluated by some calculating machinery, to pure *table-lookup* schemes in which the values of F for a large number of arguments are pre-computed and stored in a table. In the first case, a coded input situation acts as the data for a calculation, *i.e.*, a computational procedure, whereas in the second case, the coded input situation acts as a pointer, or address, to the appropriate entry in a table that contains the specification of an appropriate action. Since table access mechanisms themselves can require varying degrees of computation, the computation/table-lookup distinction is not sharp. It is clearest when one restricts attention to conventional computing devices in which both mathematical computation and table addressing schemes are well-defined, but becomes less clear when one considers the unknown forms of computation and addressing which might occur in nervous systems. We therefore refrain from attempting precise definitions and instead contrast these methods in a general way.

A major distinction between pure computation and pure table-lookup can be understood in terms of the way the controller's input situations are coded. In a pure computational scheme, the input situation is coded as some *pattern*, each component of which provides one of the arguments for the computation procedure. For a pure table-lookup scheme, on the other hand, an input situation appears as activity on a *single* pathway leading to the storage location which contains the appropriate action specification. Fig. 2 shows this in terms of a "decoder" which accepts a pattern-encoding of an input situation and transforms it into activity on one of a large number of pathways. We use the term "decoder" by analogy with the device used in computer memory circuits to transform each memory address into a signal on the wire connected to the physical storage cell having that address. Although the output of the decoder is clearly a pattern of activation, it is of a very

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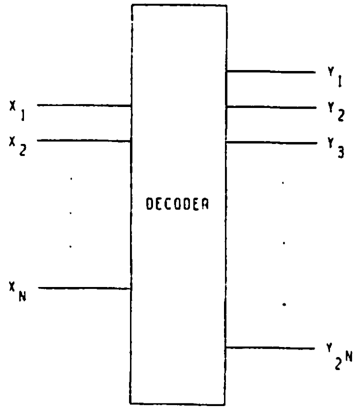

Figure 2

A binary decoder. It has N binary input channels and 2^N output channels. For each pattern of ones and zeros presented as input it selects a single corresponding output channel.

restricted form. An input situation is coded in terms of which pathway, or which storage site, is activated and not in terms of a pattern distributed over all of the pathways. While the decoding process is clearly a kind of computation which accepts patterned input, it has a simple, general structure and takes little time to complete. By a computational method we mean a process that has a complex, specialized structure and requires a sequence of computational steps.

In the case of a pure table-lookup scheme, the control surface becomes a surface in the literal, spatial sense. It has been tempting to view topographically organized neural layers as such explicit representations of control surfaces [Arbib, 1972], particularly the optic tectum [Didday, 1976]. However, one must remember that in general a control surface is a surface only in an abstract sense and that the structure and dimensionality of a control surface for motor control need have no direct relationship to the spatially organized structure of neural arrays (see [Grobstein, this volume]).

Viewed from the perspective of engineering design, pure computational and pure table lookup methods have obvious advantages and disadvantages. Table lookup methods generally yield faster response times than computational methods for equivalent tasks. Response times for tabular methods can be low irrespective of the details of the control surface, whereas the speed of a computation depends on the algorithm used, and hence on the details of the control surface. On the other hand, computational methods generally require less storage space than comparable tabular methods. The amount of space required by a computational method depends on the algorithm used, and hence on the details of the control surface, whereas the storage requirements for table lookup are uniformly large being exponentially related to the dimensionality of the control surface.

Computational and table lookup methods also differ in terms of how well they allow control surface information to be altered or "re-mapped". In the course of an animal's life, various characteristics of its motor control surfaces must change. Some changes are required because of the alteration of the mass of body parts and the lengths of limb links that occurs during growth. Other changes may be called for by the nature of specific actions, such as transporting objects of differing masses. In other words, various parameters of the control task must change. For a given control surface representation, we distinguish two types of parameters: explicit and implicit. Explicit parameters are those for which provision has already been made in the computational or storage structure. They can be viewed as input components that are distinguished only because they change infrequently or slowly. For example, symbols representing the link lengths and masses may appear explicitly in the system of equations specifying the control surface for the limb movement task described above, and a corresponding computational mechanism may have explicit inputs for altering these values when "re-mapping" is required. Explicit parameters in a table-lookup method greatly enlarge the number of table entries. For example, to make link length explicit one would need to have a separate table for each admissable length. Since computational methods for representing control surface knowledge generally do not require undue added complexity for explicit parameters, re-mapping for altered values of explicit parameters is generally easier for computational methods than it is for tabular schemes.

Implicit parameters, on the other hand, are those which determine the form of the control surface but do not appear as input components or as explicit parameters, for example, the fact that a limb has three links rather than two. Re-mapping for altered implicit parameters requires changing the algorithm used by a computational structure or changing the table entries in a tabular scheme. In either case, re-mapping involves adapting control surface specification, a topic we take up in later sections.

As mentioned above, computational and table-lookup methods for representing control surface knowledge can be combined in various ways to obtain some of the advantages of each. For example, an indexed family of computational procedures may be used in which each procedure is suitable for a given region of the space of input situations. Each table entry specifies a computational procedure, or provides parameter values to a procedure, rather than a single action (e.g. [Raibert 1977, 1978]).

Pure table-lookup becomes more computational when one considers <u>hierarchical</u> and <u>interpolating</u> tables. Hierarchical structures consist of tables that store parts of the addresses into other tables. Samuel [1959] proposed such hierarchical "signature tables" and Albus [1981] has presented a structure in which the output from high-level tables together with environmental feedback determine the entry point into a lower-level table. These methods can be helpful for reducing the exponential growth of storage requirements with increasing control surface dimension. However, memory demands may still be large, and there may not be a natural decomposition of the control surface.

Interpolating methods average neighboring table entries. A continuous space of input situations must be divided into regions that are mapped to table locations. These regions may overlap so that extraction of information corresponding to an input situation requires some process of combining the information stored for each of the regions into which the input situation falls. If the control surface is reasonably smooth, this technique can help reduce storage requirements by permitting a coarse quantization of the control

surface while retaining some degree of accuracy. Marr [1969] and Albus [1971] proposed that the granular layer of the cerebellum implements a "decoder" that is not restricted to activating a single address pathway (parallel fiber), and thus that the cerebellum, through the integrative action of the Purkinje cells, implements just this kind of interpolating table lookup representation of motor control knowledge.

4.2 Associative Memory Networks

Finally, we discuss <u>associative memory networks</u> as mechanisms for storing control information that combine aspects of computational and table-lookup methods. An associative memory network consists of a large number of processing elements that implement relatively simple primitive computations. They are therefore computational, but they compute in parallel rather than sequentially. They are also similar to tabular methods except that information can be coded in terms of distributed patterns of activity rather than in terms of specific loci, and storage "locations" may exist only in an abstract sense. Associative memory networks have been discussed by many researchers (e.g. [Amari, 1977a,b], [Anderson et al., 1977], [Kohonen, 1977], [Nakano, 1972], [Cooper, 1974], [Wigstrom, 1973], [Willshaw, Buneman, and Longuet-Higgins, 1969]) and a good overview of these structures, their applications, and their relation to neuroscience can be found in [Hinton and Anderson, 1981].

To make the nature of associative memory network storage concrete, we briefly describe one of the simplest examples known as a "correlation matrix associative memory" [Kohonen, 1977]. Suppose $X = \{X^1, X^2, \ldots, X^k\}$ is a set of input situations, or "keys", where each X^i is a vector of, say, real numbers. If we wish to associate each key X^i with some scalar control action a_i, this can be accomplished by forming a vector

$$A = \sum_{i=1}^{n} a_i X^i .$$

Retrieval of the control action associated with a key, say X^j, is accomplished by taking the inner product of A and X^j:

$$\langle A, X^j \rangle = \sum_{i=1}^{n} a_i \langle X^i, X^j \rangle .$$

Perfect retrieval of information stored in the vector A requires only that the set of vectors X is an orthonormal set. Note that one may regard the decoder used for pure table lookup (Fig. 2) as a generator of the orthonormal set of keys consisting of the standard unit basis vectors. One might therefore view the usual form of table lookup as a special case of this kind of associative memory. The unit vectors produced by the standard address decoder are orthonormal because there is no overlap of their localized nonzero values. However, vectors whose nonzero values substantially overlap can also be orthonormal such as, for example, the vectors (.5, .5, -.5, -.5) and (.5, -.5, .5, -.5).

Using such distributed but still orthonormal patterns as "keys" for storage and recall, a memory system has properties not shared by conventional lookup tables. Each entry is distributed over many physical storage locations, and each location contains the superposition of many entries. This leads to a form of generalization not possible in conventional memory systems. If a pattern were presented to the system that had not been one of the orthonormal keys used for storage, then information would be retrieved according to how similar (in the sense of the inner product) that pattern were to the keys that were used for storage. If the pattern were similar (but not necessarily identical) to a particular key, and dissimilar from all the others, then the information associated with the similar key would tend to be retrieved. For a conventional memory system, on the other hand, providing an address that is similar to, but distinct from, the desired address can yield a completely unrelated output.

The term "associative memory" is used to describe memory systems using this superposition principle and distributed patterns as keys. Interpreting this summation as neural spatial summation leads to the view that neural networks can implement this kind of information storage, with "synaptic weights" storing information and afferent patterns acting as keys. Fig. 3 shows an associative memory network, with key X, which implements a distributed lookup "table" that stores patterns Y instead of single numbers. The input lines labelled Z are used to instruct the network during the storage phase. Extensive discussion of associative memory systems and their neural

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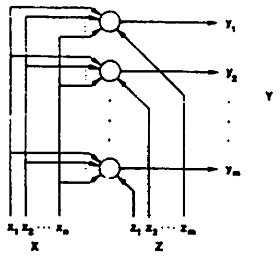

Figure 3

An associative memory network. The vector X is the input pattern or key; the vector Y is the output pattern. The lines labelled Z are used to instruct the network during the storage phase.

interpretations is provided in [Hinton and Anderson, 1981] and [Kohonen, 1977].

Associative memory networks play a dual role in the context of our present comparison of computational and tabular methods for implementing control surfaces. They are clearly computational since they require weighted sums to be formed, but they are also tabular schemes, although in a somewhat abstract sense. As pure computational schemes they can provide high reaction speed by virtue of parallel computation, but they would seem (wrongly, as we shall see) to be inadequate for even the simplest motor control tasks since they usually implement nothing more than linear transformations (possible followed by thresholding). That is, if the role of key were to be played by the "raw" input situation specification, e.g. the pattern $(X(t), X'(t), X''(t))$ for our trajectory control example, then an associative memory network such as that shown in Fig. 3 could not associate the appropriate control signals with the keys because the control surface contains essential nonlinearities when expressed in terms of these control situation variables. However, there is no reason to insist upon coordinates that arise from our own analysis of the problem. Partridge [1979] vividly makes this point: "On single nerve fibers at either the sensory or motor end, the firing rate can represent only one dimension, but that dimension involves a transformation and combination of the single dimensions usually used to describe the experimental data. If neither the input nor output operates with signals separated into the single dimensions of physics, . . . there is no obvious reason why the central processing need ever deal with the information isolated in the coordinates of our technology." (p. 221) Further, the principle of associative memory networks may be extended to include nonlinear operation [Poggio, 1975] and may be combined with more conventional computation and in hierarchical structures

in the same manner as discussed above for pure tabular representations.

Viewed as abstract versions of tabular methods, associative memory networks provide automatic interpolation, or automatic generalization, by virtue of utilizing a numerical measure of pattern similarity in retrieval. If information can be coded in such a way that this form of interpolation provides <u>correct</u> generalization, then storage requirements can be much less than for explicit tabular methods.

The general principle illustrated by associative memory networks is that of relying on structures consisting of uniform computational modules instead of special purpose computational hardware. Lack of computational generality of such structures is compensated for by the coding of control situations in terms of coordinates which lend themselves to the automatic interpolation afforded by the computational modules.

5. ACQUISITION AND MODIFICATION OF CONTROL SURFACE KNOWLEDGE

5.1 Generality vs. Generalization

The various methods discussed above for representing control surface knowledge have implications affecting methods for acquiring and modifying that knowledge. Here too, there is an important tradeoff that can be most clearly understood by contrasting pure computation and pure table-lookup. This tradeoff is between the generality of the range of information that can be acquired, or of the degree of modification that can be accommodated, and the type of generalization that can be employed to reduce the amount of experience, and hence the amount of time, required for knowledge acquisition or modification. A pure tabular method has the potential for storing very detailed and complex control surfaces since an arbitrary action specification can be stored at each table entry. It is limited only by the "grain" of the quantization used to divide the control surface into regions. The generality of a pure computational method, on the other hand, is limited by the form of the computational algorithm and its degree of parameterization. For example, if a learning process is restricted to adjusting the coefficients of a linear function of the control situation variables, then obviously only control surfaces which are linear in these variables can be formed.

The degree of constraint imposed on the set of potentially representable control surfaces by a given representational convention is directly related to the degree of generalization the convention provides. Since arbitrary entries can be stored in each location of a table, acquiring the correct contents of one table location (by means we shall discuss below) does not constrain the contents of other locations. Therefore, a learning mechanism capable of utilizing the generality of a tabular storage medium must fill in each table location separately based on knowledge acquired for the corresponding region of the control surface. Any generalization of such experience to other regions of the control surface is justified only on the basis of a priori restrictions on control surface form. For example, an interpolating tabular scheme which involves the averaging of neighboring table entries restricts the class of representable control surfaces to those which are smooth to a degree determined by the spread of the averaging function. Thus, the increase in learning speed obtained by removing the necessity to "visit" each control situation requires a priori constraints on control surface form. By virtue of imposing considerable constraint on representable control surface form, and thus considerable generalization, computational methods coupled with suitable learning algorithms can reduce the time required to acquire or "re-map" a control surface.

Any method that provides generalization can cause difficulties when that form of generalization is not correct in all circumstances. Instabilities may arise when experience in a given region A is incorrectly generalized to another region B, and subsequent experience in B leads to correction of the erroneous generalization and consequent incorrect generalization back to region A. This can occur both in computational schemes and in tablular schemes that are based on too coarse a quantization of the control space. Solutions require alterations of the form of generalization through altering the intrinsic form of the computational algorithm or altering the control situation representation (e.g. adaptively refining the grain of quantization of the input space). These problems are quite difficult and have not yielded to any uniform solution method.

5.2 Quality of Environmental Feedback

One of the most important factors affecting the design of a learning system is the quality of the information supplied to it by its environment. This information may range from explicit specification of the actions that the system is required to perform to unreliable and infrequent assessments of certain distant consequences of the system's actions. In the first case, the learning system need only remember what it is told, whereas in the second case, the system must somehow discover what actions have consequences that lead to improving assessment of performance.

Clearly, if there is a "teacher" in the environment that can tell the control system exactly what action it should take for each input situation, then "learning" is easy. For a pure table-lookup, this merely amounts to the rote storage of information, something that conventional computer memory systems accomplish very efficiently. For lookup tables implemented more abstractly as associative memory networks, the "learning" process under this high quality information is similarly rote storage. For computational schemes, this type of rote storage is generally accomplished by means of some form of regression procedure designed to adjust the parameters of a computational algorithm in order to best produce the specified actions. Some of the more sophisticated schemes for the storage of information in associative memory networks can be viewed as iterative linear regression algorithms [Sutton and Barto, 1981].

However, it is highly doubtful that this kind of teacher exists for the motor learning problems with which we are concerned here. Such a teacher would need to know, for example, how each motorneuron involved in the task should respond to each afferent volley and be able somehow to provide these motorneurons with this information. For typical motor skills, even if learning were to take place only at higher motor levels, leaving lower-level synergies fixed, it is hard to imagine where such detailed information would come from. (There are, of course, many motor tasks for which error signals <u>are</u> readily available. Reflexes provide a number of such examples, the best studied of which is the adaptation of the gain of the vestibulo-ocular reflex in response to manipulations of visual or vestibular feedback [Ito, 1982].)

A less knowledgeable teacher may know the correct control actions for just <u>some</u> of the control situations. Under these circumstances, a rote storage method that provides some form of generalization may permit correct extrapolation of the teacher's knowledge to a broader class of control situations. This type of learning problem has been extensively studied as "supervised learning pattern classification" (see, for example, [Duda and Hart, 1974]). The teacher provides the learning system with a set of input patterns together with their correct classifications (e.g., a selection of "examples" and "counterexamples" of each class), and the learning system must correctly classify these samples while extending, via its generalization capability, the classification of the samples to the set of all possible input patterns. In the context of a control problem, the input patterns correspond to patterns specifying control situations and the correct classifications correspond to the correct control action. Most of these methods are essentially iterative regression procedures that operate in real-time as classified training samples arrive. Algorithms such as that used by the ADALINE (ADaptive LINear Element [Widrow and Hoff, 1960]) are examples of these methods. They can be regarded as "error-correction" methods that adjust parameters so as to reduce the discrepancy between how they respond and how their teachers instruct them to respond. Some of these methods are also effective if the teacher's classification of even the sample patterns is unreliable. Artificial Intelligence researchers study higher-level versions of this same type of problem as "learning from examples," "concept formation," or "inductive inference" [Cohen and Feigenbaum, 1982]. Although the capacity to generalize is important for both efficient learning and storage, we do not believe that all aspects of motor learning can be accounted for by mechanisms which require such explicit information, even if it is required for only a subset of the possible input situations.

More powerful learning capabilities result from the combination of information storage methods, akin to those discussed above, with some form of problem-solving or "discovery" process. The problem-solving process determines what information needs to be stored in order to solve a given problem and provides this information to the storage medium. The role of the "teacher," then, is played by the system's own problem-solving experience. What is needed for implementing this problem-solving component is a strategy variously called "blind variation and selective survival" [Campbell, 1960], "trial-and-error search", or more recently by artificial intelligence researchers, "generate and test". This type of process generates trials whose consequences are unforseeable at the time they are generated. These trials are then evaluated and selected according to their consequences in furthering a given problem's solution. This process need only be "blind" in the sense of not knowing for sure the outcome of a trial before it is generated. Any amount of knowledge, present initially or acquired during the problem-solving process, may be used to generate trials with high likelihood of improving problem-solving performance, but true discovery requires at least some initial doubt.

A classical difficulty arises when the problem-solving process requires multiple steps for completion, as is usually the case. If success is achieved after a sequence of control decisions are made, to which individual decisions should the success be attributed (or blame, in the case of eventual failure)? Minsky [1961] called this difficulty the "credit assignment problem", and it is still a very real problem for learning systems. Perhaps the best known method for reducing the severity of this problem was implemented by Samuel in his checkers playing program [Samuel, 1959]. This method, which involves the adaptive development of a step-by-step evaluation function, is related to secondary reinforcement pehnomena in animal conditioning experiments. In Section 6.1 below a similar method is described for aiding the acquisition of a lookup table.

Learning mechanisms combining information storage with problem-solving search are probably required for solving a large class of motor learning and adaptation problems. Consider, for example, what would be required of a mechanism which is to learn the control surface for the trajectory control task discussed above while receiving only instructive information that can be determined by visually inspecting performance trials, such as the instanteous spatial error in "world" coordinates. What cannot be supplied is an instruction such as "extend the duration of activation of motoneurons in group A and diminish the duration of activity of motoneurons in group B" (where A and B are specified subsets of the motoneurons involved). The controller must use a search process to discover, via a generate-and-test process, which of its actions have as consequences the reduction of the spatial error of the movement. As these actions are discovered, they can be stored in association with a representation of the state of the limb and the task command so that eventually search will not be required in order to execute the command. A system composed only of error-correction components such as perceptrons, cannot learn to correct the spatial error unless some agency can supply individual error signals to each component. In order to do this, that agency must already know what patterns of component activity reduce the error, that is, it must already know a great deal about the operation of the controller and of the task faced.

Although it has been convenient to separate the information storage and problem-solving aspects of this type of learning in order to emphasize these roles, it does not follow that these processes need to be carried out by separate components or at separate times. In the examples which follow, neuron-like elements perform both storage and problem-solving search. Although space does not permit a thorough argument in favor of this approach, we wish to suggest that the intimate combination of these capabilities at a low level in the functional hierarchy of a learning system is important for effective learning of difficult tasks.

6. EXAMPLES OF CONTROL SURFACE ACQUISITION

In this section we provide a series of examples that illustrate many of the issues raised in the above discussion concerning both control surface representation and acquisition. The learning systems in these examples are networks of neuron-like adaptive elements which have been developed in order to explore issues in learning rather than as explicit neural models. These examples are based on a theory of associative search networks introduced by [Barto, Sutton, and Brouwer, 1981] and further developed in [Barto and Sutton, 1981], [Barto, Anderson, and Sutton, 1982], and [Barto, Sutton, and Anderson 1982]. We postpone discussion of the relevance of these examples for the acquisition and alteration of motor control surfaces until a later section.

6.1 Acquisition of a Lookup Table

This first example illustrates a control surface represented as a lookup table and its acquisition under the influence of low-quality environmental feedback (see [Barto, Sutton, and Anderson, 1982] for a complete discussion). The control task is that of balancing a pole hinged to a moveable cart (Fig. 4). the cart is free to move within the bounds of a one-dimensional track, and the pole is free to move only in the vertical plane of the cart and track. The controller can apply a "left" or "right" force F of fixed magnitude to the cart at discrete time intervals. The controller has no a priori knowledge of the cart-pole dynamics, and there is no pre-existing controller that can act as a "teacher". The controller receives a vector at each time step giving the cart-pole system's state at that instant, and if the pole falls or the cart hits the track boundary, the controller receives a failure signal, which is the only evaluative feedback provided by the environment. The controller must attempt to generate controlling forces in order to avoid the failure signal for as long as possible. It does this by constructing a control surface that assigns 'left' or 'right' to each controller input situation $(x, \dot{x}, \theta, \dot{\theta})$, where x is the position of the cart on the track, $\dot{x}$ is the cart velocity, θ is the angle of the pole, and $\dot{\theta}$ is the angular velocity of the pole. Notice that the failure signal does not directly provide the controller with an indication of what it should have done, and when it should have done it. This task is quite difficult due to the lack of a priori knowledge of the control surface and the infrequent and non-specific environmental feedback.

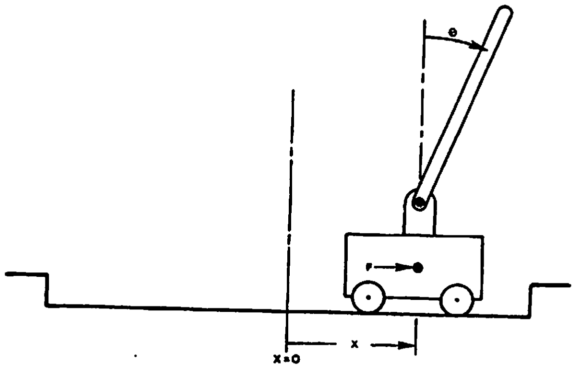

Figure 4

The cart-and-pole control problem. See text for explanation.

Much of the motivation for our solution to this problem came from a system, called 'Boxes', developed by Michie and Chambers [1968a, b]. They divided the four-dimensional space of input situations into disjoint regions ('boxes') by quantizing the four state variables. They distinguished 3 grades of position, 3 of cart velocity, 6 of pole angle, and 3 of angle velocity. This yielded 3x3x6x3=162 regions corresponding to all of the combinations of these grades. For example, one region corresponded to the cart's position being between 17 and 50 meters <u>and</u> the cart's velocity being between -2 and 2 meters/second <u>and</u> the pole angle being between 0 and 1 degrees <u>and</u> the angular velocity being between 10 and 30 degrees/second. The problem, then, is one of filling-in this lookup table of 162 entries with the appropriate control actions.

Our solution requires two adaptive elements, an Associative Search Element (ASE) and an Adaptive Critic element (ACE), each having a "reinforcement" input for evaluative feedback and 162 other input pathways for providing state information about the cart-pole system (Fig. 5). We assume the existence of a decoder that implements the quantization of the controller's input space. It has 162 output pathways, only one of which is active at a time, that act as afferents to the adaptive elements. Each adaptive element will develop a 'synaptic weight' associated with each of its input pathways. In the case of the ASE, these weights will be the entries in the control surface table, with positive weights causing a positive output (control action 'right') and negative weights causing negative output (control action 'left'). In the case of the ACE, these weights will form another table that specifies an internal evaluation function that greatly increases the speed of learning. The ACE receives the reinforcement feedback r from the external environment and uses it to construct a table of internal or "secondary" reinforcement $\hat{r}$ which it supplies to the ASE. For the pole-balancing problem, we maintain the external reinforcement r at zero until failure occurs when we momentarily set it to -1.

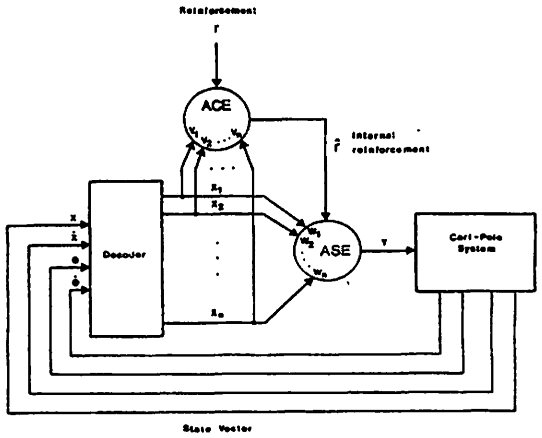

Figure 5

An adaptive network that learns to solve the cart-and-pole control problem. ASE is an Associative Search Element. ACE is an Adaptive Critic Element. See text for explanation of other symbols.

The ASE operates as follows. Let $x_i(t)$, $1 \leq i \leq 162$, denote the real-valued signal on the i^{th} non-reinforcement input pathway at time t, let y(t) denote the output at time t, and let $\hat{r}(t)$ denote the reinforcement value at time t. Reinforcement $\hat{r}$ will be provided by the ACE in such a way that positive values indicate improvement in performance and negative values indicate decrement in performance. Let $w_i(t)$ denote the value at time t of the weight associated with the i^{th} non-reinforcement input pathway. The ASE's output is determined from its input vector $X(t) = (x_1(t),\dots,x_n(t))$ as follows:

$$y(t) = f[\sum_{i=1}^{n} w_i(t)x_i(t) + noise(t)], \tag{1}$$

where noise(t) is a normally distributed random variable with a mean 0, and f is the following threshold function:

$$f(x) = \begin{cases} +1 \text{ if } x \geq 0 & \text{(control action 'right')} \\ -1 \text{ if } x < 0 & \text{(control action 'left').} \end{cases}$$

According to (1), actions are emitted even in the absence of nonzero input signals. The element's output is determined by chance, with a probability biased by the weighted sum of the input signals. If that sum is zero, the control actions 'left' and 'right' are equally probable.

The weights w_i, $1 \leq i \leq 162$, change over (discrete) time as follows:

$$w_i(t+1) = w_i(t) + \alpha \hat{r}(t)e_i(t), \tag{2}$$

where α is a positive constant determining the rate of change of w_i, $\hat{r}(t)$ is the real-valued internal reinforcement at time t, and $e_i(t)$ is the *eligibility* at time t of input pathway i. The eligibility of a pathway reflects the extent to which input activity on that pathway was paired *in the past* with element output activity. The eligibility of pathway i at time t is therefore

a *trace* of the product $y(\tau)x_i(\tau)$ for times τ preceding t. For computational simplicity, we generate exponentially decaying eligibility traces e_i using the following linear difference equation:

$$e_i(t+1) = \beta e_i(t) + (1-\beta)y(t)x_i(t), \tag{3}$$

where β, $0 \leq \beta < 1$. determines the trace decay rate. Note that each 'synapse' has its own local eligibility trace.

The basic idea expressed by (2) and (3) is that a pathway's weight changes depending on the reinforcement received during periods of that pathway's eligibility. If the reinforcement indicates improved performance ($\hat{r}(t) > 0$), then the weights of the eligible pathways are changed so as to make the element more likely to 'do whatever it did' that made those pathways eligible and, perhaps, caused the improvement. If reinforcement indicates decreased performance ($\hat{r}(t) < 0$), then the weights of the eligible pathways are changed to make the element more likely to do something else. The term 'eligibility' and this weight update scheme are derived from the theory of Klopf [1972, 1982], and have precursors in the work of Farley and Clark [1954], Minsky [1954], and others. The ASE implements the view of instrumental learning represented by Thorndike's "Law of Effect" [1911].

One reason this task is difficult is that since the external evaluative feedback occurs only after a long sequence of actions, there is difficulty in assigning credit to individual actions. The ACE reduces the severity of this credit-assignment problem by adaptively developing a more informative evaluation function than the one directly available from the learning system's environment. The ACE acts as an adaptive 'internal critic' of the learning system. It implements a method closely related to the method used by Samuel [1959] in his learning checkers playing program, and its behavior captures important aspects of animal behavior in classical conditioning experiments. Sutton and Barto [1981] extensively discuss a closely related adaptive element, and further discussion of the ACE can be found in [Barto, Sutton, and Anderson, 1982].

The ACE constructs a table of 'predictions' or 'expectations' of reinforcement whose entries are the weights associated with the ACE's input pathways. The ACE uses these predictions to determine an internal reinforcement signal as a function of cart-pole state which it delivers to the ASE, thus permitting learning to occur throughout a pole-balancing trial rather than solely upon failure. The system effectively learns how 'safe' or how 'dangerous' are the cart-pole states. It punishes itself for moving from a state to a more dangerous state, and it rewards itself for moving from a state to a more safe state. The cart-pole states act in a manner similar to secondary reinforcement of animal learning studies [Gormezano and Kehoe, in press]. The learning process automatically stops when all externally supplied reinforcement is fully predicted by the ACE.

We implemented the ASE/ACE system shown in Fig. 5, and to provide a reference point for learning performance, we implemented the Boxes system described in [Michie and Chambers 1968a, b]. The cart-pole system was simulated by digital computer using a very detailed mathematical model of the physical system. We simulated a series of runs of each learning system attempting to balance the pole. Each run consisted of a sequence of trials where each trial began with the cart-pole state $x=0$, $\dot{x}=0$, $\theta=0$, and $\dot{\theta}=0$, and ended with a failure signal. The learning systems were naive at the start of each run, and different seeds were supplied to the pseudo random number generator for each run. Runs consisted of 100 trials unless the run's duration exceeded 500,000 time steps (approximately 14 hours of simulated real time), in which case the run was terminated.

Fig. 6 shows the results of these simulations. The graphs of Fig. 6 are averages of performance over 10 runs. A single point is plotted for each bin of 5 trials giving average time-until-failure over the bin. It is clear that both the Boxes system and the ASE/ACE system were able to improve their performance with experience, with the ASE/ACE system showing dramatic

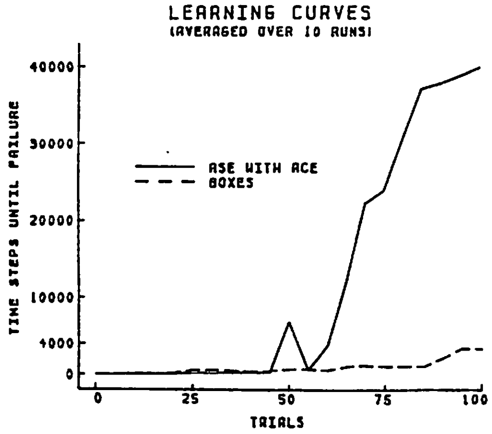

Figure 6

Network performance on the cart-and-pole task, averaged over 10 runs, compared with performance of the BOXES algorithm. Each point represents a bin of 5 trials, giving average time-until-failure over the bin, averaged over 10 runs.

improvement after about 50 trials. This improvement comes about as the ACE acquires the ability to provide internal evaluation in the absence of failure. Further details of these results are provided in [Barto, Sutton, and Anderson, 1982].

These results show how a lookup table can be acquired from experience even when no knowledgeable 'teacher' is available to specify its entries. It should be clear that such a learning system would be able to modify its existing tabular entries if various implicit parameters of the control tasks were changed, for example, if the cart mass, pole length, etc. were changed. Such an alteration would cause the system to receive reinforcement that differed from the expected level for certain cart-pole states, thereby automatically reactivating the learning process for those states.

6.2 Acquiring a Computational Control Surface

The control surface acquired in the following example may be thought of as represented either by a simple computation or by an associative memory network, depending on what aspects of the representational scheme one emphasizes. In this example, a learning system faces a simple spatial learning task which was devised by Barto and Sutton [1981] as a simple illustration of the learning capabilities of an associative search network.

Fig. 7A shows the spatial environment of a simple "organism" which is represented by the asterisk. The tree in the center of the figure is the organism's target and emits an "attractant odor" whose strength decays with distance from the tree. Each of the landmarks at the cardinal points also emits a distinct "odor", decaying with distance, which does not act as an attractant (i.e. is neutral) but can serve as a cue to location in space. The organism's task in this environment is to approach the tree as efficiently as possible and remain in its vicinity. In order to do this, it acquires a control surface that tells the organism which way to go from every place in its environment. The inputs to this controller are the patterns of "odors" from the neutral landmarks, and actions determine movement in space. Once in possession of an adequate control surface, the organism can use it to move directly to the place where the attractant peak usually appeared even in the complete absence of the attractant distribution. The organism is then able to "control" its spatial environment in the sense of being able to drive it to a desired state.

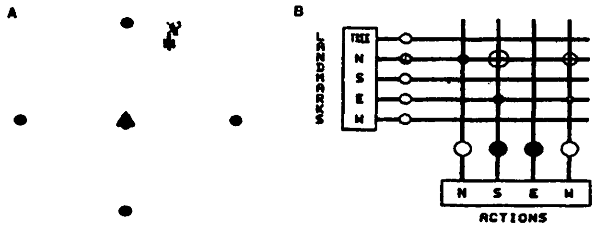

Figure 7

A. The spatial environment of a simple "organism," shown as an asterisk. The tree in the center is source of an "attractant odor" and the four disks represent landmarks which emit their own "odor" distributions, serving as cues to spatial location. B. The "organism's" "brain", a network of four adaptive elements controlling motions in the four cardinal directions. Connection weights between landmark inputs and action outputs are shown as circles centered on the intersections of input lines with adaptive element "dendrites". Positive weights appear as hollow circles, and negative weights appear as shaded circles.

The organism's "nervous system" is shown in Fig. 7B. The four adaptive elements control motions in the respective cardinal directions. Connection weights between input and output elements are shown as circles centered on the intersections of the input pathways with the element "dendrites". Positive weights appear as hollow circles, and negative weights appear as shaded circles. The size of a circle codes the weight's magnitude. The action commanded by the network is to move North if element 1 fires, South if element 2 fires, etc. We implemented a kind of crossed inhibition to ensure that if, for example, the South and North elements were both active, the organism would take a step north if the north element were more activated than the south element and vice versa. In case two non-opposing elements fire simultaneously, then the appropriate compound move is made, e.g., Northwest. We assume that each move is a fixed distance and is always completed in one time step. The control surface is to be stored as a matrix of weights connecting the neutral landmark inputs with the action-generating elements.

The problem of acquiring this control surface is similar to that of acquiring the pole-balancing control surface, and we used adaptive elements that are very similar to the ASE discussed above. Unlike that problem, however, evaluative feedback is available directly from the environment immediately after every action in the form of an indication as to whether the chosen direction of movement was up the attractant gradient or down. We therefore do not need to use prolonged eligibility traces or an ACE. In particular, $\hat{r}(t)$ in (2) is equal to $z(t) - z(t-1)$, where $z(t)$ is the attractant level sensed by the organism at time t, and $e_i(t) = y(t-1)x_i(t-1)$ (which is the result of setting $\beta = 0$ in Eq. 3).

The four adaptive elements form associations between places in space (signaled by vectors of landmark "odors") and actions leading up the attractant gradient. The weight associated with an input pathway from a given landmark to an element controlling movement in a particular direction increases if a step in that direction is taken in the presence of that landmark's signal and the resulting movement is up the attractant gradient. With sufficient experience, the organism learns to respond to the olfactory cues at each place with the action that is optimal for that place.

Fig. 8 illustrates the performance of this network. In this case, noise has been added to the attractant level in order to make the hill-climbing task more difficult. Fig. 8A shows the trail of an inexperienced organism that starts near the northern neutral landmark. It eventually remains in the vicinity of the tree. Fig. 8B shows the trail produced by replacing the

Figure 8

Example of network performance. A. The trail of an inexperienced "organism" in the presence of a noisy attractant distribution. B. The trail of the same "organism", replaced at its starting point after having undergone the experience shown in A. The network has learned how to climb the attractant gradient.

organism at its original starting point after it has undergone the experience shown in Fig. 8A. It now proceeds directly to the tree, clearly benefiting from its earlier experiences. Fig. 9A shows the network after learning. Nonzero weights have appeared so that, for example, proximity to the northern landmark causes a high probability of movement south since the "odor" of the northern landmark excites the element that causes movement south and inhibits the one that causes movement north. Fig. 9B shows the results of learning as a vector field in which each vector shows the average direction that the organism will take on its first step from any place. The vector field is the organism's map of its environment (it is never literally present in the environment). Moreover, it should be clear that the organism will follow this map even if the tree and its attractant distribution were to be removed (so long as the neutral landmarks remained). The organism has formed a control surface so that on future encounters with a similar environment, it need not perform trial-and-error search but can use its control surface to directly

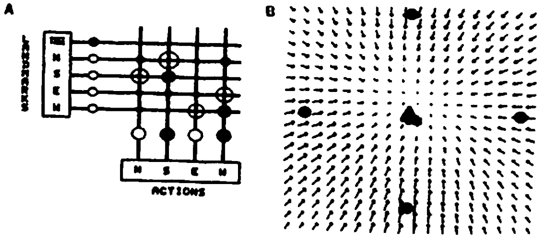

Figure 9

A. The network of Figure 7B after learning, corresponding to the behavior shown in Figure 8B. B. The results of learning shown as a vector field of the average directions that the "organism" would take on its first step from each position in the environment.

find out in which direction it is best to move. The generalization capability of the present storage method is illustrated by the fact that the control surface is defined for places never before visited by the organism. Of course, the problem faced by the organism is simple enough that this linear extrapolation turns out to be correct, but this clearly need not always be true.

Although this control surface specifies a direction of movement for each point in space, it is represented by just 16 "synaptic" weights. It is not stored as a real physical surface; the vector field shown in Fig. 9 does not literally exist as a spatial map in the network. We may regard this network as an example of an associative memory network where the role of "key" is played by the afferent patterns of "odors" and the associated "recollections" are the actions which lead up the attractant distribution, although the learning process differs from the one usually studied for associative memory networks (see Section 5.2 above).

A table lookup approach to this problem would correspond to there there being a separate landmark, with a corresponding input pathway to the network, located in each small region of space. If each landmark's "odor" could only be sensed in its own region, then the landmark "odors" would correspond to table addresses. An interpolating tabular scheme would correspond to having a landmark for each small region but letting it have an "odor" distribution broader than its own region (the storage scheme of the present example could be considered an interpolating lookup-table with 4 entries).

Let us look at an example which shows how re-mapping can occur in response to the alteration of an implicit parameter of the control problem. After the organism acquired the control surface shown in Fig. 9, we interchanged the East and West landmarks. Fig. 10A shows the vector field resulting from evaluating the old control surface in this new environment. Starting from a place near the tree, the organism is "misled" by its sensory information and follows the vector field away from the tree (Fig. 10B1). Since the movement is down the attractant gradient, the learning rule alters the weights to the East and West output elements from the input labelled East (which now responds to the landmark to the West). This relearning results in the network of Fig. 10B2 and the vector field of Fig. 10B3. A similar excursion to the east modifies the weights to the East and West output elements from the input labelled West (which now responds to the landmark to the East) as shown in Figs. 10C1, C2, and C3. The system "rewrites" its control surface, thus erasing traces of previous learning. Note, however, that the associations from the North and South landmarks remain correct for the new environment and constrain movement to a band that is narrow in the north-south direction, thereby permitting the relearning of the new map to occur faster than the acquisition of the original map. Comparison of the incorrect vector field of Fig. 10A with the correct one of Fig. 10C3 shows that re-mapping has occurred in regions of the space that were not visited in the east-west excursions. It is clear that re-mapping is made easy because the generalization produced by the storage method is suitable. If the control surface had been represented by a lookup table, then each address would have to be visited for complete re-mapping. Finally, note that transferring the re-mapped organism back to the original environment will result in the relearning of the original control surface after sufficient experience.

In the landmark-learning examples just described, we did not attempt to model the actual spatial behavior of any particular organism. It is interesting, however, to compare the behavior of our fictitious organism with that of actual organisms, and it may be an interesting topic for future

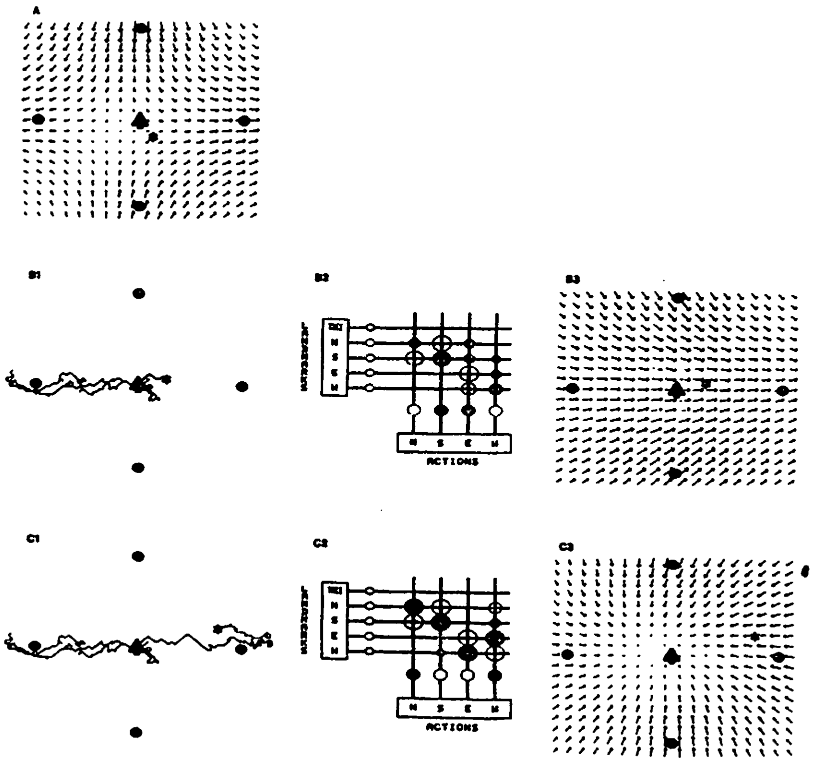

Figure 10

A. Vector field showing the behavior of the control surface of Fig. 9 in an environment in which the East and West landmarks have been exchanged. B1. Path of an organism "misled" in this altered environment. B2. The network after the experience shown in B1. B3 The corresponding vector field after the experience shown in B1. C1. Continuation of the path of B1, giving experience with the new East landmark. C2, C3. The network and vector fields, respectively, showing the control surface after the experience shown in C1; the organism has relearned its map of the environment.

research to attempt to develop realistic models of spatial learning behavior based upon similar principles. Of particular relevance is the model presented by Cartwright and Collett [1982] for how honey bees use landmarks to quide their return to a food source. These authors also present vector field representations of their models' behavior.

6.3 From Landmark Learning to Motor Control

Although the control problems of the preceding examples are far less complicated than most motor control problems routinely solved by animals, these examples can help us address, in a simple and concrete way, some of the issues that arise in realistic cases. In particular, the landmark learning example provides an easily visualized setting for some concepts that may be useful in more difficult control tasks. Recognizing that there is a wide gap between the capabilities of the landmark learning network and the capabilities required of an adaptive motor controller, let us nevertheless consider some correspondences.

If one views the spatial position of the organism in the landmark learning example as corresponding to the spatial position of a limb-tip, then the attractant level sensed by the organism might correspond to an evaluation of positioning accuracy provided by a visual system overseeing the workspace. The "odors" of the four cardinal landmarks sensed by the organism might then correspond to proprioceptive signals giving the current position of the limb in some internal coordinate system. Viewed in this way, the system has to learn for each limb position what control actions reduce spatial error. Once this is learned, the system can position the limb accurately without the aid of vision (cf. the ability of our simulated organism to approach the tree's location in the absence of the attractant distribution). One might further

regard the re-mapping in response to interchanged East and West landmarks as being analogous to the adaptation that takes place after the introduction of inverting prisms or other types of perceptual distortions.

Thus, although we have presented the landmark learning problem in terms that suggest an actual spatial environment (e.g., "odors", landmarks, etc.), many of the ideas illustrated carry directly over to more abstract "spaces" such as the state spaces of dynamical systems. Viewed in this more abstract light, a "landmark", more specifically, the "odor" distribution of a landmark, corresponds to response characteristics of a receptor. One could regard a joint receptor, for example, as an instance of a "proprioceptive landmark" in that approach to a certain joint angle would increase the receptor's firing rate. More generally, such receptors are responsive to combinations of many dimensions, as are the landmarks in the landmark learning task, and not just one. A specific combination of east-west and north-south positions defines the peak signal from one of these landmarks.

We have found the image of landmarks in state-space having "odor" distributions of a variety of shapes to be useful for thinking about the character of information that may be required for learning control tasks involving dynamic limbs. A higher density of landmarks is required in regions of complex dynamic flow; their spread functions can be arranged in order to support a variety of forms of generalization; and one can consider mechanisms for the <u>creation</u> of landmarks having appropriate characteristics by a system during its development and learning.

The landmark learning example also illustrates an important point about what types of strategies may be necessary for learning to perform certain types of motor tasks. Unfortunately, however, the landmark learning task is not sufficiently difficult to provide a vivid demonstration since the coordinate system represented by the configuration of landmarks is not essentially different from the coordinate system in which the system's actions are defined. Thus, by simply watching the movement of the organism one would obtain enough information to provide an explicit error signal to each of the network's adaptive elements - for example, if it moved northeast but should have moved southeast, then the North and South elements were wrong and the East and West elements were correct. Given this high-quality feedback, that is, a vector of individual element errors, simpler error-correction learning methods would suffice. However, although such an error vector could have been provided to the network for this task, we provided instead only a scalar evaluation of overall network performance (the attractant "odor"), and the network had to discover, via generate-and-test, which of its actions increased this evaluation.

In more difficult problems involving more complex coordinate systems, the observation of spatial movement may not yield enough information to provide the action-generating mechanism with this type of error vector. This would be true in a trajectory control task since it would not be obvious what component actions lead to reduced error. A learning mechanism having properties similar to the one illustrated by the landmark learning problem would be necessary in order to discover what actions increase accuracy.

Obviously this discussion omits many important aspects of limb control — higher level planning, proprioceptive feedback, and compliant motion, to mention only a few — but it illustrates why the most widely studied learning methods are probably inadequate, by themselves, for many of the learning tasks that occur in the motor control domain.

7. CONCLUSION

We have shown in the context of a simple trajectory control example how a control surface is determined by the nature of a task and the abilities of an effector system. We have compared alternative representations for control surfaces, emphasizing the trade-off between table lookup and computation and considering in some detail an associative network representation that lends itself to the acquisition and adaptive modification of control surfaces by trial-and-error learning. We have discussed several potential advantages of associative search networks in representing sensorimotor control surfaces, including (1) a generalization capability that reduces memory requirements and facilitates acquisition and re-mapping of control surfaces; (2) a search or problem-solving capability that permits learning even when environmental feedback is of poor quality; and (3) a simple, uniform computational structure that seems a natural candidate for neural implementation. Whether nature herself appreciates these advantages is, of course, a matter for future research.

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Chapter 4: Detour Behavior and Depth Perception

Thomas Collett and Susan Udin: THE ROLE OF THE TOAD'S NUCLEUS ISTHMI IN PREY-CATCHING BEHAVIOR

Michael Arbib and Donald House: DEPTH AND DETOURS: TOWARD NEURAL MODELS

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The Role of the Toad's Nucleus Isthmi in Prey-catching Behavior

T.S. Collett and S.B. Udin

INTRODUCTION

Frogs and toads are renowned for their well-developed ability to catch small moving objects such as flies and worms. The most prominent of the brain structures which mediate this behavior is the optic tectum (Ingle, 1970). The tectum receives visual input and transforms it in ways which are ill-understood, to produce output which is ultimately used to direct the animal to orient toward and/or snap at a prey object. Successful prey-capture requires that the animal be able to gauge the distance of targets and be able to orient accurately to one object even when several are in view. We have examined how well the toad, Bufo marinus, performs these tasks when the tectum is deprived of one set of its inputs, the projections from the nucleus isthmi (NI).

The nucleus isthmi relays visual information between the two tecta (Gruberg and Udin, 1978; Grobstein et al., 1978). (See Fig. 1.) This link provides the major source of input from each eye to its ipsilateral tectum. The projection onto each tectum of the ipsilateral eye's visual field through the isthmic nucleus is in register with the direct retinal projection of the visual field of the contralateral eye. The two projections could, in principle, provide tectal cells with information for calculating binocular disparities. Therefore, we tested whether toads with lesions of the nucleus isthmi still use binocular cues to assess the distance of their prey. As we describe below, we found that this aspect of behavior was not disrupted by bilateral NI lesions. Our second set of experiments investigated a possible role of the NI as providing a link between the two tecta, to help ensure that both tecta "focus" on the same single object in the visual field, even

when two or more potential targets are visible. We will show that bilateral lesions of the NI can impair the ability of toads to snap successfully when two targets are present simultaneously.

METHODS

Lesions.

Bufo marinus, 10-13 cm snout-to-vent, were selected on the basis of their willingness to snap at artificial lures. Animals were anesthetized by immersion in 200 ml of 0.25% tricaine methanesulfonate (Ayerst); optimum results were achieved by immersing an animal for 15 minutes, removing it for 10 minutes, reimmersing for 15 minutes, and so forth until the corneal blink reflex was abolished. The tectum was exposed and the animal was positioned with the upper jaw horizontal. The nucleus isthmi was located by inserting a metal-filled pipette, plated with gold and platinum, through the caudal tectum to a depth of 1.5-2.0 mm, where visually evoked activity characteristic of the NI was recorded. NI units respond to light on-set and off-set [illegible] and [illegible] habituate after 2-3 stimulus repetitions (Gruberg and Lettvin, 1980). Between 6 and [illegible] lesions were made in the vicinity of each NI by passing 10 μA of current for 60-90 seconds with the electrode tip negative.

Histology.

At the conclusion of behavioral testing, brains of most experimental animals were examined histologically to assess the completeness of the lesions. Some brains were fixed, paraffin-embedded, sectioned at 10 um, and stained with cresyl violet. In later experiments, horseradish peroxidase was applied in solid form to one or both tecta. Three days later, the toads were perfused with saline followed by 2.5% glutaraldehyde in 0.1 M phosphate buffer. The brains post-fixed for 2 hours, rinsed in buffer, and sectioned in the horizontal plane. Mounted sections were reacted using benzidine dihydrochloride (Riley and Marchand, 1979).

Behavioral methods

A perspex holder was permanently mounted on the top of each toad's head and various spectacles screwed to it during testing. Toads were tested in a black painted 3 ft square arena with a video camera and floodlight mounted above, facing directly downwards. Toads snapped at yellow cylinders fixed to lengths of black-painted wire. These were hand-held and moved in a frontal plane close to the toad's midline. Animals were sometimes reluctant to respond to dummy prey and were coaxed for several days with meal worms fixed to the cylinder. It usually took several weeks to complete a series of tests on each toad.

The animals' responses to the dummy were recorded on videotape at 50 frames-sec^{-1} and later analysed frame by frame. Most measurements were taken directly off the screen of the video monitor, though sometimes responses were traced on to acetate sheeting.

Computer model

A highly simplified model of tectal-isthmic interactions was simulated in Basic on a Digital Vax computer, using a series of one dimensional isotropic arrays of 280 elements to represent each retina, tectum and isthmic nucleus. To minimize boundary effects, visual inputs were restricted to the 40 elements in the center of the array. Visual inputs were punctate, i.e., they were restricted to one element. They were specified in terms of their amplitude and position on the array. Excitation spread laterally through the array, decaying linearly with distance from the input position. Recurrent lateral inhibition was introduced in the tectal array. The level of inhibition caused by a given element was proportional to the level of

excitation in that element and spread laterally decaying with distance. Thus the level of inhibition in any given tectal element depended both on the level in that and surrounding elements. The level of excitation in each tectal element was not allowed to drop below zero. The input to each isthmic array reflected the level of excitation in the tectal array on the same side. The output of the isthmic array had an inhibitory effect on the level of inhibition in the opposite tectum. Each element of the isthmic array distributed its activity maximally to the corresponding element of the opposite tectum and less strongly to other elements, by an amount which decayed linearly with distance. When the model was given a particular pattern of inputs, it ran through several iterations and we simply watched the visual display to see how activity was distributed over the tectal array.

RESULTS

Single targets

Anurans have two cues at their disposal for judging depth: the monocular cue of accommodation (Ingle, 1972) and a form of stereopsis (Collett, 1977). Our first question was: does the nucleus isthmi play a role in measuring binocular disparities? Lesioned animals both oriented normally towards distant targets and snapped correctly at close ones. Their accurate estimation of distance could be the result either of monocular or of binocular information. In order to find out whether binocular cues persist after NI lesions, it is necessary to dissociate them from monocular ones. The prey catching behavior of lesioned toads was therefore tested when the animals viewed their prey either through prism spectacles, which change binocular disparities, or through concave lenses, which alter the accommodative state of the lens. In both cases there is a conflict between the information available from accommodative and disparity measurements.

Lesioned toads resembled unoperated controls in that their depth judgements reflected the binocular rather than the monocular information they received. Thus they undershot their prey when wearing base-out prisms (Fig. 2 and 3). And, though they underestimated distances when viewing prey monocularly through a concave lens, they did not misjudge prey distance, or did so to a much smaller degree, when vision was binocular (Fig. 4). We conclude that lesioned toads like normals exploit binocular depth cues when those cues are available.

If we neglect for the moment other binocular inputs which might contribute to disparity measurements, we are led to a model of binocular depth vision which owes more to the mantid (Rossel, 1980, 1983) than to the mammal. The tacit assumption has been that anuran binocular vision resembles that of mammals: the output of local disparity detectors is used to construct a depth map. In the mantid, binocular cues are used to measure prey distance over a range of a few cm, even though there is not a rich network of binocular connections to mediate local disparity measurements. The problem then had to be faced: what alternative methods might there be of exploiting binocular disparities? One technique is to compare the output signals from the two eyes (Fig. 5).

Suppose, reverting now to toads, that the left eye sees a target along a line of sight 10° to the right of some retinal reference point and that the right tectum generates an output signal corresponding to that retinal image. Suppose also that the same target falls upon a line of sight in the right eye 10° to the left of its retinal reference point and that the left tectum produces an output signal appropriate for that line of sight. Then, the mean of the two tectal output signals will give an orientation command related to the position of the target with respect to the animal's body axis, in this

case straight ahead. On the other hand, the difference between these two signals will be proportional to the distance of the target from the animal.

If we restrict our discussion to prey capture, then the behavior of lesioned toads lends support to a scheme of this general kind, as does the behavior of normal Bufo marinus wearing prisms which alter the apparent vertical as well as the horizontal position of their prey. Figure 6 shows the snapping response of two toads viewing dummy prey through prisms which are base-out but which are also rotated, so that the left eye looks 6.5° upwards and the right eye downwards by about the same amount. It is clear from the results displayed in Fig. 6 that this large vertical disparity does not interfere with binocular depth judgements. However, it is hard to believe that conventional small-field disparity detectors would function properly under such conditions, for the receptive fields plotted through the two eyes have roughly the same vertical positions (von der Heydt et al., 1978). However, this manipulation should not disrupt the working of a system which compares the output signals of the two tecta.

Double targets

Such a system will be fine when there is only one target in the visual field. But, as with all steroscopic mechanisms (e.g. Marr, 1982), there will be problems when the visual field is more cluttered. With two targets, for instance, some trick is needed to ensure that the two tecta agree to attend to the same target in the outside world. Figure 7 illustrates what has come to be known as the "correspondence problem". The toad might respond to one of the two targets by combining appropriately the signals to the two eyes coming from the same real target. Alternatively, if it matches the left target image through the right eye with the right target image through the left eye, the motor command will be appropriate to neither. It will lead the toad to catch a "ghost" situated between the two real targets and much closer than either. The apparent distance of the ghost is given by the expression:

$$\text{apparent distance} = \frac{0.5\ \text{eye separation} \times \text{target distance}}{0.5\ \text{eye separation} + 0.5\ \text{target separation}} \qquad (1)$$

To investigate whether the nucleus isthmi might play a role in exorcising ghosts, we tested normal and lesioned toads with two identical targets which were moved synchronously in a frontal plane and which were positioned so that one target was to the left, the other to the right of the animal's midline. Target separations were 7.5, 11.3 and 16.5 cm.

Lesioned toads often snapped at one target or the other, but they would also snap at a ghost in the middle. When they aimed at one of the real targets, the distance at which they snapped was appropriate for that target, and when they aimed midway between the two they undershot the distance of the real target (Fig. 8A). In the latter case the slope of the relationship between snapping and target distance roughly conformed to that predicted by expression (1), though the intercept was greater (Table 1). One conclusion we wish to draw from this result is that with several potential targets (real and ghost) in the toad's visual field the toad picks just one of them, and that both its orientation and distance commands are appropriate for that target. It need not have been that way. The toad might, for instance, have oriented towards a real target but extended its tongue by an amount appropriate to a ghost image. In terms of the tectal output hypothesis this means that with several potential targets imaged on one retina, just one of them is selected to generate a tectal output signal which contributes to both distance and orientation commands.

Lesioned toads were also tested when they viewed double targets through concave lenses. Ghosts were seen at the same distance as they were without spectacles (Fig. 8), indicating that the response to ghosts does not depend

on the accommodative state of the eyes. However, when wearing such spectacles, toads also underestimated, but to a smaller degree, the distance of real targets, a fact which at present we do not understand.

Normal toads behaved differently. When tested with double targets, but without spectacles, they *always* aimed at real targets and snapped at the correct distance. *Rana pipiens* and *Bufo viridis* were also tested with the same double targets and were never seen to snap at anything but real targets. *Bufo marinus* usually aimed at real targets when wearing spectacles, and again snapped at the correct distance (Fig. 9). This result is interesting in itself, for it shows that anurans can use binocular cues, not only to measure the distance of targets on the midline, but also of targets positioned at least 20° either side of it.

However, normal animals in spectacles sometimes aimed at ghosts, in which case (Fig. 10), they undershot a little less than the lesioned animals. The slope of the line relating snapping distance to target distance was greater than that predicted by the apparent position of the ghosts (Table 1). We will come back to this finding in the Discussion. We should emphasize that normal animals wearing concave lenses do not readily snap at ghosts. Some animals never did, and those that did became less and less willing to do so as testing continued. Although it is difficult to give a reliable, quantitative estimate, normal animals snapped at ghosts less frequently than lesioned ones.

Completeness of lesions was judged by several criteria. The normal NI has a distinctive structure, with a cell-dense outer cortex and a cell-sparse medullary region containing tecto-isthmic terminals and isthmic dendrites (Fig. 11A). In the best cases, this structure was completely obliterated, leaving only a glia-filled region. Most of the right NI of B16 was destroyed in this way (Fig. 11B). In some cases, the NI was still identifiable, but was shrunken, with a greatly reduced neuropil,and contained many glia. Most of the left NI of B16 had this appearance (Fig. 11C). In other cases, the NI was predominantly intact, but lesions lateral to the structure had severed many of the fibers running between the tectum and the NI. This disconnection was obvious in cases where HRP was injected in the tectum; transport was blocked at the lesion (Fig. 11D).

Using these criteria, the lesions in B7 and B16 were judged to have destroyed, damaged, or disconnected most of both NI's. Histological preservation of B8 was inadequate for assessment of lesions. In B19, only minor damage was visible in either NI; lesions were observed primarily in caudal tectum. However, in B19, as in the other toads, the functional disruption produced by the lesions was probably significantly greater than the morphology would suggest.

DISCUSSION

Our results suggest that the nucleus isthmi is not essential for the binocular assessment of distance, but that it may play a role in a toad's ability to select a single target when several are present in its visual field. We present here a speculative model of what the nucleus isthmi does. If we assume that each of a set of targets produces a peak of activity in each tectum, then the problem of selecting a single target can be reformulated as follows. First, when there are multiple peaks in each tectum, the position of only one of these should influence the amplitude of the toad's snapping or orienting response. Secondly, to avoid being fooled by ghosts, the peaks selected in the two tecta should match, that is they should represent the same real target.

As has been suggested before (Didday, 1976), a plausible mechanism for suppressing all but one peak of activity is to use a lateral inhibitory network. With this idea, we devised a model which simulated a one dimensional tectal array. Excitatory activity at any point on the array was associated with a level of inhibition within the array which spread outward from that point, decaying linearly with distance. This inhibition caused the largest peak to suppress the rest. The level of activity in one tectum was also influenced by the level of excitation in the other by way of the nucleus isthmi. This nucleus links regions of the two tecta which look at the same relatively distant point in space, and in analogy to mammalian usage we call the surface in space containing these points the horopter. The intertectal pathway inhibited the lateral inhibitory network in such a way that excitation at a point in one tectum had a disinhibitory effect which was greatest at the corresponding point of the other and decayed outwards from it. The structure of the model is shown in simplified form in Fig. 12.

When the model was tuned, it behaved roughly as we had hoped. With two targets at the same distance, the model selected the one which generated the higher level of tectal activity. With two targets at different distances from the toad, the model selected the one closer to the horopter. This happens because the target closer to the horopter produced peaks in each tectum which reinforced each other via the intertectal pathway and so suppressed the smaller peaks corresponding to the other one.

The network will not always succeed in picking out real targets. With some pairs of targets it will tend to respond to ghosts, emphasizing peaks in the two tecta which correspond to different targets. The form of the intertectal connections means that such mistakes will occur when the ghost target is close to the horopter. Figure 13 illustrates this by showing two targets and two potential horopters. When distance "g" is less than "r", the model will choose ghosts, and when "r" is the shorter it will pick real targets. For the particular targets shown in Fig. 13 a model with the horopter near to the toad would see ghosts, whereas one with the more distant horopter would aim at one of the real targets. It is intriguing to ask where the horopter should be located in order to minimize the probability of responding to ghosts.

To answer this question, we computed how often toads would aim at real targets and how often at ghosts by measuring "g" and "r" with the horopter located at different distances from the animal. The "toad" was assigned a 3 cm eye separation and viewed a pair of targets in a frontal plane. The distance between the targets was varied between 5 and 70 cm in steps of 5 cm. The position of the targets was shifted systematically through the binocular field and the separation between them grew from 1 cm in 1 cm steps until the boundary of the binocular field was reached. This procedure yielded a total of some 50,000 different target positions and separations distributed evenly within the frontal binocular field. The performance of the model was assessed in terms of how often real targets were chosen in preference to ghost ones (number of real targets chosen/number of host targets chosen). Fig. 13 plots this ratio versus the distance of the horopter for all 50,000 choices and shows that the horopter should be positioned some 60 cm from the animal to yield the greatest number of real targets. The optimal placing of the horopter depends on the range of distances in which the toad is interested. If the range is somewhat smaller, from 5 to 50 cm, the horopter should be shifted to a position 45 cm from the toad.

Few ghosts were selected with wide target separations. Indeed with a 60 cm horopter and with separations of 5 cm or more only 5 ghost images were selected out of more than 40,000 choices (with the horopter at 25 cm, the number of ghosts is 2.3 thousand). Many more ghosts were picked when the

target separation was less than 5 cm. Figure 13C plots the ratio of real targets to ghosts against the position of the horopter for such small separations. It is clear that this mechanism is then not a reliable method of discriminating real targets from ghosts.

In one respect this model behaves very differently from real toads. Animals with a choice between a near and a distant target typically select the near one; the model on the other hand will always pick the target nearest to the horopter. However, the model can be brought closer to reality by including effects generated by lens accommodation. The lens moves back and forth in the eye to focus the image of a target on to the retina. Only one depth plane at a time can be in focus, and if we suppose that accommodative scanning in the two eyes is yoked, then both eyes will tend to focus on the same object in space. If we also suppose, as is certainly true for some tectal cells, that cells respond more vigorously to focussed than to unfocussed images, then peaks of activity in the two tecta representing the same focussed image will be larger. These peaks will suppress the rest, and because they represent the same target, will automatically lead to the elimination of ghost images. Furthermore, if the toad scans with its lens from close to far distances and locks on to the first target which it detects, or if it scans near distances more often than far distances, or spends more time accommodating near distances, it will tend to snap at near targets in preference to distant targets. This mechanism would work best over the relatively short range of distances within which accommodative effects are powerful. On the other hand, the selective action of the isthmic pathway works best for more distant targets closer to the horopter. Between them these two mechanisms should be able to dispose of ghost images over a wide range of distances. However, the accommodative mechanism will not eliminate ghosts when two real stimuli are presented at the <u>same</u> distance from the toad, as we have done in our experiments.

The elimination of ghosts and the preference for close targets depends solely on the way accommodative scanning is performed and no explicit distance signal related to accommodation is required. This is not, of course, to suggest that accommodative distance signals are not available for other purposes. This model is very different from that of House (1982). He described how a combination of accommodative information and local disparity measurements could be used to construct an unambiguous 3-d representation of the animal's environment. In his model, accommodation provided a coarse map of depth which interacted with a second depth map based on disparity cues. The scheme we have suggested is far more limited in scope and is concerned with how a toad might select one out of several targets in order to respond to it. Information about the other targets is discarded.

Lastly, our model suggests why it should be that the ghosts of normal animals are further away than those of lesioned ones. Lateral inhibition within the tectum means that the largest peak in the tectum suppresses the rest. There is, however, a threshold difference in amplitude, such that if peaks are initially almost the same size, several of them can survive. The crossed tectal disinhibition weakens the lateral inhibition and in doing so increases the amplitude difference which is needed for one peak to be suppressed. Consequently, starting with two peaks of approximately equal size in each tectum, there is a greater chance in normal than in lesioned toads that both will survive the action of the lateral inhibitory network. In primates, an analogous situation leads to a tectal output signal which is a compromise between the two inputs (Robinson, 1972). If toads also produce an output signal which reflects the positions of both peaks, and if the compromise is biased towards the more nasal of the two targets, then the position of the ghost would be as we find it (Fig. 14).

In conclusion, we suggest that the lesions of the NI destroy a major pathway for information flow between the two tecta. Thus, it seems more appropriate to consider the NI primarily as a tecto-tectal link rather than as a link from the eye to the ipsilateral tectum, even though both of these descriptions are consistent with the anatomy. We have seen that our first approach to the role of the nucleus isthmi focused mistakenly on the possible part it might play in detection of disparities. This job could be more economically and rapidly performed by a *direct* ipsilateral retino-tectal projection. In fact, some salamanders which catch very rapidly moving prey *do* have substantial direct ipsilateral retino-tectal projections (Rettig and Roth, 1982); perhaps this extra projection (which is absent or very sparse in most amphibians) aids the salamanders' depth judgements. In mammals, too, the tectum receives *direct* input from both eyes and also participates in a tecto-parabigemino-tectal relay which is homologous to the amphibian tecto-isthmo-tectal relay (Graybiel, 1978). We suggest that the *direct* ipsilateral projection from the retina and the *in*direct ipsilateral projection from the parabigeminal do not perform the same functions. Rather, the parabigeminal in the mammal may help to coordinate the activities of the two tecta, a task for which the direct ipsilateral retino-tectal fibers are less well suited.

TABLE 1

REGRESSION COEFFICIENTS OF RELATION BETWEEN TARGET AND SNAPPING DISTANCE

		Double Targets. Separation:			
		7.5cm	11.3cm	16.5cm	Single Target
Slope assuming response aimed at ghost		0.286	0.209	0.154	1.0
Controls	Toad 1 (-136 specs)	0.562	0.520	0.258	
	All (5) "	0.676	0.532	0.324	0.766
Lesioned	Toad B7 (-136 specs)	0.433	0.274	0.152	0.137
	B8 (-136 specs)	0.283	0.244	0.167	0.248
	B16 (-136 specs)	0.540	0.284	0.119	0.713
	B19 (-136 specs)	----	0.285	----	0.765
	B19 (no specs)	----	0.301	0.152	----
Slope assuming response aimed at target		1.00	1.00	1.00	
Control	Toad B5 (Specs)		0.759		
	Toad B3 (Specs)			0.746	
Lesioned	B16 (Specs)	0.679	0.214	0.163	
	B19 (No Specs)		0.788		

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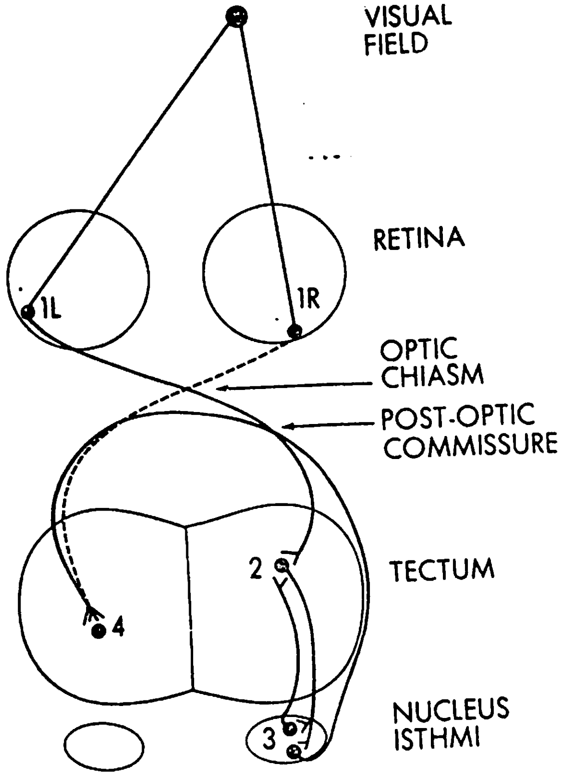


Figure 1. Schematic diagram of the neural pathways underlying ipsilateral oculotectal projections. A locus in the binocular visual field is viewed by position 1L in the left retina. Retinal ganglion cells at position 1 project directly to position 2 on the right optic tectum. This tectal site projects in turn to position 3 in the right nucleus isthmi. (The NI is actually ventral to the tectum but here is shown caudally for clarity.) Cells at position 3 in the right NI project back to position 2 on the right tectum, where they terminate in the same superficial layers where the retinal axons terminate. Other fibers leave NI position 3, run along the optic tract, decussate in the postoptic commissure, and reach position 4 in the opposite tectum. They terminate in 2 laminae near the inner and outer edges of the retinal terminal zone (Gruberg and Udin, 1978). Retinal fibers from position 1R in the right eye also project to position 4.

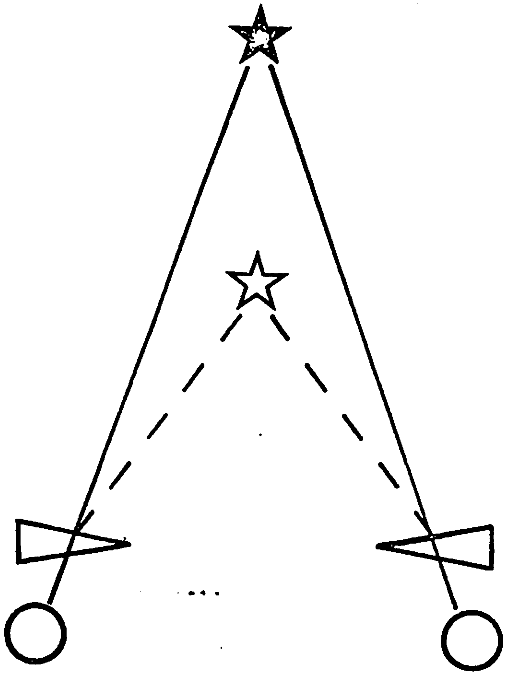


Figure 2. Base-out prisms alter binocular cues. Dashed lines indicate the apparent line of sight of the target.

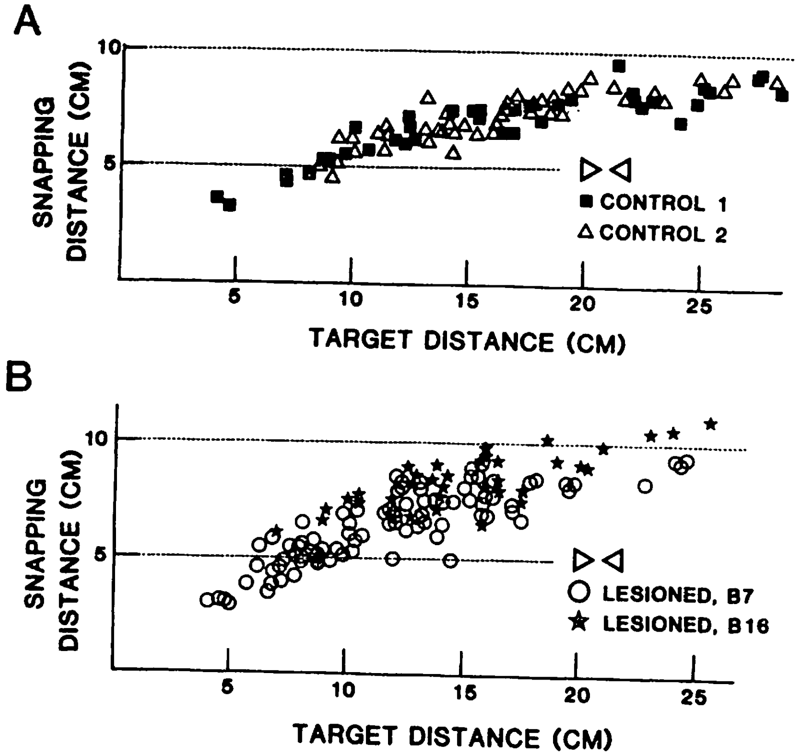


Figure 3. Snapping response of two normal toads (a) and two toads with lesions to the nucleus isthmi(b) when viewing single dummy prey binocularly through a pair of base-out prisms. Each prism displaced the target by 7.5°. Target distance is defined as the distance between the toad's eyes and the target just before it snaps, and snapping distance is defined as the distance between the toad's eyes before it snaps and the furthest point the tongue reaches.

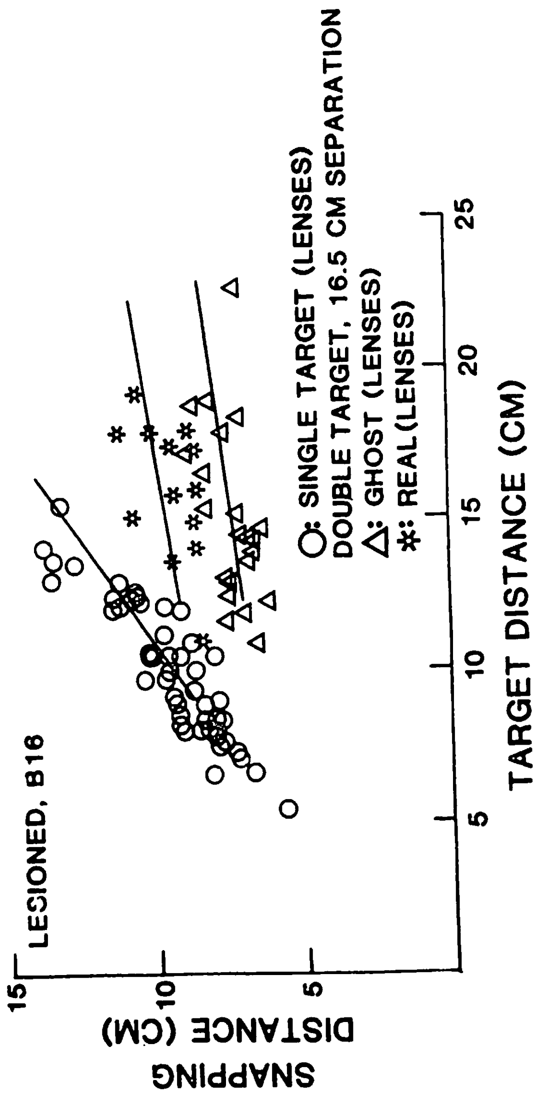


Figure 4. Snapping response of lesioned toad when viewing prey binocularly through -136 mm focal length lenses. Circles: tests with single dummy prey. Triangles and stars: double prey separated by 16.5 cm. Triangles: responses aimed at ghost. Stars: responses aimed at real targets. When tested with single targets the toad judges distance correctly, indicating that binocular cues persist despite large lesions in nucleus isthmi. Not all lesioned toads behaved as normally when viewing single target binocularly through lenses. B7, for instance, undershot considerably.

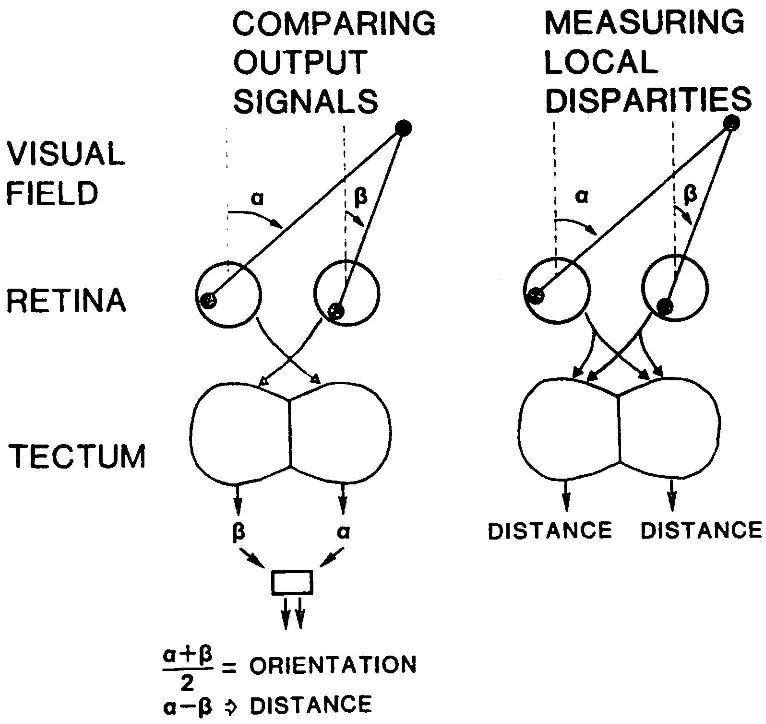


Figure 5. Two hypothetical methods of computing distance from binocular disparity. a: comparison of output signals. Toad measures position of target seen through each eye with respect to retinal reference points and then takes the mean of the signals to compute the orientation of the target with respect to its midline and the difference to derive a signal related to the distance of the target. In this case distance is computed using output signals from the two tecta. Animals with one tectum can also orient to fixate prey and may use monocular depth cues to transform a retinally related signal to one specified in head-centered coordinates. b: depth from local disparities. Since toads do not converge their eyes, horizontal disparities can be turned directly into absolute measurements of distance.

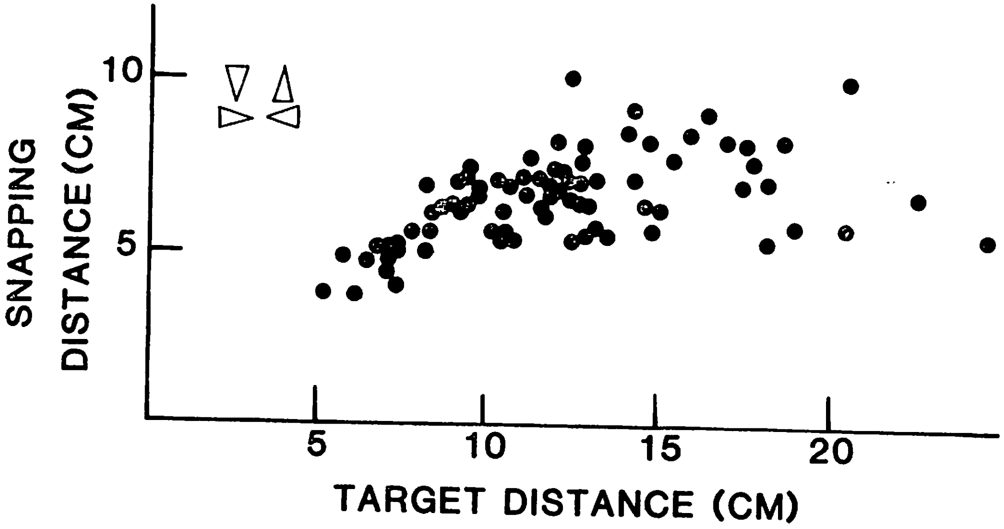


Figure 6. Snapping responses of two normal toads viewing single dummy prey objects through prisms which displaced targets both vertically and horizontally. Images in the left eye were displaced upwards by 6.5° and to the right by 5.5°; images in the right eye displaced downwards and to the left by the same amounts. Toad continues to use binocular cues to catch prey along its midline despite substantial vertical disparities.

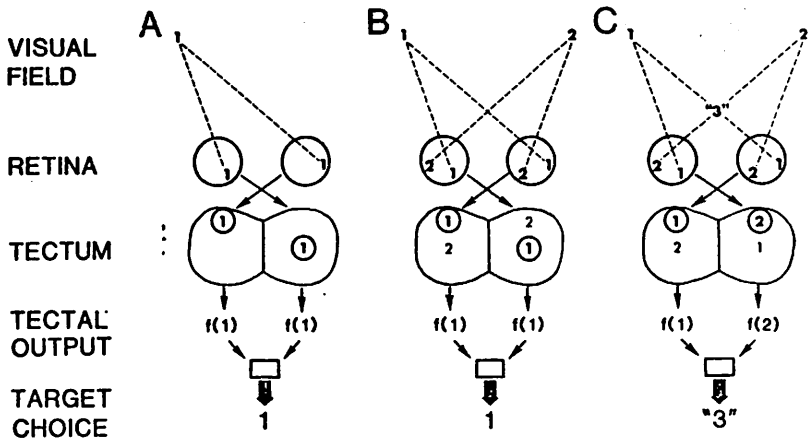
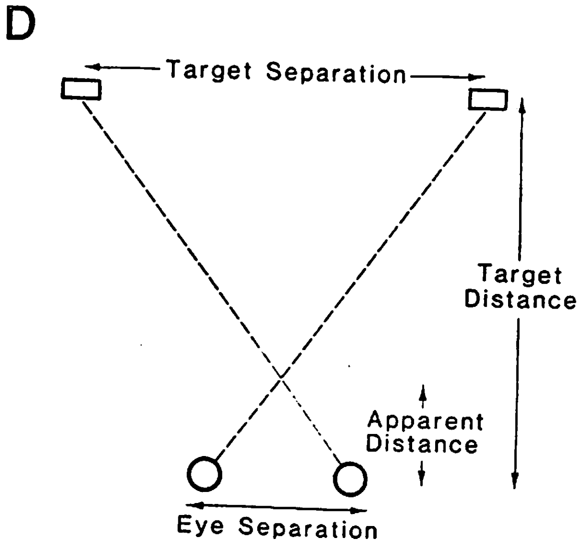


Figure 7. Double targets and the correspondence problem. A-C: If the toad matches the image of the left target through the right eye with that of the left target through the right eye, the fused image will represent neither real target but a ghost located between them and much closer than either.



D: Definition of distances for expression (1).

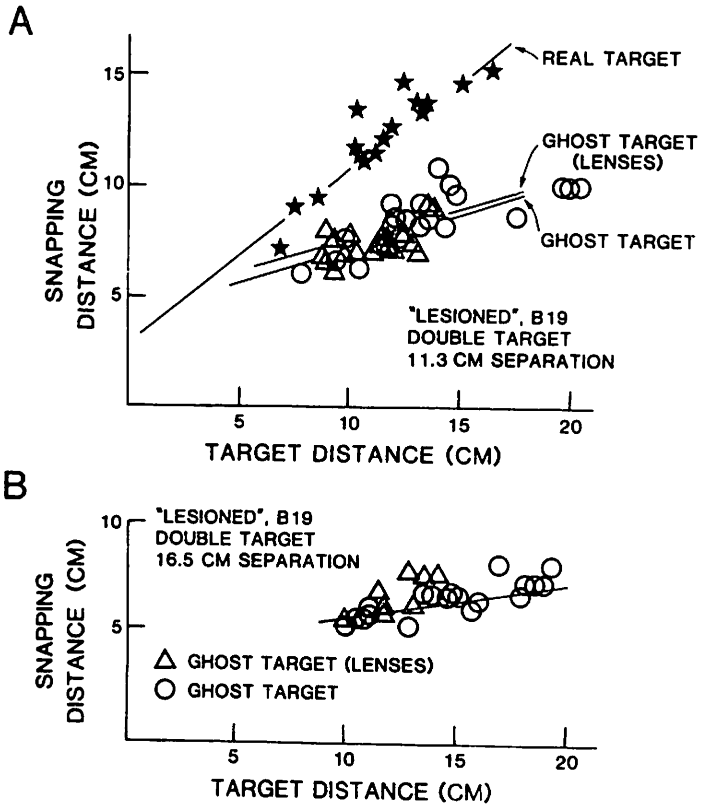


Figure 8. A: Snapping response of lesioned toad to double targets separated by 11.3 cm. Stars: responses aimed at real targets. Circles and triangles: responses aimed between targets (i.e. at ghosts). Triangles: prey viewed through -136 mm focal length lenses. The toad judges distance correctly when aiming at real targets and undershoots when aiming between them. B: Double targets separated by 16.5 cm. Line shows least squares fit to circles.

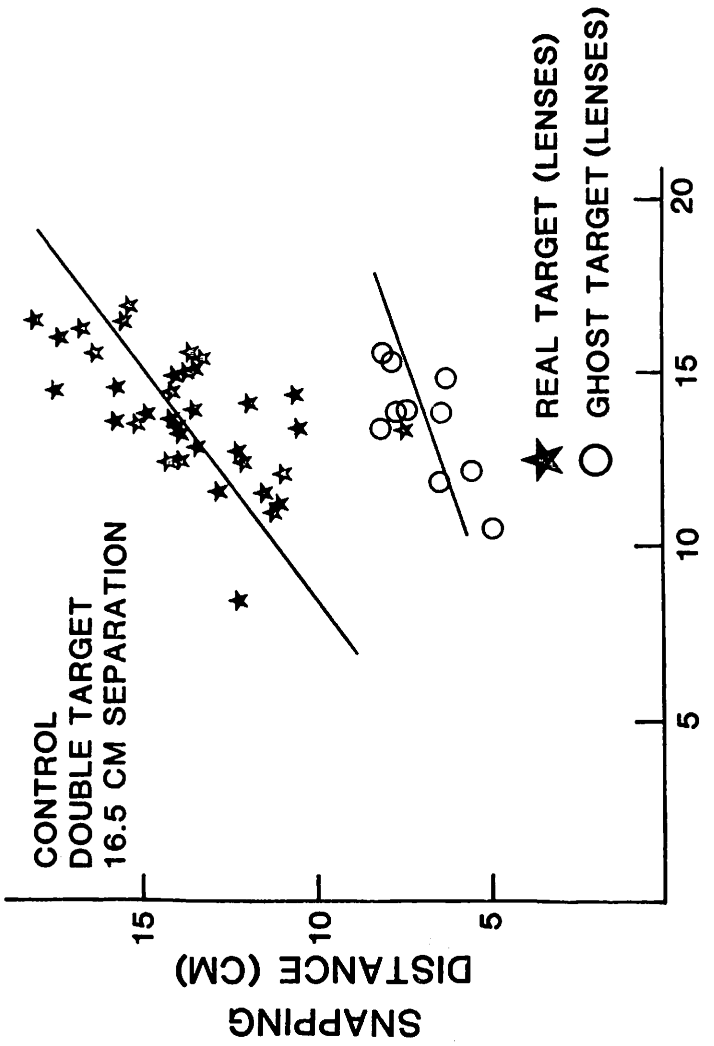


Figure 9. Normal toad viewing double targets binocularly through -136 mm focal length lenses. Real targets are 20° away from the toad's midline and responses aimed at them are normal, indicating that binocular cues are used for judging the distance of off-axis as well as on-axis targets. Responses aimed between targets fall short of the target plane.

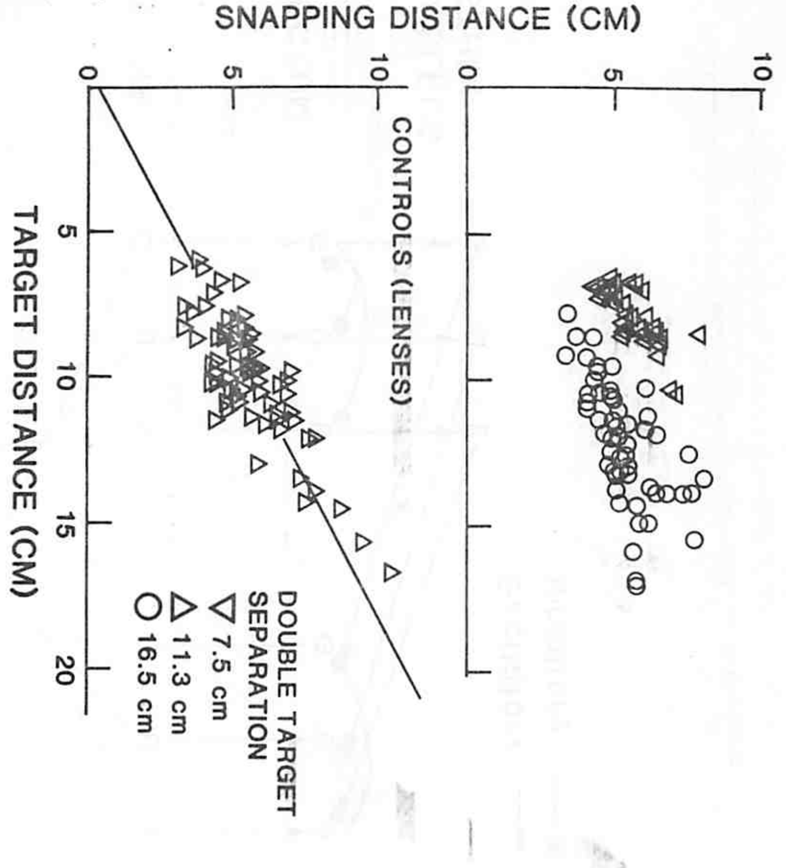


Figure 10. Relationship between target and snapping distance for 5 normal toads viewing double targets binocularly through -136 mm focal length lenses and aiming between them. The slope of the relationship between snapping and target distances is greater for normal than for lesioned toads.

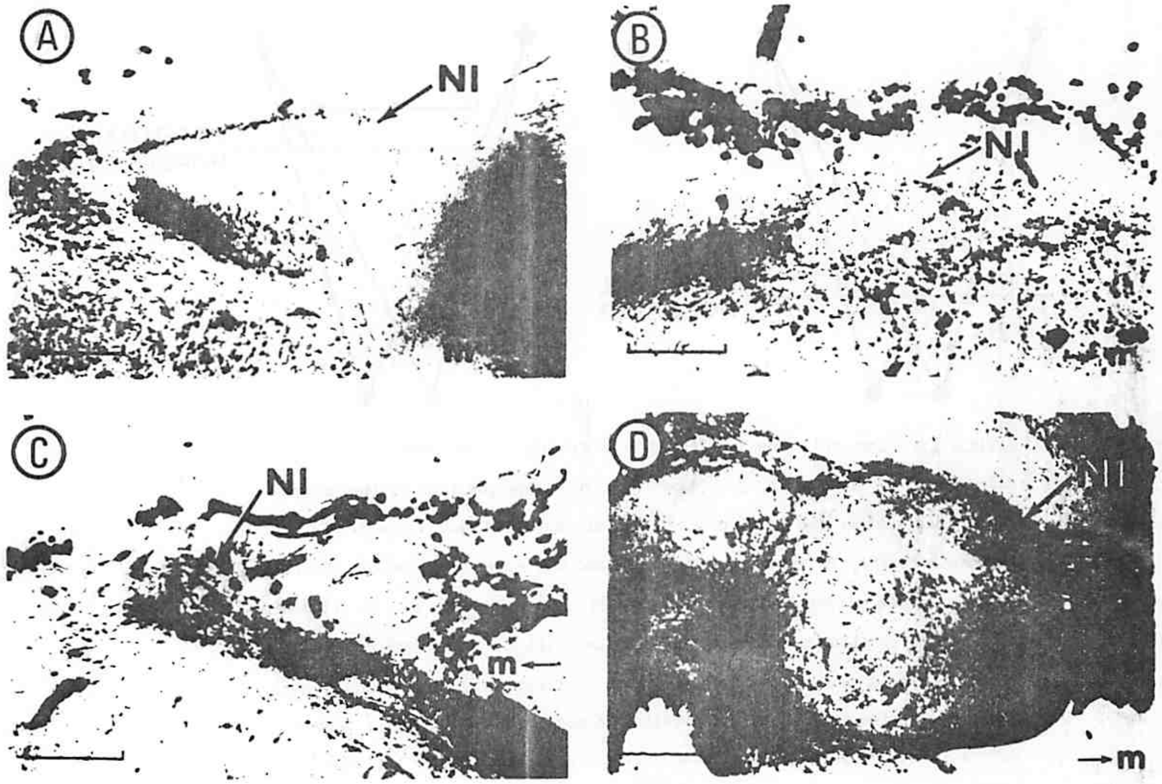


Figure 11. Photomicrographs of horizontal sections through brains of experimental toads. M: medial. Rostral is downward. For description, see text. Scale bar = 250 µm in A,B,C and 392.5 µm in D.

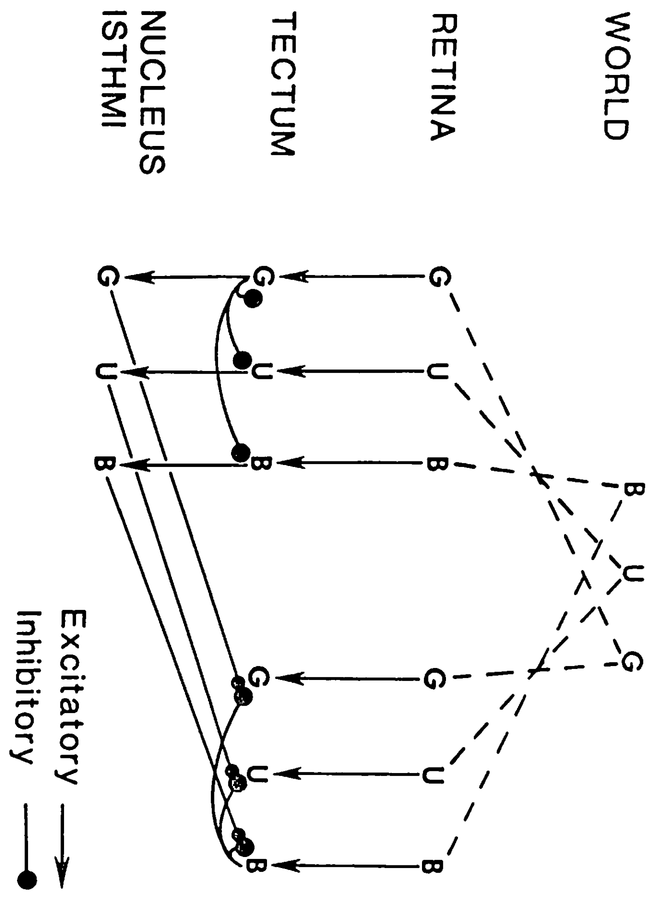


Figure 12. Simplified model showing lateral inhibitory network within tectum and disinhibition between tecta. Further explanation in text.

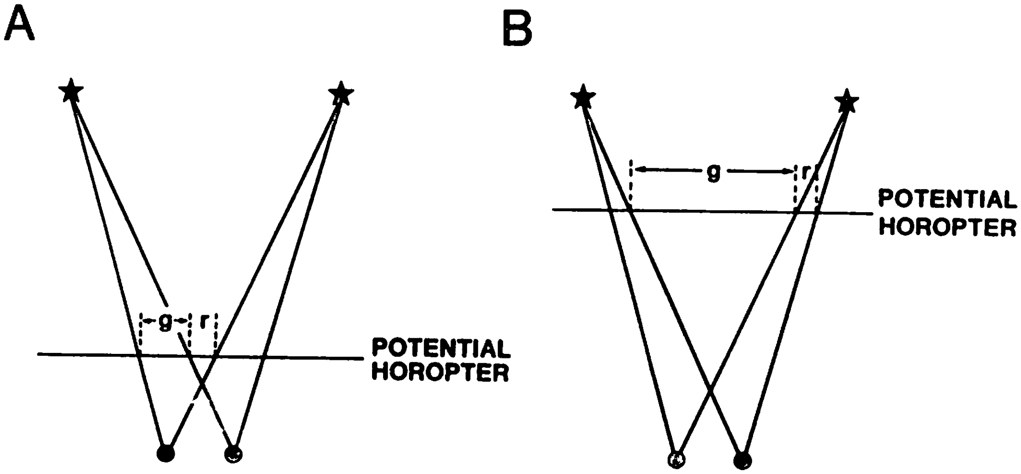


Figure 13. The relation between the position of the horopter and the elimination of ghosts. a, b: Diagrams to show how position of the horopter determines whether the model picks out ghost images or real targets. For the farther horopter, "r" is shorter than "g" and the model will select the real image; for the closer horopter, the situation is reversed. c: Relationship between the position of the horopter and the ratio of the number of times the model chooses a real target to the number of times it aims at ghost images. Model was tested with a pair of targets situated in a frontal plane between 5 and 70 cm with various separations between the targets. When the separation was small (1 to 4 cm), the model discriminated badly. When all separations are included, the model selects real targets with some reliability, provided that the horopter is situated at the correct distance. Further description in text.

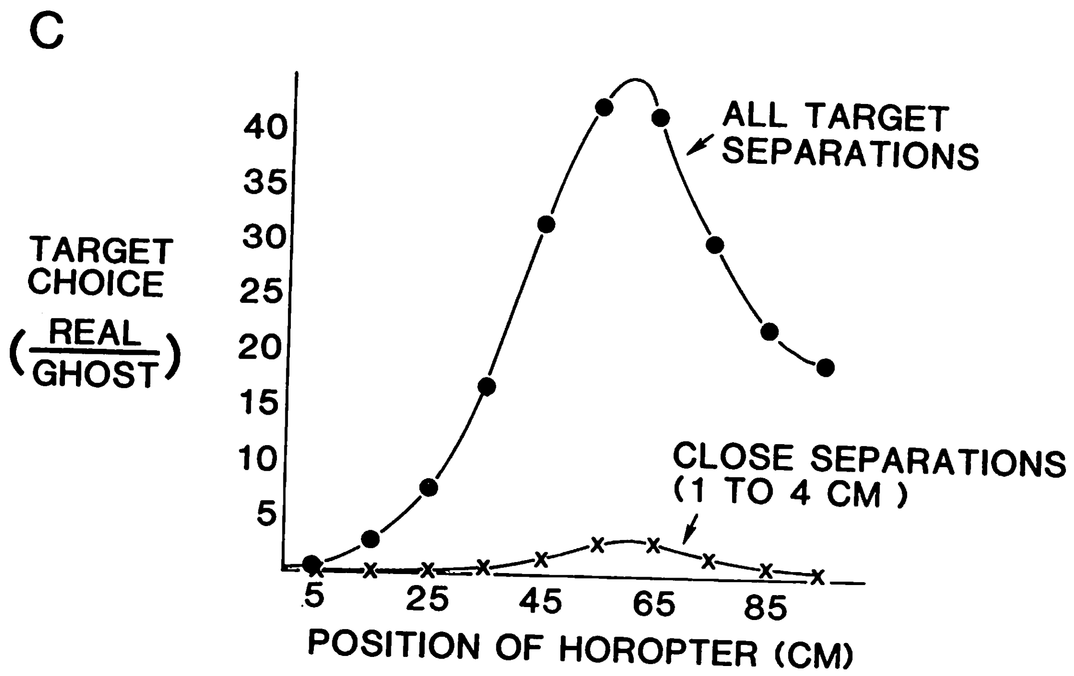

C
TARGET CHOICE
(REAL/GHOST)
40
35
30
25
20
15
10
5
ALL TARGET SEPARATIONS
CLOSE SEPARATIONS (1 TO 4 CM)
5
25
45
65
85
POSITION OF HOROPTER (CM)

Fig. 13c

Depth and Detours: Towards Neural Models[1]

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ABSTRACT

Motivated by data on the way in which a frog or toad will sidestep around a barrier to get to prey, we offer a number of alternative models for the neural networks underlying such phenomena. First, we introduce a one-dimensional model, and then compare it to experiments which show that the animal must make use of the depth of objects in determining its course of action. On this basis, we review earlier work on depth perception in frog and toad. We then turn to two models for the use of this information in detour behavior. The first builds on the one-dimensional model to indicate how the animal might 'choose' to turn to the end of a barrier or directly towards a worm. The second model indicates how the animal might come to represent in its head trajectories or a series of landmarks which can determine an overall path of action, rather than a single initial target.

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1. *Introduction*

This paper is one of a series in which we build neural models of visuomotor coordination in frog and toad to exemplify the style of neural processing which involves dynamic parallel interaction between layers of neurons, rather than a simple stimulus-response chain or a control action which can be adequately represented in terms of lumped models. Amongst the earlier studies are those of pattern recognition, which indicate how a neural network can take a spatial array of stimulation to tell prey from predator (Lara, Cervantes & Arbib, 1982), and a model of prey selection in which we explain possible mechanisms for how an animal, confronted with a spatially structured environment containing several prey objects, will come to snap at only one of them (Didday, 1976; Lara & Arbib, 1982). In the present paper we move beyond models of adequate releasers for stereotyped, though appropriately spatially directed, responses to situations in which the animal exhibits behavior which takes account of a complex spatial context. Specifically, we shall start from data on a toad viewing a vertical paling fence behind which there is a worm. It has been shown that the animal may either snap directly at the worm, or may detour around the barrier. However, it will not go around the barrier if there is no worm behind it. Thus, we may still see the worm as triggering the animal's response, but we no longer see only the stereotyped snap directly at the worm, but rather a complex trajectory dependent upon the relative spatial position of worm and barrier.

A first view of these data is given in Figure 1, from Collett (1982a) – more data will be reviewed in Section 3. The row of dots indicates a paling fence. The two circles indicate two alternative placements of worms which are to attract a toad's attention, while the T indicates an opaque barrier which prevents the toad from seeing the worms after it has moved from the start position. The position of the toad is represented by a dot for its head and a line for its orientation. The sequence of such 'arrows' on the right-hand side of the figure indicates successive positions taken by the toad in a single approach to the prey. Here we note that the animal sidesteps around the barrier, pauses for several seconds, and then continues to a position at which it stops, pointing in approximately the direction of the worm – but note that, due to the opaque barrier, the worm is no longer visible. On the left-hand side of the figure, we indicate the position of the toad on a number of different occasions, at the pause. The dashed arrows correspond to the nearer position for the worm, the solid arrows correspond to the position of the pause for the further position. What is of interest is that even though the worms are no longer visible to the toad at the time of the pause, the orientation of the animal correlates well with the position of the target. Thus, we must not only explain how it is that the animal chooses whether to proceed directly toward the prey or to sidestep around the barrier, but also come to understand how the position of the target can be encoded in such a way as to be available to guide the animal's behavior even if the target does not continue to be visible.

We may note, with Ingle and Collett, that the full detour behavior exhibited here is quite complex: the animal does not simply orient towards the prey or the end of the barrier; rather, if it does not proceed directly toward the prey, it sidesteps around the barrier orienting in a way that depends upon the position of the target and the length of the sidestep. We thus have an example of the coordination of motor schemas (Arbib, 1981) and we see that the sidestepping modulates the orienting behavior. The full analysis of such motor schema coordination is beyond the scope of the present paper, but it is worth noting that Ingle (1982a) has offered us some clues as to the possible neural correlates of the various schemas: he finds that a lesion of the crossed-tectofugal pathway will remove orienting; lesion of the crossed-pretectofugal pathway will block sidestepping; while lesion of the uncrossed-tectofugal pathway will block snapping.

The strategy of modelling in this paper will be to first develop a simple one-dimensional model of detour behavior in terms of determining the initial target for the animal: namely, directly to the prey, or to one end or the other of the barrier. This preliminary model will be developed in Section 2. Then, after reviewing further data and ways of modelling depth discrimination in Section 3, we shall turn in Section 4 to a somewhat more sophisticated model where the choosing of the direction in which to turn is augmented by the formation of an appropriate depth map to represent how far away the first target is in the given direction. Then, in Section 5, we look at a first model for generating the full spectrum of information that should be available for a variety of motor schemas to not simply determine orientation and distance but to actually determine the target for an initial sidestepping, the direction for the orienting at the end of this sidestep, and the approach to the prey. It is our intention that, by considering a variety of models, we can create a space of alternatives in which the design of a rich set of neuro-ethological and neurophysiological experiments will be possible. Thus, Section 6 is devoted to a discussion of experiments suggested by the models and some of the open questions to be addressed by modellers.

2. *The One-Dimensional Mode*

In the one-dimensional model, we represent the retinal input in terms of a map of neural firing rates indexed by the possible directions that the animal could turn in a horizontal plane. One of the first models of this kind (Didday, 1970, 1976) addressed the problem of the animal confronted with two or more fly-like stimuli, and offered a distributed neural network model of how the animal could come, in general, to snap at just one of these targets. This model was given mathematical form by Amari and Arbib

(1977), and their primitive competition model is shown in Figure 2. Here, the 'tectum' is represented by an array of n cells, whose membrane potential at any time is u_i, with corresponding firing rate $f(u_i)$ – with the conversion of potential to firing rate shown by the graph of f at the bottom left hand of the figure. Each of these cells is driven by an input s_i which indicates the output of a preprocessing element corresponding to the likelihood that a prey is present in the corresponding portion of the visual field. The cells are re-excited as shown, and also drive an inhibitory cell whose membrane potential v is converted into a firing rate g(v) which provides inhibition distributed to all the cells. Basically, with appropriately adjusted synaptic weights, we have that a cell will be able to continue its firing, thanks to its recurrent self-excitation, so long as its initial stimulation is high enough to allow it to win out over the pooled inhibition of the other cells. Typical results of the mathematical analysis are that at most one element can be excited in an equilibrium, and that if all the u_i's are initially the same, and an element remains excited in the equilibrium, it is the one receiving the maximum stimulus. However, once the model has responded to one pattern of stimulation, the build-up of inhibition will be such that the system exhibits *hysteresis* – it will not necessarily respond to the new maximal stimulus. However, a temporary change of threshold of all the units can be used to 'release' a 'blocked' response to a *new* maximal stimulus. It has been posited that this function is carried out in tectum by the newness cells.

Our first detour model (Epstein, 1979), then, is simply the Amari-Arbib model with a different input for prey and barrier stimuli. In Figure 3a (Epstein used a gerbil responding to sunflower seeds rather than a frog responding to flies or a toad responding to worms in his computer graphics) we see that each prey-like stimulus is represented as a tectal input with a sharp peak at the tectal location corresponding to the position of the stimulus in the visual field, and with an exponential decay away from the peak. Note also that the size of the peak decreases with eccentricity. On the other hand, as shown in Figure 3b, each segment of fence is represented by one trough of inhibition whose extent on tectum is just slightly greater than corresponds to the extent of the fence in the visual field. The net effect of this excitation and inhibition when the three prey stimuli and the two barriers are combined is shown in Figure 3c. Here we have simply added together the excitation shown in Figure 3a and the inhibition shown in Figure 3b to yield the curve in which we see that the combined excitation of the two central stimuli is heavily lowered by the trough of the left barrier, but is still able to yield positive contributions at spatial locations just beyond the end of either barrier. Given the nature of the Amari-Arbib model of Figure 2, it then comes as no surprise that when we run a computer simulation of the effect of such an input we come up with the situation shown in Figure 3d in which it is the cells corresponding to the right-most end of that left-most barrier which first attain a sufficiently high level of firing to command the overt response of the animal as a move towards that end of the barrier. While our task in the next sections will be to refine this model in terms of the depth dimension, it seems worth exhibiting this sample run here because the logic of this model will constitute an essential subsystem of the model shown in Section 4.

Before closing this discussion we note one important feature of the data which we shall review in the next section – namely, that Ingle and Collett, in looking at the behavior of the animal confronted with prey and barrier, do not find a single unequivocal direction, but rather plot a histogram of directions of response over a number of trials. Collett (1983) reports that, except for very few animals which exhibit a strong directional preference, the qualitative nature of these histograms does not appear to differ significantly for multiple trials with single animals from that obtained with a population. Thus, it is important that a model yield not a single unequivocal response, but rather that it be capable of yielding a histogram of preferred directions. The first strategy that suggests itself is to replace deterministic neurons by stochastic neurons whose output is driven by a noise term as well as by the other inputs. A second strategy, and an important one for many classes of non-linear models, is to vary initial conditions while keeping the elements of the models deterministic. However, a third strategy will be followed here, and that is to identify an explicit model parameter which is likely to be subject to significant variation due to motivational state and immediate experience of the animal, and whose variation will readily affect the model's convergence characteristics. For example, in Section 4 we show how such a variation in the spread of excitation due to prey-like stimuli can have significant effects on the behavior of a model of orientation behavior.

3. *Introducing the Depth Dimension*

In this section we will briefly view data indicating the need to take the depth dimension into account in any model of detour behavior in the toad. After that, we will sketch the general setting for our models of Sections 4 and 5, and close the section by briefly comparing two recent models of depth discrimination.

Figure 4 (Collett, 1982a) shows a number of experiments on detour behavior. In each case the solid square with tail indicates the initial position of the toad, the row of dots indicates the position of barriers, and the rectangle with squiggles represents the position of the worm. Arrows are then labelled with percentages to show the directions chosen by the animal over a large number of trials. 4a shows that the animal will prefer to detour around an uninterrupted barrier, while 4b shows that the animal will prefer to go through a gap rather than detour. It is interesting to contrast 4c with 4a. In 4c we still have the uninterrupted fence at the same position relative to toad and worm, but now there is the fence with a gap as in 4b in front. In this case, the animal discounts the

rear fence by choosing to go through the gap, more than half the time, even though it would have detoured around the rear fence 3/4 of the time in the situation shown in 4a. Thus, it would seem that, to a first approximation, the response of the animal is a weighted sum of its responses to the individual fences, with the effectiveness of a fence in the sum declining with distance. In 4d, we see that the animal's tendency to detour is strong when both the near and far fences are uninterrupted, while in 4e we see that with a large gap in the front fence, the toad overwhelmingly chooses to go through the gap even when, as in this case, there are side fences joining the front and rear fences so that the animal's behavior is in fact to enter a cage. Such results lend weight to the search for a model which does take the depth dimension into account, but which is not highly cognitive in the sense that the animal would be posited to use representations of such high-level constructs as one fence vs. two, or a gap vs. a cage.

In Figure 5 we have superimposed two possible coordinate systems for representing the ground plane in front of a frog or toad. In this figure we also introduce the graphical notation to be used to describe the visual scenes which form the input to the models of Sections 4 and 5. The T shaped object at the bottom of the figure represents the animal, with the disks at the ends of the cross-bar indicating its eye positions. The small disks within the grid area represent fenceposts and the solid rectangle a prey object. The 40 cm. by 40 cm. ground plane is divided into a cartesian grid with an interval size of 10 cm. The radial coordinate system overlaid upon this grid is centered on the midpoint between the two eyes. The radial lines of this system are placed at intervals of 7.5 degrees. The curved lines are lines of constant visual disparity, spaced apart by a constant disparity increment.

We posit that rather than the rectangular coordinates, neurons may be more appropriately indexed by the radial system. The use of an angular measure is clearly motivated by the way in which an image is projected onto the retinal surface. Also, since disparity cues, like other depth cues, are more acute closer to the animal, the curves are longer and further apart with increasing radial distance from the animal. Thus, they have a general appeal as a system for the representation of depth, and we would posit, represent regions which have approximately the same density of neural representatives. Note, however, that we are here simply representing the ground plane of the animal, rather than the full visual field. One structure which could support this representation is a mapping of the whole ground plane onto a linear strip of cells in the brain, with each small region in that strip corresponding to a single angular direction, but a full range of depth, with the proportion of cells representing nearer depths much greater than the proportion of cells representing further depths. In summary, we represent the ground plane by neurons indexed by an orientation coordinate θ, and a discrete depth zone coordinate d, but do not posit that θ and d also function as the coordinates for a two-dimensional array of neurons.

The general scheme of the detour model is then as shown in Figure 6. The visual input to the retinas provides two maps based on the θ coordinate which can be further processed to yield depth mappings. We have made the assumption that the barriers are recognized by one population of cells and processed for depth separately from worm-like stimuli which are represented by a separate depth mapping. This assumption is supported by the work of Ingle (1977) and of Ewert (1976) who demonstrated the likelihood that processing of prey stimuli is localized to the tectum whereas contraindicative stimuli are processed in the pretectal region. By this assumption it is possible for these two mappings, indexed by the (θ,d) coordinates, to be separately convolved – the barrier depth mapping B being convolved with a kernel I which assigns inhibitory weight to barriers, and the worm depth mapping W being convolved with a kernel E which assigns an excitatory weight to the prey. The resulting sum $B*I + W*E$ then provides the input for the target selector and the output of this target selector can be combined with the barrier and worm depth maps to provide the necessary input to coordinated motor schemas for the motor output for snapping, sidestepping, orienting, jumping, etc. We shall provide two different instantiations of this general model scheme in Sections 4 and 5. In the rest of this section, we briefly describe recent work on modelling depth perception.

Recent Models of Depth Perception

As is well known (Julesz, 1971), the input to a single eye at a given time does not in and of itself convey depth information. Among possible mechanisms for extracting depth information are lens accommodation, binocular disparity matching, and optic flow from the change in input to a single eye over time.

Ingle (1976) has shown that a monocular frog will snap accurately within its monocular field and in the ipsilateral portion of its normal binocular field. However, estimates are systematically distorted within the contralateral binocular field in a way which might be predicted by the decreasing resolving power of the lens with increasing eccentricity. On the other hand, Collett (1977) has shown by experiments with toads fitted with prisms that in the binocular toad and with stimuli within the binocular field, stereopsis appears to be far more effective in determining the animal's depth discrimination than does accommodation.

This evidence for multiple depth cues led us (House, 1982) to develop a model which extended earlier depth perception models by Dev (1975) and Amari and Arbib (1977). This model utilized both accommodative and disparity-matching cues, through a process of competition and cooperation in neural nets, to segment a visual scene into depth regions.

The model attempted to address the problem of collecting the kind of depth information necessary for the general barrier navigation problem explored in the next two sections. However, Collett and Udin (1983) have found evidence through lesion experiments that, at least for the more limited problem of unobstructed prey-catching, toads may use a neurally-implemented triangulation process (probably assisted by lens accommodation) to localize prey, rather than a process of disparity matching.

Since the depth perception model of Collett and Udin does not address as broad a range of visual data as does that of House, it does not necessarily refute the conceptual framework of the latter model. It may well be that here again we have a case of various neural strategies functioning either cooperatively or alternatively to cope with the vast array of visuo-motor tasks required of the freely functioning animal. Further modelling and experimental work is clearly needed to explore the open questions left by these two models, and to capitalize upon their strengths.

An important assumption which will be made in the models of barrier negotiation is that perception of the depth of both prey and barrier objects is simultaneously available. Behavioral evidence, already presented, clearly supports this assumption. A further assumption that this information is either determined by different neural substrates or is at least separable by object category will also be made. This assumption is implicit in the depth model of House and is not addressed in that by Collett and Udin.

4. *A Model for Choosing Orientations*

In this section we offer our first model of detour behavior which takes depth into account. We specialize the general scheme of Figure 6 in the manner shown in Figure 7a. Here, the depth map for prey is convolved with the excitatory mask shown in Figure 7b and the depth map for the barrier is convolved with the inhibitory mask shown in 7c to yield two two-dimensional arrays whose sum is shown as array E in Figure 7a. The shapes of the two masks were chosen to take into account the way in which toads, when confronted with a 'prey behind barrier' configuration, make the choice between turning around the barrier or proceeding directly towards the prey. Collett (1982b) reported that what governed the path selection was (1) the distance of the worm from the fence, and (2) the absolute length of the fence. Within a 20 to 30 cm. distance from the toad, neither the distance of the toad from the fence nor the visual angle subtended by the fence seemed to be important. Thus, the mask for barrier edges (fence-posts) was chosen to project behind the edge at a constant maximum height after an initial rise to that maximum, i.e. there is a short distance behind the edge in which there is little inhibition, after which inhibition is equally strong at all distances. The mask for prey objects projects very broadly in a lateral direction and somewhat less broadly in the forward direction. The net result is that with a prey object significantly far behind a barrier the barrier projection substantially reduces the prey projection except beyond the barrier ends. For prey close to the barrier the prey projection is not significantly reduced and is thus strongest directly in front of the prey. To approximate the 'size-constancy' exhibited by actual animals the effects of the non-cartesian coordinate system are partially counteracted by decreasing the spread effect of the masks by a linear factor with increasing distance from the toad.

The input depth-maps D_b and D_p are assumed to be cleanly segmented as to depth, so that there is one preferred depth for barrier and one preferred depth for prey in each visual direction. This is not the case in E, which represents the superposition of the convolutions applied to these two arrays. We thus subject E to two independent processes in the present model. In the left-hand path of Figure 7a, we integrate the total excitation along each visual direction, to provide a one-dimensional map which is then fed to an orientation selector model which will extract the orientation θ of maximal total excitation. Thus, this portion of the model is an extension of the one-dimensional model exhibited in Section 2. However, the present model also postulates the simultaneous subjection of the map E to a further process of depth segmentation. Thus, when the orientation selector returns an angle through which the animal is to turn, the motor schemas can also consult the depth segmentation model to provide the depth at which the target at orientation θ is to be found. Note that the target being considered now may not correspond to the initial prey stimulus. Instead, it represents the point in space to which motor activity will be directed. If this point corresponds to the prey location the object is achieved. Otherwise, we suggest that further processing will ensue upon reaching this target.

Figure 8 shows the operation of this model on the single worm behind a single barrier configuration of Figure 8a. The arrows at the base of 8b correspond to the total excitation G(θ) which is provided as input to the orientation selector model for each angle θ. The array of squares and ovals represents the input E to the depth segmentation model, with ovals corresponding to inhibition and squares corresponding to excitation. Intensity of excitation or inhibition is encoded by the size of the corresponding symbol. As we see in 8c, the direction chosen by the orientation selector model in this case is that of the left-hand end of the barrier, and the squares indicate that the depth returned by the depth segmentation model does indeed correspond to the end of the barrier.

Figure 9 shows the ability of the model to replicate some of Collett's behavioral data. Figure 9a depicts a fence and worm configuration identical to that of Figure 8 except for a gap in the center of the fence. To the left is the model input and to the right is the converged state of the model. Here we see that the preferred direction is now straight ahead, and that depth information is provided for the edges of the gap and for the worm. Figure 9b shows data for the case of a solid fence moved back to a position near to the worm. Here the preferred direction is also straight ahead. In Figure 9c we have the net result of placing a fence with a gap in front of a fence near to the worm. Again, the directional preference is straight ahead towards the worm. Finally, the cage of Figure 9d gives similar results.

In order to address the variable orientation preference indicated by Collett's histograms (Figure 4) we present the set of experiments with this model shown in Figure 10. These 9 runs were made with three different distances of a solid fence from a single worm. For each fence distance three choices of the prey spread function were made. The minimum spread necessary to cause selection of a fence end for the farthest fence distance was chosen as the base spread. The figures show model input, with the large circle indicating the spatial region selected by the model when run against this input. The left-hand column of figures was made with a spread 33 percent greater than this amount, the central column with the base spread, and the right-hand column with a spread 33 percent less than the base value. We see here that the model shifts preference between the fence ends and the fence middle depending upon the extent of spread. In no case does the model converge upon an orientation other than towards a fence end or directly towards the worm. The variation in the sensitivity of orientation preference as a function of the distance of the fence from the prey is consistent with behavioral results previously demonstrated by Collett (1982b).

The final set of experiments with the orientation model is depicted in Figure 11. Here we show the sensitivity of the model to the position of the prey behind the fence. Figure 11a shows the converged state of the model with the fence-worm configuration carefully chosen to present a nearly balanced preference between the two fence ends. In this case the model has failed to make a clean choice between the right and left fence ends although it has clearly rejected the choice to head straight for the worm. In Figure 11b we show corresponding runs for the situation where the worm is shifted slightly to the left of the balanced position of 11a. With this small shift of position the model makes an unequivocal choice of the left fence end.

5. *A Model for Planning Paths*

Both the preliminary model of Section 2, and the depth-based model of Section 4 serve simply to choose the direction and, in the latter model, the depth of the target for the animal's first move. It is not clear from such a model how the animal would determine whether that target is the target for a sidestep as in detouring around a barrier, or for a snap, as in direct approach to the prey, nor is it clear how such a model would explain how the animal has in its brain the necessary information to determine the subsequent orientation following a sidestep if that is what first occurs. In the present section, then, we turn from models based on the selection of a single target to models which suggest how the brain might go about planning overall paths of action which would require the coordination of several motor schemas. We present the two models of Sections 4 and 5 side by side because we believe that at this preliminary stage of the search for the neural substrates of detour behavior, it is premature to focus on a single model. It is hoped that the very contrast between these models will serve to stimulate the design of new behavioral and physiological experiments. We also stress that the models are not tightly constrained, in that they do not attempt to specify what particular neurons are doing in the posited behaviors. Rather, they represent processing schemes which could plausibly be carried out in neural structures, and thus represent postulates that there are populations of neurons which carry out the indicated operations. We pose it as an important challenge to lesion studier in collaboration with neuro-ethology, neurophysiology and neuroanatomy to determine whether indeed there are neural structures which do perform these operations, and then to determine whether the posited functional interactions do indeed take place between the layers thus identified. We expect that the refinement of our models will go hand in hand with the development of further data of this kind, and that both theory and experiment will each provide an important stimulus to the other.

The depth selection portion of model of Figure 7 had an excitatory field whose neurons were specified by two coordinates, one for angular direction, and one for depth or disparity. We then postulated that the activity of the neuron with coordinates (θ,d) was to be seen as a measure of confidence that there was indeed a feature in the external world at the corresponding position in the visual field. The function of the model was to converge upon a configuration in which only one depth was given a high confidence level for each visual direction. In the present model, we associate with each coordinate not a single number but a vector, and this vector is to indicate the preferred direction of motion of the animal were it to follow a path through the corresponding point. For conceptual simplicity, and not because of any change in thinking about what internal representation is most likely, the coordinate system used in this model is the Cartesian (x,y) system. Our task with this model will be twofold: to specify how the vector field is generated; and to specify how the vector field is processed to determine the appropriate parameters for the coordinated activation of motor schemas. In the technical jargon of differential geometry, then, the neural surface corresponds to a manifold representing space in some internal coordinate system, while the firing of a group of neurons associated with a particular coordinate is to represent the vectors of a tangent field, or flow. The question is how those local vectors are to be integrated to determine an overall trajectory for the animal.

At the current stage of our research, we would wish to suggest that the model that follows is meant to indicate a style, rather than to be seen as a fully articulated hypothesis about the nature of the vector fields that could be represented in the visuomotor system of the frog or toad -- or the gerbil. Our first choice is shown in Figure 12. 12a suggests that a single prey will set up an attractant field, in which from every point in the animal's representation of space there is an arrow suggesting a choice of movement toward the prey, with the length of the vector (the strength of choice for a movement in the given direction) being the greater, the closer is the point to the prey. 12b shows that we have associated a repellant field with a single fencepost, with the strength of the field contributing mostly to determine a lateral movement relative to the position of the fencepost from the viewpoint of the animal. Finally, in 12c we have the animal's representation of itself within this field. This representation simply consists of a set of vectors radiating out in all directions from the animal's current position with a decay similar to that for the prey field. Figure 13 shows the various effects obtained by summing the vectors for each point of the manifold. In Figure 13a we have the bug attractant field in interaction with the animal's self-representation. In 13b we see the summed effect of the fenceposts corresponding to a field which repels from the fence as a whole but with especially strong lateral flow at the edges of the barrier. Finally, in 13c we have the overall net field set up by a scene containing a single worm behind a fence.

The total field may be interpreted as representing the 'net motor effect' of the scene upon the animal, whether the animal is an essentially ballistic creature like a frog or a toad, or a more 'tracking' creature like a gerbil. In the case of the gerbil (Ingle, 1982b) we would postulate that the vector field is integrated to yield a variety of trajectories, with a weight factor for each trajectory. We would then see that this field has two 'bundles' of trajectories receiving high weight, that bundle which goes round the left end of the barrier to approach the worm, and that which goes around the right end of the barrier to approach the worm. Thus, if we change 'worm' to 'sunflower seed', we would posit that the gerbil actually builds within its brain a representation of the entire path, one of the paths is selected, and this path regulates the pattern of footfalls that will move the animal along this trajectory. In yet more sophisticated models, we could see the path not as being generated once and for all, but rather as being dynamically updated on the basis of optic flow as the animal proceeds along a chosen direction.

In frog or toad, however, we would postulate that the vector field is processed not to yield a continuous trajectory -- or a bundle of continuous trajectories of which one is to be chosen -- but rather serves to generate a map of motor targets, appropriately labelled as to type. The divergence operator is a likely candidate for this form of processing. Once a suitably constructed representation of a vector field is set up, the computation of divergence is a simple local process which may be carried out in the parallel distributed fashion associated with neural mechanisms. Further, the divergence of a vector field is a scalar field. The negative of the divergence will contain peaks where the flow lines in the field tend to converge and valleys where they tend to diverge. Figure 14 is a display of the negative of the divergence of the net field of Figure 13c. This contour indicates a trough of high divergence in front of the fence, peaks of convergence corresponding to the two edges of the fence, and a third peak corresponding to the worm. We would postulate that a scalar field of this sort could be played down upon motor schemas so that one of the fence ends is chosen as the motor target for a sidestep, but the simultaneous availability of the relative position of the worm is available to determine the coordinates for the orienting schema, and for the subsequent second leg of the motor sequence that we saw to follow the pause in the trajectory shown in the right-hand side of Figure 1.

In Figure 15, we offer corresponding analyses for the cases of a fence at the position of the fence in Figure 13c but with a central gap (15a), a solid fence near to the prey (15b), a solid fence behind a fence with a gap (15c), and a cage (15d). Our research has not yet resulted in isolating the most suitable algorithm for extracting a path from data of this sort. However, these preliminary results are suggestive of a strong agreement with the behavioral data. In particular, the powerfully attractive quality of fence gaps noted by Collett (1982a, 1982b) is especially apparent.

6. *Discussion*

The detour model of Section 4 is successful in several ways in replicating data obtained from behavioral studies. First, in the prey-barrier configurations tested it always converged upon an orientation to either a fence-end or the prey. Since actual animals rarely choose any other orientation, this test is critical. Second, the selection made between a turn to a fence end or a movement towards the prey can be modulated for a variety of fence distances by a simple modification of a single model parameter – the extent of the lateral spread of prey information. This is also critical since it suggests a mechanism to explain the apparent discrepancy between the deterministic character of the computer model and the stochastic (or at least variable) character of the actual animal's response to a particular configuration.

The fact that the histogram results of the behavioral trials can be explained simply in terms of the prey stimulus spread effect suggests the need for physiological studies of the susceptibility of tectal cell receptive field sizes to modulation based upon motivational state and experience. If receptive field sizes are prone to significant variation then the difference between the behavior of animals and this style of model will have at least one plausible source.

The extreme sensitivity of the orientation model to the position of the prey behind the barrier (i.e. the balance of the visual stimulus) suggests the need for a series of behavioral experiments to see whether or not animals also exhibit this quality. What needs to be determined is whether histograms of turn preference show a marked shift in peak orientation preference or whether there is a smooth shift in preference when the visual scene is gradually shifted from a central bias to (for instance) a left bias. An example of this sort of behavior is the 'snap zone' of frogs as reported by Ingle (1982b). Here the animal snaps at prey within the zone, orients to or hops towards prey outside the zone, and exhibits ambiguous behavior within a narrow band between the zones.

The vector model presented in Section 5 differs significantly from the simple orientation model of Section 4. The primary source of the difference is that here visual stimuli are not seen as setting up a simple decision surface which can be processed to select among several optional actions. Rather, what is set up is a spatially encoded map of potential motor activity which in some sense is the net result of the interaction of all of the pertinent visual stimuli. Although in the simple Cartesian representation used in this paper the vectors are described in terms of components of forward and lateral motion, there is no reason to expect that the nervous system would encode vector quantities in this way. What is more likely is that they would be encoded in terms of the various types of schematized motor patterns available to the animal. For instance, a particular vector could be envisioned as having components governing side-stepping, turning, and snapping. The coordinate system for such a vector field would, most appropriately, be body-centered rather than eye-centered.

Ingle (1982b) also suggests a model for detour behavior based upon principles similar to those employed in our simple orientation model. In this model he envisions wide-field tectal neurons driven by retinal prey-detectors as providing the kind of spread-effect we hypothesised in our model. He proposes that if inhibition from pretectal cells driven by barrier detectors is sufficient to suppress excitation in narrow-field tectal neurons, the effect of the wide-field neurons will be to provide a lateral shift of the locus of tectal excitation. This shift in locus would then be translated into a corresponding shift in orientation turning angle. However, his model is of a quite different character from either of the ones which we propose. He has shown that pretectum governs side-stepping and tectum governs orientation turning and snapping. This has led him to suggest that the signals to the motor area from tectum and pretectum are of the nature of commands which are intended to be executed in a coordinated way by the motor area. In our models, however, we see these signals as describing a field of potential motor activity which contains within it a spatial model of the animal's visual world. We would agree with Ingle's placement of the barrier related field in pretectum and that associated with prey in tectum. Further, we agree that final processing and decision making based upon this kind of scheme must take place in the motor area. However, we differ in that we do not see the nature of this process being to select among and coordinate independent motor commands. Rather, we see it as being a process of deriving appropriate motor responses based upon a set of spatially distributed motor cues which already contain within themselves the results of an interaction among the various visual cues.

In apparent confirmation of the notion of the global interaction embodied, especially, in our vector model is the report of Grobstein et al. (1982). Their findings indicate that tectal locus cannot be the unique determiner of orientation preference. For instance, lesions to the tectum abolish visually guided orientation turning but leave orientation to tactile stimuli intact. Conversely, lesions to the *lateral torus semicirculus* abolish tactile orientation but do not affect visual orientation. More dramatically, they have shown that small lesions of the neuraxis do not produce orientation scotomas but, rather, result in inaccurate turning and undershooting throughout the disturbed hemifield. Their conclusion is that these small lesions do not destroy linkages between particular tectal loci and turn-generating circuits but produce a more global disturbance for all tectal regions ipsilateral to the lesion.

If the vector model is to adequately represent spatially directed activity, the vector field set up by the fence-posts should probably be represented by a field which survives translation of the toad's position within the field. The present model does not account for this since the fence-post field shape depends upon the position of the toad – this is in contrast to the prey field which is radially symmetric about the prey's position. Further studies with the model are needed to correct this.

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FIGURE LEGENDS

Fig. 1 – Toad Trajectories

Reprinted by permission from Collett (1982b). Fence, opaque barrier, prey configuration. Solid lines to right indicate orientation of the body axis of a toad and its snout position (dots) at intervals along its path towards prey. For this case, prey objects are those shown enclosed within the solid circle. After it begins its movement, the T shaped opaque barrier prevents the toad from seeing the prey. Solid lines to the left show the orientation of the toad's body axis, for several trials, during its pause at the fence end. Dashed lines are similar but for prey positioned within the dashed circle. These data make clear the toad's ability to 1) extract depth information from its visual world, 2) maintain a short-term memory of this depth information, and 3) integrate this memory with some notion of its own body movement.

Fig. 2 – Amari-Arbib Primitive Competition Model

This model selects the maximum stimulus from an input vector s by a non-linear, distributed, competitive process. When the model converges, the element w_i corresponding with the maximal input element s_i will be above its firing threshold. All other elements will be below threshold.

Fig. 3 – Epstein's Prey Selection Model

a) The presence of three prey objects (diamonds) results in the overlapping pattern of excitation shown in the plot at the bottom of the figure, whereas b) barriers result in a trough of inhibition extending a small distance beyond each barrier end. c) The excitatory/inhibitory input obtained by summing the effects of the prey and barrier objects is shown here. The presence of inhibition due to barriers leaves the maximally excited position to the right of the left fence. d) This run of the model shows that it converges with all orientations suppressed except for the one corresponding with the initial maximal input.

Fig. 4 – Orientation, Behavioral Results

Reprinted by permission from Collett (1982b). Histograms of the initial orientation response of a toad presented with various prey/barrier configurations. In all cases the animal elects to go either straight ahead towards the prey or aims towards one of the fence ends. Percentages shown for orientations to the fence end are combined totals for turns to either end.

Fig. 5 – Coordinate Systems Used for Orientation Models

Cartesian and radial coordinate systems used in the models. The area shown represents a 40 cm. by 40 cm. square. In the radial system the radial lines are at equal angular increments from the toad's midline. Arcs are lines of constant disparity spaced at equal increments of disparity. The spacing of the equi-disparity arcs illustrates the decrease of depth acuity with increasing distance from the animal. Object below the grid area is a schematic representation of a frog or toad with eye positions indicated by the large disks. Within the grid the small disks represent fence posts and the solid rectangle represents a prey object.

Fig. 6 – Conceptual Schematic of Visual/Motor Pathway

Assumptions made in this diagram are 1) that separate depth maps are maintained for prey and barrier stimuli, 2) direction for an orientation turn is obtained by combining information from these two depth maps, and 3) information on preferred orientation and depth of prey and barriers is available simultaneously to motor schemas. These schemas are capable of integrating this information to produce a coordinated motor-output.

Fig. 7 – Orientation Model, Implementation Schematic

The general model of Fig. 6 is shown here in a specific implementation. a) shows the information flow and indicates the operations performed. b) and c) show the shapes of the spread-functions which are convolved with the prey and barrier depth-maps to produce selection surface E. E is resegmented in depth via a Full Amari-Arbib Model in order to provide a single depth target at each visual direction. The orientation target is provided by a Primitive Amari-Arbib Model driven by an input vector obtained by integrating total excitation along each visual direction in surface E.

Fig. 8 – Orientation Model, Test Case

a) The scene used as input to the model, showing a single prey behind an unbroken fence. b) The selection surface E is shown superimposed upon the original scene. Square blocks indicate areas of excitation due to spread of the prey stimulus. Ovals indicate inhibition from fence-posts. Strength of excitation or inhibition is indicated by the size of the corresponding symbol. The arrows indicate the visual direction and strength of the elements of the input vector G. c) After nearing equilibrium the model has selected a single orientation preference to the left end of the fence, and a localized set of preferred depths (indicated by the squares near the left fence end).

Fig. 9 – Orientation Model, Comparison with Behavioral Experiments

The selection surface and equilibrium state for several configurations used in behavioral studies. a) Fence with gap. b) Solid fence close to prey. c) Fence with gap in front of solid fence. d) Cage. The model results are consistent with behavioral results (compare with Figure 4).

Fig. 10 – Model Performance for Various Fence Distances and Spread Parameters

The nine trials shown here were made with three distances of the fence from the prey and, for each distance, three settings of the prey attractant spread parameter. The images shown are the model input for each configuration, with the approximate spatial target selected by the model indicated by a large circle. The "base spread" used in the central images was that which just caused the model to select a fence-end for the farthest fence distance. The model's choice of fence-end vs. direct approach to prey is highly sensitive to this parameter, thus suggesting a way in which the variation in actual animal behavior might be explained.

Fig. 11 – Visual Balance vs. Selected Orientation

a) A careful balancing of the prey/barrier configuration results in the detour model being unable to make a clean choice between the two fence ends, although it clearly has rejected the "direct approach" choice. b) A small displacement of the prey from the balanced position of a) results in the model being able to rapidly select the left fence end.

Fig. 12 – Vector Field Model, Primitive Fields

The vector field model envisions objects in the animal's visual world as determining a space of potential motor activities. The fields depicted here represent a first exploratory attempt at defining a set of primitive fields which will interact in interpreting a more complex scene. a) A single prey object sets up a symmetric attractant field with attractive strength decaying gradually with distance from the prey. b) A single barrier object sets up a repellant field which decays more rapidly with distance than does the prey field. Here, the field is not symmetrical but has a lateral component much stronger but decaying more rapidly than its opposing component. c) The vector field model also contains a representation of the animal itself. This representation is simply the converse of the prey representation, i.e. it is symmetric but repelling from the position of the animal.

Fig. 13 – Interaction of Primitive Vector Fields

The three types of primitive field of Figure 12 are shown here in interaction. a) The prey attractant field in interaction with the animal's self-representation produces a field suggesting various curved paths terminating at the position of the prey. b) The effect of the interaction of the fields from several barrier objects arranged to form a fence is to provide a strong lateral thrust at the fence ends. The lateral components produced by the interior posts is effectively cancelled by neighboring posts. c) The net field produced by the interaction of all of the elements of the configuration has a set of paths most of which are diverted around the fence ends.

Fig. 14 – Divergence of the Net Vector Field

The negative of the divergence of the net field of Figure 13c is shown here as a 3-Dimensional plot. Peaks on this plot represent regions of strong path convergence or bundling of paths, whereas valleys represent a strong divergence. The two fence-ends and the prey are associated with the three peaks. There is a trough of divergence in front of the fence.

Fig. 15 – Vector Model, Comparison with Behavioral Experiments

Although an analysis has not yet been completed to identify a specific means for deriving motor activity from the vector fields, these figures indicate that the relevant information is efficiently encoded by the vector model. a) Fence with gap. b) Fence near to prey. c) Fence with gap in front of a solid fence. d) Cage. The model results are consistent with behavioral results (compare with Figure 4).

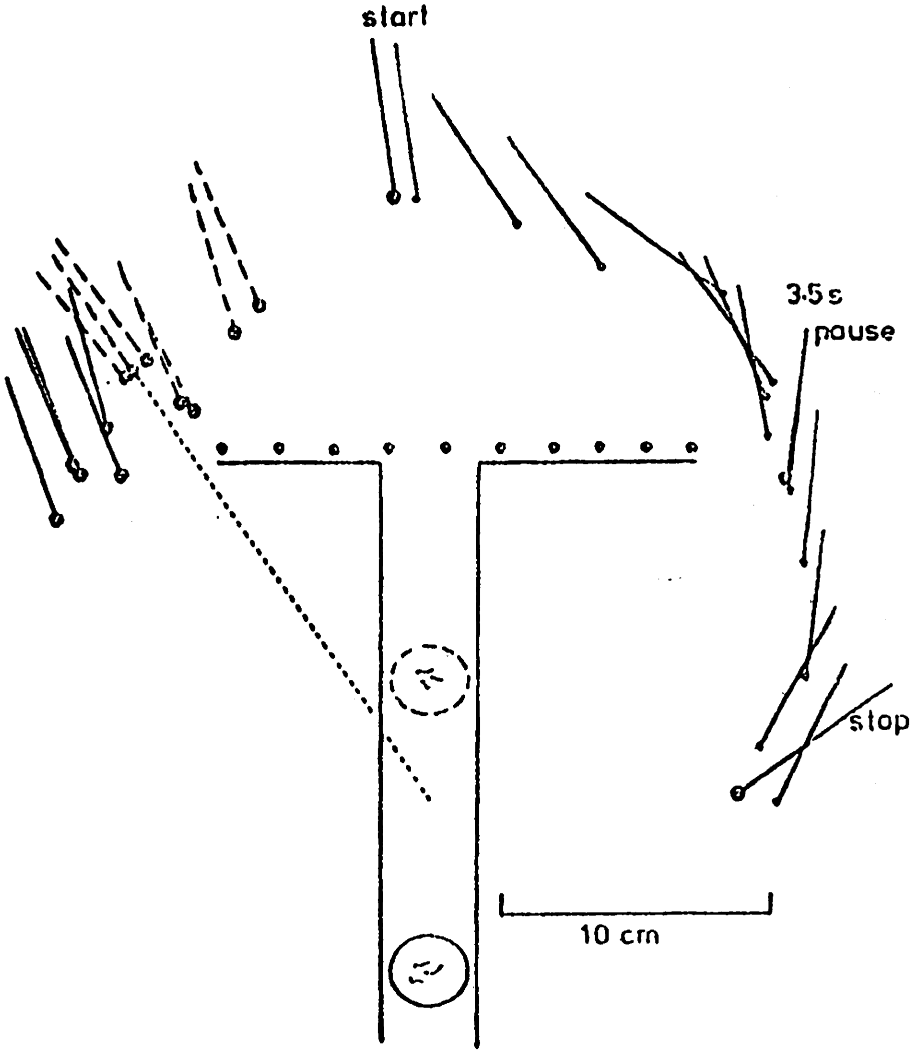
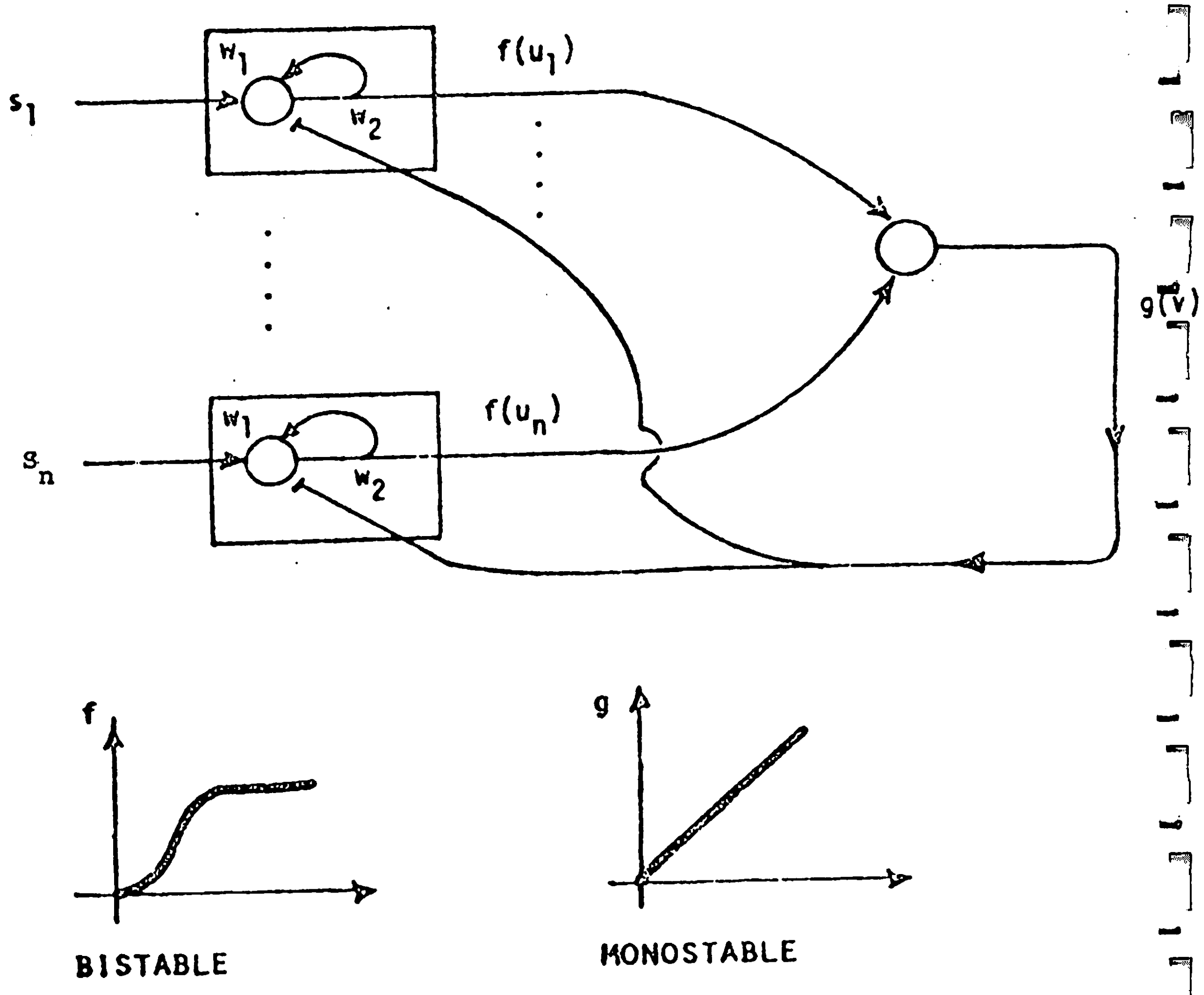


Fig. 1. Toad Trajectories

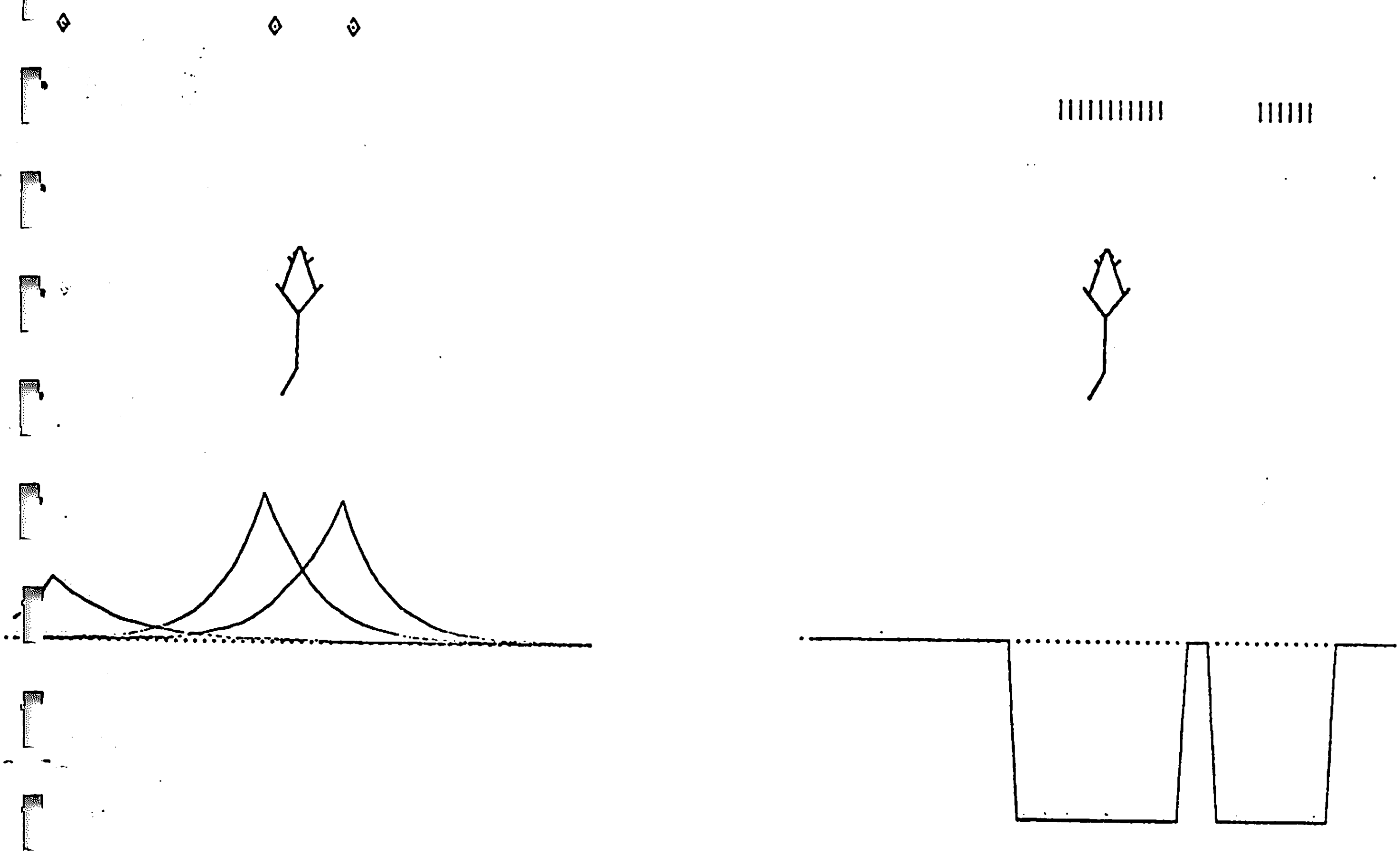
AMARI-ARBIB PRIMITIVE COMPETITION MODEL



BISTABLE

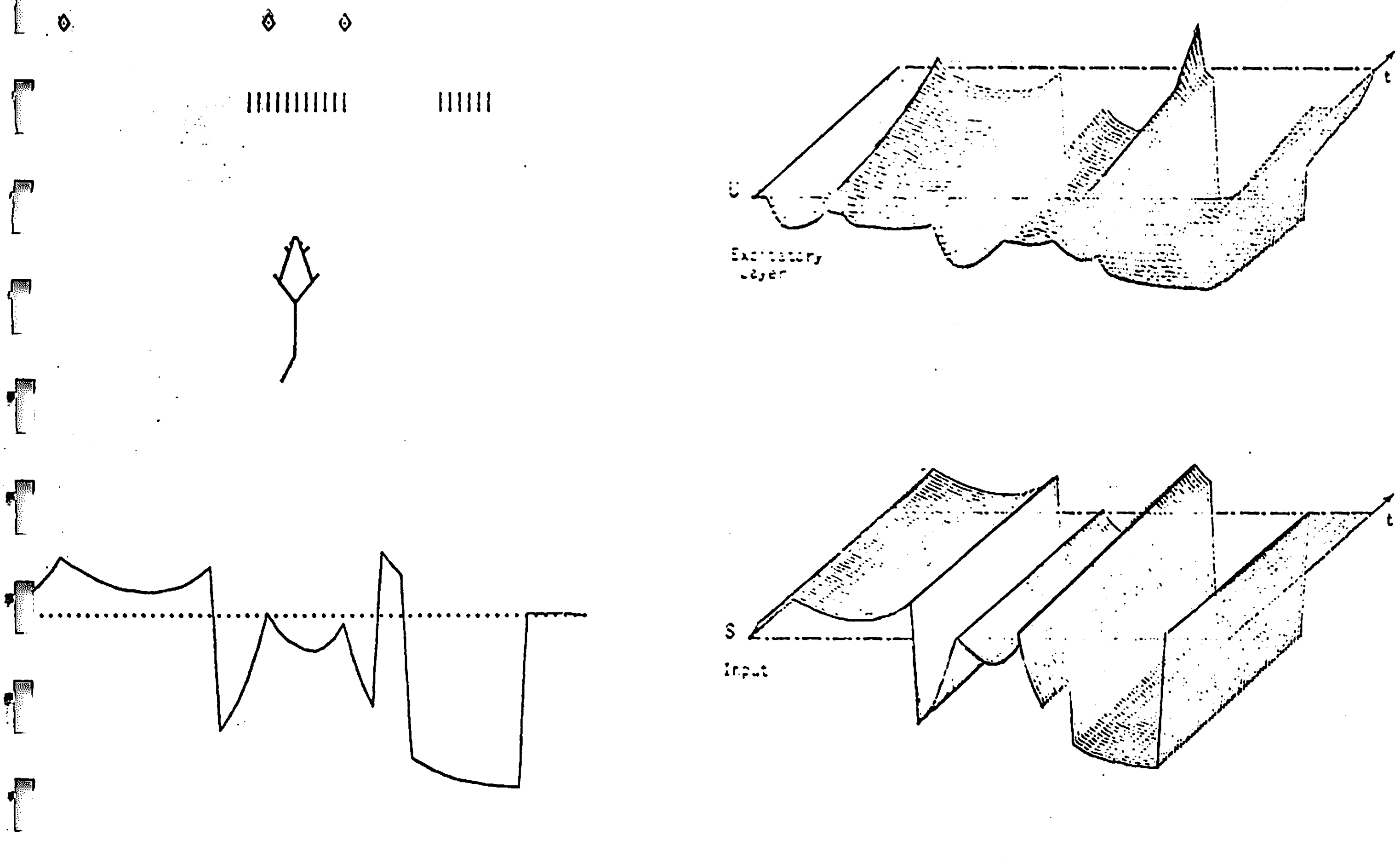
MONOSTABLE

Fig. 2



a) Excitation due to prey

b) Inhibition due to barriers



c) Summed excitation and inhibition

d) Time course

Fig. 3. Epstein's Prey Selection Model

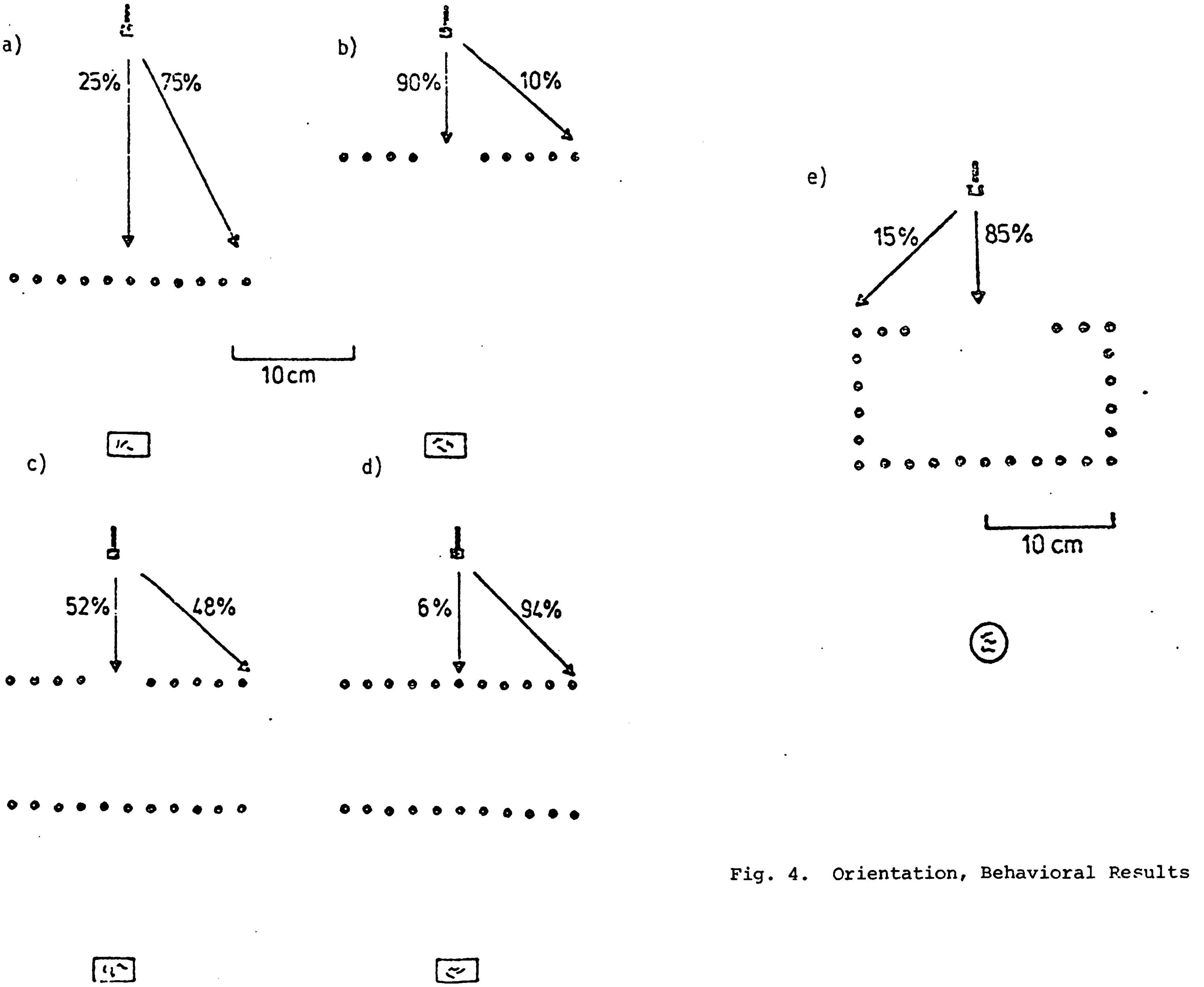


Fig. 4. Orientation, Behavioral Results

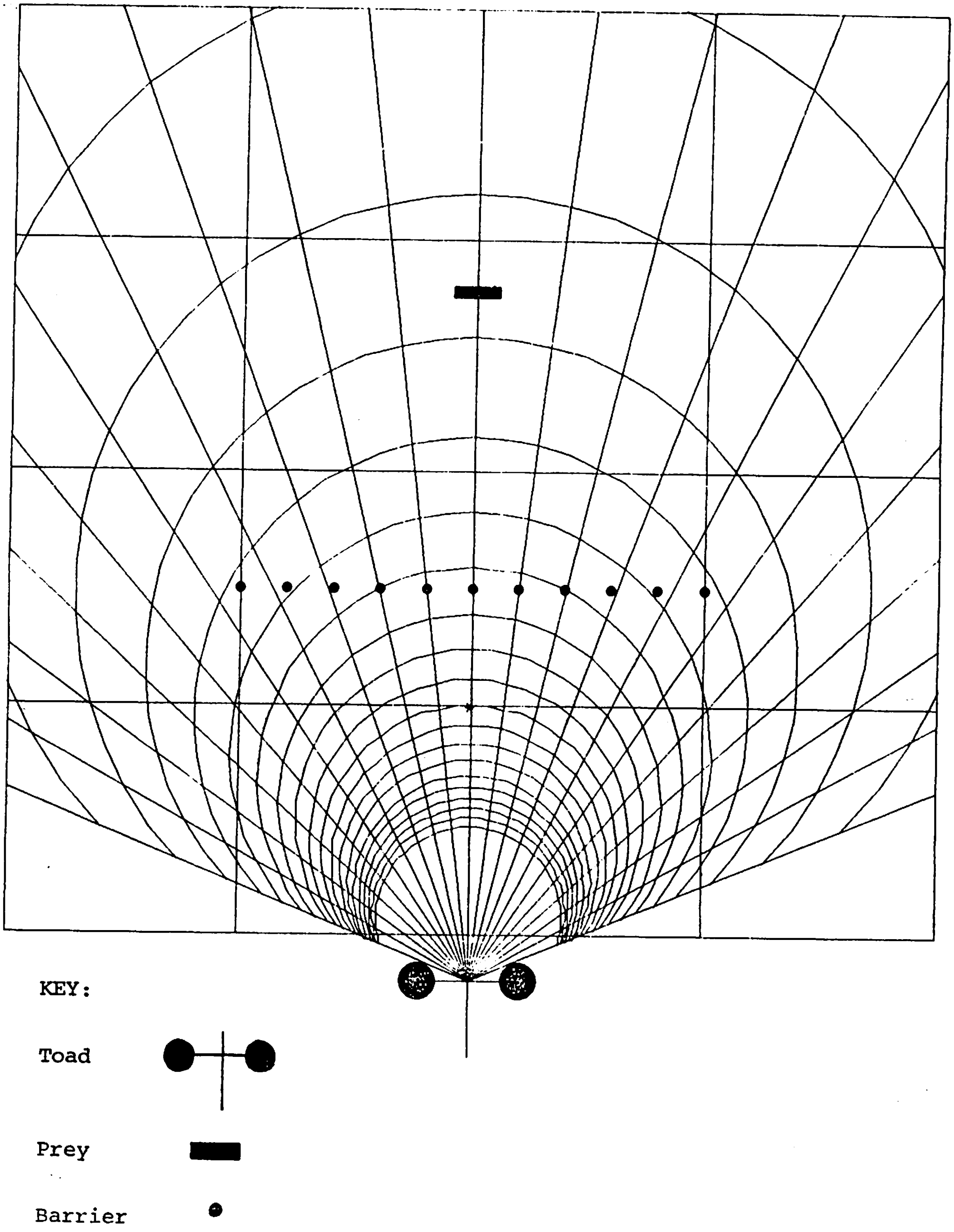


Fig. 5. Coordinate System Used for Orientation Models

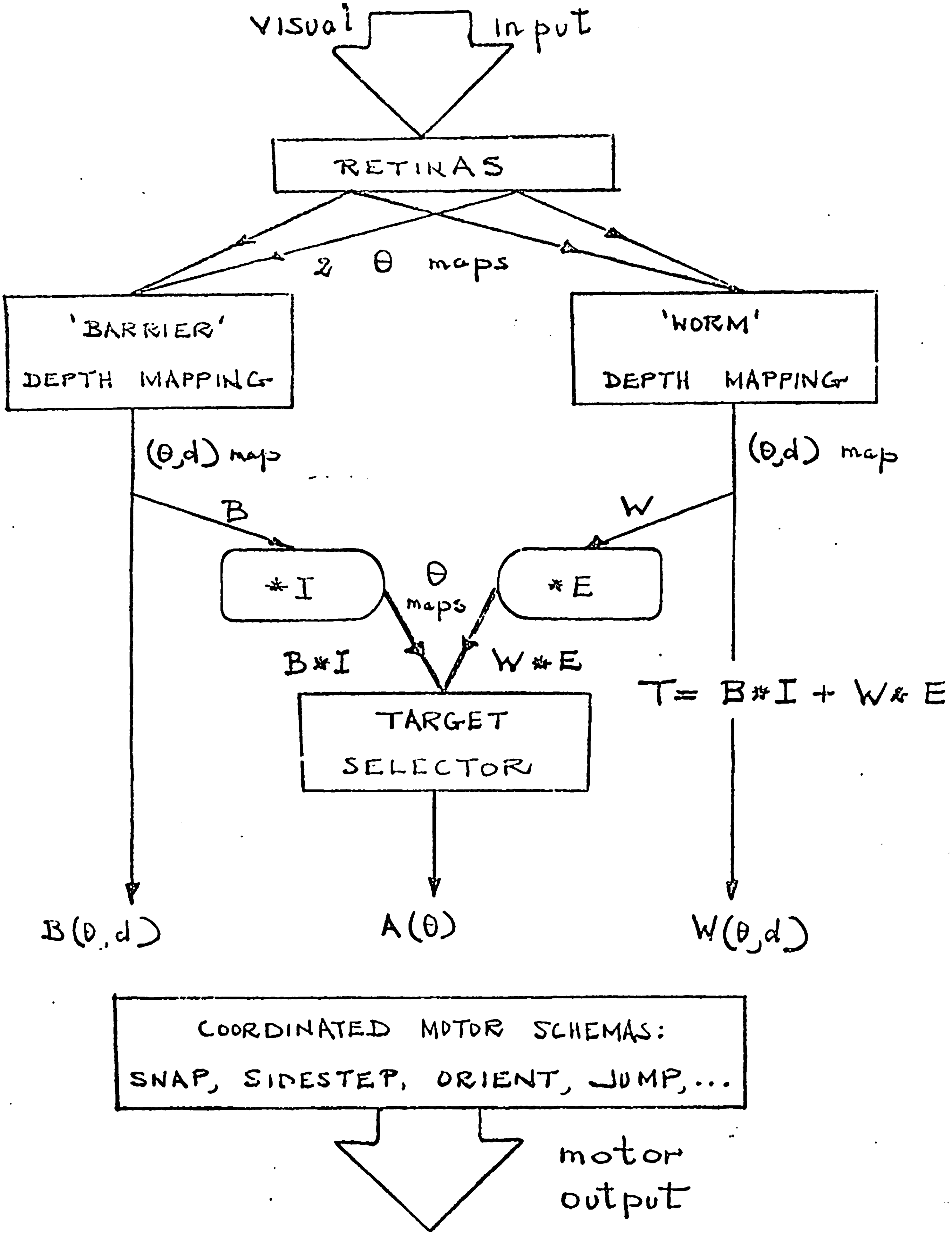


Fig. 6. Conceptual Schematic of Visual/Motor Pathway

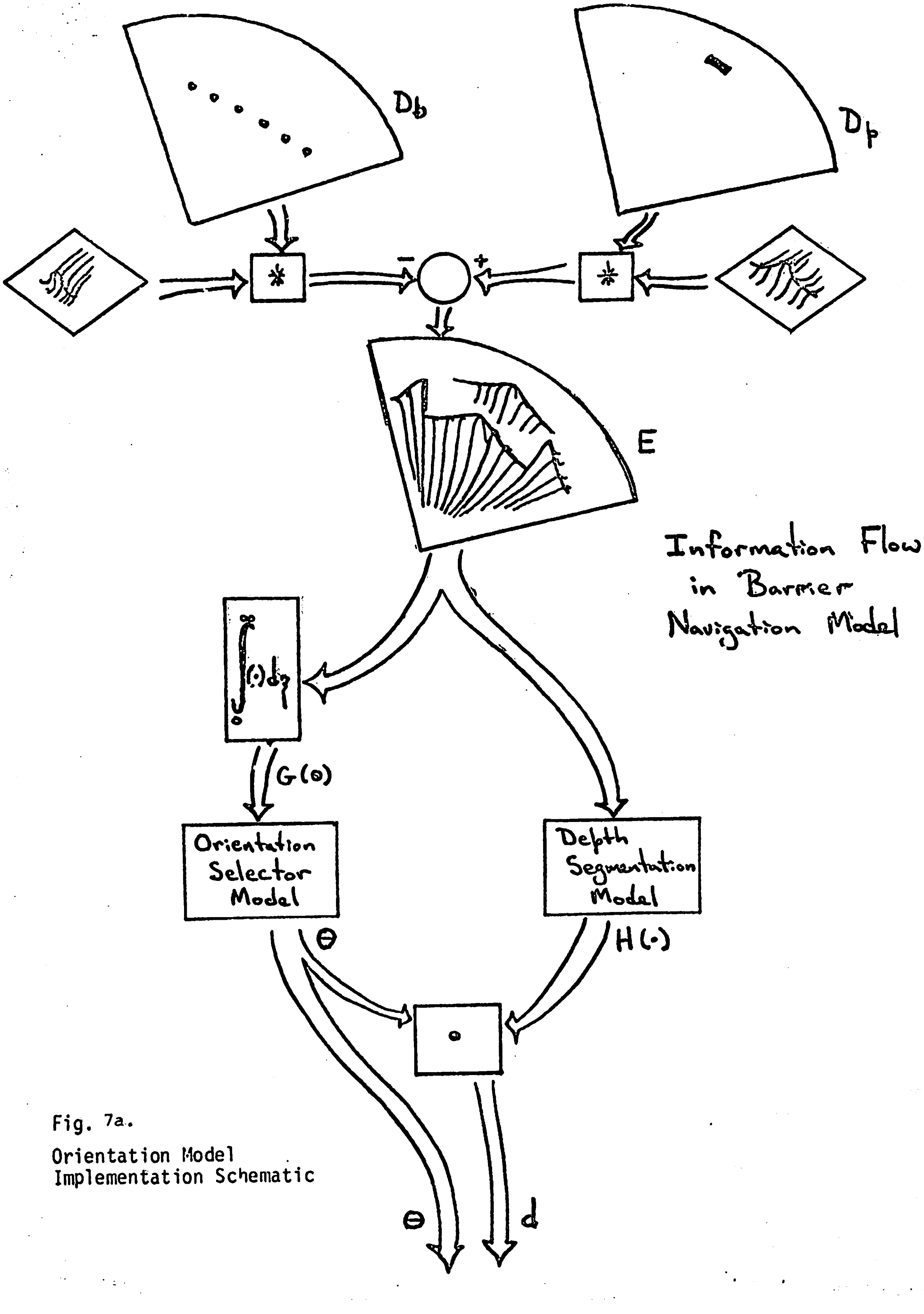


Fig. 7a.

Orientation Model Implementation Schematic

Spread of Excitation Due to Prey Object

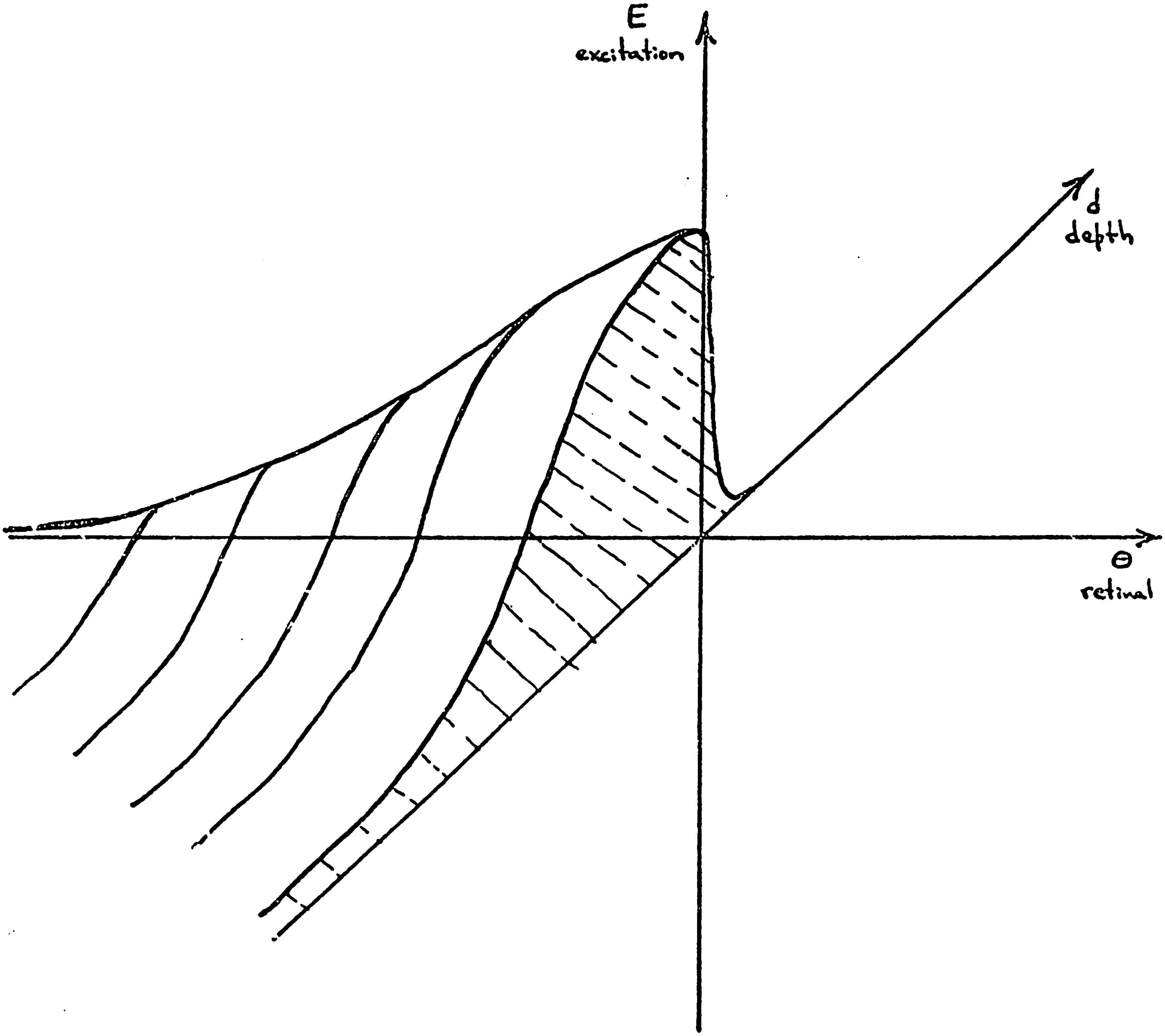


Fig. 7b. Prey Excitation Kernel (Cutaway)

Spread of Inhibition Due to Barrier Object

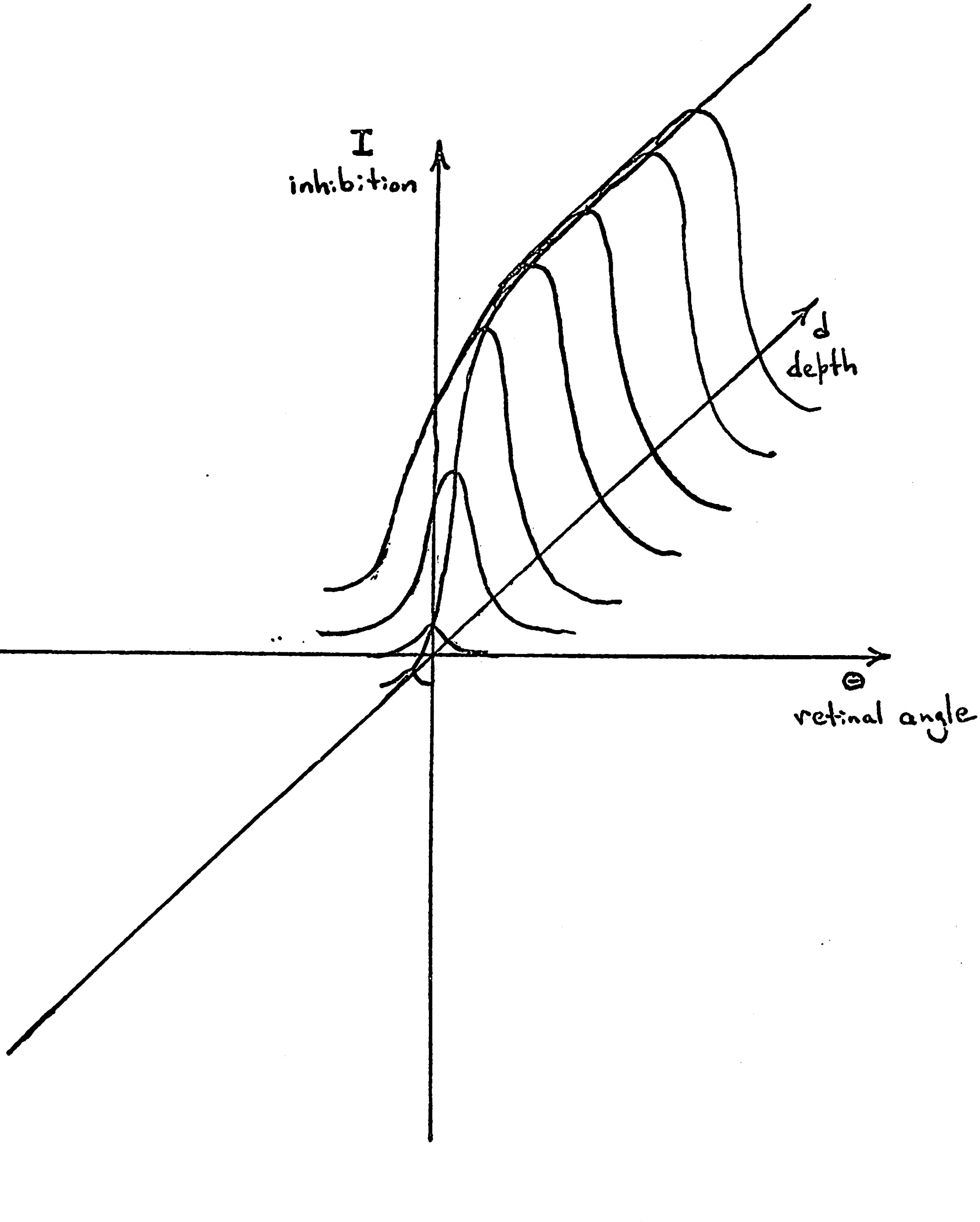
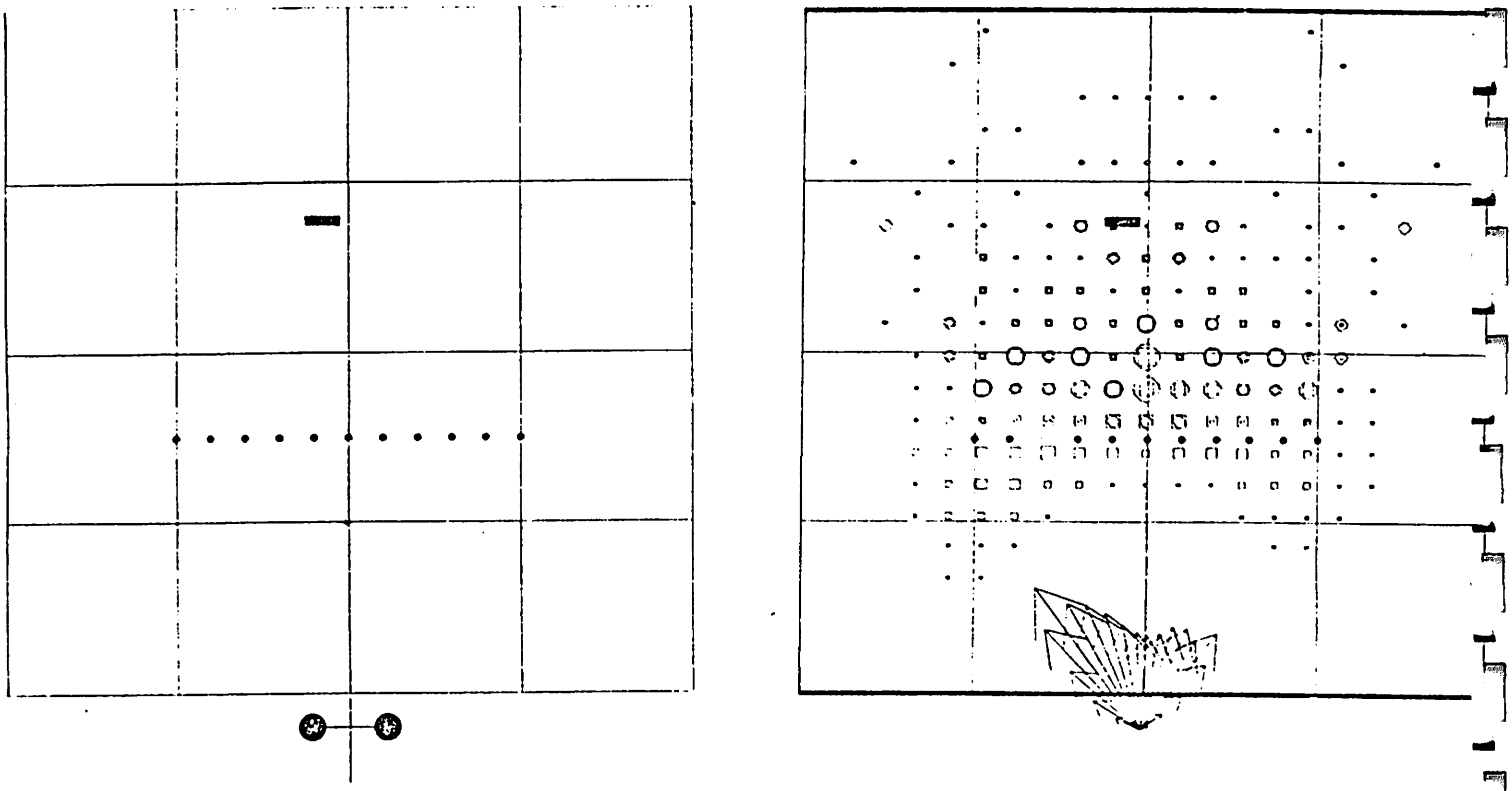


Fig. 7c. Barrier Inhibition Kernel



a) Prey/Barrier configuration

b) Model input

c) Model near equilibrium

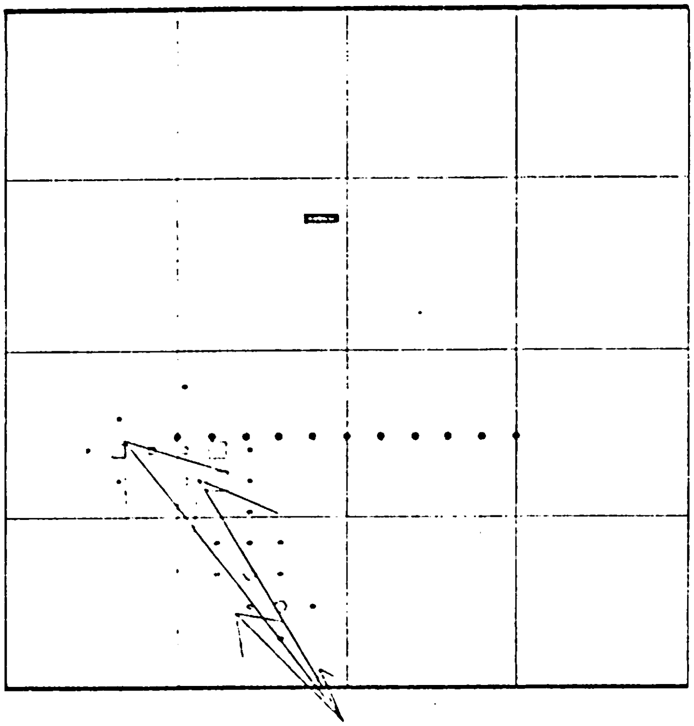
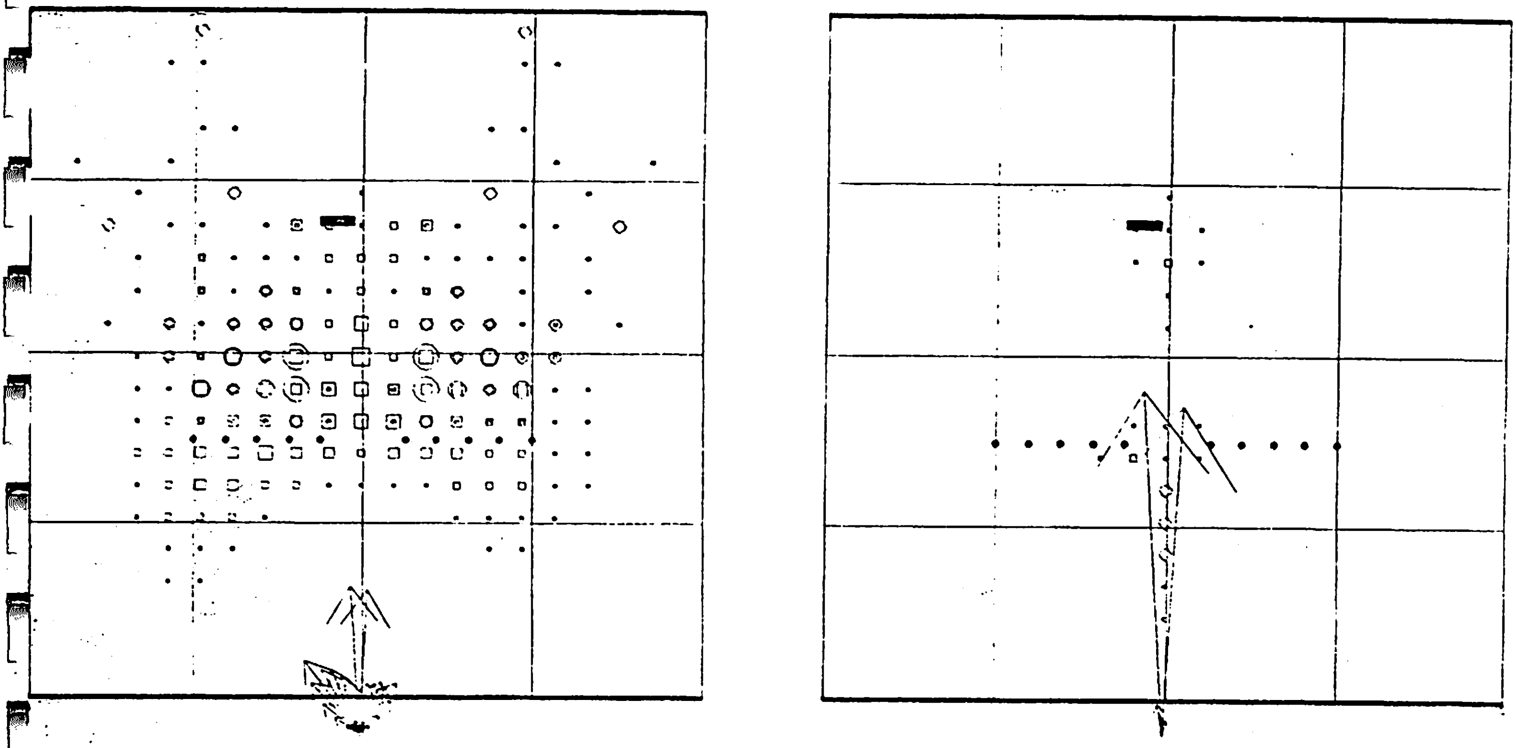


Fig. 8. Orientation Model, Test Case

INPUT NEAR EQUILIBRIUM

a) Fence with gap



b) Fence near prey

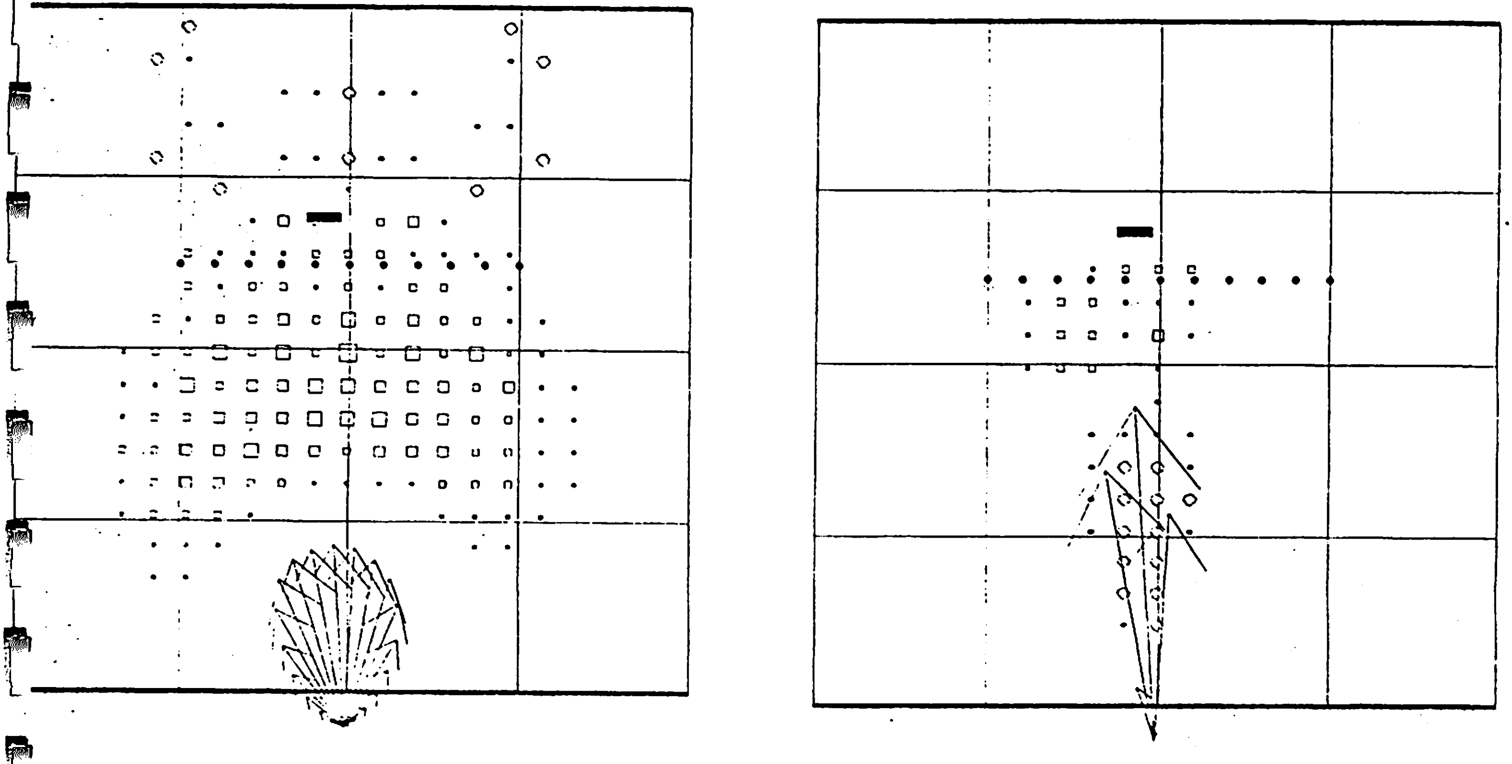
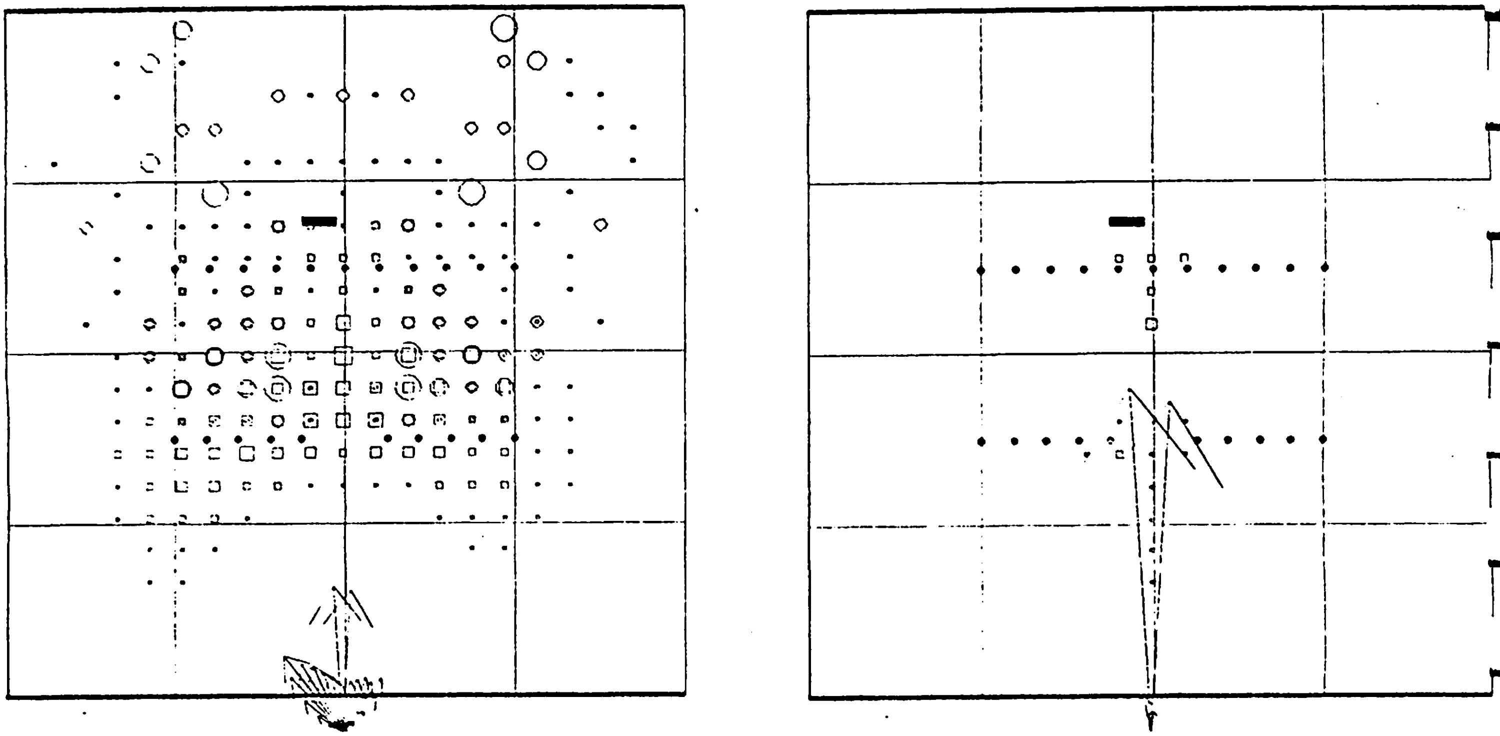


Fig. 9. Orientation Model, Comparison with Behavioral Experiments

INPUT NEAR EQUILIBRIUM

c) Fence with gap in front of solid fence



d) Cage

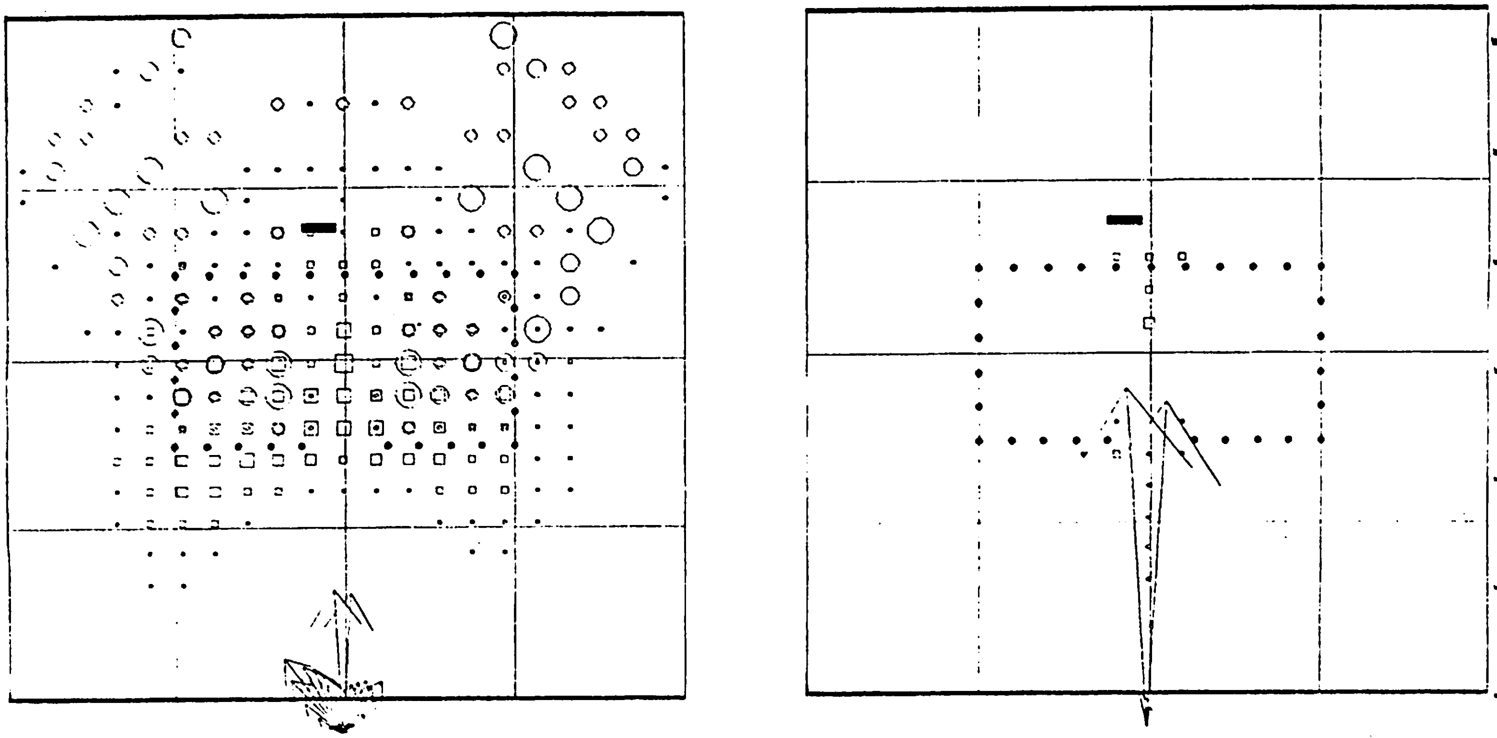
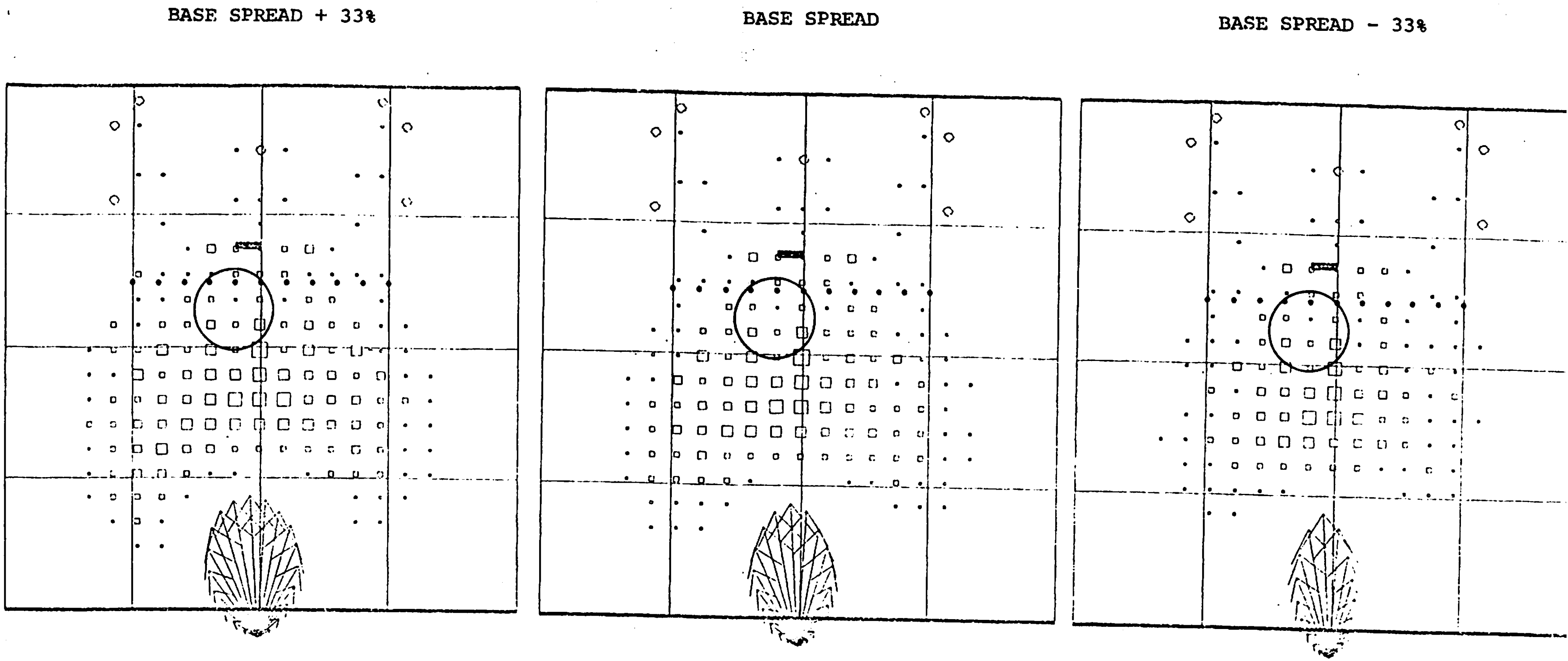


Fig. 9. (continued)

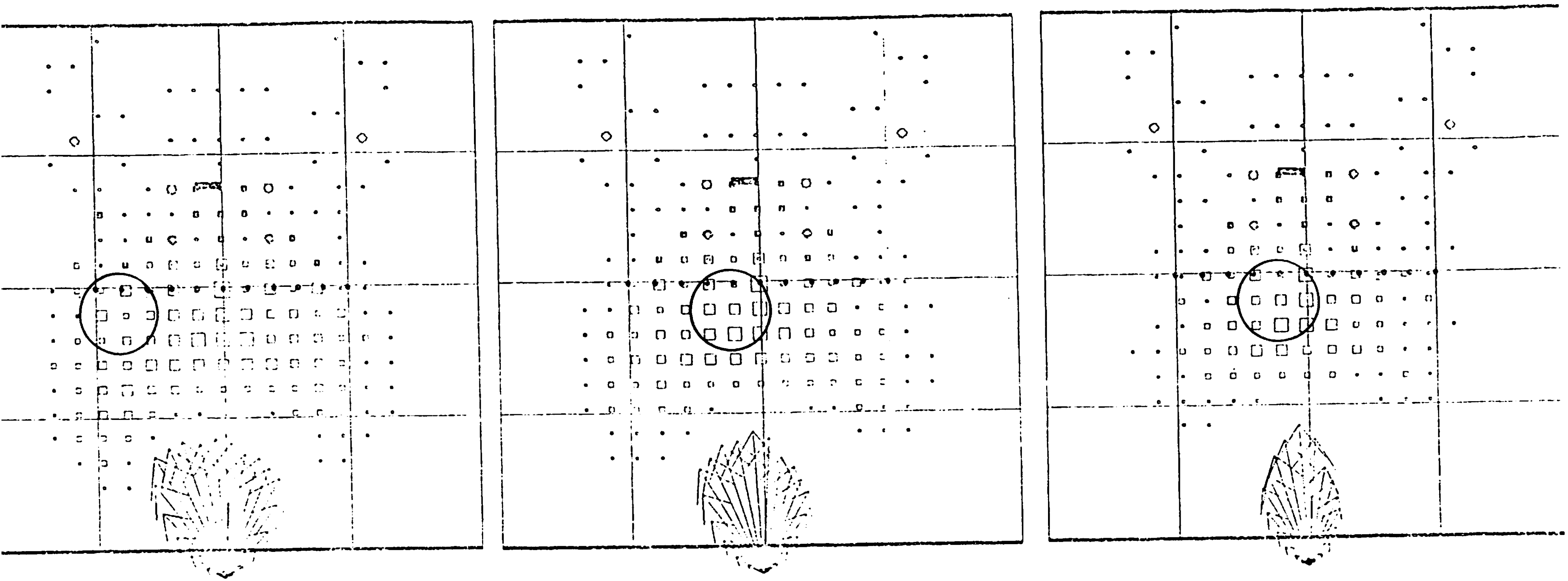


BASE SPREAD + 33%

BASE SPREAD

BASE SPREAD - 33%

Fig. 10. Model Performance for Various Fence Distances and Prey Spread Parameters

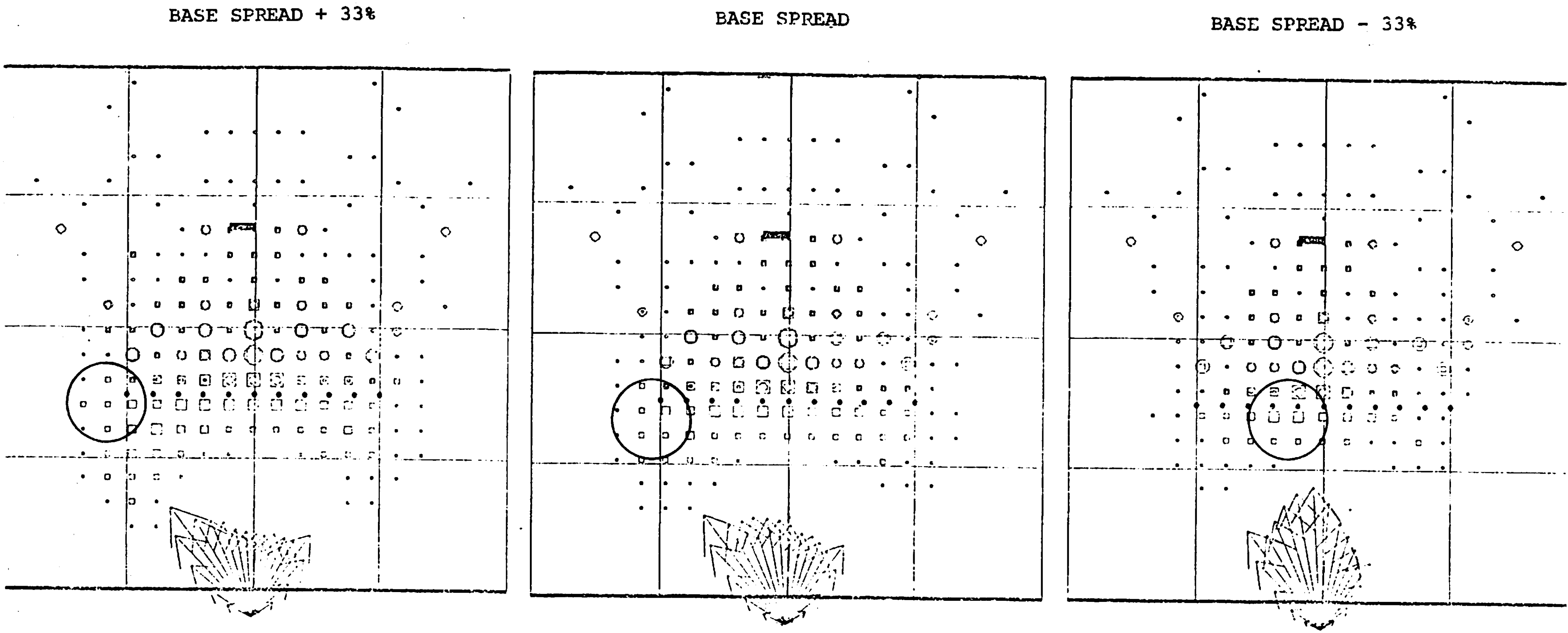


BASE SPREAD + 33%

BASE SPREAD

BASE SPREAD - 33%

Fig. 10. (continued)



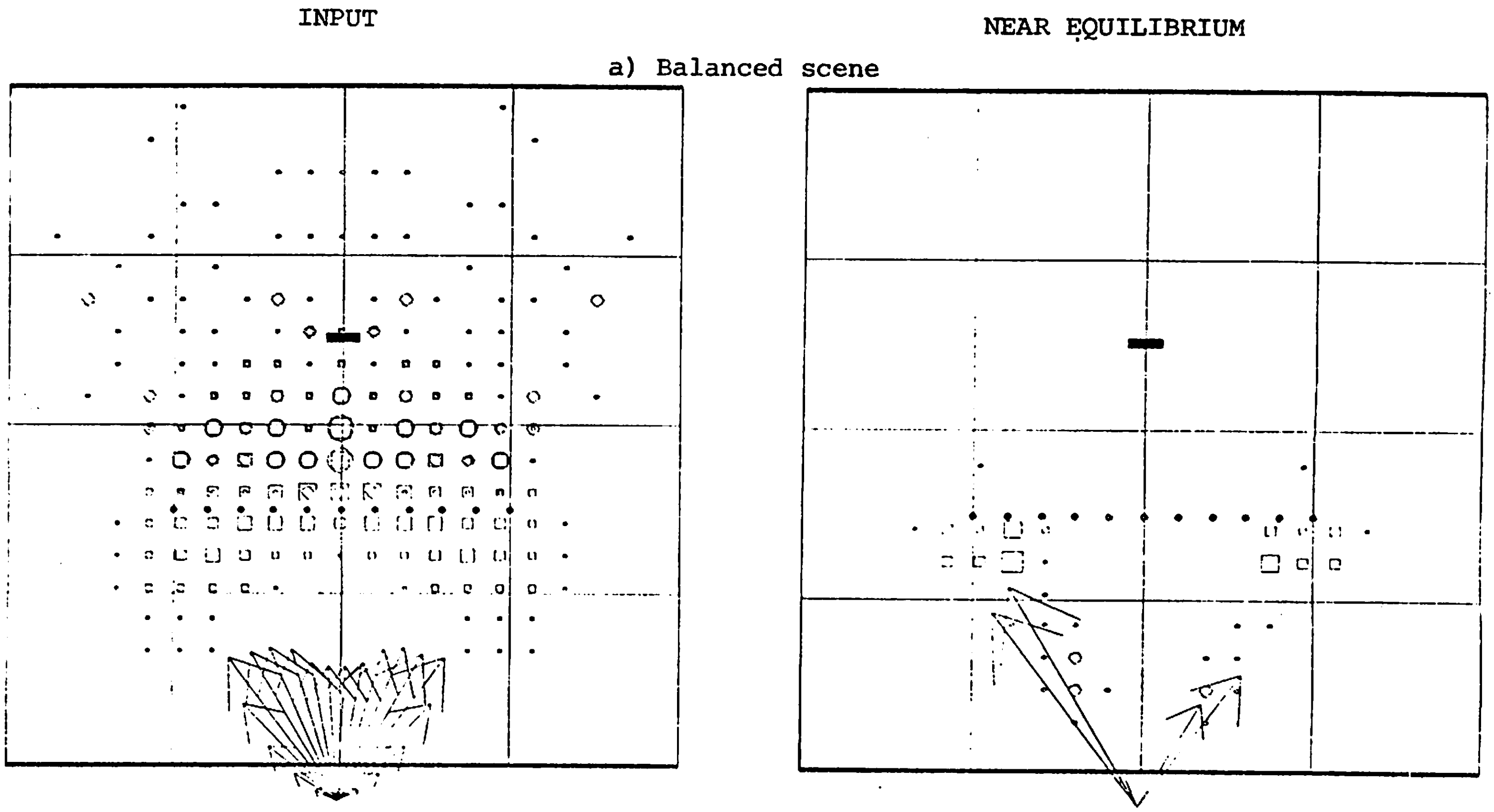
BASE SPREAD + 33%

BASE SPREAD

BASE SPREAD - 33%

Fig. 10. (continued)

a) Balanced scene



b) Prey off-center

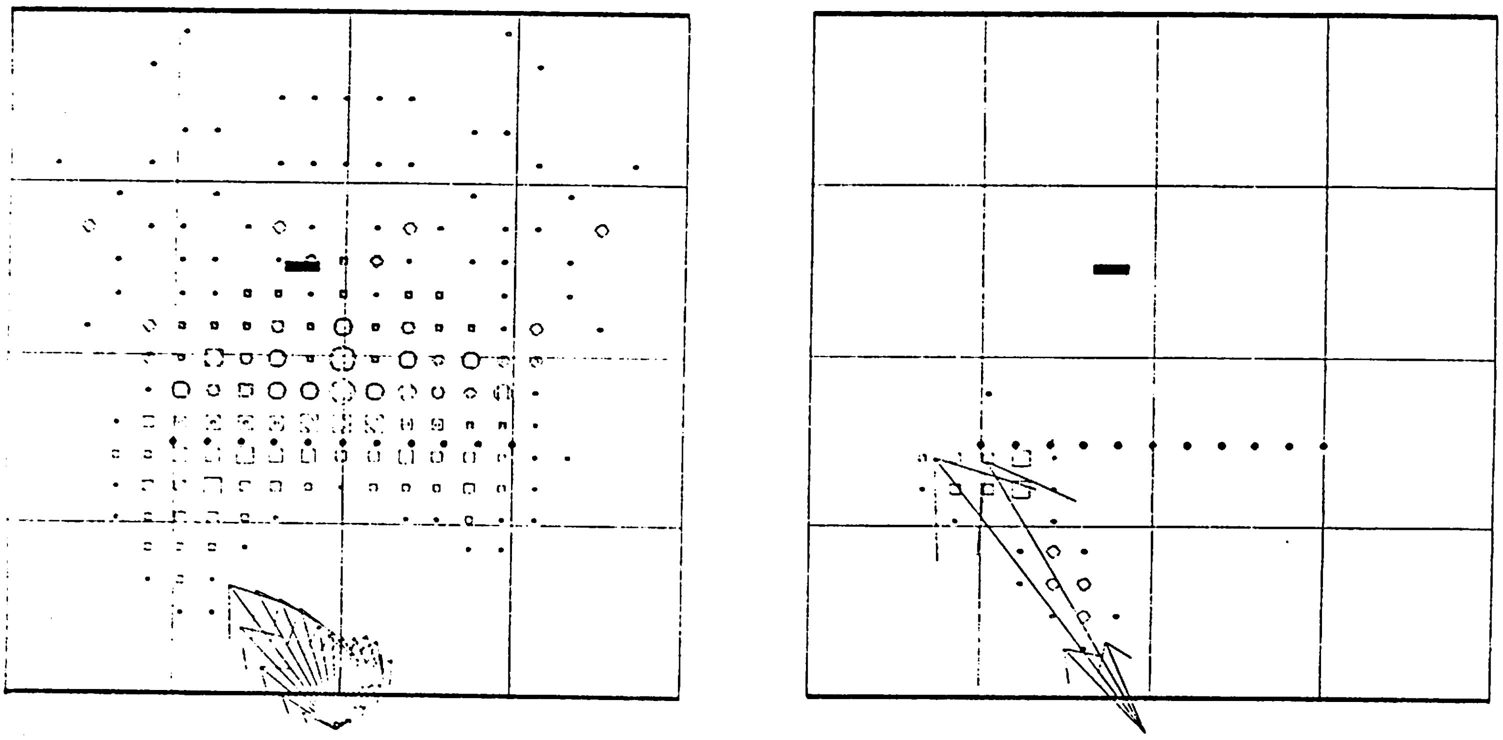
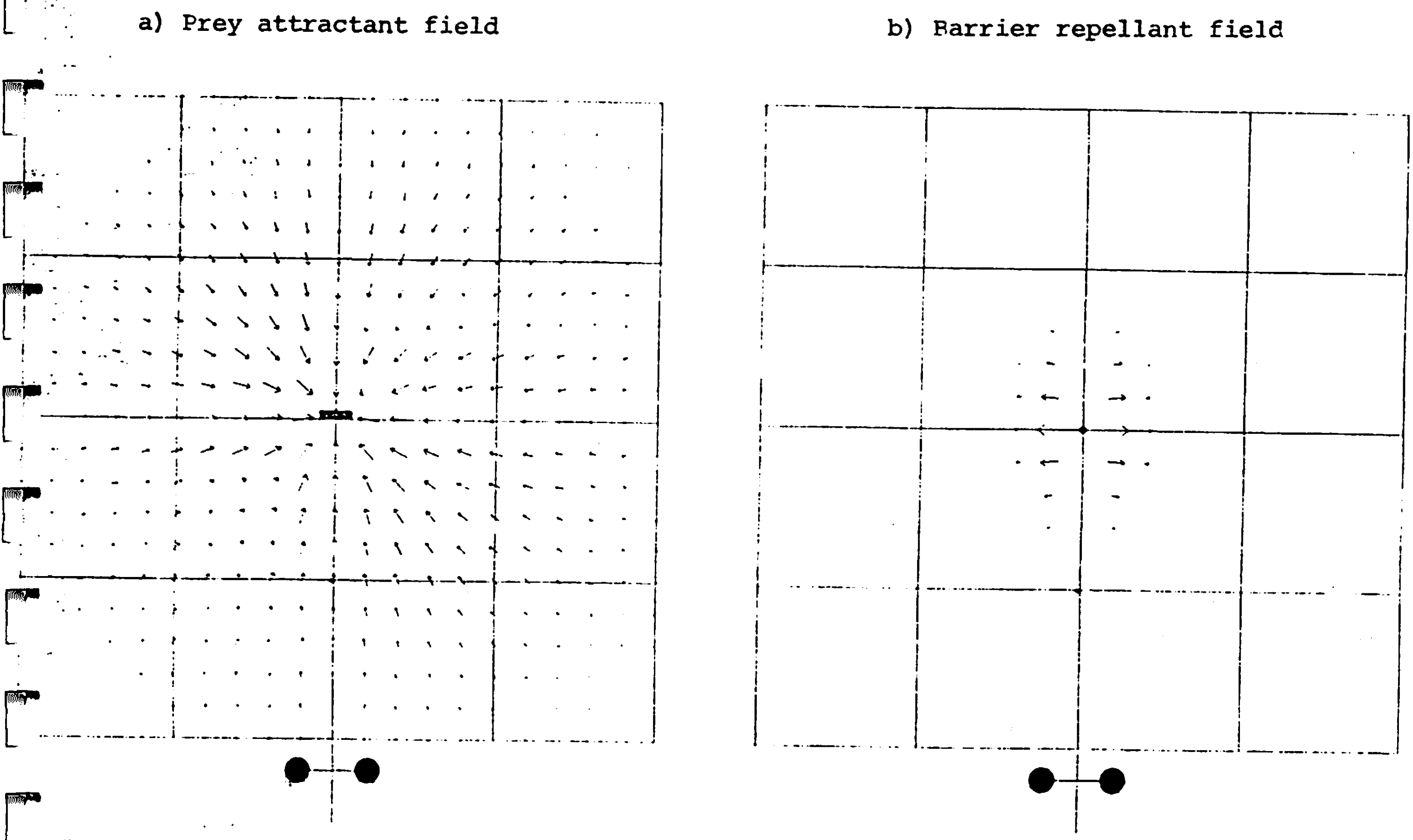


Fig. 11. Visual Balance vs. Selected Orientation



a) Prey attractant field

b) Barrier repellant field

c) Animal's self representation

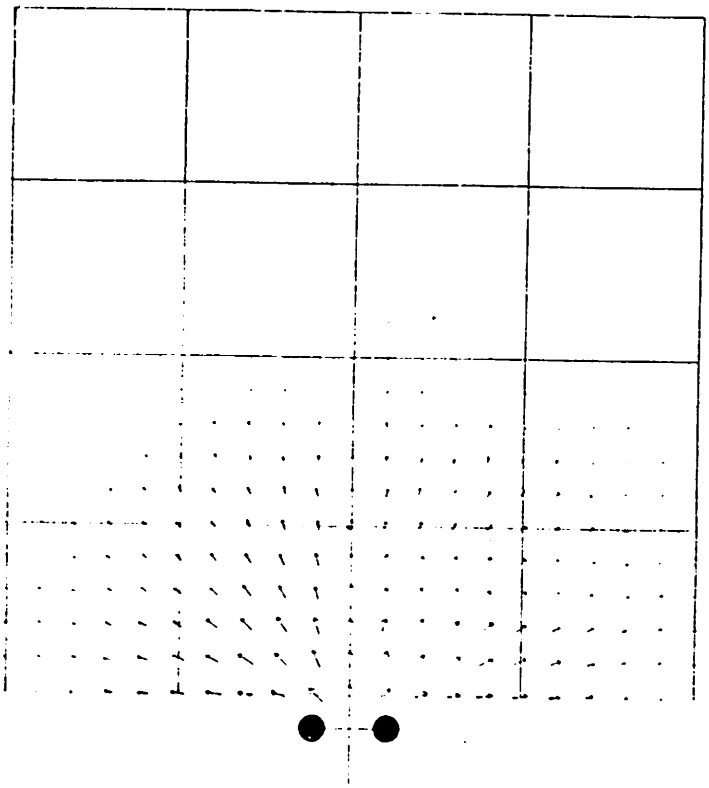
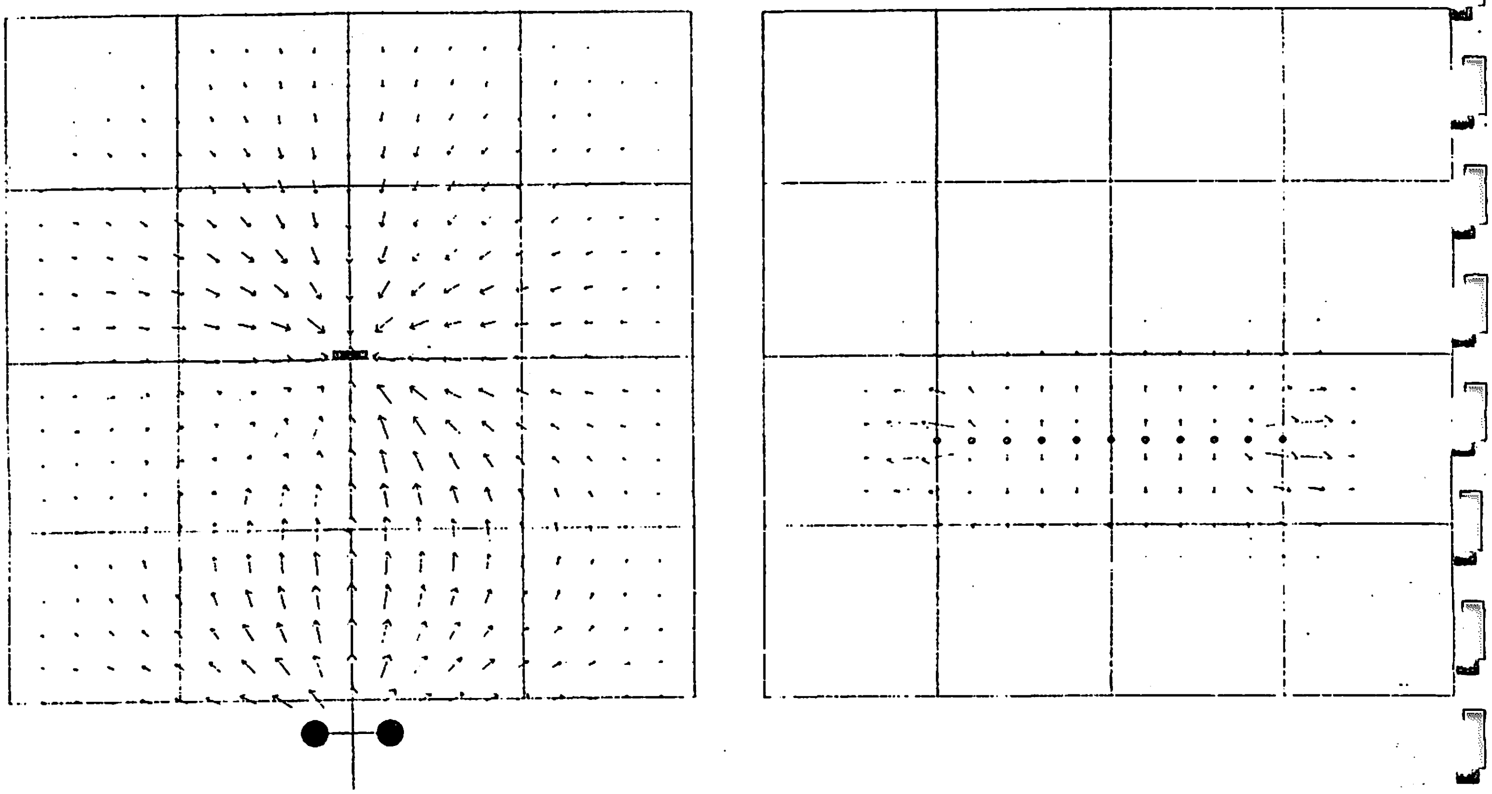


Fig. 12. Vector Field Model, Primitive Fields



a) Animal and prey

b) Barriers arranged as fence

c) Net field

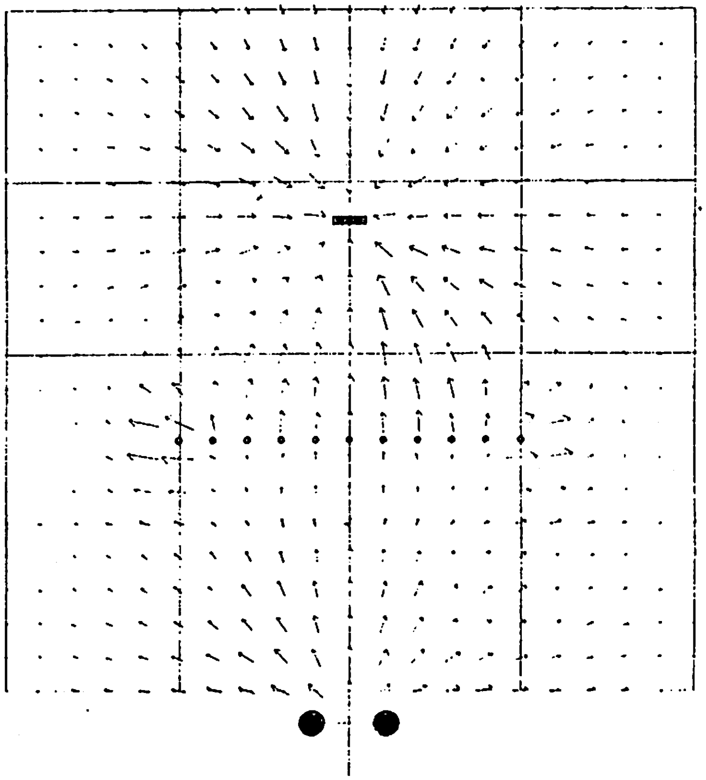


Fig. 13. Interaction of Primitive Fields

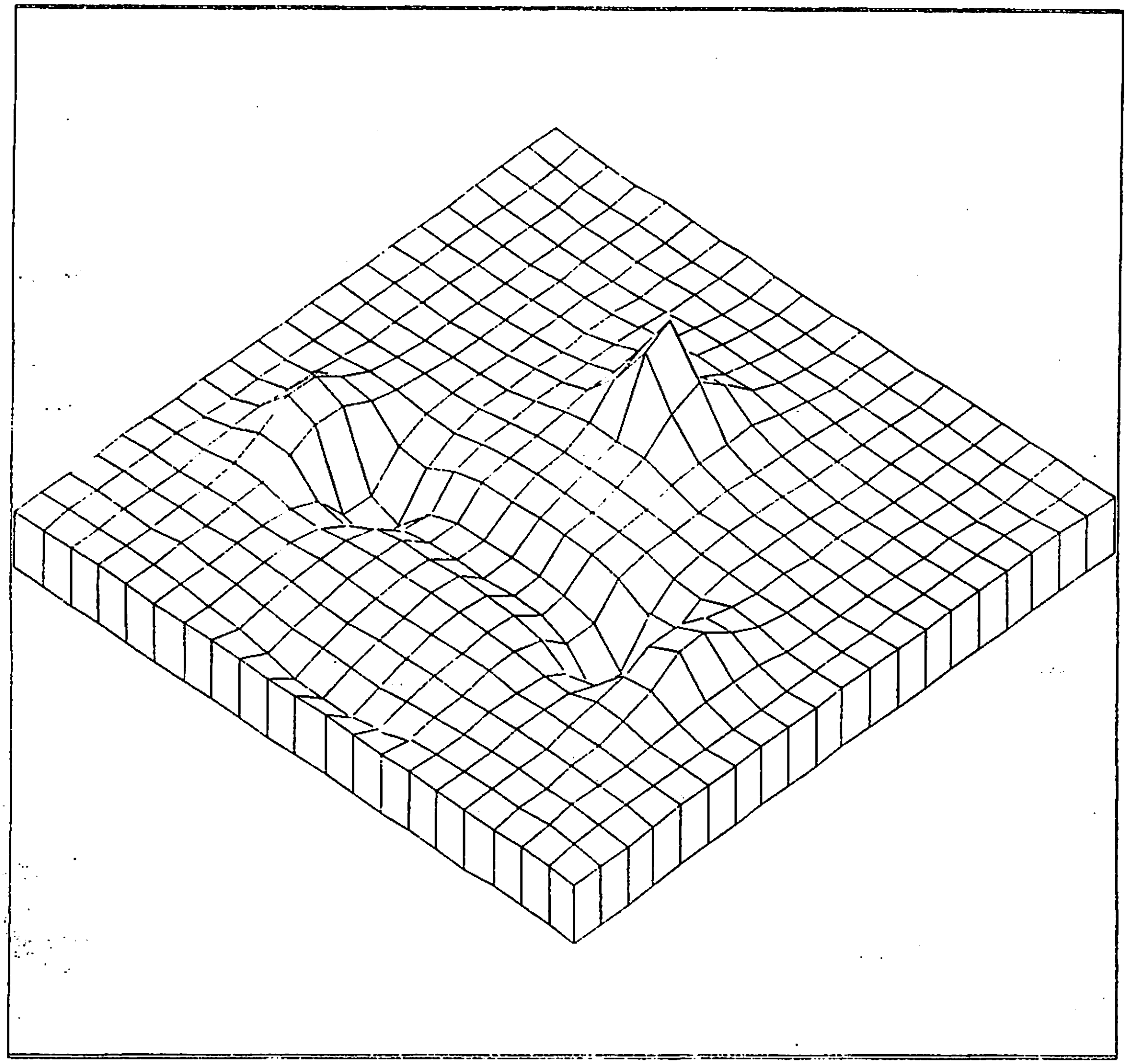
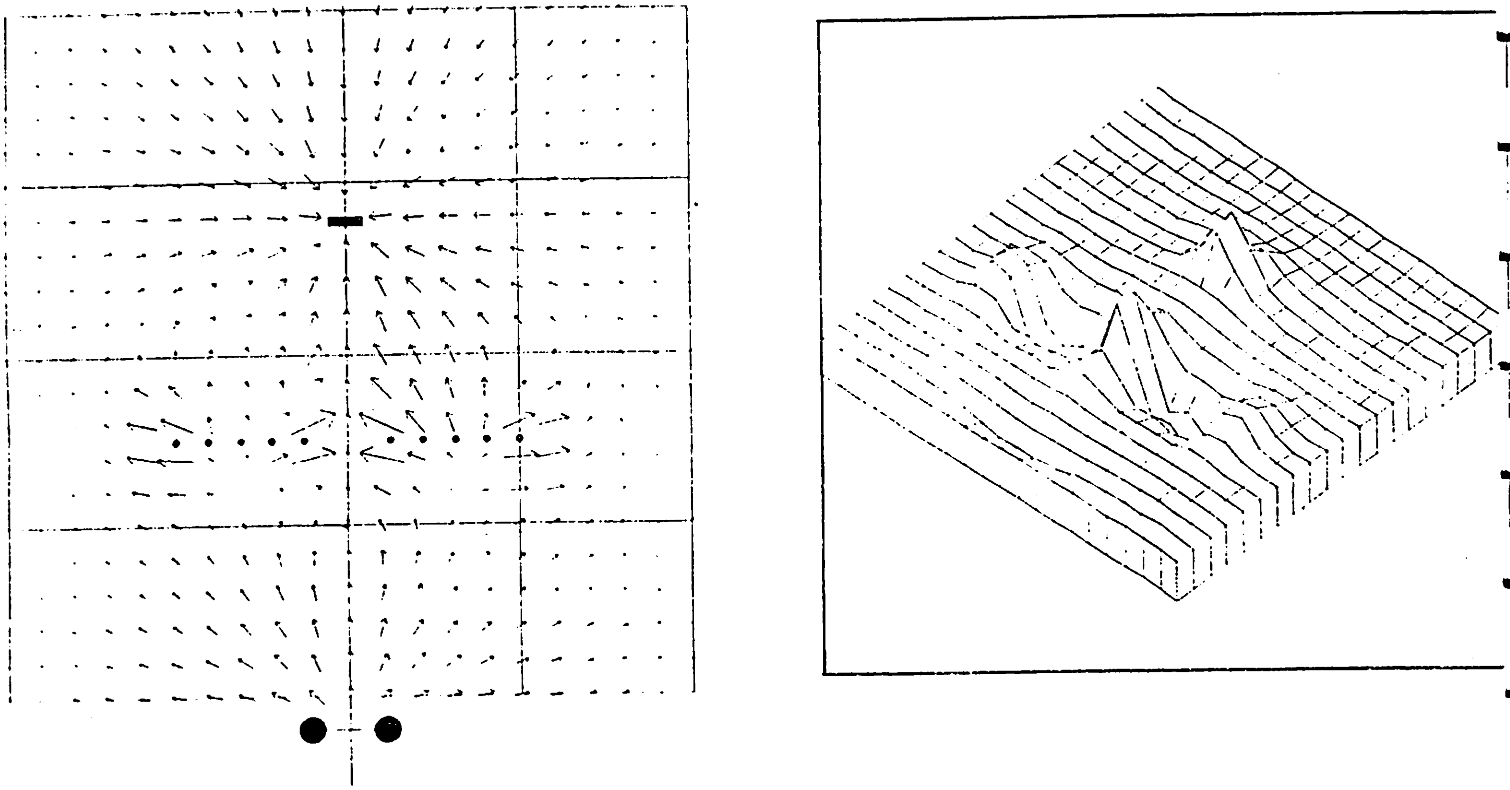


Fig. 14. Divergence of Net Vector Field

a) Fence with gap



b) Fence near to prey

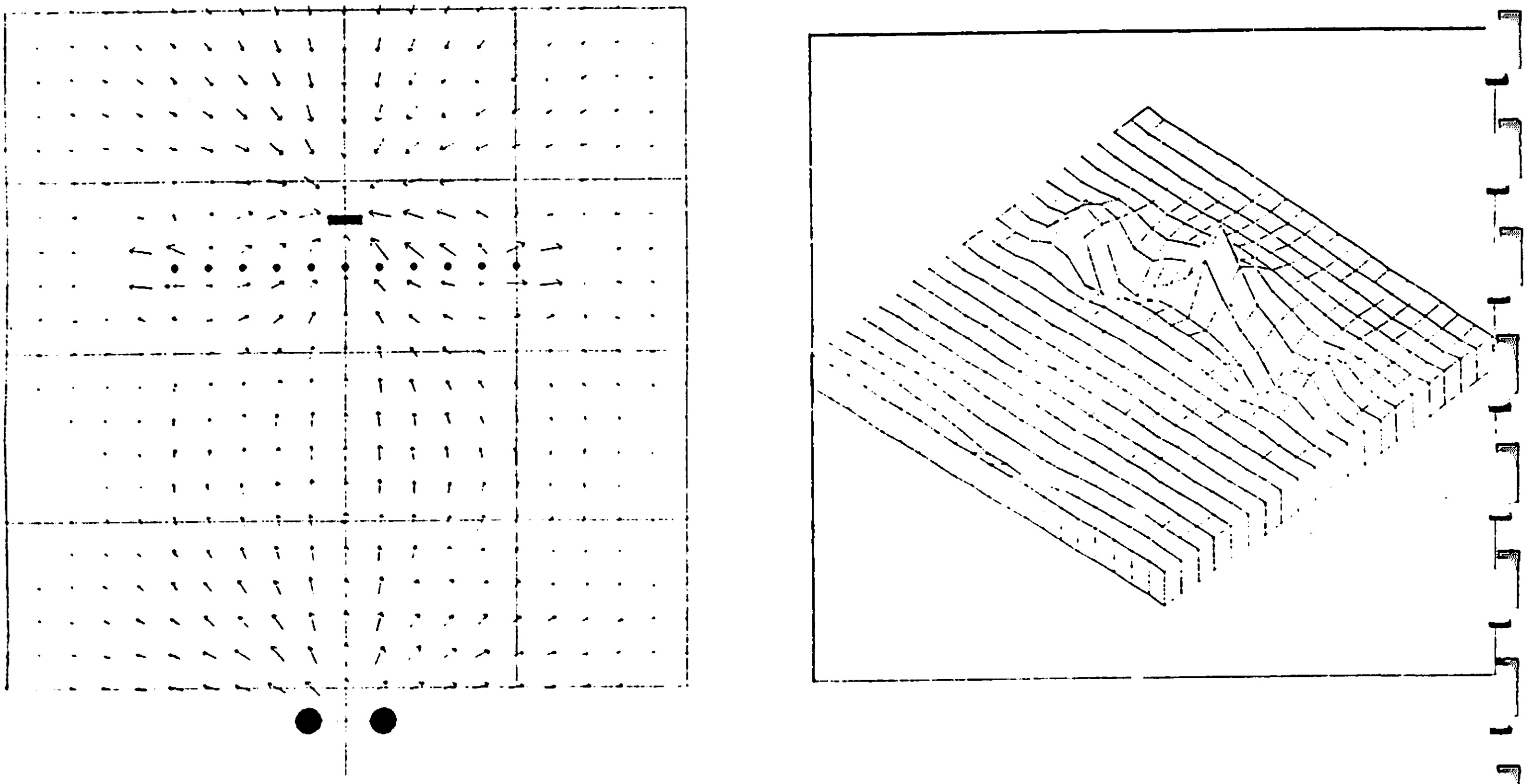
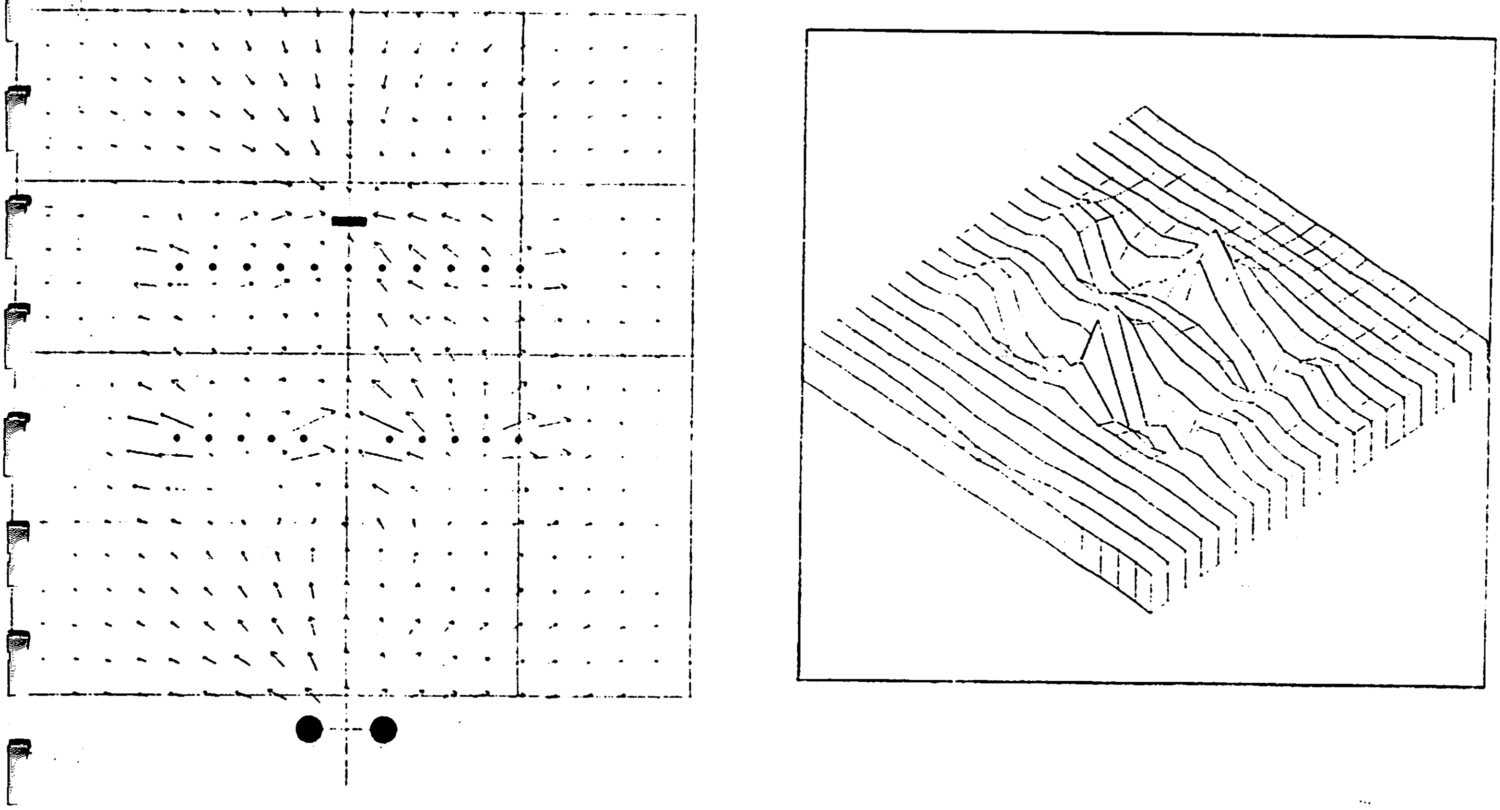


Fig. 15. Vector Model, Comparison with Behavioral Experiments

c) Fence with gap in front of solid fence



d) Cage

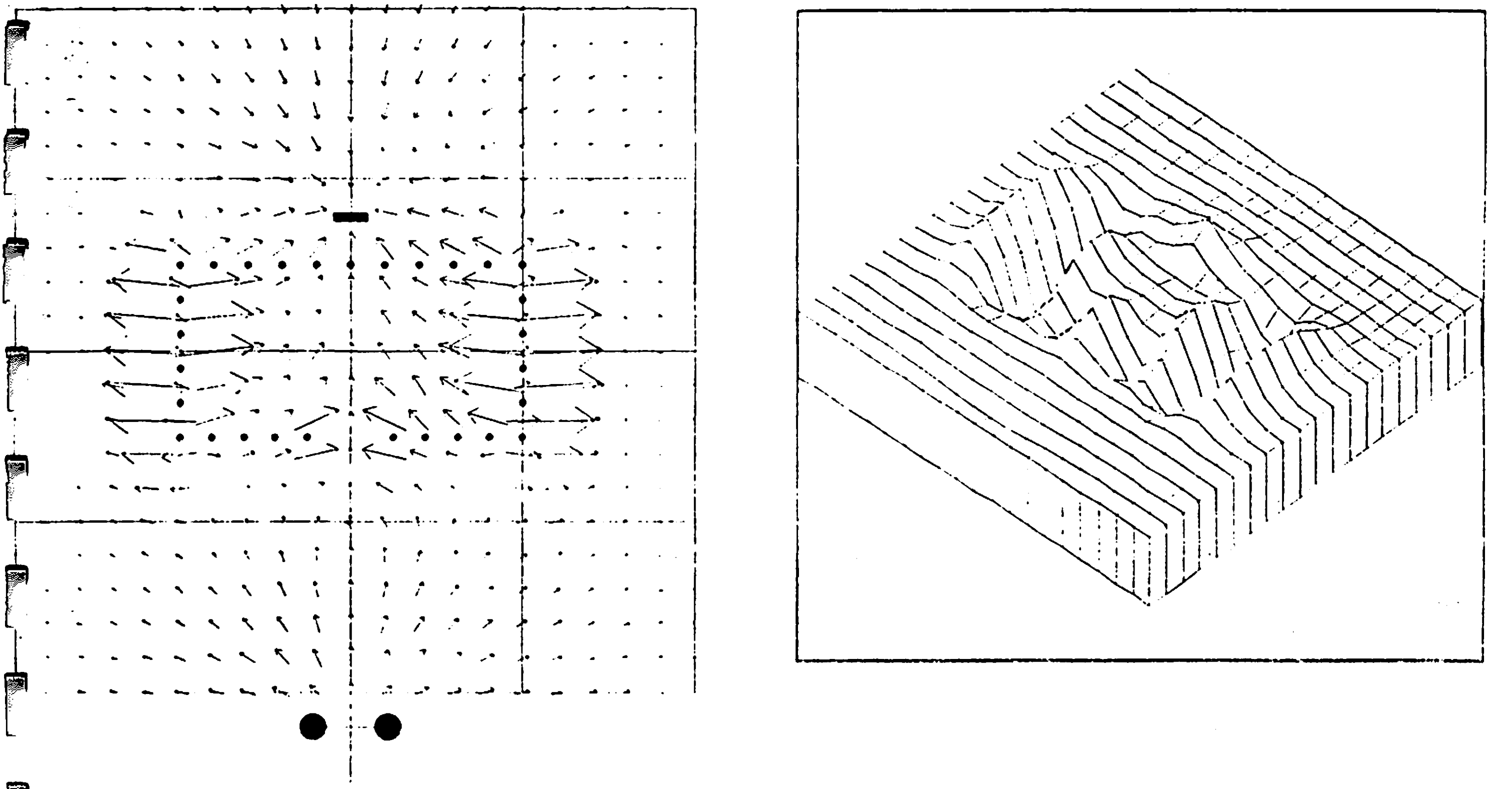


Fig. 15. (continued)

VISUAL NUCLEI AS A SOCIETY INVOLVED IN VISUOMOTOR COORDINATION IN TOADS

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INTRODUCTION

One of the main goals in the studies of artificial intelligence and robotics is the design and implementation of intelligent systems that can interact adaptatively with their surroundings.

Since the beginning of artificial intelligence, the way in which the nervous system processes information has been a source of inspiration for the design of more versatile and intelligent machines. However, this inspiration has been limited by the boundaries imposed by even the most simple processing of information.

Several disciplines, such as cognitive psychology (Bartlett, 1964; Piaget, 1947), brain theory (Arbib, 1978, 1980) and artificial intelligence (Newel and Simmon, 1972; Winston, 1979; Minsky, 1976, 1977) have proposed theories of the possible mechanisms of intelligence that allow an animal to interact adaptatively with the external world. These theories, however, do not contain enough detail to understand how the nervous systems performs these operations, or how these ideas may be implemented in the computer.

On the other hand, present neuroethological studies, done mostly in invertebrates (Kandel, 1976) and in lower vertebrates (Ewert, 1980), have allowed us a more informed guess as to the manner in which the nervous system processes information in order to control sensori-motor behavior. Based on these studies, several theoretical models proposing global theories of sensori-motor coordination have appeared (Ewert, 1982; Lara, this volume). These models, however, do not yet reach the prerequisite generality needed for the complex processing of information that give origin to the symbolic, more intelligent operations of higher vertebrates.

In the present paper, we propose a theory which integrates some general concepts on the processing of information by the nervous system, steming from studies on artificial intelligence, brain theory, cognitive psychology, and neuroethology that allow us to understand, in simple conceptual terms, how visuomotor coordination may be performed in toads (with the motivation of finding the fore-mentioned prerequisites), through its ease of implemention in the computer. This theory may be used either for the design of intelligent machines or for the visuomotor coordination of robots.

THE THEORY

The main postulates of our theory for the processing of information by the nervous system are the following:

1) Visuomotor coordination is the result of the interaction, in a Society of task-oriented hierarchy, of non-intelligent agents that process the visual information in a parallel, distributive way (Pitts and McCulloch, 1947; Kilmer, McCulloch and Blum, 1969; Piaget, 1947; Arbib, 1981; Minsky, 1977).

2) The same task can be performed by different communities of agents (Luria, 1973; Piaget, 1947).

3) The agents can have two functions: first, to recognize specific features of the stimulus in a symbolic scene version, thus acting as perceptual schemas, such as the "wormness" or "predatorness" of a given stimulus; and second, to perform specific motor actions (or 'methods'), thus acting as motor schemas that can be taken as preprogramed simple motor actions (Piaget, 1947; Arbib, 1981; Lara, this volume).

One should keep in mind that agents are constituted, after all, by a matrix of units, each unit is constituted by a group (net) of neurons with a specific function, thus constituting entities such as neural columns (Hubel and Wiesel, 1962; Lara and Arbib, 1982).

4) There is no common language among the communicating agents, but each agent can generate a data source (DS), from which other agents can pick-up needed information. The DS can be available to several agents (community), but not to all of them. (Minsky, 1977). The DS can store one of two types of information: features of the visual stimulus for selection by the motor schema (command system), or information for the performance of the selected motor schema (performance system) (Lara, this volume).

5) The processing of information of the interacting agents for a specific task give origin to what we may call (following Minsky, 1977) the short term memory (STM) of the nervous system, while long-term memory (LTM) is constituted by all the DS which potential agents, present for the control of a specific task, can eventually carry.

6) Potential conflicts between agents become problems to be solved by other agents which are in a higher hierarchy (Kilmer, McCulloch and Blum, 1969; Didday, 1976; Lara and Arbib, 1982; Lesser, Fennel, Erman and Reddy, 1975; Minsky, 1977).

7) In a nearby hierarchy, the agents have different functions: the highest agents designate the competitive-nuclei participants; depending on "context", the middle ones solve conflicts among nuclei by giving priority to competitors; and the lowest, generate data specific for the task. Agents with their DS used above their inputs are useful in analytic recognition; agents with outputs below their hierarchy level are "method" or "effector-like" (Minsky, 1977).

COMPUTER PROGRAMMING IMPLEMENTATION

We chose a functional programming language, LISP, for the implementation of our theory because we find a close matching between this language and the theory.

NOTATION:

Figure 1 shows the notation we are going to follow in order to discuss the programming.

1) The most general idea was to represent a function as a machine denoted by boxes, each carrying its corresponding name with its input and output specified. Since we used NILADIC functions, no input was present in the notation.

2) The DS variables are represented in the notation with their names encircled. When encircled inside a function, the variable was LOCAL; when encircled outside, GLOBAL.

3) Functions not considered as nuclei are represented as rectangles in the same plane as their master function. Satellite nuclei of a function are represented as if outside the plane of the master function, thus denoting independent anatomical location (chips ?).

4) A nucleus can call itself in a recursive sense and this recursiveness is represented in the same way as a satellite nucleus may be called, by loopingback to the same plane. (A shortened notation for this is a small circle surrounded by four arrows; each circle contains a letter indicating which box-corners the arrows are pointing to).

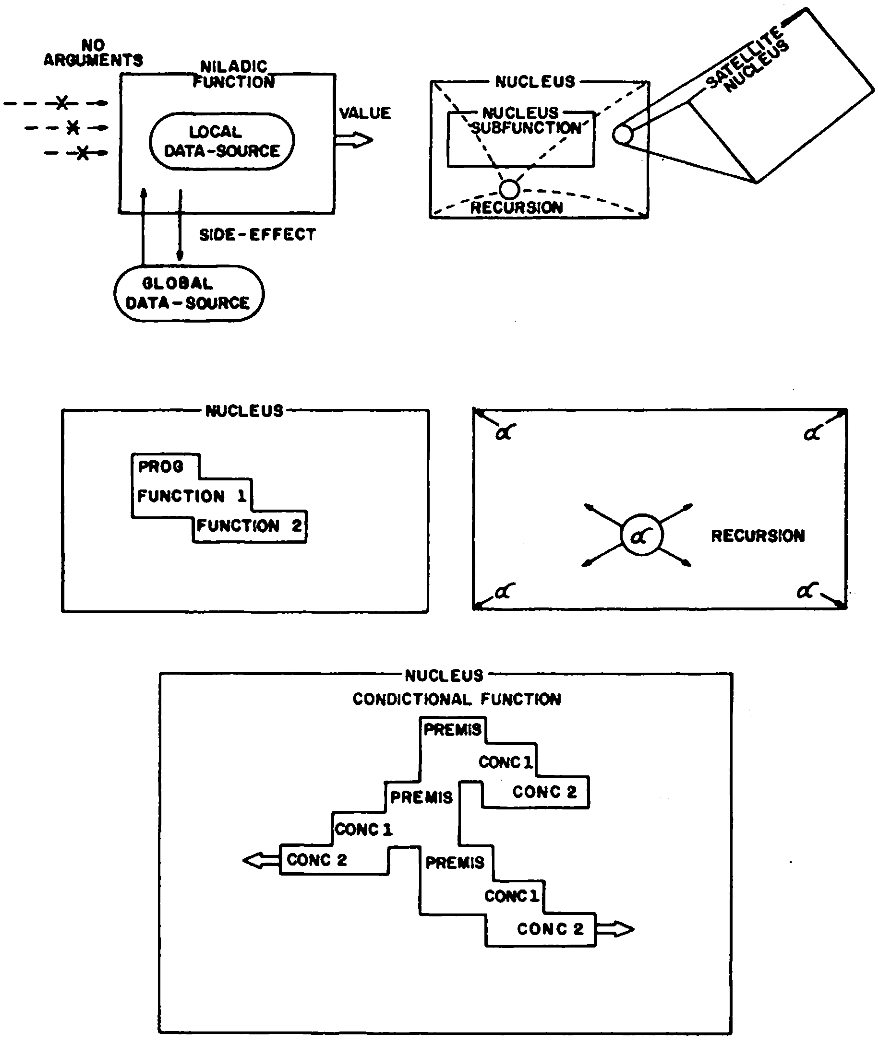
5) PROGram (sequential) functions were represented as a staircase-like contour and CONDitional (logic) function as a 'pine tree', the trunk of which was formed by the premises and the branches by the conclusions (represented by PROGram functions).

GENERAL IMPLEMENTATION

a) Nuclei were represented as functions.

b) Only NILADIC functions (without arguments) were used for the CNS pro-

FIG. 1


NO ARGUMENTS
NILADIC FUNCTION
LOCAL DATA-SOURCE
VALUE
SIDE-EFFECT
GLOBAL DATA-SOURCE
NUCLEUS
NUCLEUS SUBFUNCTION
RECURSION
SATELLITE NUCLEUS
NUCLEUS
PROG
FUNCTION 1
FUNCTION 2
α
α
α
RECURSION
α
α
NUCLEUS
CONDICTIONAL FUNCTION
PREMIS
CONC 1
CONC 2
PREMIS
CONC 1
CONC 2
PREMIS
CONC 1
CONC 2

gramming. The side effects of this functions, not their values, were used as DS generators.

c) CNS lesions were simulated by NOT-ALLOWING the information from the lesioned nuclei to become part of a DS.

d) CNS stimulation was simulated by USER information introduced in a DS.

e) Microelectrode information was considered as machine-language expression of a member of a DS or as a machine-language argument of a generating function of a DS member. This proposition was not implemented.

f) The work-space of the functional language in a micro-computer was used as the STM residence and diskette memory as the long-term-memory.

g) Nucleus functions were not LISP DEFINed functions, but LAMBDA expressions to be APPLYed. This was done in order to simulate their vanishing from STM when not called.

h) Figure 2 represents the typical module of our programming, in which we can define three main functions. The first, denominated MASTER, defines the nuclei that will be activated (COMPETITORS), and the threshold levels for each of the competitor function; it also activates the second function DECISOR. The second function uses the DS (of COMPETITOR names) to bring them in to play. First, COMPETITOR1 which gives a scene version and is then compared with its respective threshold level to define if it will or will not give a response (command system). If no response is obtained, then COMPETITOR2 is called into action (not shown in the figure). COMPETITOR2 also gives a scene version which is then compared with its threshold level to give a response. If the threshold is not reached, then DECISOR calls a function denominated SOLVE, which changes the threshold values of the competitors and again call DECISOR. If none of the nuclei gives a scene version which reaches the threshold value, then no motor response is obtained and the function

MASTER is again called to restart a new visuomotor processing.

PREY-PREDATOR RECOGNITION IN TOAD'S BRAIN AS AN EXAMPLE OF THE IMPLEMENTATION OF OUR THEORY

Figure 3 respresents a detail of the third level of the model of prey-predator recognition in toads when the MASTER function has chosen TH-3 cells and TECTAL-COLUMNS as the competitors nuclei. In order to have its scene, TH-3 calls GANGLION-III cells. If the scene value does not reach the TH-3 possible-action threshold, no action is taken; it passes the AVOID threshold, an AVOID action is taken. If the scene value lies between the afore mentioned thresholds, then TECTAL-COLUMNS is called. If TECTAL-COLUMNS decides to act, but the scene value is below ORIENT threshold, then a T value results in the calling of the SOLVE function. This function will redefine the threshold values in order to get a response, either ORIENT or AVOID.

When no action is generated by TH-3, then a NO-ACTION function calls TECTAL-COLUMNS in which the process is repeated.

Please note that the serial calling of COMPETITORS is a programming simulation of a parallel, simultaneous competition.

SUMMARY AND CONCLUSIONS

I) An AI CNS function theory was proposed and assayed in an amphibian model: neuroanatomical, neurophysiological, and ethological phenomenology associated with visuomotor-coordination in toads.

II) Amphibia CNS programming can be simulated within the theory with a modular structure of three hierarchical levels of nuclei: the nuclei in the highest position designate the potential conflicting nuclei; the middle ones solve the possible conflict; and the lowest are the conflicting agents themselves (i.e., TH3-CELLS and TECTAL-COLUMNS).

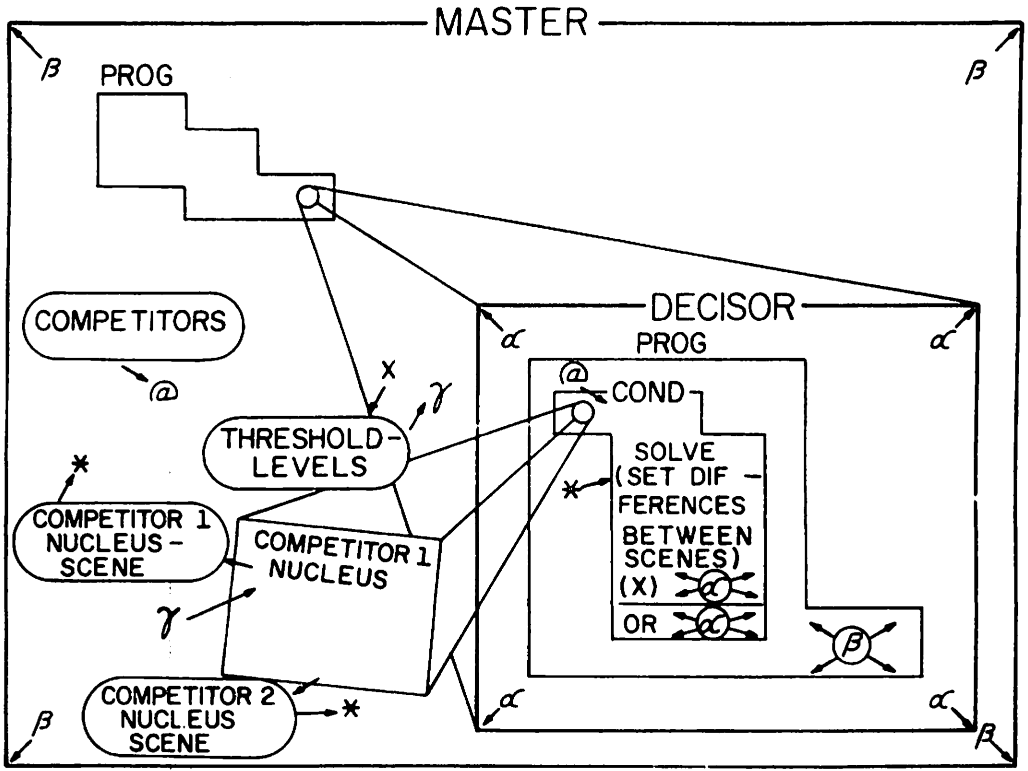

MASTER
β
β
PROG
COMPETITORS
@
X
γ
THRESHOLD-LEVELS
DECISOR
α
α
PROG
@
COND
SOLVE (SET DIFFERENCES BETWEEN SCENES) (X)
α
OR
α
β
*
*
COMPETITOR 1 NUCLEUS-SCENE
COMPETITOR 1 NUCLEUS
γ
COMPETITOR 2 NUCLEUS SCENE
*
β
α
α
β

FIG. 2

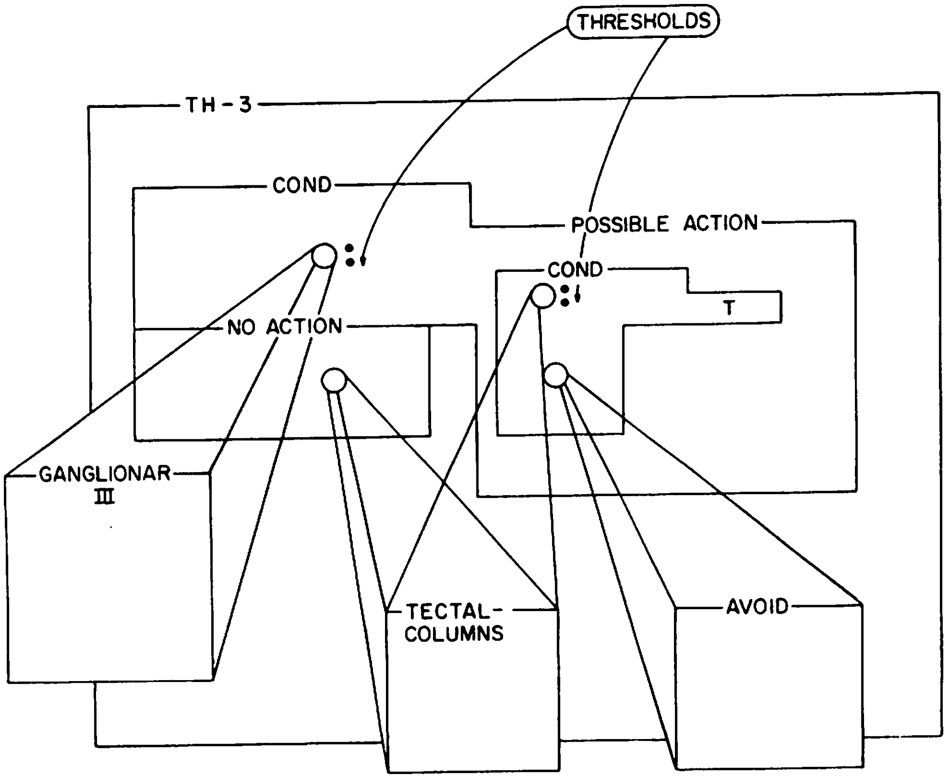

THRESHOLDS
TH-3
COND
POSSIBLE ACTION
COND
T
NO ACTION
GANGLIONAR III
TECTAL-COLUMNS
AVOID

FIG 3

III) In every case, it was possible to consider a module as recursive.

IV) The visual world of Amphibia was considered as being distributed by CNS in several symbolical versions (scene-versions or perceptual-schemas), resident in data sources (DS) of nuclei specialists. These versions were used for nuclei decisions (command system), thus resulting in prey-predator behavior through a performance system.

V) A given scene-version was resident in the common DS of the interacting nuclei in the STM.

VI) The competence level of this proto-model extends to lesions, visual-stimulation, electrical-stimulation, and behavior.

VII) From the AI point of view this CNS programming simulation is a deep-first ACTION-OR-METHOD search with the provision of a lower OR-exclusive situation in which an upper mechanism sets the potential lower OR situations. OR situations are decided first by exclusive competition and, then on "draw" conditions by an upper level.

VIII) The present theory does not yet deal with the problem of the creation or transformation of nuclei due to experience. Clues may be found by attempts to incorporate habituation and learning within the second postulate of the theory.

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A GLOBAL MODEL OF THE NEURAL MECHANISMS RESPONSIBLE FOR VISUOMOTOR COORDINATION IN TOADS

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(Second draft, January, 1983)

ABSTRACT

A model of how the nervous system of toads process the visual information to control the motor response is proposed. The model tries to integrate the anatomical, physiological, and behavioral studies done in these animals to postulate specific hypothesis that could be tested experimentally. The model postulates that the visual information is processed in a parallel, distributive way by a multiple group of layers whose interaction give origin to a command and an information channel which choose and control the proper motor action, respectively. The group of layers can be divided in: perceptual, command, information, and motor layers. The motor output is the result of the coordination of simple motor actions that we call motor schemas.

INTRODUCTION

It has been of interest for philosophy and science to understand the means by which animals, including human beings, are able to cope inteligently and adaptatively with the external world, from the sensori-motor intelligence of invertebrates and lower vertebrates to the symbolic attitude of the most developed vertebrates. Problems initially considered as part of philosophy, as the way we perceive the universe, understanding, intelligence, planning, etc., are now approached from a scientific point of view by several disciplines, such as cognitive psychology, ethology, brain theory and artificial intelligence.

All these disciplines coincide that the brain is basically a center of sensori-motor coordination where stimuli both external and internal release a motor response to solve the situation in such a way as to preserve the life of the animal. In animals with a simple nervous system, the motor response is observed as a specific action; but in animals with a more complex nervous system the action can be symbolically represented and compared with other possible acts to give the animal a more versatile system of adaptation. Furthermore, these disciplines have postulated that the brain contains structures of information with the capacity to relate a group of sensory stimulation with a motor response, which have been denominated schemas, frames, etc. These structures are able to interact with each other and to build super-structures as well as to create new ones, depending on the capacity of the nervous system of the animal. However, nothing is known of how the nervous system could give origin to this complicated processing of information.

For this reason, some of these disciplines have concentrated on animals with a comparatively simple nervous system where some of these processes could be studied at a neural level and could give us some information of the nature of the mechanisms that the nervous system uses to control the motor response of the animal. A great number of studies have been done in invertebrates where it has been possible to identify how the sensory information produces a motor responses; these studies, however, can only say a few things on how more complicated nervous systems could perform the appropiate sensorimotor coordination, because the number of neurons and the complexity of interaction is greatly augmented and possibly they do not use the same mechanisms as those animals do. A compromise is needed, then, where one should choose an animal with a comparatively simple nervous system, but with enough complexity as to give us an idea how the brain processes the sensory information to give a motor response with a minimum level of sophistication, that will allow us to postulate how the nervous system of these animals process the visual information to give a motor response.

This preparation is, we think, that of frogs and toads. Behavioral studies on these animals have shown:

1.- They orient to animals whose longest axis is in the direction of motion, and the orienting response is inhibited to stimuli whose longest axis moves perpendicular to the direction of motion(1).

2.- They avoid animals that cover an area greater than 20 degrees(1,2).

3.- They show size constancy within 30 cm of their position(3-4).

4.- They habituate to stimuli which is repetitively presented (5,6).

5.- They can see and interact with fixed objects (7).

6.- They plan their route to the prey stimuli without feedback information. If the stimulus is moved outside the visual field of the animal, he does not search for it which indicates that they do not have a permanent representation of the object (7-9).

7.- In a complex environment, in which there are barriers and chasms, they plan their route to the prey depending on the specific situation in terms of the relation of prey and obstacles and on the dimensions of the obstacle. This suggests that the motor response is chosen in terms of the three dimensional representation of the world (8-11).

All these studies suggests that different sequences of motor responses are chosen by the animal, depending on the specific sensory stimuli that is receiving, in terms of fixed and moving objects.

Anatomical studies in the toad and frog(12,13) have also shown that the retina sends in a retinotopic way fibres to several brain regions, such as the tectum, the posterior thalamus, the nucleus of Bellonci, the pretectum, and the uncinate nucleus. The tectum forms close loop interactions with the posterior thalamus and the pretectum and several brain regions in the thalamus establish close loop interactionas with the telencephalon, either directly or through the tectum. This suggest that the retinal information is processed by several layers that interact among each other to define the proper motor response of the animal (Fig. 1). Physiological studies in the tectum have shown (1) that this region have cells that may play a role in prey-predator recognition (T5-2), predator recognition (T5-3), depth perception (T2,T1); while physiological studies in the pretectum-thalamus (14) have shown that there are cells that may play a role in predator recognition (TH-3), in sensing fixed objects (TH-10), and in the habituation of the orienting response (TH-9?) (1,14).

Theoretical models have appeared which try to explain how the animal could recognize a prey from a predator (15,16), the recognition of predators (17), habituation of the orienting response(18), prey selection(19), depth perception(20), and motor control (21).

These studies, however, say very few things on how the sensory information is processed in the nervous system of these animals to choose, for every specific situation, the proper motor action.

In the present paper, we propose a global model of the possible neural mechanisms responsible for the visuomotor coordiantion in toads and the processing of information needed so that these animals choose a specific motor response or a sequence of motor responses depending on the present sensory stimulation. The model is based on our models of prey-predator recognition, predator recognition, habituation of prey orienting behavior, and prey selection. We have added new parts including a model of depth perception, fixed objects detectors, and gap detectors.

THE MODEL

The main postulates of the model are the following:

1.- The retinal ganglion cells initiate the visual processing of information defining the speed, contrast and size of the moving stimulus and the size of fixed objects.

2.- The retinal ganglion cells give origin to a matrix, planar representation of the world.

3.- The scene matrix of the retina is sent to several brain regions where new matrices are computed both through internal processes and as a result of the interaction with other layers.

4.- The tectum has a multitask group of columns with the following functions:
    a) prey-predator recognition.
    b) predator recognition.
    c) depth perception for prey and predators.
    d) size constancy.

5.- The thalamus-pretectum has a multitask group of columns with the following functions:
    a) predator recognition.
    b) fixed objects recognition, either obstacles or chasms.
    c) gap detector.
    d) depth perception of predators and fixed objects.
    e) prey-object distance.
    f) size constancy.

6.- The telecephalon has the following functions.
    a) motivational state of the animal.
    b) habituation of the orienting and avoidance response.

7.- The information coming from both tectum and pretectum can activate different motor actions, which we have considered, following Gernstein and Arbib(21), preprogramed and we denominate motor schemas. Motor schemas to be active need two sources of information: the command signal, depending on the cells activated; and the information signal, where the motor schema sets the proper parameters that controls its action, such as distance for approach, position for orient, etc. We have considered the following motor schemas:

1.- Approach.
2.- Orient.
3.- Snap.
4.- Avoid.
5.- Leap.
6.- Step.
7.- Climb.
8.- Go away.

GENERAL ARCHITECTURE AND BEHAVIOR OF THE MODEL

The model is constituted by a group of layers, i.e. matrices, where the retinotopic information from the retina is maintained (Fig 2). Each layer process a specific feature of the stimulus, and several layers could coexist in the same region. In the tectum we have layers that process the recognition of prey with its position (T5-2 neuron of Ewert (1)) in combination with pretectal layers; layers that process predator sensitivity and position, also in combination with pretectal layers (T5-3 of Ewert (22)); and layers that process both prey and predator depths (T1 and T2 of Ewert (1). The interaction of the prey position and the depth of prey layers in the tectum with the pretectal predator sensitive layers and fixed objects sensors layers give origin to three command layers: a layer that controls the orient response if the stimulus is in the visual field and it is not in the binocular position (b-); a layer thet controls the snapping response if the object is in the binocular field and within snapping distance (b+, d-); and a layer that controls the approach schema if the object is in the binocular field but it is farther than the snapping distance (b+, d+). Finally the avoidance command in the tectum is controlled by the joint activity of predator tectal(T5-3) and pretectal neurons (TH-3).

The thalamus has a group of layers that process the following properties of the visual image: predators and their position (TH-3 of Ewert (1), fixed objects and their position(TH-10 (14), predator and fixed object depths (?).The layer that measures fixed-object depths is further processed to give origin to a group of layers that recognize if the fixed object is a barrier -- measuring its height and prey-barrier distance-- a chasm -- measuring width and depth -- a distance, and gaps -- measuring the most attractove gap with respect to its size, depth and prey position. The combination of these layers give origin to three command layers both for barriers and chasms: for barriers, when the prey-object distance is within snapping distance (dpo-), the approach-barrier schema is activated; when the prey-object distance is long (dpo+) there are two options: if the height of the barrier is

small (h-), then the jump schema is activated; while if the height is big (h+), then the detour schema responds. For chasms we have that if the width is small (w-), the leap schema is activated; while if the width is large (w+), we have two options depending if the chasm is shallow (d-) or deep (d+), the cross or the go-away schemas are activated, respectively (9-11).

Finally, the motor schemas are shown as subroutines where a command signal activates it and an information signal (figure 3 and 4) defines the proper parameters for the proper motor performance. A motor schema can be a relatively simple motor action, such as approach or leap; but it can be a structure that coordinates the action of several simple schemas. For example, in figure 2 we show that the cross schema is activated, but this schema is constituted (Fig 4) by the coordination fo the approach, step, and climb schemas. A similar case happens with the leap, jump, and detour schemas, shown in figure 2 and figure 4, in the latter figure are shown the schemas that are part of the superschema and how they are coordinated. We have postulated that the coordination of motor schemas is a local function of each schema when aspecific situation is present, and they act as part of the command system for the activation of the next schema, but it can also be controlled by a single region, such as the cerebellum as has been described elsewhere (23), as it is shown in figure 5. Notice, then, that a simple motor schema can be activated by different command and information layers, depending on the specific visual scene of the animal, as it is shown in figures 3 and 4. In these figures we show that the command layer enables an information later that the motor schema will use for its proper performance. In this way, the approach schema, for example, some times is controlled by the prey command and the prey-distance information layers, if there is not a fixed object between the animal and the prey; while the approach schema will be controlled by the gap barrier command and the gap-detector information layers if a barrier is between the animal and its prey and the prey-barrier distance is farther than the snapping distance. Each time each of these schemas is activated, the visual image takes again control of the system and the new motor schema is then chosen depending on the present visual scene.

SUBPARTS OF THE MODEL

In this section, we will define in detail each of the steps of the proposed processing of information of the nervous system of toads to control its behavior in terms of neural networks. Some of these networks do not have any anatomical or physiological bases, but we propose them as a specific hypothesis that could be tested experimentally.

PREY-PREDATOR RECOGNITION

We have described elsewhere(16) how the interactions between retina-tectum-thalamus pretectum could account for the group of cells that are sensitive to prey-predator recognition. Briefly, we propose that the tectum is constituted by columns where the visual input from the retinal ganglion cells arrives at the glomerulo--constituted by the dendrites of large pear shaped and small pear-shaped cells, and axons of both retinal fibres and recurrent axons from large and small pear neurons--, the large and small pear-shaped cells and the pyramidal neuron, which is the efferent cell of the tectal column. The recurrent axons of the large pear neuron, besides its recurrent effect over the glomerulus, excites the stellate neuron which exerts an inhibitory effect over the large and small pear cells, controlling in this way the state of excitation of the column. The pyramidal neuron gives a response whenever the ganglion cells. the large and small pear neurons are simultaneously activated. We have simulated the fact that the interaction among diferent tectl columns yields the tectum to be mostly sensitive to the elongation of the situmulus along the direction of motion. Following Ewert's hypothesis, we then postulated that the pretectal neurons which receive ganglion cell type 3 and 4 as inputs and are mostly sensitive to predator like stimulus, inhibit the activity of the large and small pear shaped cells and the pyramidal neuron. thus the response of the pyramidal neuron is inhibited when the stimulus elongates perpendicularly to de direction of motion which simulates the response of tectal T5-2 neurons and the orienting response of toads towards this type of stimuli (Fig 6).

MODEL OF PREDATOR AVOIDANCE

Following, again, Ewert's hypothesis, we postulated that there are another groups of neurons in the tectum that are sensitive to predator-like stimulus and that tha joint activity of these cells with the pretectal neurons gives origin to the avoidance response. Both cells are mostly driven by ganglion cells type 3 and 4 (Fig 6) (17).

MODEL OF DEPTH PERCEPTION

Ewert has also found that there are cells in the tectum that are sensitive to the depth of the prey stimulus (1). Ingle and Collet have shown that depth perception in frogs is controlled by monocular and binocular mechanisms(24,25). House(2 has postulated that these mechanisms may be binocular disparity and accomodation. We have followed House postulates but we have changed the general architecture of the system that is able to compute ocular disparity and accomodation(Fig 7).

For ocular disparity we have proposed that each tectal neuron, which represents a point in space of the contralateral field, receives afferents from the ipsilateral eye which could represent a point in space (see Fig 7), and this neuron code the spatial distance of synaptic action as a measure of depth of the object, measured as the frequency of reponse in the following way:

$$fr=f(ci-pj)$$

which is a measure of the disparity between cell i, ci, and the ipsilateral affernt j, pj. Naturally there could be several points of disparity, generating the ghost objects. We postulate that the accomodation system is used as a cue for the proper disparity of the real object and the convergence is obtained through synaptic competitive interactions between the different synapse arriving at the same neuron. This is expressed mathematically as follows:

$$\frac{dwj}{dt}= TRLi*TRLj- TRLk-abs(fd-fac)$$

where wj is the weight of the jth. ipsilateral synapses; TRL is the transmiter liberated by the ith contralateral, kth and jth, both ipsilateral, synapse respectively; and fd and fac is the frecuency of response of the disparity and the accommodation neurons, respectively.

This equation symply shows that the weight of a synapse is increased depending on its own activity (TRLi*TRLj), but a competitive interaction exist with other synapses simultneously activated (TRLk). Moreover, the convergence to a given synapse is biased by the similarity of the output response of the cell controlled by a given disparity and that given by the accomodation system [fd-fac]. In this way the response of the output neuron is controlled by that ipsilateral projection which gives a closer response to the accomodation system output.

The accomodation system is simulated in the following way:

$$\frac{dAc}{dt}= E$$

where Ac is the accommodation system and the error, E, is defined as follows:

$$E= fr(t)-fr(t-1)$$

or

$$E= f(d)-fr(t)$$

where fr is the frequency of response of the neuron that codes the depth of the accommodation system; and f(d) is a function that defines the frequency of response when the immage at a given distance, d, is in focus. The frequency of response of the accomodation neuron is given by the following function:

$$fr(t)=f(d)e^{-[f(d)-Ac]}$$

where fr(t)=f(d) when teh image is in focus, f(d)=Ac. This depth percetion model is also applyed for sensing fixed objects.

MODEL OF DISCRIMINATION OF FIXED OBJECTS

Our previous models give us a group of layers, i.e. matrices, where the position and depth of fixed and moving objects are coded; from these matrices we still need to define if a fixed object is in the trajectory from toad to prey and the nature and properties of these objects. For this reason, we postulate that the depth-perception matrix of fixed objects is further processed to define if the depth measure corresponds to a distance, a barrier or a chasm.

We postulate that this discrimination may be performed by a neural structure similar to that shown in figure 8. This group of cells represents the group of neurons that are coding the trajectory between toad and prey, and is a mesure of depth. When a border is detected in the visual field of the animal, it is coded as a depth measure in the matrix in the planar representation of space in the toad's brain, which as was shown above, gives a specific frequency of response that codes distance. The group of neurons in the lower layers can be of three types, which corresponds to distances, barriers and chasms detectors, respectively: These neurons compute the difference between two subsequent depth-measure of borders: if the distance of the second border is equal to that of the first one, then the body is recognized as a barrier; if the second border is greater than the first, then it is a distance; but if the intermediate neurons between the two borders have a depth value bigger than that corresponding to a plane then the distance between these borders is a chasm. These cells act as disparity neurons but instead of measuring the difference between right and left-eye, they measure the difference between two representations of visual space in the following way:

$$fr=f(pi-pj)$$

which means that the rate of response of these cells is proportional to the spatial distance between neurons i and j that correspond to a specific location in space. In the case of barrier detection the response of this cell codes the position of the border, by the position of the cell in the matrix, and the height of the barrier by the frequency of response of this neuron. In the case of the distance matrix, it codes the distance of the second border with respect to the first, that could actually be the position of the toad. Finally for the case of a chasm we need three measures: the position, given by the position of the cell, the width, given by the frequency of response of this neuron, and the depth, given by another groups of neurons, similar to those that measure the height of the barrier.

MODEL OF GAP DETECTOR

We still need to process gap detection and gap selection measured as the relation between objects and prey position. To simulate how neurons could perform these functions, we propose a circuit as shown in figure 9, where the first layer of cells corresponds to a row of the planar representation of space but where depth is coded as the rate of response of neurons. The second row are neurons with the function of subtraction the i+1 to the i input, thus they sense any difference of depth between column i and column i+1. If the difference is positive, then the neuron codes the width, again trough a space-disparity function, to the next-to-right activated neuron; while if the difference is negative, the neuron codes the width through the next-to-left activated neuron. Thus the output of these cells will be proportional to the depth and width of the gap in the following way:

$$fr=a*d+b*w$$

where d is depth; w is width; and a and b are constants.

MODEL OF GAP DISCRIMINATION

For the gap discrimination system we propose a circuit as shown in figure 10, where it can be seen that the selection of the gap depends on three factors: width and depth of the gap, given by the frequency of response of the gap detector, and the position of the prey with respect to the different gaps, thus the above equation is defined as follows:

$$fr=a*d+b*w+c*f(p)$$

where f(p) is a gaussian function where the peak is in the prey position and c is a constant.
The selection is obtained through a system similar to the one that Didday (26) and later Lara and Arbib(19) proposed for prey selection. In this case the competitive interaction between gap detectors is given by a gaussian distribution of the prey input which bias the final convergence to the most atractive gap.

MODEL OF PREY-OBJECT DISTANCE

The final operation we are propossing is a matrix that measures prey-object distance, as shown in figure 11. The output neuron is again a space-disparity cell which responds to the spatial difference between object and prey. in the following way:

$$fr=f(foi-pi)$$

where foi is the position of the fixed object in row i and pi is the position of prey in row j. If the difference is positive it means that the fixed object is away from the prey; while for a negative difference, it means that the prey is behind the fixed object.

SIZE CONSTANCY

It has been shown that toads can show size constancy for moving and fixed objects within a given distance (3,4). We propose, following Vurpillot (27), that this function can be computed by a simple function performed by a layer of neurons in the following way:

$$sc=fr.dim$$

where sc is the output response of the size constancy neuron; fr is the response of the depth neuron and dim is the area covered by the stimulus in the retina. In this way, for stimuli far away, fr is big while dim is small; while for close stimuli, fr is small and dim is big. For a given distance this product has to be constant.

THE COMMAND SYSTEM

The command system is constituted by an exclusive or function of the different command matrices and it is simply implemented so that only one command system could be active at the same time. This is obtained through the interaction of the different matrices, as described above, and through the specific processing of information that allow the system to discriminate different situations, as we described above.

The command system, besides the activation of the different motor schemas or group of motor schemas, enables the proper infrmation matrices that will control the differen schemas, as shown in figures 3 and 4.

MOTOR SCHEMAS

As we mentioned above, motor schemas are considered as preprogramed circuits that yield to simple motor behavior that can be activated by different matrices depending on the specific situation of the three dimensional space. Some of these schemas are closely associated with other ones constituting super-schemas, that have been linked possibly as a result of evolution for a more adequate adaptation to the external world of the animal. This coordination may be a function of the proper schema or may be is linked by an external system, such as the cerebelum, as has been described elsewhere. In the present model we did not touch how the motor schemas are organized in terms of the anatomical and physiological studies on toads.

COMPUTER SIMULATION

We have simulated the above model in a digital computer Bourroughs 7800.

We have assumed some simplifications in order to show the behavior of the global model. We have considered that the simulated toad has a receptive field of 170 degrees, 85 to the left and 85 to the right, and 32 degrees in the vertical direction. Thus the retinal and other brain layers in the model are of 170x32 units, represented by neurons. We also considered that the prey is in a fixed position, thus the prey-predator recognition matrix is simply a point in space; when we introduce prey movement, the complete prey-predator recognition model should be integrated. For depth perception, we used a simplified version of the described model where we calculated the depth of each object by a disparity function and the chosen synapses was simply done through a comparisson between the measure given by the accomodation system and the disparity function. We did not simulate the fact that objects change the area covered in the retina depending on their depth, but we simply represent the real size in the retinal layer, not considering the needed transformation for size constancy, as postulated above.

The way to study the behavior of the global model was to define a space where prey position, toad position, obstacles position and dimensions are specified. The toad first orients toward the prey, then the depth matrix is generated both for fixed objects, with their dimensions, and for the prey. After this, the gap matrix is genereated and the most attractive one is selected, depending on depth width and prey position. At the same time the definition of the barrier and chasm is done. With this internal representation of the world, then the proper motor schema is selected according to the specific situation, as we will show with several examples.

Collet (8-10) has studied that toads plan their routes depending on the specific situation of its three dimensional world. He has found that if a barrier is between toad and its prey, and the prey is far away from the barrier, the toad makes a detour 75% of the times. Fig 12 A shows the results of the computer simulation of the toad behavior in this situation, where it can be seen that the toad (R) detours the barrier (B) to get the prey (P).

The numbers in the upper part of the figure are the weights of the two gaps that the toad sees before him before the beginning of his action. Because they have the same weight, he choses either of them. In order to obtain a convergence in the gap competition model we simply introduced some random noise, thus biasing the chosen gap. Fig 12 B shows that, in the presence of two barriers one of them with a gap in the middle line of the toad, the animal prefers to walk first through the gap and then detour. The numbers show the strong preference for the middle gap but the behavior is also biased by the conflict between two different motor schemas: approach and detour, which explain why the animal detours 48% of the trials. Figure 13 A shows that the toad has a strong preference to approach the prey through the gap of the barrier rather than for deotouring it; while figure 13 B shows that, in the presence of two barriers, detour behavior is preferred. Figure 14 A shows that the toad cannot deal properly with a closed barrier, because he most of the time (85%) goes inside rather than detours. In the model the middle gap is stronger (88%) than the two other gaps, thus the animal approaches directly to the prey. Figure 14 B shows that, in the presence of two barriers, one of them with a gap away from the middle line of the toad, the toad has a strong preference for the closer gap in the barrier. Figure 15 A and B show how the gap's depth may define the trajectory followed by the toad. When two gaps are present in a barrier with approximately the same weight, the toad always prefers the closer gap; however, if the farther gap is deeper (Fig 15 B), then the toad chooses either of them with the same probability. Figure 16 A and B show the behavior of the toad with chasms, where he crosses (Fig 16 A) or leaps (fig. 16B) depending on the depth and width of the chasm, as Collet has shown.

DISCUSSION

In the present paper we have proposed a global model of the visuomotor coordination in toads depending on the specific external circumstances of the world. The general features of the present model are that the visual information is processed by multiple layers in a distributive way and that these layers perform different functions within the same region and communicate with other layers to define which is the proper action for that specific situation. The final outcome of these processing of information is a command and an informations system which select and inform the motor schema for adequate function. In this way, each motor schema can be activated by different command sytems and with different information depending on the specific situation of the external world. The command system can activate a single motor schema or a group of coordinated motor schemas which only release the system command when the last of the schema has ended its function. For example the detour behavior is the coordination of the orient gap response, approach gap, and reorient to prey, possibly this las step is the result of the liberation of the command system that now can freely orint to the prey stimuli.

Bergson (28) and later Piaget (29) have postulated that the brain is organized in specific sensorimotor structures which are activated by a specifc group of sensory stimuli, which they called schemas. The sensorimotor schema has basically two fuctions: assimilation and accomodation, the first meaning the capacity of the schema to be activated by similar stimuli, that is how the animal represents the external world according to the infrmation structures loacated in the brain of the animal. Accomodation, on the other hand, is how the external world can modify the sensori motor schemas to adapt them to the specific situation that the animal is perceiving. These operations, however, can act not only to the external world but within other sensorimotor schemas thus orginizing a more complex structures of information.

Later, Arbib (21) has postulated that the brain is constituted by perceptual and motor schemas, and that these schemas can interact among each other through cooperative and competitive interactions to choose which one of them will be the activated. This author also postulated that the animal can generate an internal representation of the world and that there is a program of coordination of the motor response, which basically follows a serial order where the result of the action is the stimulation of the next schema.

Minsky (30), on the other hand, proposed that the brain is constituted by strucures of information that he called frames, and the groups of frames can interact among each other performing simple functions and without transmission of informations as a community of nuclei. The final response is obtained as consensus of the group of nuclei presently activated.

Ewert (22) has also proposed that toad's behavior is controlled by a group of and command functions, where depending on the cell activated, the response of the animal.

Grusser (31) and later Roth (32) have, on the contrary, proposed that toad's behavior is given as a result of a group of neurons, rather than a single unit controlling the whole response, and that the termination of the motor response is given by new activation of other cells.

We consider that our model give specific postulates of the nature of all these processes in the toad's brain. We think that the equivalent of a perceptual schema, of Arbib, is equivalent to the proposed prey, predator, barrier, chasm, distance, prey-object distance, and gap detector and selector. The command system constituted by these matrices is the equivalent to the assimilation process of Piaget, where a group of sensory stimuli gives a specifc response, and to the and command system of Ewert. The information system, on the other hand, could be considered as a short term process of accomodation where the motor schema has to respond to a specific situation of the environment. The command and the information system, on the other hand, constitute the internal representation of the world, proposed by Arbib, but, as Luria (33) postulates, it is not a single region where a very complex processing of information is occurring, but it is the joint activity of various regions and subregions in the region with very simple operations, that give origin to this internal representation of the world. This representation, as Piaget, Arbib and Minsky have potulated, is the result of the coordiantion and communication of different schemas, layers, or nuclei. The command system, however, can activate a group of schemas rather than a single schema for specific situations of the world, which simulates the coordination of motor schemas proposed by Piaget as a result of accomodation and assimilation between schemas. This point has not been illustrated in the present paper, but could be considered as an accomodation function at a long-term manner depending on the mistakes, or trial and error of the animal through evolution. The idea of Arbib of a program of coordination of motor behavior, in terms of our model, could be interpreted as a region that is actually functioning as a serial command system, as Boylls (23) has proposed for the cerebellum, or simply through simple operations between the same motor schemas. The ideas of Grusser and Roth, in spite of the fact that they do not consider the presence of perceptual schemas, is also in agreements with the fact that motor behavior is the conjoint activity of different cells and regions, rather than a single neuron.

The model, in general, has a lot of ad-hoc functions for the different postulates of the processing of infrmation performaed by the toad's brain, but they can be considered as one of a family of models that should be postulated that could be tested experimentlly
and that could also be the bases of a more anatomically and physilogically tied model for the future.

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Figure 1.- General organization of the visuomotor system of toads. The retina sends their fibres in a retinotopic way to the tectum, pretectum and anterior thalamus. The tectum establishes closed-loop interactions with the pretectum and the anterior thalamus. The pretectum, at its turn, establishes closed-loop interactions with the teleencephalic structure the striatum. The tectum, through the anterior thalamus, the medial and the anterior palium, and the hypothalamus, establishes a closed-loop interaction with the telencephalon. The tectum and the pretectum, possibly in combination with the tegmentum, may control the motor response of the animal through their projections to the spinal chord.

Figure 2.- General architecture of the command system of the global model of visuomotor coordination in toads. The retinal layer, which represents the retinal map of the different ganglion cells, is projected in a retinotopic way to both tectum and to several brain regions in the thalamus. In the tectum we postulate the existence of three perceptual types of layers: prey-recognition layer (prey), prey-depth layer (prey-dep), and predator recognition layer (pred); four command layers: one controlling prey orienting if the prey is not in the binocular field (b+), the second controlling prey sanpping if the prey is within the snapping distance (d-), prey-approach if the prey is farther than the snapping distance (d+) and there is not a fixed object between the prey and the animal, and the avoidance command which is activated by the joint activity of tectum and pretectum. The thalamus has two layers which are sensitive to predators and to fixed objects (F.O.). The F.O. layer is further processed by other layers to define if the object is a barrier (barr)-- with height, distance, and prey-barrier distance (prey-obj dist)-- a chasm-- with width (w), depth (d), and distance-- or a gap. These layers give origin to two command layers which, for the case of the barrier, activate the approach schema if the prey-object distance (dpo) is within snapping distance (dpo-): if dpo is farther than the snapping distance (dpo+) and the barrier height is big (h+), then the detour schema is activated; while the jump schema is activated if the height is low (h-). For the case of a chasm, if the width is small (w-), the leap schema is activated; but if the chasm is large (w+) and shallow (d-), then the cross schema is activated; but if the chasm is large (w+) and deep (d+), then the go-away schema is activated. Notice that the command system is an "exclusive or" function of "and" type of commands.

Figure 3.- Information flux in the global model of visuomotor coordination in toads. This figure shows that the same motor schema may be activated by different command and information layers. The information layer sends a parameter to the motor schema to define specifically how it should operate. The command lines, shown in Fig 2, enable (dot) the information layer to control properly the performance of the motor schema. The snap schema is activated by the prey command that enables the prey-distance and position information layers so that the sanapping be directed with the proper depth. The orient schema can be used to prey-orient or to gap-orient, the position given by the prey-position or gap-position respectively; and the approach schema can be controlled by prey, barrier, gap, or chasm layer, depending on the nature of the fixed object.

Figure 4.- Information, command flux and coordination of motor schemas in the global model of visuomotor coordination in toads. The command system enables, through switches, the information layers to contro the performance of the motor schema. Notice that the detour, jump, leap, and cross scemas of figure 2 are now represented as a group of coordinated schemas: detour= orient-gap, approach-gap; jump= approach-barrier, jump-barrier; leap= approach-chasm, leap-chasm; cross= approach-chasm, step, approach-border, climb. The command layers activate the schema and select the information layer that the motor schema will use.

Figure 5.- An alternative interpretation of the coordination of motor schemas in the global model of visuomotor coordinatin in toads. The coordination of motor schemas is controlled by a specific region depending on the specific circunstances given by the command layers.

Figure 6.- Neural model of prey-predator recognition, predator avoidance, and habituation. The tectum is constituted by the tectal columns which are inhibited by the predator sensitive cells in the pretectum. The joint activity of the predator sensitive cells in both tectum and pretectum activate the avoidance neuron. The habituation columns are constituted by a modeller neuron, which generates a model of the spatio-temporal pattern, either in the tectum or in the pretectum, produced by the stimulus, which is then compared with the actual stimulus pattern; if they are equal, the habituation cell start to build-up an inhibitory effect over either tectum or pretectum to habituate the motor response; but if model and stimulus are different then dishabituation occurs, through a desinhibition of the habituation neuron and the activation of the comparisson cell.

Figure 7.- Neural mnodel of dep-th perception. The right and the left retina project retinotopically to the left and the right tectum, respectively, shown in the figure in the same side for clarity. Each tectal cell of the left tectum receives afferent from the ipsilateral eye which may correspond to a specific point in space. This neuron responds depending on the spatial disparity between the contralateral and the ipsilateral projection. The final

response, however, is biased by the accommodation system which independently has a depth estimation of the stimulus.

Figure 8.- Neural model of fixed object detectors. The group of neurons in the upper layer represents a column in the fixed-object depth layer, which may account for the trajectory between the animal and the prey once the animal has oriented. The lower layer reperesents the tree types of detectors which measure the disparity between two subsequent activated distances, i.e. borders. If the two depth measures are the same, the object is defined as a barrier in the barrier-layer, and the response of this cell is a measure of the height of the barrier. If the two distances are different, then the object is recognized as a distance, but if the intermediate neurons show a value that is lower than that corresponding to a plane, then the distance is classified as a chasm.

Figure 9.- Neural model of gap detector. The first row of neurons represents a row in the retinal map that is projected to other brain regions that measure fixed object depth. The second row measures the difference in depth between two neighbouring neurons. The third row computes the gap size, again by a disparity fuction between two differential neurons activated and as a function of the difference in depth. The gap size can be measured in both ways: if the differential neuron gives a postive value, meaning that the i column is farther than the i+1 column, the left-disparity function is computed; while the inverse occurs if the difference is negative.

Figure 10.- Neural model of gap selection. The first row represents the incoming input from a row of the prey-position layer where the prey is located. The second row is the output of the gap detector described in figure 9. The third row represents the discriminatory cells which inhibit all cells except the one that activates them from the gap-detector layer. The gap detector layer receives an excitatory effect from the prey-postion layer, thus biasing the selection of the most attractive gap depending on the frequency of response of the gap detector layer, which measures size and depth of gap, and the prey position.

Figure 11.- Neural model of prey-object distance layer. The prey-object distance neurons are activated by the fixed object layers, either a chasm or a barrier, and the prey postition layer. The response of this cell is a measure of the spatial disparity between the fixed object and the prey position (dotted lines).

Figure 12.- Computer simulation of the global model of visuomotor coordination in toads (R) in a primitive space with barriers (B) and prey (P). When the prey is away fro the barrier, the toad detours (A). The numbers indicate the weight of attraction of each gap in the visual field of the animal. On the right it is shown the probability of response in the toad obtained experimentally by Collet ( ). In the presence of two barriers, one of them with a gap in teh middle, the toad prefers to walk through the gap and then detour the second barrier. The experimental results show that there is a slight prefernce for walking through the gap than detouring ( ).

Figure 13.- Computer simulation of the global model of the behavior of the toad in the presence of barriers. When a barrier has a gap in the middle line between toad and prey, the animal has a strong preference to walk through the gap (A). In the presence of two barriers, the animal has a strong preference to detour. These results reproduce the experimental observations as shown on the right.

Figure 14.- Computer simulation of viusomotor behavior in the toad in the presence of barriers. In the presence of a cage barrier, the toad has a strong preference to walk inside (A). While the toad prefers to walk through the closer of two gaps (B). These results can be compared with the experimental studies, shown on the right ( ).

Figure 15.- Computer simulation of taod's behavior in the presence of barriers and the change in the trajectory depending on the gap's depth. In A the toad always prefer the closer gaps but if the farther gap is deeper (B), then the choice is almost the same for both gaps. In the right part of the figure we show the experimental results obtained by Collet ( ).

Figure 16.- Computer simulation of taod's behavior in the presence of chasms (Z) and barriers (B). For wide and shallow chasms (A), the animal crosses it; while for narrow ones, either deep or narrow, the animal leaps. This is in agreement with wxperimental observations ( ).

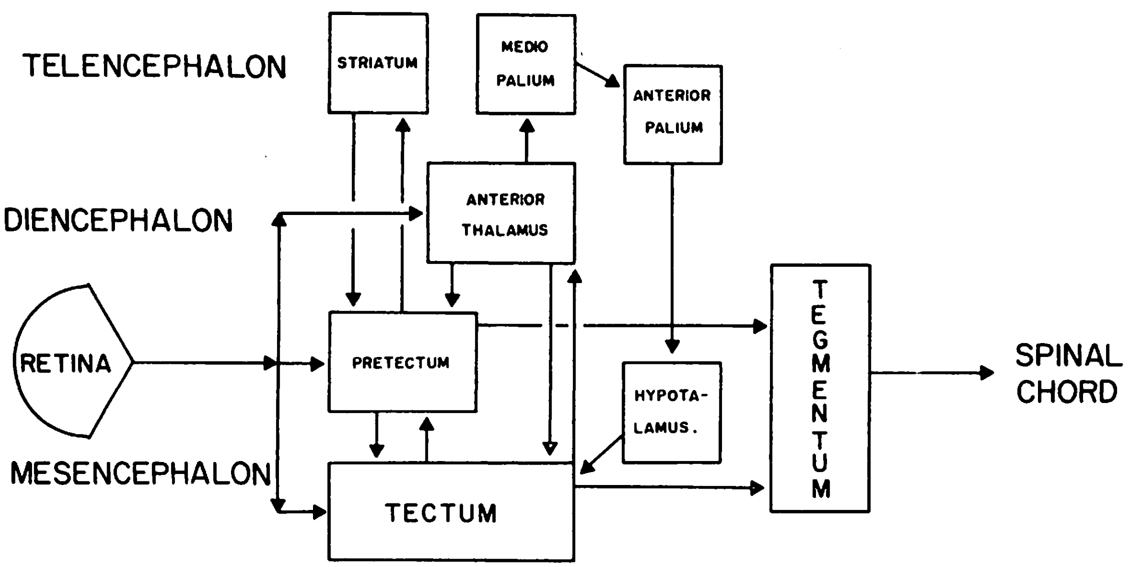

TELENCEPHALON
STRIATUM
MEDIO PALIUM
ANTERIOR PALIUM
DIENCEPHALON
ANTERIOR THALAMUS
RETINA
PRETECTUM
TEGMENTUM
SPINAL CHORD
HYPOTA-LAMUS.
MESENCEPHALON
TECTUM

Fig. 1

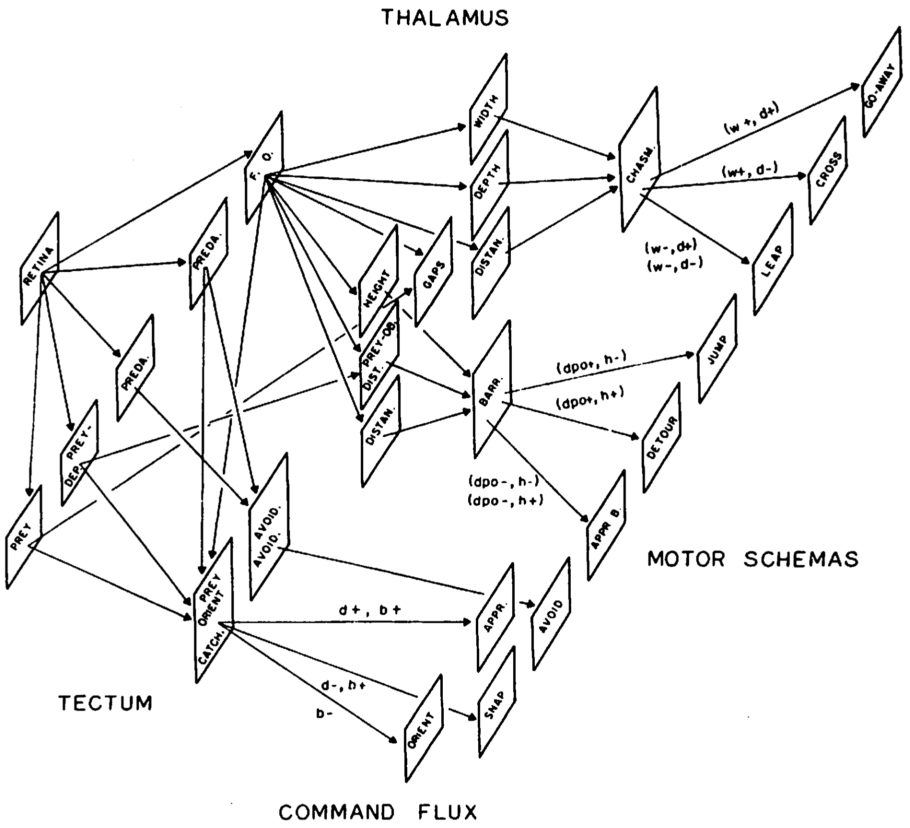
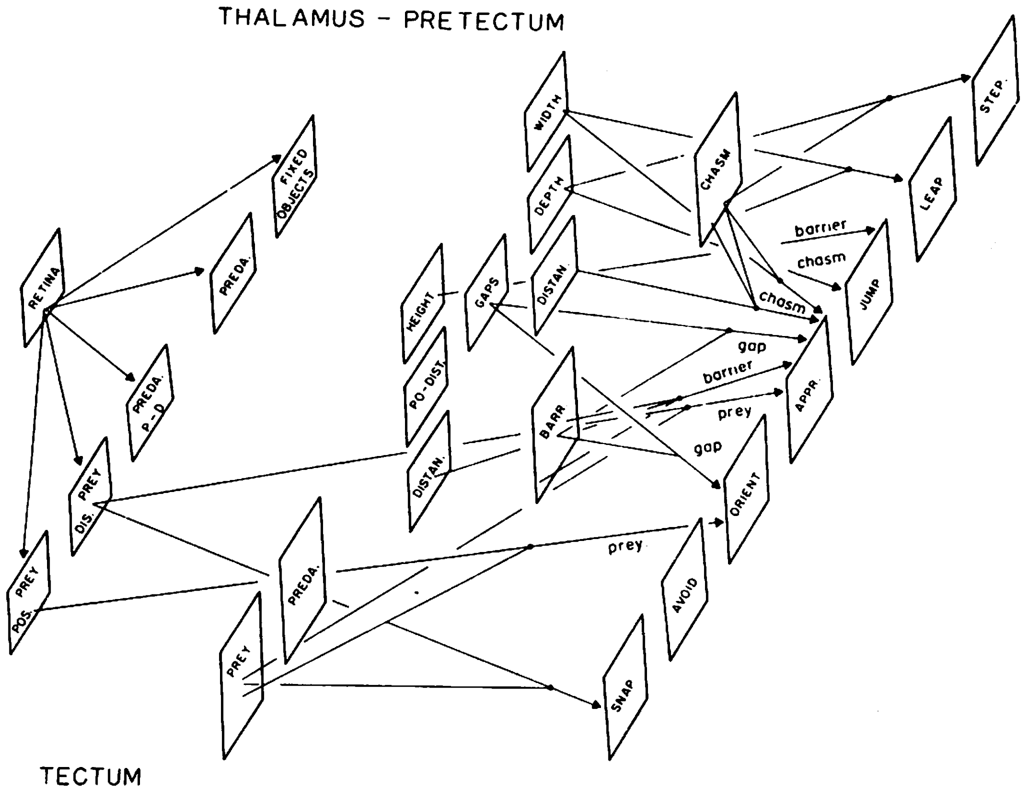
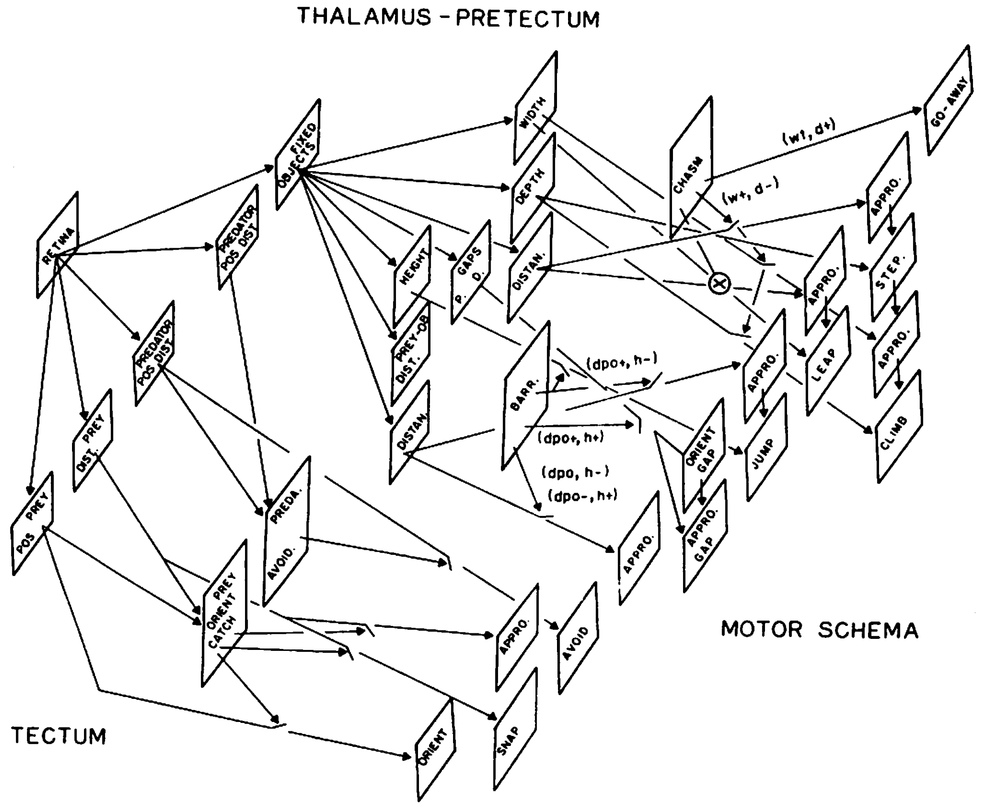

THALAMUS
RETINA
F. O.
PREDA.
WIDTH
DEPTH
DISTAN.
CHASM.
(w +, d+)
(w+, d-)
(w-, d+)
(w-, d-)
GO-AWAY
CROSS
LEAP
HEIGHT
GAPS
PREY-OB. DIST.
DISTAN.
BARR.
(dpo+, h-)
(dpo+, h+)
(dpo-, h-)
(dpo-, h+)
JUMP
DETOUR
APPR B.
PREDA.
PREY-DEP.
PREY
AVOID. AVOID.
PREY ORIENT CATCH.
MOTOR SCHEMAS
d+, b+
d-, b+
b-
APPR.
AVOID
SNAP
ORIENT
TECTUM
COMMAND FLUX

Fig. 2



INFORMATION FLUX

Fig. 3



INFORMATION, COMMAND FLUX AND COORDINATION OF MOTOR SCHEMAS

Fig. 4

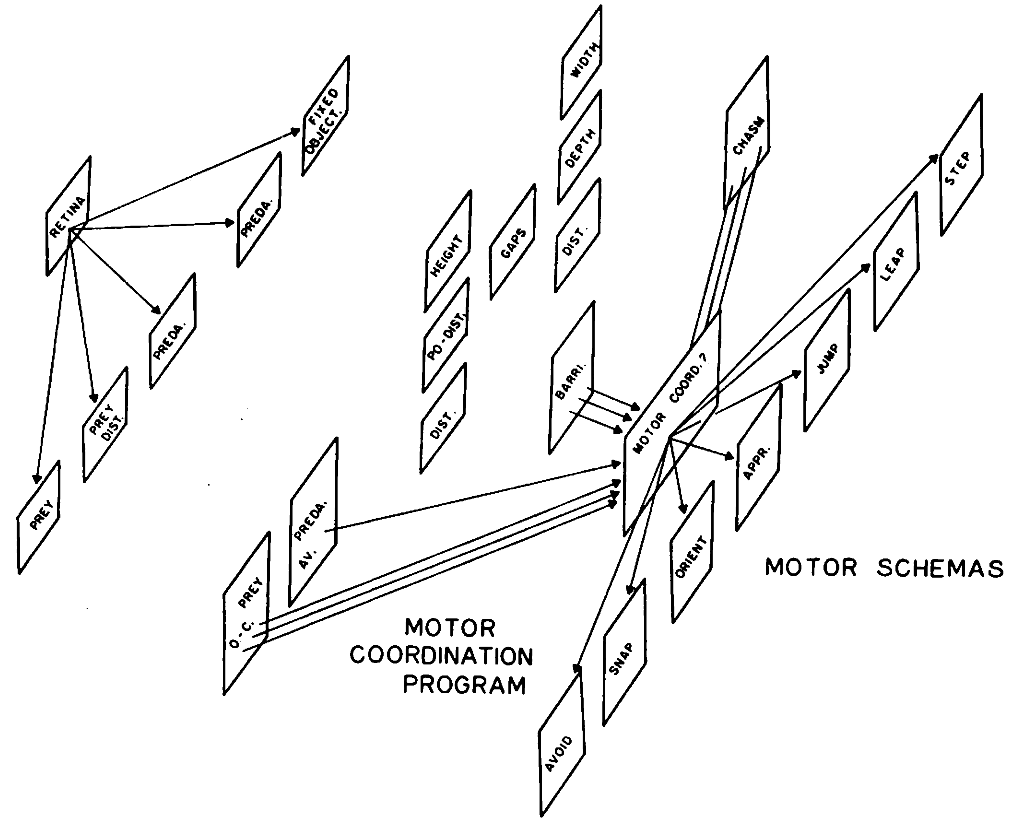

RETINA
FIXED OBJECT.
PREDA.
PREDA.
PREY DIST.
PREY
WIDTH
DEPTH
DIST.
HEIGHT
GAPS
PO-DIST.
DIST.
BARRI.
CHASM
STEP
LEAP
JUMP
MOTOR COORD.?
APPR.
ORIENT
SNAP
AVOID
PREDA. AV.
PREY O.-C.
MOTOR SCHEMAS
MOTOR COORDINATION PROGRAM

Fig. 5

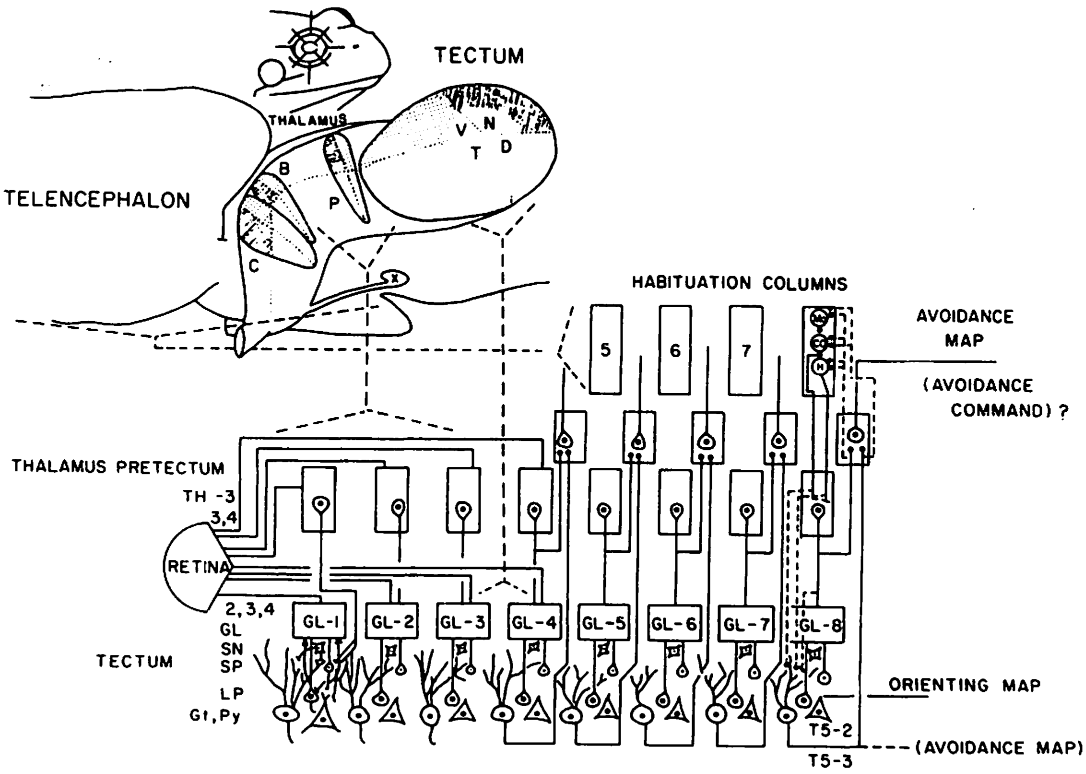

TECTUM
THALAMUS
V
N
T
D
B
P
C
X
TELENCEPHALON
HABITUATION COLUMNS
5
6
7
AVOIDANCE MAP
(AVOIDANCE COMMAND)?
THALAMUS PRETECTUM
TH -3
3,4
RETINA
2,3,4
GL
SN
SP
LP
Gt,Py
TECTUM
GL-1
GL-2
GL-3
GL-4
GL-5
GL-6
GL-7
GL-8
ORIENTING MAP
T5-2
T5-3
----(AVOIDANCE MAP)

Fig. 6

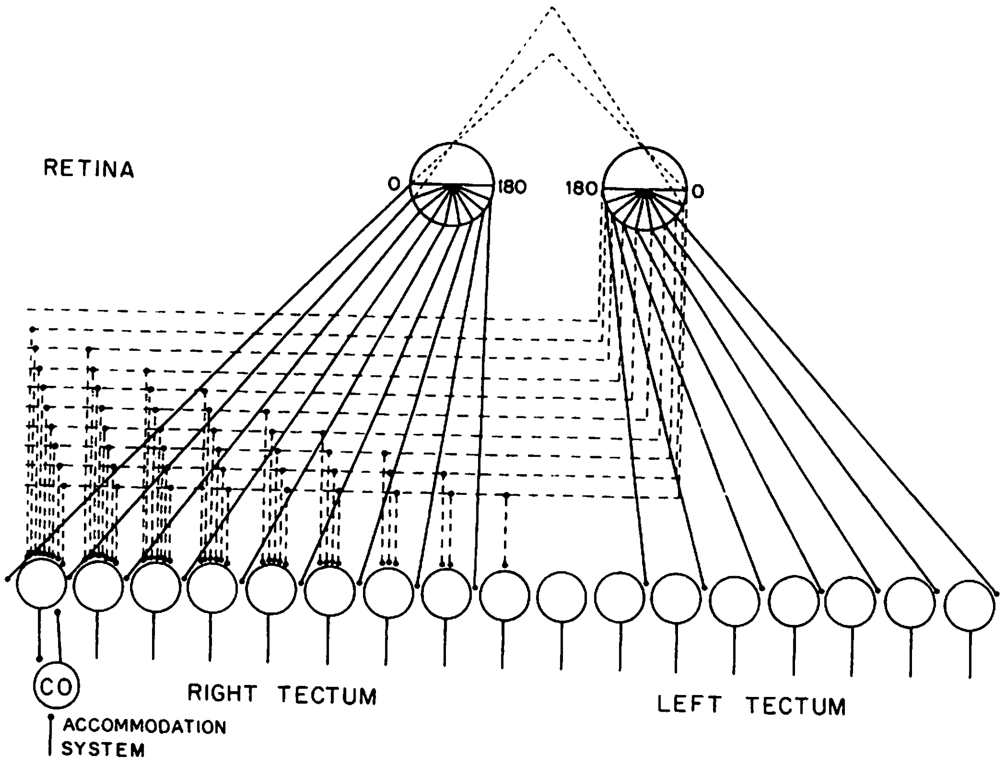

RETINA
0
180
180
0
CO
RIGHT TECTUM
LEFT TECTUM
ACCOMMODATION
SYSTEM

Fig. 7

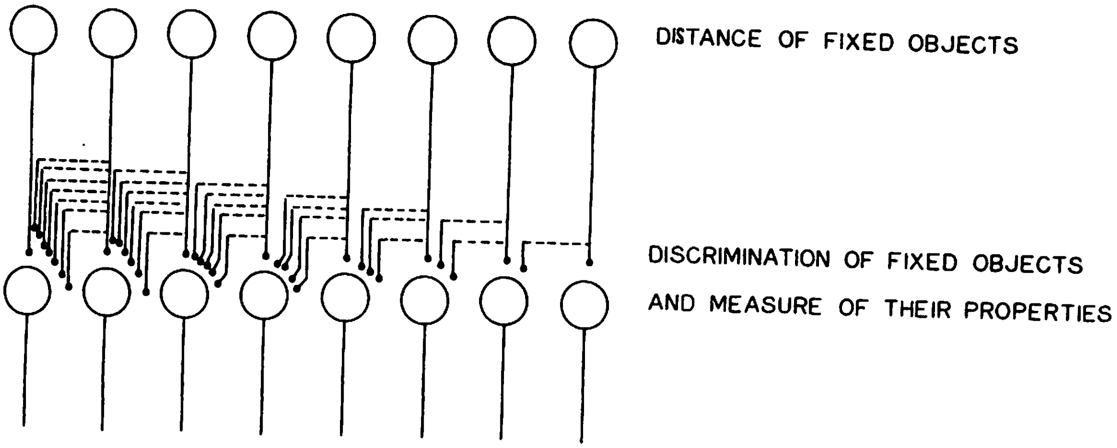

DISTANCE OF FIXED OBJECTS
DISCRIMINATION OF FIXED OBJECTS
AND MEASURE OF THEIR PROPERTIES

Fig. 8

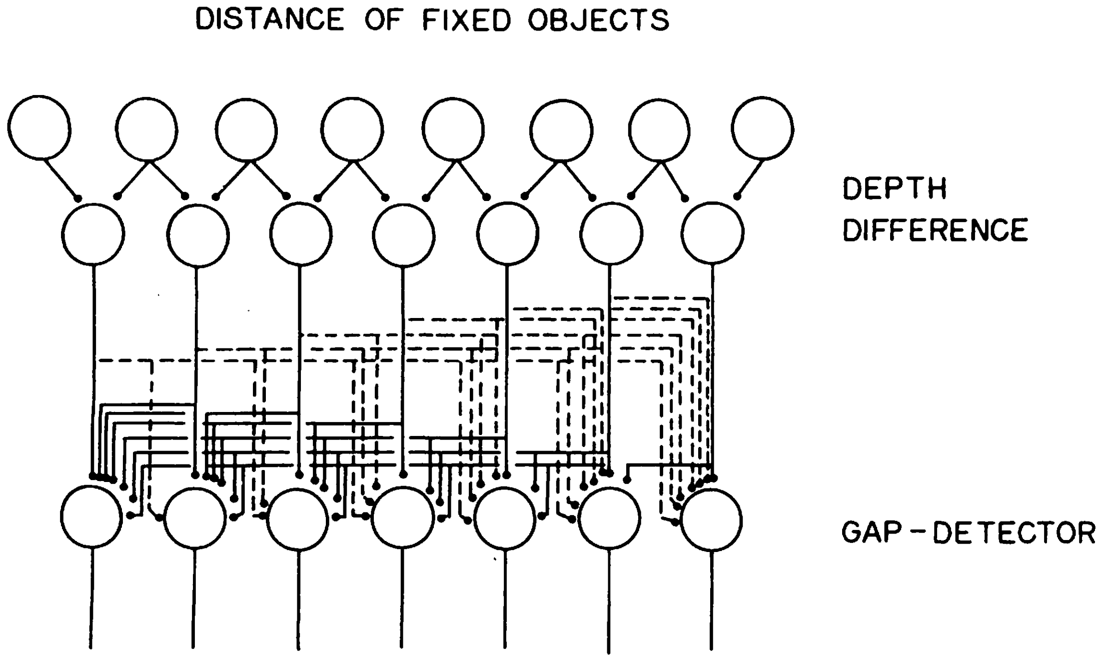

DISTANCE OF FIXED OBJECTS
DEPTH DIFFERENCE
GAP-DETECTOR

Fig. 9

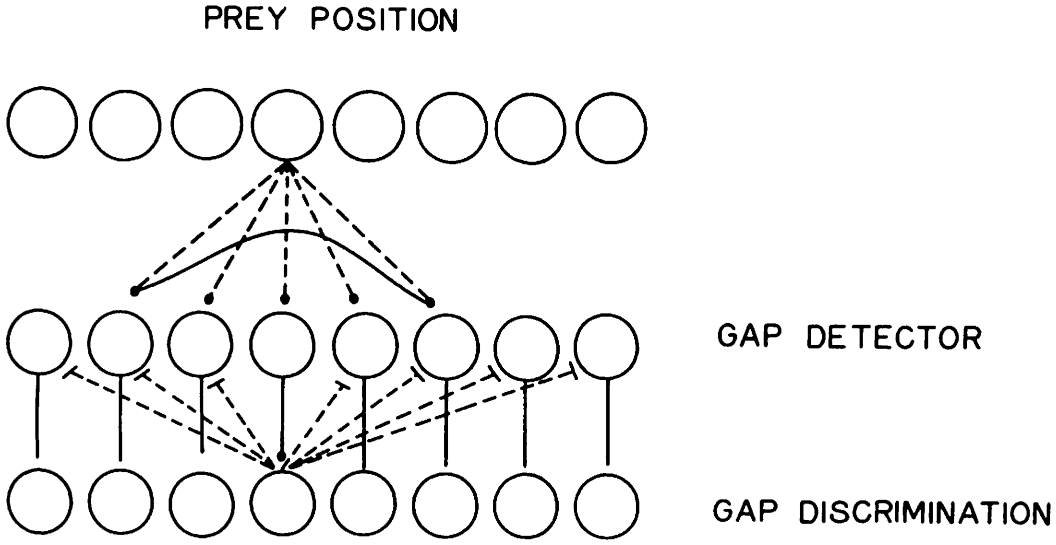

PREY POSITION
GAP DETECTOR
GAP DISCRIMINATION

Fig. 10

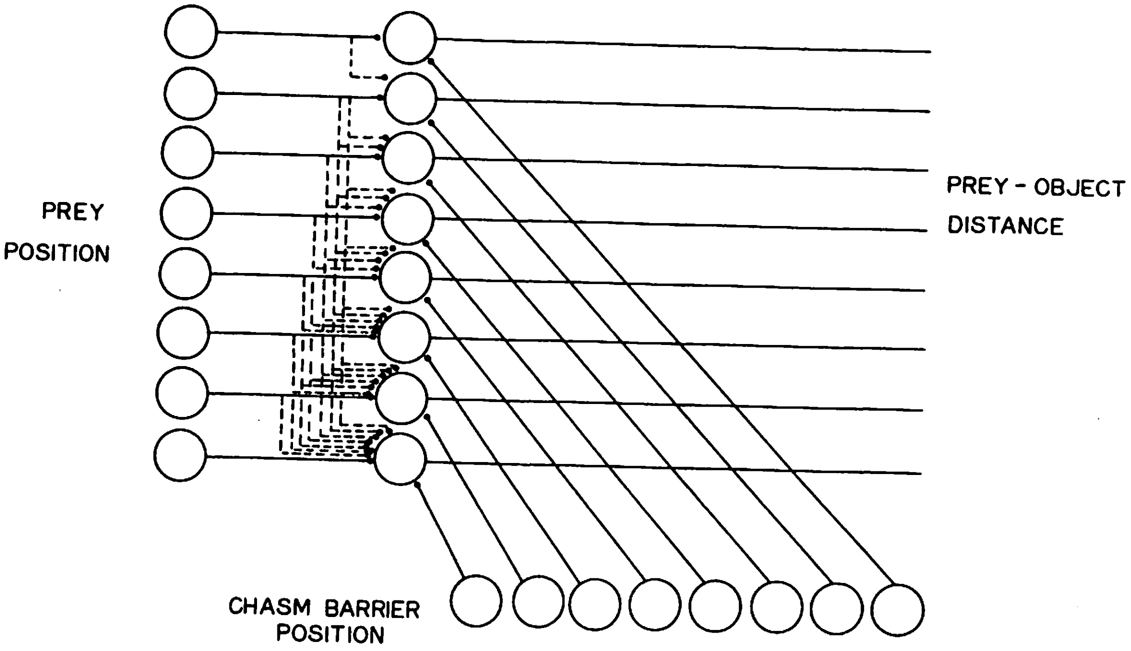

PREY
POSITION
PREY - OBJECT
DISTANCE
CHASM BARRIER
POSITION

Fig. 11

Fig. 12

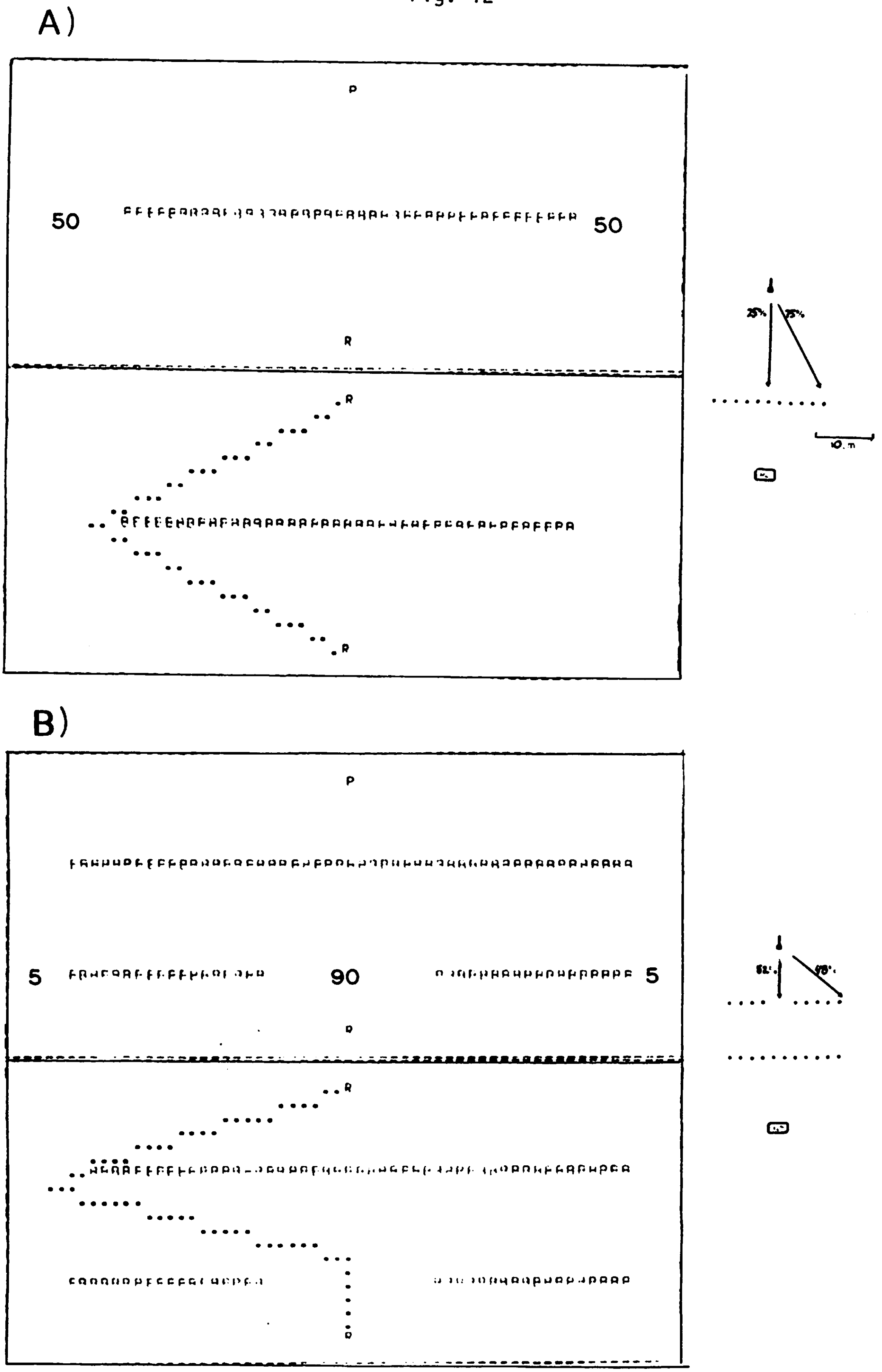


Fig. 13

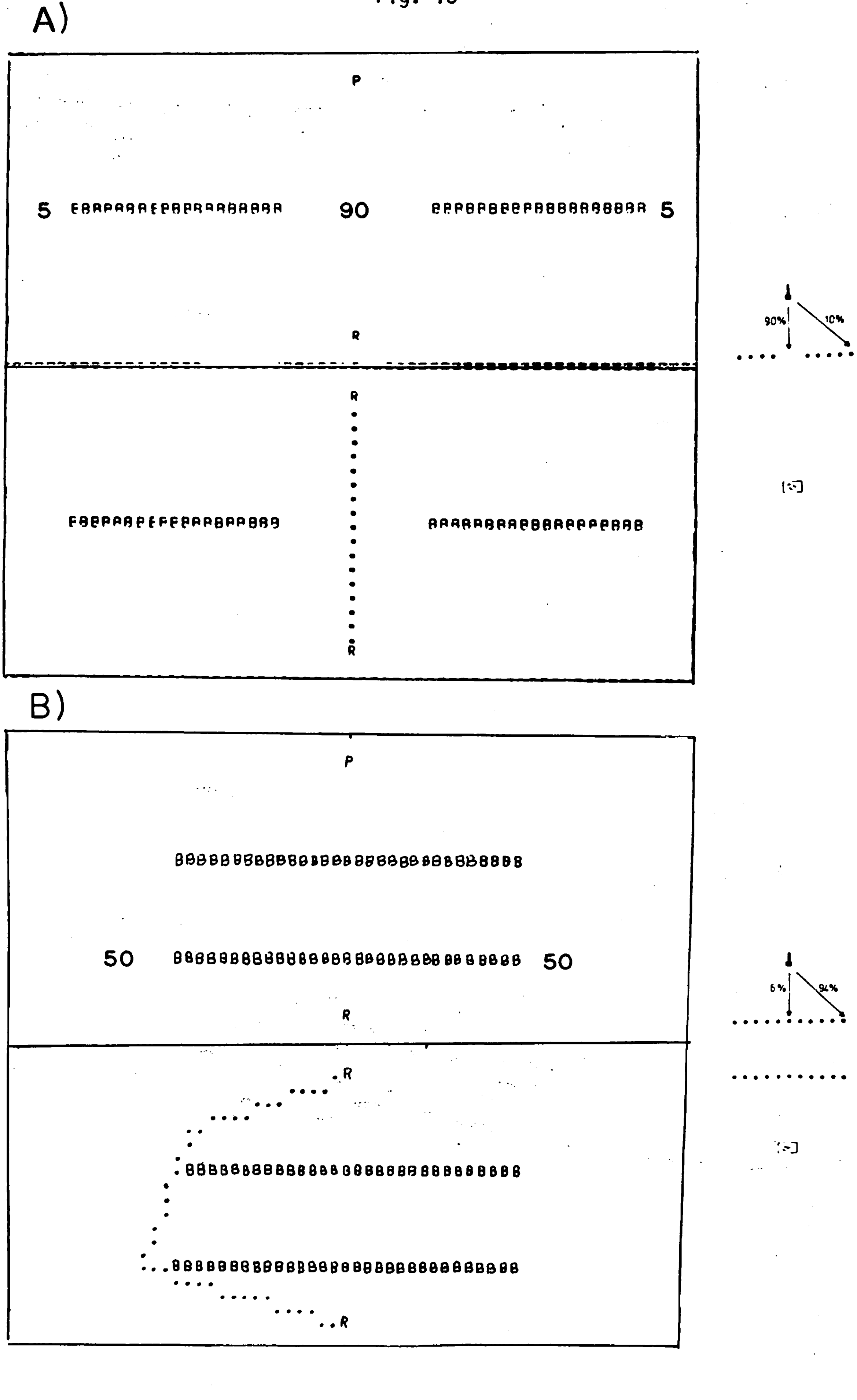


Fig. 14

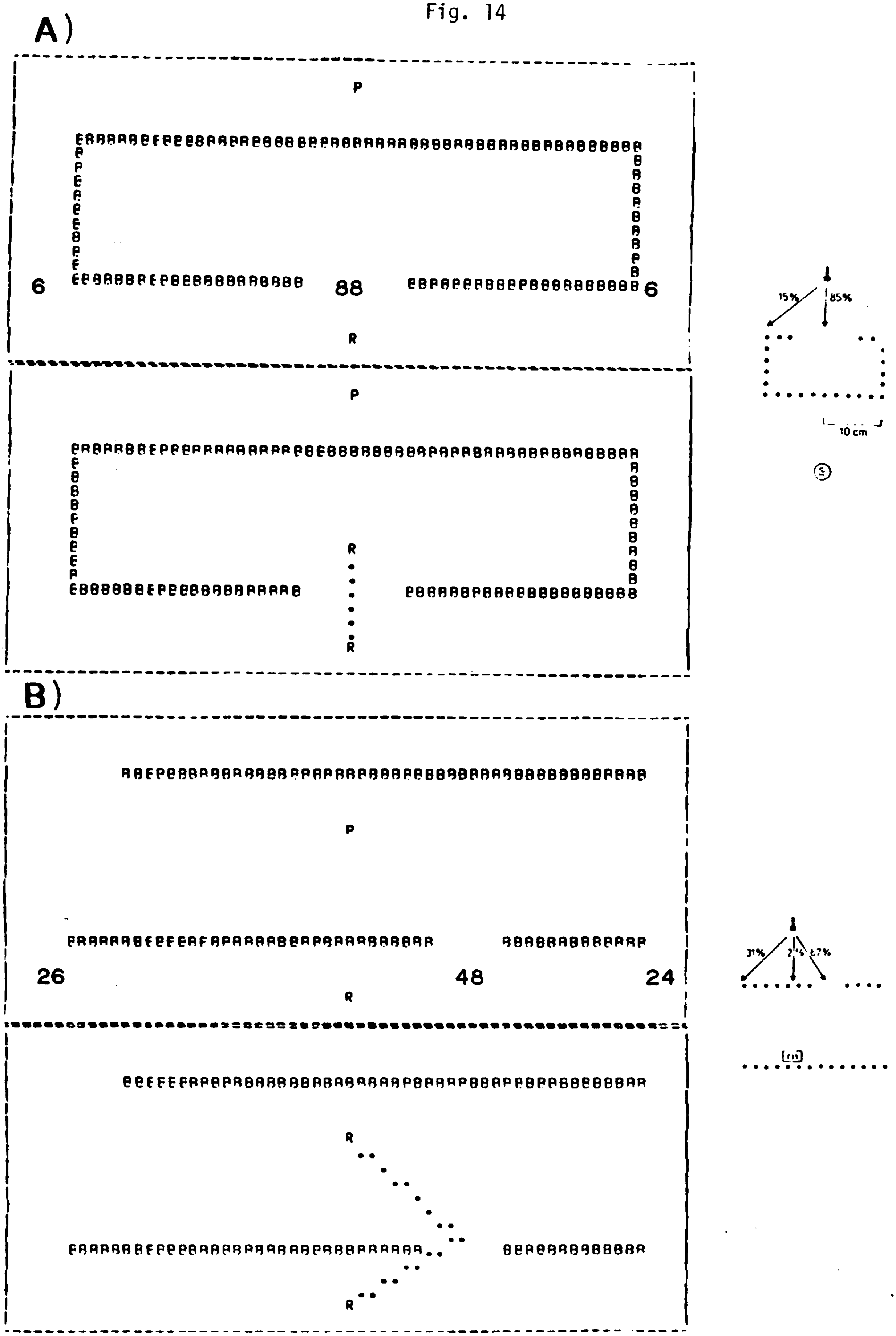


Fig. 15

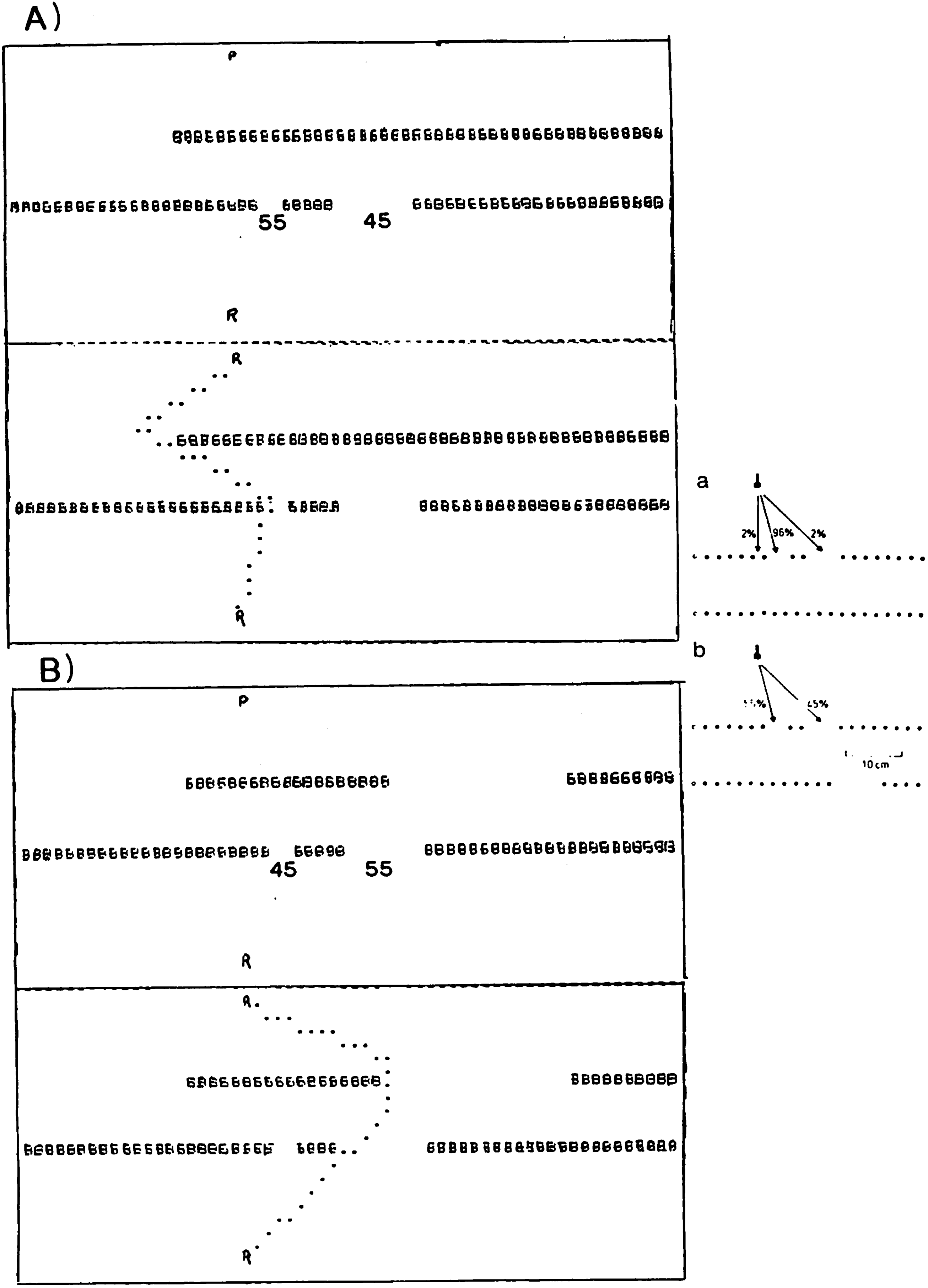
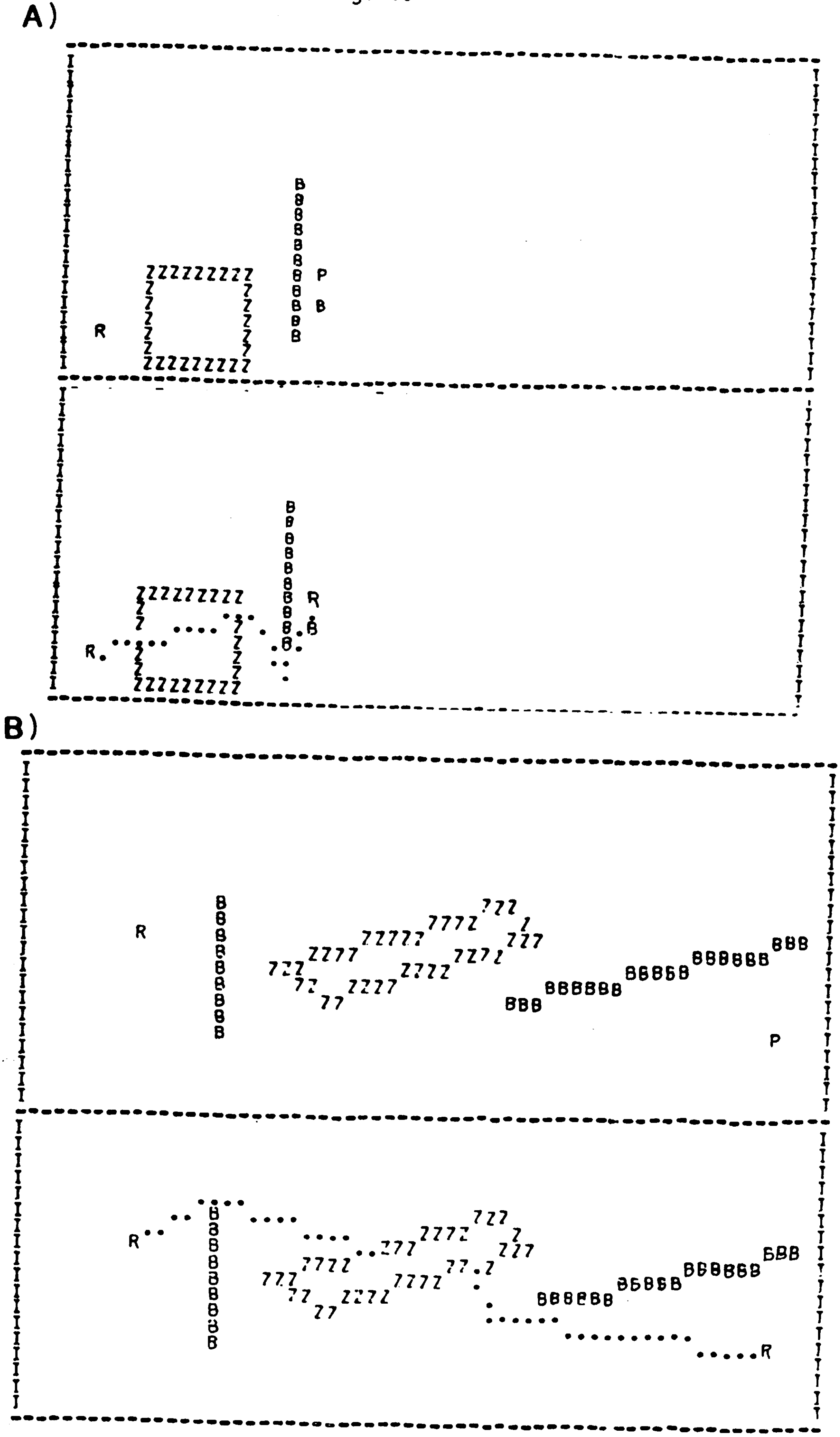


Fig. 16



Chapter 7: Neurochemical Studies

M.E. Sandoval, L. Massieu and S. Canizal: POSSIBLE NEUROTRANSMITTERS IN THE FROG OPTIC TECTUM

POSSIBLE NEUROTRANSMITTERS IN THE FROG OPTIC TECTUM

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The study of synaptic functions may be an useful tool for understanding the control of interneuronal communication. Our present knowledge of the synapses arises basically from anatomical and physiological studies; only recently the biochemical approach has been incorporated to the study of synaptic events.

In the vertebrate's nervous system the transfer of information in most of the synapses is given by chemical signals called neurotransmitters. It is known that at the nerve endings exists the biochemical machinery for the synthesis, storage and release of neurotransmitters. Studies on neurotransmitters have showed that they may be of different chemical nature. There is increasing evidence that amino acids as glutamic acid, aspartic acid, γ-aminobutyric acid (GABA) as well as norepinephrine (NE), dopamine (DA), serotonin (5-HT) and acetylcholine may be neurotransmitters in the central nervous system of vertebrates.

- SYNAPTIC TRANSMISSION

When an action potential arrives at the nerve terminal specific calcium channels, that are voltage-sensitive, are opened; the calcium ions enter to the nerve ending increasing the internal calcium concentration, which then triggers neurotransmitter release through an unknown mechanism (1, 6, 15). In the synaptic cleft the neurotransmitter molecules diffuse towards the postsynaptic membrane where they bind to a specific receptor. The interaction of the neurotransmitter with its receptor leads to a change in the membrane permeability to either sodium, potassium or chloride ions changing the polarity of the membrane. The neurotransmitter inactivation can take place in two ways: 1) an enzymatic modification of the molecule in the synaptic cleft or 2) transmitter uptake by the nerve ending. (Fig. 1).

IDENTIFICATION OF NEUROTRANSMITTERS.

Two approaches have been clasically applied to the study of neurotransmitter substances: the physiological point of view and the neurochemical one. From these studies arise the criteria for identification of neurotransmitters. (17, 18, 24).

1. Physiological Criteria.

1.1 Changes in the neuronal excitability.

A putative neurotransmitter must modify the neuronal excitability. This change in excitability may be due to an increase or an decrease in the neuronal firing or in the membrane potential. (18, 24).

1.2 Identity of Action.

When a putative neurotransmitter is applied to a neuronal membrane it must mimic the response of the neurone to the stimulation of the respective pathway. That is, it should lead to a specific postsynaptic response similar to that elicited by the release of the natural neurotransmitter. (18, 24).

1.3 Specificity of the postsynaptic receptor.

The action of the putative neurotransmitter on the postsynaptic membrane must be enhanced by agonists of the natural transmitter or inhibited by the antagonists agents. (18, 24).

2. Neurochemical Criteria

2.1 Localization at the nerve ending.

The postulated neurotransmitter must be naturally present at the nerve ending.

2.2 Synthesis and storage at the nerve endings

The synaptic terminal must have the biochemical machinery to synthesize and store the neurotransmitter. It is known for well established neurotransmitters that they can be synthesized either in the nerve ending or in the cell body and then transported to the nerve terminal through the axoplasmic flow. At the nerve ending the neurotransmitter may be stored in the synaptic vesicles or in a soluble pool. (13, 21).

2.3 Calcium-dependent release from the nerve ending.

The postulated neurotransmitter must be released in a calcium-dependent manner from nerve endings when a stimulus that mimic the action potential is given. This criteria is perhaps one of the most critical to postulate a substance as a neurotransmitter. (8, 17).

2.4 Specific postsynaptic receptor

The interaction of the neurotransmitter with its postsynaptic receptor must be specific. The agonist and antagonist agents of the natural transmitter must displace or inhibit the binding of the putative neurotransmitter to its receptor, respectively. (7, 22).

2.5 Neurotransmitter inactivation.

A specific mechanism to terminate the action of the neurotransmitter must exist at the synapse. Two systems for neurotransmitter inactivation have been described. The first is related with an enzymatic system in the synaptic cleft that changes the chemical nature of the neurotransmitter to make it ineffective. The second and more common system for neurotransmitter remotion is a specific high affinity transport system in the membrane of the nerve ending that is able to accumulate neurotransmitter from the environment. This transport system requires sodium ions and it has also been demonstrated in glial cells. (8,11,14,17).

IDENTIFICATION OF NEUROTRANSMITTERS AT SPECIFIC SYNAPSES

Regarding the criteria mentioned above a large number of molecules can be listed as neurotransmitters in the vertebrate's nervous system. However, there are little information on the identification of neurotransmitters at specific nerve endings. Glutamic acid has been proposed as the neurotransmitter of the granule cells in the cerebellum, (4,9,20), in the lateral olfactory tract of the olfactory bulb (10,27) and at synapses between the enthorinal cortex and the pyramidal cells of the hippocampus (16,19); GABA has been described as the inhibitory transmitter for some interneurones and the Purkinje cells of the cerebellar cortex (23,26). However, no attempt has been made for relating the control of synaptic transmission with specific functions of the nervous system.

Since the optic tectum of Amphibia has been studied from anatomical and physiological points of view and its role on the control of the visuo-motor coordination is well known, it offers an excellent model to study the participation of neurotransmitters on the control of specific functions of the nervous system. However, little is known regarding the transmitters of the optic tectum. The aim of the present work is to apply the most critical neurochemical criteria mentioned above in order to identify the neurotransmitters in the optic tectum of Amphibia.

We use the criteria of the presence of a high affinity transport system and the calcium dependent release from nerve endings. The putative neurotransmitters that we looked for in the tectal tissue were: glutamic acid, aspartic acid, GABA, glycine, among the amino acids, and dopamine, norepinephrine and serotonin for amines.

In the study we used partially isolated nerve endings from optic tectum. It has been demonstrated that isolated nerve endings maintain the basic physiological features of the nerve terminals "in situ" such as glucose utilization, respiration, ATP synthesis, as well as those related to the synaptic transmission: synthesis and storage of neurotransmitters, membrane potential, neurotransmitter accumulation and calcium-dependent release under depolarizing conditions (2,25).

Procedures for isolating crude preparations of nerve endings from specific areas and whole brain have been described (5,25). For the uptake and release experiments we applied the methodology that has been described in similar studies in hippocampus and cerebellum (19,20). A general scheme of these procedures is shown in Fig. 2.

RESULTS

1.1 Amino Acid Neurotransmitters.

Regarding the amino acid neurotransmitters we found that GABA and glycine both inhibitory transmitters in the central nervous system of vertebrates, are rapidly accumulated by tectal nerve endings; however it was observed that GABA was mostly taken up through a sodium-dependent transport system whereas glycine was accumulated by two different mechanisms, one of which is sodium-dependent and that may resemble that related to neurotransmitter remotion, and a second one that showed to be sodium-independent. (Table I).

In contrast to GABA and glycine, aspartic and glutamic acids, amino acids postulated as excitatory transmitters in the vertebrate's central nervous system, were less accumulated by tectal nerve endings. However, it is important to note that glutamic acid uptake was mostly due to a sodium-dependent mechanism. The sodium dependency for aspartic acid accumulation was unclear (Table I).

1.2 Amine neurotransmitters

We looked for a high affinity transport system for dopamine norepinephrine and serotonin, known inhibitory amines in the nervous system of vertebrates. In contrast to amino acid transmitters, the uptake of dopamine and norepinephrine was rather small, about two orders of magnitud lower than that observed for GABA and glutamic acid. In the case of serotonin, however, its accumulation by isolated nerve endings from tectal tissue was rather similar to that described for amino acids. (Table II). Regarding the sodium dependency of the amines transport, it was lesser than that of glutamic acid or GABA and in the case of dopamine it was rather small (Table II).

2. Release studies

2.1 Glutamic acid release

Glutamic acid was released from isolated nerve endings of the tectal tissue in a calcium-dependent manner. Under unstimulated conditions the transmitter substances are released spontaneously from the nerve ending. In Fig. 1 it is shown the spontaneous or baseline efflux of $[^{14}C]$glutamic acid from tectal nerve endings. When nerve endings were

Table I

Uptake of Amino Acid Neurotransmitters by Tectal Nerve Endings

nmoles/mg protein/5 min

	Total Activity	Activity in Na^+-free medium	Na^+-dependent uptake (% total)
GABA	5.98 ± 0.57 (9)	0.78 ± 0.07 (9)	87.0
Glycine	5.35 ± 0.61 (7)	2.02 ± 0.33 (7)	62.3
Glutamic acid	0.94 ± 0.07 (9)	0.15 ± 0.01 (9)	84.0
Aspartic acid	1.26 ± 0.15 (3)	0.58 ± 0.08 (3)	54.0

Table II

Uptake of Amine Neurotransmitters by Tectal Nerve Endings

pmoles/mg protein/5 min

	Total Activity	Activity in Na^+-free medium	Na^+-dependent uptake (% total)
Norepinephrine	21.5 ± 4.8 (5)	9.48 ± 1.34 (5)	56
Dopamine	2.61 ± 0.32 (8)	1.55 ± 0.26 (7)	40.7
Serotonin	2580 ± 460 (5)	1200 ± 330 (5)	53.5

stimulated with depolarizing agents that mimic the action potential (56 mM KCl or veratrine) in the presence of calcium ions, a two fold increase in efflux was obtained. In addition, when calcium ions were removed from the incubation medium, glutamic acid efflux decreased about 50%. (Fig. 3).

2.2 GABA Release

In contrast to glutamic acid, GABA was released from tectal nerve endings in a calcium-independent manner. The efflux of GABA was increased two folds in relation to the baseline efflux after stimulation with 56 mM KCl, however, this efflux was unchanged after the removal of calcium ions from the incubation medium. (Fig. 4).

DISCUSSION

The rate of amino acid neurotransmitters efflux observed in the isolated nerve endings from frog tectal tissue are similar to those reported for these amino acids in other areas from the nervous system in similar preparations and to those observed in the pigeon tectum. (3,12, 19-21). Thus it seems that the high affinity transport system for glutamic acid, GABA and glycine observed in the frog's optic tectum has the same characteristics than those reported for well established neurotransmitters: the requirement of sodium ions and the high transport activity at very low amino acid concentration. (3,8,12,20,21) Thus, it can be suggested that this transport system for glutamic acid, GABA and glycine may be related to the removal of neurotransmitter from the synaptic cleft in the tectum (14).

The role of amines in the synaptic transmission of the pigeon optic tectum has been poorly studied. Both dopamine and serotonin are accumulated by isolated nerve endings from the pigeon tectum; serotonin is taken up by an high affinity system whereas dopamine is accumulated by a low affinity transport mechanism. A transport system for norepinephrine has not been observed in the pigeon optic tectum (3,12). Regarding the results mentioned in this paper we may suggest that only serotonin may have an important role on the synaptic transmission of the tectum tissue. However, it is necessary to study other parameters in order to confirm this possibility.

We used the calcium-dependent test as a second criteria to study the possible role of different substances as neurotransmitters in the frog optic tectum. Our results showed that glutamic acid is released in a calcium-dependent manner, while GABA release is calcium-independent. These results strongly suggest that glutamic acid may play a role as a neurotransmitter in the frog optic tectum, while the role of GABA is still unclear.

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Synaptic Transmission

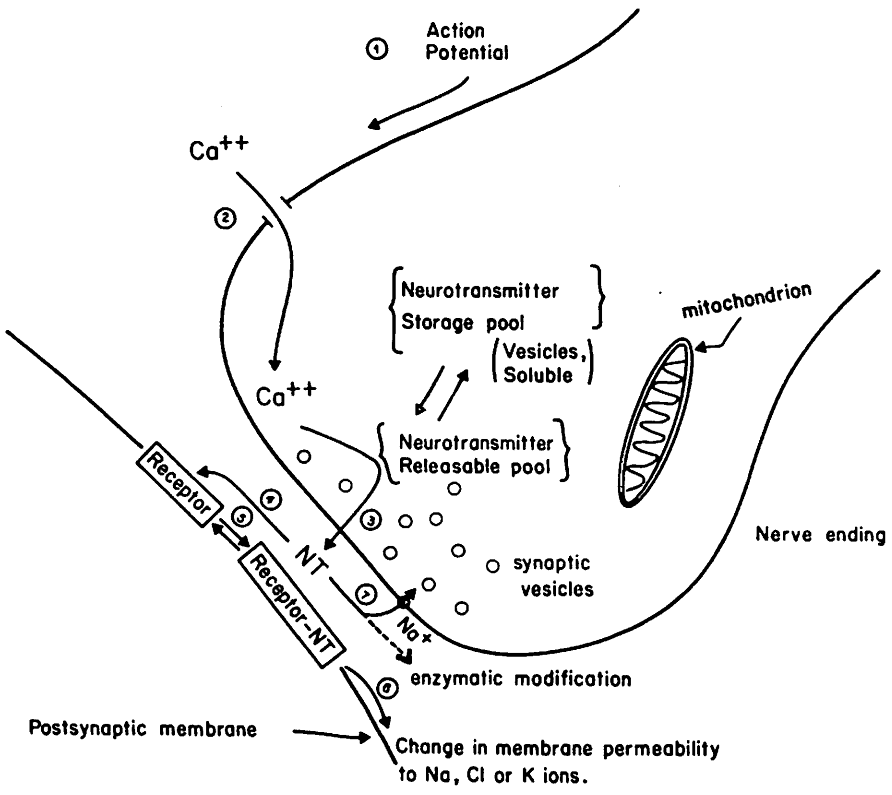

Fig. 1. Events during chemical synaptic transmission

1) An action potential arrives at the nerve ending; 2) the voltage-sensitive calcium channels are opened and calcium ions enter to the nerve ending; 3) the increased calcium concentration triggers transmitter release; 4) transmitter molecules diffuse across the synaptic cleft towards the postsynaptic membrane; 5) transmitter molecules bind to the postsynaptic receptor; 6) the membrane permeability to Na, Cl or K ions changes; 7) the neurotransmitter molecules are removed from the synaptic cleft either by an enzymatic system "in situ" or accumulation by the nerve ending.

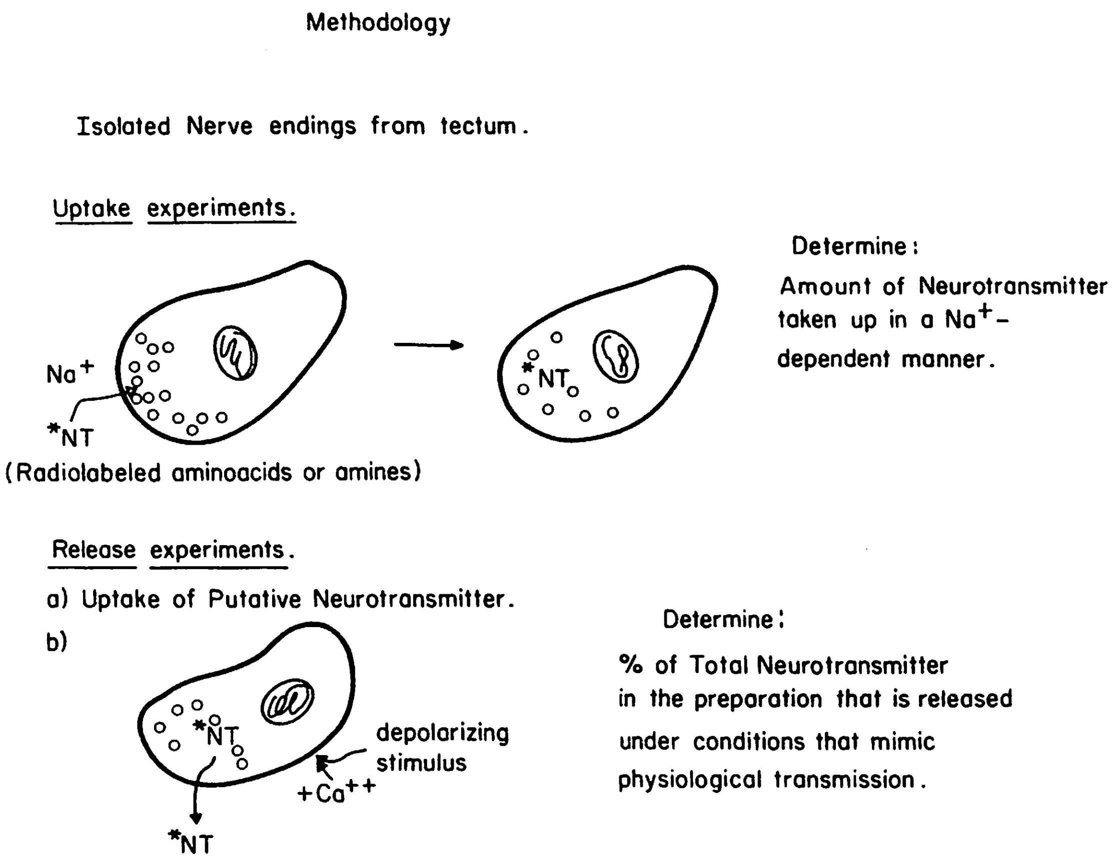

Fig. 2. General procedure for the uptake and release experiments. Methods have been described earlier (see refs. 19 and 20).

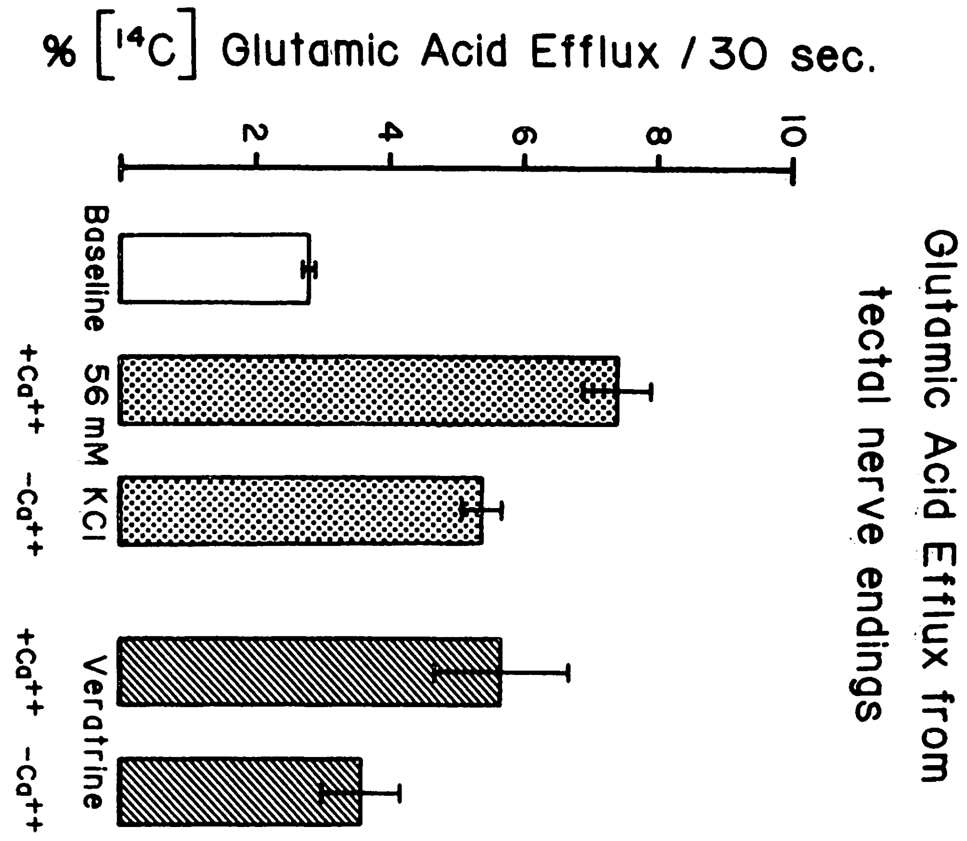

Fig. 3. [^{14}C]Glutamic acid efflux from tectal nerve endings. Baseline efflux represents the spontaneous release of the transmitter under nonstimulated conditions. % efflux = $\frac{\text{Radioactivity released/30 sec}}{\text{Total radioactivity in the tissue}} \times 100$

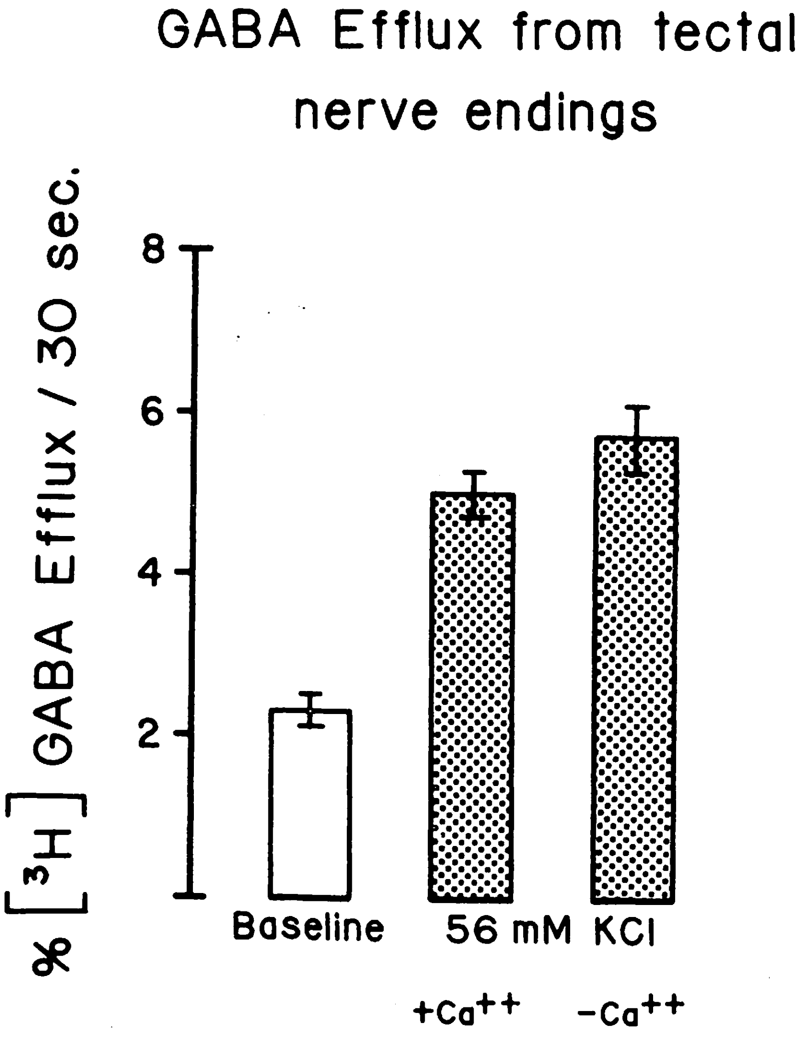

Fig. 4. [^{3}H]GABA efflux from tectal nerve endings.