THE PHYSIOLOGY OF HIGH-ORDER VISUAL NEURONS IN THE JUMPING SPIDER (SALTICIDAE) and THE VOCALIZATIONS OF FREE RANGING OWL MONKEYS.

Thesis by

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ABSTRACT

Jumping spiders have a highly specialized visual system for the detection and analysis of prey. The retina of each of the anterior medial eyes has a compact, high-resolution, three-dimensional array of receptors that can scan, saccade, and engage in slow tracking. Quaiitative study, computer-controlled data collection, and randomized stimulus presentation were used in an electrophysiological study of the properties of high-order visual neurons.

Receptive field mapping revealed neurons with well-defined, positionally stable, receptive fields. Some of these receptive fields had an angular extent greater than that of the static retinal array. The stability with respect to the cephalothorax and the angular extent of these receptive fields suggest integration of retinal information and eye position, to yield position constancy. Most neurons had receptive fields of constant angular subtense as the distance to the tangent screen varied. Some neurons have receptive fields that remain relatively constant in absolute physical size (changing in angular extent) as screen distance varies. Such size constant cells may be useful in assessing prey suitability. These characteristics require integration of depth information. These cells are driven monocularly, ruling out disparity cues. Jumping spiders do not use muscular accommodation. Instead, the retina has a layered, tiered structure. Depth of focus cues are probably the source of this information, as hypothesized previously by Land (1969a).

Quantitative assessment of velocity preferences revealed cells with medial eye input responding optimally to velocities of 16°/second, and other cells responding to higher velocities. Tuning for direction of movement orientation was also observed and quantified. The degree of tuning correlates with a measure of latency.

Results are also presented in a separate section from a primate behavior study on the vocalizations of the owl monkey, in which the vocal repertoire of two populations was recorded. Field recordings were analyzed for temporal and spectral properties of both the vocalizations and the acoustic context. We found no systematic variations of calls between populations, except for the number of syllables in the loud call. We examined behavioral context and probable function of inter and intragroup vocalizations. We found that the loud call may carry gender information, with a bimodal distribution of the spectral bandwidth of the fundamental.

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INTRODUCTION

Chapter 1

Jumping spiders (Figure 1.1) have always attracted attention, even amongst those who have little interest in spiders. Their bright colors catch the eye, but what wins the attention of observers is their visually guided behavior. It is easy to empathize with a creature that turns to look at you as you walk past, and will wave at a reflection in a mirror. It is much harder to imagine conducting your life by an analysis of substrate vibrations, as do most other arachnids. Jumping spiders are well represented in the arachnid fauna. The superfamily characteristic of eyes arranged in three rows (Figure 1.2) dates back at least to the Oligocene (Petrunkevitch, 1955).

Most of the results I will present are derived from neurophysiological studies. These results in isolation will mean little without the ethological context, so I will sketch not only brain but visual behaviors, as well.

NEUROANATOMY - HISTORICAL TIMELINE

Since the early work of Georges Saint-Remy (1887), describing the variation of visual masses in several families of spiders, many anatomical techniques have been developed, but few have been applied to spiders. There is nothing like the pioneering studies of pathfinder neurons in other arthropods (i.e., Goodman, 1982) and the field has been little colored by application of various dyes, HRP, or monoclonals. This is because the primary focus of arachnological research has been taxonomy, and the morphological research which has been done was generally concerned with homologies.

Figure 1.1 Frontal view of a mature female Phidippus johnsonii.

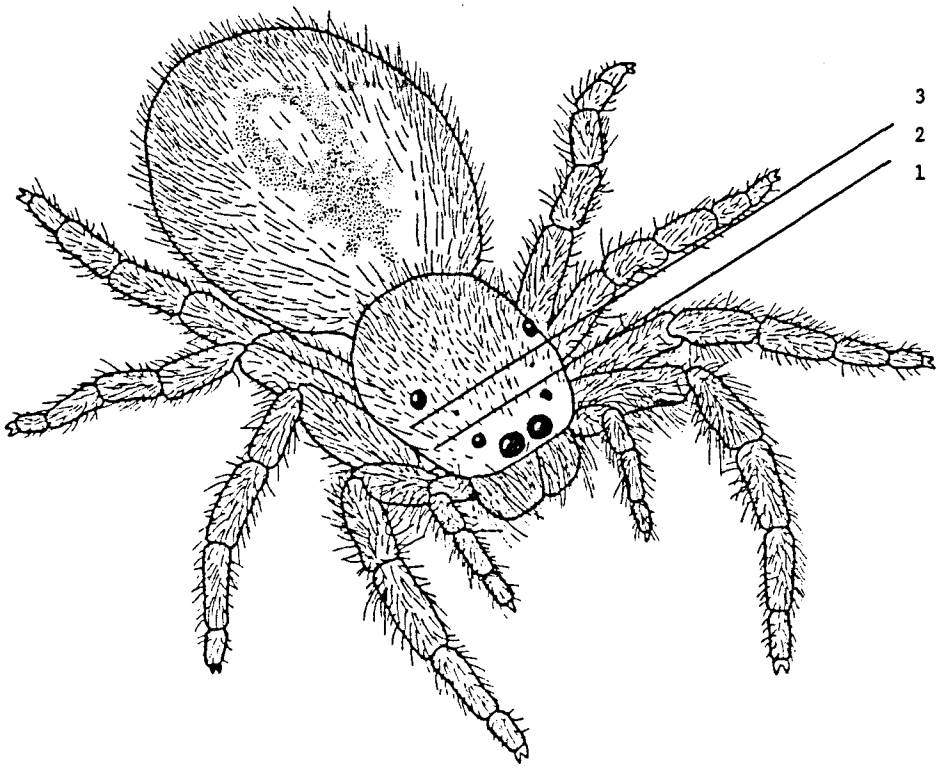


Figure 1.2 The superfamily characteristic of salticids is the arrangement of eyes in three or four rows. P. johnsonii, as drawn, has eyes arranged in three rows, in contrast to more "primitive" salticids such as Lyssomanes.

Reviews of work prior to 1939 may be found in Bonnet (1945-1962). Millot (1949) provides a review of araneid biology. Legendre (1959) gives a review of morphology and development, and Bullock and Horridge (1965) give an extensive review of invertebrate nervous systems. The most current general listing of and review is Neurobiology of Arachnids, edited by F. G. Barth.

A major contribution to our understanding of the araneid nervous system comes from the work of Hanstrom (1919, 1921, 1923, 1928). He used Golgi techniques to study the system on a cellular level, as well as gross nervous structure. His comparative studies demonstrated structural differences that are related to differences in sensory specialization, and included other arachnids in addition to spiders.

Legendre's (1959) review and study cover the central and sympathetic nervous system and development. He notes the musculature for movement of the anterior medial eyes, which is of great importance for the jumping spiders.

The first of many papers to come from Babu (1965) is a comparative anatomical study of the cental nervous system of five orders of arachnids, using silver impregnation to study fiber tracts, as well as several basic stains.

The last two decades have seen many more anatomical studies, including Meier (1967), Trujillo-Cenoz and Melamed (1967), Satija (1970), Hill (1975), Oberdorfer (1977), Tsvileneva (1982), Babu (1985).

Many of the early studies remarked on the optic lobes of salticids in passing, but not until the last twenty years have studies been devoted to visual systems. Melamed and Trujillo-Cenoz (1966, 1967) studied the optic nerve and synaptic structure in the visual system. Satija et al. (1970) provide sketches of the optic lobes of a cribellate spider. Tsvileneva and Titova (1982) studied the visual system cellular morphology in sedentary orb weavers.

Salticids were found early on to have the most highly specialized visual system, with optic ganglia comprising 25% of the total brain mass, as compared to 3-4% in sedentary species (Hanstrom, 1928). Even in the visual wolf spiders, the optic masses make up only 7-12% of the brain volume. This should not be surprising, in the light of the extreme development of the jumping spider's principal eyes, and heavy reliance on visually guided behaviors.

Hill's (1975) thesis contains an excellent description of salticids of the genus Phidippus, with horizontal sections that detail the fiber tracts, and a few sketches of sagittal sections in different instars. These are quite useful in lieu of an anatomical atlas.

Oberdorfer (1977) gives a detailed description of synaptic structure in the first optic ganglion of the principal eye of two salticids, both with light microscopy and electron microscopy, discovering ribbon synapses and synaptic glomeruli similar to some found in vertebrate sensory systems.

No physiological studies have been published on the central nervous system of salticids. Physiological studies of the eyes (DeVoe, 1975; Yamashita and Tateda, 1976; Blest et al., 1981) have determined different spectral sensitivities in retinal receptor populations.

Study of central nervous system neurotransmitters has just begun. Meyer and Idel (1977a) and Meyer and Pospiech (1977b) have assayed the distribution of acetylcholinesterase in araneids, salticids, and lycosids, finding relatively high concentrations in the active CNS visual systems of the latter two.

The number of studies of arachnid neuroanatomy is minute compared to the number of species and great diversity found in this group. Babu (1985) observed, "...the central nervous system of arachnids is a rich, unexplored field, ready for harvesting. Our knowledge of the finer anatomy and physiology of the CNS of arachnids is much behind what is known in insects and crustaceans."

Sensory and general neuroanatomy

Figure 1.3 shows the fused ganglia of the salticid nervous system. Sensory processing takes place in the protocerebrum and associated supraesophageal ganglia (collectively called the syncerebrum), and motor processing takes place in the subesophageal ganglion. There are a few exceptions to this generalization, such as the motor control for the chelicerae, which is located above the esophagus, and sensory information coming in from the legs.

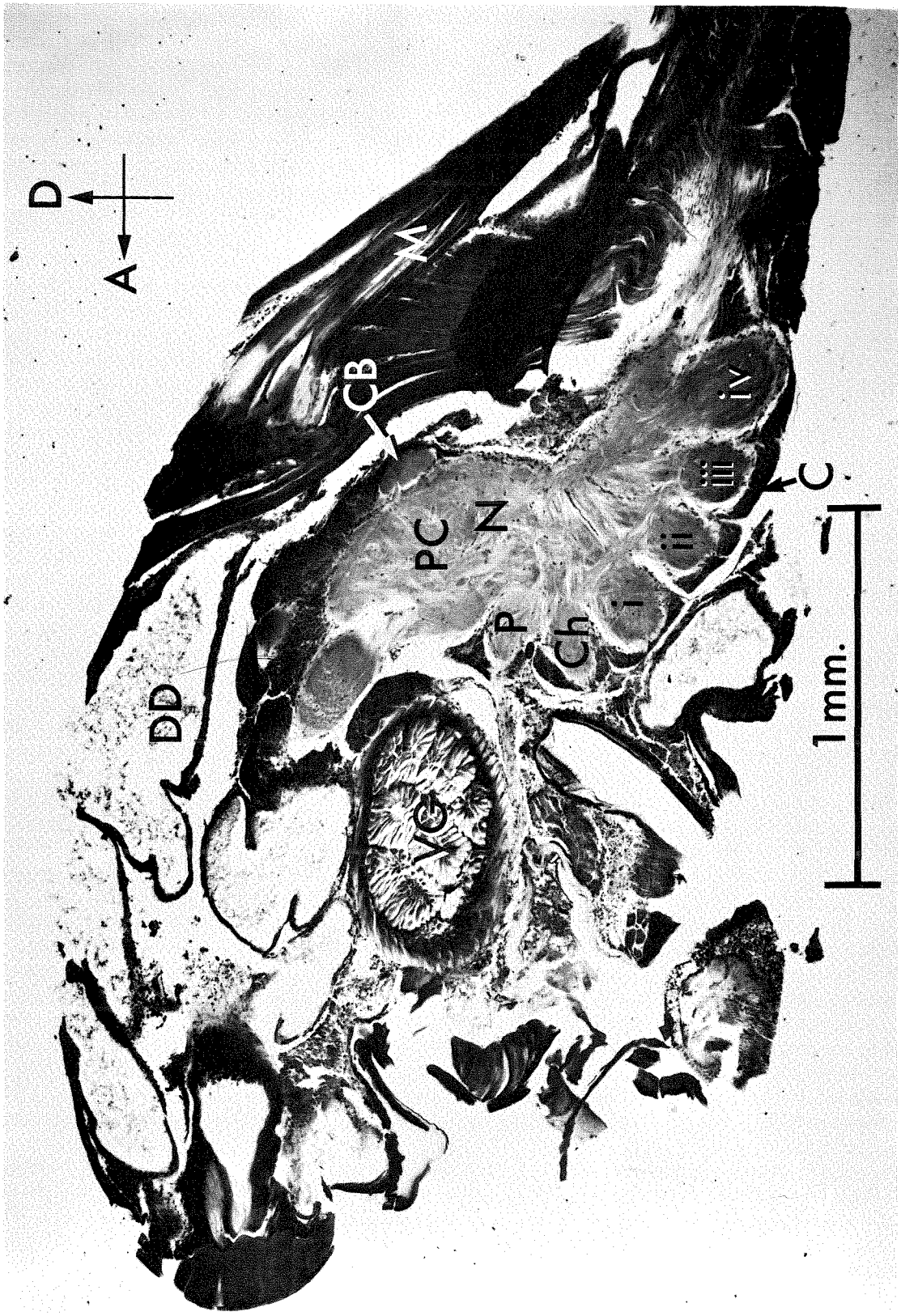
Central nervous system

The brain consists of a core area of neuropil, which is composed of all the ramifications of neural processes. The cell bodies are clumped around this core in a rind, called the cortex. Synapses have not been found in the cellular cortex (Babu, 1985). The entire structure is sheathed in a neural lamella, consisting of a single layer of compact cells (Hill, 1975).

The brain receives a variety of sensory input. Yamashita and Tateda (1983) have described extraocular input to the visual system of some spiders, in addition to the input of the eight eyes. Mechanical stimulation is sensed through several different channels. Trichobothria, with their hair cell-like innervation, sense airborne vibration. Lyriform organs and slit sensilla sense cuticle deformation, providing information about substrate vibration. Proprioceptors sense internal joint stresses. There are several chemical sensing inputs as well, such as chemosensitive hairs that sense pheromones. There are tarsal pits that may be involved in sensing moisture. There are certainly other chemosensitive channels, which remain to be described.

Babu and Barth (1984) found that the brain consists of between fifty thousand and one hundred thousand neurons in Cupiennius. Histological studies have revealed several types of glial cells, and four or five categories of cells,

Figure 1.3 Internal gross morphology of the cephalothorax, parasagittal view. In this and in subsequent figures, A=anterior, D=dorsal, P=posterior, V=ventral. Other abbreviations will be defined in their first figure of appearance. A complete list of abbreviations may be found in Appendix A. C=Cell bodies, CB=Central Body, Ch=Cheliceral ganglion, DD=Digestive Diverticula, M=Muscle, N=Neuropil (cellular processes, dendrites), P=Pedipalpal ganglion, PC=ProtoCerebrum, VG=Venom Gland, I-IV=leg ganglia 1-4. (Plate)


D
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based on nuclear and cell size, quantity of chromatin, location, etc. A consensus has yet to emerge, but the largest cells are usually 30-80 μm (up to 140 μm) in somata size and are motor neurons. Globuli cells, rich in chromatin and possessing a nucleus of 6-8 μm, are associated with the mushroom bodies.

Central Body

This two-layered structure lies dorsal to the mass of the protocerebrum. It receives axons from the protocerebrum, and tracts to and from the subesophageal ganglion as well. It has been considered the final integration center for vision, a multimodal "association" center, and a center for genetically programmed behavior. Witt et al. (1972) observed that orb weavers do not learn to build webs, and that they have large central bodies, relative to other spiders, suggesting the latter hypothesis may be correct for orb weavers.

Rostral Ganglion

This structure consists of the two bilaterally symmetric lobes that have fused. It lies dorsal to the anterior portion of the esophagus and coordinates the pharynx and the sucking stomach.

Cardiac Ganglion

This structure consists of 60-80 neurons, and drives the heart neurogenically, as in the lobster (Bursey and Sherman, 1970).

Cheliceral Ganglion

This structure corresponds to the tritocerebrum of other arthropods. It lies above the esophagus, but is considered part of the motor system.

Pedipalp and Legs I-IV Ganglia

These ganglia, together with the cauda equina, comprise the subseophageal ganglion. There is a well-delineated region of neuropil for each of the two pedipalps and eight legs.

Deutocerebrum

There appears to be no trace of this structure, common in other arthropods. It is usually driven by antennal input, which may make its absence less surprising, as spiders lack antennae.

Protocerebrum

The protocerebral neuromere is the site of high order visual integration in salticids. Most of the cell bodies lie packed together anterior to the mass of neuropil.

Supraesophageal Ganglion

This term covers the central body, the protocerebrum, visual centers, and the rostral and cheliceral ganglia.

Corpora pedunculata

This pair of ganglia (one per side) is the site where visual information from the anterior lateral and posterior lateral eye converges.

Cauda Equina

This structure lies ventrally, symmetrically disposed about the midline. It controls opisthosomal functions, such as the pedicel, abdomen, spinnerets, epigynum, and book lungs.

Development

The number of neurons seems to remain constant during development, from instars one through adult. Hill (1975) shows that the nervous system occupies almost the entire volume of the cephalothorax in second instar spiders, decreasing to a much smaller portion in the adult. The size increase is due to increase in cellular volume, glial cell number and size, and increases in the neuropil (Babu and Barth, 1984).

ECOLOGY AND BEHAVIOR

Chapter 2

Although species numbers for arthropods are constantly being revised upwards (Conniff, 1986), jumping spiders can be said to comprise about ten per cent (3,000 of 30,000) of all described spider species, indicating that heavy reliance on high-resolution vision can be a viable strategy in arthropods of this size class. These successful leapers are most numerous in tropical climes, but worldwide in distribution, excluded only from polar tundra, ranging from 69 degrees North to 47.5 degrees South (Cutler, 1982). Their unique visual system has allowed an adaptive radiation into a variety of niches, from subnivean habitats to tropical rainforest, and from subsealevel xeric environments to the 22,000 foot level of Mt. Everest, where they live as top predator in a restricted food chain (Wanless, 1975).

This powerful visual system serves as a general tool, supporting a diversity of prey utilization and other behaviors, as might be expected from the range of habitats. Ant-like salticids live within the protection of an ant colony, and in some species feed upon the colony as well. Some salticids are almost exclusively arachnivorous, stroking the web of their prey as would a potential mate, and varying the vibrational pattern until they observe a response (Jackson, 1985). If they stalk another salticid, they adopt visual deceit, using body parts to camouflage the distinctive salticid features that might reveal them to their prey. Jackson and Blest (1982) advance an attractive hypothesis for web invasion and arachnivory as the original step in the evolution of jumping spiders, as exemplified by Portia.

Phidippus is a large (12-13 mm body size for adult females), colorful spider with a squarish cephalothorax and is represented by about forty species in North America (Hill, 1975). I used P. johnsonii (Peckham, 1883) for most experiments and for most of my behavioral observation as well. Some of my experiments were conducted using a Phidippus from Sedona, Arizona, which resembles johnsonii. The taxonomy of western Phidippus is being revised by G. B. Edwards. I also observed P. rimator, P. octopunctatus, P. audax, P. apacheanus, and a variety of Philippine, Australasian, and Peruvian genera in captivity. In addition to Phidippus, other local genera such as Thiodina, Pellenes, Menemerus, and Metaphidippus were also observed.

The life history of P. johnsonii covers a period of a year to eighteen months. Although some captive specimens live two years, they are usually quite decrepit, and this age group is not well represented in field collection. Adult males mature a few weeks earlier than the females and die months sooner. The adult males (body length about 10 mm) become conspicuous to the casual observer in early March, and the adult females (12-13 mm) a few weeks later. These and subsequent dates are based on observations in Pasadena. The specific season will vary for Phidippus in other habitats. After courtship and sperm transfer, a well-fed female will soon produce an egg sac, containing up to 60 eggs wrapped in protective silk. She may produce as many as five of these over the next few months. The spiderlings develop rapidly, and in as little as two weeks, second instar spiders may emerge, having spent the first instar without food in the protective confines of the silk egg sac. (An instar is the stage between molts; a second instar spider has molted once.) At this stage the spiderlings have a body length of approximately 1 mm, and are a fraction of a percent of the adult volume, yet are capable of distinguishing between their cohort and their potential prey, such as Drosophila, small lepidopteran larvae,

insect larvae, etc. Much of the interior of their cephalothorax is occupied by the central nervous system at this point (Hill, 1975). Within a few days of emergence and after a few abortive capture attempts, most are quite accurate in their pursuit and capture of prey. Manly and Forster (1979) showed that naive Trite auricoma would orient to prey and succeed in capture 9% of the time for a first capture, with success rising to 38% and 61% for second and third captures. The unsuccessful spiders sink into torpor and expire. After sufficient feeding, the spiderling is ready to molt its rigid exterior to allow further growth. He spins a small silk shelter, secretes enzymes that partially digest the chitin from within, then splits open the carapace with elevated internal pressure.

Spiderlings lose much of their gregarious tolerance of siblings during the third or fourth instar and will consume their siblings in the absence of suitable prey.

The spider usually overwinters as a subadult. This seems to be a period of low activity, spent primarily in the silk shelter at the base of a plant or under stones.

After eight or nine molts, the jumping spider is mature, with complete sexual characteristics (pedipalps, epigynum) appearing on emergence from the last molt.

Phidippus johnsonii is most seen at this stage. The spider frequents sunny surfaces offering a good visual vantage point (Figure 2.1), allowing ready detection of prey and potential threats, such as wasps.

Visually guided behavior

The jumping spider has two pairs of lateral eyes. Their combined field of view covers all but a small arc behind the spider. As shown by Land (1972a), the spider can use these eyes to detect the translation of a one-degree turn, which

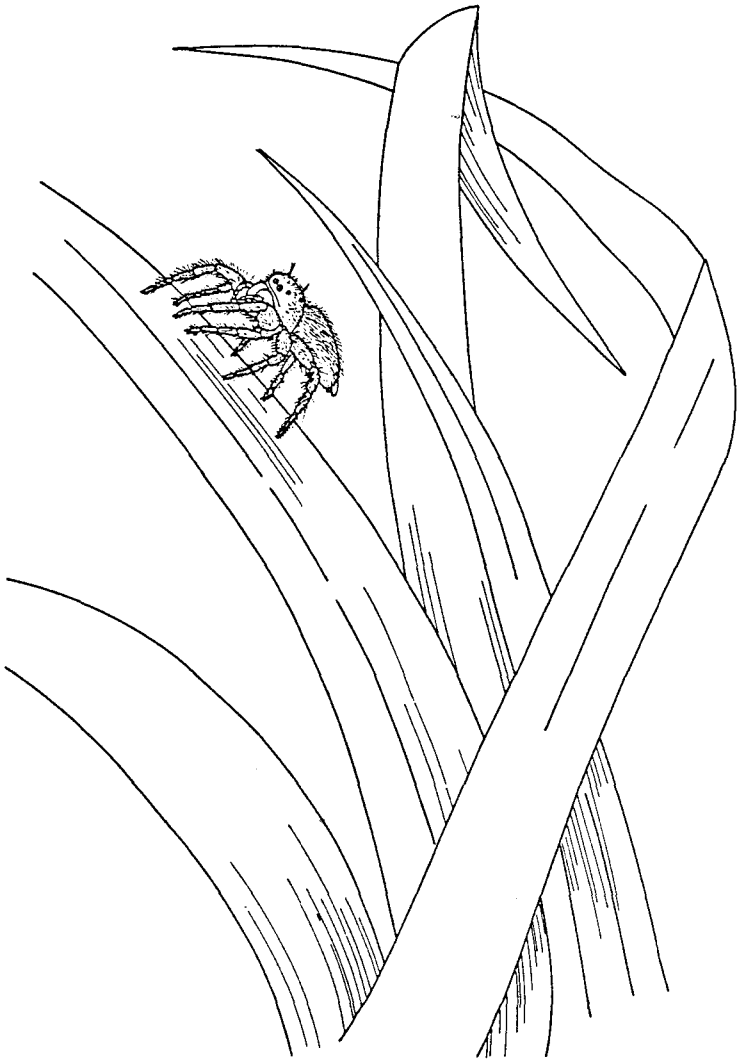

Figure 2.1 P. johnsonii on a day lily leaf, a common sight on sunny spring days. The spider moves to the underside of the leaf, and runs to the base of the plant when threatened.

accurately positions the stimulus in the field of view of the high-resolution principal eyes.

Perception of form by jumping spiders was studied by Drees (1952), who presented stimuli, graded from simple geometric forms to a frontal profile of another spider (Figure 2.2 A, C). He found that the spider consistently attacked simple geometric forms and fly shapes, but as he added spider features to the profile the attack frequency declined. It seems that the spider is checking for the presence of certain features that indicate a dangerous prey item; in their absence, if the prey is not too large, he will attack.

Each principal retina of P. johnsonii subtends a width of 1-2 degrees and a height of 20 degrees (Figure 2.2D). At a typical laboratory capture distance of 28 mm (about two body lengths), the view of a fruit fly (Drosophila melanogaster, 3 mm long, 1.5 mm high) from lateral aspect subtends about 6 degrees horizontally and 3 degrees vertically. About one third of the length of the fly would fall on the retina, covering about one hundred receptors in each of the two high-resolution retinal layers.

Land estimates a minimum receptor separation in the central retina of the principal eyes of nine minutes. Hyperacuity, utilizing the array of retinal receptors, could improve this performance.

High visual accuity is also evident from behavioral experiments. Drees reported different responses to winged versus non-winged prey (Figure 2.2B). Land (1979) reported tht a salticid could discriminate another spider when it was at such a distance as to cover only thirty receptors. I have noticed in collecting specimens that when I sight them on a bush from ten meters, they are already tracking my movements. C. Kristensen, who supplied many of the specimens, uses binoculars to scan likely habitat to locate salticids before they take evasive action.

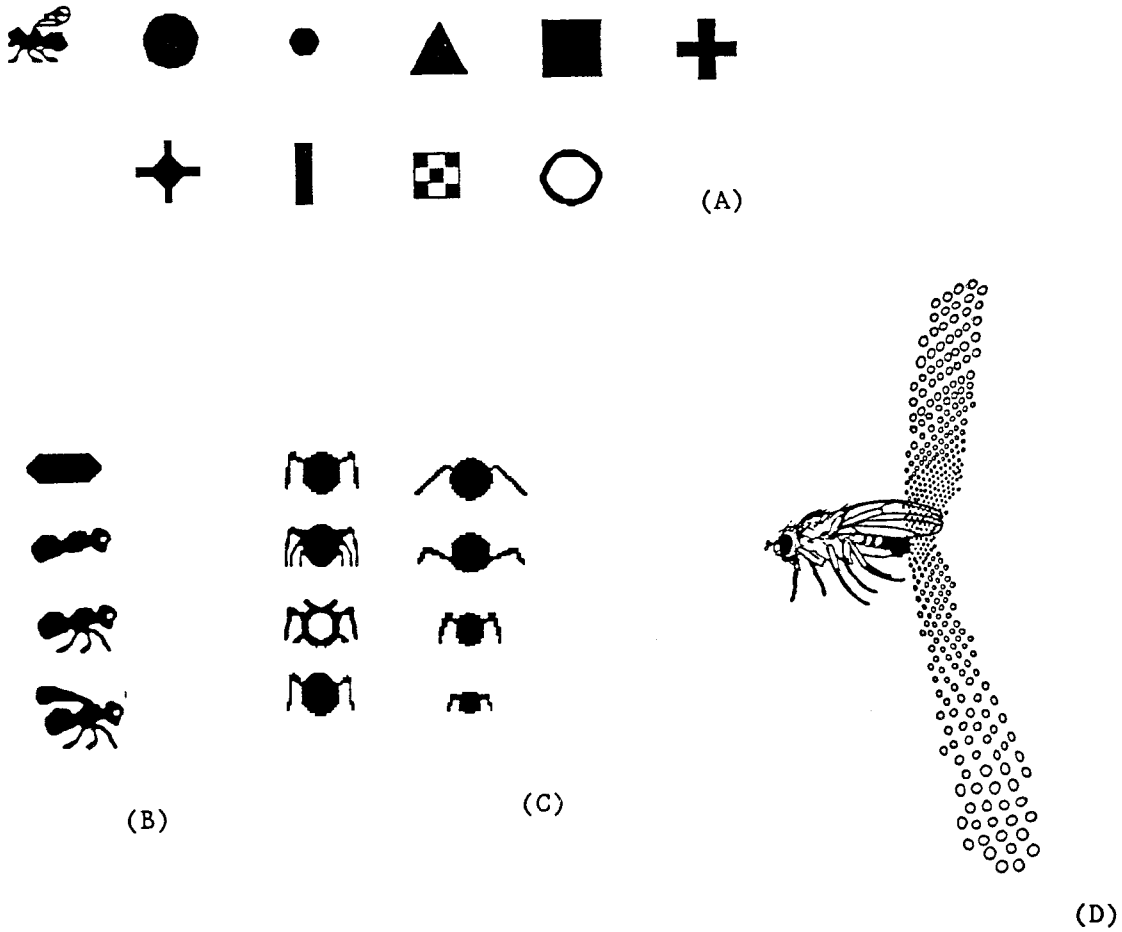

Figure 2.2 Drees (1952) used a variety of two-dimensional stimuli to explore the nature of form vision in salticids.

(A) Items treated as prey.

(B) Response varies with presence of wings.

(C) Propensity to attack the stimulus diminished as "spiderlike" features were added.

(D) Drosophila melanogaster, as it would appear on the layer 1 retinal mosaic at a typical capture distance (28 mm) observed in the laboratory. Prey are identified at greater distances.

Prey capture occurs typically from distances of 6 cm or less. The spider orients to the prey and makes a quick leap. If the prey is on the move, the spider may give chase. Forster (1982) has shown that this decision is largely mediated by the frontally directed lateral eyes (AL eyes).

If the desirable prey item is distant, the spider then uses eye movements and slight turns to survey possible approach pathways to the prey. Land (1979) has commented on the catlike nature of the subsequent stalk, with low crouching, creeping, freezing, and indirect approach, until within pouncing range. If the approach is on a three-dimensional substrate such as a branching tree, the spider will lose principal eye contact on its circuitous route. He nevertheless seems to retain an accurate spatial map of the prey location. Hill (1979) demonstrated that as the spider makes this approach, he will occasionally make a ballistic turn that will point his principal eyes at the prey location, though visual barriers may intervene. This orientation may be a combination of gravitational reference, idiothetic navigation, and use of visual landmarks. Stalking and approach behaviors may vary, based on the nature of the prey.

Visual courtship displays begin typically at distances of 10-12 cm. The male's front legs rock from side to side and move inwards and laterally in ever decreasing arcs. The motions and legs used vary among species, and this display facilitates identification of conspecifics. In addition, many salticids are marked by distinctive tufts of hair, leg adornments, and color patterns. If receptive, the female will freeze and allow the male to reach over from the front and side and rotate her abdomen, so that his pedipalps, precharged with sperm, can be inserted into the epigynum. This process can last for over thirty minutes, after which they go their separate ways. If the female is not receptive, or the display is inappropriate, she will attack the male. The attack appears vigorous, and the female is larger than the male, but I have not observed fatal results. Indeed, the

male often persists and approaches a few more times. I have not observed success resulting from this persistence.

THE EYE: OPTICS, RECEPTORS, MUSCLES

Chapter 3

Introduction

Most spiders have eight simple eyes located on the cephalothorax. They consist of a cornea, a lens, crystalline cone cells (a vitreous body), and a retina, comprised of sensory and support cells.

The great variation in the details of the eye structures reflects the diversity of lifestyles among the spiders. The number of receptors in a single eye can be as high as 16,000 in some visually guided spiders, or entire eyes can disappear during development in cavernicolous species. Most spiders possess a tapetum, a reflective layer behind the receptors analogous to the tapetum lucidum found in some nocturnal vertebrates. This layer increases sensitivity, albeit at the cost of resolution.

Terminology

Salticids have four pairs of eyes, which are categorized by function and position. The secondary eyes are the anterior lateral (AL), posterior medial (PM), and posterior lateral (PL) eye pairs. The principal or main eyes are the anterior medial (AM) eyes.

Secondary eyes

The structure of the secondary eyes of salticids is similar to that of the typical spider described above, except that the tapetum is lacking entirely (Eakin and Brandenburger, 1971).

The cornea (Figure 3.1) is a cuticular structure, several microns thick, consisting of many laminations, densely packed. It is shed as part of the exuvia with each molt.

The lens is a biconvex, laminated structure. The laminae are made up of microfibrils, each 20 nm in diameter (Munoz-Cuevas, 1984). The laminae are less dense than in the cornea. The lens is secreted by the crystalline cone cells. Focal lengths for the frontally directed AL eye and the laterally directed PL eye are given in Table 3.1 (from Land, 1969a). Some of the optical data come from the hanging drop preparation of Homann (1928), and Land (1969a), in which the lens is dissected free of the carapace and suspended on a drop of water, allowing direct measurement. The PM eye has a small lens and only a few hundred receptors, and has yet to receive a thorough study.

The structure and optics of salticid eyes have been studied by Scheuring (1914), Homann (1928, 1971), Land (1969 a, b, 1971), Eakin and Brandenburger (1971), Blest et al. (1981, 1983, 1984, 1988), and others. Most of the information that follows pertaining to Phidippus johnsonii comes from the electron microscopy of Eakin and Brandenburger (1971) and the optical microscopy of Land (1969a).

The retina of the lateral eye is classed as an indirect retina and consists of sensory cells and two types of support cells (Eakin and Brandenburger, 1971). The sensory cells are unipolar. The cell bodies lie in a band outside the retina, encircling the eye. The projection from the cell is an axonlike fiber. After it bends into a path normal to the local curvature of the retinal surface, arrays of microvilli sprout from two of its sides, forming two rhabdomeres. After the rhabdomeric section, the microvilli cease, and the axon continues on, ultimately to synapse in the first lateral eye ganglion.

Figure 3.1 A parasagittal section through the anterior lateral eye, showing receptive cell layer and pigmented surrounds of the lateral eye. AL=Anterior Lateral eye, Co=Cornea, Le=Lens, O=Optic nerve, R=Retinal receptors.

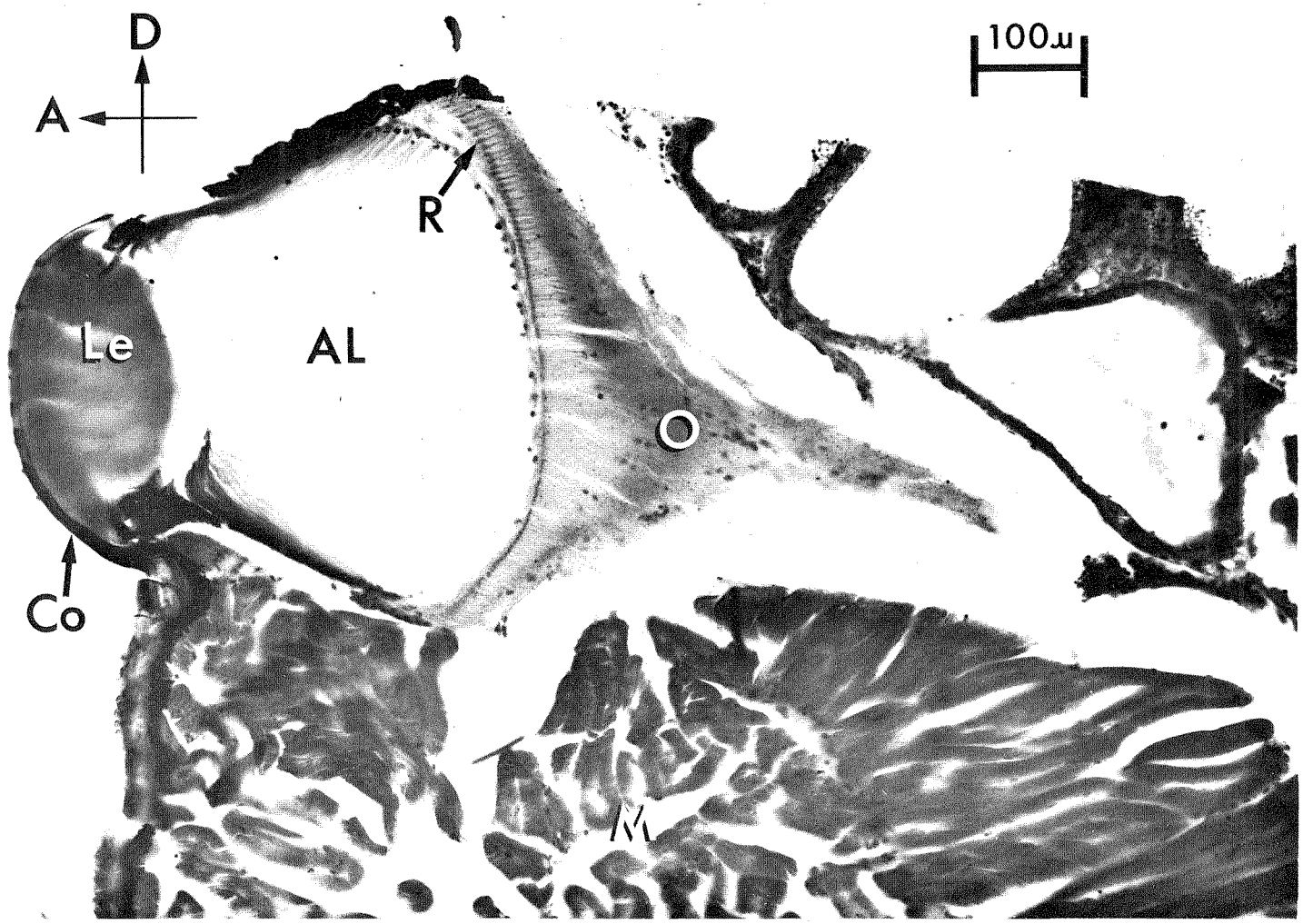
D
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TABLE 3.1

	AM	AL	PL	UNITS
FOCAL LENGTH	767	385	254	MICRONS
SEMIAPERTURE	130	100	90	MICRONS
F/#	5.9	3.8	2.8	NONE
RETINAL VIEW FIELD	2x20	60	130	DEGREES
VIEW FIELD OF LENS	60	60	130	DEGREES
RECEPTOR #	1000	6000	16000	RECEPTORS
MIN. REC. SEPARATION	2.0	3.2	4.5	MICRONS
MIN. REC. SPACING	8'	28'	60'	ARC-MINUTES
WAVELENGTH A	532	530	530	NANOMETERS
B	370			NANOMETERS

Most of these data are from Land, 1969a. Blest et al. (1988) have revised some of the particulars. Wavelength data from DeVoe (1975) for Phidippus regius.

Each axon in the retina, with its pair of rhabdomeres, is encircled by nonpigmented supportive cells. Each support cell has many arms, which flank the receptive segment of many receptor cells.

Near the outer surface of the retina lie the cell bodies of pigmented support cells. These cells flank the nonpigmented support cells to the inner end of the rhabdomeres. They are roughly triangular in cross section and form a regular array, six per receptive fiber, resulting in a space-filling pattern of

triangles and hexagons, and providing an effective optical isolation of each receptor from its neighbor.

The anterior lateral eyes each have about six thousand receptors, with the minimum receptor spacing of one-half degree in the section of the retina directed frontally, increasing to slightly more than one degree laterally. The posterior lateral eyes, with a coverage of about 130 degrees, each have about 16,000 receptors, each of which covers about one degree (Land, 1972).

Principal eyes

The principal eyes of Phidippus johnsonii have a cornea and lens similar to the secondary eyes, though of greater size and focal length. There are major differences in the pigment cells, receptor-cell morphology, receptor array, and rhabdomere form.

As shown in parasagittal section (Figure 3.2), the principal eye is a long tube, surrounded by pigment. The pigment is contained in support cells. Unlike the secondary eyes, the pigment does not surround each cell, but is located in a layer surrounding the entire receptor array, minimizing off-axis and scattered light.

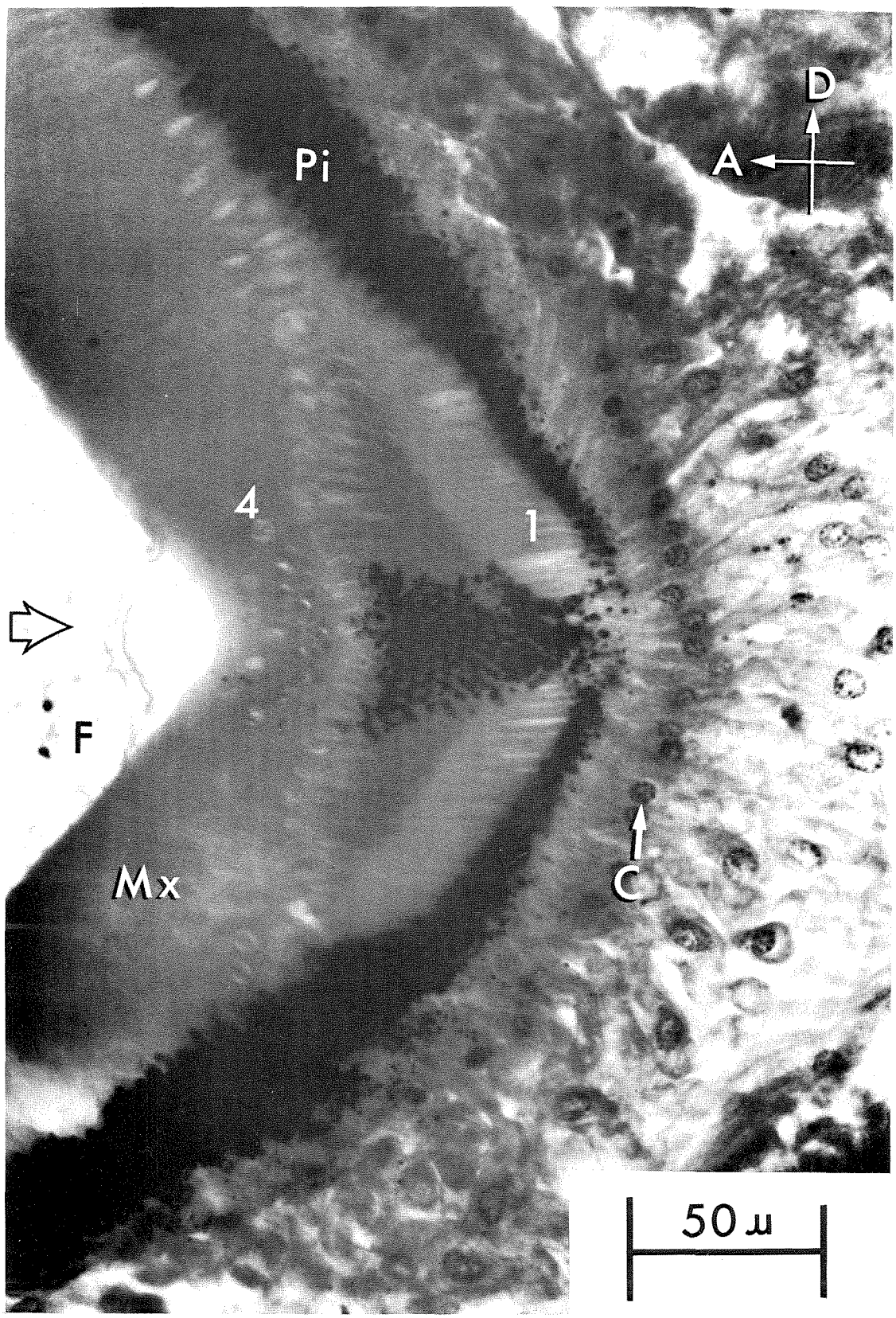
The retina is a direct retina, with receptor cells bipolar in form. The cell bodies lie outside the pigmented layer. A process enters the retina and enlarges to form a receptive segment two to six μm in diameter. The microvilli are much more variable than in the secondary eyes and may arise from between one and four sides of the process.

The receptor array (Figure 3.3) is not a flat two-dimensional sheet as is found in most other eyes. Instead, it is a three-dimensional array of receptive segments, arranged within the pigmented eye capsule in roughly four layers along the optical axis of the eye. The layers are tiered as well, such that a plane of

Figure 3.2 Parasagittal section of the anterior medial, or principal eye. The lens is not shown in this section. The open arrow indicates the direction taken by the incoming light. AM=Anterior Medial eye, C=Cell bodies (bipolar) of receptors, F=Foveal pit, Mx=supporting Matrix, Pi=Pigment capsule.


D
A
100 u
C
R
Mx
F
Pi
AM

Figure 3.3 Sagittal view of the principal retina. Receptors are arranged in layers along the optical axis of the lens. 1 indicates layer 1 receptors (high resolution layer), 4 indicates layer 4 receptors (short wavelength UV receptors).


D
A
Pi
4
1
F
Mx
C
50 µ

section normal to the optical axis may contain receptive segments of more than one layer. There are on the order of 1000 receptors in each AM retina. Land (1969a) counted 1184 axons in the optic nerve. Eakin and Brandenburger (1971) counted a total of 907 receptive segments in the different layers, as follows.

Proximal	Layer 1	344	arranged in 60 rows
	Layer 2	366	
	Layer 3	148	
Distal	Layer 4	49	

Because the layers are tiered, some of these segments may need to be reclassified to different layers. Blest and Price (1984a) have several excellent EM sections in other species of salticid that explore the layers and tiering in more detail.

Each receptive segment is sheathed by a nonpigmented process from supportive cells. The receptive segments are very tightly packed in the center of the retina, spaced at about 1.7 μm, corresponding to a visual angle of about eleven minutes.

The entire array covers a field of view of approximately two degrees lateral extent and 21 degrees vertical extent, in a slight boomerang shape (Land, 1969a).

Wavelength sensitivity

The brilliant coloration of some salticids has long stimulated investigation into color sensitivity. The rejection of painted mates (Peckham, 1894), Crane's (1949) analysis of display, and Kaestner's (1950) striped wall experiments provide behavioral evidence of color vision. Land (1969a) made optical measurements

and suggested that chromatic aberration would cause layers 1-4 each to be in focus for different wavelengths from red to ultraviolet. A number of ERG and intracellular studies, some combined with chromatic adaptation have been made on a variety of salticids and other spiders, with mixed results (Lycosid: DeVoe, 1962; Phidippus regius: DeVoe, 1975; Menemerus confusus: Yamashita and Tateda, 1976; Argiope: Yamashita and Tateda, 1983; Tiedemann et al., 1986). The ERG studies do not provide definite information on all types of receptors present and seem to be prone to coupling, presence of off-axis pigment granules, and other problems. Intracellular studies give more definite information, but are so technically difficult that most data come from cells with low internal potential and short lifetimes. The only recording, filling and recovery of marked cells (Blest et al., 1981) indicates sharply tuned ultraviolet cells in Layer 4 and broadly tuned green cells in Layer 2 and peripheral Layer 1.

Polarization sensitivity

The receptor segments in layer 4, the most distal segment, are not arranged in the regular tight pattern suggestive of form vision, and are ovoid in form and oriented at right angles to the incoming light. Optically, the segments are probably in focus for distant, ultraviolet light (350 nm).

Land (1969a) has suggested that this layer may be used for the detection of the plane of polarization. Many arthropods use e-vector patterns in the sky for navigation. It has also been shown by Magni et al. (1965) that some wolf spiders use the plane of polarization of skylight to navigate, mediated by the retina of the AM eye. No one has yet confirmed this for salticids either behaviorally or physiologically.

Principal eye movements, musculature, and innervation

The eye movements of the principal eyes of salticids have been noted, and anatomical descriptions of the underlying structure given, by Scheuring (1913-1914), Dzimirski (1959), and Land (1969b). Direct observation of the movement of the pigmented eye tubes is possible in a number of salticid species with translucent carapaces. Dzimirski (1959) noted optokinetic nystagmus in a salticid by moving a striped pattern in front of the spider. I have observed spontaneous and tracking movements through the carapace in immature (second or third instar) Mopsus mormonii, an Australian salticid. Some species of Maevia from the southeastern United States are apparently useful as well. I have also observed the blue-green flash that Land (1969b) has noted, which may be seen as the retina moves by staring into the lens of the AM eye a the correct angle.

Land (1969b) thoroughly characterized the eye movements in awake, behaving Phidippus johnsonii, using a Maxwellian view system that allowed projection of images onto the retinal surface and direct observation of the retina. He found that the two principal eyes generally do not converge on a spot stimulus, although it is within their range of movement. Instead, they track side by side. Land describes fixation, slow tracking, saccades to a target, and scanning. Scanning consists of fixation and torsional movements of the retinae. Land notes that these movements allow alignment of different images (such as portions of legs) on the retinae, and hypothesizes that these torsional movements are involved in pattern analysis.

Musculature

The musculature consists of six muscles, that move the eye capsule within the cephalothorax in a manner analogous to the movement of our eye within its orbit. Medial-to-lateral movements and ventral-to-dorsal movements can be

combined to move the center of the retina about, over a range of sixty degrees. An additional degree of freedom is a torsional movement about the optical axis.

Interestingly, these six muscles and their complex repertoire of movements are controlled through six neurons - one per muscle, from the posterior portion of the brain (Land, 1969b). No sensory fibers have been found coming from the muscle, so eye position information is probably derived from a collateral of the six motor nerves in the brain.

VISUAL PATHWAYS

Chapter 4

Introduction

The simplest overview of the flow of visual information in the salticid is shown in Figure 4.1 (adapted from Hanstrom, 1923). The information from the principal (AM) retinae and the information from the secondary (AL, PM, PL) retinae flow in parallel through two stages of processing and meet in the protocerebrum. This parallel flow can also be seen in Figure 4.2, a parasagittal section through the cephalothorax of Phidippus johnsonii. The entire principal pathway is evident, from the long cylindrical AM retina and its receptors, through the first optic ganglion (AM 1), the second optic ganglion (AM 2) and descending into the protocerebral neuropil. The retinae and first optic ganglia of the three secondary eyes on this half are in more lateral sections. Two of these (AL 1, PL 1) feed into separate areas of the corpora pedunculata, lying beneath AM 1, and then into the protocerebral neuropil. This summarizes the major details of the two parallel pathways. There are many other smaller projections (Hill, 1975).

This separation of visual pathways is strikingly analogous to mammals, where two types of information, peripheral-location-motion detection and foveal-pattern analysis separate at the level of the retina, and propagate through different cells, different layers in the geniculate, and different cortical visual areas. Salticids take this separation one step further, employing separate lenses for these different tasks.

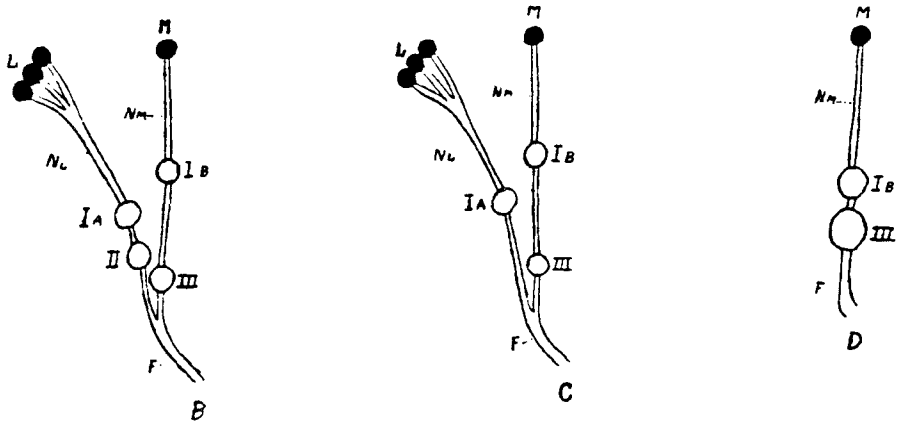


Figure 4.1 Visual pathways in spiders (after Hanstrom, 1923). Visually predaceous spiders (such as salticids, lycosids, and thomisids) have Pattern B morphology; web spinning araneids, Pattern C morphology; and phalangids (harvestmen) have Pattern D. L=lateral eyes, M=Medial eyes, IA, IB, II, III = optic masses.

Figure 4.2 A parasaggital section through the cephalothorax of a mature female Phidippus johnsonii. The chitin has been trimmed. This section is too far lateral to show leg ganglion iv, or the cauda equina.


AM
AM1
AM2
CP
PC
Ch
P
Ns
III
II
D
A
1 mm.

Secondary pathway

The secondary eyes, with their wide angle optics and low resolution array, are well suited for the localization of motion. The retinal fibers for the three pairs of secondary eyes terminate in their respective first ganglia. Figure 4.3 shows the optic nerve of the anterior lateral (AL) eye, which synapses with the first interneurons at the first ganglion of the anterior lateral eye (AL 1). This long ribbon-shaped surface is illustrated in cross section in Figure 4.4. (This is the PL 1, but the ribbon structure is similar.)

The first-order interneurons are all bifurcated, receiving input from two adjacent locations in the primary neuropile as shown by Hill (1975). This forms the anatomical substrate for Land's observations (1971), that a small (one degree) black spot, moved the distance between adjacent receptors, was adequate for accurate localization of that spot.

The bifurcated first-order interneurons each terminate in one of two structures - the glomerular layer of the corpora pedunculata and the lateral eye neuropil (discovered by Hill in 1975). The cell bodies of these first-order interneurons are distributed in the usual pattern, lying clumped together outside the neuropil, with no synapses on the cell bodies.

The corpora pedunculata, also known as pedunculate or mushroom bodies, are well developed in all visually active spiders, and reach the peak of arachnid development in salticids. Hanstrom (1928) advanced the concept of homology of this structure with the similarly named structure in insects. Arguments for analogy rather than homology can be made on morphological grounds (Meier, 1967). The sensory modality is also different, as input in insects is primarily from the antennae, via the deutocerebrum. Hill (1975) suggests that these bodies may be used for general directional orientation.

Figure 4.3 A parasagittal section of the first ganglion of the anterior lateral eye (AL 1). This figure shows some of the optic nerve, connecting receptors in the retina to the synapses with first-order interneurons in AL 1. The ordered array of retinal receptors forms a complex, three-dimensional surface. C=Cell bodies of the first-order interneurons of the lateral tracts.

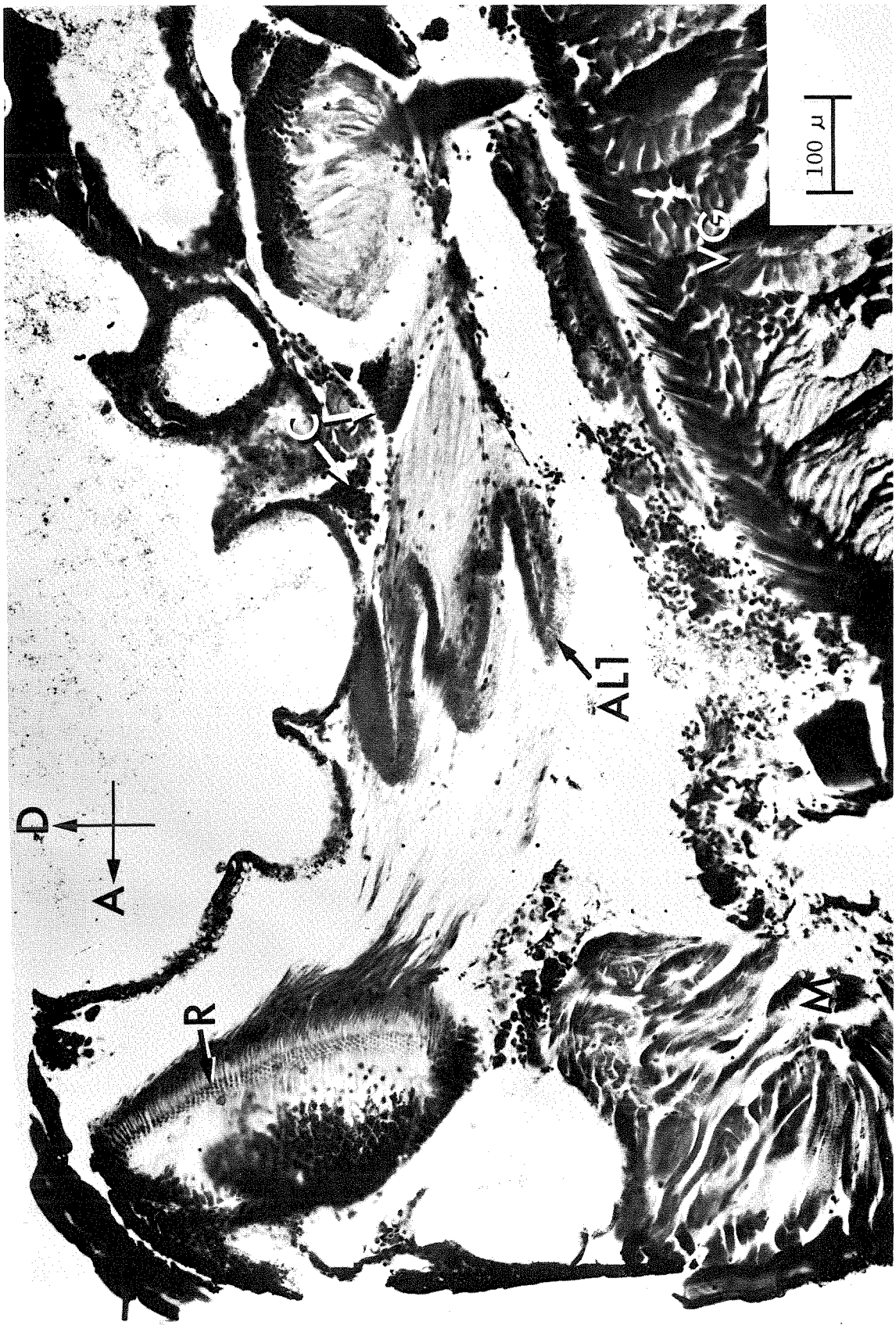
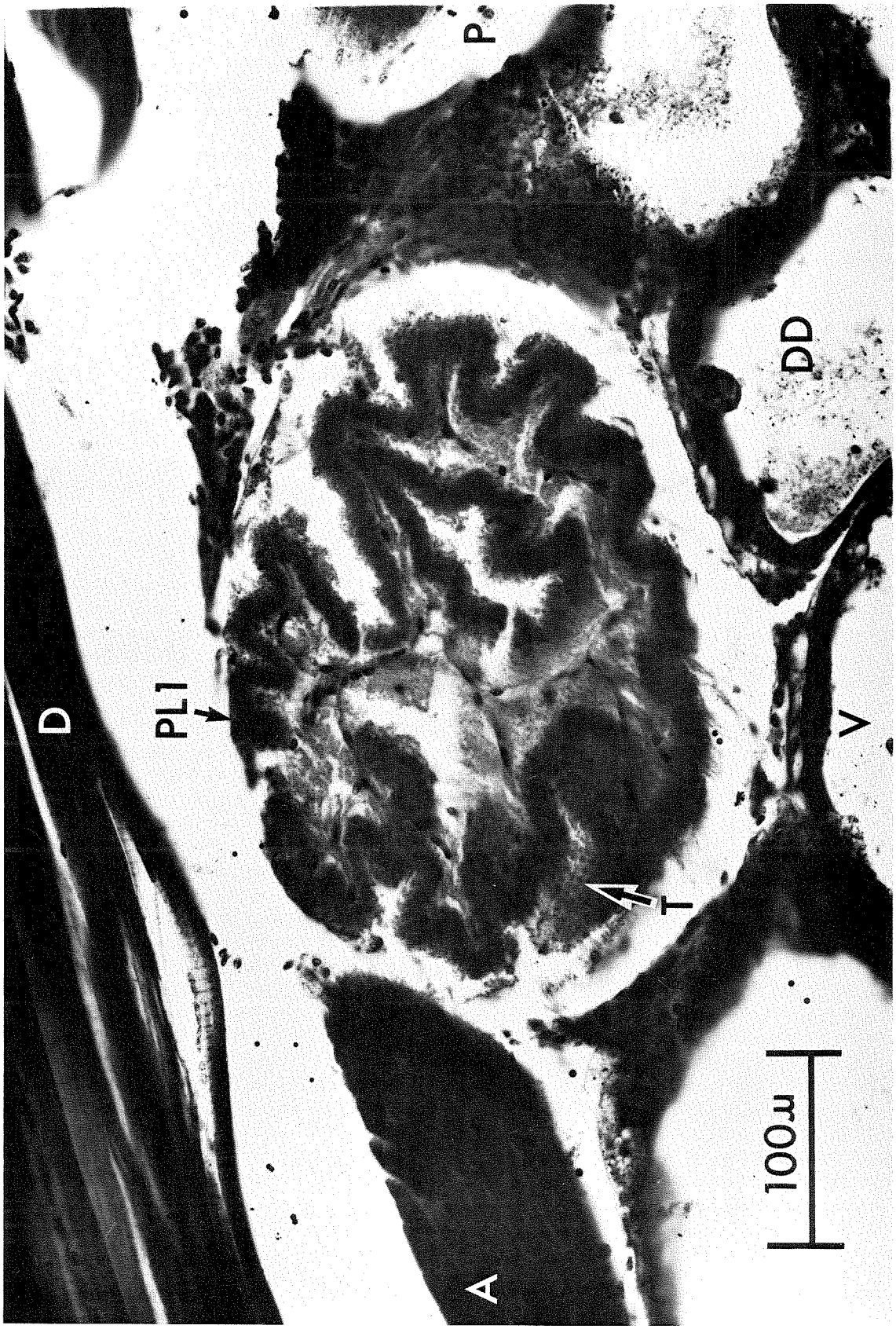

D
A
R
M
ÄL1
VG
100 µ

Figure 4.4 The first ganglion of the posterior lateral eye (PL 1), in parasagittal section, orthogonal to the direction of the optic nerve. AL 1 and PL 1 are similar in structure, and an idea of their three-dimensional structure may be gained by comparing with Figure 4.3. This structure receives input from PL retina, and outputs to the glomerular layer of the corpora pedunculata and the lateral eye neuropil. T=compact fiber terminals, which feed to the corpora pedunculata.


D
PL1
P
T
DD
A
V
100µ

The globuli cells of the corpora pedunculata give rise to intrinsic fibers, which synapse with the incoming visual information in the glomerular layer of the corpora pedunculata.

These secondary centers each have separate input from the ipsilateral AL and PL eyes. The lateral eye neuropil send a tract into the protocerebrum. Each corpus pedunculatum sends a tract into the protocerebrum, and also a tract to the contralateral corpus pedunculatum, the first point at which visual information crosses the midline. Collaterals from the lateral eye neuropil also cross in this commissure (Hill, 1975). Some of the fibers from these two secondary centers descend in a separate tract into the subesophageal ganglion.

The term protocerebrum is used in several senses in the literature. Babu (1985) uses it to refer to much of the supraesophageal ganglion (syncerebrum). I follow Hill's (1975) usage, which restricts the term protocerebrum to the neuromere of the cerebral ganglion, excluding the central body, all of the various eye centers, and rostral and cheliceral neuromeres.

The posterior medial (PM) eye is classed as a secondary eye. Although it has only a few hundred receptors, it has discrete ganglia and distinct connections with many areas. The function of this pathway remains to be elucidated.

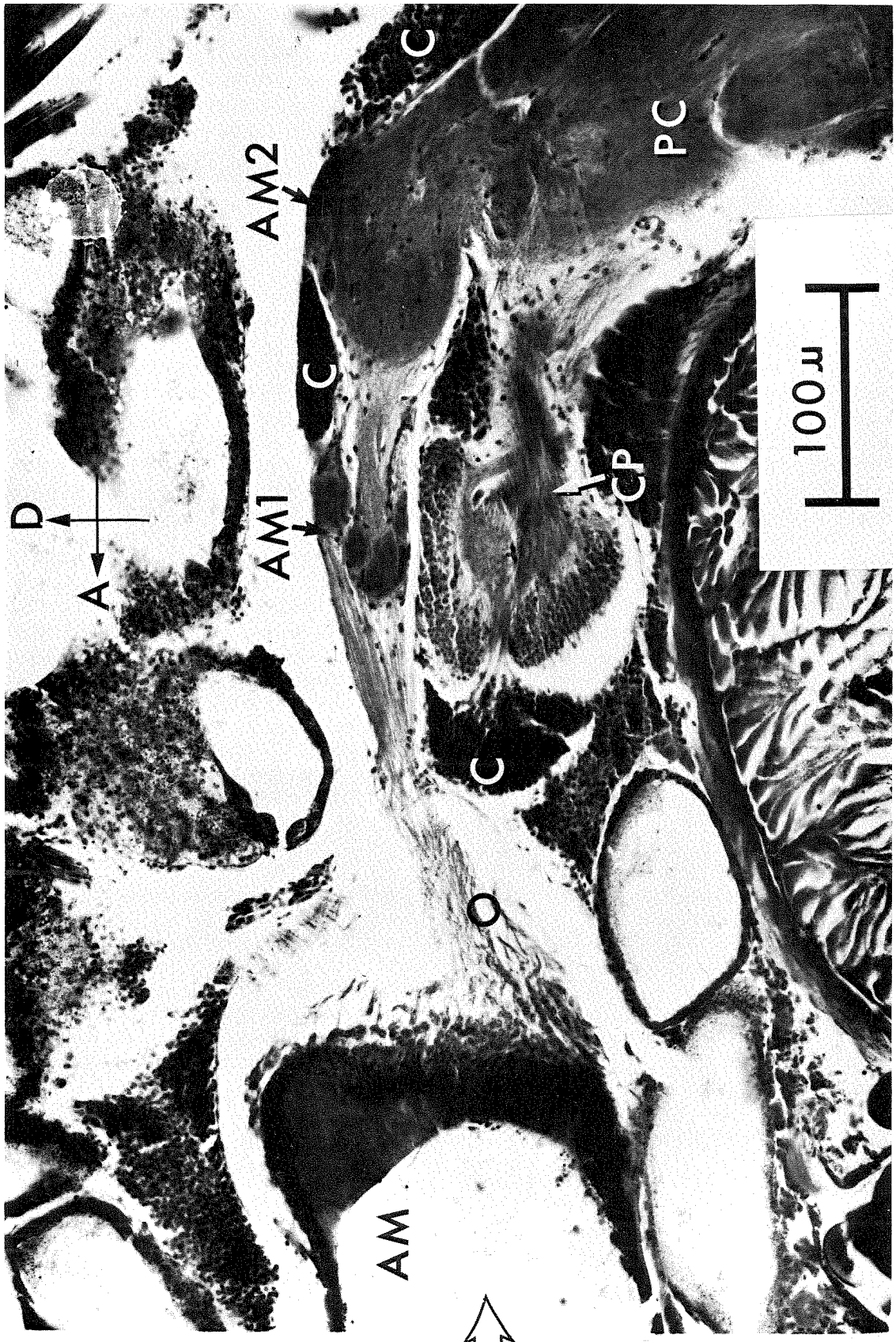
Principal eyes

The principal eye pathway is much simpler, consisting of two serial ganglia and the protocerebrum (Figure 4.5).

The optic nerve from the four layers of receptors in the AM retina terminates in an orderly fashion in the first optic ganglion of the principal eye (AM 1).

The first optic ganglion of each principal eye (AM 1) is a highly ordered structure. Oberdorfer (1977), using Salticus scenicus and Habrocestum pulex

Figure 4.5. Principal eye pathway, showing major structures and connectives involved in early visual processing. Starting at the left, the retina is connected by the optic nerve to the first optic ganglion (AM 1), which connects to the second optic ganglion, and subsequently, the protocerebrum.


D
A
AM1
AM2
C
C
C
PC
CP
O
AM
100 μ

described the retinal terminals synapsing in compact glomeruli, 20 μm long and 10 μm in diameter. The retinal terminals send out fine, postterminal fibers, which spread 40 μm, allowing communication between adjacent glomeruli. Smaller, more numerous, second-order fibers also spread enough to cover adjacent glomeruli, providing a second pathway for this interaction.

The synapses are dyad and triad ribbon synapses, similar to those seen in vertebrate retina (Oberdorfer, 1977). In addition to the retinal axons synapsing with second-order fibers, there are also serial synapses between second-order fibers.

Hanstrom (1928) proposed that the glomeruli would exist in a one-to-one relationship with the incoming optic nerve fibers. Subsequent work by Land has shown the situation to be more complex, with the ratio of fiber to glomeruli closer to 1.5 or more.

The terminal zones containing these glomeruli are separated into distinct areas (Figure 4.6), which seem to correspond to input from separate retinal layers (Land, 1969a). Layer 1 fibers synapse in the anteriormost division. Layer 2 fibers synapase in the areas posterodorsal and posteroventral to this. Hill has shown a pathway for early interaction in the form of second-order neurons, which connect AM 1 and AM 2, and synapse in one or both of these two high-resolution layers.

The connections decribed in the previous few paragraphs indicate that comparison of adjacent retinal receptor input can be made in each of the two high-resolution areas of AM 1, and comparison of equivalent receptor input between the two high-resolution layers.

Oberdorfer (1977) found that fibers leaving AM 1 toward AM 2 are still ordered into discrete bundles. Some of these bundles decussate while still in the chiasm, while others retain their integrity. Hanstrom (1928) found in a Golgi

Figure 4.6 Detailed view of the first optic ganglion of the principal eye. Layer 4 fibers terminate in the dorsal division. Layer 1 fibers terminate in the anteriomost division. The anterior-posterior striations in the anterior division are a consequence of the glomerular structure.

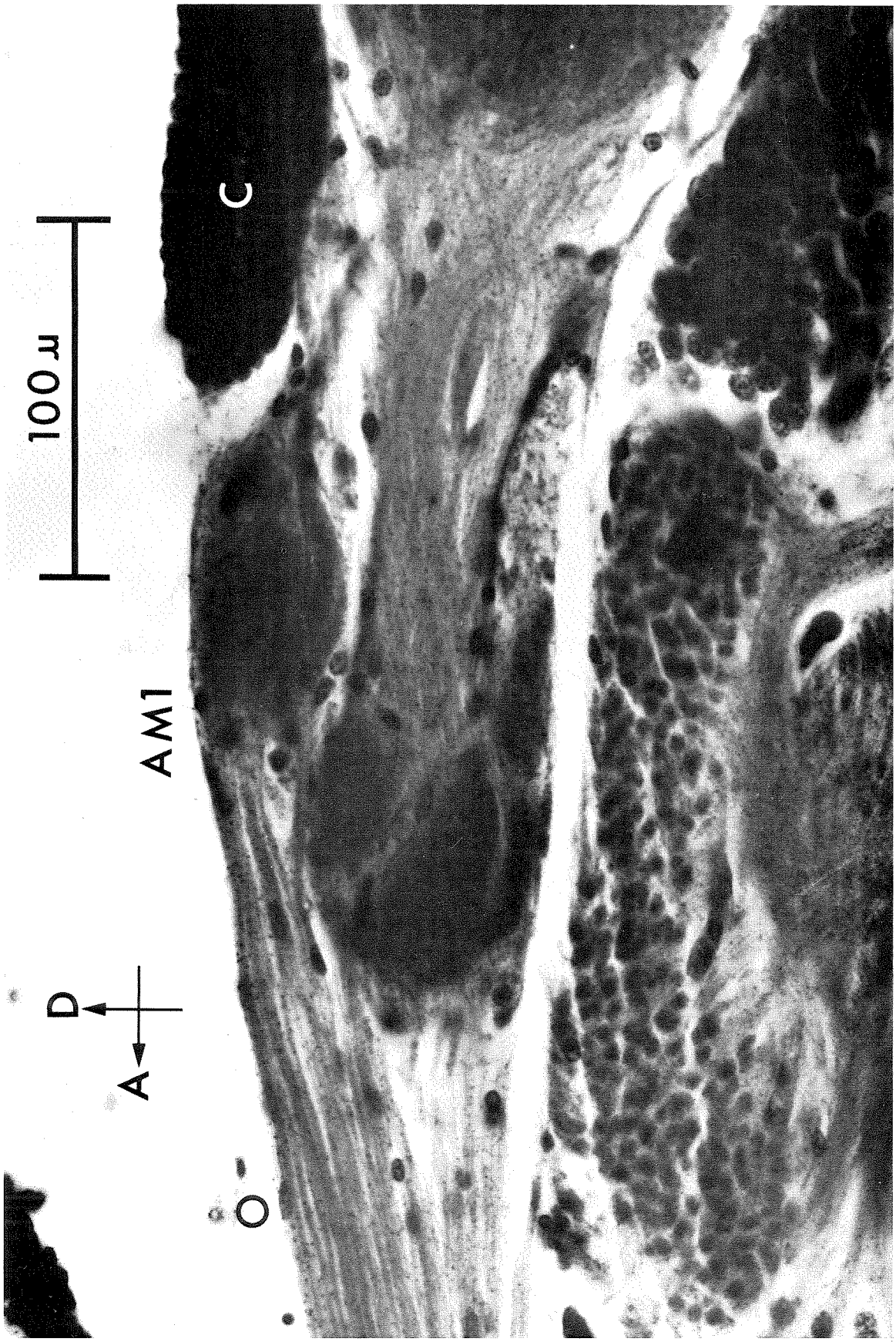
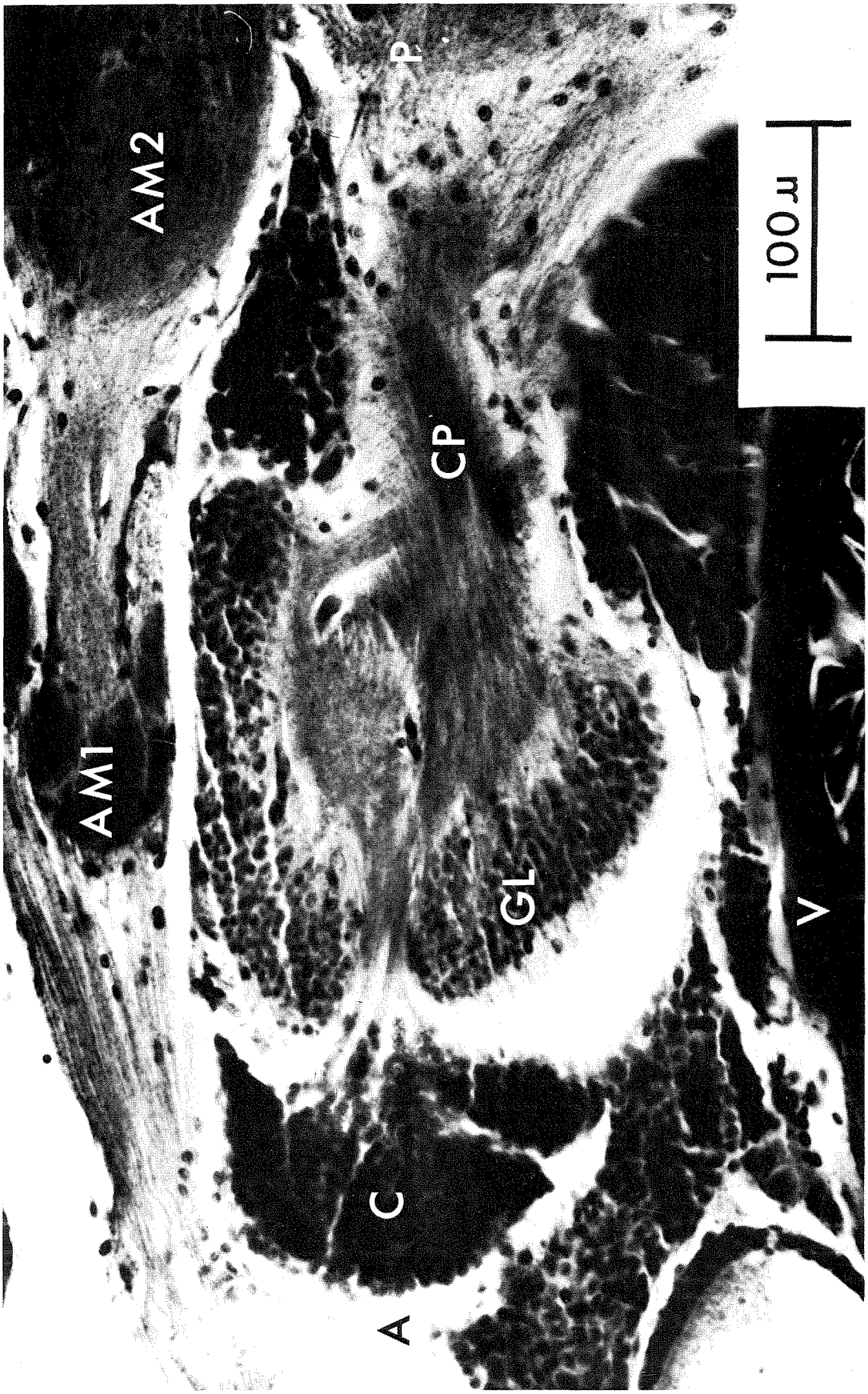

C
100 μ
D
A
AM1
O

Figure 4.7 The connectives from the first optic ganglion of the AM eye terminate diffusely in the second optic ganglion. The parallel pathway of the lateral eyes lies ventral to these structures.


AM1
AM2
P
CP
GL
C
A
V
100 µ

study that some of these interneurons pass through AM 2 and onto the central body.

Some of the visual fibers in the protocerebrum also project into the central body.

Other tracts descend from the protocerebrum to the (largely) motor areas of the subesophageal ganglion.

Figure 4.8 is a summary but by no means a complete diagram. Interneurons confined to a single ganglion are not shown, nor are possible efferents, such as the sensitivity feedback reported by Yamashita (1985).

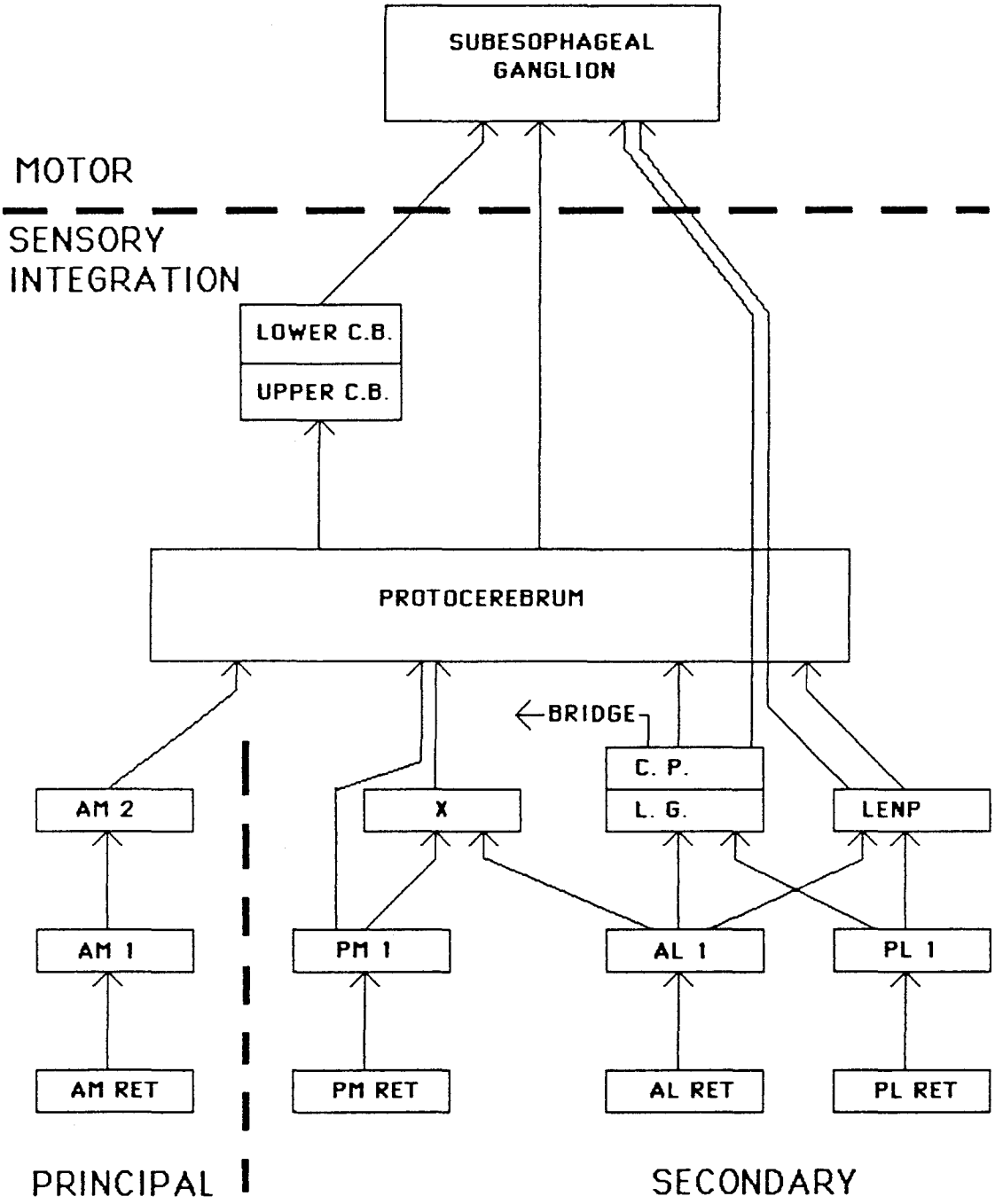


Figure 4.8 The principal and lateral visual pathways run in parallel from the retinae, to the intermediate ganglia, to the protocerebrum. This figure also indicates pathways into the subesophageal ganglion, which eventually result in motor output.

VISUAL CAPACITIES AND BEHAVIORS

Chapter 5

A detailed knowledge of visual capacities and behaviors is useful in designing experimental stimuli and in understanding the properties of neurons in the central nervous sytem.

Figure 5.1 shows the fields of view (in a horizontal plane) of each eye. The partitioning of the visual surround by the various eyes reflects the separate or cooperative functions of each. The posterior median eyes are omitted from the view diagram, as they are greatly reduced in "advanced" salticids. Land (1985a) showed that in two "primitive" genera the larger PM eyes played a role in covering the gap between the view fields of the anterior lateral and posterior lateral eyes. The larger lateral eye fields in the "advanced" salticids cover this area.

Lateral eyes

The primary function of the lateral eyes is the detection and localization of movement, which leads to a ballistic turn to place the moving object in the view of the principal (AM) eyes. This was elegantly demonstrated and quantized by Land (1972a), who took advantage of the tendency for salticids to perch on striplike substrates. By suspending them in midair from their carapace, and placing a strip of paper in their legs, Land simulated their natural perch. The ends of the strip were connected, forming a loop, along which the spider could "walk." In response to visual stimuli, the spider would step its legs in the normal turning fashion, resulting in a movement of the paper in the opposite direction equal in magnitude to the free turn. Land found that a one degree spot, moving one degree, was the minimum stimulus, which corresponds nicely with the

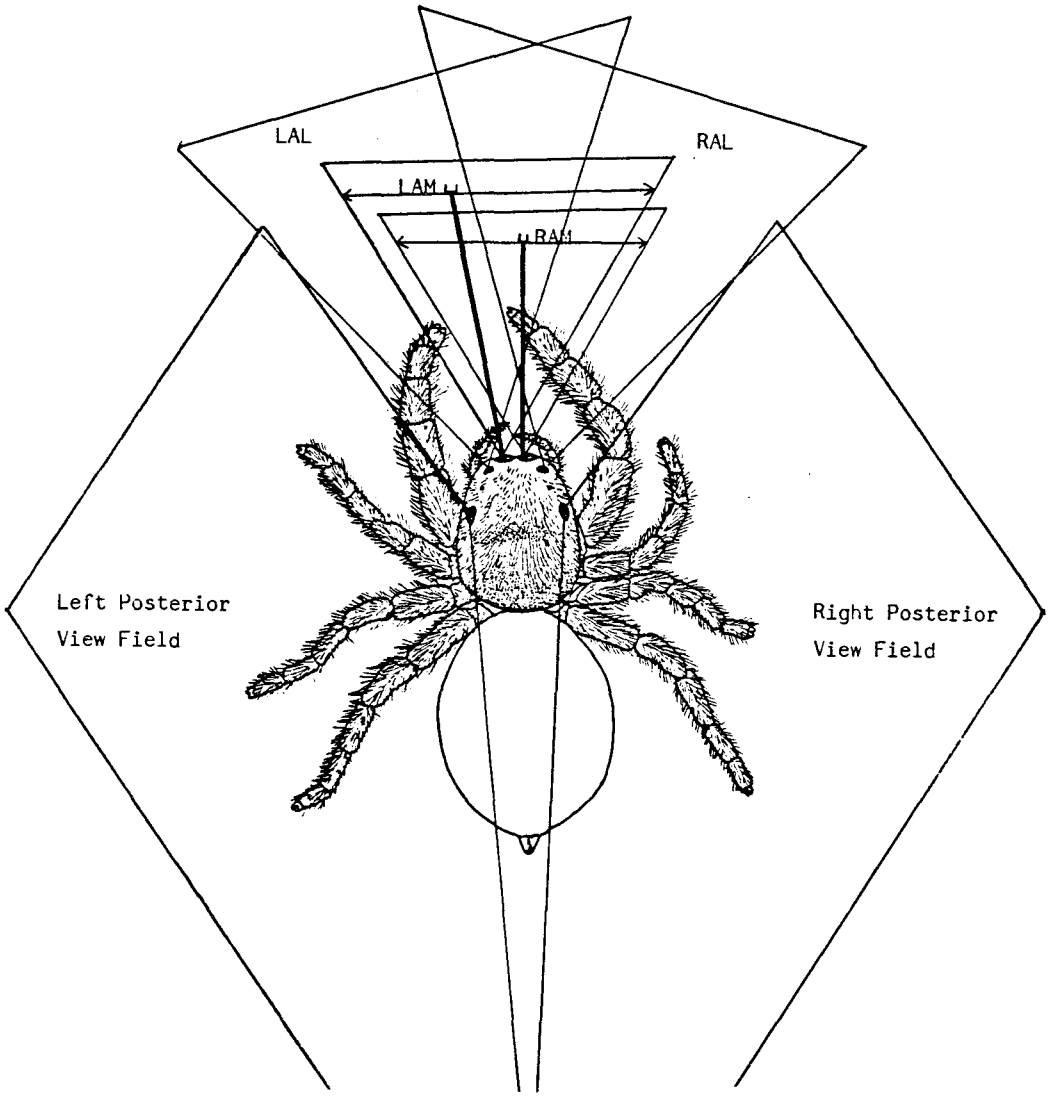


Figure 5.1 Fields of view of the eyes of P. johnsonii. Arrows indicate range of movement of the narrow retinal strip of the principal eye. The right and left AM retina are typically slightly divergent. PM eye view fields are considered unimportant in "advanced" salticids and are omitted for clarity.

receptor resolution and separation. The turns were of the correct magnitude to place the stimulus in front of the spider, in the view fields of the principal eyes. Land (1972) found that the turning response existed for stimuli with speeds up to one hundred degrees per second. This corresponds to a time difference of ten milliseconds between neighboring receptors. The theoretical time response of the system is much better than this; it may be that there is simply no relevance of such a stimuli for the spider.

Behavioral observations in the field indicate that the eyes are used at distances from a few millimeters to ten meters or more (Hill, 1977). I have observed orienting responses to my presence at ten meters. Hill reports Eris marginata responding to smaller items, such as a butterfly, at three meters, and to crawling mites at a distance of a few millimeters, and taking evasive action in response to a wasp flying by, a meter away.

An additional function for the anterior lateral eyes has been found by Forster (1979) in Trite planiceps. She extended the blinding studies of Homann (1928), in which various eyes were temporarily occluded ("blinded") by application of black acrylic paint to the cornea. After covering the principal eyes, Forster found that the AL eyes were responsible for initiating chasing behavior of moving prey, and for making short jumps toward prey moving faster than fifteen degrees per second. The distance of the short jumps toward prey were inversely correlated with target velocity, indicating confusion of proximity (rapid angular movement) and actual rapid movement. Halted flies with moving appendages did not elicit chasing behviors.

By unilateral occlusion of the frontal eyes (RAL and RAM), Forster found that the chasing movements are unilaterally driven. The hunting posture of the spider was lopsided, as the legs on the unblinded side of the spider crouched in typical cryptic hunting fashion, whilst the legs on the blinded side did not.

Forster's experiments with blinded AL eyes also indicate that the male's eyes are also necessary in courtship after a movement by the female, in order to follow her.

Principal (AM) eyes

Movements

The principal eyes each have a fixed lens and a mobile retina of about one thousand receptors, surrounded by a pigmented capsule. The retinal movements, accomplished by six muscles, cover most of the vertebrate repertoire, and some novel moves as well (Figure 5.2). Land (1969b) found that AL eye input could induce AM eye movement. He found upper and lower limits for the four types of eye movements described. Saccades involved retinal movements of over 150 degrees per second, and slow tracking movements followed targets at speeds less than 10 degrees per second. Land (1971) measured spontaneous movements between two and one hundred degrees per second, and found scanning movements with lateral displacement at fifty degrees per second (1-2 Hz) and torsional movements of fifty degrees in five to fifteen seconds.

Behavioral capabilities

Homann (1928), Crane (1949), and Forster (1979) used blinding studies to show that the AM input is necessary for inducing courtship behaviors (male dancing, female response). The AM eyes are also used after the lateral eye mediated turning response, to examine the moving object. The spider will examine stationary objects in the field of view of the AM eyes as well. Hill (1977b) reports prolonged observation of threatening stimuli at a distance, such as wasps or humans. Drees (1952) found that the spider behaved differently after using the AM eyes to inspect outline drawings of winged versus nonwinged prey.

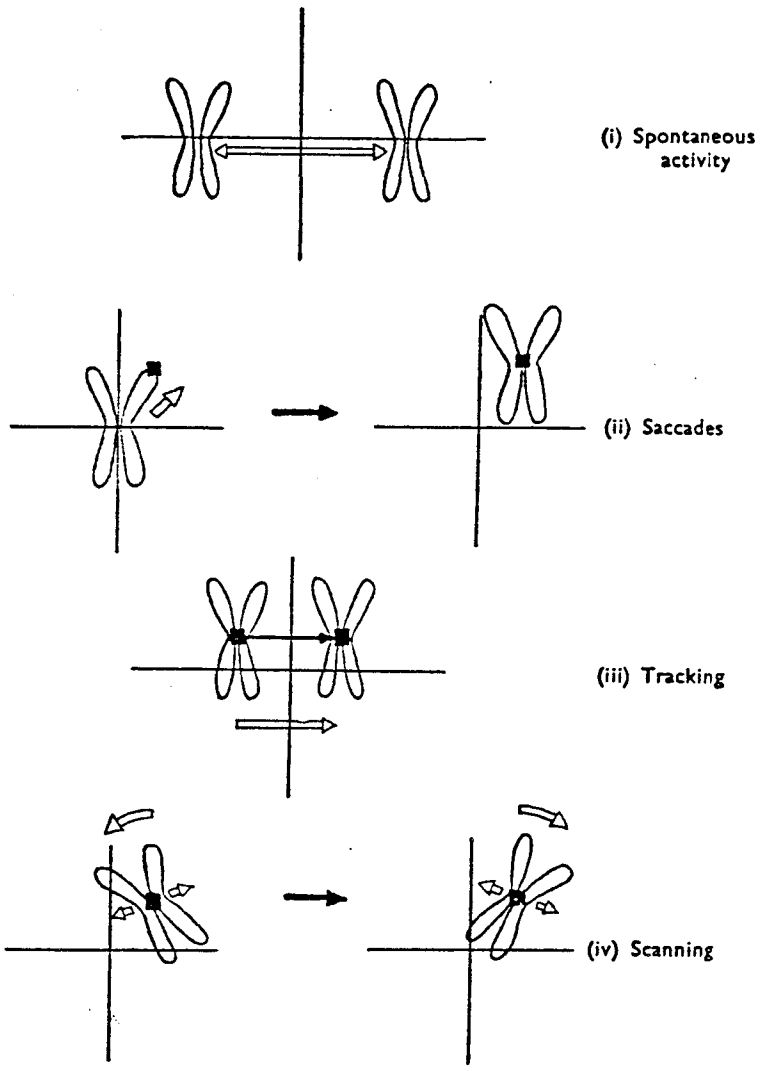


Figure 5.2 Movements of the principal eye retina (Land, 1969b).

Forster (1979) showed that the behavior of stalking stationary models was mediated by the AM eyes, with accurate estimation of depth.

The Peckhams (1894) demonstrated the color vision capabilities of frontal vision by the application of unnatural colors to the females, resulting in disruption of courtship behavior, in marked contrast to the findings of cosmetological investigations in humans. Dzimirski (1959) found that salticids (Sitticus truncorum) prefer black and white striped walls to plain walls (presumably reflecting their preference of vegetation over barren substrate) when placed in a corridor with differing walls. He also demonstrated their color abilities by making stripes of blue or orange against twenty-six background intensities, ensuring that isoluminant conditions would exist for at least one intensity/color pair. The spider always oriented to the stripes, indicating color vision.

Use of the AM eyes to discriminate stationary patterns is taken to its extreme in navigation. Hill (1977a,b) reports the systematic survey of prominent vegetation vantage points during the course of general movement. Phidippus johnsonii also returns each night to its concealed silk nest, after the day's foraging.

Hill (1977a) details indirect pursuit of prey, where the plant structure imposes a circuitous approach to the prey, with a temporary loss of AM eye contact with the prey. Hill (1979) extends this study in an artificial arena, and demonstrates that after sighting prey, the salticid is consistently successful at determining by visual inspection the best route to the prey. Enroute, the spider orients occasionally to the prey, turning the AM eyes to point in the correct direction. The ability to do this remains even when a leaf or other visual barrier is interposed, indicating the existence of some sort of internal map.

MATERIALS AND METHODS

Chapter 6

I conducted electrophysiological and anatomical experiments primarily on the genus Phidippus. I also used the following species for additional experimentation: an unidentified sheetweb species, a local species of wolf spider, a local tarantula, and Thiodina spp., and Lycosa spp.. Early experiments were conducted with specimens obtained in the campus gardens (P. johnsonii, Thiodina, an Agelenid species, and a Lycosid species). Later experiments used P. johnsonii, P. rimator, and a P. species obtained from Arizona, which superficially resembles P. johnsonii, but is probably a new species (G. B. Edwards, personal communication, 7/87). These spiders were obtained primarily from Chuck Kristensen's Spider Pharm. Identification of various species was based on personal consultation with Graeme Lowe (Caltech), Chuck Kristensen, and on the descriptions of Peckham and Peckham (1909), Kaston (1978), and Roth (1985).

I used wild-caught spiders for the significant results described in this thesis. Little work has been done to ascertain the effects of visual impoverishment on laboratory-reared specimens. Many invertebrates seem to have a substantial degree of "hard-wiring," but most advanced visual systems in which plasticity has been studied have modification by experience. The only data for salticids come from the Manly and Forster (1979) study of the development of predation, which demonstrated the effect of experience on subsequent capture success.

The spiders I used were caught as adults or in the penultimate instar. I housed the spiders in clear Petri dishes fourteen centimeters in diameter for periods of up to a year after capture. The spiders received visual stimulation

from twice weekly feedings of Drosophila, spiders in adjacent dishes, and people moving about. Lighting was controlled by a timer, corresponding to the outside light/dark cycle.

The experimental protocol evolved over the course of my studies as I developed new methods to improve survival and data collection. A consequence of this is difficulty in direct comparison of some of the data. However, qualitative data from early experiments are in agreement with the quantitative data from later experiments.

The first experiments were based on a method originated by Jack Wathey. The spider was anaesthetized with $CHCl_3$ and immobilized in a two-part chamber, which separated the cephalothorax and abdomen at the pedicel. This allowed partial dissection of the cephalothorax while immersed in Spider Ringer's solution, without impairment of air flow to the entry to the lungs located on the ventral aspect of the abdomen. After a section of dorsal carapace was removed, and as much of the digestive tract as possible, tungsten microelectrodes were placed and advanced until a visually responsive cell was located, and the receptive field was then mapped and qualitatively studied. Stimuli were presented on a 28.65 cm. (one-half visual meter) half-sphere, with the spider located at the center.

Although some visual responses were recorded, this protocol had several drawbacks. The principal optic pathway lies close to the dorsal carapace. Difficulties were encountered in sectioning and removing the tough, sclerotized, laminated chitin and muscle attachments without damage to the optic nerves lying directly beneath. Much of the digestive apparatus had to be removed as well, to prolong the viability of the preparation. Long-term recording was not possible, and injury potentials were common.

Later experiments were less invasive. The spider was anaesthetized with carbon dioxide from sublimating dry ice for about 25 minutes in its home Petri dish (135 mm. diameter). The spider was placed on an open platform. Paraffin (Paraplast 58 Centigrade) was built up beneath and around the cephalothorax, immobilizing appendages and stabilizing the cephalothorax. The abdomen was left free. The pedipalps and chelicerae were usually left free, to allow evaluation of sensory input from the palps, monitor sedation, and allow watering or feeding. When presented with a fruit fly, the spider would grasp it between the chelicerae, and consume it in the normal fashion. The electrode was placed through a small nick in the chitin, as detailed below. This preparation was simpler, and had a longer viability, without significant disruption of the visual pathway. I established the possibility of stable receptive field maps and collected qualitative data on selectivity for velocity, direction, size, and contrast. The major drawbacks were a high sensitivity to mechanical and electrical interference.

The third preparation used a machined, black-anodized aluminum chamber (Figure 6.1), which I made for the purpose in the student machine shop. The spider was placed on the block, and paraffin built up, as detailed above. The temperature of the paraffin at time of application is critical. If the molten paraffin is too cool, it will not wet the surface of the cephalothorax adequately to form a strong bond and prevent movement during surgery. If the paraffin is too hot, it will tend to flow beneath the abdomen, and block the breathing passages. The aluminum chamber also helps to rapidly cool the paraffin and prevent heat damage to the spider. A lower melting point wax was tried, but proved to be too soft. A platinum-iridium ground wire attached to the experimental chamber was inserted in the fourth leg and waxed in place. This aluminum chamber shielded the electrical interference and provided such

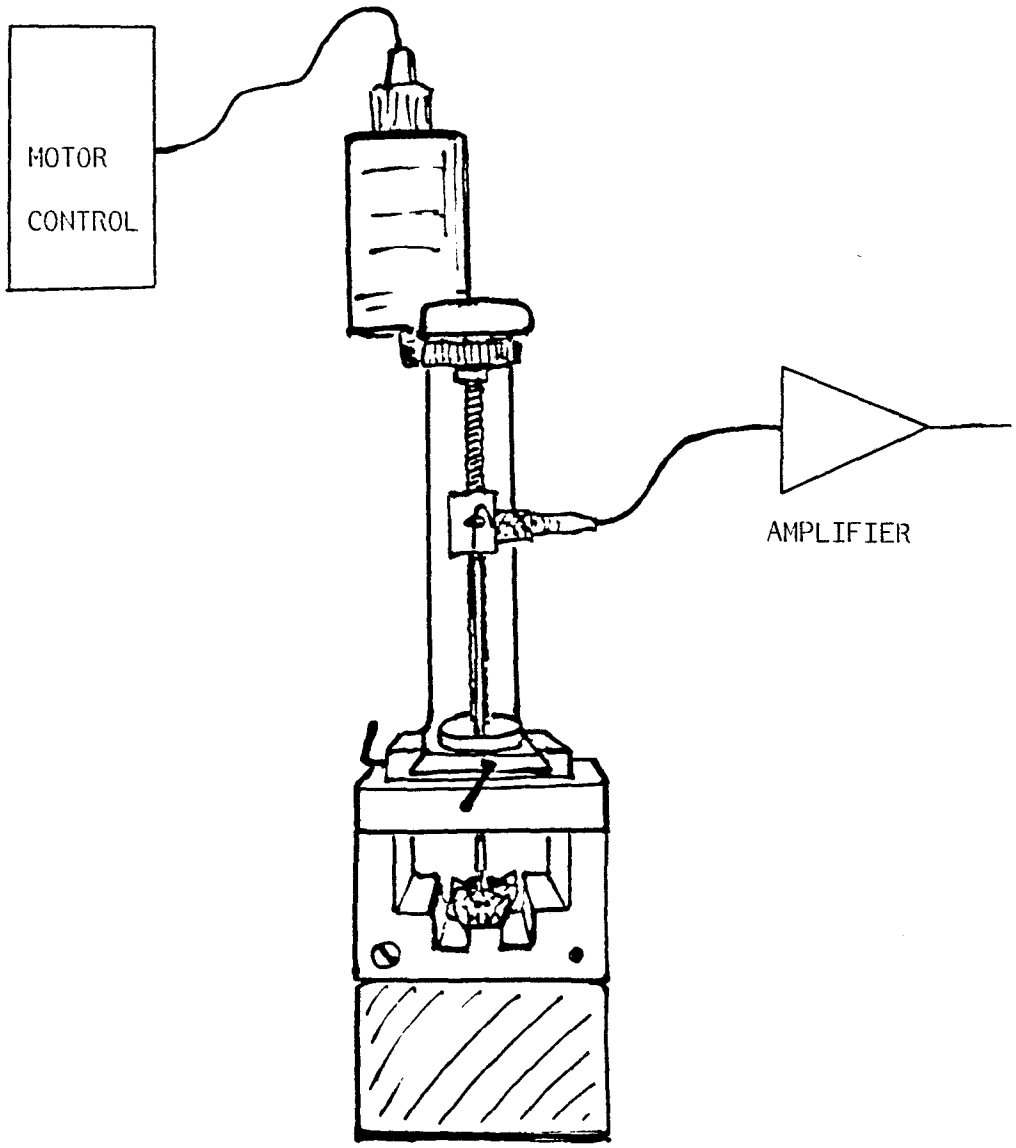


Figure 6.1 Physiological recording setup. The spider is anaesthetized and waxed to a plateau in the middle of a black-anodized block of aluminum. The microdrive adaptor is bolted to the top of the block, and the microelectrode is stepped down into the nick in the chitin. The block provides both mechanical rigidity and electrical shielding.

mechanical rigidity that the preparation could be moved without losing the cell. The recording chamber has a rotational mount and a sliding bracket, both of which lock into place. This allows for placement of the electrode at any point within the circular aperture of these components.

The final change was the introduction of computer-controlled stimulus presentation and data collection.

I determined initial placement of the electrode through a dissecting microscope based on external landmarks, previous results and histology, and the excellent drawings of Hill (1975). I found that the beveled tip of a syringe needle (Figure 6.2) made an excellent microknife (the curvature provides extra stiffness). This is necessary to penetrate the lamellae of the exocuticle. Each lamella consists of crosslinked polysaccharide microfibers in a protein matrix (Barth, 1973). This laminated composite is very tough and sometimes flexible, depending upon the degree of sclerotization. Attempts were made using a #80 twist drill to bore the insertion site, but the cutting edge tended to grab and shatter the exoskeleton. I also tried direct penetration with the glass-coated platinum-iridium microelectrode. This technique worked in freshly molted spiders. I also got it to work on mature specimens about half the time by baking a teflon coating on to the electrode, but tip damage and mechanical coupling were still major problems.

Using the syringe tip method, I would make a small incision in the dorsal cuticle of the cephalothorax overlying a portion of the supraesophageal ganglion. Total anaesthesia is critical at this point, as the already high internal pressure of the spider rises greatly when excited, resulting in a major loss of haemolymph through the incision if anaesthesia is not sufficient. I found in later experiments that cooling the entire chamber and the spider greatly decreases this problem. Cooling can not be used during initial anaesthesia, as the drop in

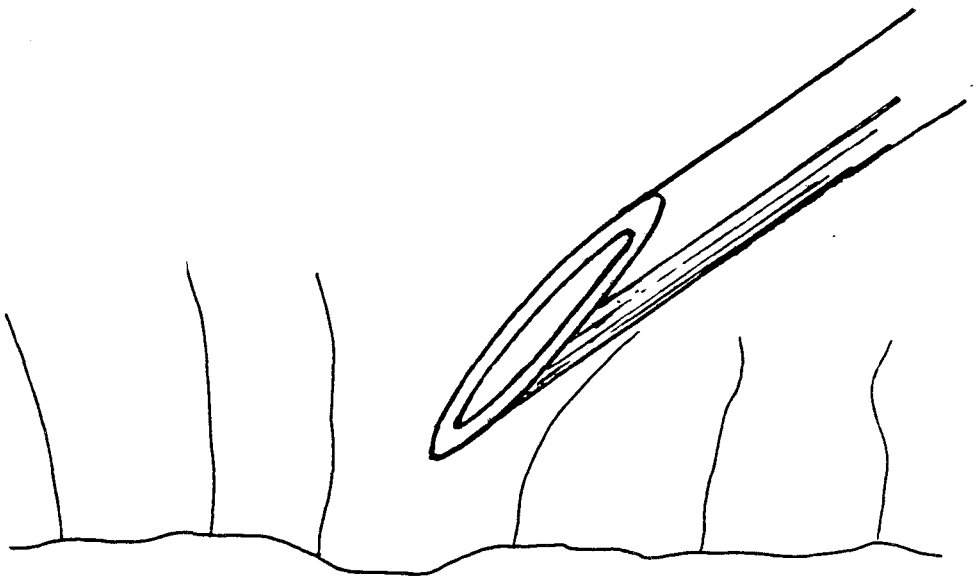


Figure 6.2 Sketch of the microknife used for surgery, adapted from disposable insulin syringes. The curvature of the bevelled tube adds stiffness to the knife.

temperature decreases the spider's breathing rate and increases the time necessary for sedation. After making the incision, I would bolt an adaptor for a microdrive to the top of the chamber. A glass-coated, platinum-iridium microelectrode mounted in the microdrive was centered and placed in the small incision. Rapid placement is necessary, as upwelling haemolymph can obscure the insertion point, decrease the spider's vitality, and prevent accurate localization of the surface necessary for later reference. The haemolymph forms a stable, fluid seal between the glass and the chitin, which prevents fluid loss for the duration of the penetration.

Immediately before electrode insertion, I prepared the surface by using a cotton tipped swab to remove the small droplet of haemolymph.

This preparation is extremely stable. Mechanical rigidity reduces microelectrode movement, making extended study of single cells possible. Access to the palps and chelicerae allow administration of water and live prey to the spider, making it possible to maintain the preparation indefinitely. This turned out to be quite important, as a large amount of data came from preparations during the third day of the experiment. A front plate fastened to the chamber decreased 60 Hz. interference.

After the electrode was in place, its entry point as seen through the dissecting microscope was sketched. A wait of approximately twenty minutes was necessary for the anaesthesia to wear off.

The preparation was centered relative to the screen. The altitude usually needed no alignment, as the spider was mounted flat on a horizontal stage. Rotation of the spider about its dorsal-ventral axis sometimes occurred, resulting in a variance of azimuth, and was compensated for by rotation of the block. The tangent screen was then brought flush with the spider, and the midpoint of the spider's visual hemifield shadow plotted on the screen, and transferred to the plotting table by alignment of the stimulator beam.

DATA COLLECTION

The signal from the microelectrode is amplified and displayed on a storage oscilloscope, a swept display, and fed to an audio amplifier to drive a loudspeaker. A window discriminator and adjustable triggering allow isolation of a waveform based on relative time and voltage parameters. Additional high- and low-pass filters allow data collection in the presence of interference from heart and muscle activity. Detection of a waveform meeting the set parameters results in storage of the time of occurrence of the waveform in a data file in the online Data General Nova 2 computer.

The microelectrode is stepped in 10-20 micron steps initially, and muscle responses and visually evoked potentials (VEP) mapped. The patterns and polarity of On and Off VEPs give an indication of distance to active neurons (see Appendix C, Table C.2). The microelectrode is stepped in 2 micron steps when approaching a neuron. The penetrations in the supraesophageal ganglion usually traversed about 1.3 mm. At this depth, visually responsive cell activity was replaced by large action potentials with a high spontaneous rate that are probably associated with the motor ganglia of the legs.

I presented stimuli to the anterior medial(AM) and anterior lateral(AL) eyes. The chamber occluded the posterior medial(PM) and posterior lateral(PL) eyes. A mask (originated by Jack Wathey, UCSD) consisting of an electrical bus strip (Figure 6.3) attached to a micropositioning device allowed selective occlusion of one or more frontal eyes during the course of the experiment.

The responses of cells driven by one or more frontal eyes were studied qualitatively and quantitatively. I studied primarily single unit responses. Multicell responses and the previously mentioned evoked potentials were also

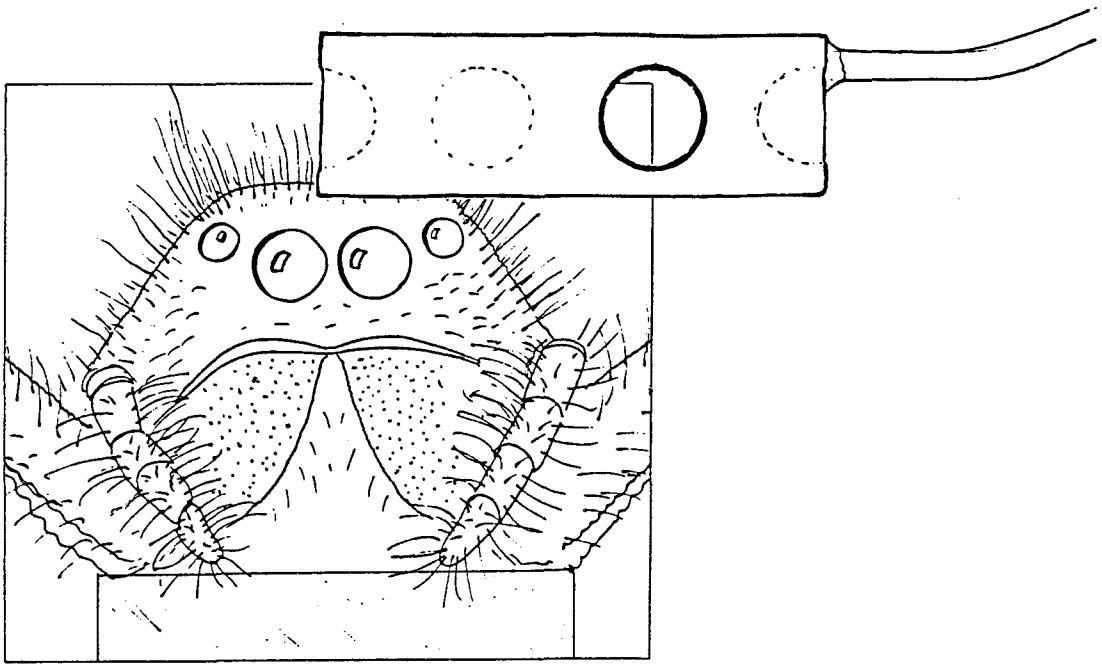


Figure 6.3 An electrical bus strip, solderd to a micromanipulator and painted flat black, allowed selection of specific frontal eyes for visual input during experiments. The posterior eye pairs are occluded by the chamber. Most of the front of the chamber is covered by a shield to reduce inductive pickup.

studied. A single unit was suitable for study if I could isolate it reliably, using the variable thresholds of the window discriminator, which were displayed on the display screen of a storage oscilloscope, along with the waveform, and if I could make a reproducible receptive field map for the isolated cell. Qualitative study consisted of mapping the receptive field by hand, using rear projected stimuli, controlled by a joystick, on a tangent screen with an intermediate beam splitter that reflected the image down to a plotting table (Figure 6.4). The oscilloscope display was augmented with an audio output of the unit's response. I assessed responsiveness to an array of colors, shapes, sizes, directions, velocities, contrasts, and a variety of ethologically significant stimuli during the initial mapping. The plotting table, projector, and tangent screen were on tracks that allowed varying the spider to stimulus distance.

Quantitative study of cell properties used computer programs developed in the Allman lab, primarily by Francis Miezin and Steven Petersen, and modified by myself for this application. A Data General Nova 2 computer and an Analogic A/D unit collected spikes in real time while controlling the rear projection systems' galvanometers, shutter, and stepping motors (Figure 6.4). I selected a 35 mm. slide (various sizes of bars, spots, textures, gratings, or ethological stimuli) and in later experiments added filters (neutral density, polarizing, and 10 nm bandwidth interference filters for spectral tests). I then selected a distance for the tangent screen.

The light source was an air-cooled, 500 watt projector bulb (DEK/DFW). The divergent light passed through a condenser and heat filter. It then passed through the center of a rotating stage containing the stimulus, and entered a projector lens. The emergent beam converged at the shutter location and passed to a pair of mirror galvanometers, which controlled the movement on screen.

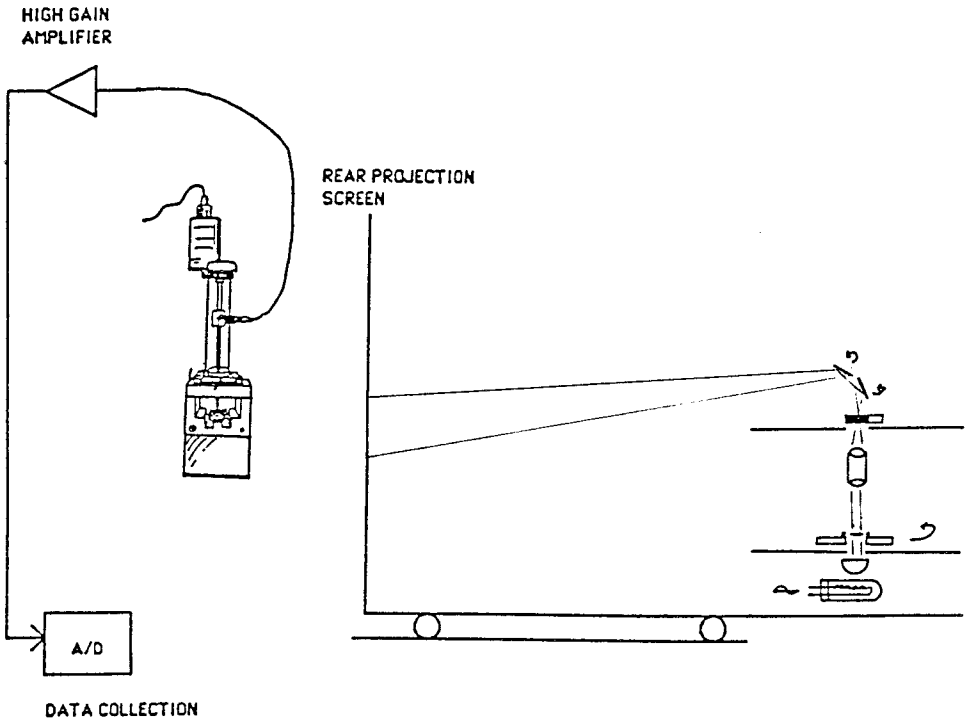


Figure 6.4 Stimuli are presented on a rear projection tangent screen. The entire stimulus apparatus is on a bearing track, allowing variation of stimulus distance. The light path of the optic stimulator is shown here. 35 mm slides in the image plane can be rotated to any orientation, and mirror galvanometers can direct the image to any specified location on the tangent screen.

The computer controlled stimulus orientation, velocity, and direction of movement. One of these variables would be selected for study and the other parameters would be held constant. The stimulus was varied over 6-12 values of the selected variable in a pseudorandom sequence. The entire sequence was usually repeated 5 times to improve signal-to-noise ratio. This method was essential, as many of these cells showed habituation to repeated presentation of nonvarying stimuli.

Velocity series would sweep the selected stimulus through a specified angle (larger than the receptive field) at velocities from two to five hundred degrees per second.

Direction series would move a spot or bar that was oriented normal to the direction of movement. Five presentations of each of twelve angles in pseudorandom sequence were swept through a specified angle on the rear projection screen, sufficient to ensure appearance and disappearance of the stimuli outside the mapped receptive field.

Results were displayed on a storage scope for immediate feedback, and stored on a magnetic disk cartridge for later analysis.

I used Fran Miezin's Single Neuron Analysis Program (SNAP1, Rev 13.0) for detailed offline analysis (Baker et al., 1981).

Histology

I made electrolytic lesions to mark penetrations (5-10 microamperes for 10 seconds). I anesthetized the spider at the end of the experiment (1-6 penetrations) and removed the appendages. I removed the abdomen at the pedicel and removed the chelicerae with a sharp razor blade. These procedures allowed better penetration of the fixative. The cephalothorax was then immersed in formol-saline (see Histology Appendix) under vacuum.

Most of the histology was done using the paraffin method of Blest (1961) and Humason (1967). I left the cephalothorax intact to facilitate localization with regard to external landmarks for future experiments. I added an extra step to improve the penetration of paraffin, as the heterogenous nature of the tissue (nerves, muscles, chitin, and the tough esophagus coursing through the center of the nervous system) sometimes resulted in fragmentation. The spider was removed from the paraffin after the initial embedding and the dorsal chitin removed. The spider was then put through the rest of the paraffin steps. In addition to allowing better penetration of the paraffin, this also gave an entry point for the microtome, so that fragmenting chitin did not tear up the sections. The spider was sectioned at 10-40 microns and stained with haemotoxylin and eosin.

CELL PROPERTIES (A journal submission)

Chapter 7

The physiology of high-order visual neurons in the brain of the jumping spider (Salticidae: Phidippus)

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Summary

Response properties of high-order, visual neurons in jumping spiders were investigated by microelectrode recordings in the supraesophageal ganglion.

1. Many of the cells driven solely by the mobile, ipsilateral, anterior medial eye possess receptive field maps that are larger than the angular extent of the retina (18 of 22 medial eye cells mapped), and have a stable location (constant position) with respect to the body (all cells mapped).

2. Some cells driven by medial eye input have receptive field maps that deceased in angular size with increasing stimulus distance.

3. Some cells driven by the AM eye are strongly selective for a stimulus velocity of 16°/second.

4. Some cells are selectively tuned for orientation and direction of movement of stimuli.

5. A measure of response latency correlated with the specificity of tuning.

Introduction

Jumping spiders (family Salticidae) have a highly specialized visual system, which they use for the detection and analysis of predators, prey, mates, and for navigation. They possess four pairs of eyes specialized for different tasks (Forster, 1979). Two lateral pairs (anterior and posterior) provide wide-angle,

low-resolution coverage of the spider's visual sphere and direct turning behaviors (Land, 1972). The principal (anterior medial) eyes each possess a high magnification telephoto lens (Blest et al., 1988), and a multilayer, high-resolution (8") retinal strip. The spider can direct this array with eye movements, including slow tracking saccades and scanning (Land, 1969b). When moving on a discontinuous substrate, and in prey capture, salticids jump, suggesting visual estimation of distance.

Visual behaviors that have been studied include courtship (Peckham and Peckham, 1894), color discrimination (Kaestner, 1950), two-dimensional form analysis (Drees, 1952), and navigation in three-dimensional mazes (Hill, 1979). Anatomical studies of eye and brain have described the visual specialization (Hanstrom, 1921; Land, 1969a; Eakin and Brandenburger, 1971; Hill, 1975; Oberdorfer, 1977; Blest et al., 1988). Physiological studies of the retina have addressed chromatic sensitivity in the retina (Blest et al., 1981). However, no visual physiology has been done beyond the level of the retina. In the present study, the extracellular responses of high-order visual neurons in the supraesophageal ganglion are examined in salticids of the genus Phidippus. These are large (13 mm body size), robust spiders whose behaviors, retina, and neural anatomy have been previously studied (Land 1969a,b; Blest et al., 1988; Hill, 1975).

Materials and Methods

Wild-caught, adult female jumping spiders with a body length of 13 mm were used. All successful recordings were from females, which have larger body size and lengthy survival time, both in the preparation and in captivity. Recordings were made from 35 Phidippus johnsonii (Peckham and Peckham, 1909), collected locally, and 15 P. sp. from Sedona, Arizona, obtained from C.

Kristensen (Spider Pharm). Specimens were maintained until needed in clear Petri dishes under normal circadian lighting on a diet of Drosophila virilis.

Recording Techniques

Spiders were anaesthetized with CO_2 from sublimating dry ice in their Petri dish, and immobilized with normal posture in an aluminum chamber by flowing wax (Paraplast, m.p. 58°C) around the ventral cephalothorax and appendages, leaving the abdomen clear.

A hypodermic syringe tip was used as a microknife to cut a small incision in the dorsal chitin overlying the supraesophageal ganglion, at a point determined by external landmarks (Figure 1A). Extracellular potentials were recorded with a glass-insulated, platinum-iridium microelectrode (Wolbarsht, 1960), which was advanced by a stepping motor microdrive. Proximity to recording sites was determined by polarity reversal of visually evoked potentials. Cells recorded from were typically 1100 microns from the dorsal surface (Figure 1B). Cell responses were displayed on a storage oscilloscope, and stored on magnetic tape for offline analysis.

Visual Stimulation and Data Collection

Visual stimuli were presented on a rear projection tangent screen and mapping table. The entire apparatus could be moved on bearings located in fixed tracks aligned parallel to the spider's body axis, to allow mapping at different spider-to-screen distances. Receptive fields were mapped for single and multiunit responses. Quantitative studies of velocity, direction, and orientation were conducted using an automated stimulus presentation and data collection system, as detailed in Baker, Petersen, Newsome, and Allman (1981). Briefly, the system recorded time of occurrence of spikes of a specific waveform, as

selected by a window discriminator, while sweeping a selected stimulus across the tangent screen at controlled velocities and angles in a pseudorandom sequence. Detailed analysis of response properties was conducted offline (Baker et al., 1981).

Results

One hundred and eight penetrations were made (one to six penetrations per spider) in the protocerebral cortex, a rind of cell bodies anterior to the protocerebrum (Figure 1B). Cells could not always be isolated; recordings were made from one hundred and fifty single or multiple units (cluster responses), including sixty-four visually responsive units. Nonvisual neurons responded to somatosensory stimulation, substrate or airborne vibrations, had periodic discharge rates (0.5-5 Hz), or could not be driven. Figure 2 shows the extracellular record of a single spike from an isolated single unit. Fifty of the sixty-four visual units were mapped.

The preparation was stable. Cells encountered could be held for hours. Many experiments involved multiple penetrations over several days. Cells responded to light and/or dark contours. Repeated presentation of a stimulus with no variation of speed, size, etc. resulted in habituation, which could be reversed by nonvisual stimuli.

Position constancy

The high-resolution layer (layer 1) of the retina of the anterior medial (AM) eye of P. johnsonii is a boomerang-shaped strip, two degrees in horizontal extent and twenty degrees in vertical extent. The eye capsule containing the thousand receptors comprising this retina moves in response to stimuli (Land, 1969b).

Out of 64 visually driven units, I was able to map 50 receptive fields. The frontal field of view of the spider is covered by the two AM eyes and a pair of anterior lateral eyes as well. By using a visual occluder, I mapped cells driven exclusively by input from a single AM eye. Two significant and related observations were recorded. Receptive field dimensions exceeded the static view field of the retinal array (Figure 3). Receptive field maps did not move with respect to the cephalothorax. Mapped receptive field centers (and boundaries) were never observed to shift in position, even in cells held for many hours.

Receptive fields of cells driven by medial eye input were on the average smaller than those of cells with lateral or lateral and medial eye input. The receptive field sizes for medial-eye-driven cells ranged from 8.7 to 1255 deg^2, with a median size of 77 deg^2 ($\bar{x}$ = 234 deg^2, s = 348 deg^2, n = 22). Receptive field sizes for lateral-eye-driven cells (n=6), and for cells receiving both medial and lateral eye input (n=3), ranged from 118 to 6200 deg^2, with a median size of 1481 deg^2 ($\bar{x}$ = 2375 deg^2, s = 1959 deg^2). The ocular input(s) for 19 cells were not positively identified by occlusion. The receptive field sizes of these cells ranged from 1.2 to 1128 deg^2, with a median size of 58 deg^2 ($\bar{x}$ = 178 deg^2, s = 334 deg^2). This distribution is similar to that of medial-eye-driven cells.

Size constant cells

Eighteen cells were mapped at two to five distances between 7 and 114 cm. Two of these cells had large receptive fields and input from all four anterior eyes. Five cells were definitely identified with the occluder as driven exclusively by the ipsilateral AM eye. Ten units had small receptive fields, suggesting medial eye input. One cell with only lateral eye input was included for comparison.

Two categories of receptive field variation were encountered. The first category consisted of cells whose receptive field maps covered a constant solid angle. Receptive field dimension varied linearly with screen distance. Doubling the distance to the tangent screen doubled the width and length of the receptive field.

The second category of cells had a nonlinear variation of angular receptive field size over distance. Most of the medial eye cells (14/18) studied fell into this category. Five of the cells had very small receptive field dimensions. Although they appeared to vary in a nonlinear fashion, they are not used as evidence, since a small mapping error could contribute a large percentage of size variation. The nine remaining cells had larger receptive field dimensions that would require mapping errors of centimeters to account for the variation in size from a divergent solid angle. An additional control was provided in the separate measures of x and y dimensions (Figure 4B-D). The systematic covariation of these two dimensions at different screen distances indicates that any mapping uncertainty which would affect them independently would be less than a few millimeters.

Many of these cells with a nonlinear change of receptive field size had properties suggesting a designator of "size-constant." These cells followed the normal divergence pattern up to a certain distance, at which point the metric dimensions remained constant as the screen distance increased, resulting in a decreasing solid angle.

Quantitative evaluation of cell properties

Seventeen cells were quantitatively analyzed with computer-controlled, pseudorandom stimulus presentation and data collection, by comparison of mean response values to multiple presentations of a range of velocities, orientations, and directions of movement.

Velocity tuning

Cells were tested for velocity preferences, usually with an illuminated bar, oriented normal to the preferred direction of movement, swept in that direction at seven different velocity values, presented five times each in pseudorandom order. Velocity values used ranged typically from 2 to 128 deg/s, by powers of two. Twelve of the seventeen cells studied had clear velocity preferences.

Cell responses could be grouped into two categories (Figure 5). The first group (n=7) had a maximal response to stimuli moving at 16 deg/s. For three of those cells the mean response was down over 50% at adjacent velocities of 8 and 32 deg/s. Each of these seven cells was driven exclusively by the ipsilateral AM eye. The second response category consisted of cells that responded best to velocities of 128 deg/s or more (n=5). Three of these cells were driven by medial eye input. The other two received input from both AL eyes and AM eyes. The preferred direction for these cells was for movement along the long axis of the retinal strip.

Tuning for Direction and Orientation

Direction and tuning preferences for cells were assessed as follows. After qualitative evaluation of velocity preference, stimulus dimension, and receptive field boundaries, the stimulus (usually a light bar) was presented and swept across the receptive field at twelve angles, five presentations each, in pseudorandom order. Stimulus display was shutter-controlled, and sweep initiation and termination positions were selected to ensure that the stimulus was outside the mapped receptive field.

Cell responses to each angle were computed by comparison of rate of response during presentation to that of the three second foreperiod immediately

preceding it, compensating for any change in excitability over the five minutes of presentations.

Two response indices were calculated as a measure of directional selectivity and orientation selectivity. The direction index (D.I.) is a measure of the bidirectionality of the cell:

$$D.I. = 1 - (R_p - R_{180})/R_p$$

where R_p is the response to stimulus movement in the preferred direction and R_{180} is the response to movement in the opposite direction. A D.I. of 0 indicates equal response for the preferred direction and its opposite. The tuning index (T.I.) is a measure of the selectivity of the cell for direction of movement. It is averaged over presentation angles within 90 deg of the peak response. A T.I. of 1 is a sharply tuned cell. Complete details of the analyses of these indices may be found in Baker et al. (1981).

Sixteen cells were quantitatively studied with a light bar stimulus under comparable parameters and had adequate S/N ratios for analysis. The variation of orientation and direction of movement in the series were not as effective in preventing habituation as was the variation of velocity. Nevertheless, most cells showed direction selectivity. Both single direction and bidirectional cells were found (Figure 6A, B).

The mean value for sixteen cells of the directional index (D.I.) was $\bar{x} = 0.77$, $s = 0.43$. The mean value of the tuning index was $\bar{x} = 0.56$, $s = 0.22$ (Figure 7). Three of the cells studied had input from the AL eyes, with values in the range of the medial eye cell values. In one cell where all four frontal eyes contributed input, multiple series were run. Tuning was sharper when the cell was driven solely through a medial eye.

The preferred direction of movement had a biased distribution. Eight of sixteen cells responded best to the stimulus moving upwards (90 deg). Four of these eight cells had down (270 deg) as the second preferred direction. Medial to lateral (0 deg) motion was first of second preferred direction for five of the sixteen cells.

Response latency and tuning

Response latency was measured two ways. For seven cells, a light bar was presented in a flashed orientation series. These cells responded transiently to stimulus termination with a range of delays from 30 to 95 ms ($\bar{x}$ = 62.9, SD = 20.8), with latency defined as the mean delay to response onset for thirty trials. The second latency measure resulted from the observation of a delayed "off" response to the termination of the stimulus in light and dark orientation series. This delay ranged from 40 to 255 ms ($\bar{x}$ = 125, SD = 62.8, n = 15), followed by a sustained response, and was calculatd from the mean delay to response of 12 histograms, each of the average of five trials (Fig.8A). The delayed "off" latency correlated with the tuning index (Fig. 8B).

Discussion

In this investigation of the salticid supraesophageal ganglion, the main findings were: (i) high-order neurons exist that are selectively tuned for specific stimulus velocity, orientation and direction of movement; (ii) a correlation exists between a measure of latency and degree of tuning specificity; (iii) retinal information and eye position/movement information are combined to generate large, position constant and size constant receptive fields.

Velocity tuning

One category of cells responded best to 16 deg/s. These cells were driven by an AM eye. Some of the retinal movements described by Land (1969b, 1971) are in this range. The scanning motion described for investigating a stationary stimulus can occur at 50 deg/s. Tracking movements are slower, less than 10 deg/sec. Saccades occur at speeds of 150 dg/s. Because of the tiered retinal mosaic and the distribution of distance information behind the focal point, it would seem that a scanning motion of a slow (16 deg/s) moving object at a higher rate could extract distance information along with the other image parameters. Sixteen degrees per second represents a rate of 1 cm/s at a distance of 3.5 cm from the spider, well within behaviorally significant range.

The other category of cells responded preferentially to higher velocities, in some cases in excess of 100 deg/s. Most of these cells had lateral eye input. Land (1972) found 100 deg/s as the maximum velocity to elicit a behavioral response (turning). This is not necessarily a contradiction. For a receptor spacing of 1 deg, a 100 deg/s stimulus produces 10 ms delay between neighbors, well within the dynamic range of most neurons. The absence of a behavioral response may be due to a lack of behavioral relevance.

Forster (1979) has demonstrated the role of the AL eyes in inducing pursuit of moving prey by lacquering over different sets of eyes. With occluded AM eyes, prey are pursued, followed by a short jump. The shortfall is inversely correlated with target speed, indicating a confusion of proximity and target velocity. The input from the AM eyes is necessary for accurate distance estimation.

Velocity tuning in salticid CNS can be compared with data from other visual systems possessing frontally directed, mobile eyes. Studies conducted in primate area MT have found cells responsive to visual motion. In the owl

monkey, Baker et al. (1981) have found cells in MT that respond over similar velocity values, with the greatest number of cells responding to 10 and 25 deg/s. In the macaque, Maunsell and Van Essen (1984) have found cells optimally tuned for velocities from 2 deg/s to 256 deg/s, with the grestest number of responses at 32 deg/s and 16 deg/s.

Tuning to direction of movement orientation

Cells were found that were tuned to the direction of movement and orientation. True orientation selectivity could not be assessed from the presentations, as the long axis of the bar was always perpendicular to the direction of movement. Flashed orientation series, designed to assess orientation selectivity without stimulus motion (Hubel and Wiesel, 1962), resulted in large, highly variable, non-specific responses to stimulus onset and termination. Hence, the direction and tuning indices should be regarded as measures of response to motion.

An additional factor in perceiving motion and orientation is the AM retina. The 2 X 20 deg boomerang shape of the retinal mosaic can be rotated through about 50 deg (Land, 1969b). Land suggested that these rotations act to align the retina with image elements to pick out contours. Drees (1952) has shown oriented contours in 2D images to be an effective component of spider recognition.

The measurement of a consistent direction preference may indicate that retinal rotation information has been processed out before reaching these cells, or that the viewing is performed at a consistent angle. The tuning curves measured could be as shown, or the result of a more selective curve smeared by retinal rotation during the series.

Latency and tuning

The tuning indices were found to correlate with a measure of delayed off-response latency for both light and dark stimuli. Several aspects of this measure need to be considered. The delayed off-response latency is different from a pure flash latency measure, which produces a short latency transient off-response. The delayed off-response is usually a sustained response, preceded by inhibition, and occurs after stimulus disappearance. In the case of a dark stimulus, the shutter action results in a full-field background illumination change. In the case of a light stimulus, no change occurs within the mapped receptive field, but a delayed off-response occurs, indicating that the cells receive some input from outside the mapped receptive field. The response was to the disappearance of the preferred stimulus after it had moved through the mapped receptive field. No consistent variation of this measure was observed for light versus dark stimuli, or large versus small stimuli.

The evidence suggests that this measure reflects some assessment of processing delay, either in number of cells involved or in feedback time constants, and this delay increases for sharper tuning.

Directionally selective cells have been found in a range of vertebrate and invertebrates. Hertel, Schäfer and Maronde (1987) report direction selective responses from the inferior and anterior optic commissures of honeybees. Hubel and Wiesel (1962) found orientation and direction selective cells in the cat. The data from the jumping spider are directly comparable to the tuning data from Baker et al. (1981) in the owl monkey and Maunsell and Van Essen (1984) in the macaque, and, although based on a much smaller sample, are similar to results in the medial temporal area of these primates (see Table 7.1).

The appearance of similar results in phylogenetically diverse species with separately evolved visual systems suggests that the same sort of high-level visual

processing solution has occurred in response to a similar set of constraints. Other similarities to vertebrates such as ribbon synapses (Oberdorfer, 1977), arrangement of eye muscles and degrees of freedom of movement (Land, 1969b), and frontal eye alignment as in primates (Allman, 1977) suggest that the optical and physiological constraints may limit the possible range of solutions.

Position constancy

High-resolution scanning retinae have evolved separately a number of times: several genera of heteropod molluscs (Land, 1982), and an isopod, Copilia quadrata, (Gregory, 1964) use a mobile retina. By sacrificing resolution in the time domain, high-resolution spatial imaging of a large field is possible, in a fashion analogous to the mobile primate fovea. The question of how retinal movement can occur without blurring the image remains open.

Fifty of sixty-four visually responsive cells were mapped. The remaining 14 cells could not be mapped. This could be solely visual information, uncorrected for the retinal movements of the awake spider. These cells are probably underrepresented in the study sample, since the protocol tended to select cells that could be mapped.

The position constant cells suggest an integration of retinal information and eye position or movement information. These cells appear to be positionally constant with respect to the body. The situation may be more complex. Wiersma and Yanagisawa (1971) found fibers in rock lobster optic nerve that were modulated by gravity ("space constant") and the receptive field would shift as the crustacean was rotated to remain in an upper quadrant, regardless of the dorsoventral orientation. There is evidence (Hill, 1979) that salticids retain the spatial position of their prey during circuitous approach entailing loss of visual contact. Such issues could not be addressed with the immobilized preparation used in the present study.

Schlag et al. (1980) describe absolute position cells in the thalamic internal medullary lamina in alert cats and argue that a combination of stimulus retinocentric coordinates and eye position coordinates are used to compute "stimulus absolute" coordinates. A position constant, gaze-independent, reference frame facilitates movement computation, and agrees with our conscious perception of the visual world, which maintains positional constancy despite eye and head movements. Some evidence of modulation of retinal information by eye position has been found in the posterior parietal cortex of primates (Mountcastle et al., 1975; Robinson et al., 1978; Anderson and Mountcastle, 1983; Sakata et al., 1983). Zipser and Anderson (1988) used awake, fixating monkeys and found that in area 7a (posterior parietal cortex) 57% of the cells were "spatially tuned," combining eye position and visual input; they also reproduced these cell properties with a neural network model.

Mammalian position constancy must rely solely on combined retinal and eye position information. Salticids have an additional resource, as the anterior lateral eyes cover the area in which the anterior medial eyes move, providing a coarse, low-resolution map. The occlusion data suggest that position constant fields exist using only retinal and eye-position information from the medial eye, but do not exclude the possibility of registration with the anterior lateral eyes. Three cells recorded from received a combined input from anterior medial and anterior lateral eyes. Land (1972) has described how lateral eye input translates directly to behavioral output, with stepping movements of the legs to place the stimulus on body axis and in the fields of the anterior medial eyes. The presence of position constancy in such diverse visual systems suggests that this abstraction of the world is useful and may provide an effective base for motor input.

Size constancy

As small visual predators, salticids require accurate assessment of size and distance of potential prey to evaluate suitability of prey and to initiate capture. The size constant cells provide a substrate for this assessment. The occlusion data in the present study show that input from a single ipsilateral anterior medial eye is adequate to generate this constancy, ruling out binocular cues. The most likely source of distance information comes from the plane of best focus, as suggested by Land (1969a). Accommodation by alteration of lens curvature does not exist in this system. The four layers of receptors are arranged in such a way as to give an optimal image at the deepest layer (Blest, 1988), which is densely packed in an ordered array 2 deg horizontally by 20 deg vertically. This array is tiered horizontally, so that a lateral eye movement results in a succession of layer 1 receptors imaging a given point at different distances from the focal point. As an object comes nearer, its point of best focus shifts farther behind the focal point of the lens. Best focus is relatively simple to determine, by finding the largest difference between two adjacent receptors. The layer 1 receptors act as light guides (Blest, 1988) allowing light to enter only at their anterior end, maintaining image quality.

The simple lens of the AM eye has a significant amount of longitudinal chromatic aberration (Land, 1969a), which could complicate the focal distance information. How are these components separated? Some attenuation of longer wavelengths may occur from absorption in the eye (Blest, personal communication). The laminar lens structure may act as an interference filter around 560 nm (based on layer spacing data from Eakin and Brandenburger, 1971). Differential chromatic sensitivity of receptors is unlikely: intracellular recordings of cells in identified layers (Blest et al., 1981) showed that the receptors in the high-resolution layer 1 had broad chromatic tuning curves

centered at 535 nm. The best possibility may lie in layer 2, which is similar to layer 1, albeit coarser, and could play a role by sampling the image at a second point, allowing comparison of the differences, and facilitating reconstruction.

Acknowledgements

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Figure Legends

Figure 1. (A) The electrode was placed in a small incision on the dorsal surface, near the cephalothoracic fovea, at the intersection of a line that passed through the RAM eye parallel to the anterior posterior axis and a line that passed posterior to the RPL eye, normal to the a.p. axis. (B) Cells recorded from were most likely anterior to the protocerebral mass, based on range of electrode depths (1), surface insertion point (2), location of cellular cortex (3), and presence of large-signal, high spontaneous rate cells at greater depth (4). (Parasagittal line drawing adapted from Hill, 1975.)

Figure 2. Extracellular action potential recorded from a visually responsive neurons in the supraesophageal ganglion of a jumping spider.

Figure 3. A spider's eye view of the tangent screen, with the projection of layer 1, the high-resolution retinal layer (adapted from Land, 1969a). The arrows show the 60 deg range of retinal movement. All mapped receptive fields remained positionally constant, and most exceeded the static retinal coverage. The nine receptive field maps illustrated received input exclusively from the AM eye.

Figure 4. The horizontal and vertical dimensions of receptive field maps were modulated by stimulus distance. (A) shows the spider and the tangent screen at two distances. The diverging lines mark a constant angular field. The parallel lines indicate a size constant field. (B,C,D) show the pattern of variation of linear receptive field dimensions with distance. The x-axis of each plot is the spider-to-screen distance. The y-axis is the measured receptive field dimension

in cm. The horizontal (x) and vertical (y) dimensions of the receptive field are both plotted for each map. Nine of eighteen multiple-mapped cells clearly did not have a constant angular field.

Figure 5. Cells fell into two categories of velocity preference. One category was sharply tuned and preferred velocities of about 16 deg/s (n=7). The other category consisted of cells that responded best to much higher velocities (n=5). Bars indicate the standard errors of the means.

Figure 6. Cell preferences for orientation and direction of movement were measured. A bar of preferred size and contrast was moved at the preferred velocity through the receptive field at twelve different angles, in pseudorandom order to minimize habituation. Responses were calculated by comparing cell discharge rates during stimulus presentation with the spontaneous rate of the foreperiod. The stimulus appeared and disappeared outside the mapped receptive field to minimize flash responses. Averaged responses of five presentations at each of twelve angles are shown. The direction index (D.I.) is the ratio of response in the preferred direction to the response to motion in the anti-preferred (180 deg) direction. Tuning index (T.I.) is equal to one minus the area underneath the curve for the preferred direction ± ninety deg. See Baker et al. (1981) for complete details of these indices. Bars indicate the standard errors of the means.

Figure 7. Distribution of direction and tuning index values among quantitatively studied cells.

Figure 8. A positive correlation was found between direction and tuning indices and a measure of latency. (A) Cell latency was calculated by plotting averaged response histograms for each presentation angle and measuring the delay of the off-response to the end of stimulus presentation. (B) Latency vs tuning index and latency vs direction index for fourteen cells.

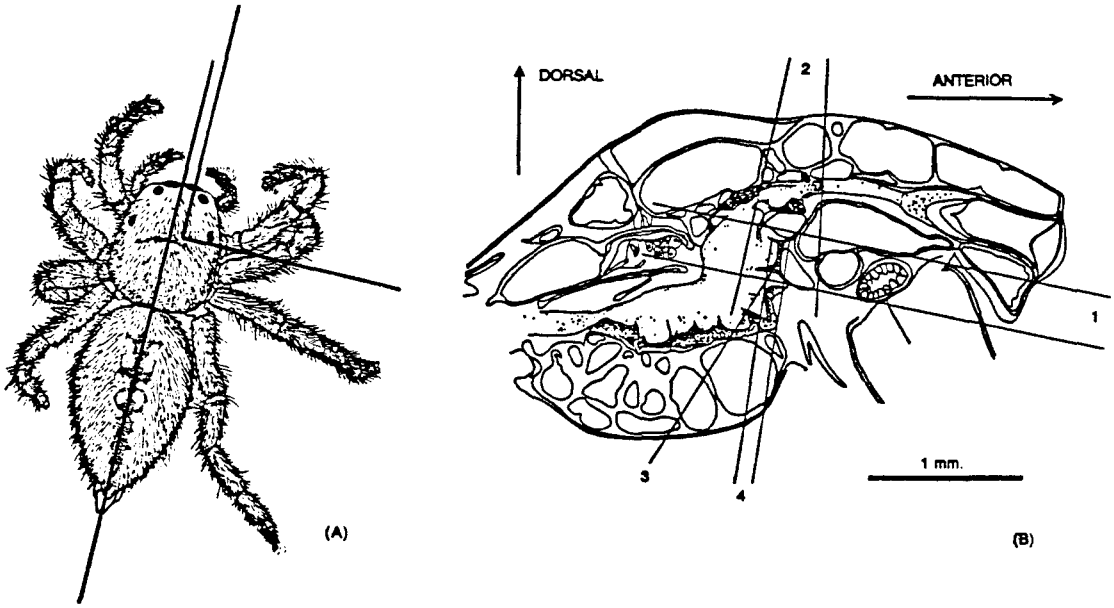


Figure 1

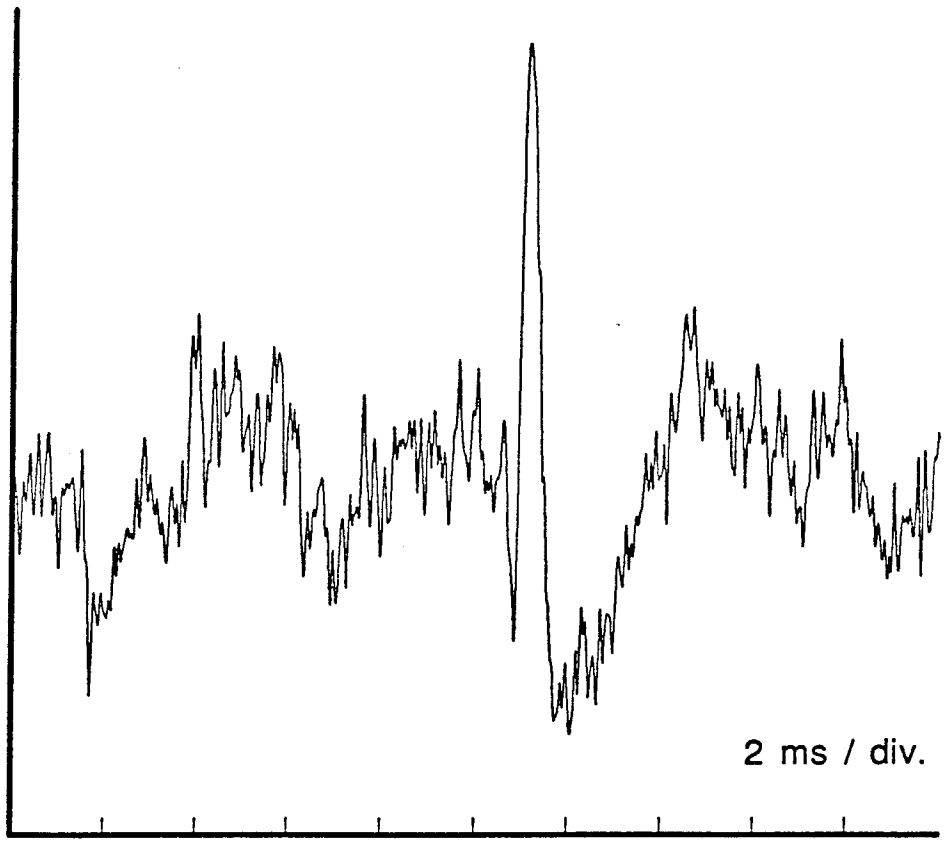
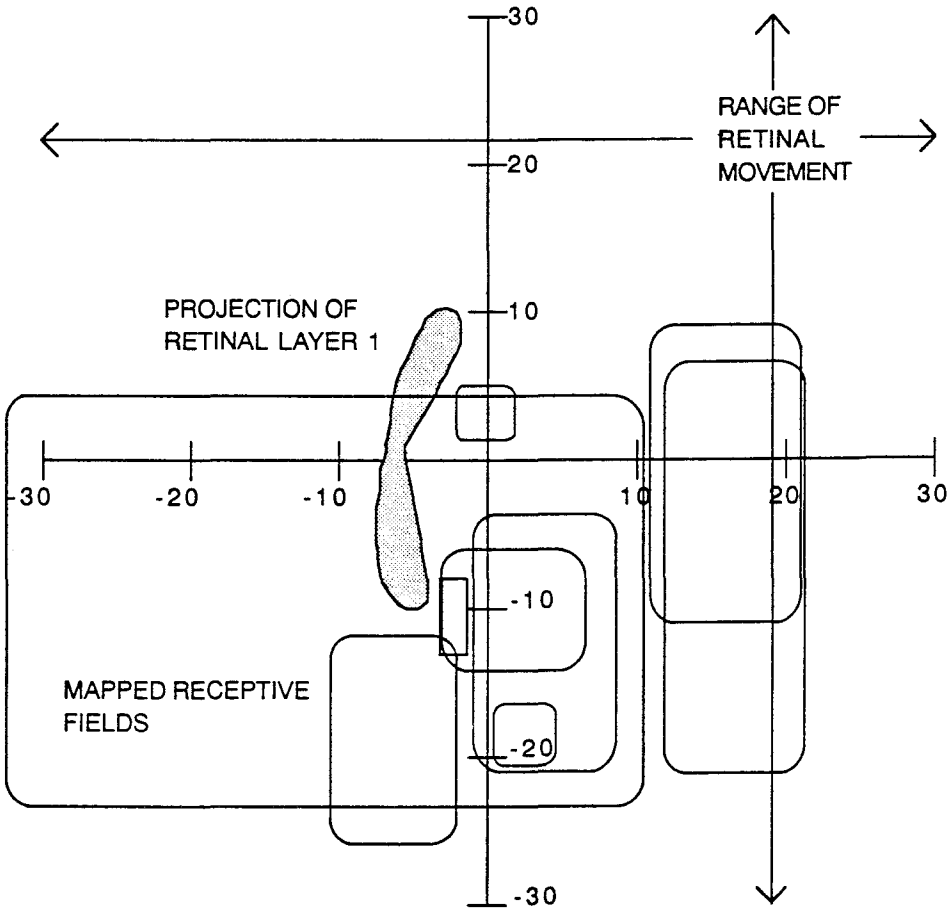


Figure 2


30
20
10
-10
-20
-30
-30
-20
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10
20
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RANGE OF
RETINAL
MOVEMENT
PROJECTION OF
RETINAL LAYER 1
MAPPED RECEPTIVE
FIELDS

Figure 3

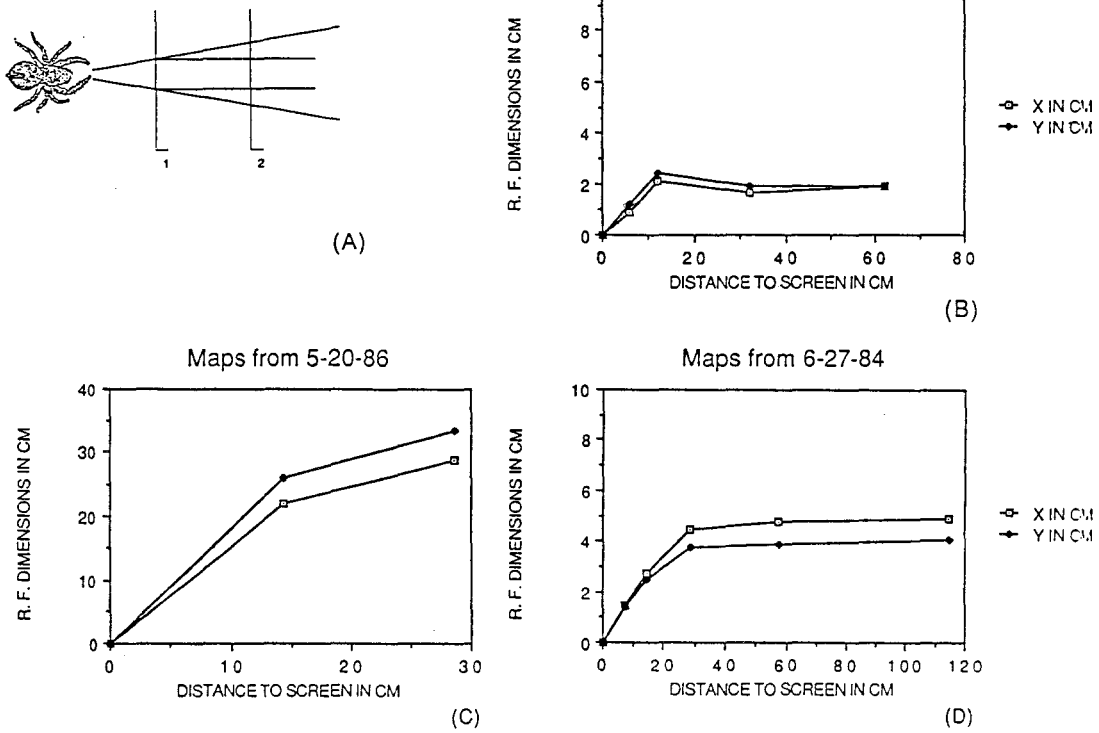
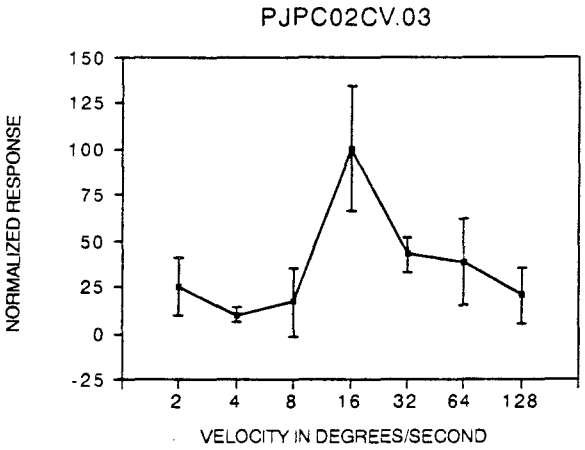

1
2
(A)
Maps from 8-11-82A
R. F. DIMENSIONS IN CM
DISTANCE TO SCREEN IN CM
X IN CM
Y IN CM
(B)
Maps from 5-20-86
R. F. DIMENSIONS IN CM
DISTANCE TO SCREEN IN CM
(C)
Maps from 6-27-84
R. F. DIMENSIONS IN CM
DISTANCE TO SCREEN IN CM
X IN CM
Y IN CM
(D)

Figure 4

MAX. RESPONSE = 60 SPIKES/SECOND

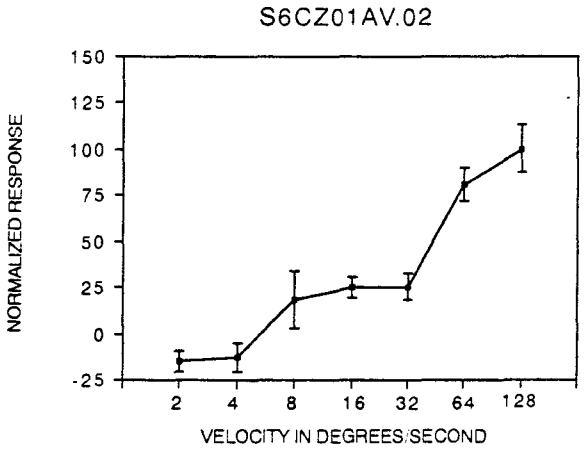
S/N = 6.27



(A)

MAX. RESPONSE = 51 SPIKES/SECOND

S/N = 4.0

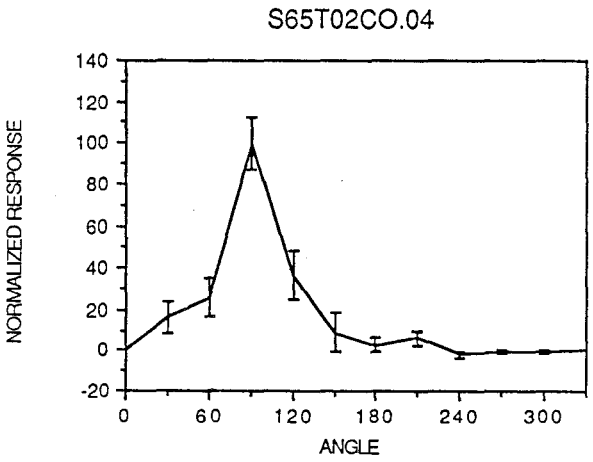


(B)

Figure 5

D.I. = 1.007
T.I. = .685
S/N= 48.00

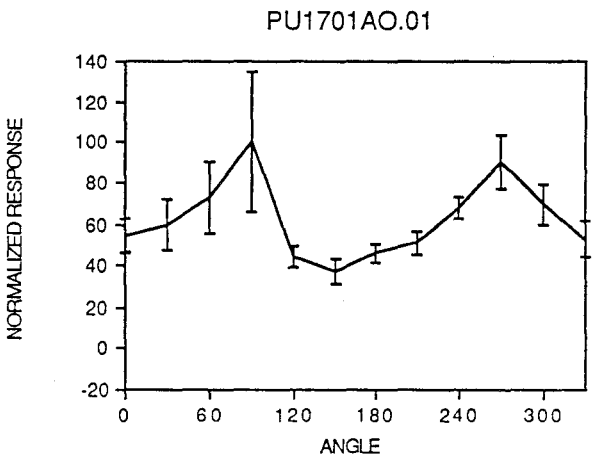
MAX. RESPONSE = 9.6 SPIKES/SECOND



(A)

D.I. = .030
T.I. = .494
S/N= 27.73

MAX. RESPONSE = 20.48 SPIKES/SECOND



(B)

Figure 6

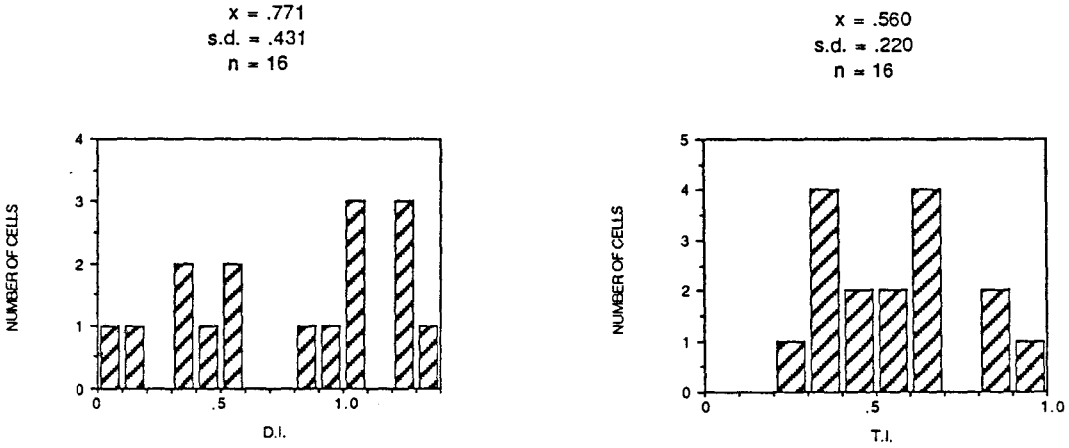
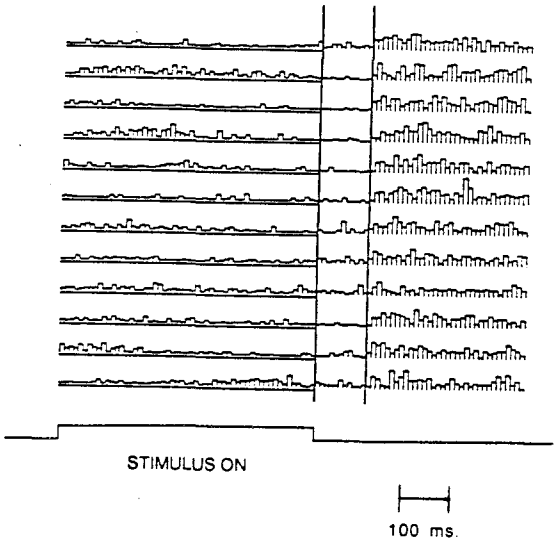
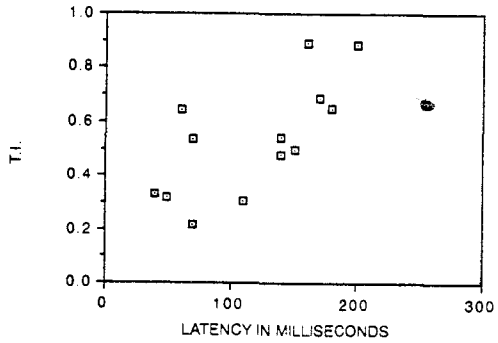

x = .771
s.d. = .431
n = 16
NUMBER OF CELLS
0
1
2
3
4
0
.5
1.0
D.I.
x = .560
s.d. = .220
n = 16
NUMBER OF CELLS
0
1
2
3
4
5
0
.5
1.0
T.I.

Figure 7



(A)



PEARSON PRODUCT MOMENT CORRELATION = .662

(p<.001)

(B)

Figure 8

Table 7.1

	D.I.		T.I.		
	$\bar{x}$	SD	$\bar{x}$	SD	n
jumping spider protocerebrum	0.771		0.432	0.560	0.220 16
owl monkey area MT	0.806		0.299	0.567	0.246 ...129
macaque monkey area MT	0.932		0.372	0.557	0.329 ...163

COMPARATIVE SURVEY AND GENERAL CONCLUSIONS

Chapter 8

Scanning retinal systems

The scanning retinae of the salticidae are unique amongst the Arachnids. Although most spiders have rudimentary musculature for moving the retinae of the anterior medial eye, none have the high degree of development of muscle, lens and retina that yield the high-resolution vision essential to the salticid lifestyle.

There exist a few other scanning retinal systems, found in copepods and molluscs. By comparative study, we can ascertain the costs and benefits of this system, and look for common features in the lifestyles of the scanners.

The most extreme example of scanning vision was described by Exner (1891) in the copepod Copilia. Gregory, Ross, and Moray (1964) have restudied this system in female Copilia quadrata. The following summary is based on their description.

Each lateral eye consists of a large, fixed, anterior lens, and a posterior lens 650 microns distant (Figure 8.1). Five receptors lie behind this lens and may function as a single unit. The optic nerve from these receptors terminates in the supraesophageal ganglion.

Under the experimental conditions, each of the two posterior lenses moved rapidly and continuously across the (probable) image plane of their respective anterior lenses. The posterior lenses and receptors move in a synchronous sawtooth, consisting of rapid movement medially, and slower movement laterally (resulting in a projected scan of the visual world with a slow medial movement (Figure 8.2)). The authors' (1964) analogy to a television raster suggests that

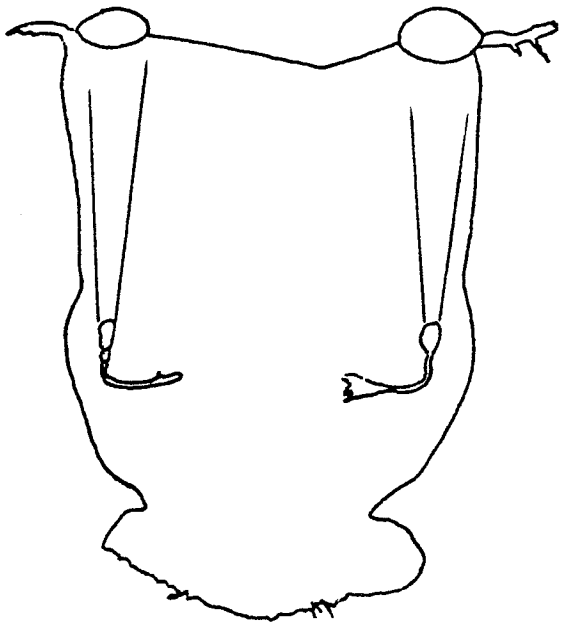


Figure 8.1. Lateral eyes of Copilia quadrata (from Gregory et al., 1964).

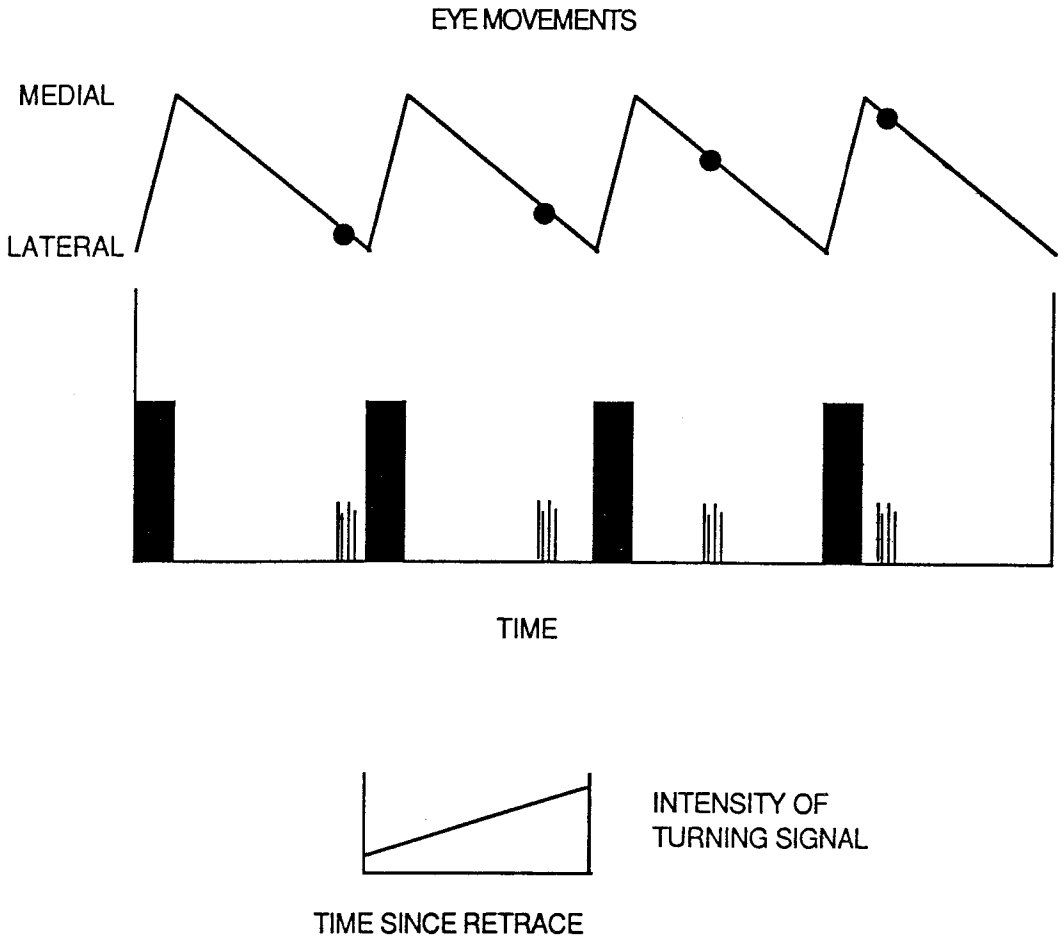


Figure 8.2. Scanning eye movements of Copilia quadrata and information for turning behaviors.

there may be movement in the dorsal-ventral plane as well as side-to-side, but this is not explicitly stated.

Ethological data of the visually guided behaviors would be useful in understanding the function of this system, and comparing it to that of salticids. The continuous scan is a necessity imposed by the single receptor and could be used to construct a template of the visual world from the serial string of retinal information and the oscillating position of the retina. Figure 8.2 shows how this system could be used to generate turning behaviors (not necessarily using a template) to orient the midline of the animal to a contrast point (typical behavior in many visual creatures). For further discussion of scanning in Copilia and other copepod genera, see Land (1981).

Another scanning system, which is more analogous to that of the salticids, has been described in several genera of gastropod molluscs (Hesse, 1900; Bruel, 1924a, 1924b; Messenger, 1981; Land, 1984). Prosobranch strombid and heteropod genera that have had scanning systems described include Pterotrachea, Oxygyrus, Carinaria, and Atlanta.

As these pelagic carnivores are difficult to acquire and maintain, few studies have been made of their scanning behaviors, with the notable exception of a study by Land (1982), who succeeded in studying the scanning movements of the eye of Oxygyrus keraudrenii.

Oxygyrus has two laterally directed, statocyst stabilized eyes. The retina of each is a horizontal strip, three receptors (subtending 3.2°) vertically by about 410 receptors (160°) horizontally, behind a lens of about 540 microns focal length.

Oxygyrus alternates one or two second swimming bouts with ten second bouts of slow, downward drifting, during which scanning takes place. The eye flicks downward, covering 100 degrees in 200-300 ms, followed immediately by a

slow (600-1100 ms) return upwards. The eye movements are sometimes synchronous. Land also mentions that some Atlanta species with frontally directed eyes have conjugate movements.

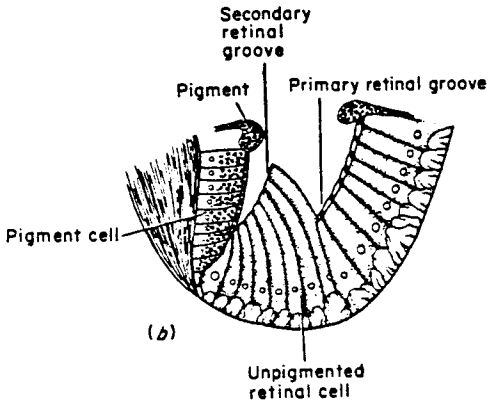
The keel of the shell may be sticky and act as a net. Although prey catching studies have not been conducted, it is likely that this scanning visual system is used to detect prey and direct subsequent capture behaviors, possibly using a turning scheme such as that advanced for Copilia.

In addition to a striplike retina, some heteropod molluscs possess an additional similarity to salticids, that of retinal tiering and a second strip (Figure 8.3). Gardiner (1972) describes the receptor location in Carinaria mediterranea: "These lie in a groove, divided into two secondary grooves. The cells in the dorsal groove become progressively taller toward the center of the vesicle, while those in the ventral groove are of uniform height." Gardiner suggests that the two surfaces allow calculation of distance. These two bands are contained in a simple eye which can be moved by muscles.

A major question in salticid vision is the function of Layer 2. Initial proposals assumed selective photopigments for sorting chromatic information, but evidence for them is lacking. Blest (1988) has pointed out the compromised image quality of this layer and the connections between adjacent receptor segments.

The appearance of a similar scheme in scanning molluscs suggests the second layer does play an important role. One possibility is that as the high-quality, tiered receptor layer scans and derives precise depth information, the low-resolution layer helps register the relative position of this information. More investigation is needed.

The position constancy found in salticids is taken one step further in rock lobsters. Wiersma and Yanagisawa (1971) found space constant fibers in the



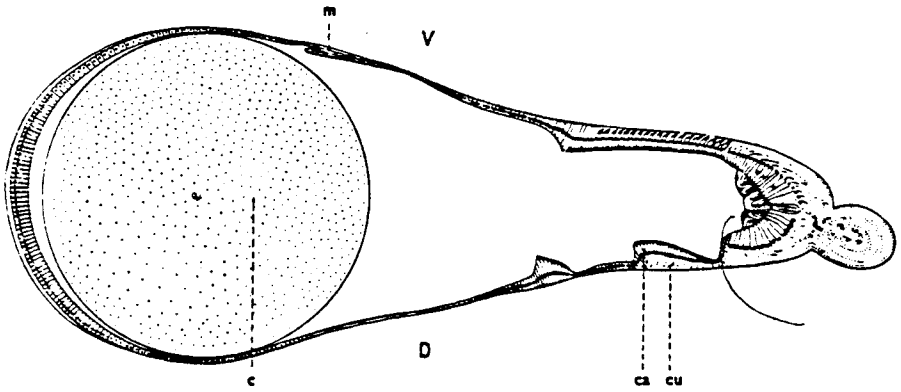


FIG. 122. — Coupe sagittale d'œil de *Pterotrachea coronata*. *c*, cristallin ; *ca*, cellules visuelles accessoires ; *cu*, cellules nerveuses unipolaires ; *m*, muscles ; *D* et *V*, côtés dorsal et ventral (d'après HESSE).

Figure 8.3. The retinae of Carinaria mediterranea (from Gardiner, 1972) and Pterotrachea coronata (Grassé, 1968), showing the two bands of receptors.

optics tract, which shifted the area of visual response with body movements, presumably in response to statocyst input. A similar image stabilization scheme is found in the octopus, where statocyst information maintains a horizontal orientation of the pupil (Budelmann and Young, 1984).

What are the common ecological niche requirements for scanning visual systems? Salticids are r-strategists, occupying seasonal habitats, with small body size and weak social behavior. Salticids are small predators. Following Allman's (1977) discussion of the problems of a visually directed predator, I compare primates and salticids. Effective capture requires prey in the frontal sector, especially in labidognath spiders, allowing not only effective grasp with limbs, but effective envenomation and maceration as well, because of the biomechanics of the opposed cheliceral structure. The optical axes of primate and salticid eyes are directed directly forward, yielding maximum image quality and avoiding numerous aberrations encountered off-axis. Early primates needed this because low light levels (nocturnal) require a wide aperture to gather more light, increasing off-axis aberrations. Salticids need this because of the small size of their system. The "advantage" salticids have over primates is the global coverage of their vision, a lack primates have compensated for (in some cases) with social behavior.

Two innovations allowed the adaptive radiation of salticids. The first was the labidognath jaw structure, which allowed reduced body size for a similar prey category. The second is the visual system. Arachnids extend their sensory range with silk lines. Salticids extend their sensory range even further, with visual specialization, which has resulted in an explosive proliferation of species.

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Appendix A

Abbreviations

A anterior

AL first ganglion of the anterior lateral eye

AM1 first ganglion of the anterior medial (principal) eye

AM2 second ganglion of the anterior medial eye

C cell bodies

CB central body

CC crystalline cone cells

Ch cheliceral ganglion

Co cornea

CP corpora pedunculata

D dorsal

DD digestive diverticula

E esophagus

F fovea

GL glomerular layer

I-IV ganglia for legs 1-4

L lateral

Lenp lateral eye neuropil

M medial

Mu muscle

Mx matrix surrounding receptors

N neuropil

Ns neurosecretory

O optic nerve

P posterior

PC protocerebrum

Pi pigment surround

PL 1 first ganglion of the posterior lateral eye

R receptor

Rh rhabdomere

S sucking stomach

T terminals (fiber)

V ventral

X posterior medial nucleus

Equivalences

AM 1 = AME 1 = FOG (first optic ganglion of the principal eye)

AM 2 = AME 2 = 20G (second optic ganglion)

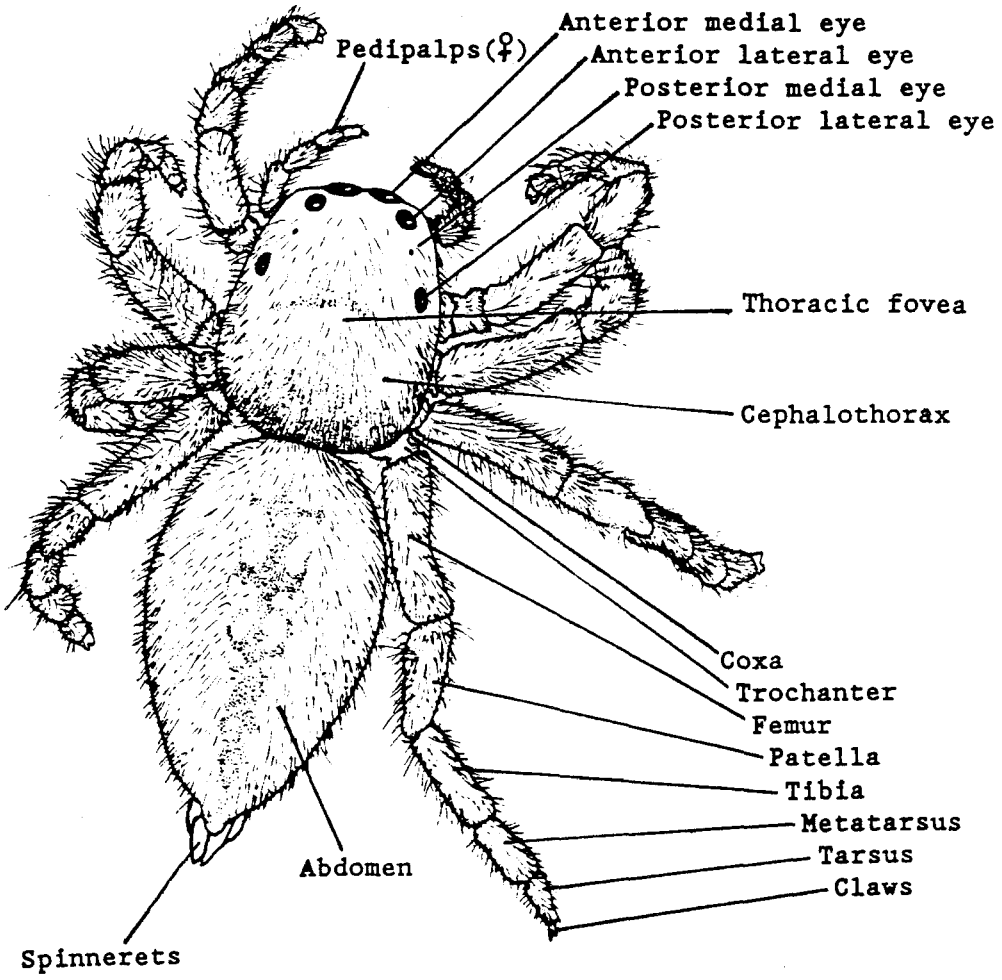


Figure A.1. External morphology of P. johnsonii, dorsal view.

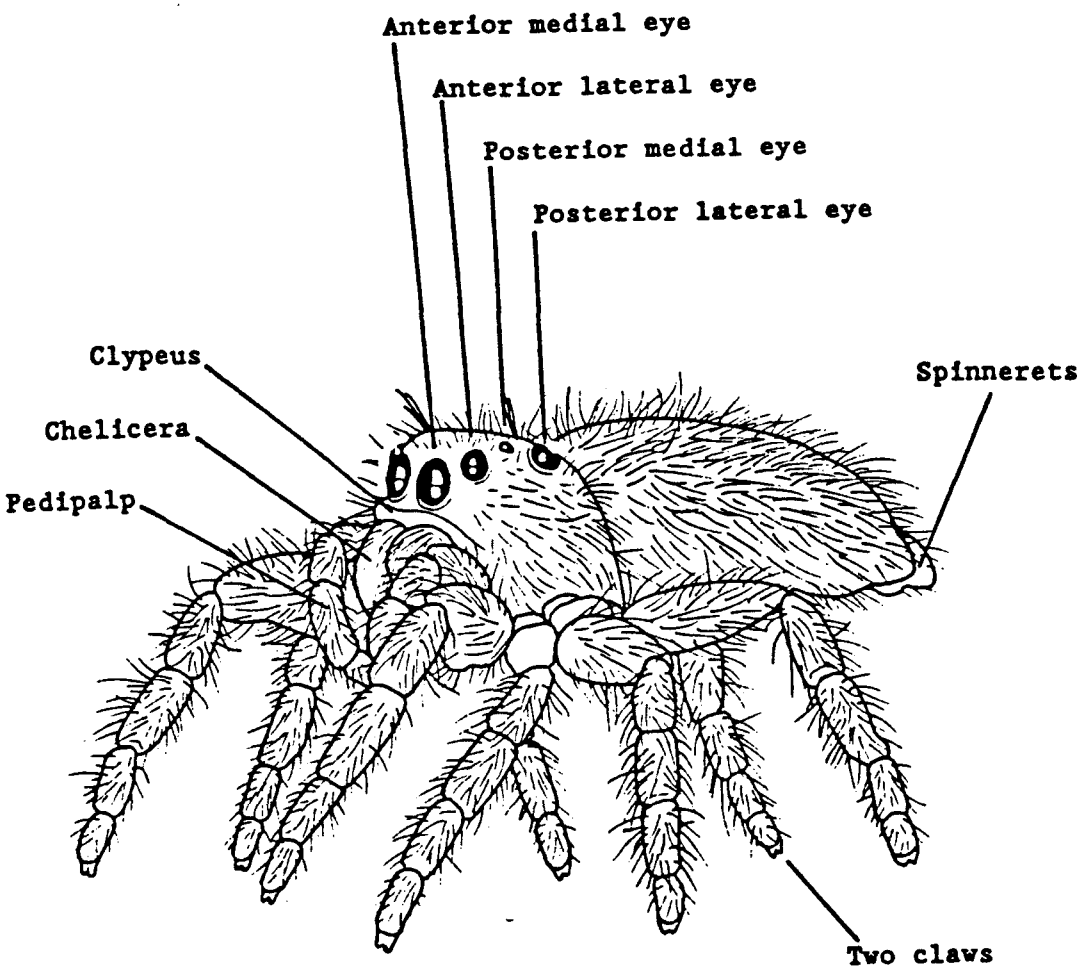
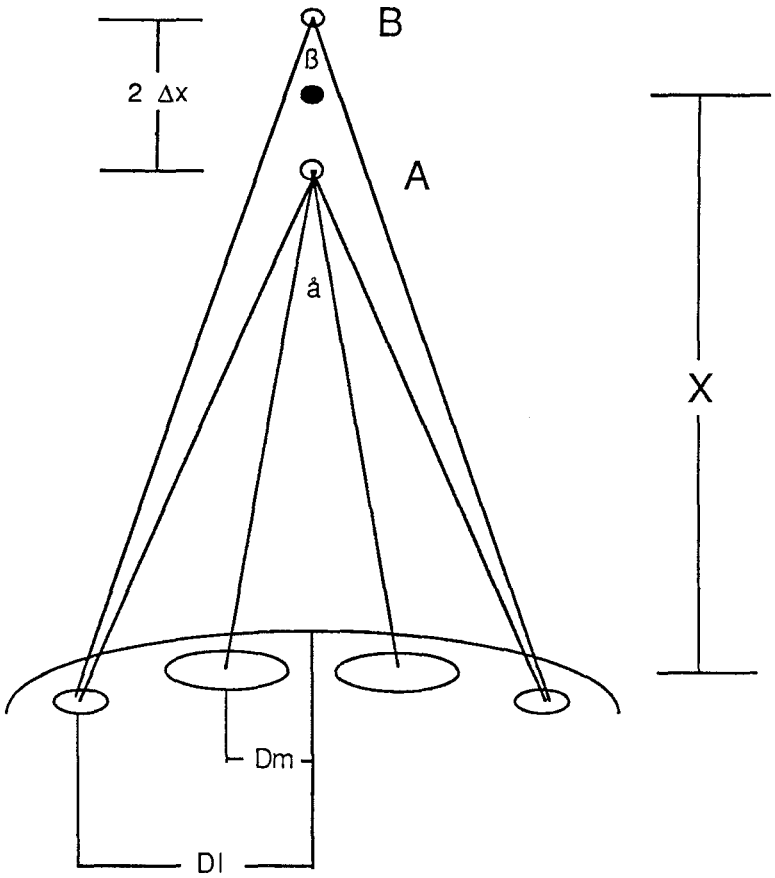


Figure A.2. External morphology of P. johnsonii, lateral view.

Appendix B



ΔØ = RECEPTOR SEPARATION = å - ß
X = TARGET DISTANCE
2D = INTEROCULAR DISTANCE
Δx = DEPTH ERROR

$$\Delta x = \sqrt{(D \cot(\Delta Ø/2))^2 + X^2 + D^2} - D \cot(\Delta Ø/2)$$

For a strike at 5 cm.,

ΔØm = 9'	Dm = .4 mm.	Δxm = 4.06 mm.	Medial eyes
ΔØl = 30'	Dl = 1.5 mm	Δxl = 12.8 mm.	Lateral eyes

Lines defining ß for the medial eyes omitted for clarity.
Drawing not to scale.

(after J. C. Wathey)

Appendix C

Other results

Many types of other activity meriting study were recorded in the jumping spider central nervous system. Table C.1 summarizes them.

The mapped, visually responsive units have been described. Cells that were visually responsive and not mapped were also qualitatively studied. The absence of a receptive field could be due to an intermittent response over the field, as would be caused by the combination of a retinotopic cell and retinal movements. Most of the unmappable cells were located less than 400 mm from the dorsal surface.

Shallow cells were found driven by lateral eyes or medial eyes. One of the shallow cells was directionally tuned to 90^{o}, and like one other, responded best to novel stimuli, habituating rapidly. Different cells responded to a range of different stimuli, including dark edges, specific directions of movement, novel stimuli, and small (1^{o}) dark or light spots (contrast insensitive).

I tested several mapped cells (two anterior radial input, one anterior lateral input) for chromatic sensitivity over a range of values by inserting interference filters into the path of the visual stimulator and characterizing the response. This provided a reasonable map of wavelength sensitivity (Figure C.1). UV sensitivity (350 nm) could not be tested with the setup.

Other sensory cells noted include cells that respond to vibration, or puffs of air. Cells responding to vibration could be very tightly tuned for frequency. Figure C.2 shows records from a cell that responded to a very narrow range of frequencies around 43 Hz. The stimulus consisted of airborne transmission of low frequency tones from a dynamic loudspeaker driven by a sinewave function generator. The loudspeaker introduced distortion, so that the 40 Hz signals had

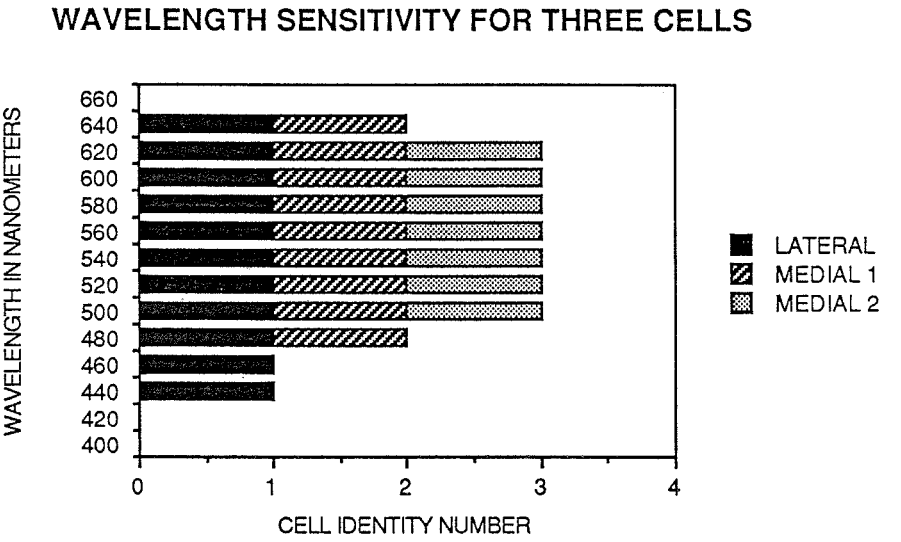


Figure C.1. Apparent range of wavelengths over which cells driven by anterior medial and anterior lateral eyes respond.

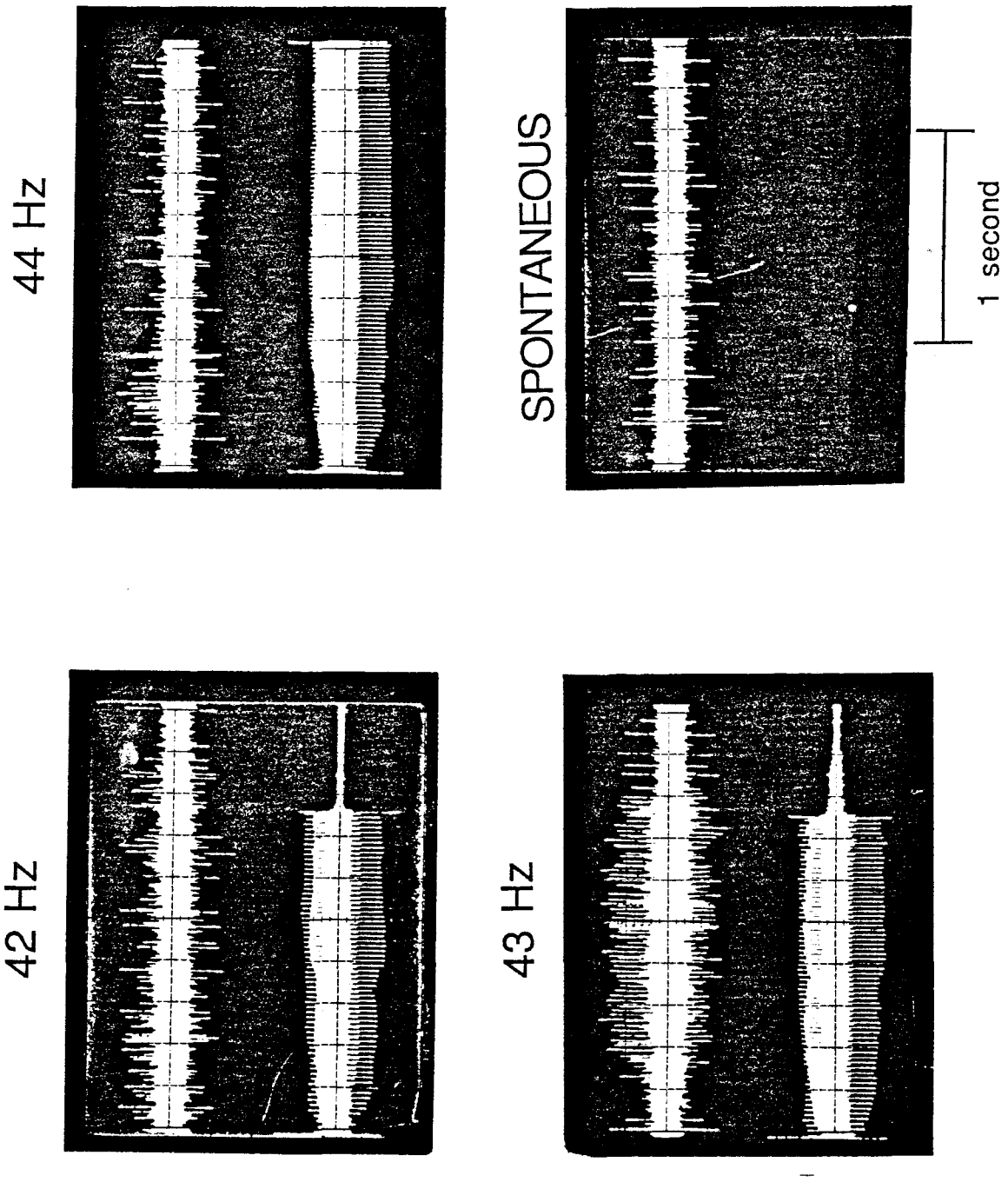


Figure C.2. Response records at different frequencies of a vibration-tuned cell.

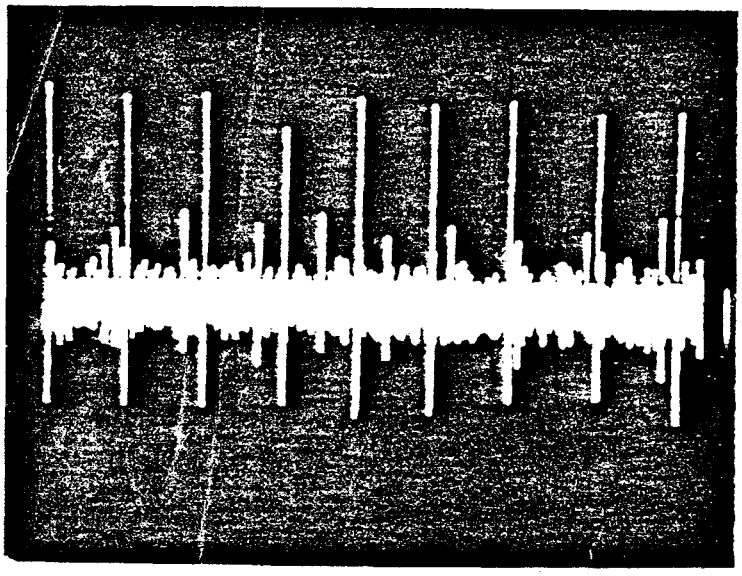
additional harmonic content. The sensory channel was not isolated. Two likely candidates are the lyriform organs or trichobothria. Most of the ventral cephalothorax was encased in wax, but lyriform organs can be quite sensitive. Trichobothria have been shown to respond to airborne vibration, and many were left exposed.

I also found seven somatosensory cells, which responded to a light touch or breath of air on the pedipalps. The pedipalps are highly ennervated, and covered with numerous sensory hairs.

About twenty cells were found with extremely periodic spiking activity, which for convenience in discussion I will term rhythmic cells. Uttal (1976) has pointed out the unfortunate baggage of implications that come with a descriptive label, but it facilitates discussion. The rhythmic cells were, for the most part, extremely regular over periods of minutes to hours. Figure C.3 depicts the position of the second spike on an oscilloscope display triggering off the first spike. This figure represents lumped data for several hundred spikes, with even the outliers within 5 percent of the center value.

A few rhythmic cells had basic response rates that could be modulated by visual or other sensory stimulation, resulting in a temporary (30 seconds) increase in frequency.

Rhythmic pulses were also frequently encountered. Although regular in the short term, they were variable over a few minutes, and the period was inversely related to arousal. Pulse frequencies varied from .5 Hz to 5 Hz, with slow timecourse waveforms. These responses are most likely the result of motor activity, with several possible sources, the most prominent of which is the heart. Although the cardiac muscle is located in the relatively isolated abdomen, a major blood vessel supplying the brain runs along the dorsal side of the subesophogeal ganglion. Heart rates fall into the frequency range as well.



100 ms

Figure C.3. Response record from a "clock" cell. These cells were fairly common, and usually frequency stable over hours.

Some of the rhythmic pulses would appear and disappear suddenly. These could be accounted for by muscular activity of the sucking stomach with the esophagus, or the lateral esophageal dilator, both of which are quite near the recording site, or movements of the jaws or attempted movements of the wax-embedded legs.

Evoked potential responses were extremely useful in determining proximity to the recording site.

The visually evoked potential elicited in response to a full field illumination onset or termination on a screen at 1/4 visual meter was a complex waveform. The polarity and order of major peaks for the ON and OFF visually evoked potentials typically followed an ordered sequence with depth. A typical sequence is shown in Table C.2.

Two cells were found that had nonhomogeneous response properties over the extent of a large receptive field. These cells,
driven by all four frontal eyes, were sensitive to the sign and degree of contrast. The sensitivity varied over the extent of the field. They responded optimally to a small (1^{o}) black spot, although larger stimuli could drive them. Response was to motion onset, but only after a stationary foreperiod, which varied in temporal magnitude over the extent of the field (Figure C.4).

A succession of jerky movements of the spot resulted in continuing discharge.

Discussion

Vibration sensitivity is the primary sensory input for most arachnids. Despite the strong visual system, vibrations still carry important information for salticids. It is used for nonvisual courtship in the nest (Jackson and Blest, 1982), and other functions, as well.

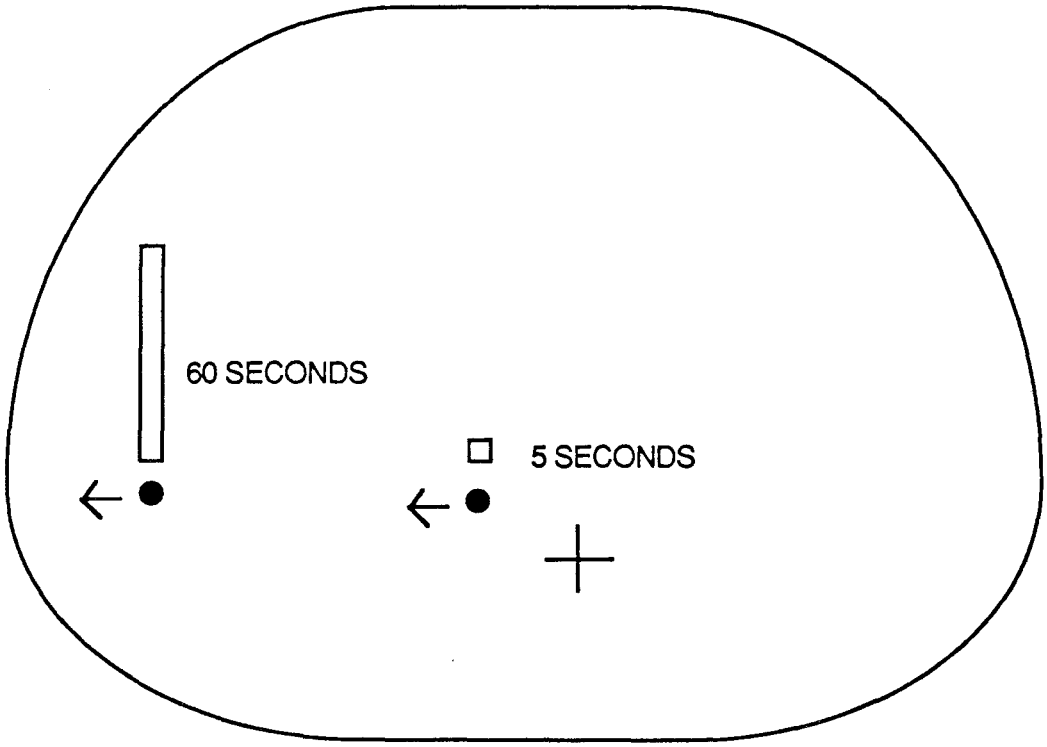


Figure C.4. A cell that responds to onset of motion, after an appropriate stationary foreperiod. Variation of length of foreperiod is indicated by vertical bars.

The distorted 40 Hz signal has several features to which the cell could be responding. The most likely feature is the periodicity of the fundamental. Although higher harmonics were present as a result of the distortion, frequency multiples of the optimal stimulus were not effective. The vibration sensitive cells were encountered at greater depths than the visual cells. Sensory information from the legs enters via the subesophageal ganglion, suggesting the origin of the input for these cells.

Blest and Collett (1965) found rhythmic discharge patterns in the ventral nerve cord of several species of Lepidoptera. They also found units in the medial protocerebrum whose activities were linked to this pattern. This response was, however, coupled to sudden illumination. The rhythmic cells I found in the vicinity of the medial protocerebrum (20 cells) were typically not modulated by visual or other sensory stimuli. Further research is needed to elucidate the function of these periodic cells.

The movement onset cells described could be used for visual attention. The stimulus described suggests prey movement. The anterior lateral eyes play a role in directing medial eye movements, such as tracking and saccades. It is likely that these neurons play a role in this system.

TABLE C.1 TOTAL ACTIVITIES SAMPLED

Visually responsive units	67
Mappable receptive fields	(53)
Nonresponsive spontaneous neurons*	52
Rhythmic cells	20
Somatosensory cells	7
Airborne vibration cells	4
Multimodal cells	2
Motor activity*	23
Rhythmic pulses* (muscle activity)	60

*These items were not under study. They were encountered so frequently that they were not always noted.

TABLE C.2

Surface = 0

Depth	OFF VEP	ON VEP	ACTIVITY
0	.	.	
100	.	.	
200	.	.	
300	+weak		
400	+weak		
500	+	-	
600	+	-	
700	+	-	
800	-+	+-	
900	-+	+-	Visual neurons
1000	-+	+-	Visual neurons
1100	+	-	Visual neurons
1200	+	-	Giant spikes motor activity

Structure and Function of the Calls of the Night Monkey (Aotus trivirgatus) in Peru and Paraguay

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Abstract--Vocalizations of night monkeys were recorded from 10 groups at two sites in the rain forest of Peru during 18 months of study and two groups at one site in the chaco of Paraguay during an additional four months. Frequency and temporal measurements from spectrograms of recordings revealed that loud calls which could be heard up to 500 meters were of low frequency (250-415 Hz), whereas intragroup calls such as alarm calls, were higher in frequency (1000-3000 Hz). All Aotus calls were of lower frequency than the ambient background of insect and amphibian calls. Loud calls made by night monkeys in Paraguay and Peru do not differ more than loud calls made by neighboring monkeys in either Peru or Paraguay. However, a bimodal distribution of "splatter," or spectral bandwidth, of loud calls in both Peru and Paraguay suggests the possibility that male loud calls may be distinguished from female calls.

Introduction

Aotus, the only nocturnal monkey, ranges from forests in Panama south to Northern Argentina. Most authors have recognized only one species in the genus Aotus: Aotus trivirgatus (Hershkovitz, 1949; Napier and Napier, 1967; Thorington and Vorek, 1976). However, cytogenetic studies have shown that Aotus is comprised of at least nine populations differing in chromosome morphology and number (DeBoer, 1974; Brumback, 1974; Ma *et al.*, 1981). Hershkovitz (1983) has recognized each of these nine different karyotypes as different species. Since acoustic analysis of loud calls of different populations has helped clarify taxonomic relationships within groups of red colobus (Struhsaker, 1970), gibbons (Marshall and Marshall, 1976), black and white colobus (Oates and Trocco, 1983), and pygmy marmosets (Snowdon *et al.*, 1985) examining the loud calls of two disjunct populations of Aotus may help clarify whether there is one or more species.

Because Aotus is nocturnal, loud calls are given in a different acoustic environment than other South American monkey calls. Diurnal monkey calls must compete with a wide range of bird calls as well as calls of other monkey species. But at night it is insect and amphibian noise that produces the most acoustic interference. Loud calls of diurnal monkeys have been studied and it has been determined that low frequency sounds have less attenuation and will carry farther in the rain forest than high frequency sounds (Waser and Waser, 1977; McGeorge, 1978). We examine the structure of the loud call of Aotus and compare frequency modulation and distribution as well as duration of the call in light of the night time environment.

Other monogamous primates such as Indri, Hylobates, Callicebus, and Tarsius spectrum give territorial duets (Pollock, 1986; Marshall and Marshall, 1976; Robinson, 1979; MacKinnon and MacKinnon, 1980). Aotus is strictly monogamous, yet the loud call is given by only one animal in each group. Although it is known that both male and female Aotus can give the loud call hoot in captivity (Moynihan, 1964), it is not known if both sexes give the loud call hoot in the wild, or if male hoots can be distinguished from female hoots. Since loud calls can function either to confirm territoriality or to attract mates, or just as spacing mechanisms, examining the structure of these calls could help to clarify the function.

Materials and Methods

One of us (Patricia C. Wright) examined populations in two sites in undisturbed primary rain forest in southeastern Peru (Cocha Cashu Biological Research Station in the Manu National Park and Quebrado Romero located at 30 miles downstream from Cocha Cashu; both located at 71d 22m W., 11d 52m S.) in and one site in the chaco of Paraguay (La Golondrina Ranch, Villa Hays at 57d W., 24.5d S.) (Fig. 1). The Cocha Cashu populations were studied for one full year (September, 1980 - August, 1981), incorporating all seasons and then studied for three months one year later (October - December, 1982). The calls from Quebrado Romero were studied for one night (October 2, 1982). In Paraguay the population was studied from May - September, 1982 during the winter and spring months.

Although tape recordings were made of four different call types, special attention was paid to the intergroup call termed a "hoot" (Moynihan, 1964). A focal group of Aotus was followed for at least five complete nights (dusk to dawn) each month at Cocha Cashu for a year. Any hoots given by the group were

noted, and tape recorded when possible. Compass readings were taken on hoots from neighboring groups, and number of hoots of those groups noted. Ten additional nights each month censuses were conducted throughout the square kilometer study area in order to locate Aotus hoots. In Paraguay the focal Aotus group was followed for twelve 24 hour periods from July to September and for ten additional nights each month the study area was censused for hoots.

When a monkey began to hoot, calls were recorded on a Sony TCM 5000 cassette deck or an Aiwa TPS-30 cassette deck with a Sennheiser ME-88 directional microphone and power booster or a Sennheiser MD 402 U microphone. When possible, entire hoot sessions were recorded (1-2 hours). Monkeys were followed closely as they hooted and the locations of hoot routes were later mapped. The hoot is often contagious and hoots of other groups were noted and counted and compass readings taken (1-6 groups might hoot in the study area on a given night). Phase of the moon, position of moon in sky, and weather conditions were noted every half hour during hoot sessions.

To determine the extent of individual variation, ten calls of two of the hooters were randomly selected for each night that those individuals called (two nights for one hooter and three nights for the other). Five hoots each were randomly selected from an additional eleven Aotus. Sound spectrograms of these calls were made on a Kay Sona-graph 6061B (85-16,000 Hz), incorporating a Kay 6076C Scale Magnifier to increase frequency resolution. Temporal characteristics of each call were measured from 300 Hz bandwidth spectrograms and frequency characteristics from 45 Hz bandwidth spectrograms.

From each complete call (n = 105) bandwidth was measured for 1) duration, 2) fundamental frequency at the temporal midpoint of the dominant band, 3) range in frequency during each syllable.

Sound spectrograms were also made of intragroup calls. Since these low intensity alarm calls and fighting calls have been described by Moynihan (1964) for Aotus in Panama, and because these calls did not vary much between our study groups, we did not study these calls intensively. However, these vocalizations designated "clicks," "perks," and "resonant whoops" were recorded from several groups, and subsequently analyzed on the Kay 6061B. Insect and amphibian noise was also recorded and analyzed from all three study sites, at various times of year.

Results

Description of repertoire: Aotus have a repertoire of eight discrete calls (Moynihan, 1964; Wright, 1978, 1981), but all of these calls could not be recorded in the wild. The calls can be divided into two classes: 1) calls that can be heard up to 500 meters (the hoot), and 2) calls that can be heard up to 75 meters (the gruff grunts), the sneeze-grunts (clicks), the gulps (perks), and the resonant-grunts (resonant whoops). The former have the potential for long range communication and have all the characteristics of "loud calls" (Marler, 1965) found in other primates to be used for intergroup communication. The calls in the latter group seem to be used to convey to other group members various degrees of alarm, or as in the case of resonant whoops, perhaps to other groups that are within 50 meters and opponents in battle.

1) Calls that carry 500 meters (Loud call)

Behavior accompanying hoots

Hoots were given by one individual in each group and most hooters were separate from the group when they called. Short hoot series of from 1-20 hoots were given throughout the lunar month, but longer hoot series of from

25-500 hoots were given in nights of bright moonlight when the moon was directly overhead. Most hooters traveled from 50-300 meters during a continuous hoot session. The paths of these hooters consistently went in a U shape from the center of a territory to a border, and back. Different borders were often visited at different months. Directed answers to the individual hooter were not heard. Individual hoot consistently in the same territory month after month. An exception to this is a solitary individual which we followed for three kilometers as it hooted 1500 hoots in eight hours. This individual traveled through about ten Aotus territories in a nearly straight line following the river. It is possible that this individual was perhaps trying to find a mate or a vacant territory. There was no answer to its call and no Aotus attacked or joined it during the eight hour journey. An exception to this is a solitary individual which we followed for three kilometers as it hooted 1500 hoots in eight hours (Fig. 2D). Figure 4 shows two recordings made in exactly the same location at Cocha Cashu, but six months apart. Since individual hooters could be distinguished by human ears, we can say with some confidence that this one individual hooted in one Aotus territory from September, 1980, to August, 1981. However, in November and December, 1982, the individual that hooted in this territory (Fig. 2E) differed from the 1980-1981 hooter. Likewise, the gruff hooter from near the lake in 1981 (Fig. 2G) differed from the gruff hooter recorded in the same location in 1982 (Fig. 2I), as did the south hooter for those two years. Since monogamous pairs are stable over a period of years, this yearly change may indicate that subadult group members are hooting. It would be unusual if the subadult was calling only for territorial advertisement, and it seems likely that the subadult would be advertising its sex and trying to attract a mate. Aotus subadults emigrate from the family group at 3 years of age, but information about dispersal and establishing a new territory is unknown.

However, hooting individuals were followed each month and were never observed to pair up or join another Aotus, but, rather, hooted to territorial borders and then returned to the center of the territory.

Description of hoot

A hoot is usually composed of a sequence of from two to eight pulses (syllables), each lasting a mean of 170 ms (Table 1, Fig. 3D). Most hoots have little or no harmonic structure and little frequency variation. Hoot frequencies ranged from 250 Hz to 415 Hz. Each hoot in a series varied little in frequency from other hoots in the series. In 53% of the hoots the second syllable is slightly (25 Hz) higher than the first syllable. In 42% of the hoots, the second syllable is the same frequency as the first syllable, and in the remaining 5% the second syllable is lower in frequency than the first. In 50% of the three note hoots the third syllable is the same frequency as the first syllable, and in 50% of the three note hoots the third syllable is the same frequency as the second syllable.

Intervals between hoots ranged from 250-680 ms. In all but one individual the interval between the first two syllables was smaller than the interval between the second and third syllables (mean difference = 137 ms).

Structural variation

We examined the hoots of several individuals in order to determine 1) if local variation in hoots from neighboring groups was greater or less than the distant variation between night monkey groups in Paraguay and Peru. 2) If hoots were structurally divided into two types, suggesting the possibility that night monkeys can discriminate the sex of the hooter.

Table 1 shows the variation between groups at Cocha Cashu and the hooters from Paraguay. Due to the small number of individuals from Paraguay

(n=2) we were unable to test significance level of differences between the two sets. Figure 2 shows spectrograms of typical hoots of each of the twelve groups of Aotus and it can be seen that the the calls of individual 2A from Paraguay are more similar to many Cocha Cashu calls (2D-L) and the Romero hooter's (2C) than to the calls of the other individual from Paraguay (2B). The A hooter and the B hooter were solitary individuals that shared the same forest together. The authors perceived that they could identify different hooters, even when these hooters called during different months. In light of recent work on species specific specialization in perception of vocalization (Zoloth *et al.*, 1979), this suggests that night monkeys may also distinguish individual hooters, and recognize neighbors using only acoustic cues. Although there is no significant difference between sets of hoots in regards to interval length, frequency, or temporal duration, the hoots do seem to separate into two sets. The hoots in Figure 2 show five hoots (A, C, E, G, I) with a wide band of spectral splatter and seven hoots (B, D, F, H, J, K, L) that are narrow band, relatively pure tones. The former are best described as gruff barks, and the latter are owl-like hoots. It is difficult to sex night monkeys in the field, but it was determined that Hooter A in Paraguay was a male (sexual identification was made at dawn).

2) Calls that carry 75 meters or less

Description of calls

Alarm and/or mob calls

Gulps (perks): This short call lasts about 60 ms and is modulated in both frequency and amplitude. The call begins at approximately 2 KHz, rapidly sweeps up to 2.8 KHz, then descends again. Gulps can be made in rapid succession for periods of up to ten minutes by all members of the group. The call is given in a mildly threatening situation (Fig. 3A).

Sneeze-grunts (clicks): These very short, broadband pulses last less than 50 ms. They have a distribution of spectral energy from 200 Hz to more than 8 KHz. Often sneeze-grunts are given in rapid succession and followed by a low, gruff moan. All group members give the sneeze-grunts (Fig. 3B).

Gulps and sneeze-grunts are often given together in threatening situations. Although in some monkeys there is a graded continuum in threat and alarm calls (Rowell, 1962; Gautier, 1974), or discrete alarm calls designating different classes of predators (Struhsaker, 1967; Seyfarth *et al.*, 1980; Macedonia, in press), Aotus appears to use these discrete alarm or mob calls either together or singly for any mildly threatening situation. Amplitude and intensity increase with the intensity of the stimulus, reminiscent of squirrels (Emmons, 1978).

Battle or threat call

Resonant-grunts (resonant whoops): This call is a continuous series of eight to twenty low pitched, frequency-modulated syllables of moderate amplitude. The spectral energy is concentrated below 200 Hz. The syllables last about 15 ms, and the entire resonant-grunt series lasts from two to five seconds, beginning quietly, but becoming louder as the call progresses. The resonant quality of the call is produced by expanding the gular sac (throat pouch). The call is given by both adult males and females in the midst of, or immediately after a battle with another group of Aotus. I have noted up to fifteen resonant-grunts given in one battle, but the average number is eight per fight, often given by 2-4 animals in alternation (n=15 fights). The winners of the fight usually give the last two resonant-grunts (Fig. 3C).

Structure of ambient night noise

In both Peru and Paraguay the background noise, consisting mainly of calls of amphibians and insects, was recorded at various times during the night. Although there was some variability in the loudness of the insect/amphibian band according to season, hour, and location, the spectral energy of these calls ranged from 3-8 KHz in both Peru and Paraguay under all conditions (Fig. 3A, 3B).

Most calls given by mammals (jaguars, pacas, capybara) were infrequent, but were of low frequency and given in short, explosive pulses. Olingos and kinkajous gave high frequency alarm calls, and bamboo rats gave 20 minute calls nightly (Emmons, 1981). In Peru calls given by owls and other nocturnal birds were given for long intervals, and were easily distinguished from Aotus hoots by temporal patterning and increasing or decreasing frequencies. In Paraguay the great horned owl (Bubo virgineanus) called at low frequencies (200-400 Hz) with 4-5 syllables. During the owl breeding season (June), the pair duetted every ten minutes, but calling decreased after the chicks were born. Aotus calls were distinguished from Bubo call by temporal patterning differences. Bubo gave a series of 4-5 syllables, while Aotus at that site rarely gave more than two syllables.

Discussion

The effective transmission of primate calls over long distances in the forest depends on frequency of the call (Marler, 1955; Waser and Waser, 1977) acoustic interference (Morton, 1975, 1977; Marten *et al.*, 1977; McGeorge, 1978; Schwartz and Wells, 1983), and stereotypy of the call (Waser, 1977) for species recognition. Calls of low frequency are less attenuated in the rain forest than higher frequencies, and can be heard for greater distances (Waser and Waser, 1977). Existing data shows that calls of high volume and low frequency do tend

to be used for intergroup communication by many diurnal monkeys (Gautier, 1974; Chivers, 1976; Marler, 1973; Oates, 1974; Waser, 1977; McGeorge, 1978, Robinson, 1979; Mitani, 1985). During the day a primate loud call is in competition with calls from hundreds of species of birds, other species of primates, and several species of squirrels. Therefore, the diurnal loud calls will be characterized not only by the features that transmit most effectively through the forest, but also by features that serve to distinguish it from competing sounds (Morton, 1975, 1977; McGeorge, 1978). Diurnal monkey calls are often complex, encompassing a wide range of frequencies, harmonic structures, and temporal patterning.

But Aotus transmits its loud calls in a very different acoustic environment than other monkeys. During the night in the forests of South America there are few bird species that call and there are no other species of monkey that consistently call. Alouatta do make predawn roars (Sekulic, 1983), but Aotus rarely call at this time. There are mammals that give night vocalizations (jaguars, capybara, paca) of low frequency, but only on rare occasions (estrus or alarm), and some mammals that give calls of high frequencies (kinkajous and olingos) several times a night, but only the bamboo rat Dactylomys dactylinus gives nightly low frequency calls. These staccato, explosive pulses at 125-1300 Hz often continue for 20 minutes and are given 1-2 times each night (Emmons, 1981).

However, the night in South America is by no means quiet. A din of amphibian and insect noise is nearly constant, becoming louder in the early part of the night and at predawn. This constant noise level occurs from 2.5-8 KHz and is maintained primarily by frogs, toads, and large Orthopterans such as katydids, grasshoppers, and crickets. There are seasonal differences in amplitude, with more species of amphibians calling in the wet season in the rain

forest, and more calls from both amphibians and insects in the hot season of the chaco than during the cold winter months.

The night monkey's loud call is low in frequency (250-415 Hz) as might be predicted in order to carry long distances in the forest, but the hoot is singular in its simplicity and monotony. There are few or no harmonics, and little frequency or amplitude modulation compared to the elaborate calls of most diurnal monkeys. However, the large amplitude of insect and amphibian noise at night would obscure many components of diurnal monkey calls, especially the higher harmonics. The hoot is well below the loud insect and amphibian noise and can easily be distinguished by temporal patterning from the calls of the bamboo rat. It is plausible that with lack of competition at this frequency and time period, hoots have never evolved more complexity, analogous to the case of some island birdsongs, which decrease in complexity when compared with mainland song (Marler, 1960).

But what about intragroup calls that must be heard at close range, but need not carry far in the forest? Alarm and aggressive calls are effective when heard by group members or opponents at close range, but offer no advantage if heard at greater distances. The night monkeys have two low intensity alarm calls which are often given together. Although the "gulps" are of high frequency, they are still beneath the insect/amphibian din, and "sneeze-grunts" cover a broad band of frequencies from 1-8 KHz in each short call. These calls, when taken together, are broad in their scope and guarantee that no matter what the interference or competition, the message will get through to other group members. The threat or triumph call of Aotus given in and immediately after fights with other groups is of lower frequency than the hoots. In this case, low frequency may signify age, experience, and physical size. Older Aotus have larger gular sacs and consequently produce lower frequencies. Sekulic (1983)

found that older, more dominant howler monkeys give calls of lower frequencies. Perhaps the resonant whoop of the night monkey is the audio version of the lion's mane, making the monkey sound larger than he is.

Structural variation of the hoots

The loud calls of monogamous primates might be considered to function in mate attraction (Aldrich-Blake and Chivers, 1973; Tilson, 1981; Tenaza, 1975; Wright, 1984, Mitani, 1985) or in territorial advertisement (Robinson, 1979; Tenaza, 1976; Gittens, 1980; MacKinnon and MacKinnon, 1980; Pollock, 1986). There is evidence in gibbons that loud calls function as reproductive isolation mechanisms among different sympatric species (Brockelman, 1978). Because of their potential as isolating mechanisms, the structure of primate loud calls have been studied to give insight into taxonomic relationships between populations. Marshall and Marshall (1976) distinguished different species of gibbons by examining loud calls. Struhsaker (1970) divided up red colobus species by differences in loud calls and Oates and Trocco (1983) found loud calls useful, but not definitive, in distinguishing different species of black-and-white colobus. Macedonia and Taylor (1985) could distinguish two subspecies of ruffed lemur from their loud calls, and Snowdon *et al.* (1985, 1986) have distinguished populations of new world monkeys.

Since Aotus is currently in a state of flux (Thorington and Vorek, 1976; Ma 1981; Hershkovitz, 1983), we decided to examine the structure of loud calls of two different taxa of Aotus in hopes that our data might clarify the systematics. Since the populations chosen were separated by 2000 km, lived in very different habitats (chaco vs. rain forest), were different karyotypes, and were classified by Hershkovitz as different species (Paraguay population Aotus azarae, male karyotype 2n=51, female karyotype 2n=52; Peruvian popula-

tion Aotus nigriceps, male karyotype 2n=49, female karyotype 2n=50), we predicted that there would be greater variation in hoot structure between populations in Peru and Paraguay than between neighboring individuals. Our results did not verify this prediction. In fact local differences often exceeded differences between individuals in Peru vs. Paraguay. These results are more striking when hoots recorded in Panama at the northern limits of the Aotus range (Moynihan, 1964) are compared with the hoots I recorded from the southernmost populations of Aotus in Paraguay. Although Moynihan's hoots are analyzed with a wider bandwidth than we used, the similarities in frequency, pattern, and structure are readily apparent.

There are two possible explanations for these results. 1) The two populations in Peru and Paraguay belong to one species or, 2) as discussed earlier, the loud call of Aotus is subject to very little competition and variation in acoustic interference and, therefore, is not as subject to selection pressures and has not evolved variations.

There is some evidence that the latter explanation may not be true. Emmons (1981) found that the loud calls of the bamboo rat (Dactylomys dactylinus), which is both monogamous and territorial, were distinctly different in temporal patterning and structure when recorded in Limoncocha, Ecuador, Tzapino, Ecuador, and Cocha Cashu, Peru. Although the frequency of the bamboo rat calls is higher (750-1300 Hz) than Aotus calls (250-415 Hz) there is little competition for either frequency range. Loud call variations between populations have evolved despite this lack of acoustic interference, while loud call variations between populations of night monkeys examined have remained minimal.

Bird songs can vary according to the complexity of the environment (Marler, 1970) and indeed there is some evidence that Aotus calls may vary

slightly in Paraguay where the great horned owl gives calls at similar frequencies. Although our sample size is too small to be conclusive, the number of syllables given per hoot is less in Paraguay than in the Peruvian rain forest where great horned owls are rare or absent. Great horned owls give calls with 4-6 syllables. The variation in temporal patterning allows both animals to use the same frequency band (200-400 Hz).

Although the number of hooters we recorded is too small to make any definitive statement, our results do not support the use of vocalizations as a taxonomic criterion for the division of Aotus into different species. Future work should be done recording hoots from other populations and doing playback of hoots of one karyotype to individuals of another karyotype to determine if an answer is forthcoming.

Sexual differences in hoots

In the territorial duets of Hylobates, Symphalangus, Callicebus, and Tarsius spectrum the call of the female is different from that of the male. In Aotus, males and females do not duet, and it is difficult to differentiate the sex of the hooter in the forest, even in bright moonlight. It was known that both male and female Aotus hoot in captivity (Moynihan, 1964, Wright, 1981), but Moynihan had attributed the different structure of the hoots of two individuals to age differences rather than sex differences, and Wright had only heard a female hoot.

As data were collected from different individuals, two different types of hoots could be differentiated. The hoot that sounded like a gruff bark had a fundamental with a great bandwidth (several hundred Hz). The owl-like pure tone hoot had a very narrow spectral bandwith (less than 45 Hz, the filter bandwidth). In Paraguay the gruff hooter (2A) was positively identified as a

solitary male. Moynihan's Panamanian male and female gave gruff and pure hoots, respectively. Two captive females have also given pure tone hoots. It remains to do playbacks and induce more captive Aotus to hoot to verify if all gruff hooters are male and all pure tone hooters female, or if other factors may explain this difference.

The question that should be resolved is why would a paired male or female Aotus leave its group once a month in the full moonlight and hoot alone on the boundaries of its territory? Since pairs are inseparable at all other times of the month, foraging and traveling within 1-25 meters of one another, this behavior is quite puzzling. From our data it also seems that a male in one territory will hoot month after month, while a female in another territory will hoot every month. Again, the spectrograms were a revelation. The hooters in certain territories at Cocha Cashu in 1982 were different from those noted in 1981, yet the territories and stereotyped routes traveled in those territories had not changed. It is unlikely that the composition of the adult pairs in these territories changed. A reasonable explanation might be that the 2.5-3 year old subadult in each group is the individual that hoots. When it disperses from the family group, the subadult hoots while traveling (like 2D, who traveled more than 3 km in one night, hooting over 1500 times). If the subadult doesn't find a mate, it continues to hoot alone each month until it does attract a mate, or hear one at a distance. Although structure of the hoots recorded so far does give insights into the function of the loud call of Aotus, further work is necessary to clarify the role this vocalization plays.

Summary

1) The structure and behavioral context of four calls of Aotus populations in Peru and Paraguay are described on the basis of studies of wild individuals.

2) Frequency and temporal measurements from spectrograms revealed that loud calls (which could be heard up to 500 meters by humans) were of low frequency (250-415 Hz), while intragroup calls, such as alarm and mobbing calls, were higher in frequency (1000-2800 Hz). All calls of Aotus were of lower frequency than the ambient insect and amphibian noise, thereby avoiding the highest amplitude and most constant acoustic interference in the night.

3) With the exception of the number of notes most commonly used, differences between hoots in Peru and those recorded 2,000 km away in Paraguay fall within the range of variation of adjacent individuals at either site, suggesting strong stabilizing selection. Implications for taxonomy are that the loud call is not acting as a mechanism for reproductive isolation in a karyotypically diverse group.

4) A bimodal distribution of spectral bandwidth of loud calls in both Peru and Paraguay suggests that male loud calls may be distinguished from female loud calls.

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Table 1

Loud Call of *Aotus* (Hoot):

Frequency (Hz), Duration (Ms) and Interpulse Duration (Ms)

INDIVIDUAL	# NOTES	(N=)	NOTE 1 Hz	NOTE 1 Ms	INT A Ms	NOTE 2 Hz	NOTE 2 Ms	INT B Ms	NOTE 3 Hz	NOTE 3 Ms
PARAGUAY										
A										
(Boot 82)	2	(37)	351	168	446	362	142	-	-	-
	c.v.		21.45	33.9	31.4	30.1	11.1	-	-	-
B										
(High 82)	2	(20)	303	176	383	368	172	-	-	-
	c.v.		17.0	35.3	46.2	29.4	38.2	-	-	-
PERU										
C										
(Romero 82)	2	(2)	287	165	500	312	220	-	-	
	3	(2)	307	175	495	325	227	455	320	220
D										
(LONE RANG)	2	(2)	292	190	420	312	220	-	-	
	3	(2)	300	215	315	317	162	553	553	320
E										
(GRUFF 82)	2	(2)	285	120	335	280	135	-	-	
	3	(2)	283	135	270	305	145	340	295	155
F										
(RIV 81)	2	(6)	304	117	498	316	121	-	-	
	3	(5)	306	115	384	324	122	596	304	126
G										
(GRUFF 81)	2	(2)	300	100	530	300	120	-	-	
	3	(2)	293	95	450	293	135	610	300	98
H										
(N-81)	2	(2)	310	155	408	313	145	-	-	
	3	(2)	310	140	330	323	200	483	300	
I										
(NSR-81)	2	(2)	280	115	325	280	107	-	-	
	3	(2)	268	135	265	300	110	360	308	113
J										
(R-82)	2	(2)	293	155	365	293	160	-	-	
	3	(2)	288	185	305	288	175	500	273	188
K										
(SB-82)	2	(4)	285	138	571	328	143	-	-	
	3	(2)	348	160	425	333	123	588	333	125
L										
(SA-82)	2	(0)	-	-	-	-	-	-	-	
	3	(6)	327	87	495	341	102	602	343	93

Fig. 1. Map of South America with the study sites marked by stars. Cocha Coshu Biological Research Station, Manu National park, Madre de Dios, Peru and La Golondrina Ranch, Villa Hayes, Paraguay.

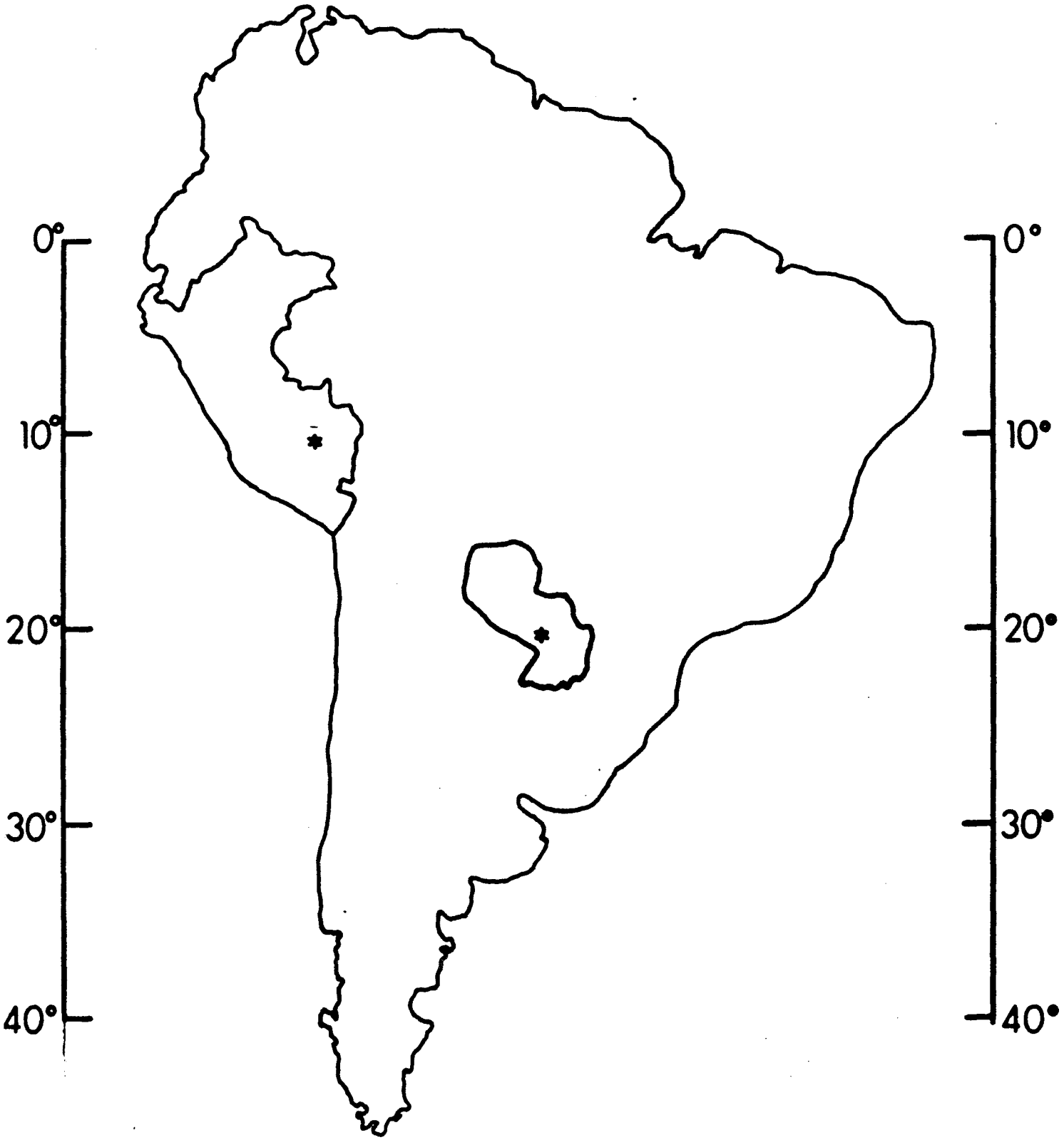

0°
10°
20°
30°
40°
0°
10°
20°
30°
40°

Fig. 2. Long call ("hoot") vocalizations of 12 individuals.

2A, B Aotus individuals in Paraguay; 2C Individual from Quebrado Romero;

2D-L Individuals from Cocha Cashu, Peru.

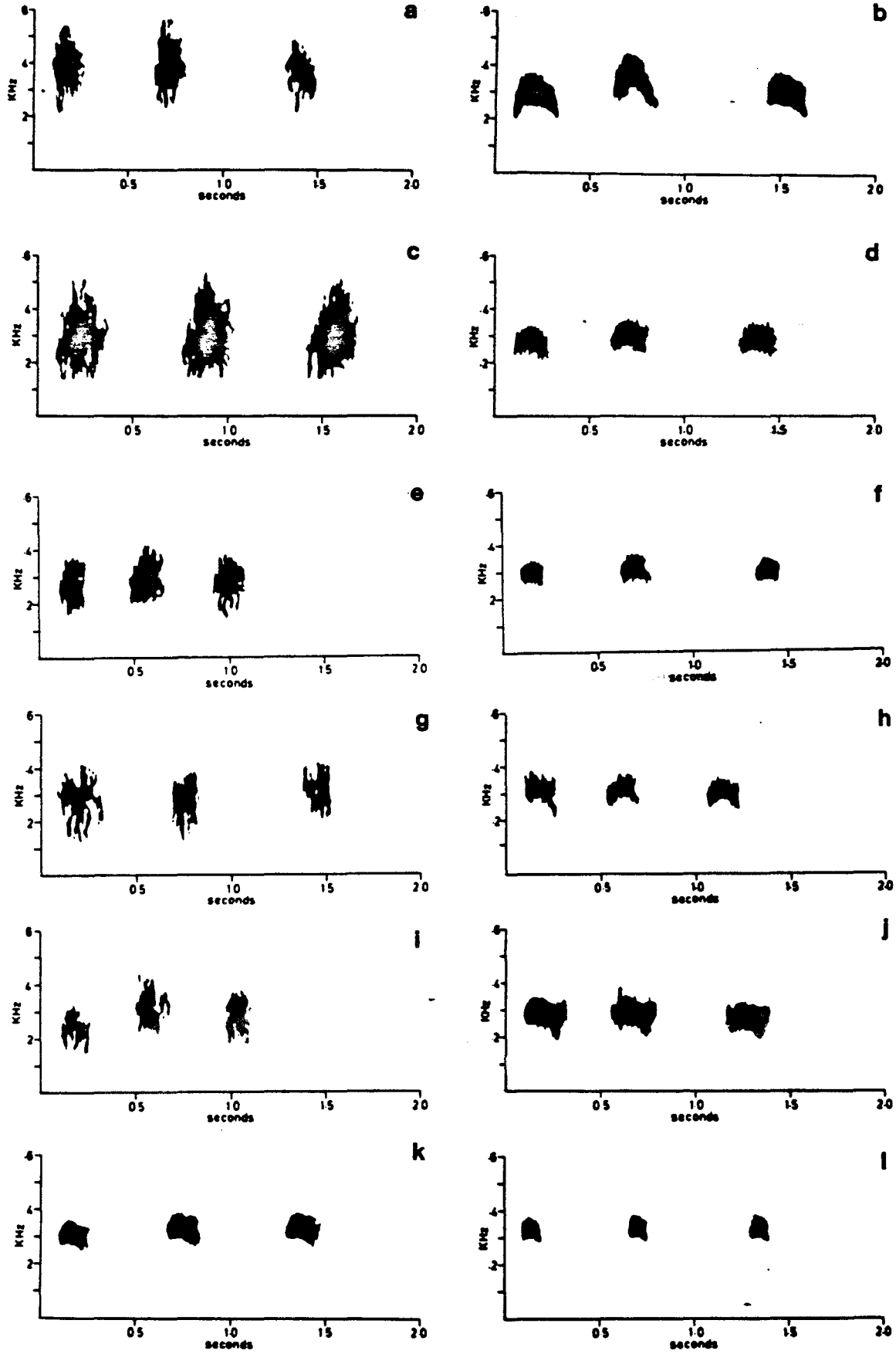
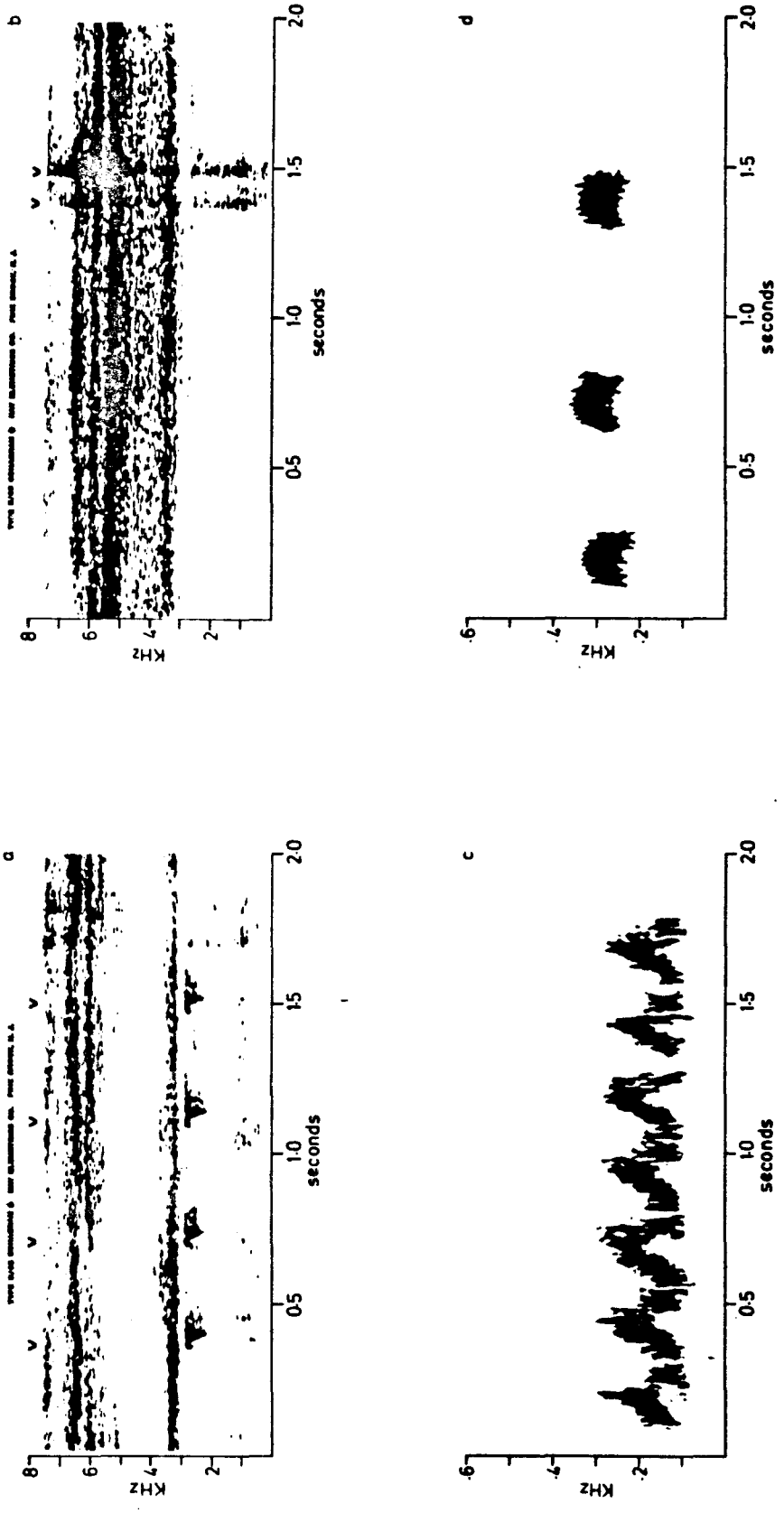

a
b
c
d
e
f
g
h
i
j
k
l
KHz
seconds
0.5
1.0
1.5
2.0

Fig. 3. Sonograms of other Aotus vocalizations. 3A "Perks" shown with the ambient background levels of competing insect sounds. 3B "Clicks", with a broad spectrum energy distribution, are audible over a range of ecological interferences. 3C "Resonant whoop" given during and after territorial border disputes. 3D "Hoot", a repetitive low frequency long call, audible to human observers at 500 m.


a
b
c
d
KHz
seconds
0.5
1.0
1.5
2.0
2
4
6
8
.2
.4
.6