

NERVOUS SYSTEM



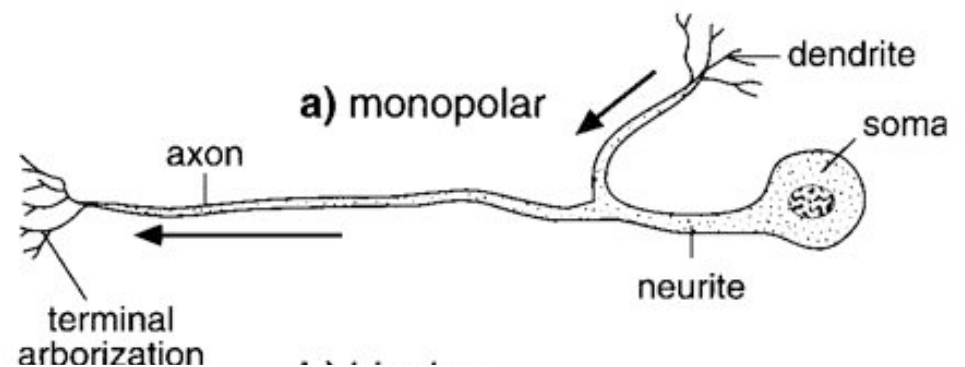
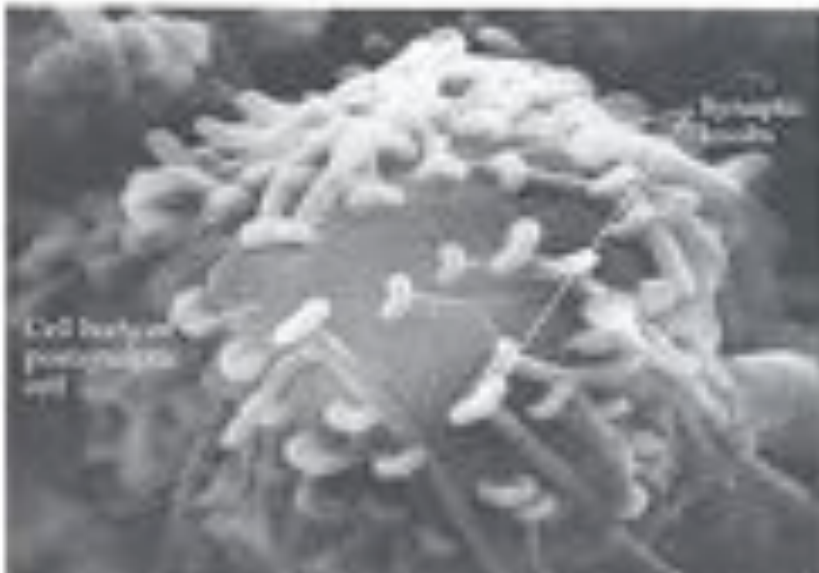
Differences between the human and insect nervous systems

HUMAN

1. Dorsal nervous system
2. Soma or perikarya can have synaptic input on them
3. No monopolar neurons
4. Cell bodies not on periphery of ganglia
5. Have myelinated neurons
6. CNS has about 10^{10} neurons

INSECT

1. Ventral nervous system
2. Soma or perikarya do not have synaptic input on them
3. Most common neuron is
4. Cell bodies on periphery of ganglia
5. Lack classical myelin sheaths
6. CNS has about 10^5 - 10^6 neurons



FUNCTIONS OF THE NERVOUS SYSTEM

- 1. To provide an information processing and conducting system for coordination of events involving most of the other systems that are under nervous control**
- 2. To provide for feedback from various parts of the insect that then can impact the central nervous system**
- 3. To act as the ‘windows’ of the insect by providing sensory input from the various sense organs, sensilla, receptors or better known as the **affectors****
- 4. Provides rapid response and feedback from its peripheral receptors**
- 5. Rapid transfer of information concerning short-term events and also the coordination of these short-term events**
- 6. Transfer of messages to the **effectors** (i.e., muscles and glands)**

Major developments that give us better understanding of the nervous system

1. Microscopic

- a. Light microscopy
- b. TEM, SEM and freeze fracture

2. 'Listening in' to what is going on in the nerve

Electronic recording advances:

- a. Sharp metal and glass-filled electrodes plus suction electrodes for patch clamp technique
- b. Cathode ray oscilloscope
- c. Amplifiers
- d. Recording devices of the action potentials

3. Visualization techniques

- a. Stains
 - (1) Methylene blue
 - (2) Cobalt filling
 - (3) Fluorescent-Lucifer yellow and dextran-rhodamine
 - (4) Immunological stains (fluorescent antibodies)

BASIC COMPONENTS OF THE NERVOUS SYTEM

1. Neuron
2. Glial cells

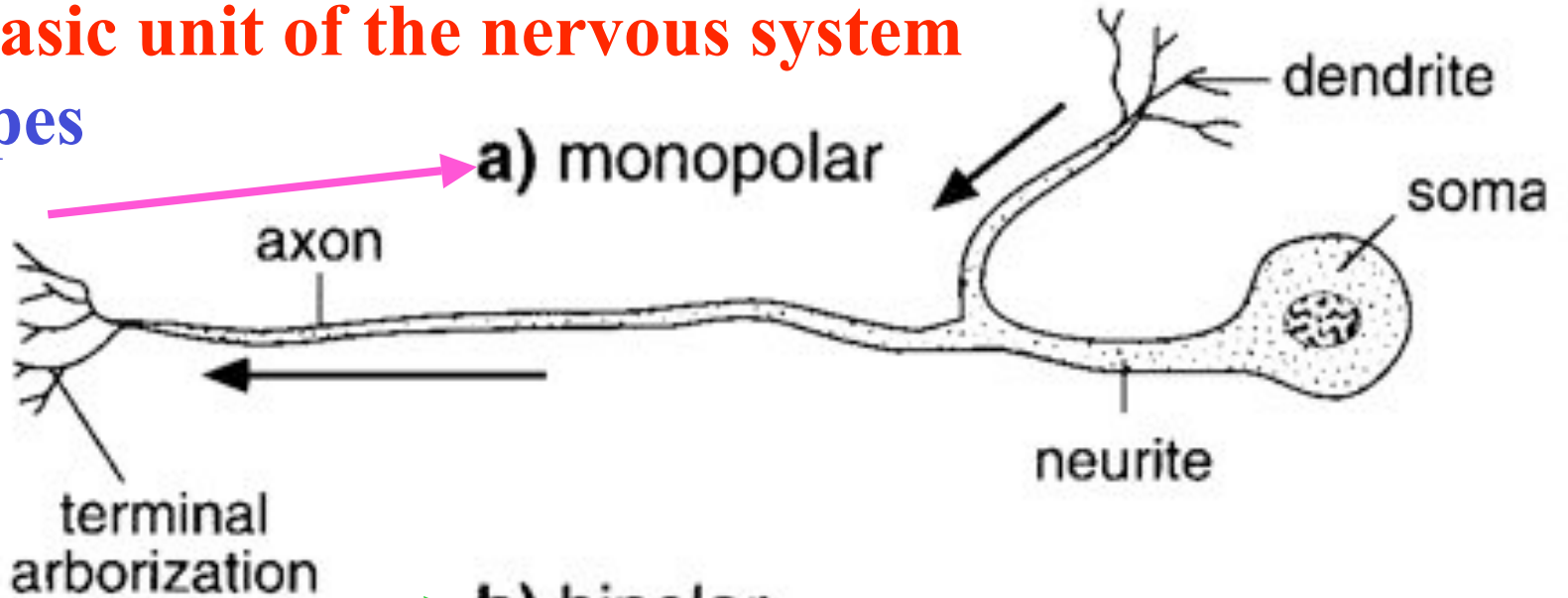
BASIC FUNCTIONS

1. Electrical properties of the neuron
2. Signal transmission
3. Action potential
4. Events at the synapse
5. Electrical synapses
6. Ionic environments of the neurons
7. Chemical messengers of the neurons
 - a. Neurotransmitters
 - b. Neuromodulators
 - c. Neuropeptides
 - d. Neurohormones

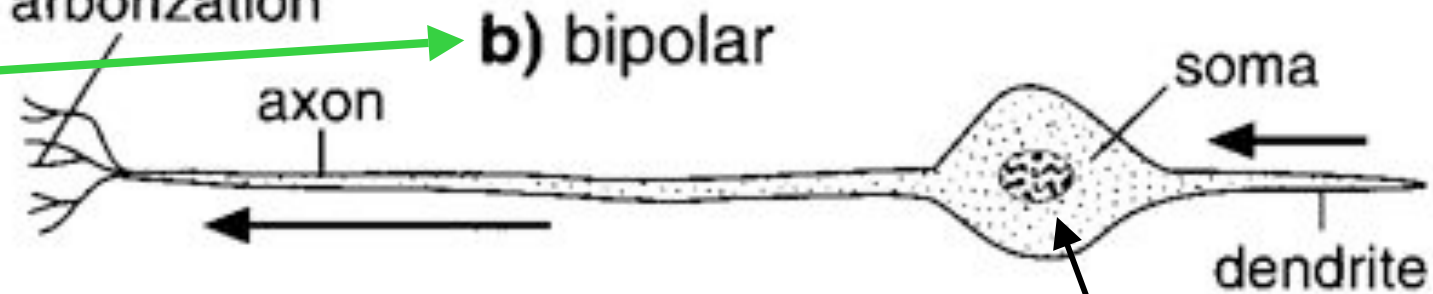
Neuron-Basic unit of the nervous system

3 basic types

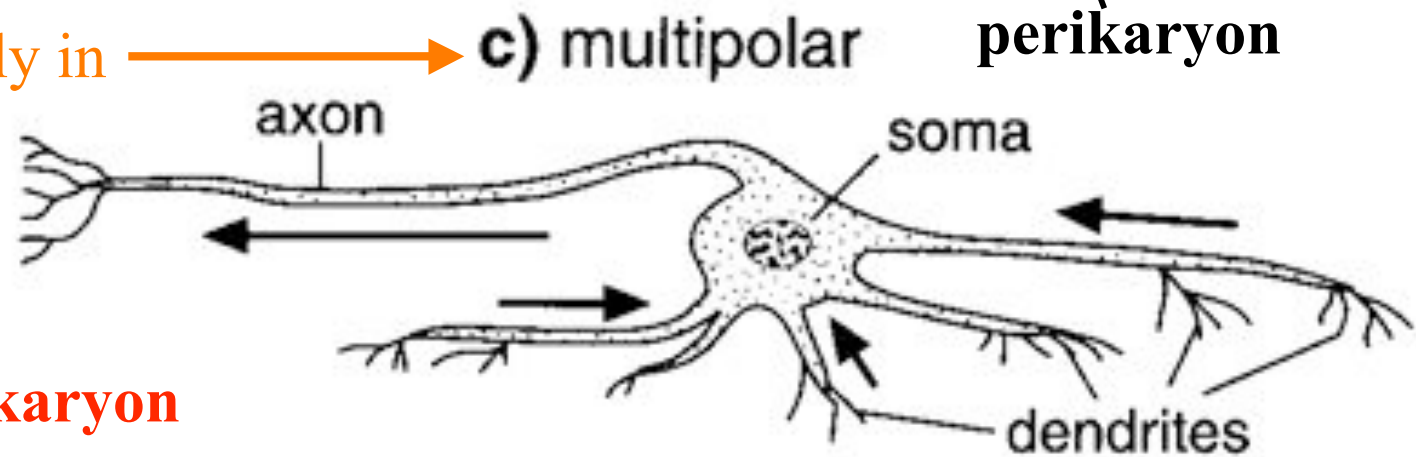
Most common in insects



Peripheral sense cells are bipolar



Occur usually in the ganglia



soma=perikaryon

Classification of the different types of neurons

- I. Relationship to type of input or output
 - A. Sensory or afferent
 - B. Motor or efferent
 - C. Interneuron, association, or internuncial
- II. Type of action on postsynaptic neurons
 - A. Excitatory
 - B. Inhibitory
- III. Chemical taxonomy using immunocytochemical techniques with antibodies developed against various neurotransmitters released by the neuron
 - A. Cholinergic
 - B. Glutaminergic
 - C. Aminergic
 - D. Peptidergic

Cell body or perikaryon=master of the neuron; protein synthesis occurs here

Dendrite=specialized for reception of information

Axon=carries information to other cells

Terminal arborizations=end in synapses

Synaptic cleft or synapse=space between pre and postsynaptic neurons

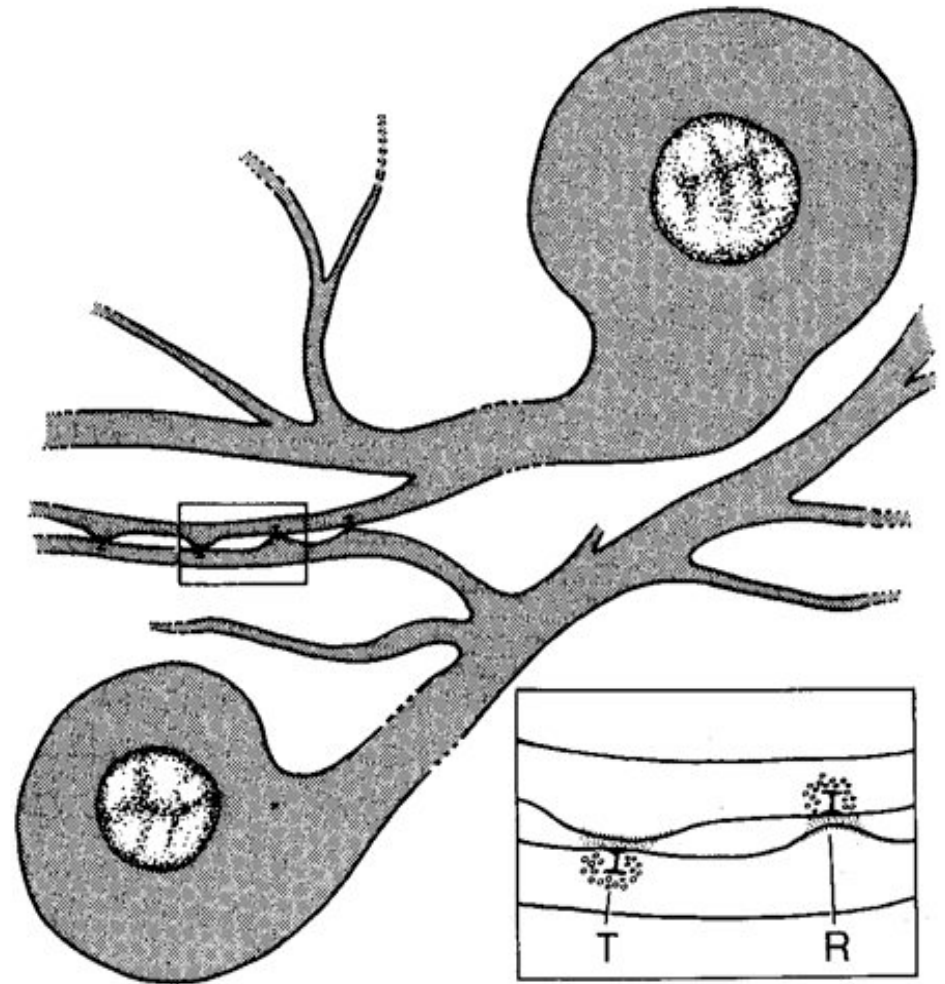
What is a synapse and What kinds are there?

A synapse is a space or region between the presynaptic neuron and the postsynaptic region where the information (either chemical or electrical is exchanged)

Presynaptic neuron=the sending or transmitting neuron

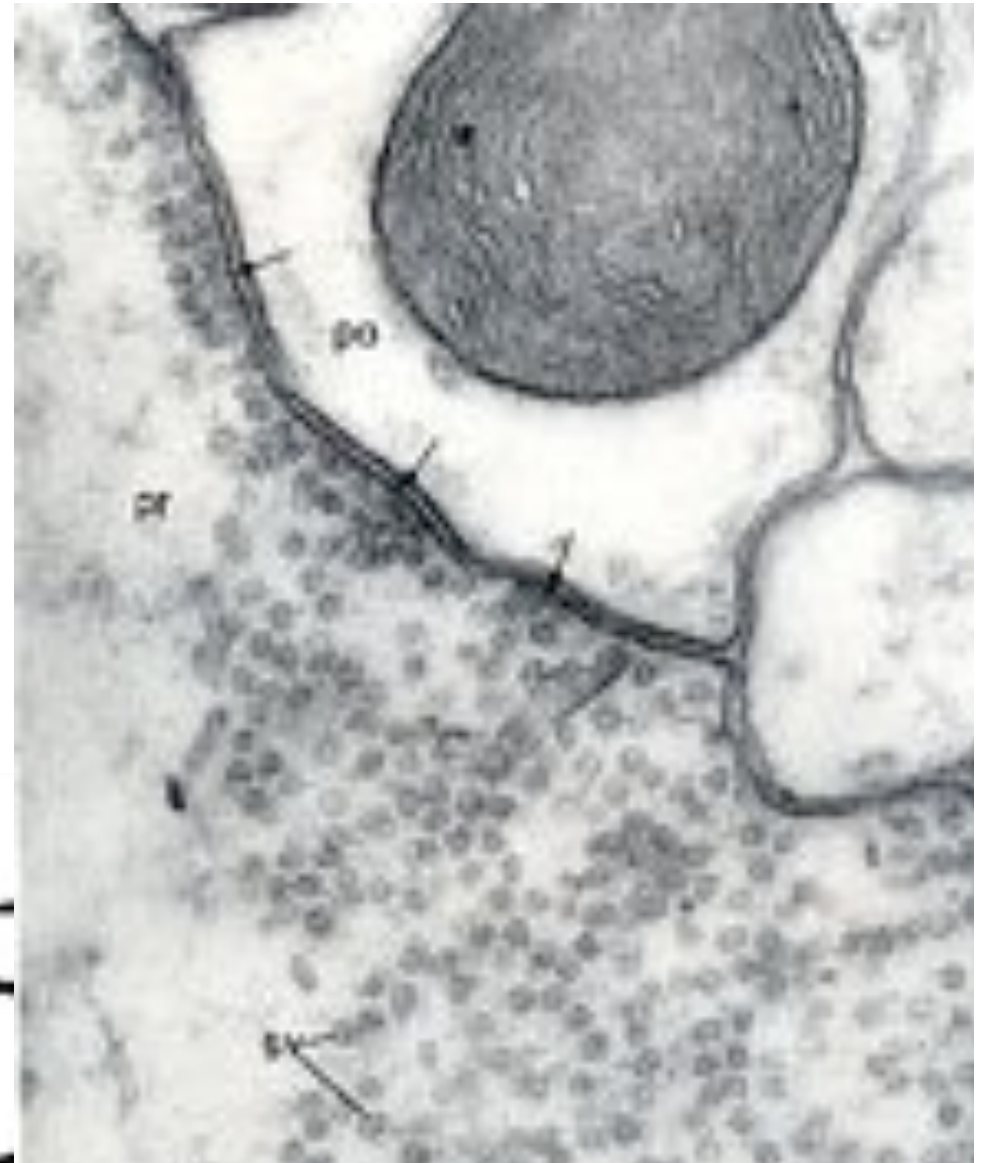
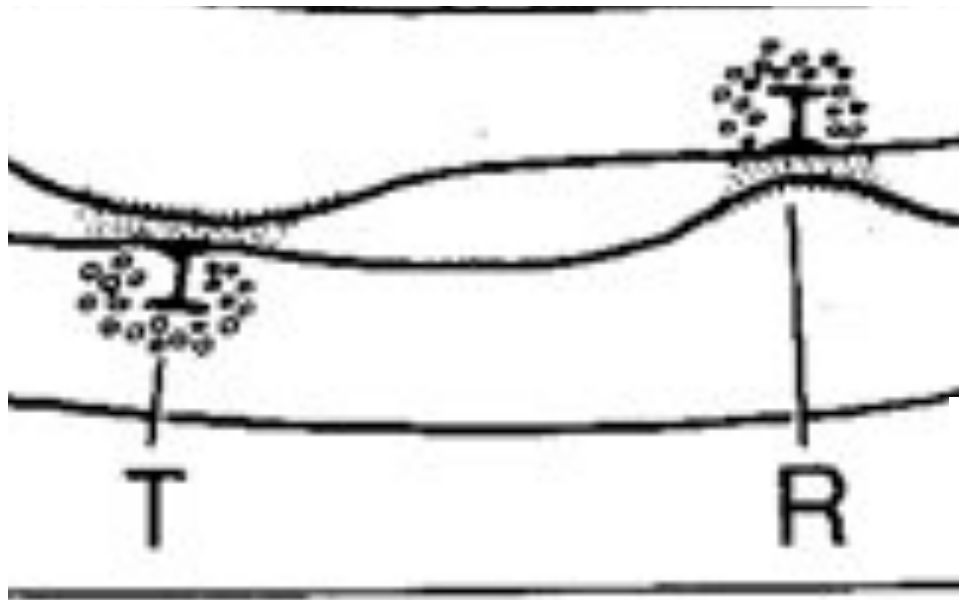
Postsynaptic neuron=the receiving neuron

Note the diagram to the right showing the presynaptic neuron or transmitting neuron (T) and the postsynaptic or receiving (R) neuron. Note what it looks like at the synaptic area or cleft.

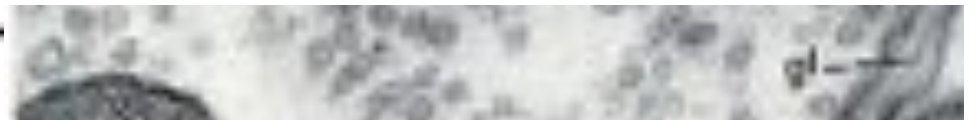


Below is a drawing showing the arrangement of the presynaptic or transmitting cell (T) and what it looks like. To the right is a TEM showing what this looks like for a neuropile region of the cockroach.

Note the synaptic cleft area



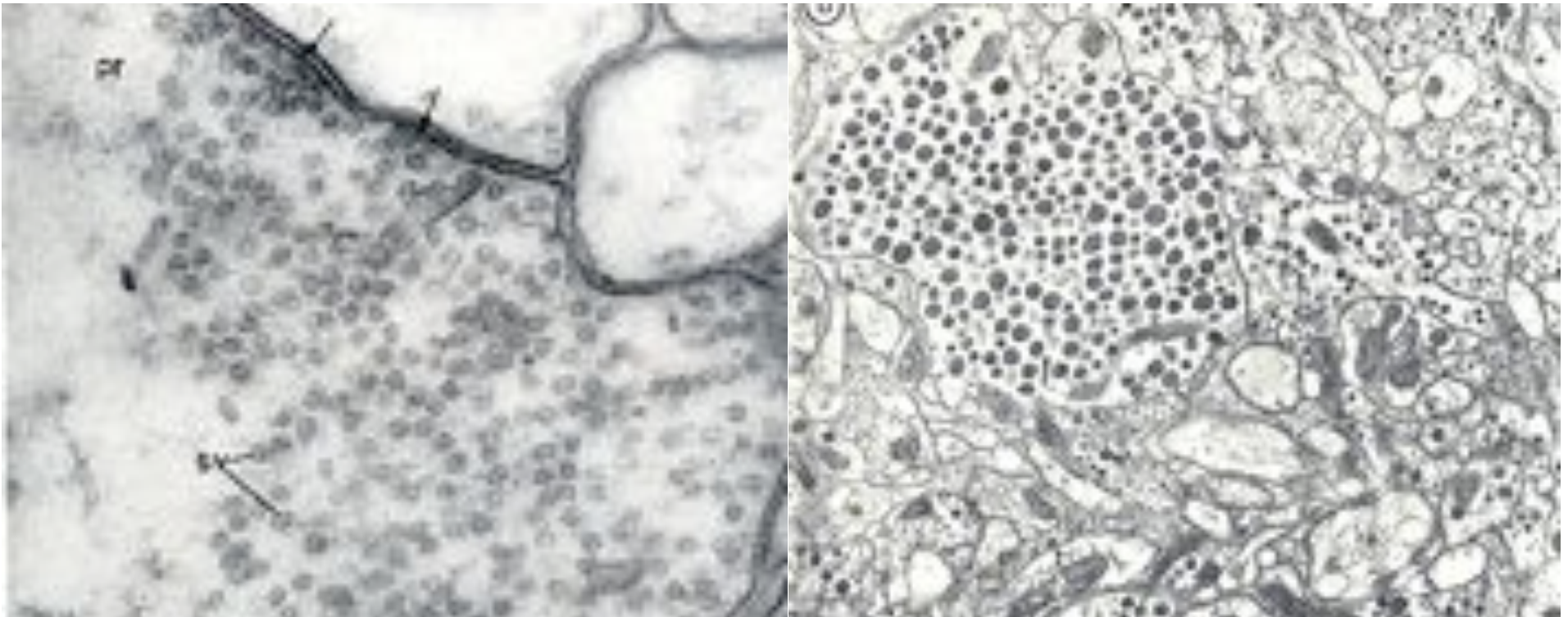
po=postsynaptic neuron; pr=presynaptic neuron; gl=glial cell; sv=synaptic vesicle



The two TEMs below of insect tissue show an important difference between two types of chemical messengers.

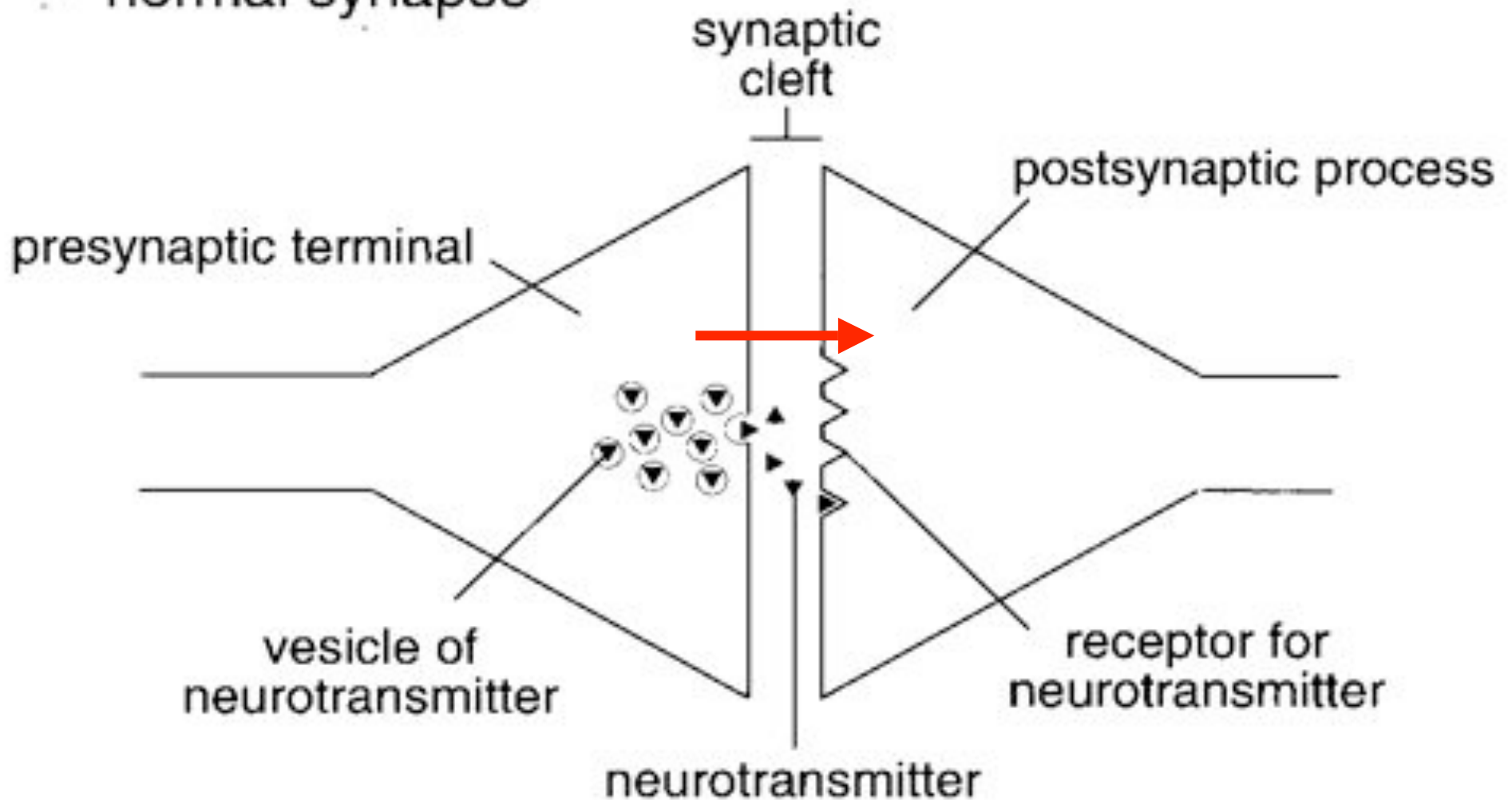
Can you see any differences between the two photos?

The one on the left has electron-lucent vesicles, that are indicative of a **neurotransmitter** while the one on the right has electron-dense material, that is indicative of **neurosecretory** material. Also note in the right photo that an electron-dense material, not due to the vesicles, is evident on the presynaptic side. It appears dense because of the proteins that are involved in the release of the neurotransmitter material from the vesicles.



Events at the synapse-The release of the neurotransmitter occurs when the vesicle moves to the membrane and its membrane unites with that of the neuron and through **exocytosis** is deposited into the synaptic cleft.

normal synapse

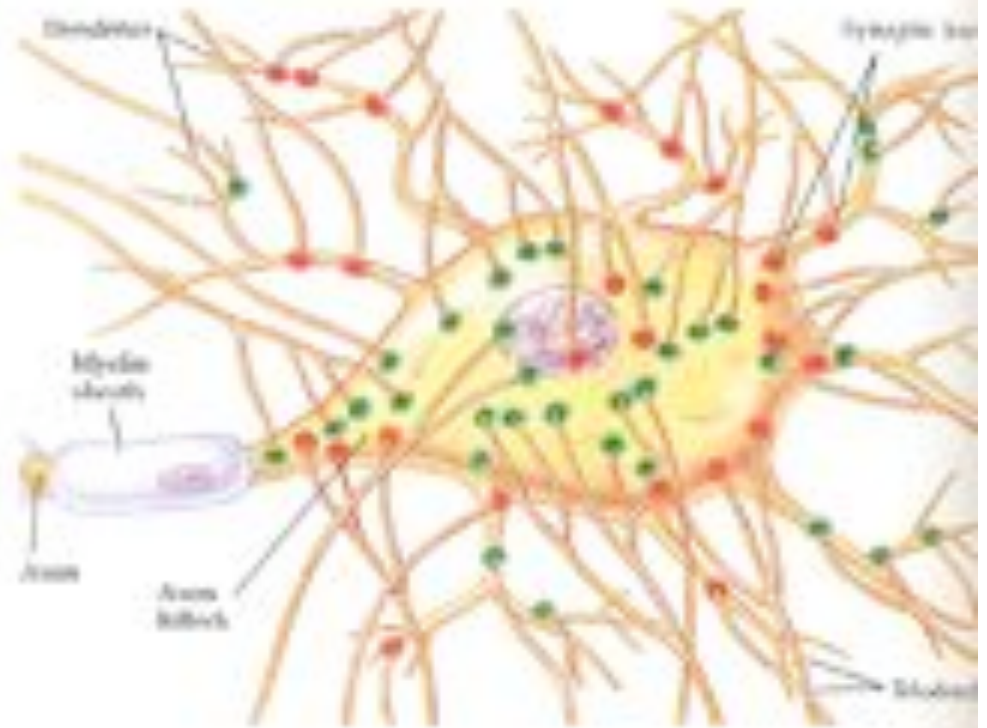


Electrical synapses

Neurons may be in direct electrical contact with another neuron. Thus, the transfer of information from the presynaptic neuron to the postsynaptic neuron is not via a chemical messenger but, involves the **direct exchange of ions** between the two. The gap between the two is only about 3.5 nm. Thus, the two cells are linked via this gap. This type of cell connection is called a **gap junction**.

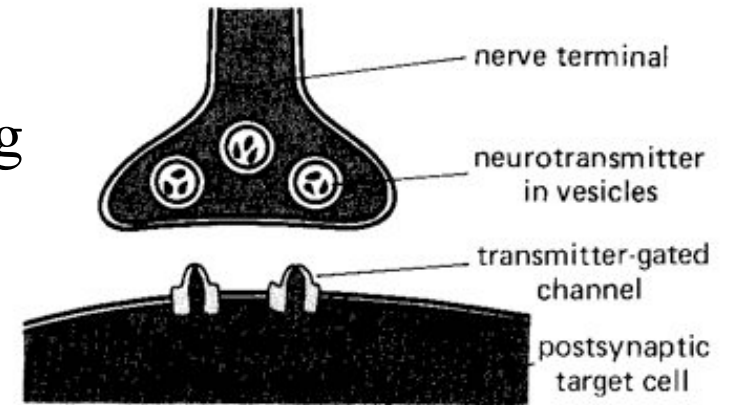
	<u>transmitter vesicles present</u>	<u>size between cells</u>
Chemical synapse	yes	20-25 nm
Electrical synapse	no	3.5 nm

This diagram and SEM are from a vertebrate system since insects do not have synapses on the soma or perikaryon. Regardless, it is an excellent SEM showing how the dendrites that end in synapses can impinge on a postsynaptic neuron. In fact, some of these can produce an **excitatory stimulus** (Green) while others can produce an **inhibitory stimulus** (Red).



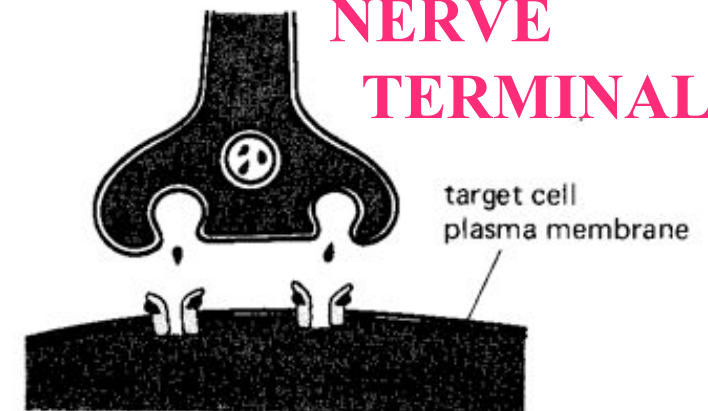
Transmitter-gated ion channels-

1. Each channel has a high selective binding site for its particular neurotransmitter
2. Unlike voltage gated ion channels responsible for action potentials, these ion channels are relatively insensitive to surrounding membrane potential changes

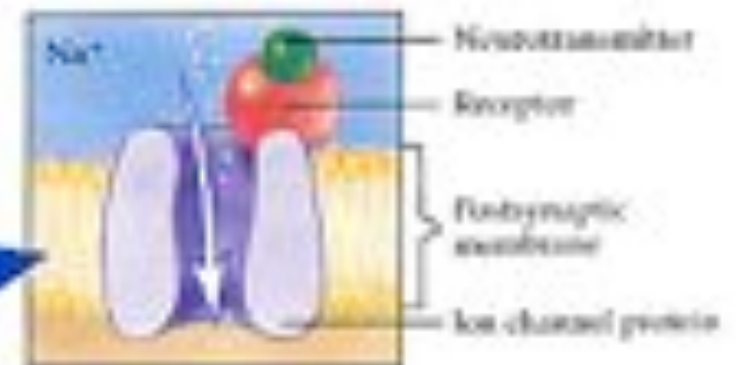
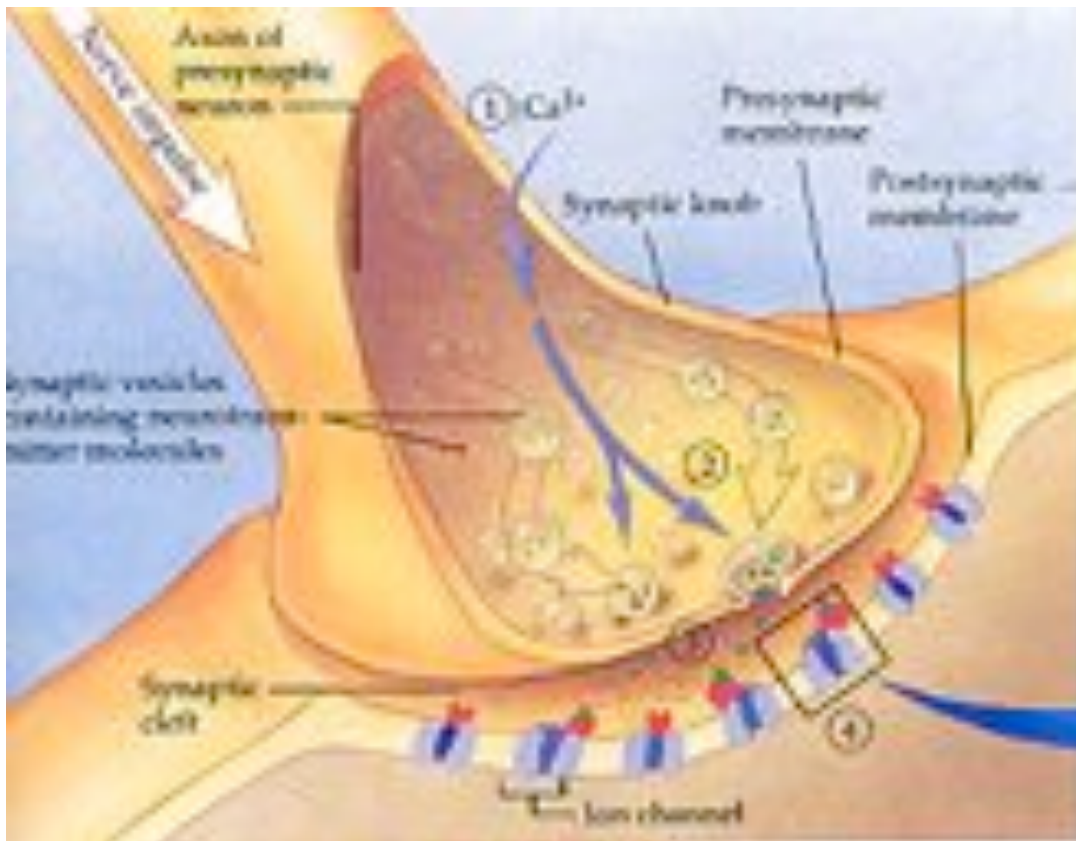


RESTING CHEMICAL SYNAPSE

EXOCYTOSIS AT NERVE TERMINAL



ACTIVE CHEMICAL SYNAPSE



Glial cells

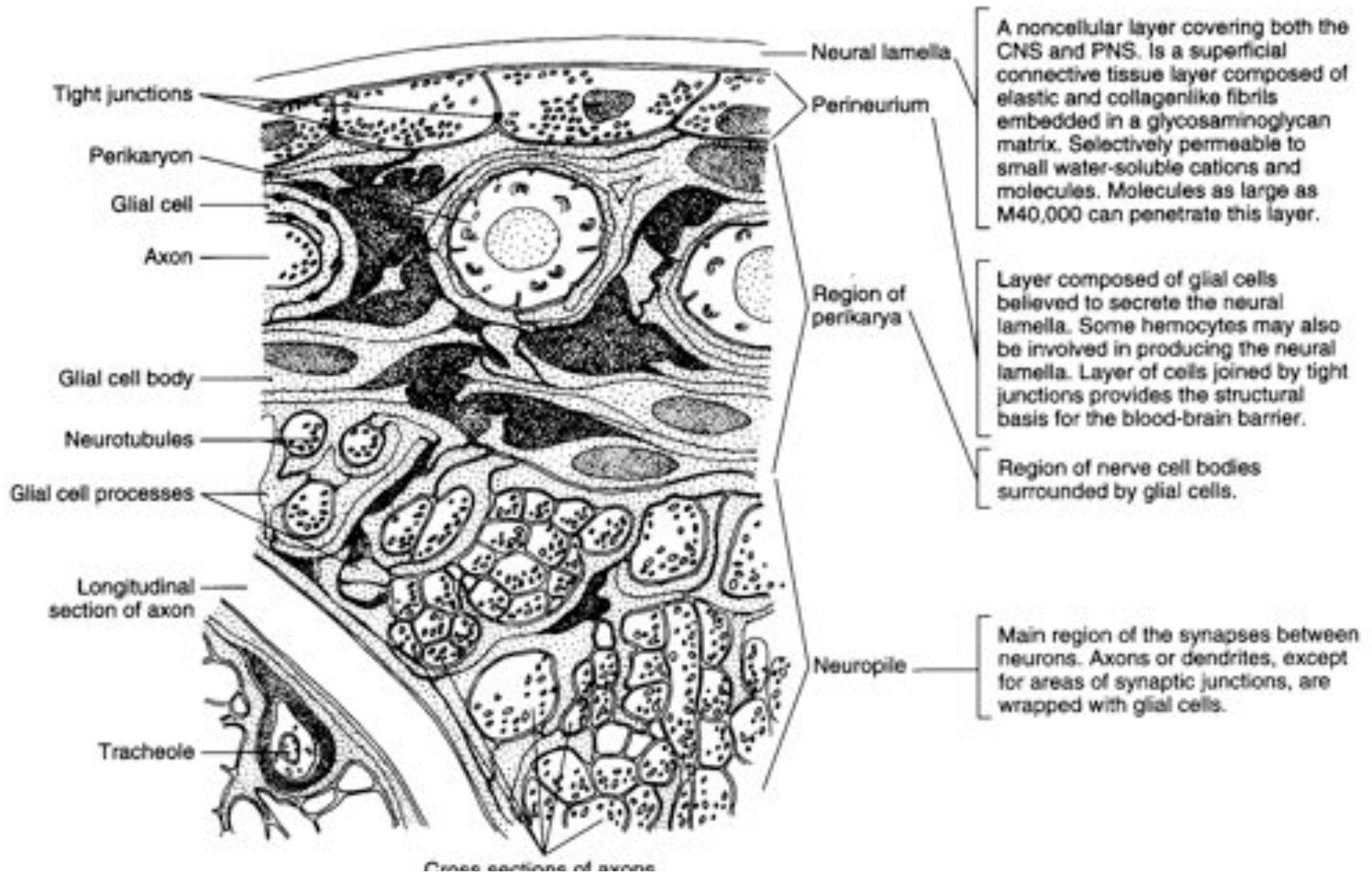
Special cells that encircle or wrap around the neuron, **except** at the area of a synapse. These cells may wrap around a neuron several times, which are called glial windings.

Functions of the glial cells:

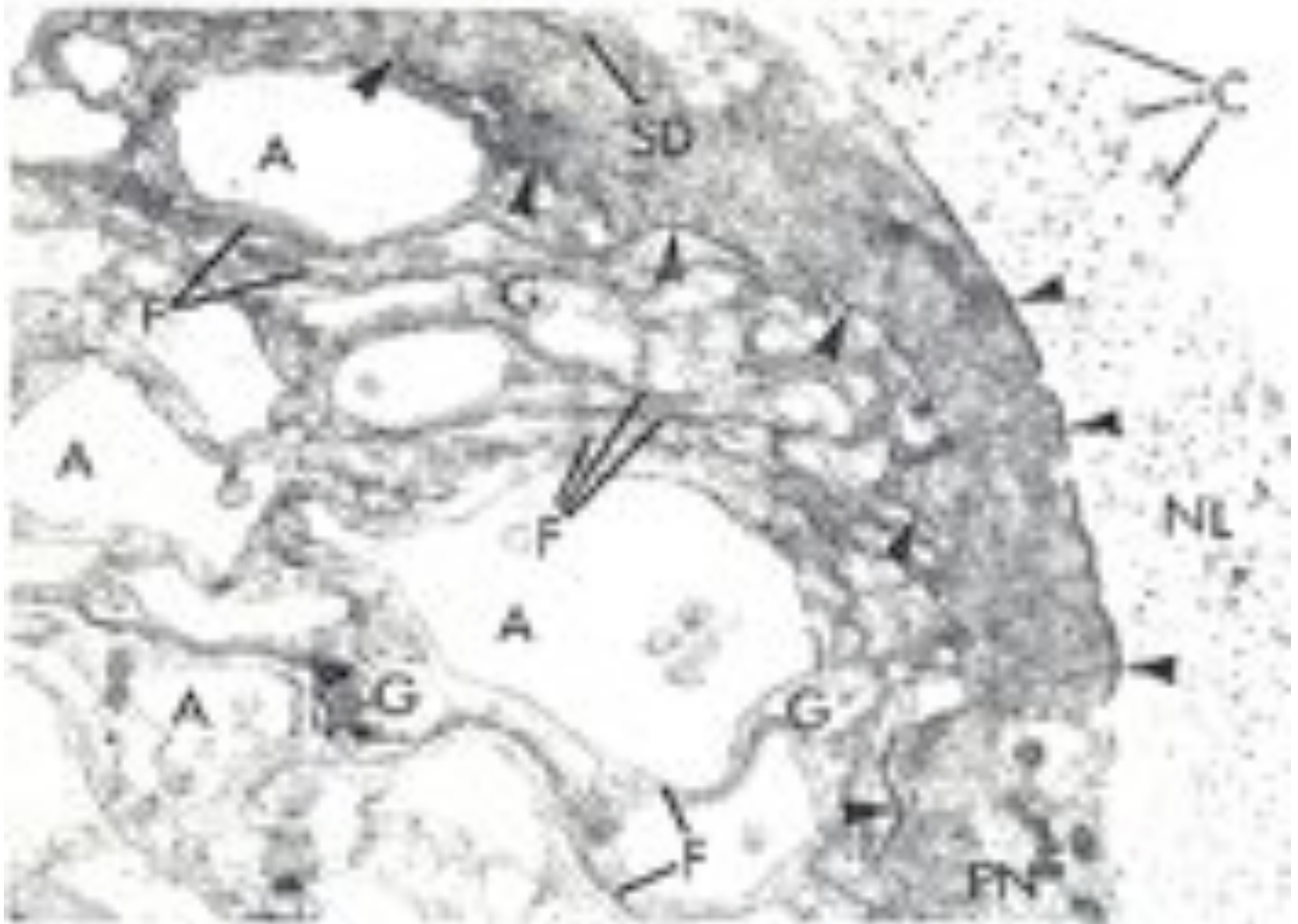
- a. Bathe the neurons and influences its electrical properties
- b. Pass nutrients to neurons
- c. A special group of glial cells known as the perineurium. They are involved in keeping the ionic environment nearly constant, separating the blood from the neurons.

These cells are linked together by tight gap junctions, thus forming the **blood-brain barrier** and permitting only certain substances to enter from the hemolymph. Cells of the perineurium secrete the thick basal lamina known as the neural lamella.

Cross-section of cockroach ganglion



A=axons; G=glial wrappings and cells; NL=neural lamella;
PN=perineurium. From abdominal nerve cord of stick insect.

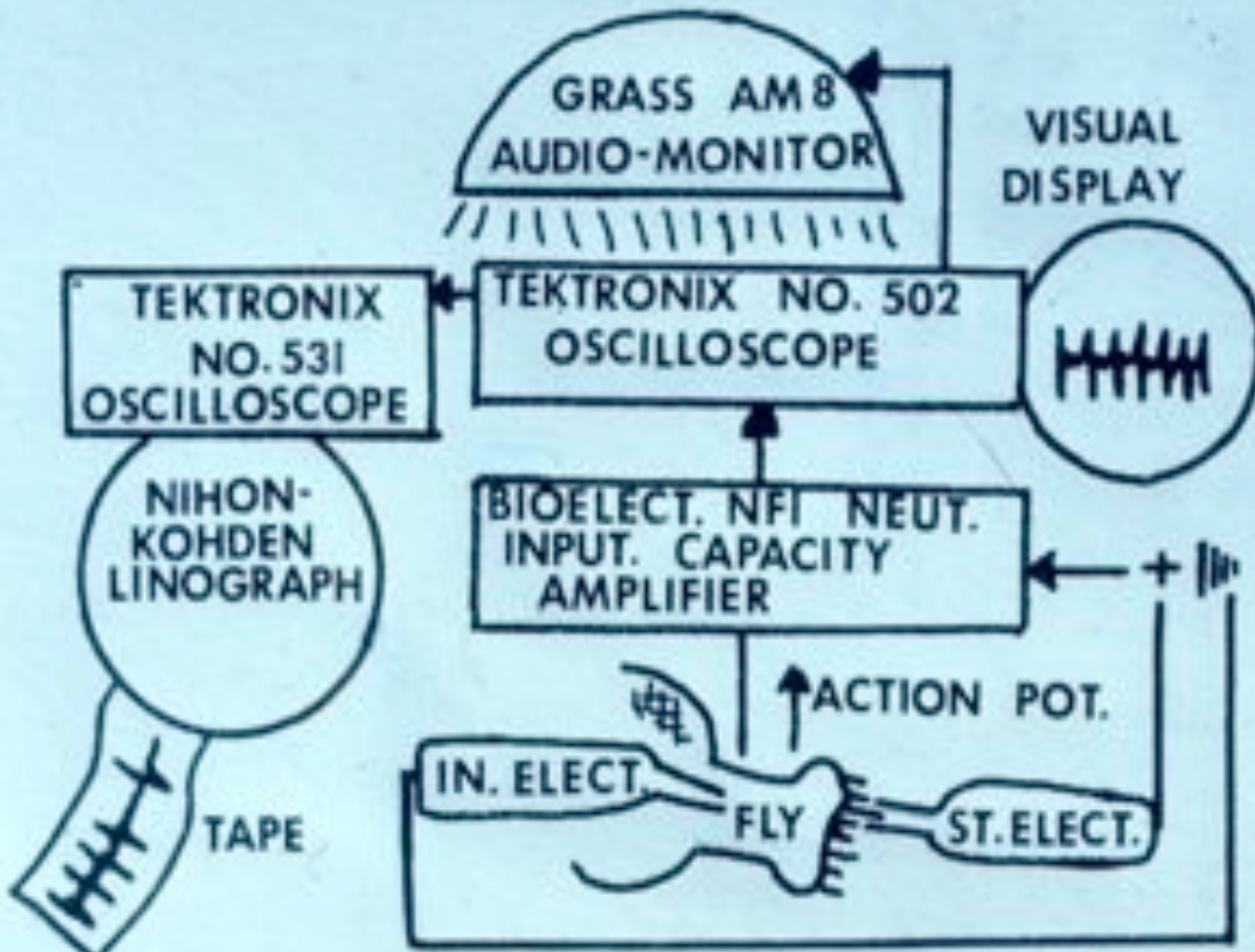


Different ways of recording action potentials:

1. Along a neuron
2. At the tip of a chemoreceptor (over the hair)
3. Using patch clamp for ion channels
4. Electrode insertion into muscle
5. Olfactory insect receptors

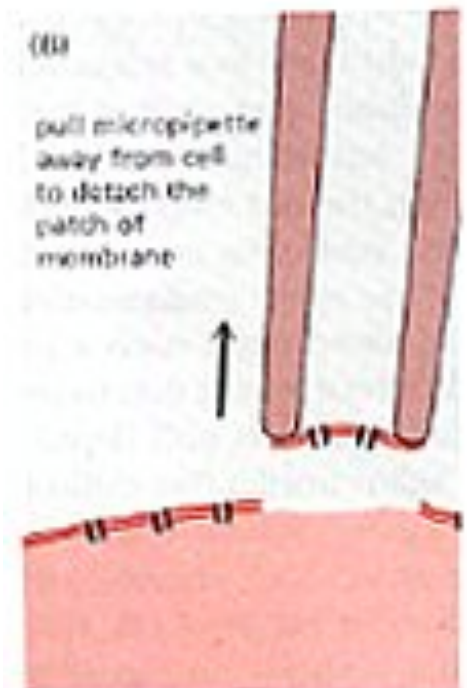
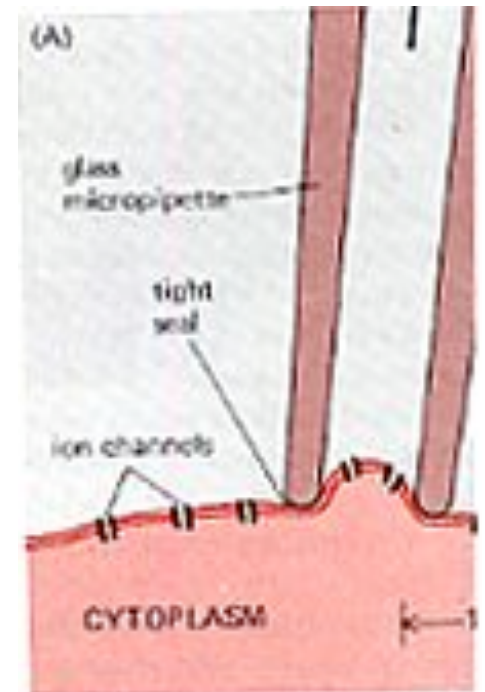


ELECTROPHYSIOLOGY SET-UP



Over the hair recording from a labellar chemosensillum

Patch clamp technique-This technique was extremely important for neurobiologists to better understand what was really taking place at the membrane of the neurons. The presence of ion channels needed to be studied experimentally and this technique provided the technology. Using a suction electrode (glass micropipette in top right) to suck onto a piece of membrane, which by gentle pulling breaks away but, remains on the end of the pipette. This isolates some channels, shown here as two black channels. Now, by changing the concentration of ions outside or inside one could study the effect of various chemicals, such as a suspected neurotransmitter, on these ion gated channels. Also, it permits individuals to study the effects of pesticides, transmitters, and other compounds that might open or close the gates.



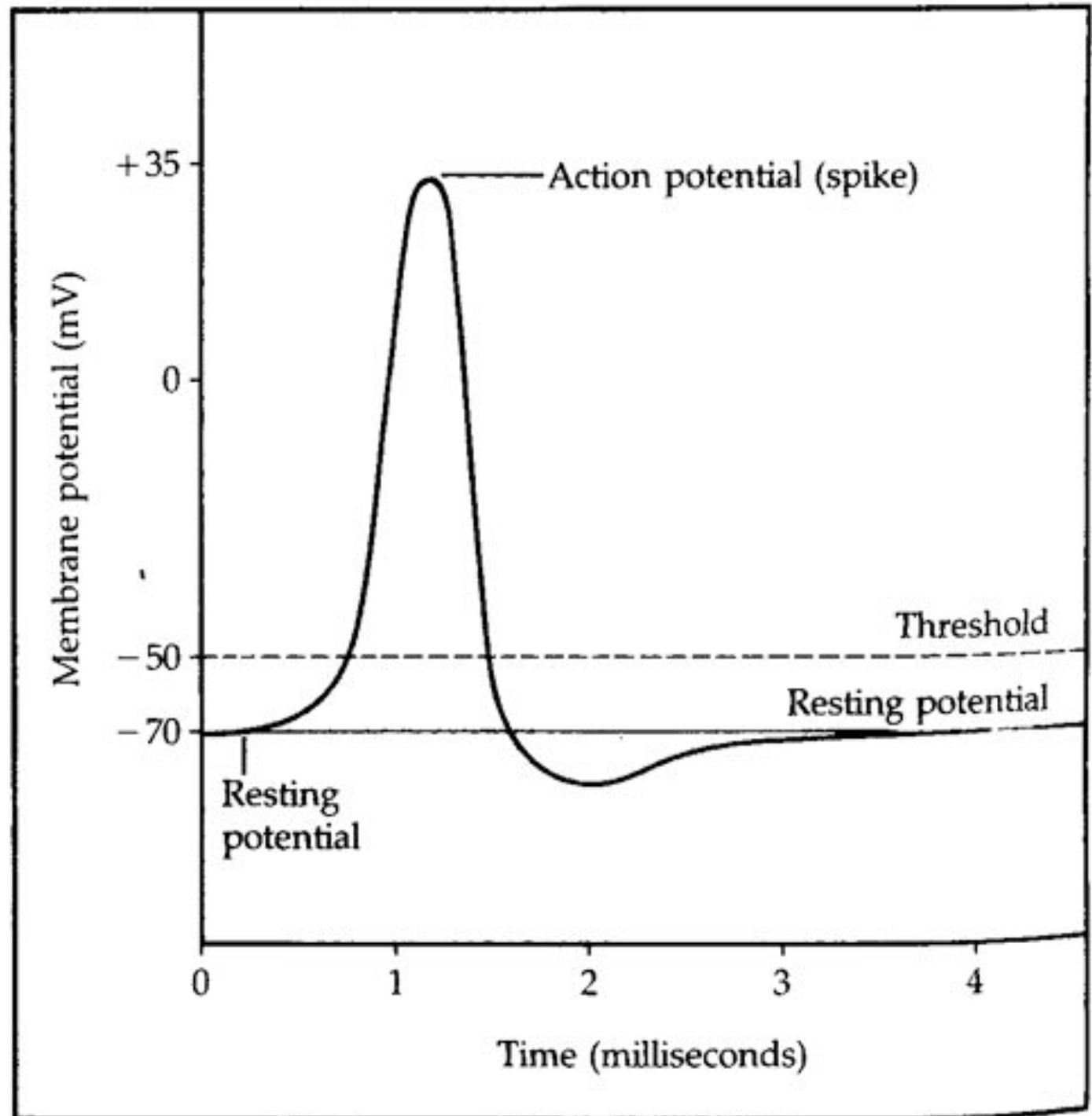
Different kinds of thresholds:

1. Electrophysiological

- a. Neuronal
- b. Receptor

2. Behavioral

- a. Recognition
- b. Acceptance
- c. Rejection

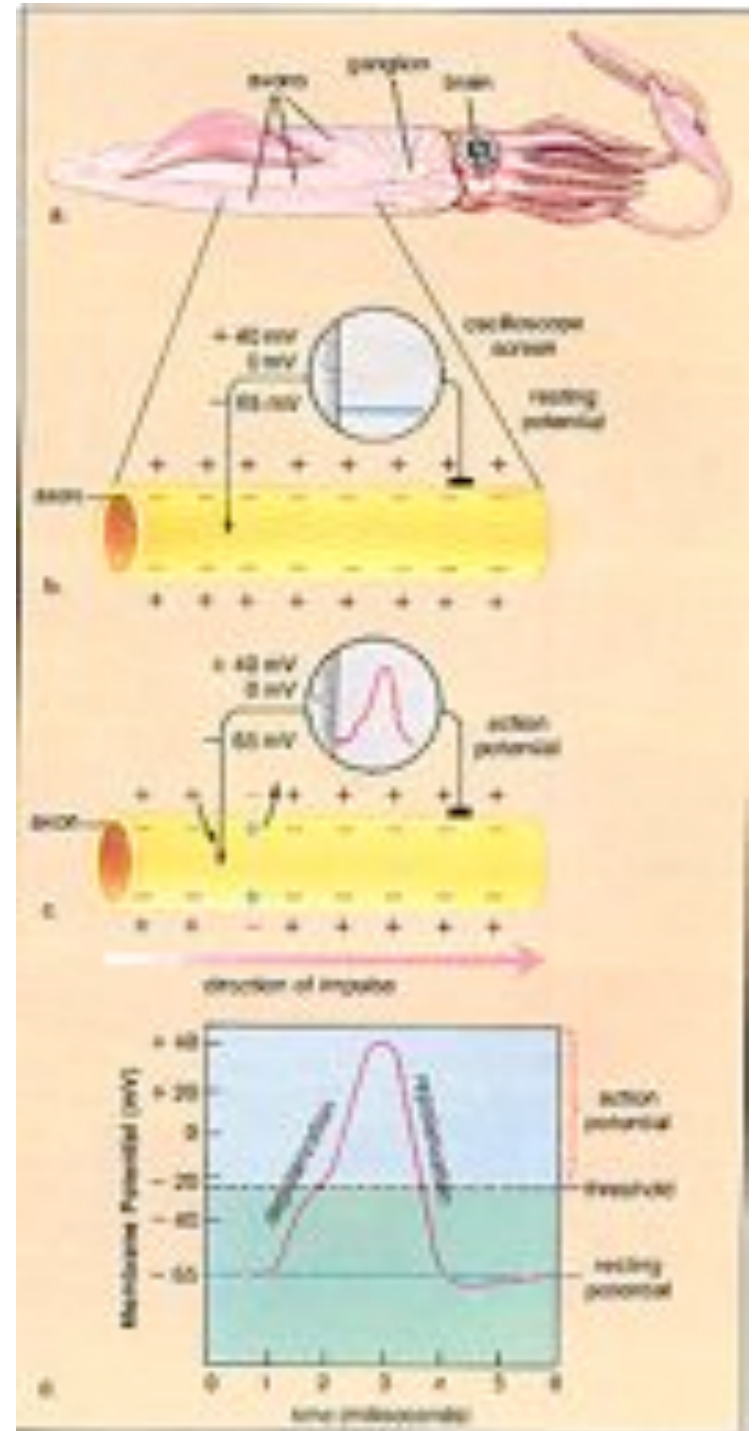


The original nerve impulse studies were done using the giant axon of the squid and a voltage recording instrument known as an oscilloscope.

Note at the resting potential, the outside of the nerve is positive in relation to the inside which is negative.

If the threshold of that nerve is reached, the sodium gate on the outside opens and lets sodium in. This depolarizes the axon causing the outside to now become negative while the inside is positive.

Recovery occurs when the sodium gates close and the potassium gates open. This allows K to leave, thus restoring the membrane potential.





- 1. Chemical messengers of the neurons**
 - a. acetylcholine**
 - b. biogenic amines**
 - Octopamine**
 - Dopamine**
 - Serotonin (5-hydroxytryptamine)**
 - c. amino acids**
 - alpha amino butyric acid (inhibitory)**
 - glutamate (excitatory for muscles)**
 - d. peptides**
 - dromysuppressin**
- 2. Chemical messengers can act as:**
 - a. Neurotransmitters**
 - b. Neuromodulators**
 - c. Neurohormones**

Neurotransmitter-a chemical that is released from the synaptic knobs into the synaptic cleft, binds to a receptor and stimulates the postsynaptic cell. In TEM they are electron lucent vesicles.

Neuromodulator-chemicals that can modulate or change the type of response that may occur as a result of a stimulus. They can act on the pre- or postsynaptic cells and do so by altering the ionic permeability of the membranes.

Neurohormones-The cells producing neurohormones are called neurosecretory cells. They are found in various ganglia of the central nervous. In TEM they are electron dense vesicles.

Table 20.2. *Substances secreted by neurons in the central nervous system and their principal functions*

Chemical	Neurotransmitter	Neuromodulator	Neurohormone
<i>Acetylcholine</i>	+++ (excitatory in CNS)		
<i>Biogenic amines</i>			
Dopamine	+	+	
Histamine	+		
Serotonin (5-hydroxytryptamine)		++	+
Octopamine	+	+++	+
<i>Amino acids</i>			
γ -aminobutyric acid (GABA)	+++ (inhibitory)		
Glutamate	+++ (excitatory at muscles)		
<i>Peptides</i>			
Adipokinetic hormone			+++
Allatotropin		+	+
Allatostatin		+	+
Cardioactive peptide			+++
Diuretic peptide			+++
FMRamide		+	
Leucokinin		+	
Pheromone biosynthesis (PBAN)		+	++
Proctolin	+	+++	+
Prothoracicotropic hormone			+++

INSECT NERVOUS SYSTEM

A. Central nervous system (CNS)

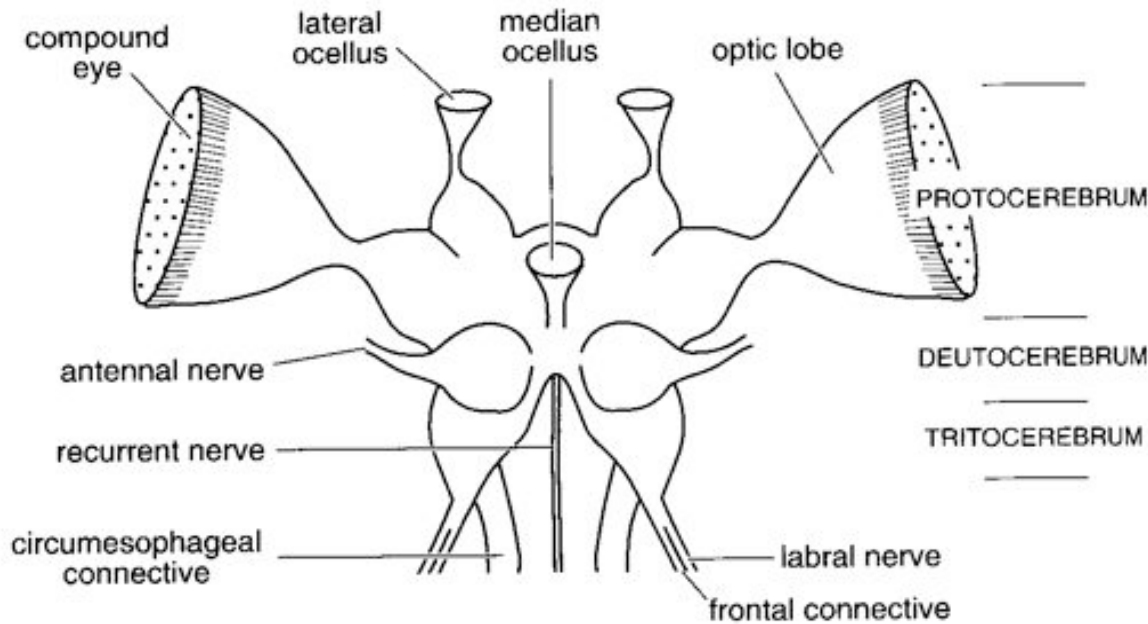
1. Brain-supraesophageal ganglion. Is the result of the fusion of ganglion 1 in early ancestors
 - a. Protocerebrum
 - b. Deutocerebrum
 - c. Tritocerebrum
2. Ventral nerve cord and segmental ganglia
 - a. Subesophageal ganglion. Is the result of the fusion of ganglia 2,3 and 4 in early ancestors

B. Stomatogastric, stomodaeal or visceral nervous system (VNS)

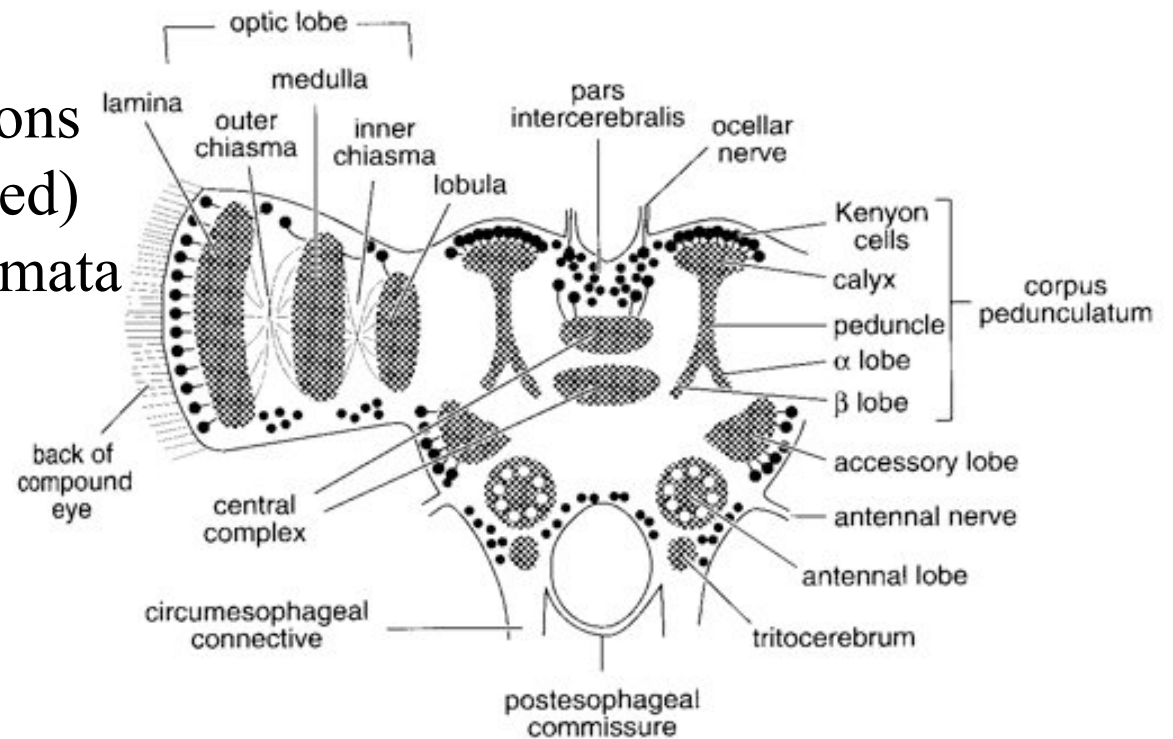
1. Frontal ganglion
2. Recurrent nerve and NCCI and NCCII
3. Hypocerebral ganglion complex

C. Peripheral nervous system (PNS)

1. Receptor-cell or part of a cell that converts stimuli into nerve impulses
example=chemoreceptor, mechanoreceptor
2. Sensillum (sensilla, pl)-a simple sense organ composed of a few neurons
example=chemosensillum
3. Sense organs-grouping of several kinds of cells or tissues built around a group of receptor cells of a specialized type. Example=eye, antenna

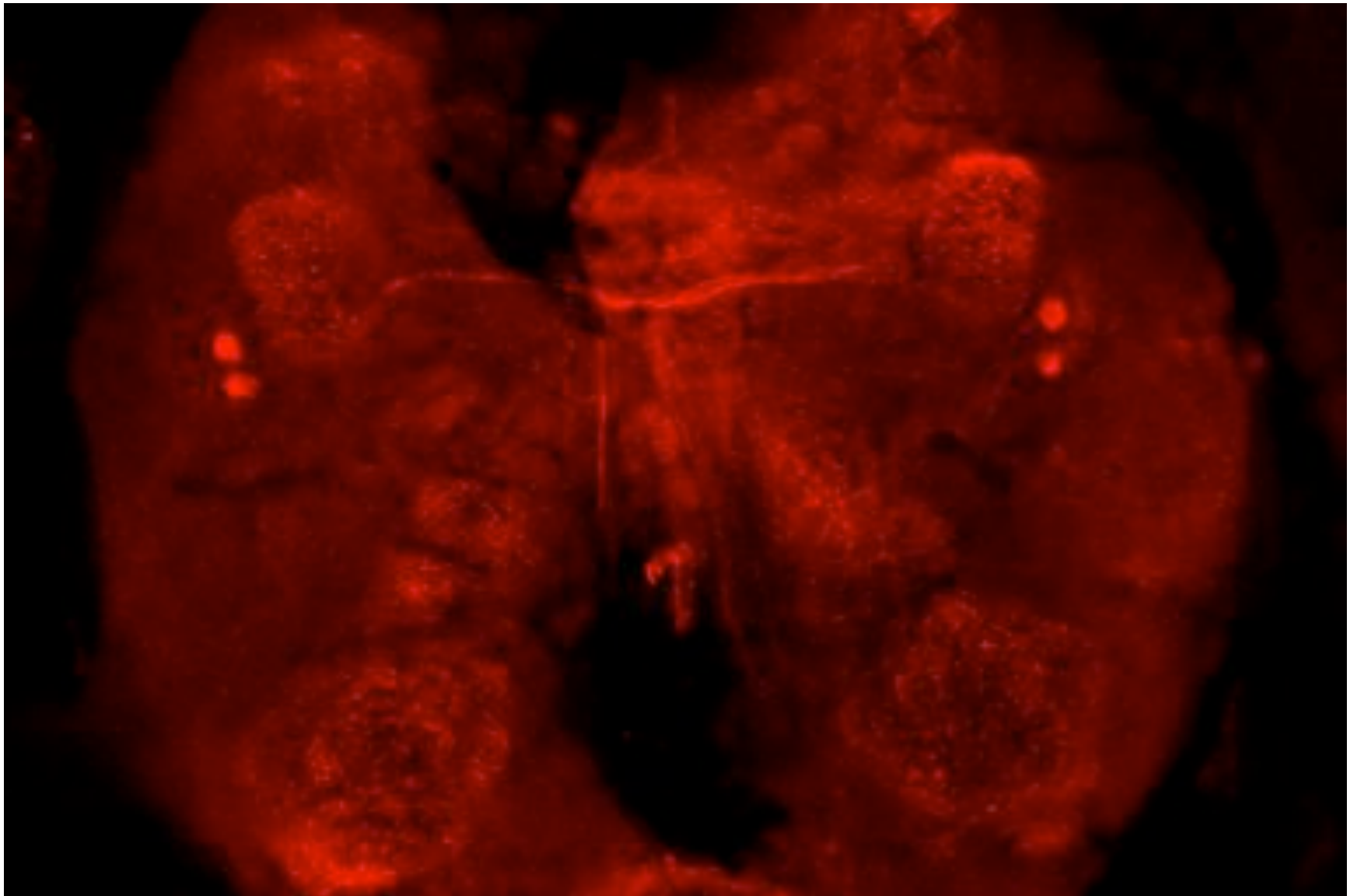


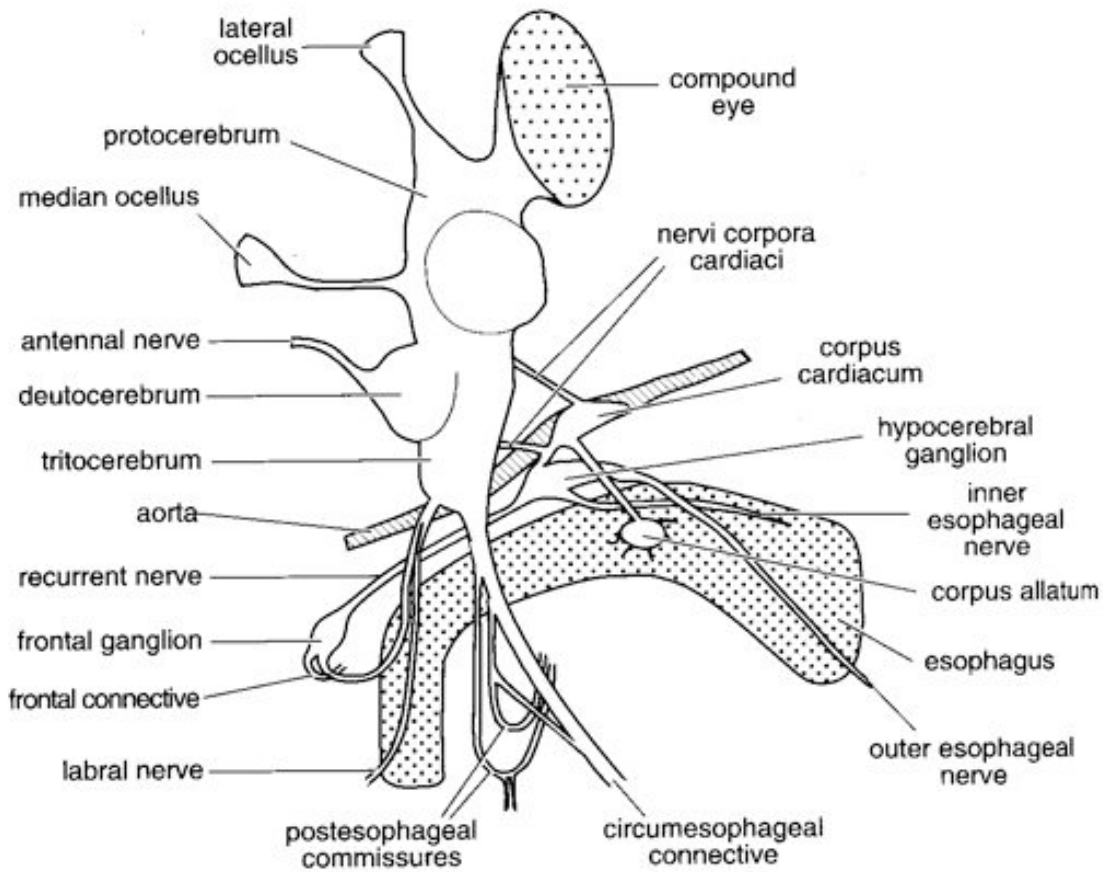
Brain showing the main regions of organized neuropile (shaded) and the distribution of the somata shown as black dots.



5-HT immunoreactivity in the brain of the horse fly

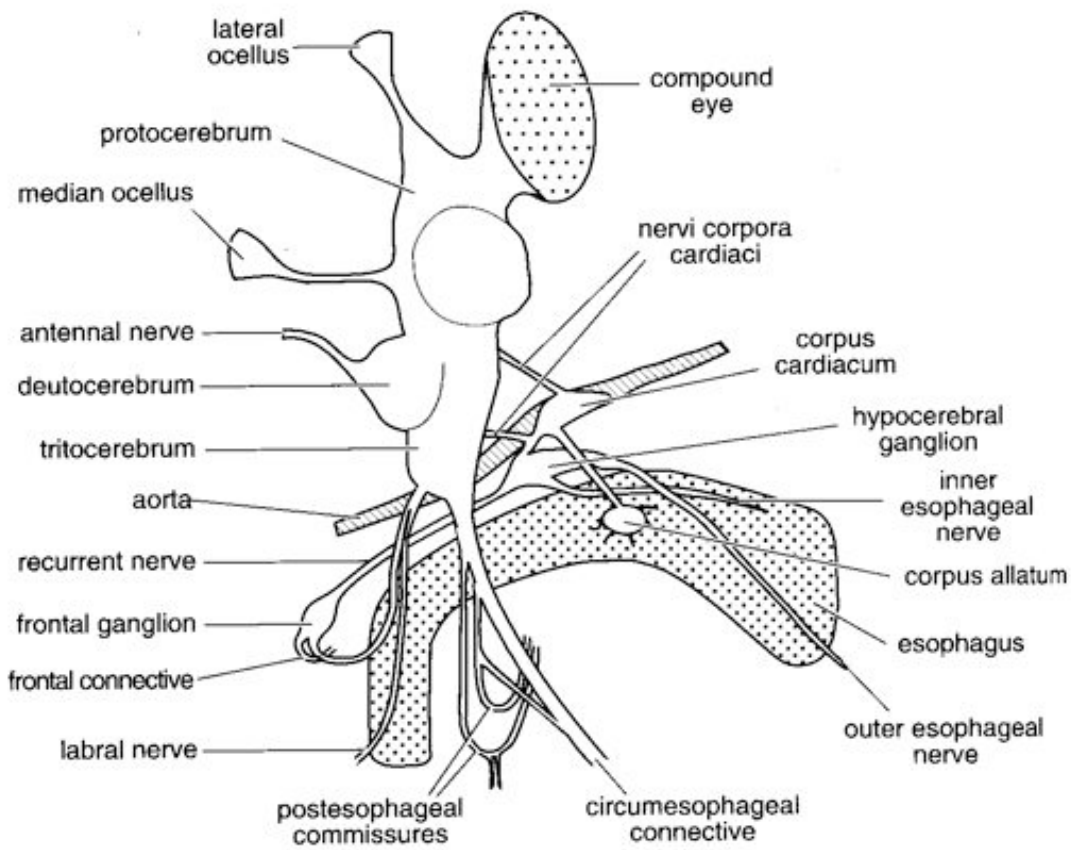
Notice the regions of organized neuropile





CNS of a locust

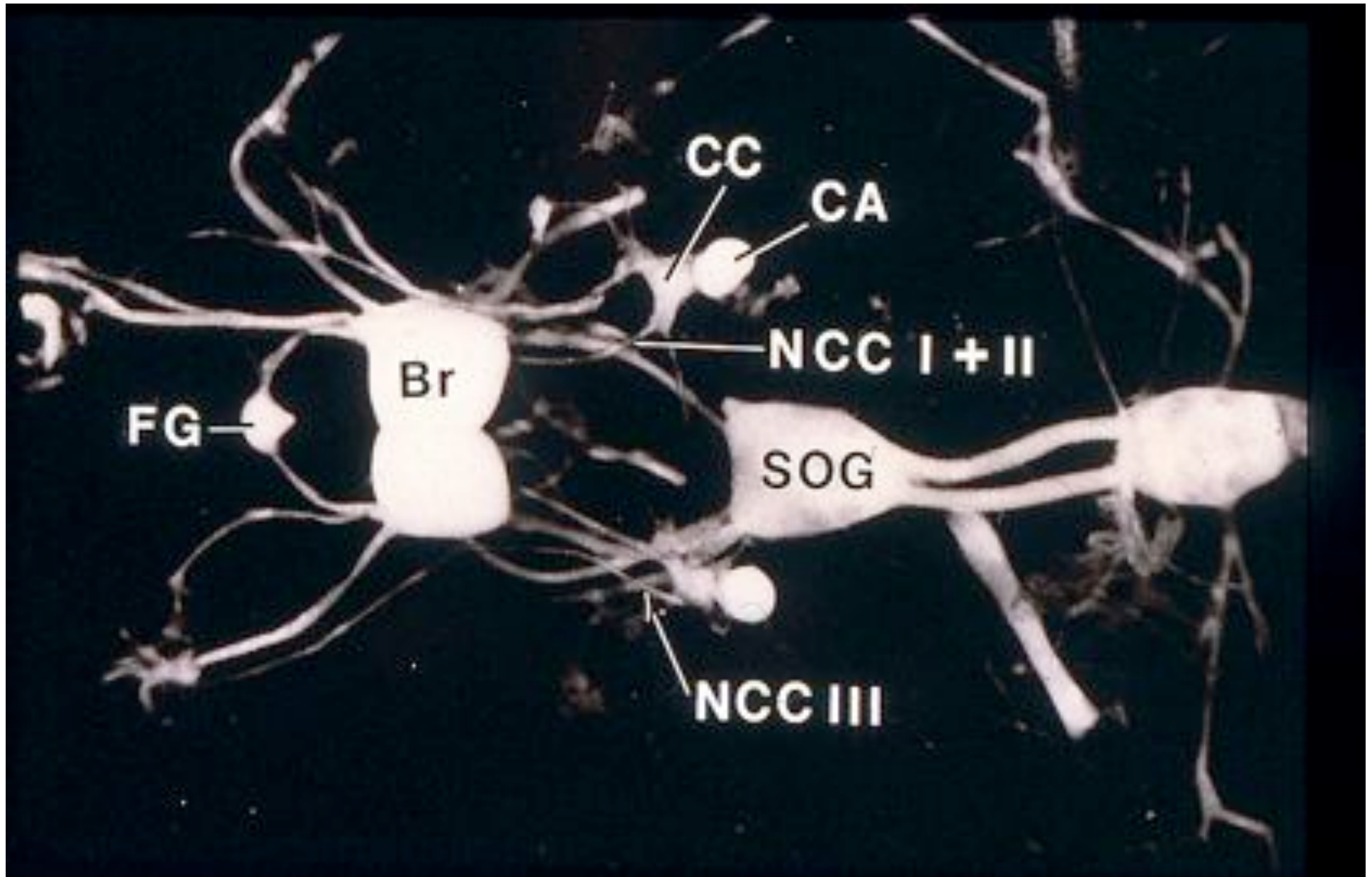


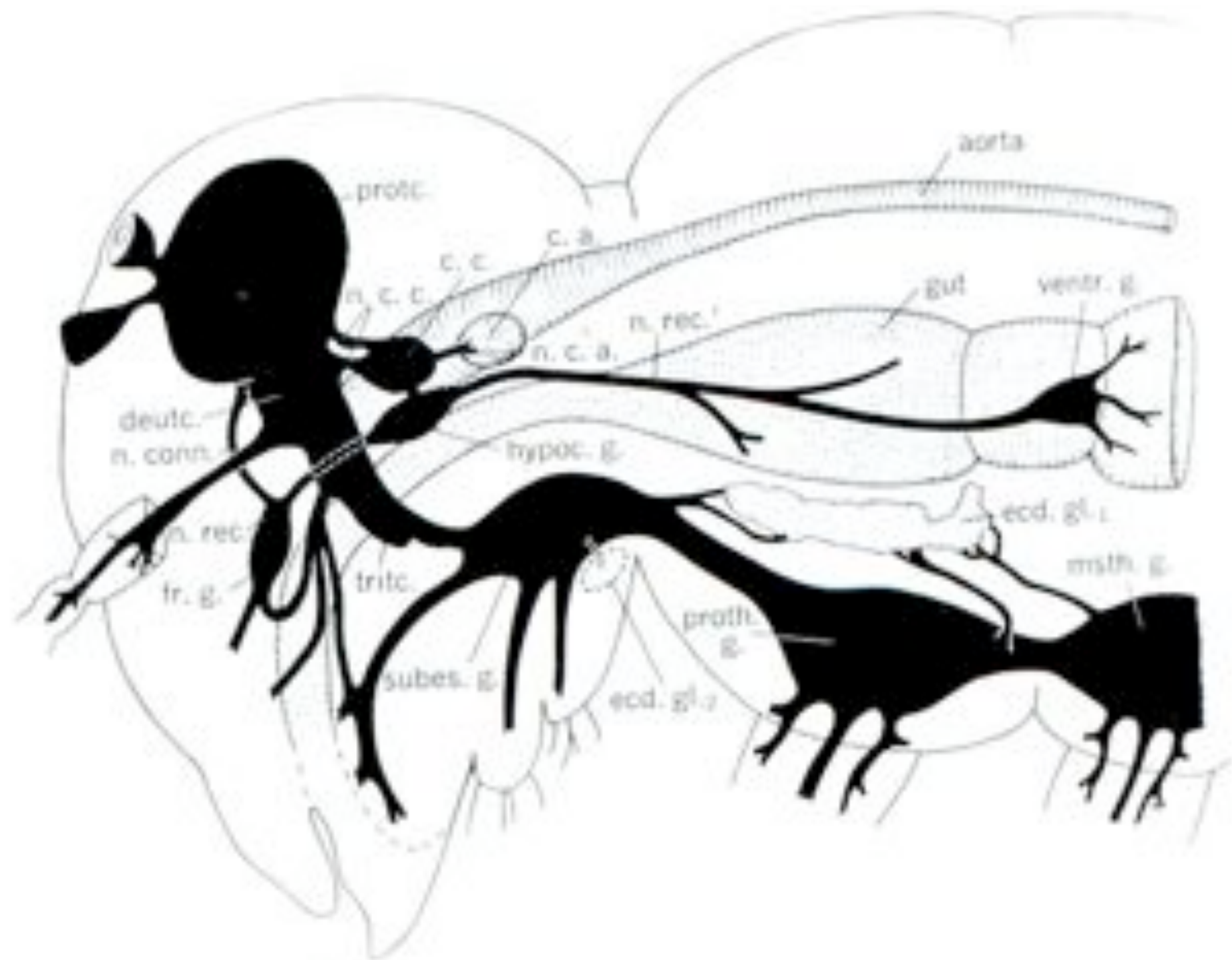


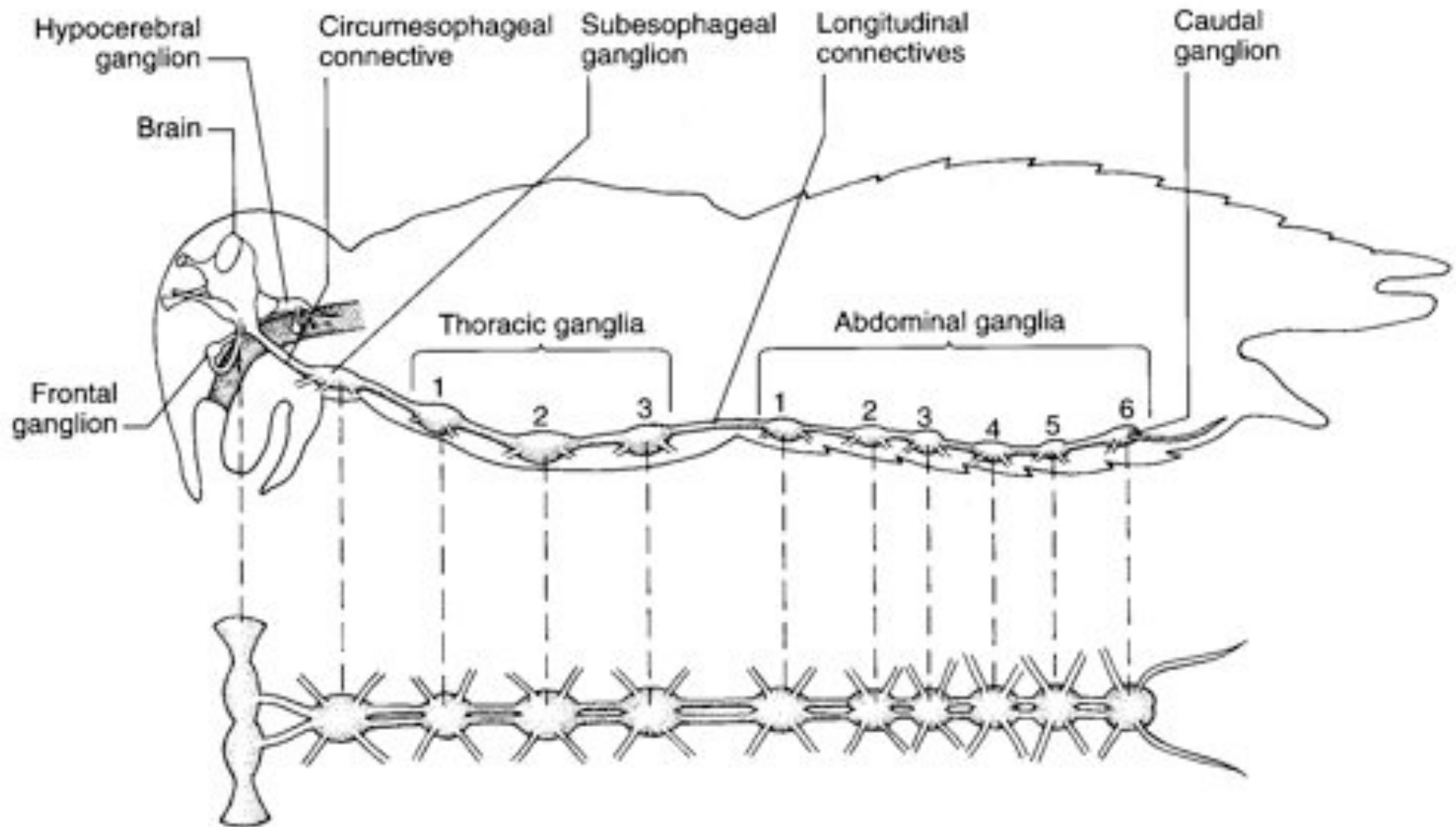
CNS of a locust



Whole mount dissection of part of the central nervous and endocrine system of the gypsy moth larva.







Ganglion=a collection of neurons. Note the CNS is composed of a double chain of ganglia joined by lateral and longitudinal connectives. In many insects the ganglia have fused (e.g., the Diptera).

Variations in the concentration or fusion of the ventral chain ganglia

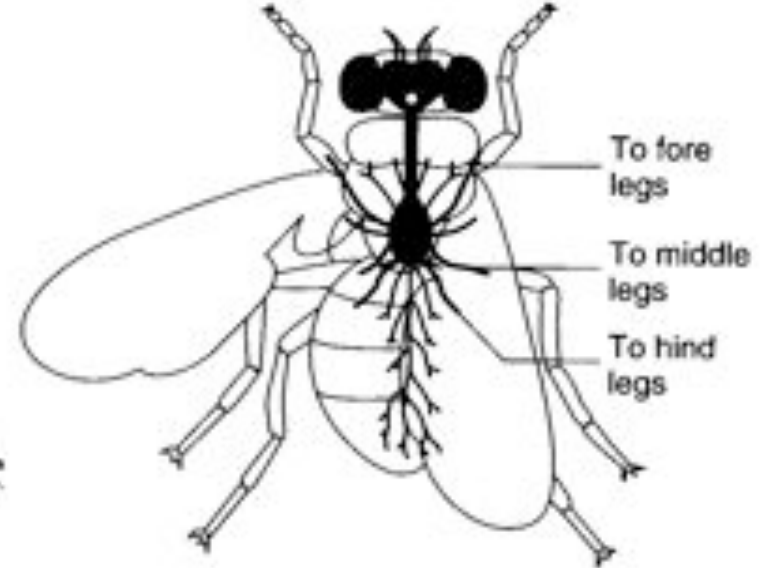
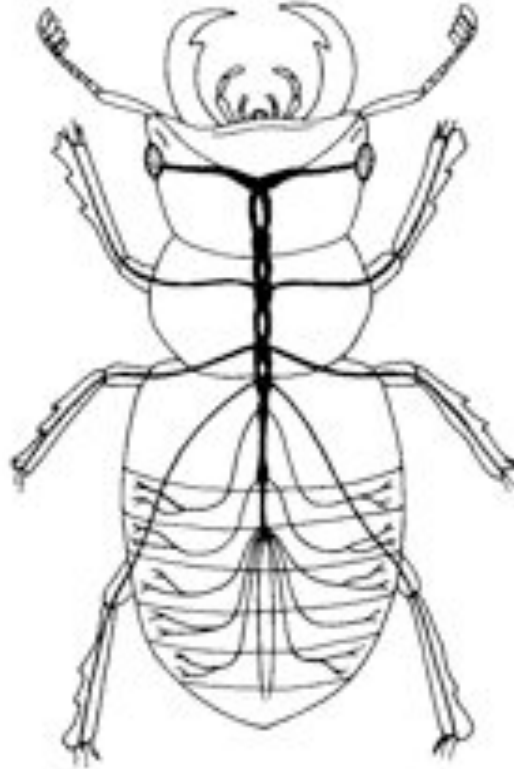
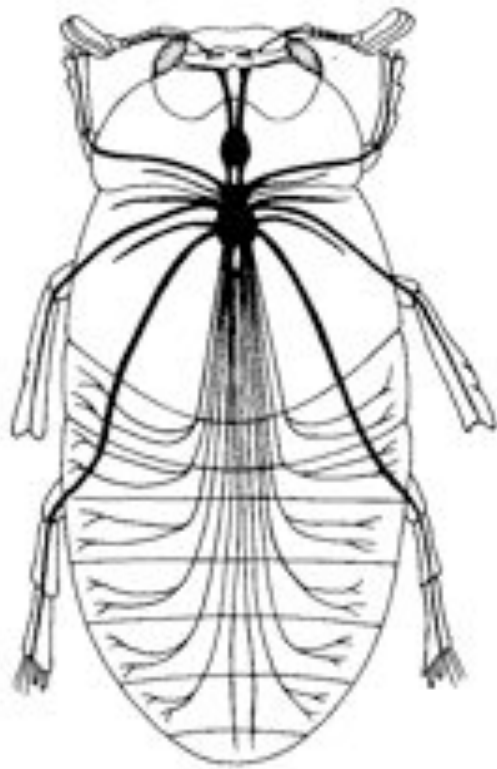
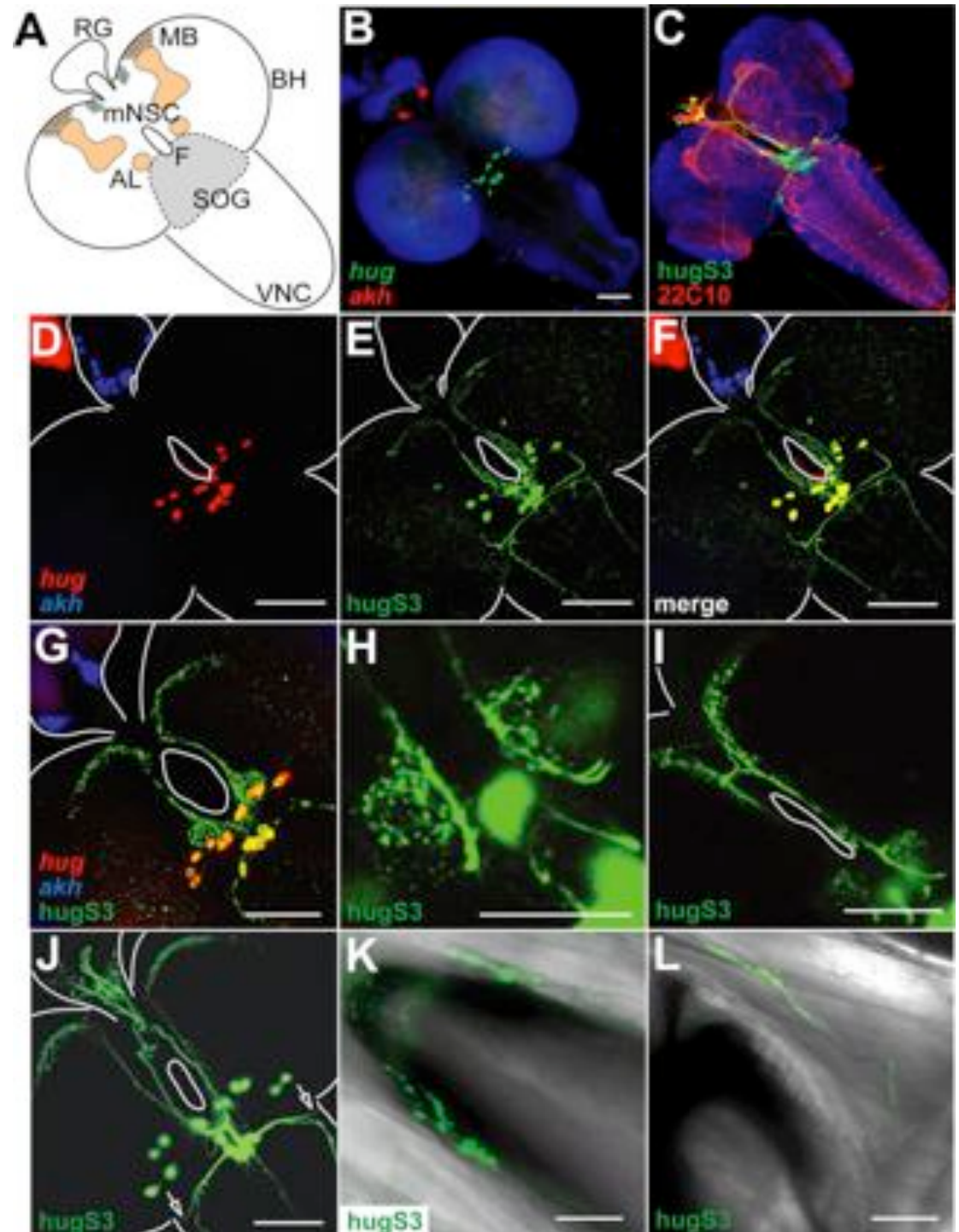
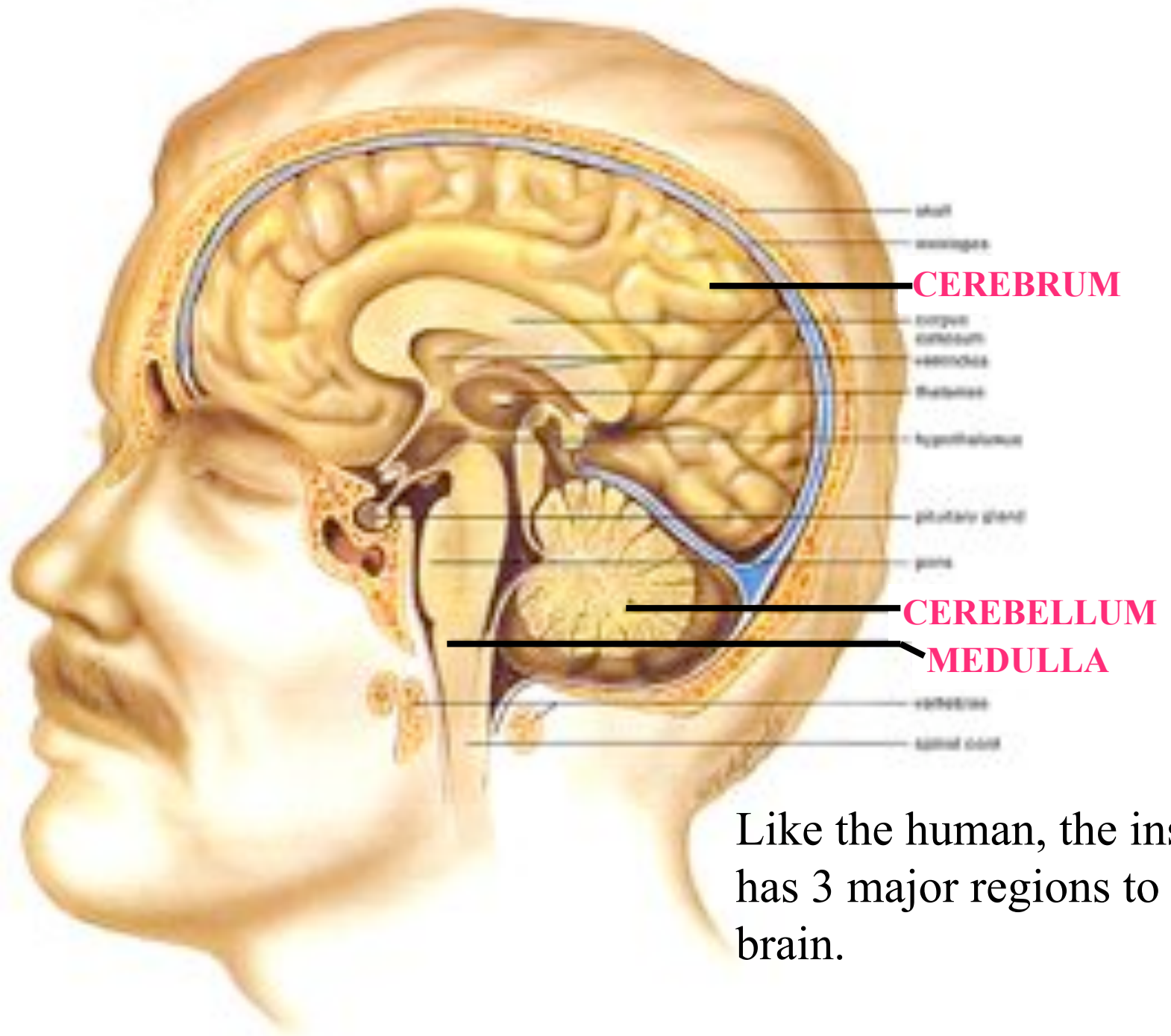


Figure 5 Neuroanatomical Analysis of *hug* Interneurons in Adults

PLoS Biol. 2005 September; 3(9): e305. Published online 2005 August 30. doi: 10.1371/journal.pbio.0030305. Copyright © 2005 Melcher et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. **Candidate Gustatory Interneurons Modulating Feeding Behavior in the *Drosophila* Brain** Christoph Melcher¹ and Michael J Pankratz¹ ¹Institut für Genetik, Forschungszentrum Karlsruhe, Karlsruhe, Germany

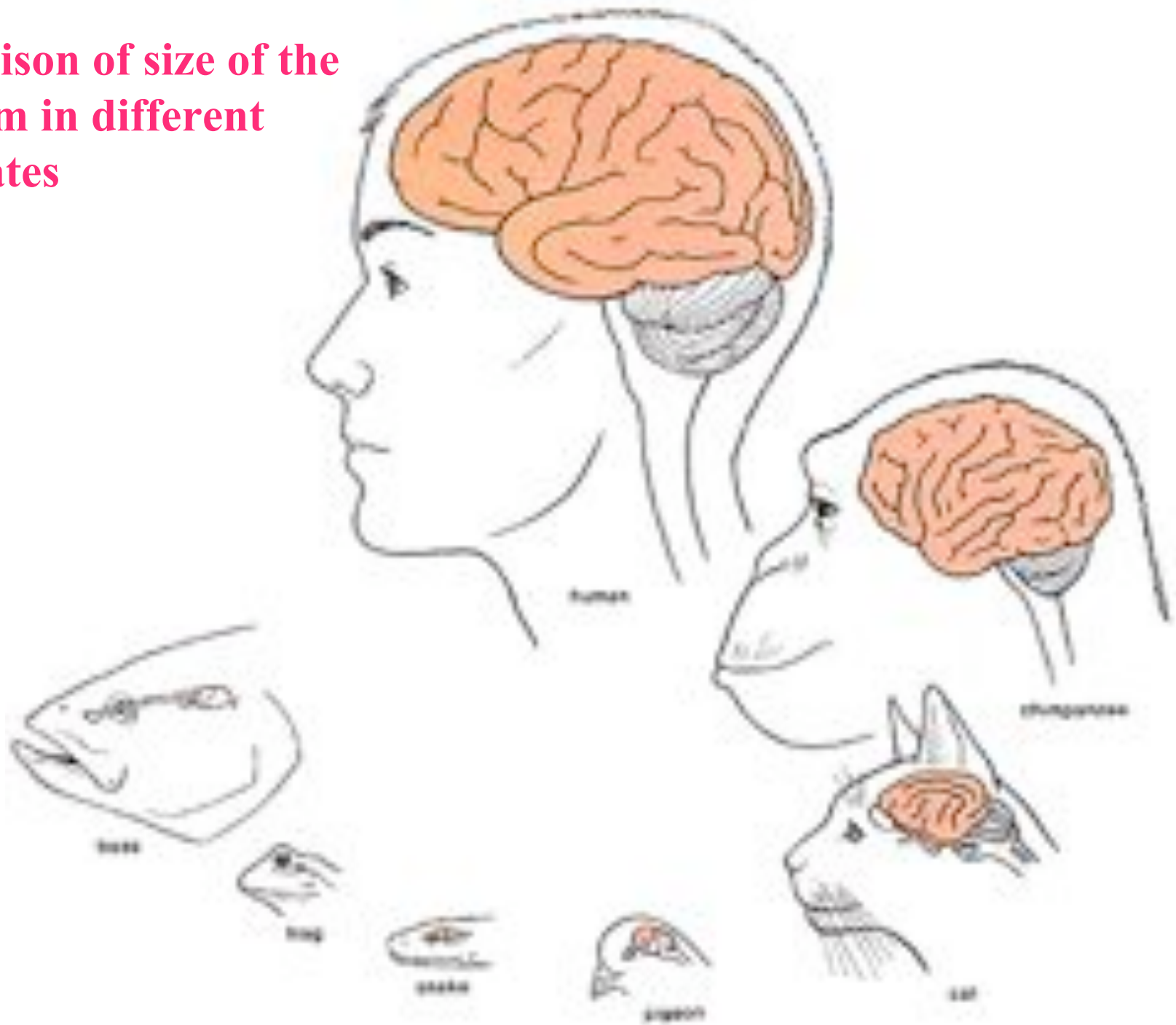


- I. Brain or supraesophageal ganglion (see the next slide for the human brain)
 - A. **Protocerebrum**-Innervates compound eyes and ocelli and is the area where complex behaviors are summated and integrated.
In insects that have a well developed directional sense to return to a nest the corpus pedunculatum is large compared to other insects. Tactile spiders have small corpus pedunculatum while in hunting spiders it is large (see 2nd slide)
 - B. **Deutocerebrum**-Innervates and coordinates information from the antennae.
 - C. **Tritocerebrum**-Connects brain to visceral nervous system via the recurrent nerve and to the ventral nerve cord via the **circumesophageal connectives**.
Connect to the frontal ganglion and innervates the labrum.
- II. **Ventral nerve cord**-Conducts impulses to and from the brain and ganglion from the peripheral nervous system.
- III. **Ventral ganglia**-Thoracic- control flight, locomotion and breathing while the abdominal control breathing, reproductive tract, copulation and ovipositioning.
CENTERS FOR VARIOUS PREPROGRAMMED MOTOR OUTPUTS.
States rights
- IV. **Subesophageal ganglion**-Resulted from the fusion of the 2,3 and 4 ganglia of early ancestors. It innervates the muscles and sense organs associated with the mouthparts (excluding the labrum), plus the salivary glands. In some insects it has an excitatory and inhibitory influence on motor activity in the whole insect.

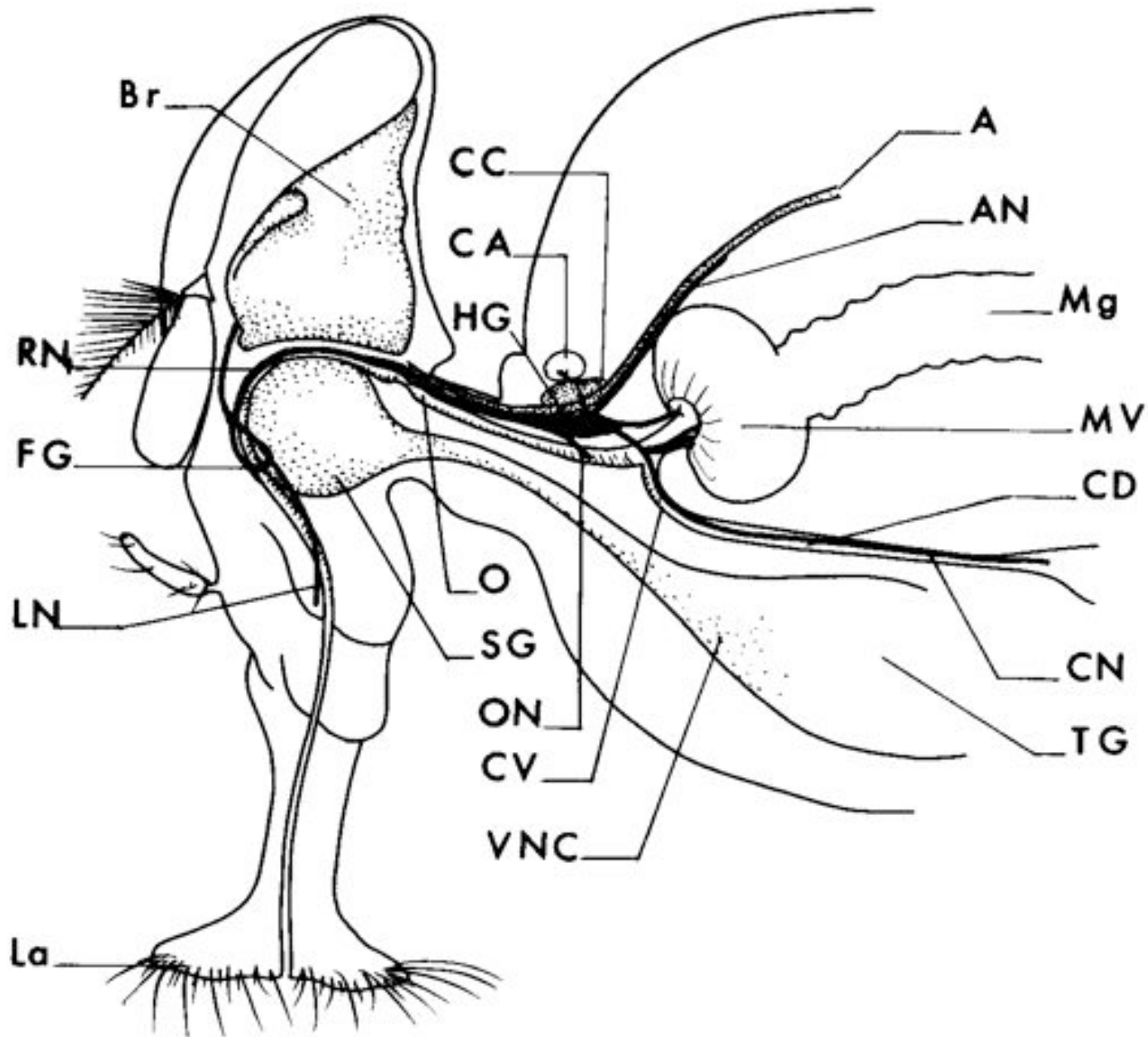


Like the human, the insect has 3 major regions to its brain.

Comparison of size of the cerebrum in different vertebrates



Adult dipteran nervous system



**Central nervous system of adult
Phormia regina, the queen blowfly.**

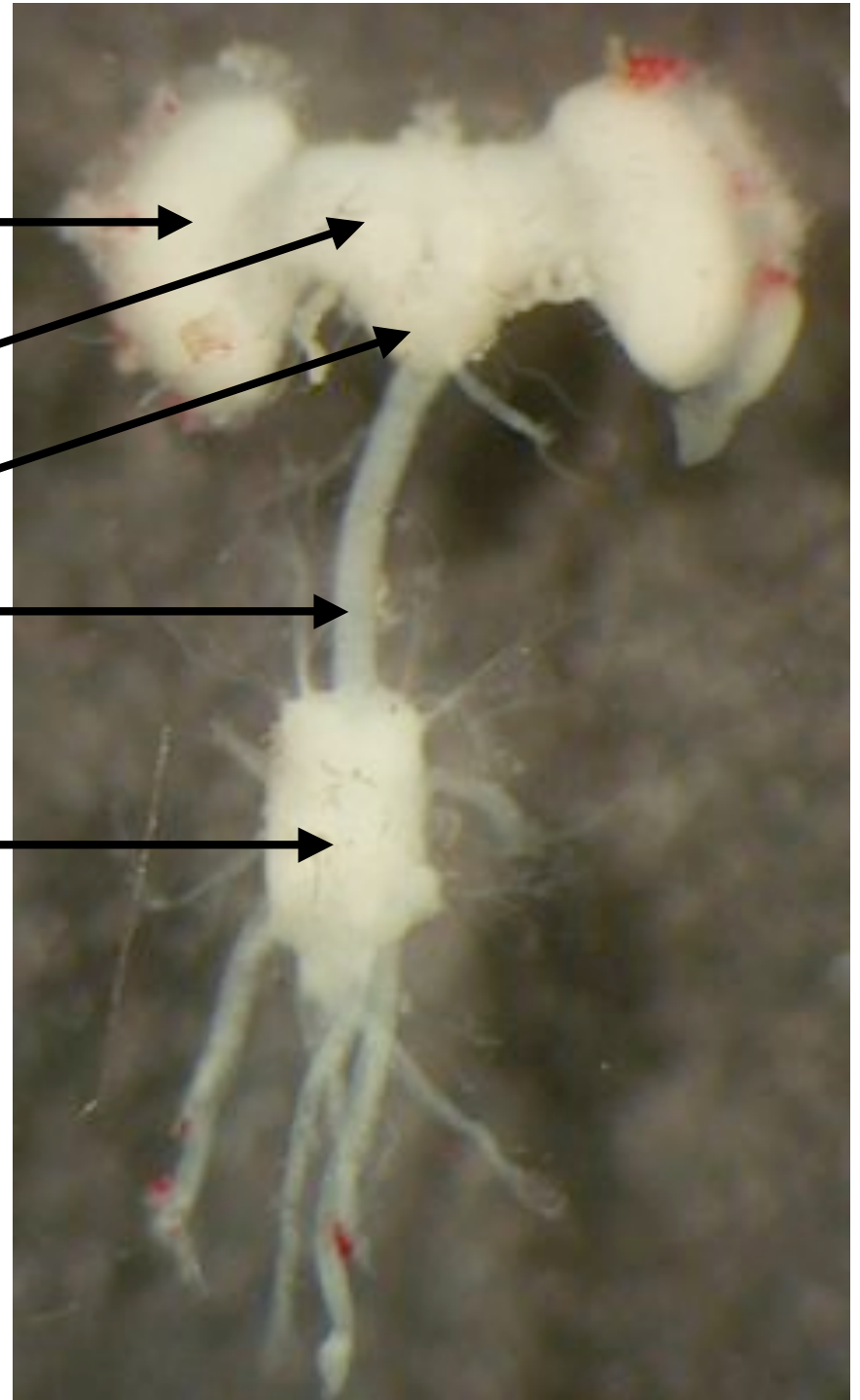
Optic lobes →

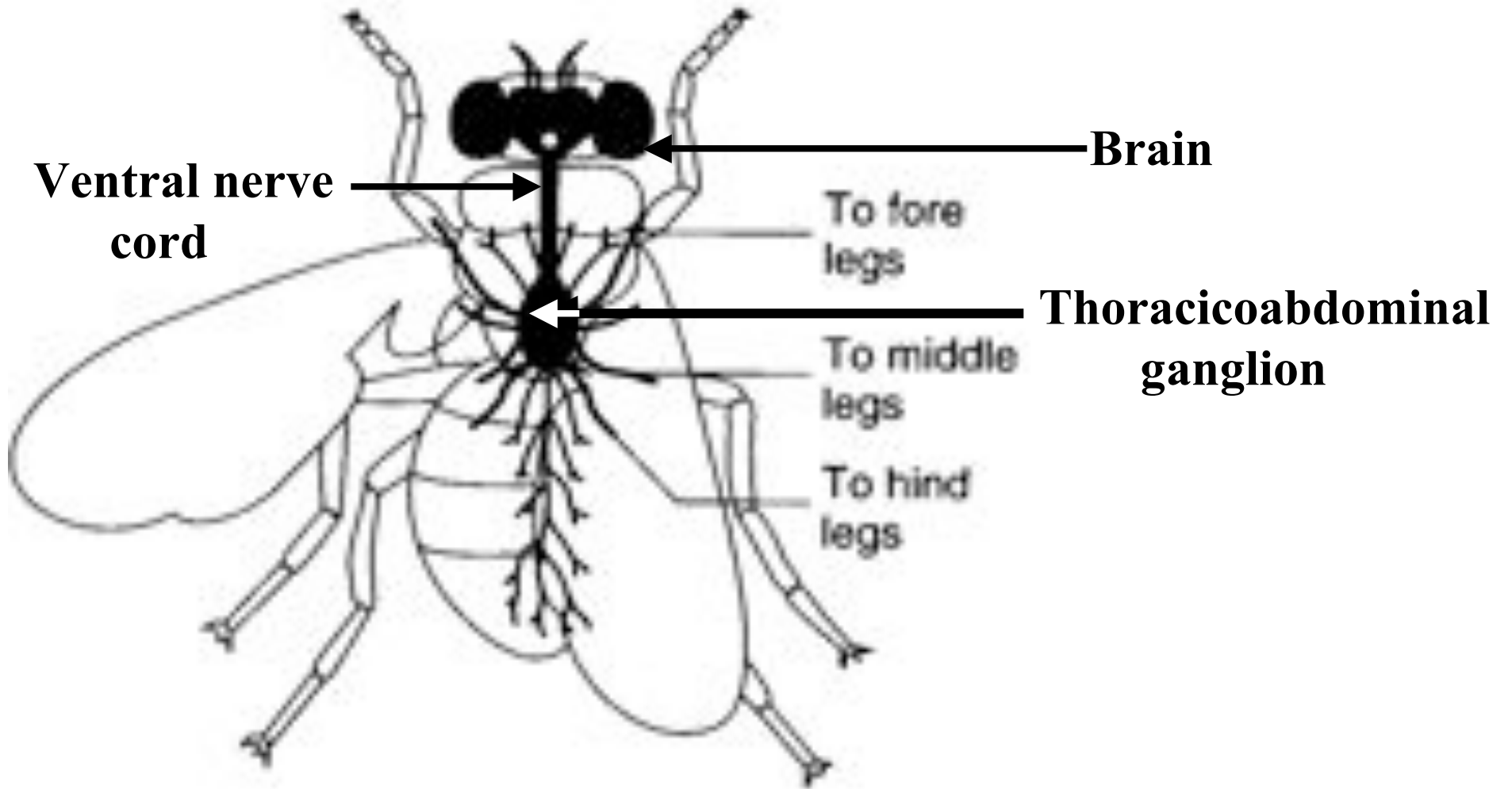
Brain →

Subesophageal ganglion →

Ventral nerve cord →

Thoracoabdominal ganglion →

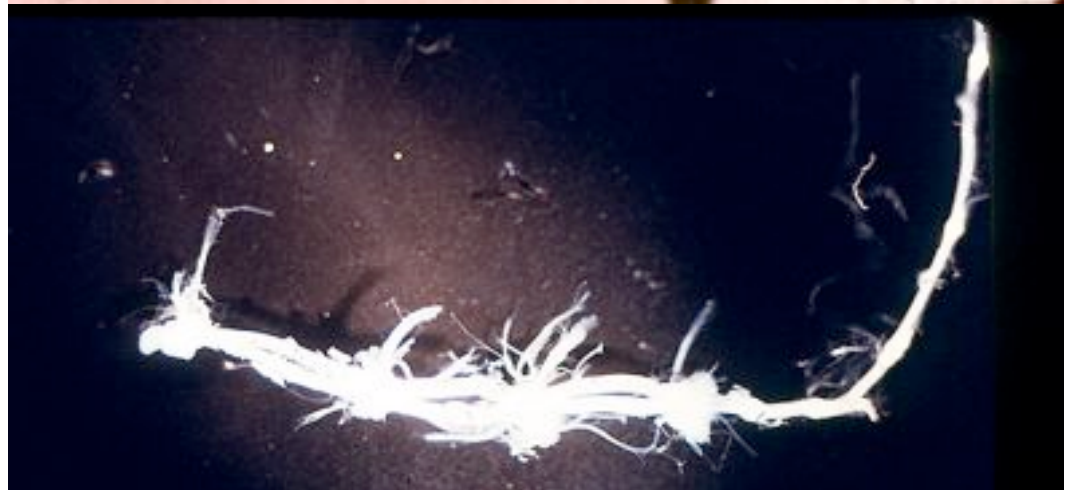




Photos of Lubber grasshopper nervous system

In the photo on the right one can see the ventral nerve cord and the nerves going from the various ganglia to either effectors, such as muscles, or coming from affectors, such as external receptors.

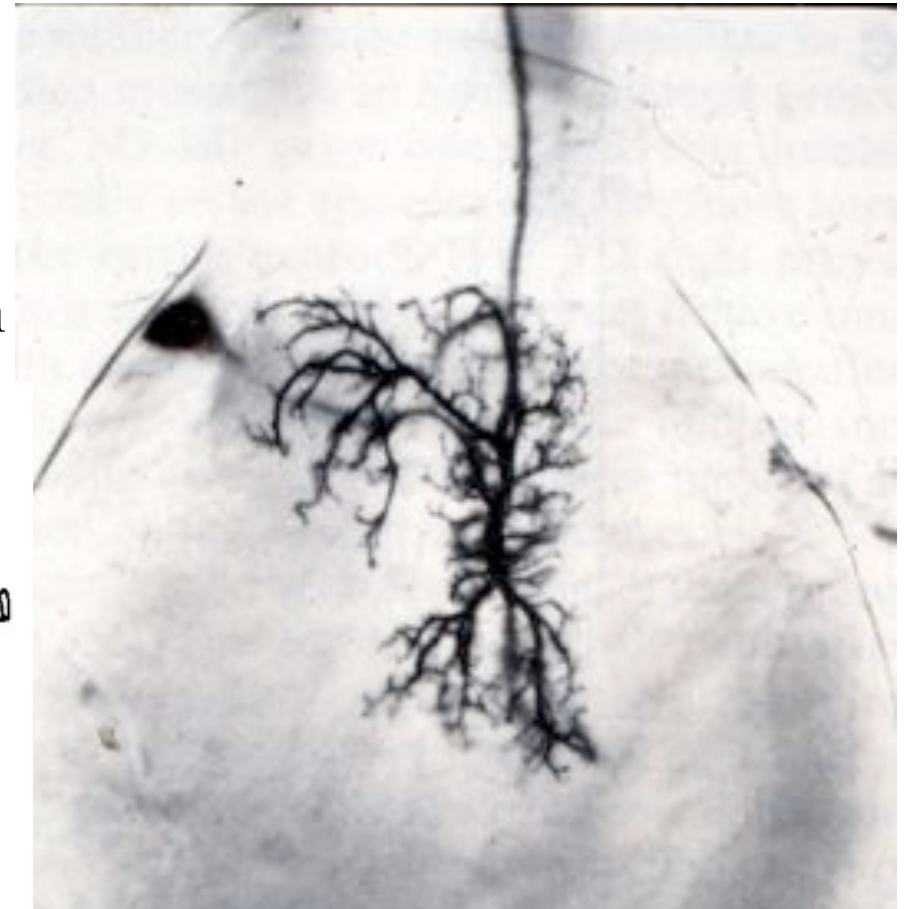
Below note that the nerve cord in some primitive insects is double with a fused ganglion in each segment.



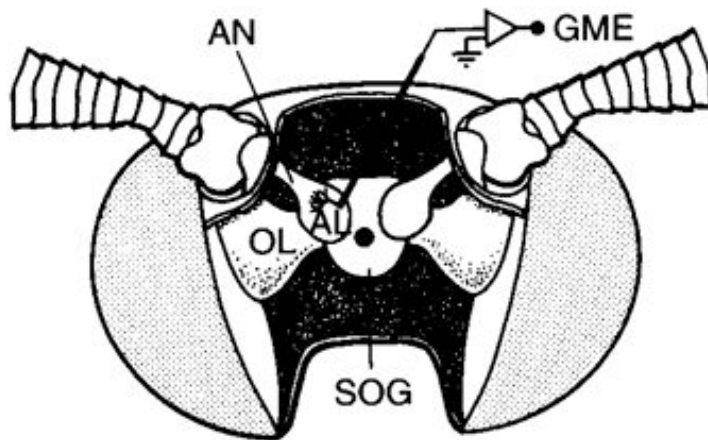
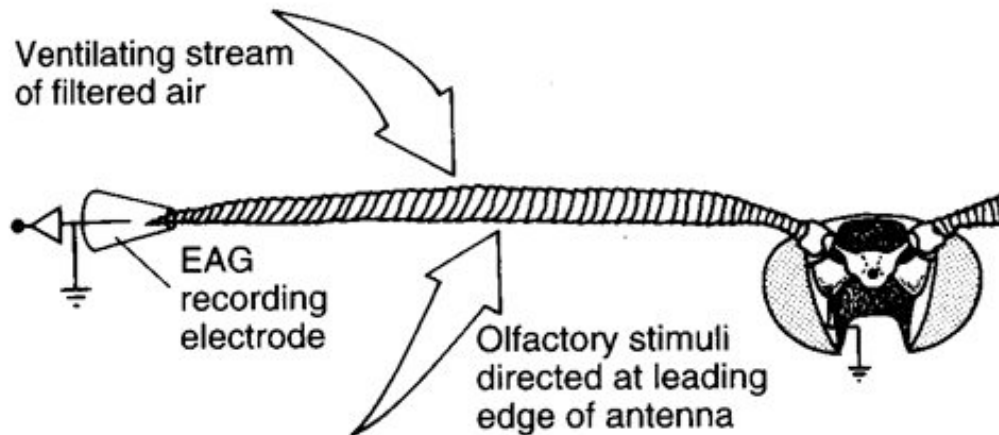
**FOLLOWING ARE EXAMPLES OF VARIOUS TECHNIQUES
USED TO MAP AND IDENTIFY SPECIFIC CELL TYPES IN
THE INSECT**

1. Use of cobaltic chloride while recording, injection using a glass electrode and filling and/or cutting nerve and backfilling
2. The use of various fluorescent labeled antibodies or immunolabeling

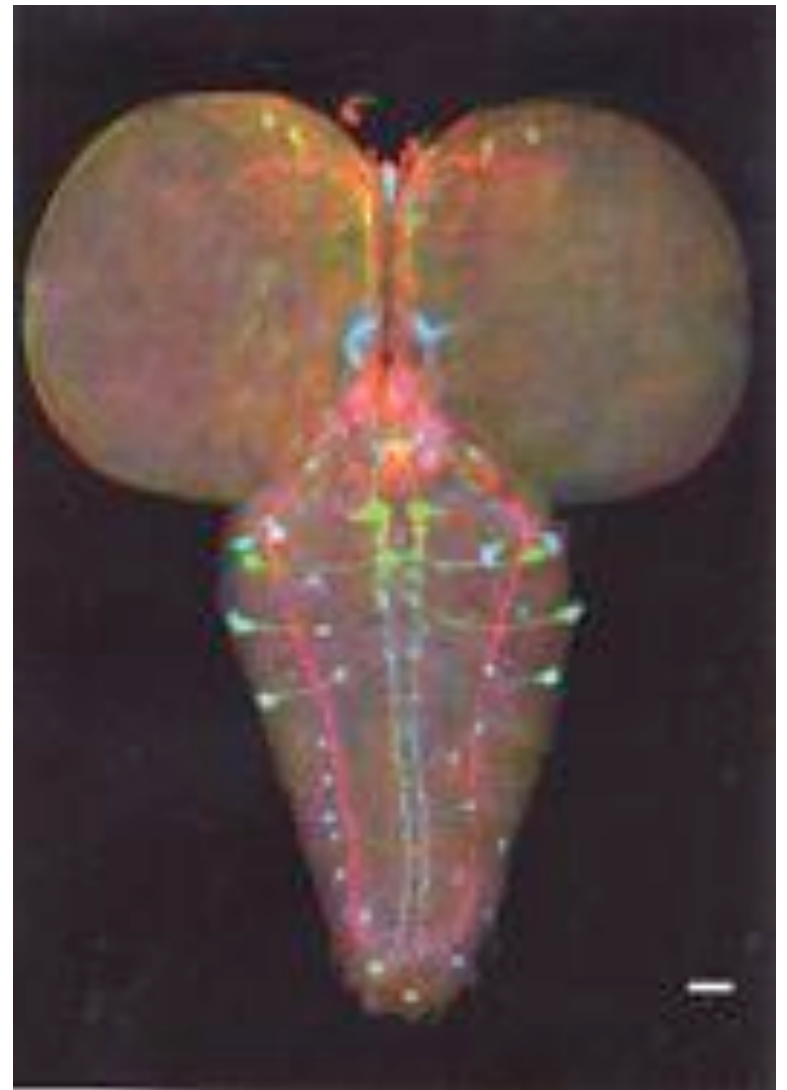
On the right is a whole mount of the terminal abdominal ganglion of a cricket showing neuron stained with cobaltic chloride. Below shows technique of EAG and labelling neuron



Now use computers to map the ganglion. Neurons can be imaged in different colors and the whole system (3-D) can be rotated.



Immunolabelling of larval *D. melanogaster* CNS. FMRFamide antisera of whole CNS. Triple immunolabelling of whole CNS using 3 different FMRFamide-containing peptide-specific antisera.



Dromyosuppressin (DMS) and crop contractions

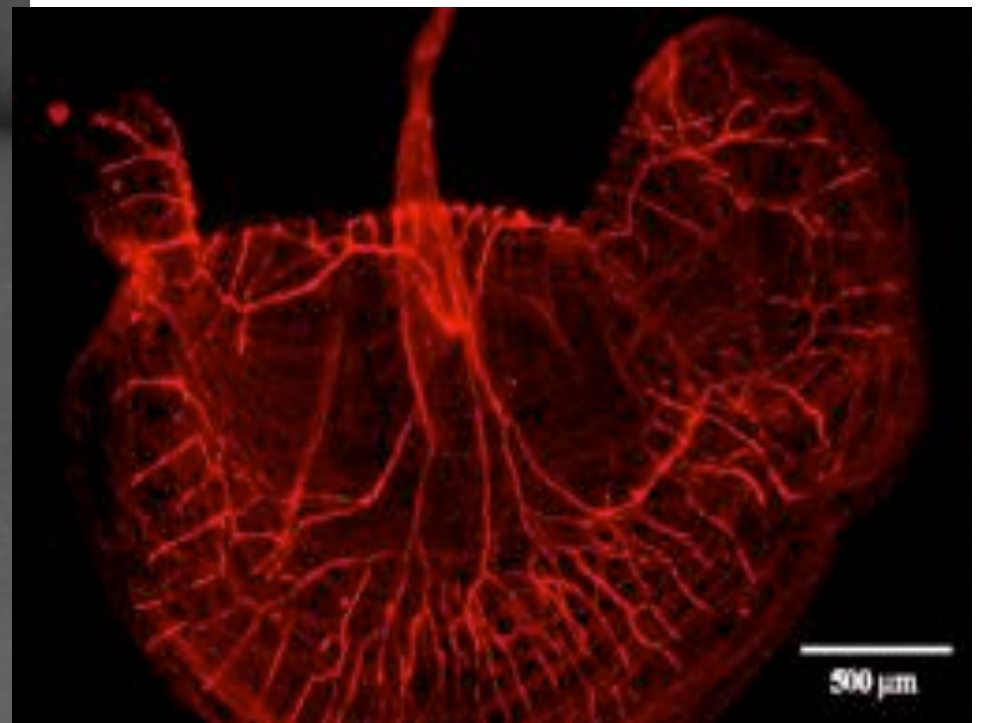
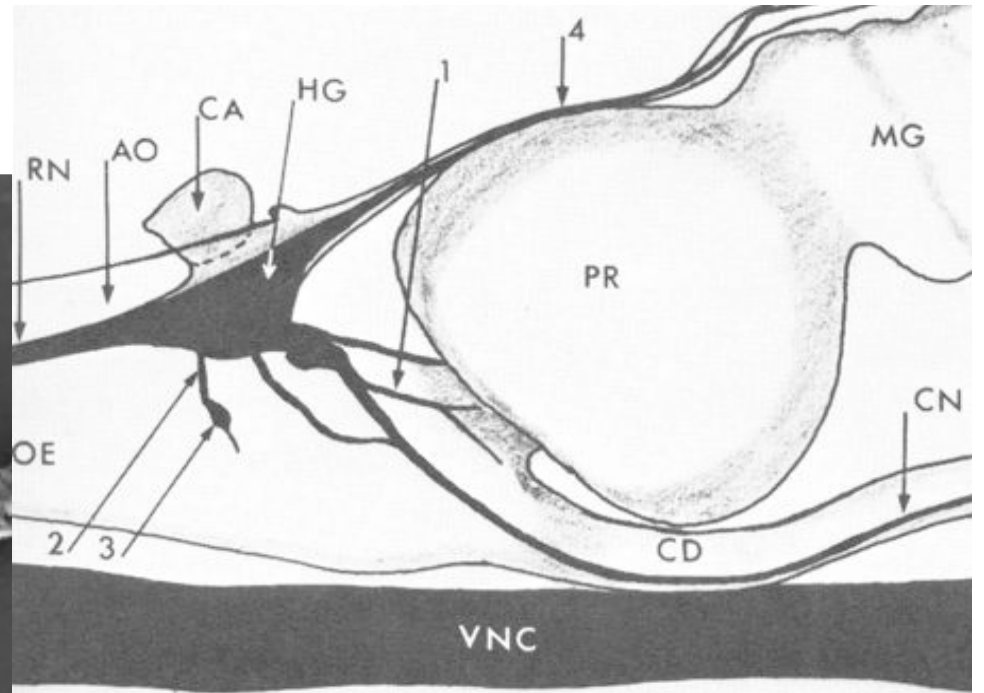
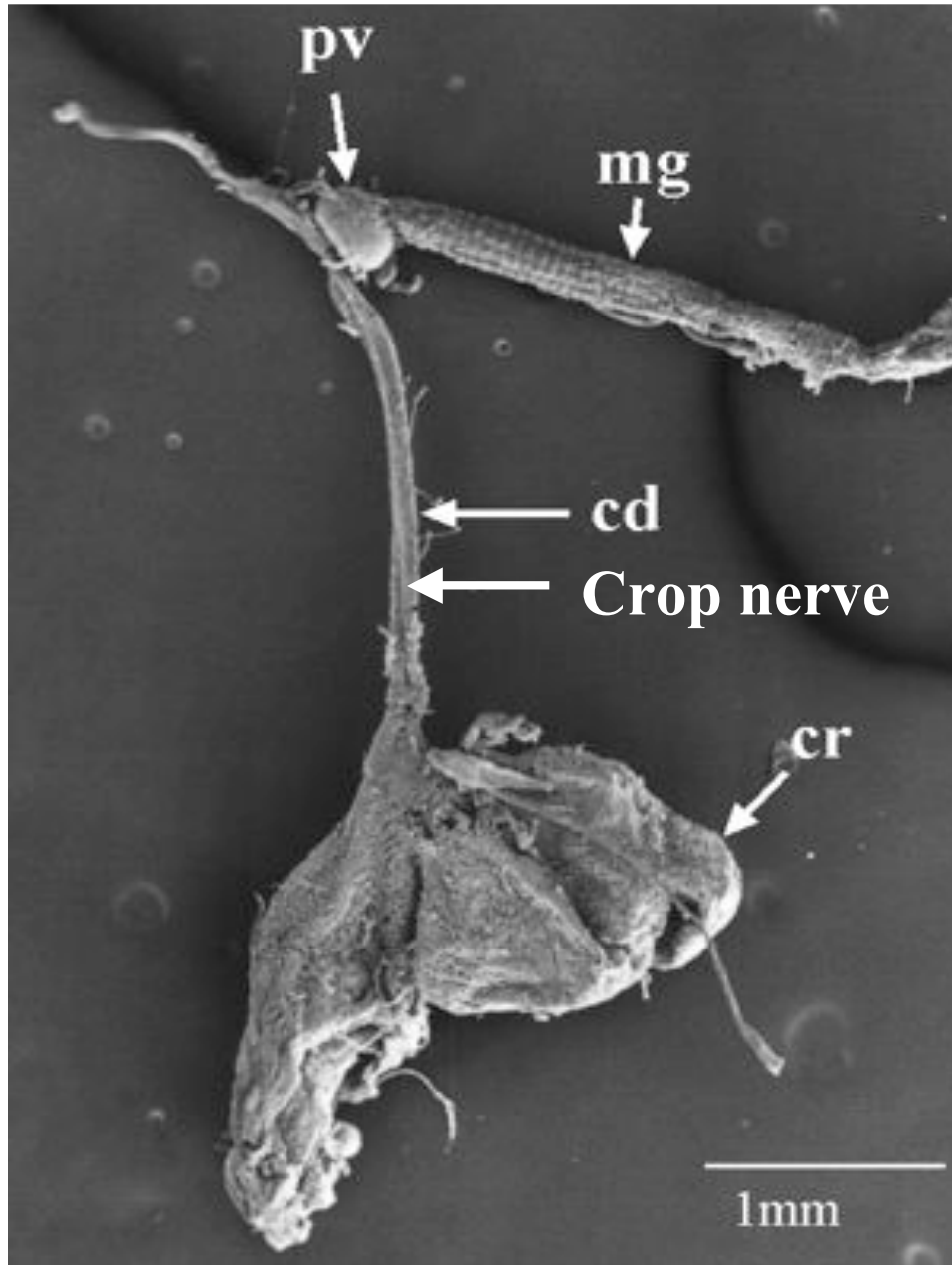
- myosuppressins isolated from several insects, including *Drosophila*
- myotropic myoinhibitors
- dromyosuppressin (DMS) structure: TDVDHVFLRFamide
- CNS, alimentary tract with DMS IR cells and processes
- DMS applied to *in vitro* crop preparation

DMS and crop contractions

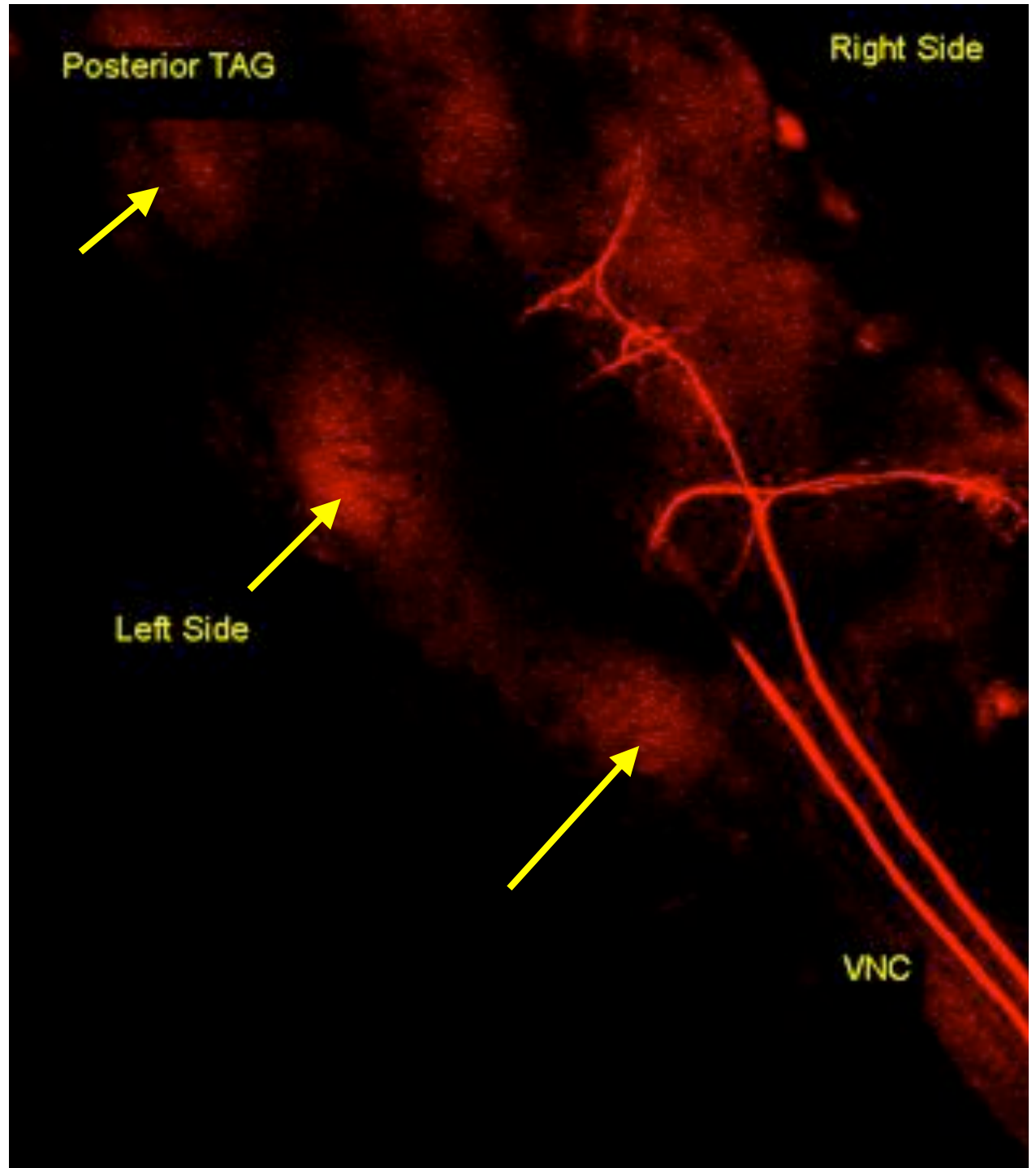


Application of 10^{-6} M DMS reduced crop contractions by 95% (from 46 to 2 contr./min)

Dromyosuppressin antibody on crop nerves of a fly



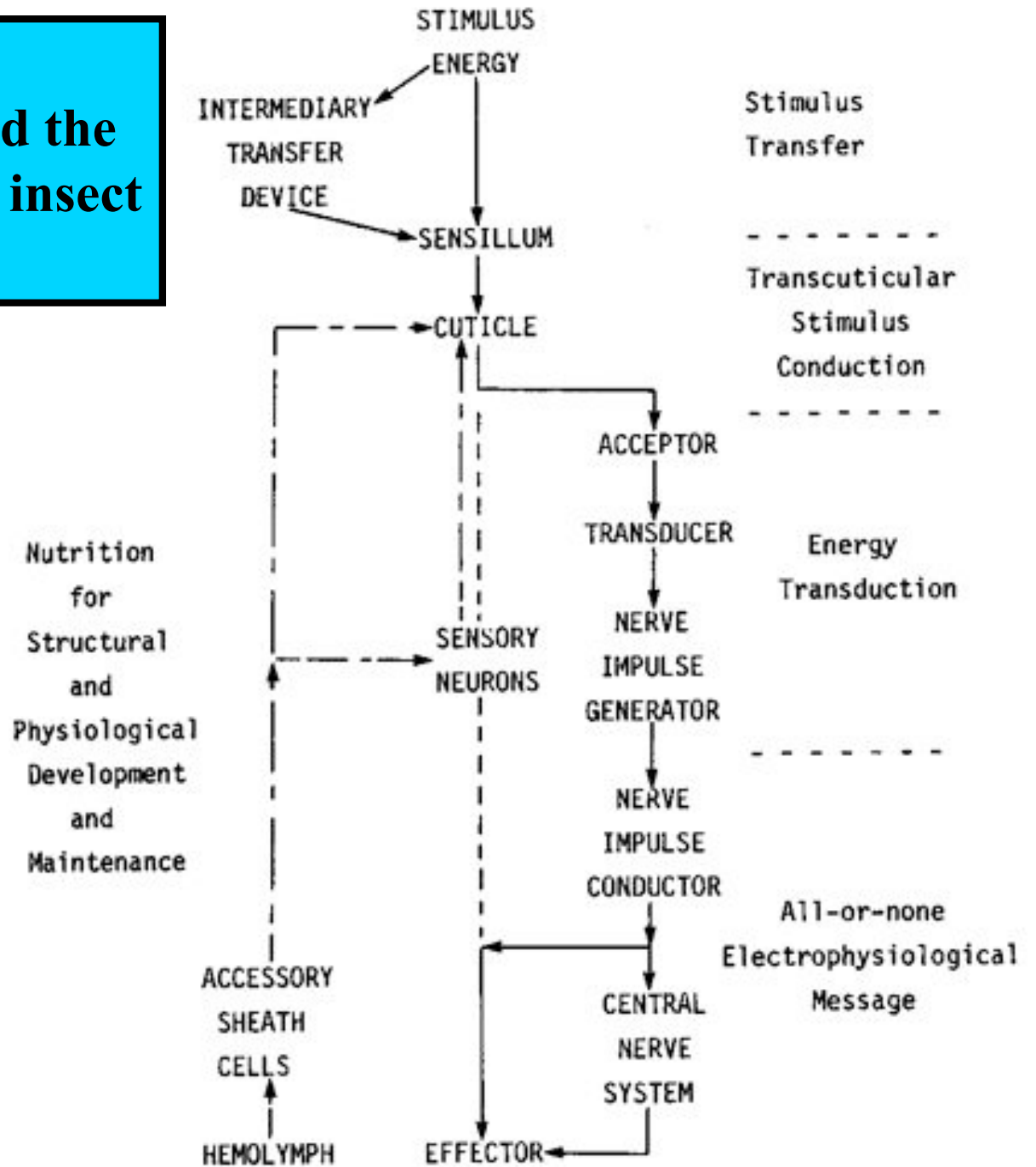
Dextran-rhodamine backfilling from the fly antenna down to the thoracicobdominal ganglion. Note the 3 major divisions of the thoracicoabdominal ganglion (see yellow arrows).



LIST OF RECEPTOR TYPES

1. Mechanoreceptors
2. Chemoreceptors
3. Proprioceptors
4. Thermoreceptors
 - a. IR receptors
5. Osmoreceptors
6. Nociceptors
7. Photoreceptors
8. Hygroreceptors

Schematic showing the pathways of function and the mechanisms involved in insect cuticular sensilla



MECHANORECEPTORS

Mechanoreception is the perception of distortion of the body caused by mechanical energy, which may originate either internally or externally.

Produces the senses of

- a. gravity
- b. pressure
- c. touch
- d. position
- e. current flow (air or water)
- f. vibration
- g. hearing

Chordotonal sensilla-composed of special sensilla, the scolopidia, that are associated with support.

Scolopidia contain a **scolopale**, that is an intracellular structure composed of electron-dense material deposited around longitudinally oriented microtubules. Is an integral part of mechanoreceptors.

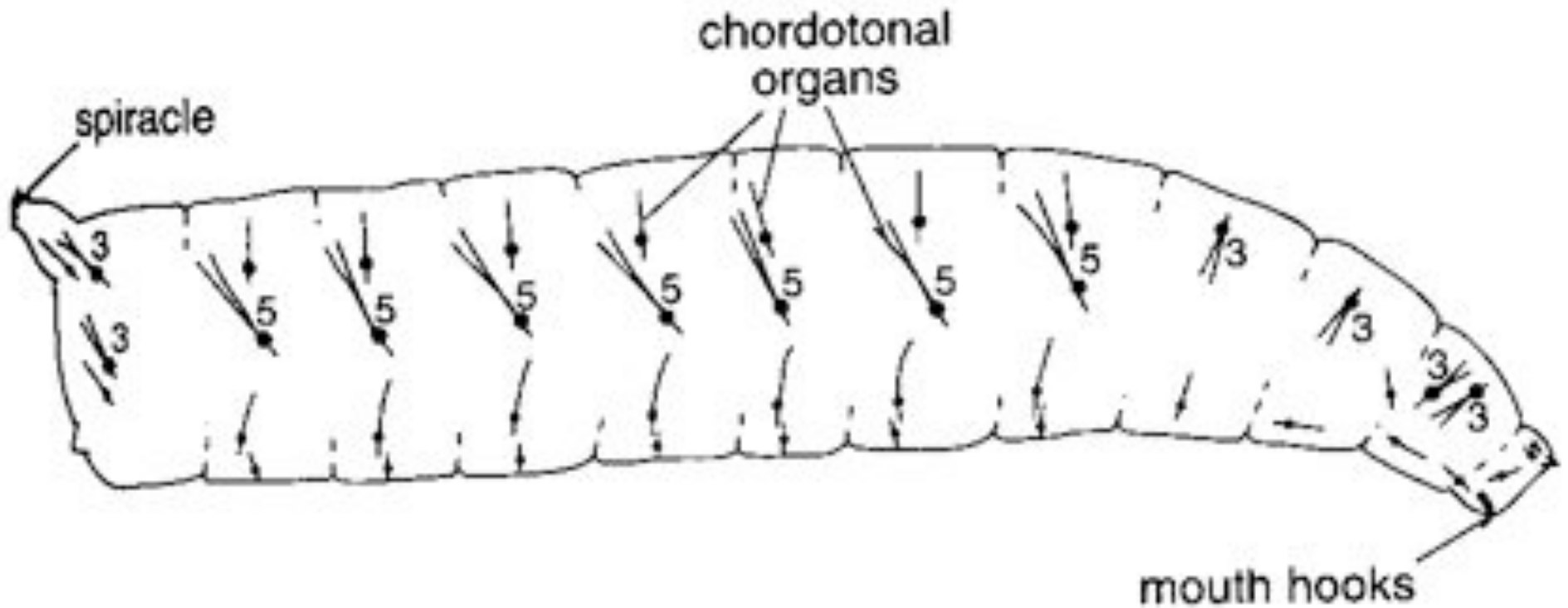
Note below the scolopophorous (so) or chordotonal organ of a short house fly larva just prior to pupation.

The scolopale is stimulated by tension due to body changes. Structure also found in:

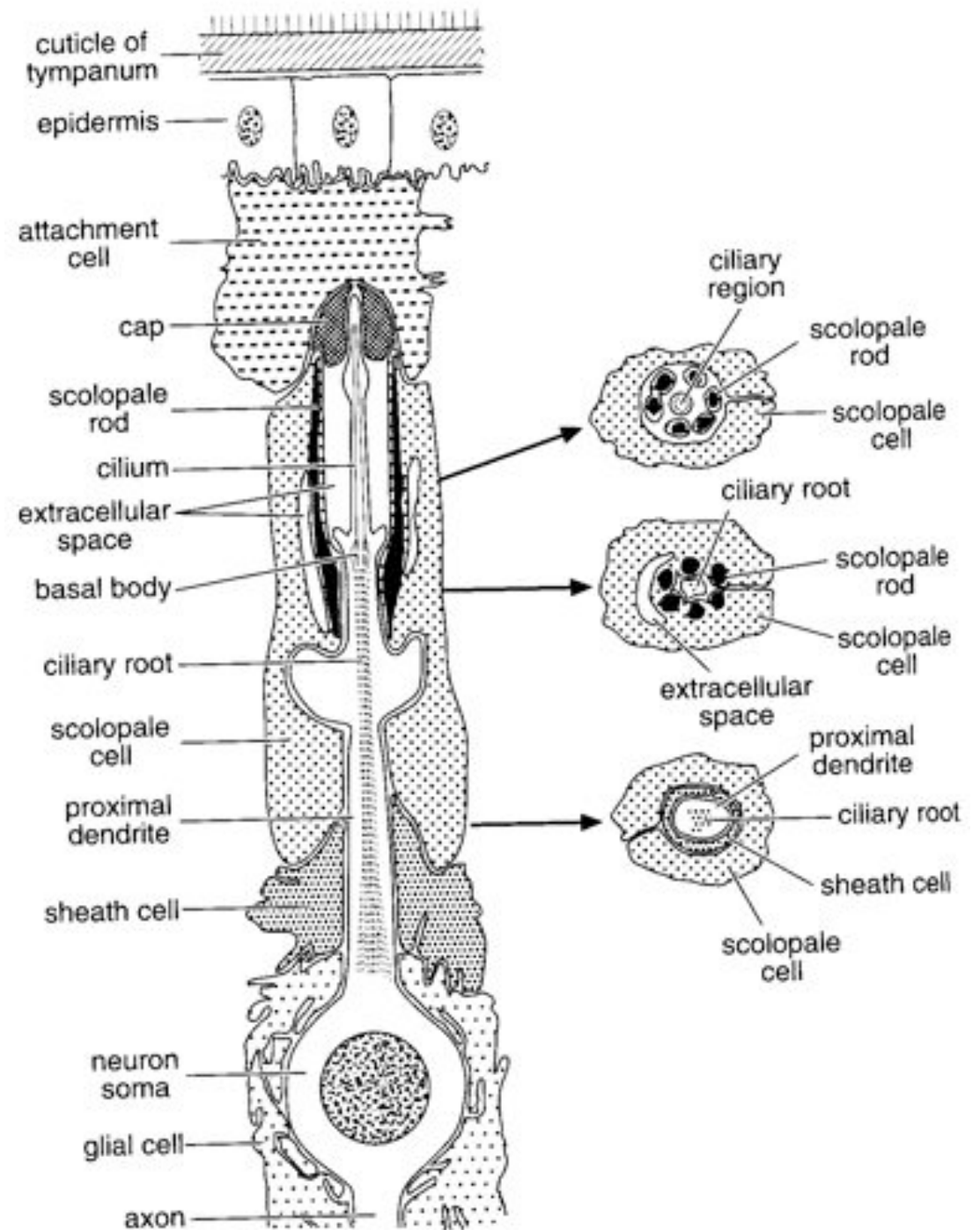
1. Subgenual organ
2. Johnston's organ
3. Tympanal organ



Drosophila larvae have 90 chordotonal organs

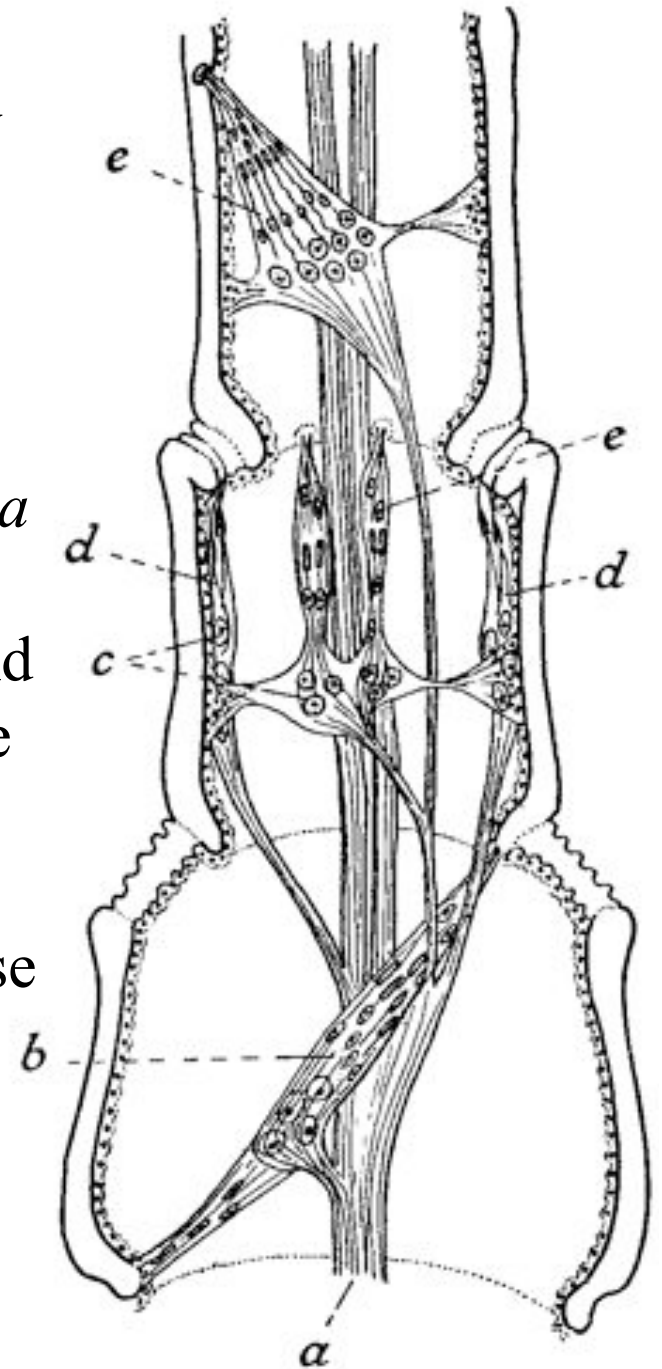


Scolopidium from the tympanum organ of the locust.



Chordotonal organs-

- a. A key characteristic is that they are usually stretched between two parts of the insects cuticle, thus responding to tension.
- b. To the right is a photo showing two chordotonal organs (b and e) in the three basal segments of the antenna of *Meconema varium*.
- c. Common throughout the insect body. Found in legs, antennae, palps, wing bases and the general body cavity. Respiratory siphon of *Culex* larvae contains 3 pairs. Occur at the base of wings in Lepidoptera and at the base of wing and halteres in Diptera.



Subgenual organ-A type of chordotonal organ but located in the proximal region of the tibia, not associated with the joints.

Specifically adapted to perceive vibration signals from a solid substrate.

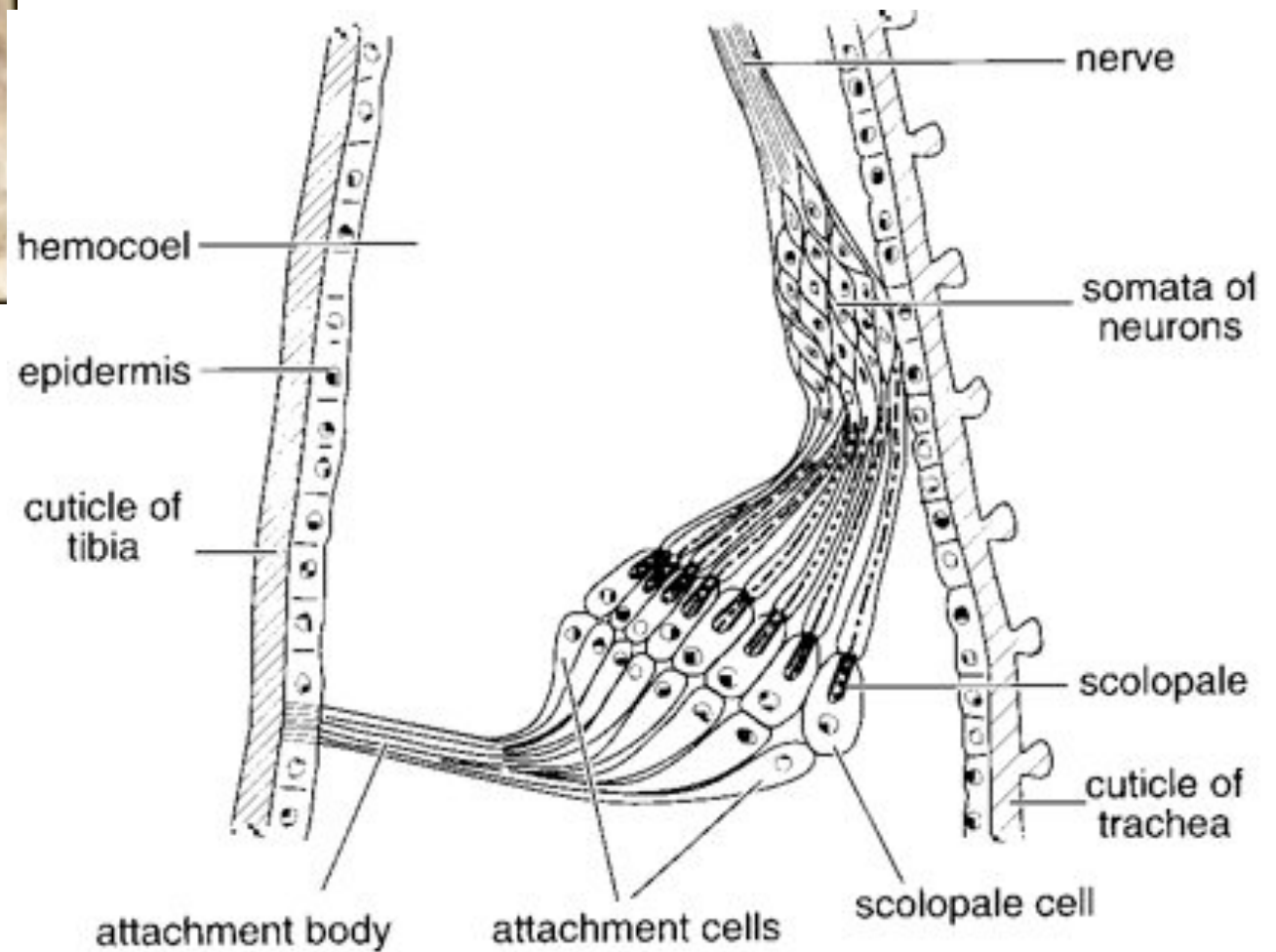
Cokl, A. and M. V-Doberlet. 2003. Communication with substrate-borne signals in small plant-dwelling insects. Ann. Rev. Ent. 48: 29-50.

“The subgenual organ, joint chordotonal organs, campaniform sensilla and mechanoreceptors, such as the Johnston’s organ in antennae, are used to detect these vibratory signals.” “Species-specific songs facilitate mate location and recognition, and less species-specific signals provide information about enemies or rival mates.”

Subgenual organ of *Formica sanguinea*.



located in the proximal region of the tibia, not associated with the joints and responds to substrate vibrations

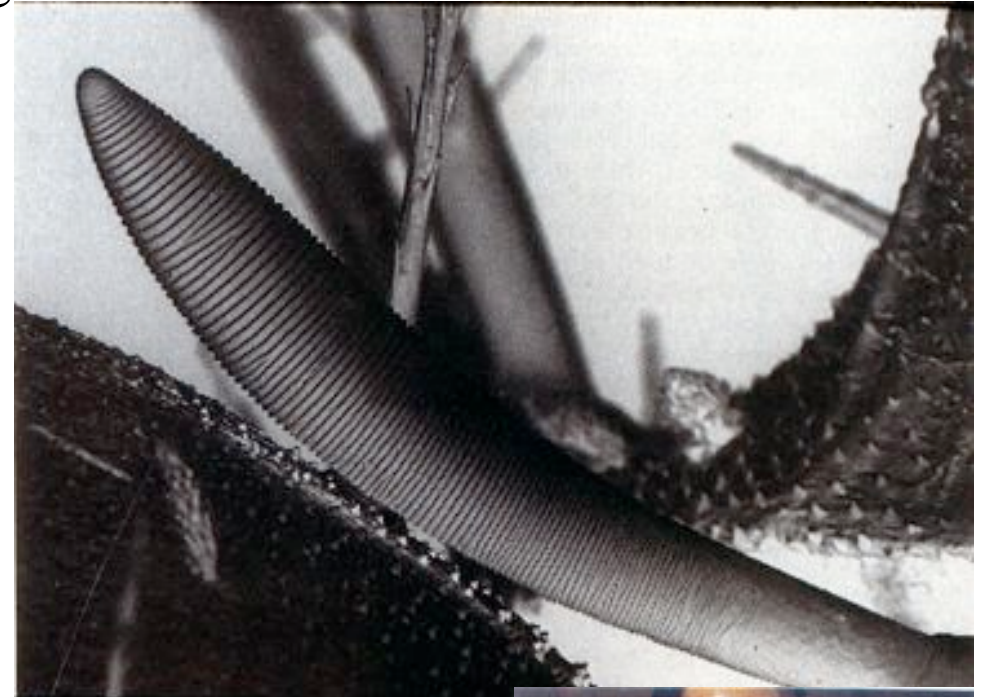
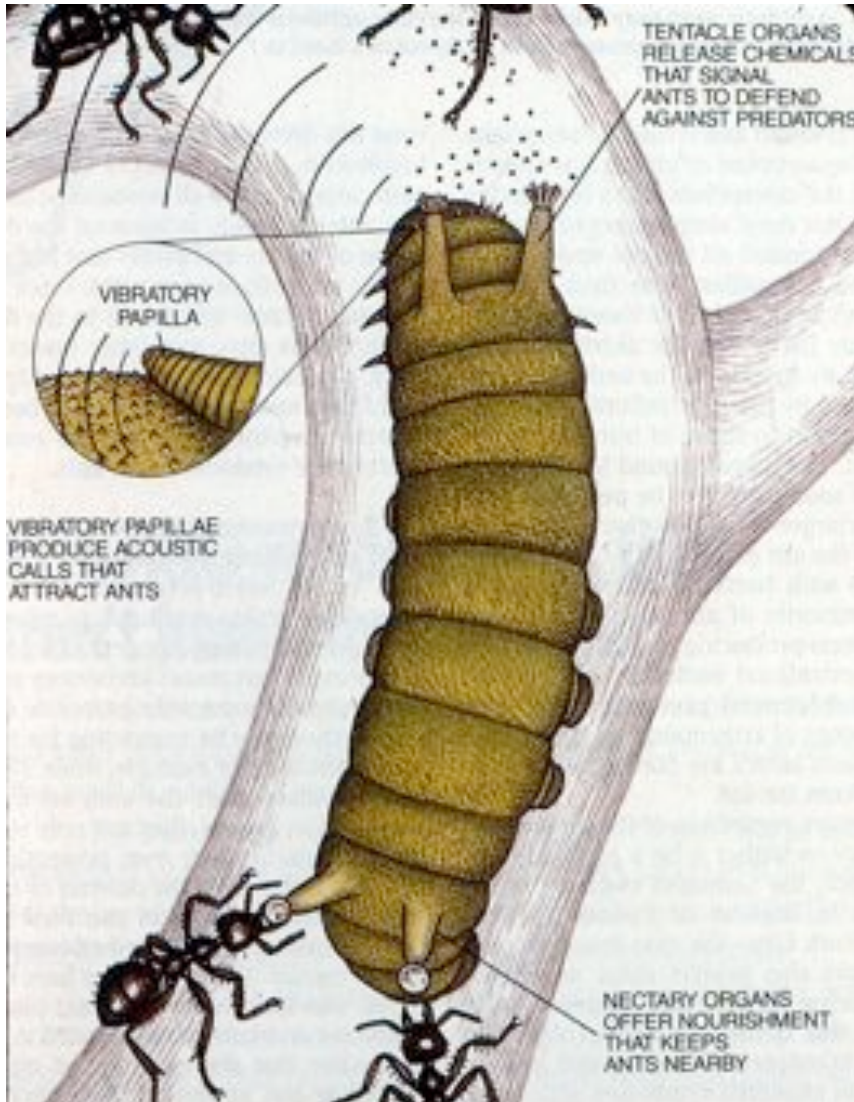


Ants tending to lycaenids

How do the ants find the caterpillars?



Lycaneid caterpillar stridulates with a special structure on its head + this is what ants cue into as they walk around at the base of or on the plants. Ants use subgenual organs in the legs to perceive this vibratory signal.

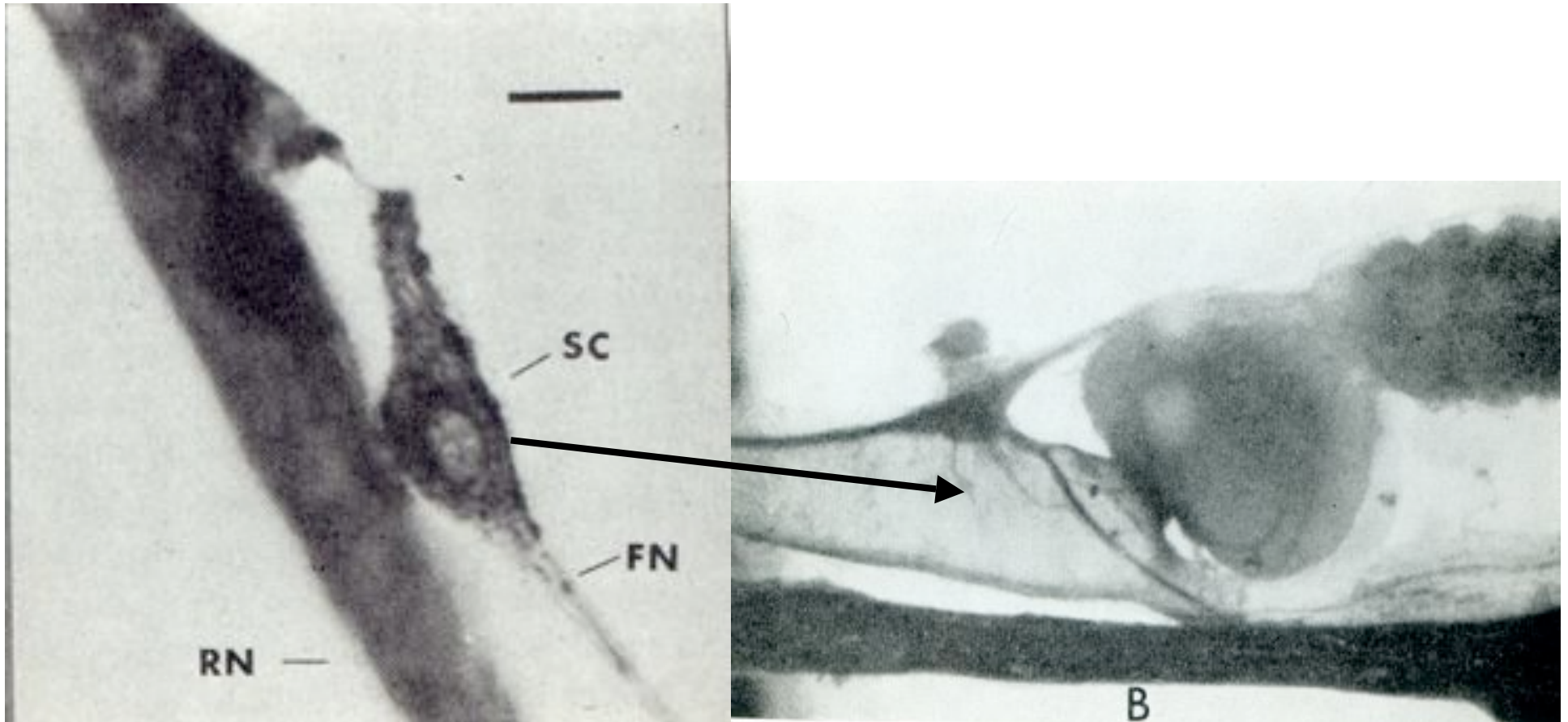


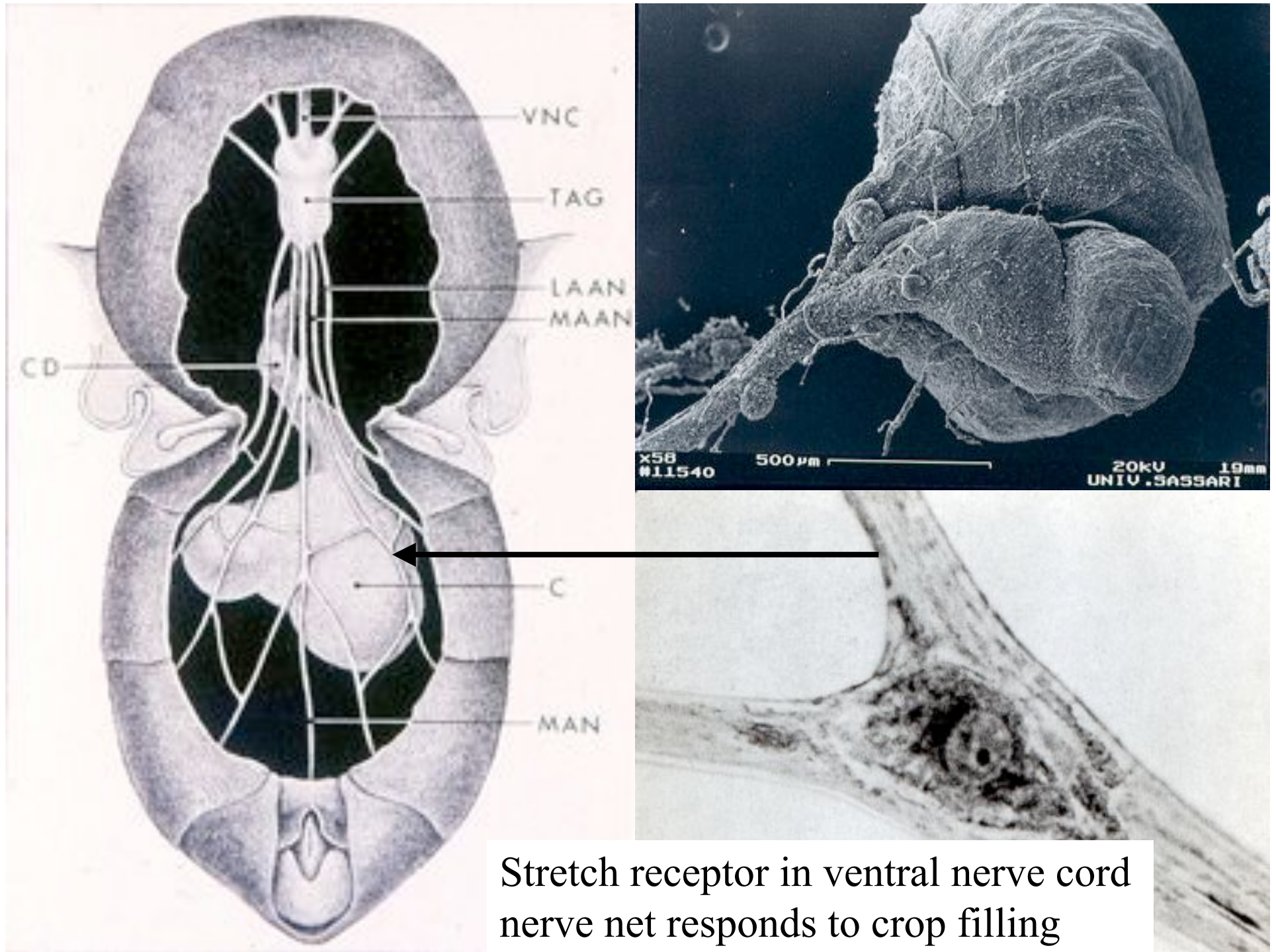
Guero or musical instrument of P.R. + similar to the stridulatory structure on the caterpillar.



Stretch receptors

Stretch receptor of the recurrent nerve attached to the esophageal area in adult *Phormia regina*.



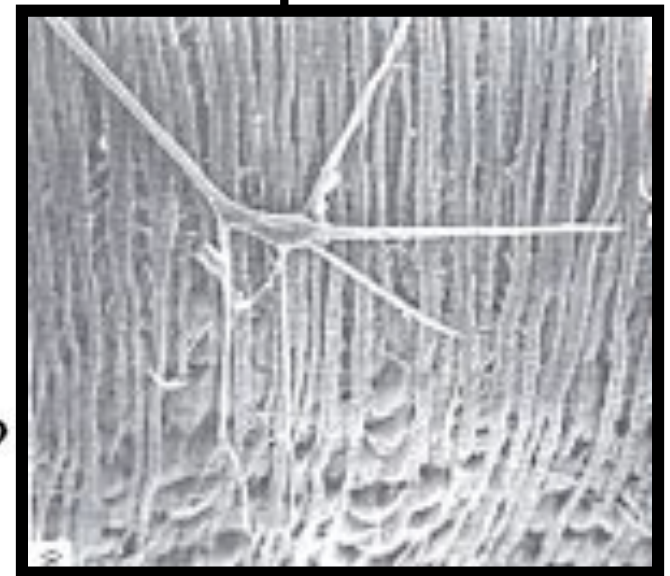
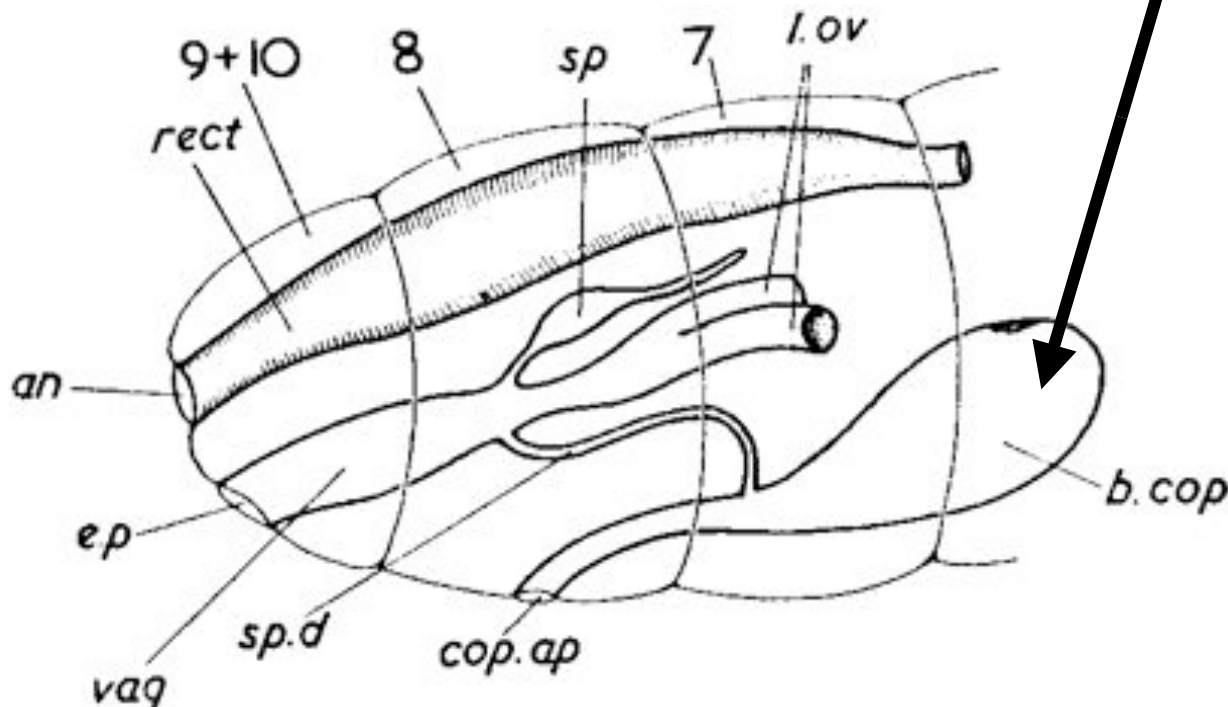
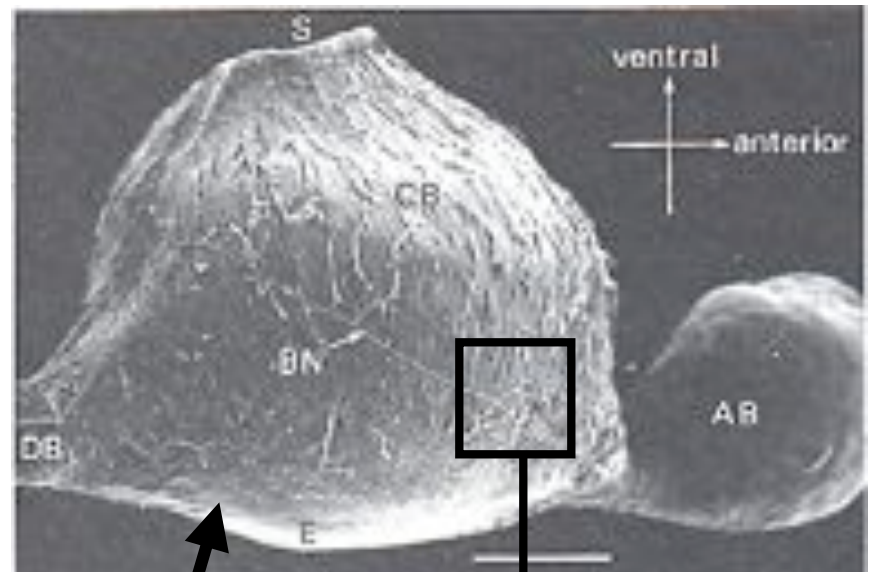


Stretch receptor in ventral nerve cord
nerve net responds to crop filling

Stretch receptor on the internal (hemolymph side) of the bursa copulatrix of adult *Pieris*. Note the musculature of the bursa and the multibranched stretch receptor. As the bursa enlarges, the stretch receptor (BN) that is anchored at each point to the bursa (inside the box) becomes stretched.

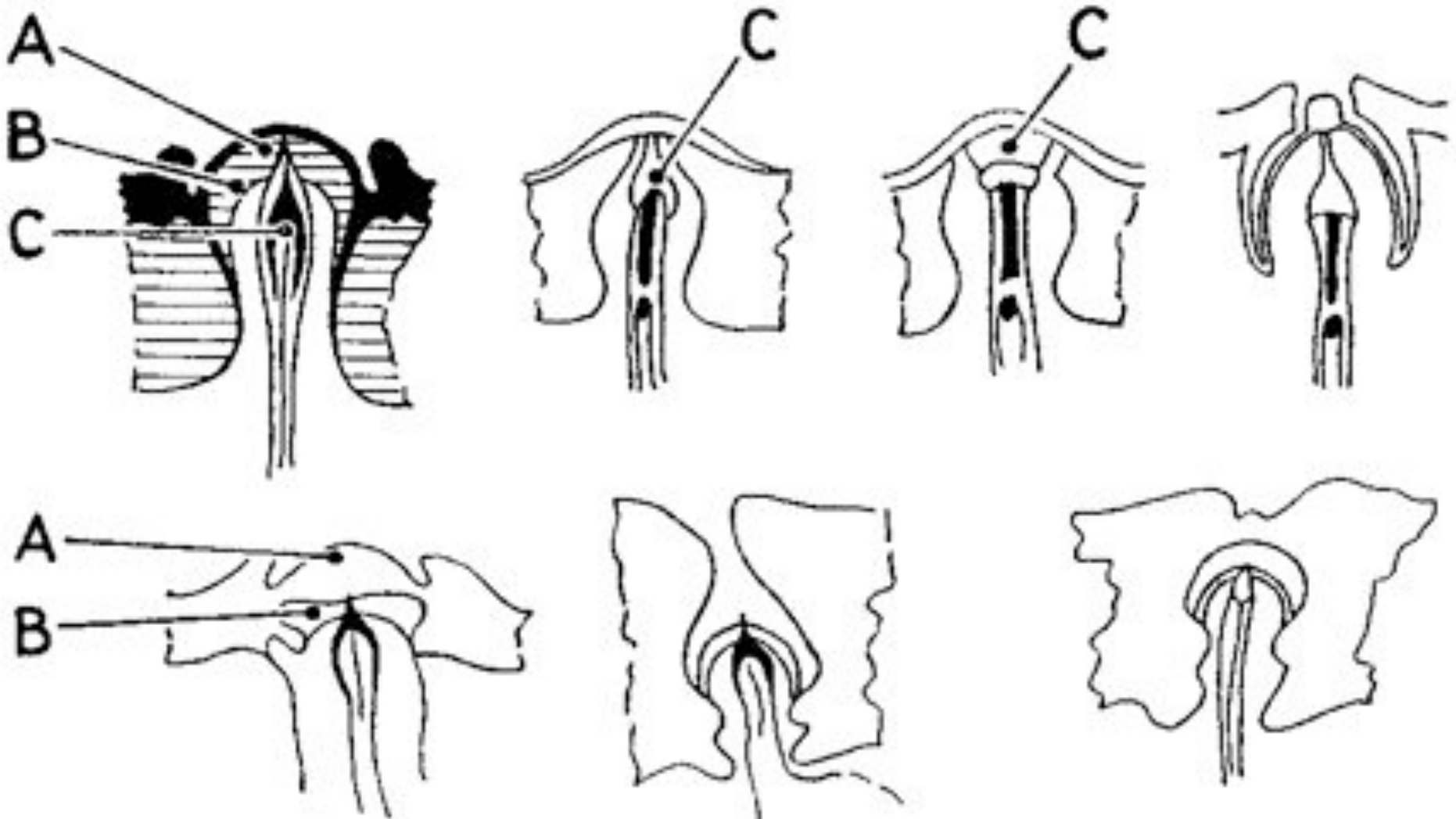
What is deposited in the bursa copulatrix during mating?

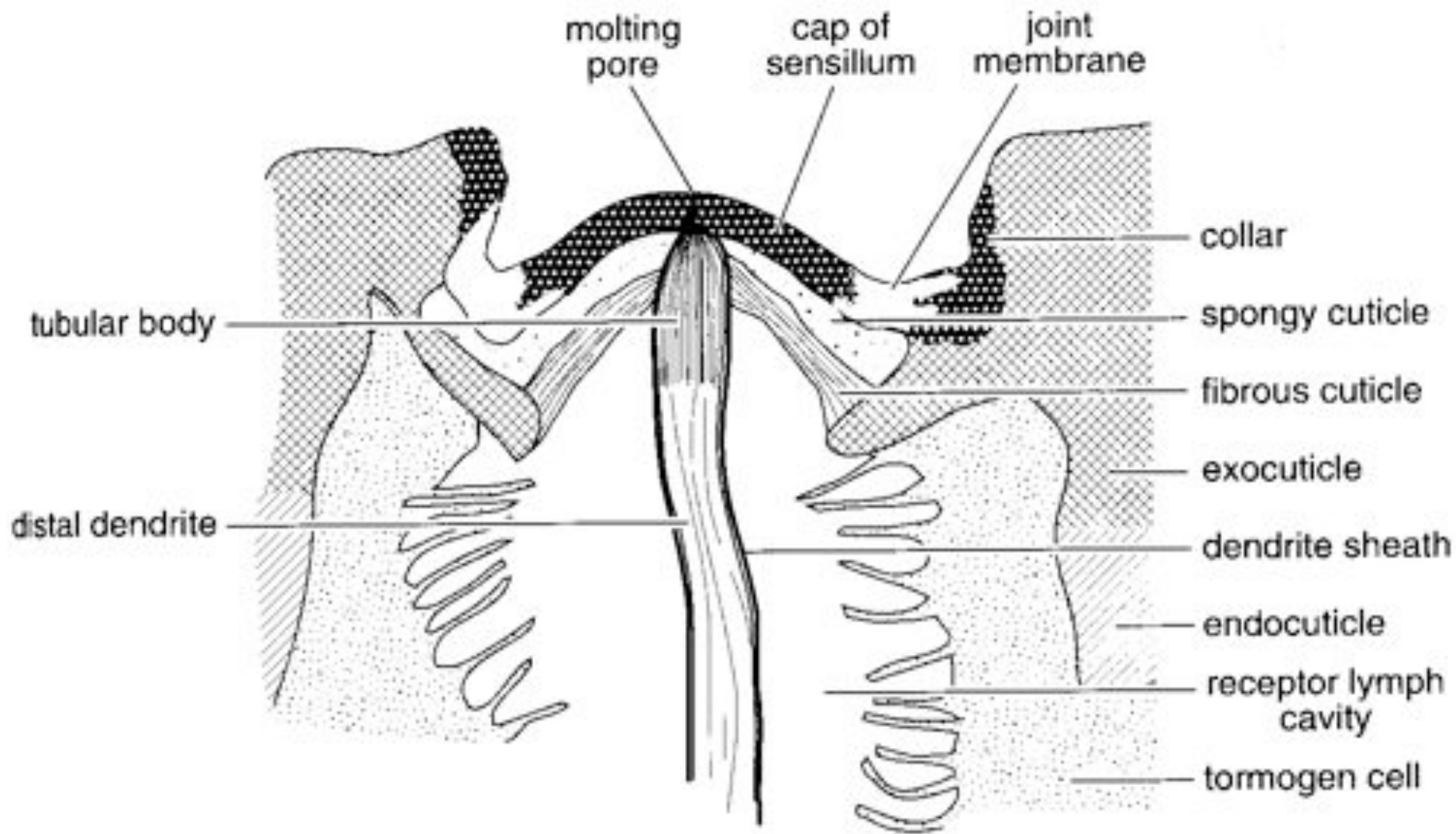
A spermatophore



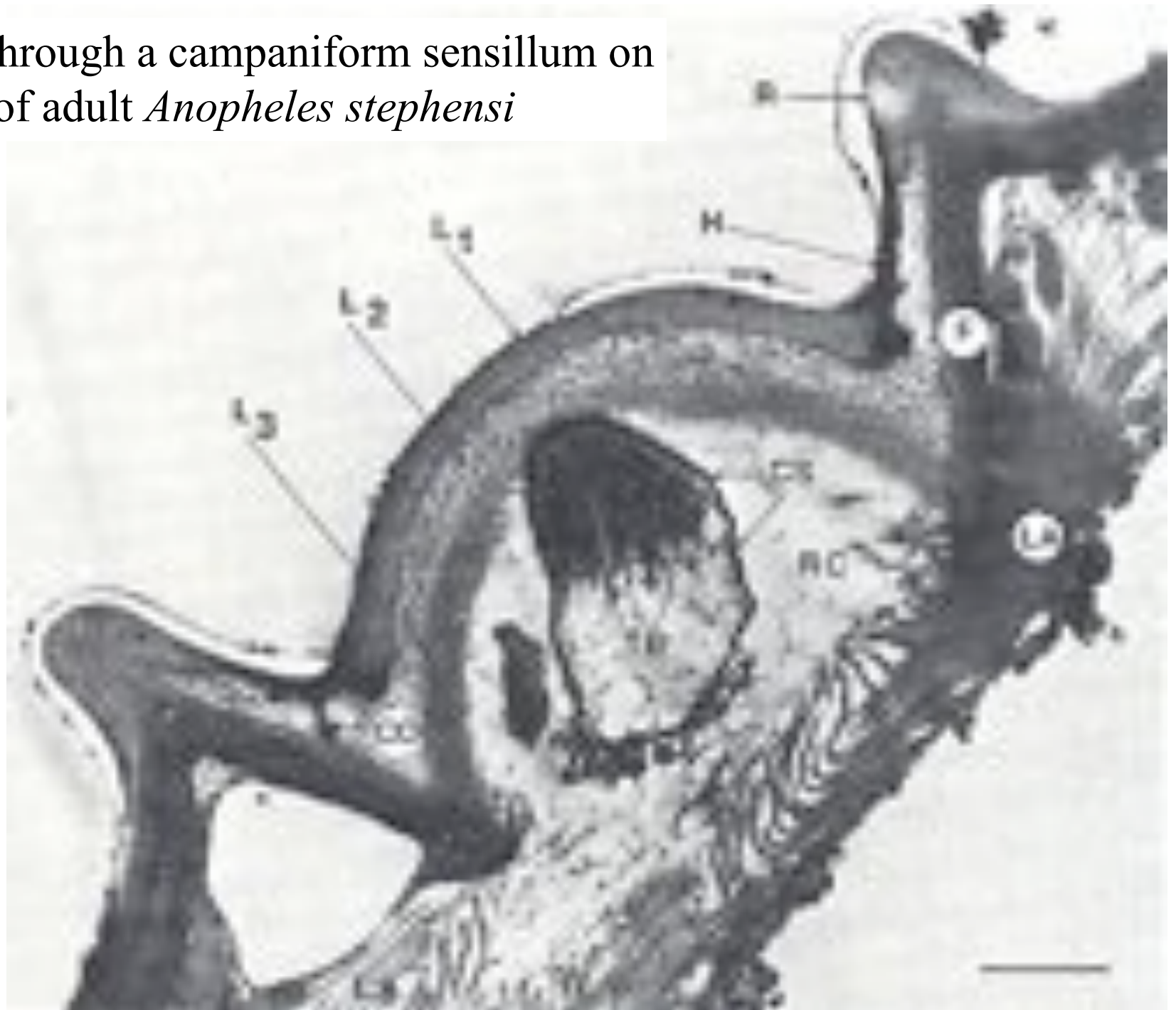
Campaniform sensilla

Structurally a key characteristic is that they have a cap or dome-like piece at the cuticular side that responds to distortion and/or compression





Section through a campaniform sensillum on the palp of adult *Anopheles stephensi*



Specializations of areas on the ovipositor

What sorts of problems does the apple maggot female face when she attempts to lay an egg in a fruit?

- 1. Hardness of the fruit**
- 2. Quality of the fruit**

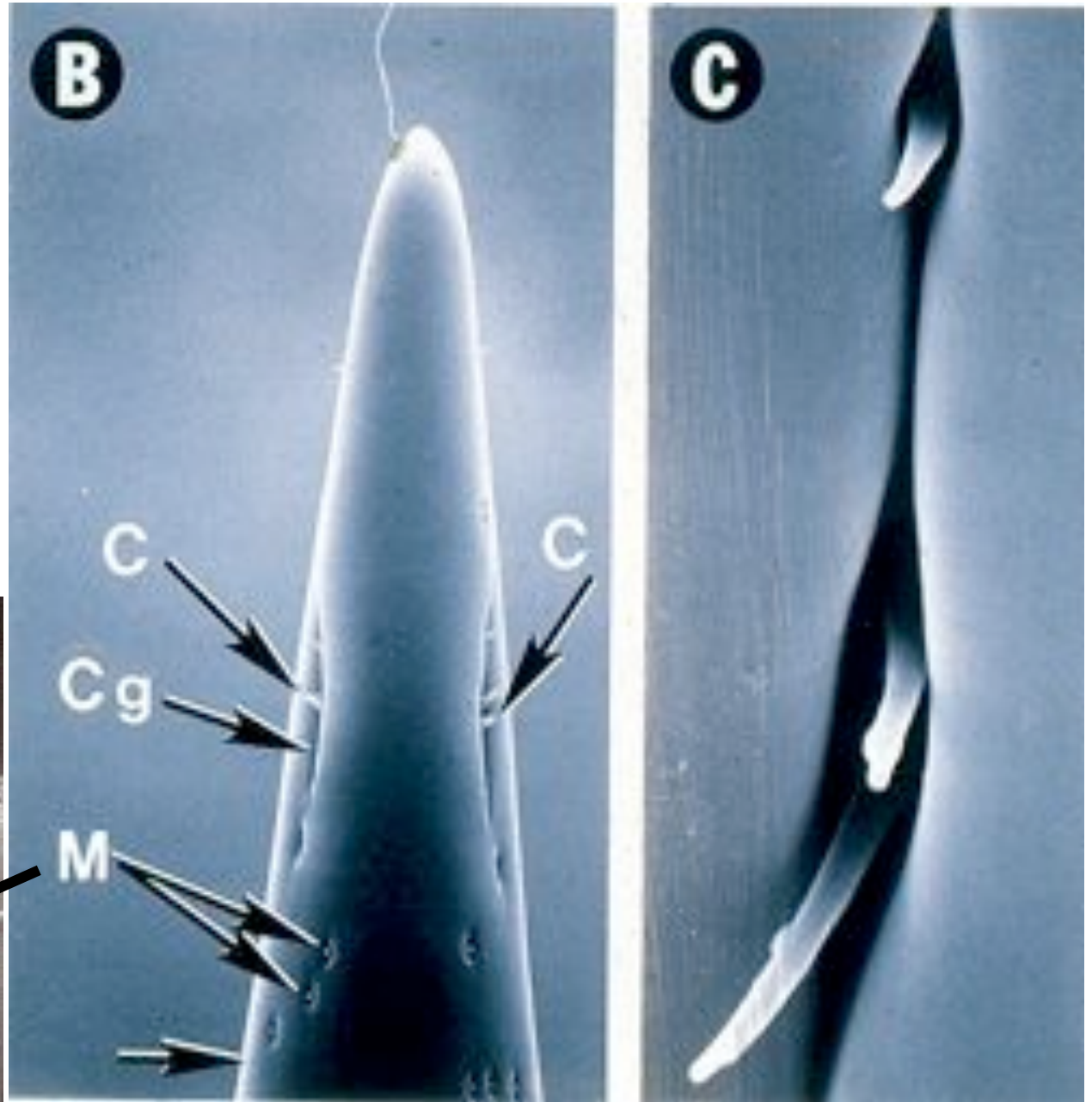
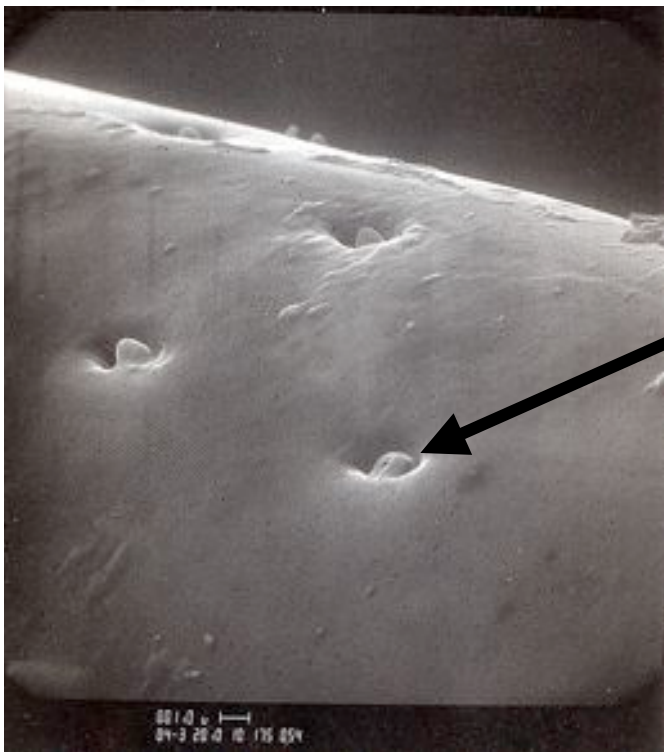
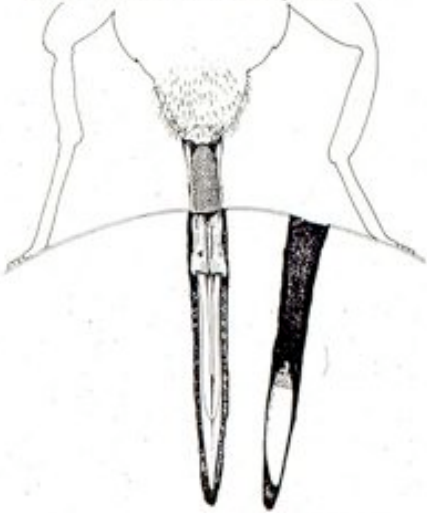
How does the cuticle come into play in this situation?



OVIPOSITION BEHAVIOR IN THE TEPHRITIDS

BY

JOHN G. STOFFOLANO, JR.



M=campaniform sensilla; C=chemosensilla

Most parasites/parasitoids place their eggs into the hemocoel of the host. They do this using their ovipositor and sensing the internal environment of the hemolymph. Very few parasites/parasitoids attack the adults. This may be due to a couple of things:

- 1. Adult cuticle is more difficult to penetrate and**
- 2. The hemocytic response of adults has not been studied that well but suggests that they have fewer hemocytes.**
- 3. Adults may live a short time compared to the immatures, thus shorter time to develop**



Tachinid eggs laid on adult Japanese beetle

1st exam

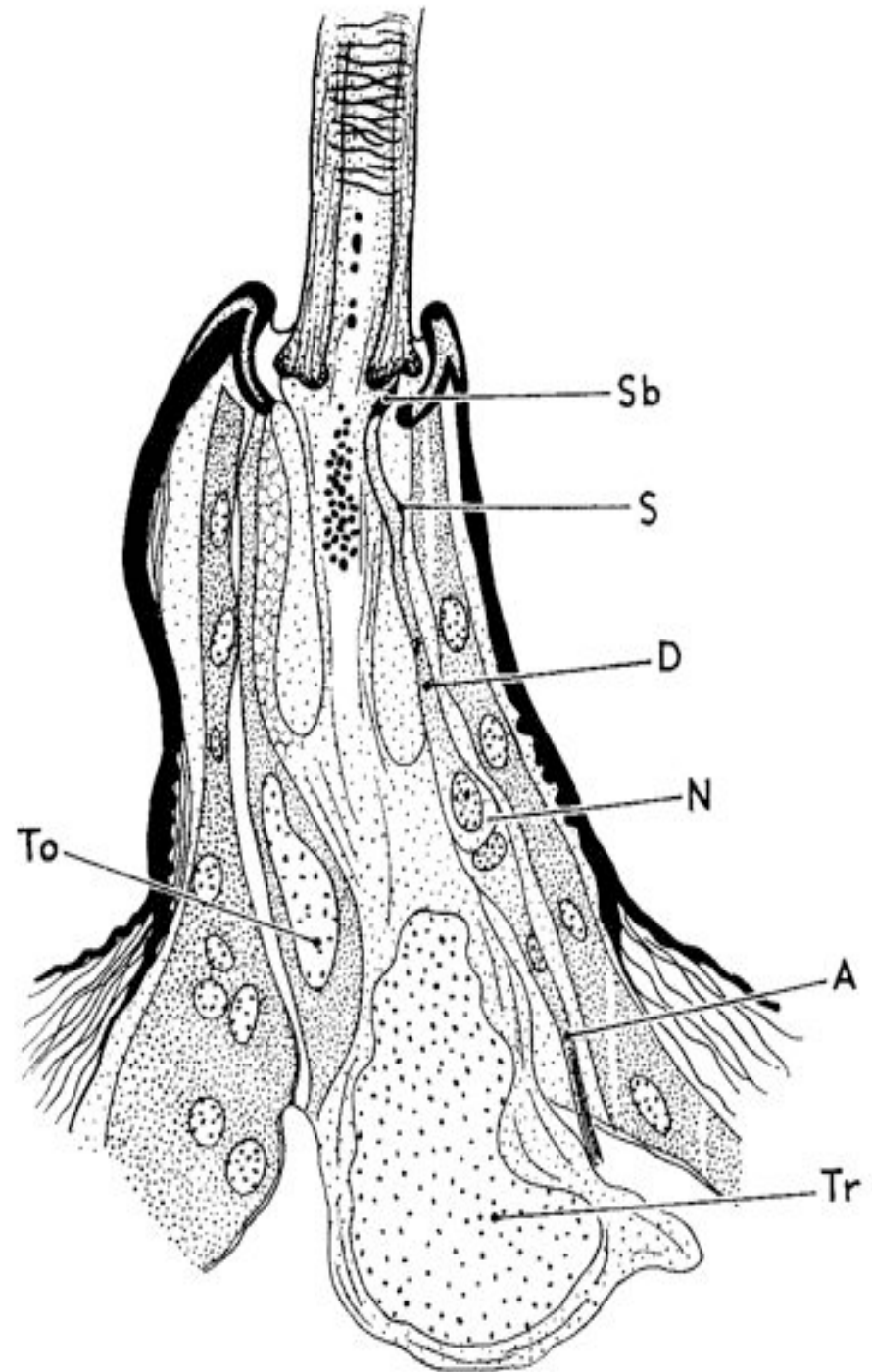
original score	with 7 points added
93%	100%-----A
83%	90%-----A-
80%	87%-----B+
75%	82%-----B
71%	78%-----B-
51%	58%-----F
40%	48%-----F

Hair sensillum

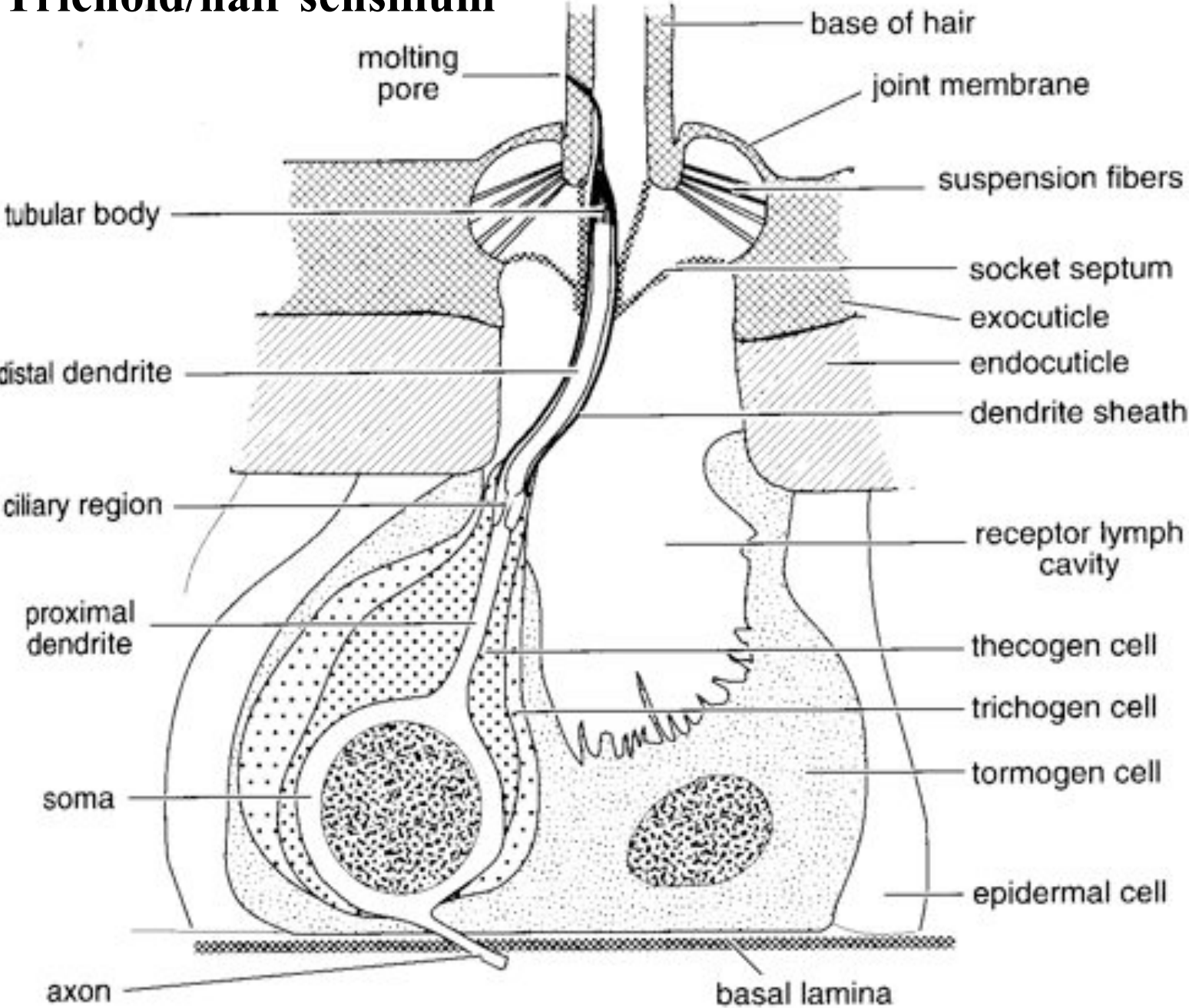
These are moveable structures that are sensory. They do not have a pore to the outside.

They have a scolopoid body (Sb) that aids in the transduction process when the hair moves. This causes the bipolar neuron (N) to depolarize and send an impulse to the CNS.

Note the tormogen (To) cell that produces the hair socket and the trichogen (Tr) cell that produces the hair itself.



Trichoid/hair sensillum



Hair sensilla serve various functions in the insect:

1. Sense of touch

- a. All over the body
- b. Ovipositor
- c. Cerci
- d. Antennae
- e. Mouthparts including palps

2. Air movement

- a. Antenna
- b. Cerci
- c. Front and top of head for monitoring air flow when in flight.
Responsible for maintaining wing beat; aerodynamic sense organs. Are directionally sensitive so control yaw
- d. Caterpillar hairs respond to wing beat frequency of wasp

Hair sensilla serve various functions in the insect:

3. Orientation with respect to gravity

Usually involved proprioceptors

- a. In desert locust they have specialized hairs with swollen bulbs at the tip that are located on the cerci. Center of gravity is presumed to be inside the bulb.
- b. Some have statolith-like structure but they have not been clearly demonstrated to be gravity receptors

4. Pressure receptors-Found in some aquatic insects to monitor depth they are at and/or head/body orientation

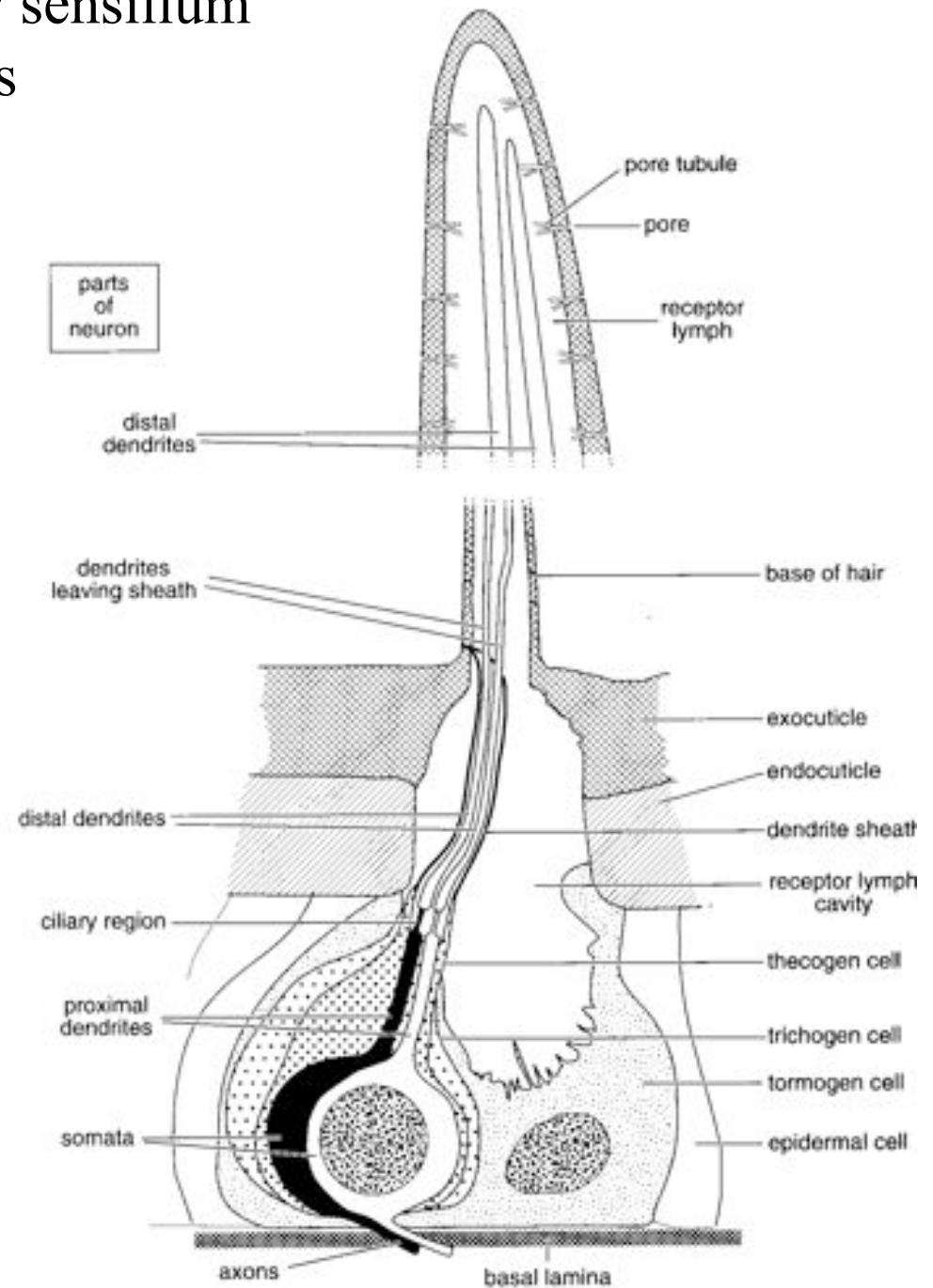
5. Proprioceptors-Mechanoreceptors that usually signal movements or position of parts of the body. Respond to deformations (changes in length) and stresses (tension and compressions) of the body. “The insect maintains position by assessing much information from a multitude of receptors.”

CHEMORECEPTORS

Olfaction-

- 1. The sense of smell or response to volatile or gaseous chemicals**
- 2. Axons from the olfactory receptors terminates in antennal lobes**
- 3. Sensilla are multiporous**
- 4. Usually no socket region to hair**
- 5. Number of neurons in each olfactory sensillum varies from 2 to 20**
- 6. Axons end, without synapses, in the antennal lobes that form arborizations known as the olfactory glomeruli in the deutocerebrum**
- 7. Pheromone-binding protein is produced by the trichogen and tormogen cells**
- 8. Located on:**
 - a. antenna**
 - b. palps**
 - c. genitalia**

Note that this SEM of an olfactory sensillum clearly shows that it is multiporous



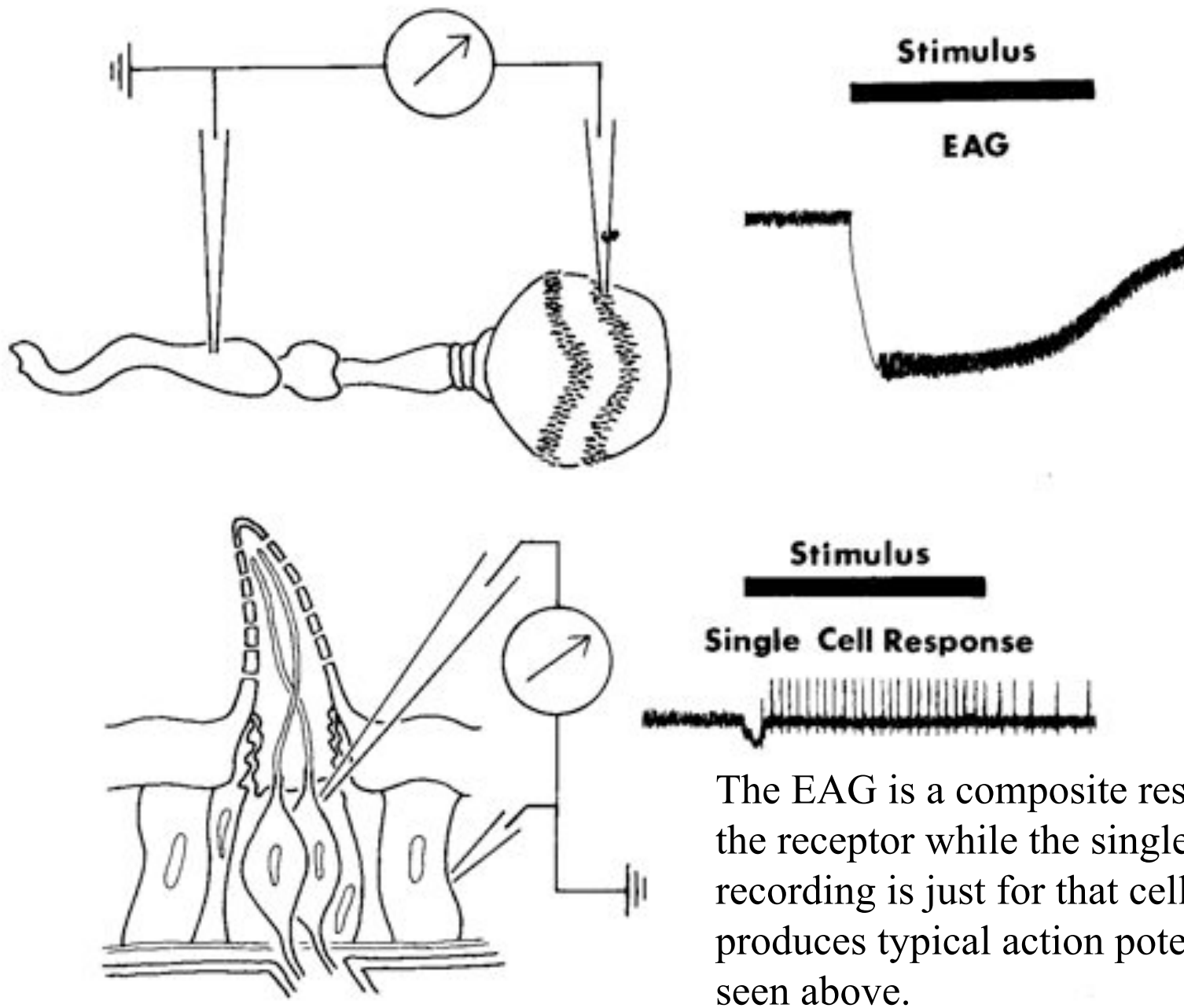


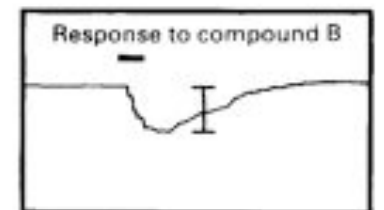
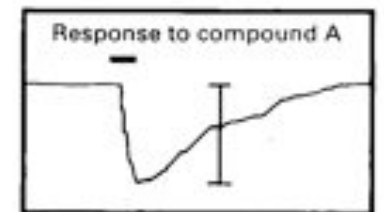
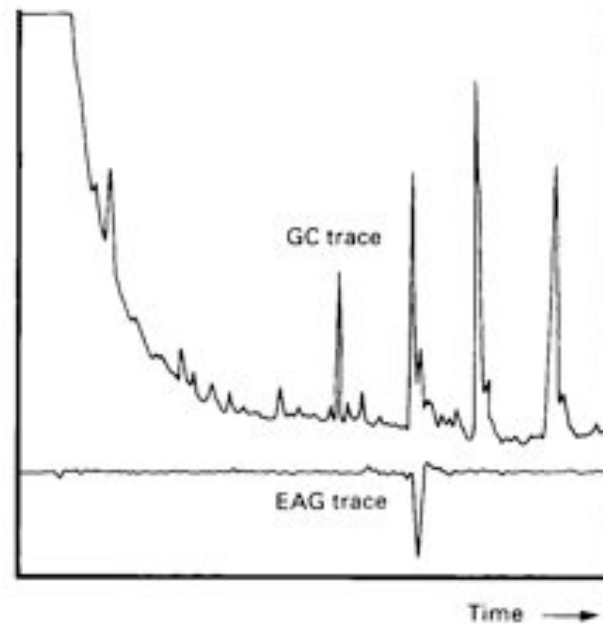
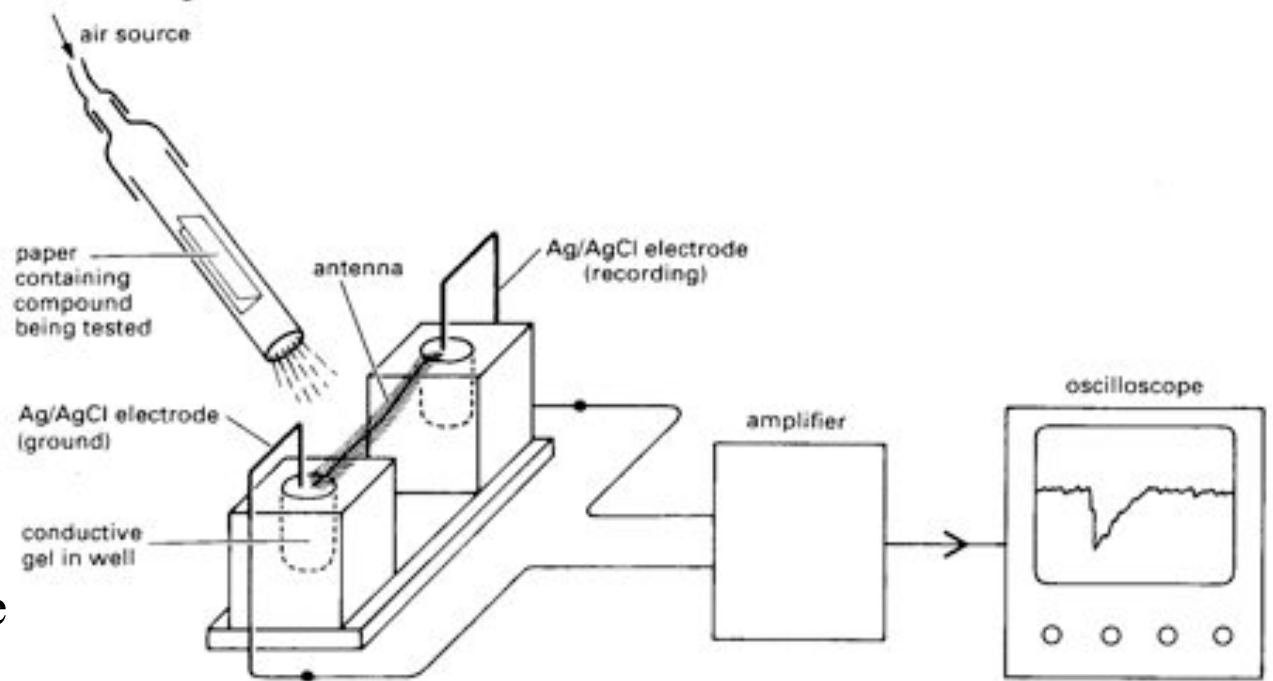
Fig. 3.1. Schematic diagram of the electroantennogram (EAG) and single cell recording techniques.

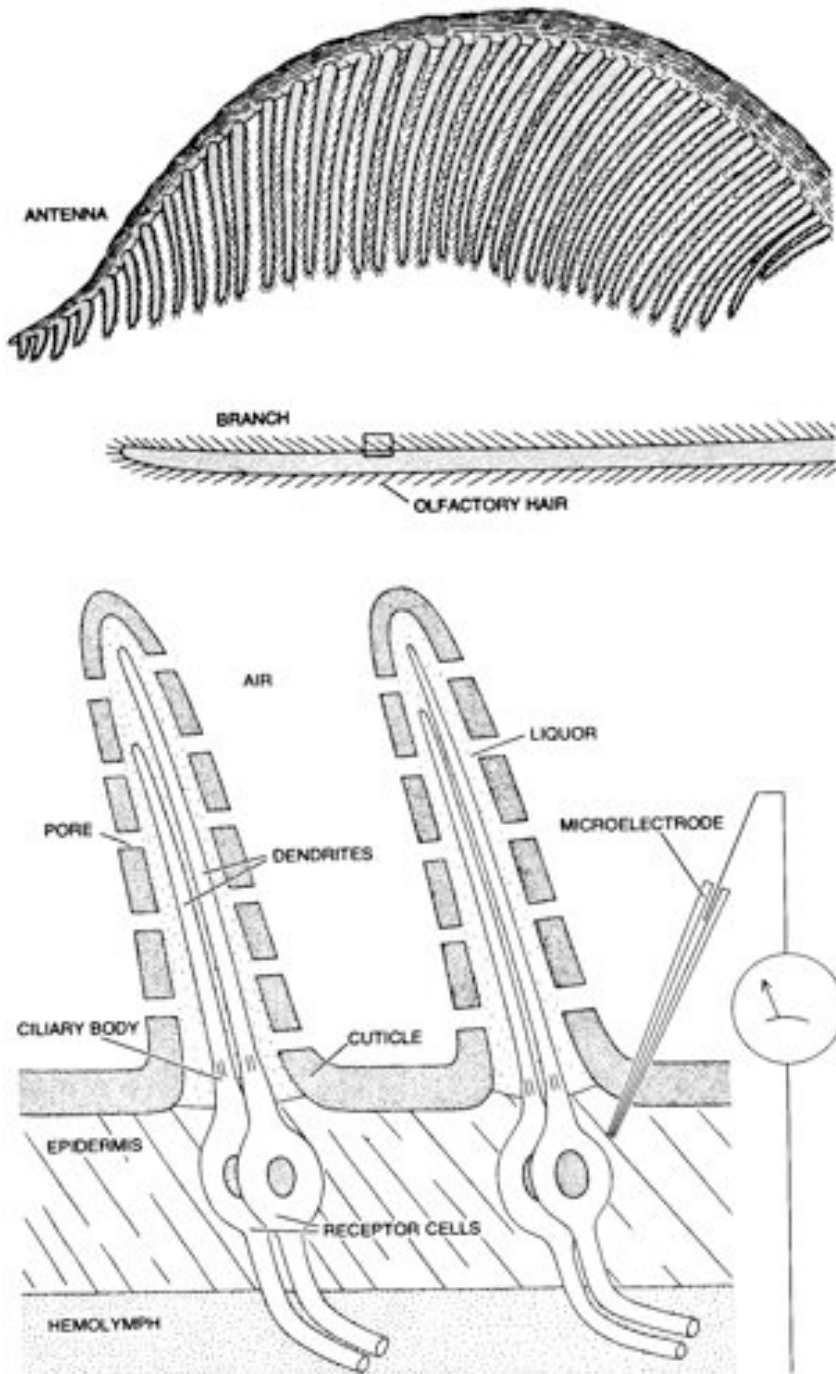
The EAG is a composite response of the receptor while the single cell recording is just for that cell and produces typical action potentials as seen above.

Evaluating the olfactory antennal response to various chemicals using the EAG (electroantennogram) technique.

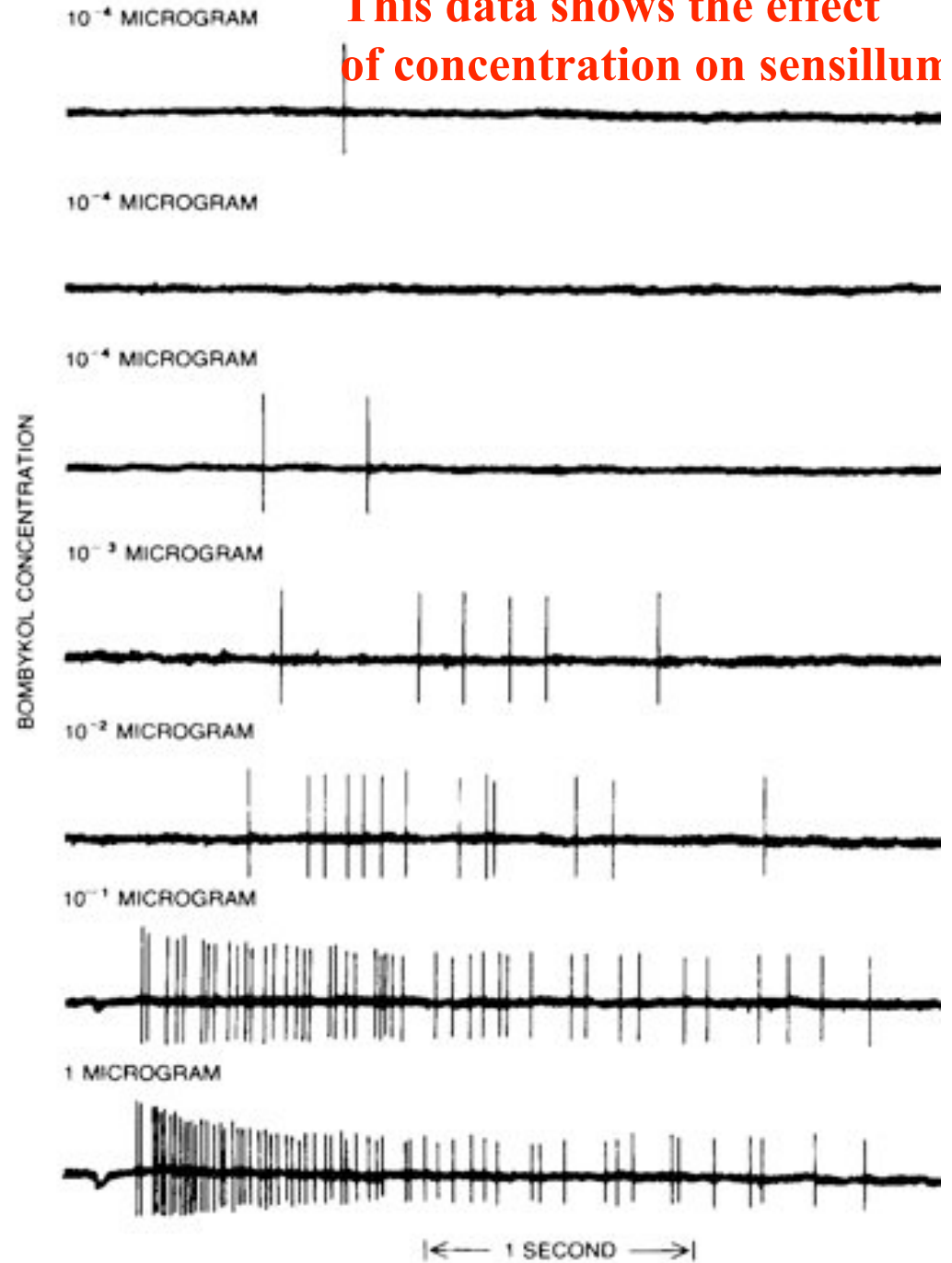
By using the EAG technique in conjunction with the HPLC technique, one is able to identify which compounds in the HPLC the insect's antenna is responding to based on the EAG response.

Box 4.2 The electroantennogram





This data shows the effect of concentration on sensillum

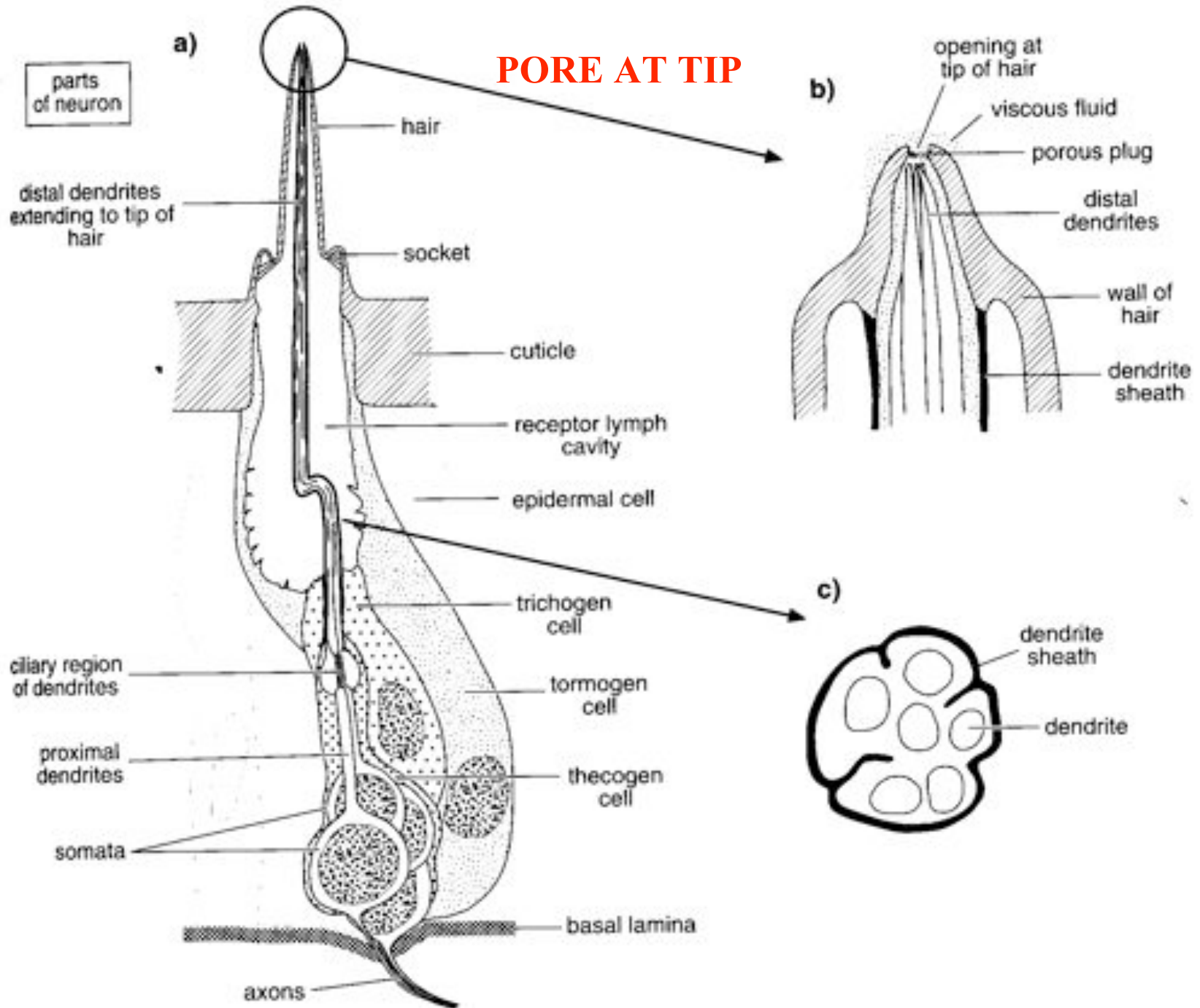


CHEMORECEPTORS

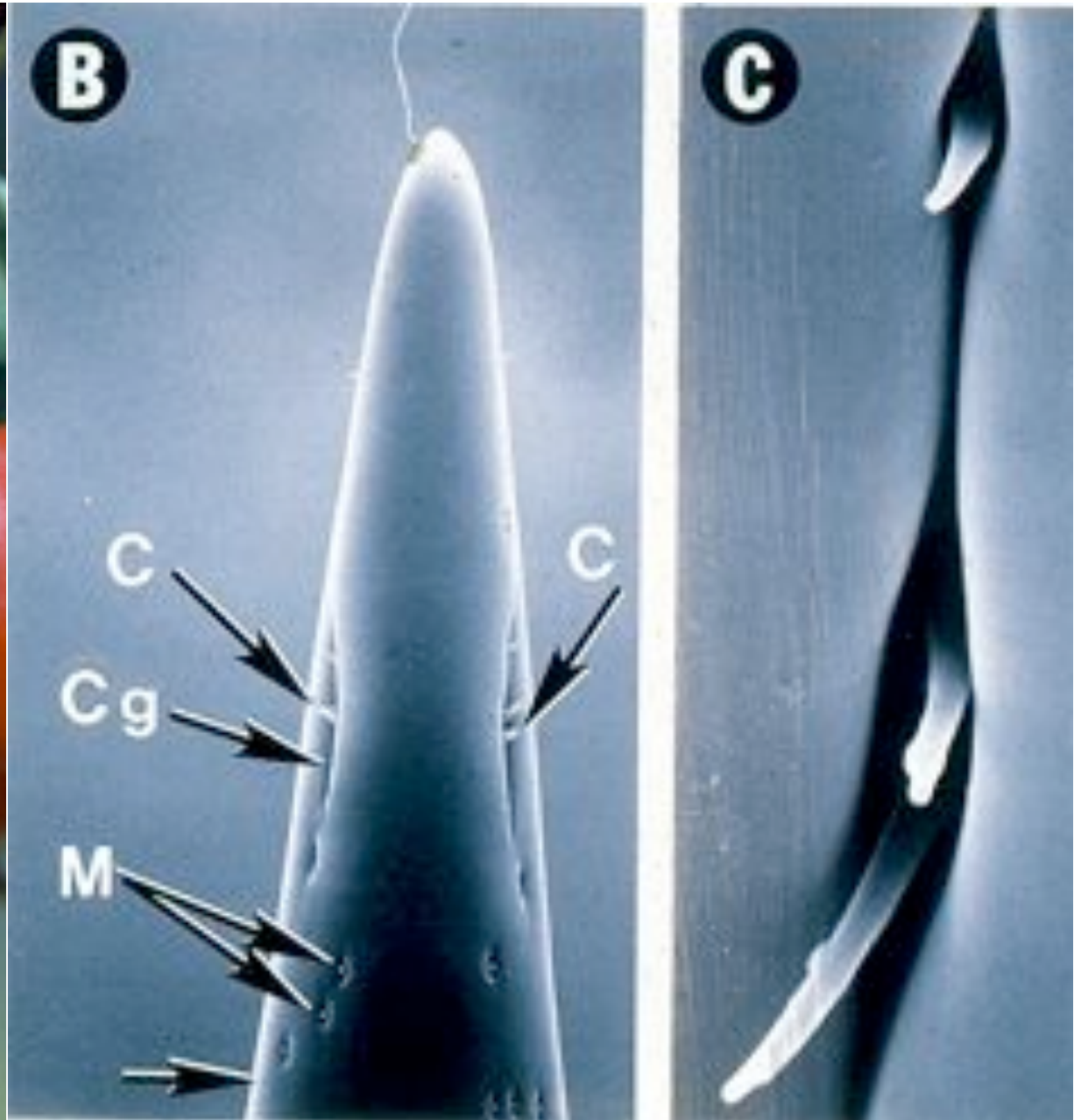
Gustation or Contact

chemoreception-

- 1. Detection of chemicals by contact**
- 2. Axons from the contact chemoreceptors terminate in the ganglion in which the receptors are located**
- 3. Sensilla are uniporous with pore at tip**
- 4. Usually has a socket region to hair giving it some mobility**
- 5. Usually have 4 chemosensitive neurons**
- 6. They can be located any where on the body but are found on:**
 - a. labrum**
 - b. maxillae**
 - c. labium**
 - d. antenna**
 - e. tarsi**
 - f. ovipositor**



Contact chemosensilla (C) on the ovipositor of the apple maggot, *Rhagoletis pomonella*.



OVIPOSITION BEHAVIOR IN THE TEPHRITIDS

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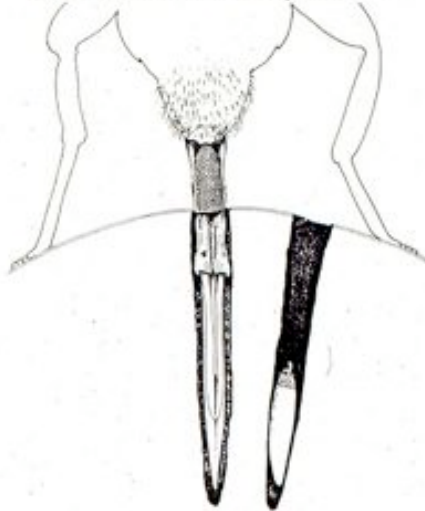
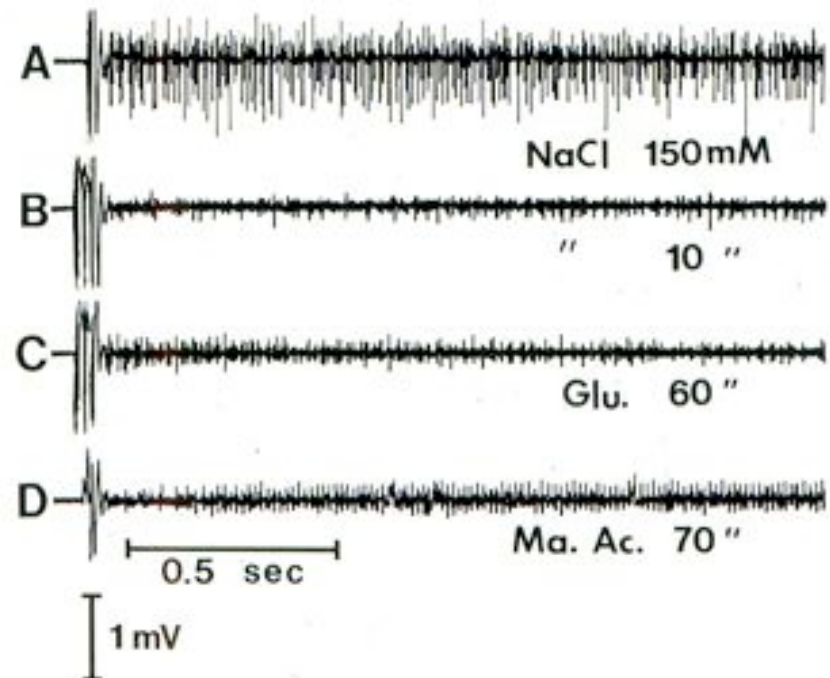


Table 2.-The effect of chemical treatment of the ovipositor sensilla with NaOH on oviposition behavior of *R. pomonella*.

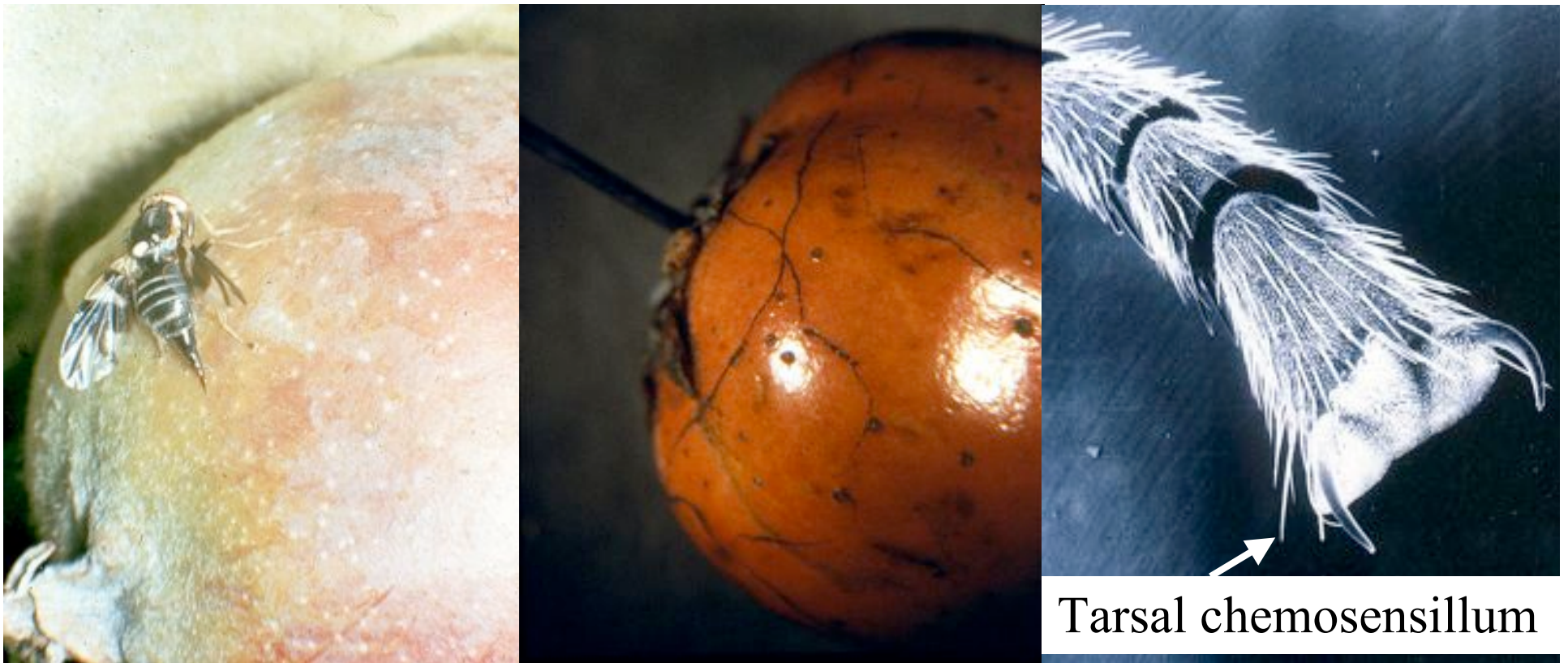
Condition of ovipositor	Treated		Control	
	Holes	Eggs	Holes	Eggs
Untreated	20	17	23	2
Treated-.1M NaOH	14	12	10	3
Treated- 1M NaOH	35	25	34	23

Treated domes contain 100 mM fructose

Using the over the hair recording technique one can test various substances, such as malic acid, to see if the chemosensilla responded to them and to see what kinds of chemical cues inside the fruit the female is cueing into when making the decision to lay an egg.



Below is a female *Rhagoletis pomonella* using her ovipositor to mark the fruit with the oviposition deterrent pheromone. In order to show that a fluid is secreted, powder from the copy machines was sprinkled onto the fruit and when the secretion was laid down it formed trails. To the right is an SEM of a tarsal contact chemsensing that responds specifically to this pheromone. Stadler, E., B. Ernst, J. Hurter & E. Boller. Tarsal contact chemoreceptor for the host marking pheromone of the cherry fruit fly, *Rhagoletis cerasi*: responses to natural and synthetic compounds. *Physiol. Entomol.* 19: 139-151.



Contact chemoreceptors are uniporous or have one pore (black arrow) usually located at the tip. Below are two chemoreceptor hairs from adult *Phormia regina*

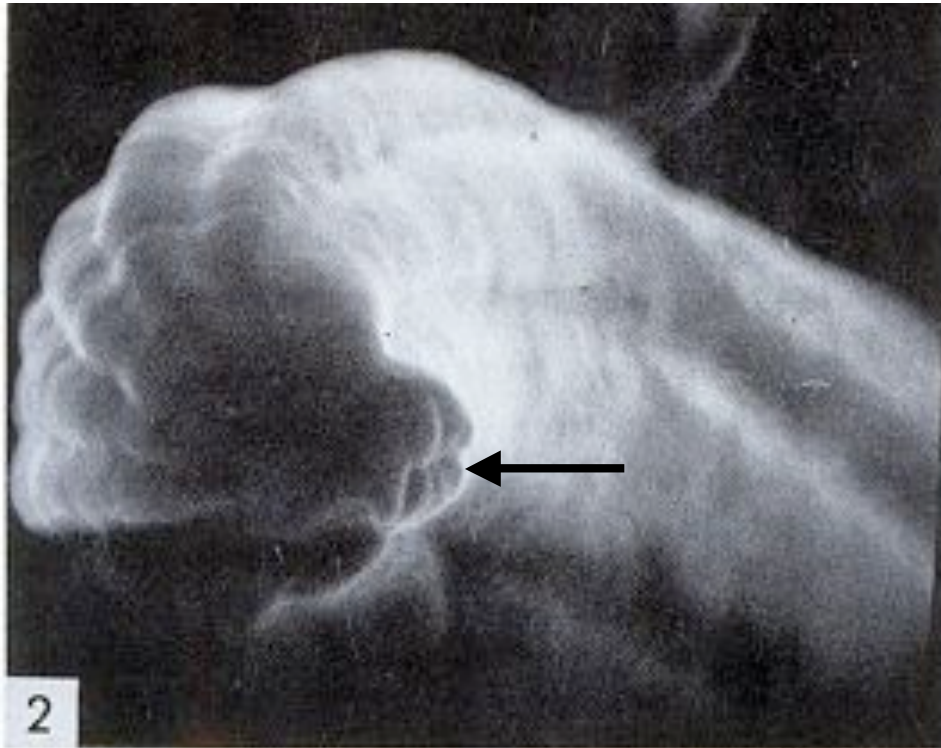
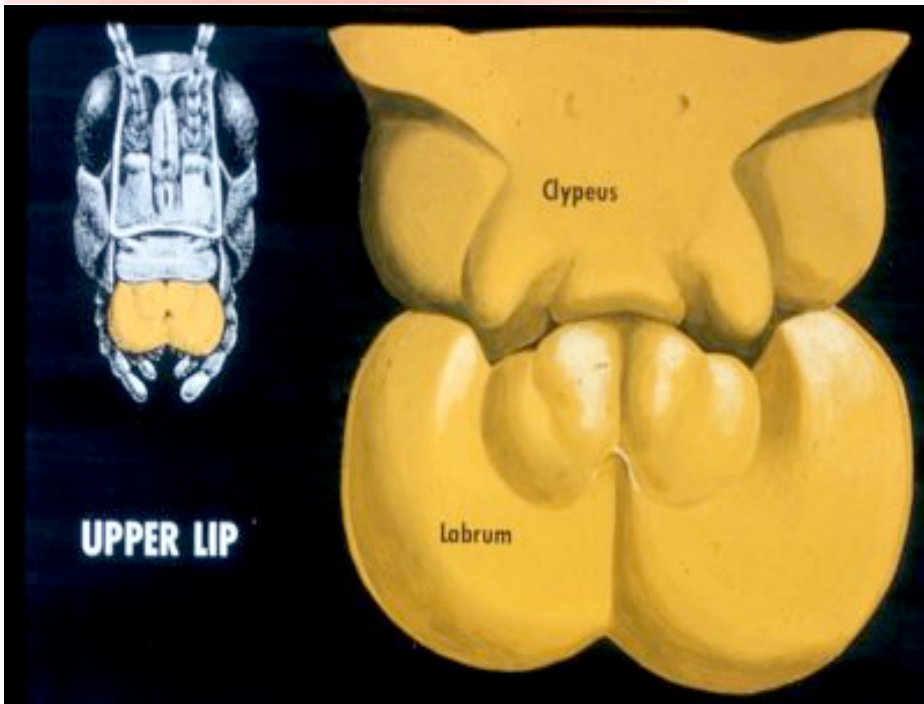
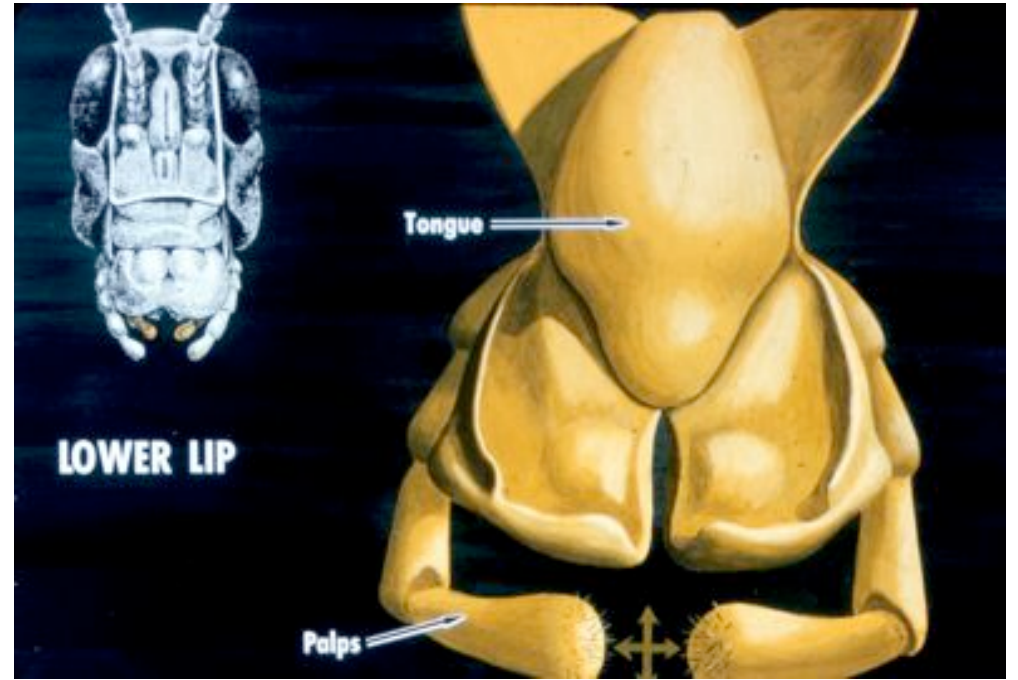


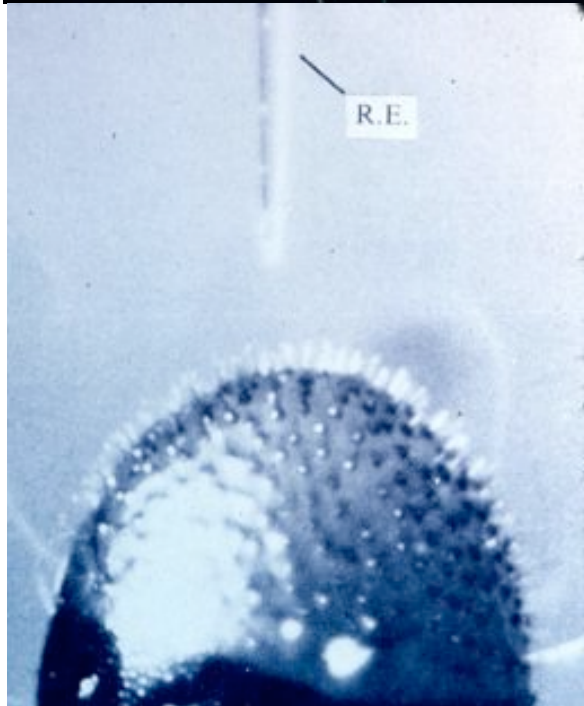
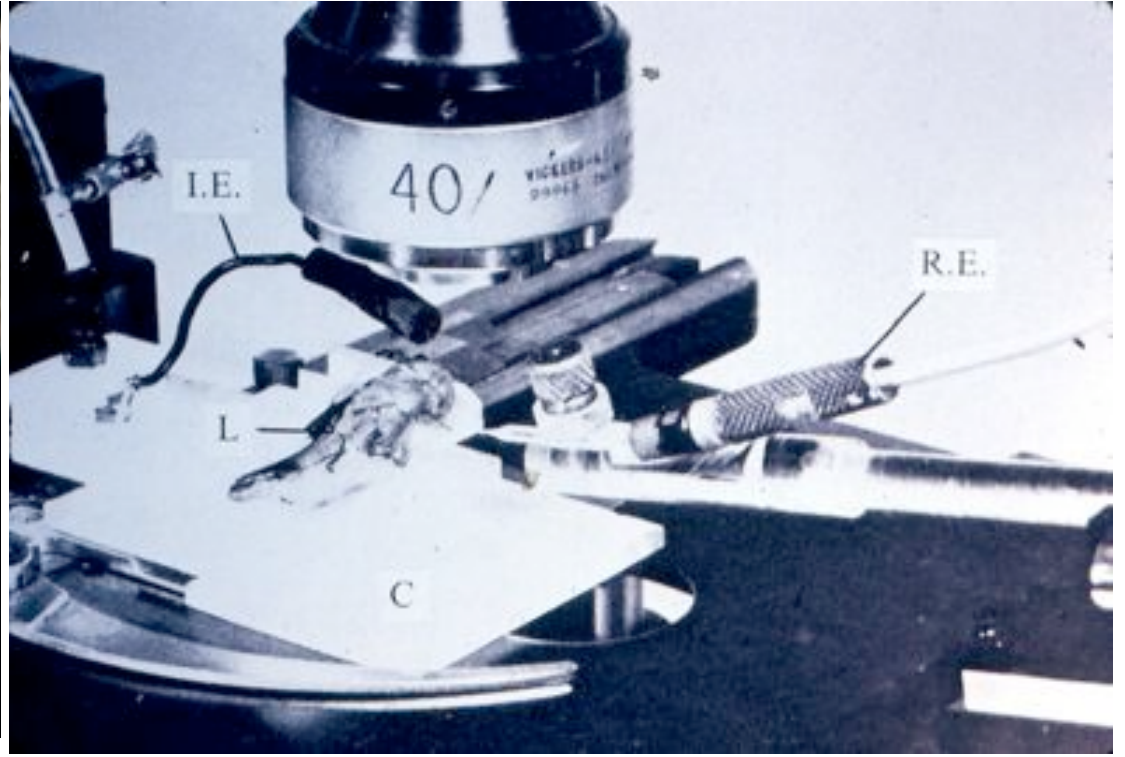
FIG. 2. Recurved type A tarsal hair showing dimpled tip free of exudate ($\times 20,000$) (Photographed with the scanning electron microscope at Florida State University, V. G. Dethier and R. Parker.)

FIG. 1. Largest type of labellar hair showing exudate at tip. ($\times 12,000$) (Photographed with the scanning electron microscope at Florida State University, V. G. Dethier and R. Parker.)

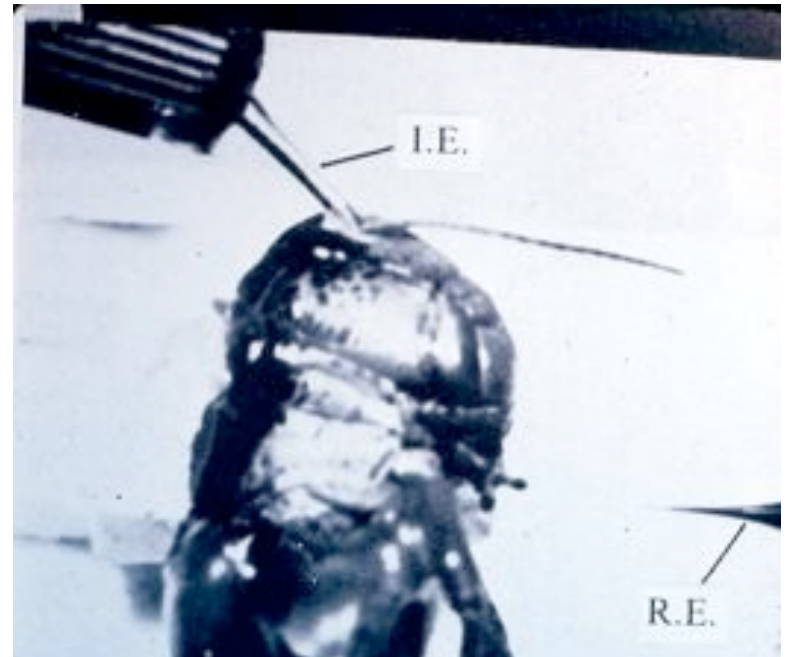


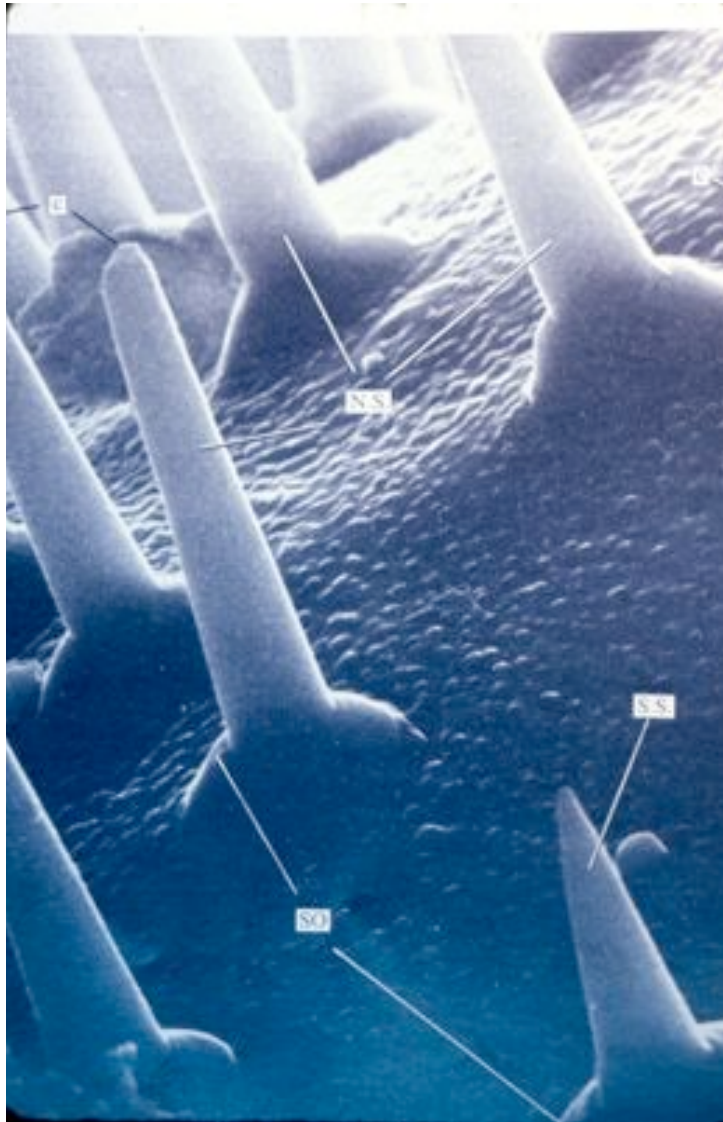
Gustatory sensilla
on the inner
surface of the
labrum



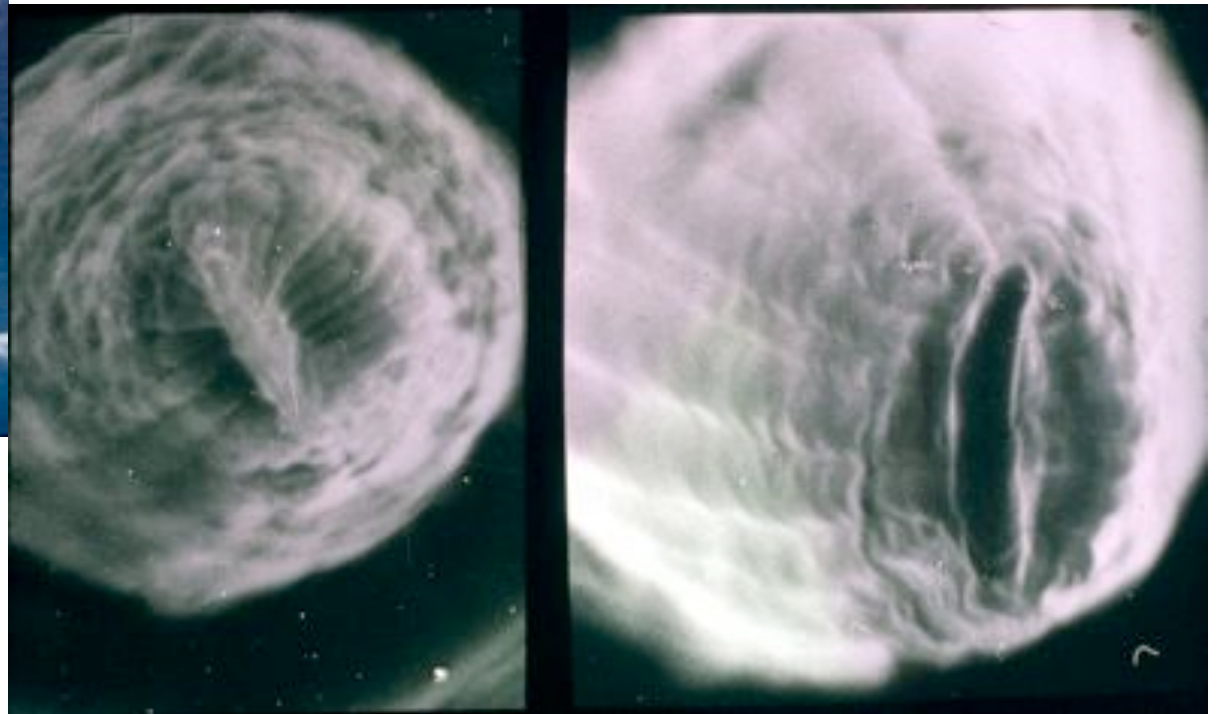


PALPS





Neurobiologists want to know if things are modulated or controlled by the peripheral nervous system and/or the central nervous system. One of the few cases of peripheral modulation by a sensillum is with the locust that is able to close the tip of the chemoreceptors on the palps, thus influencing stimulation and input. It is believed the closing of the tip is influenced by hormones or chemicals in the hemolymph that are released depending on feeding.



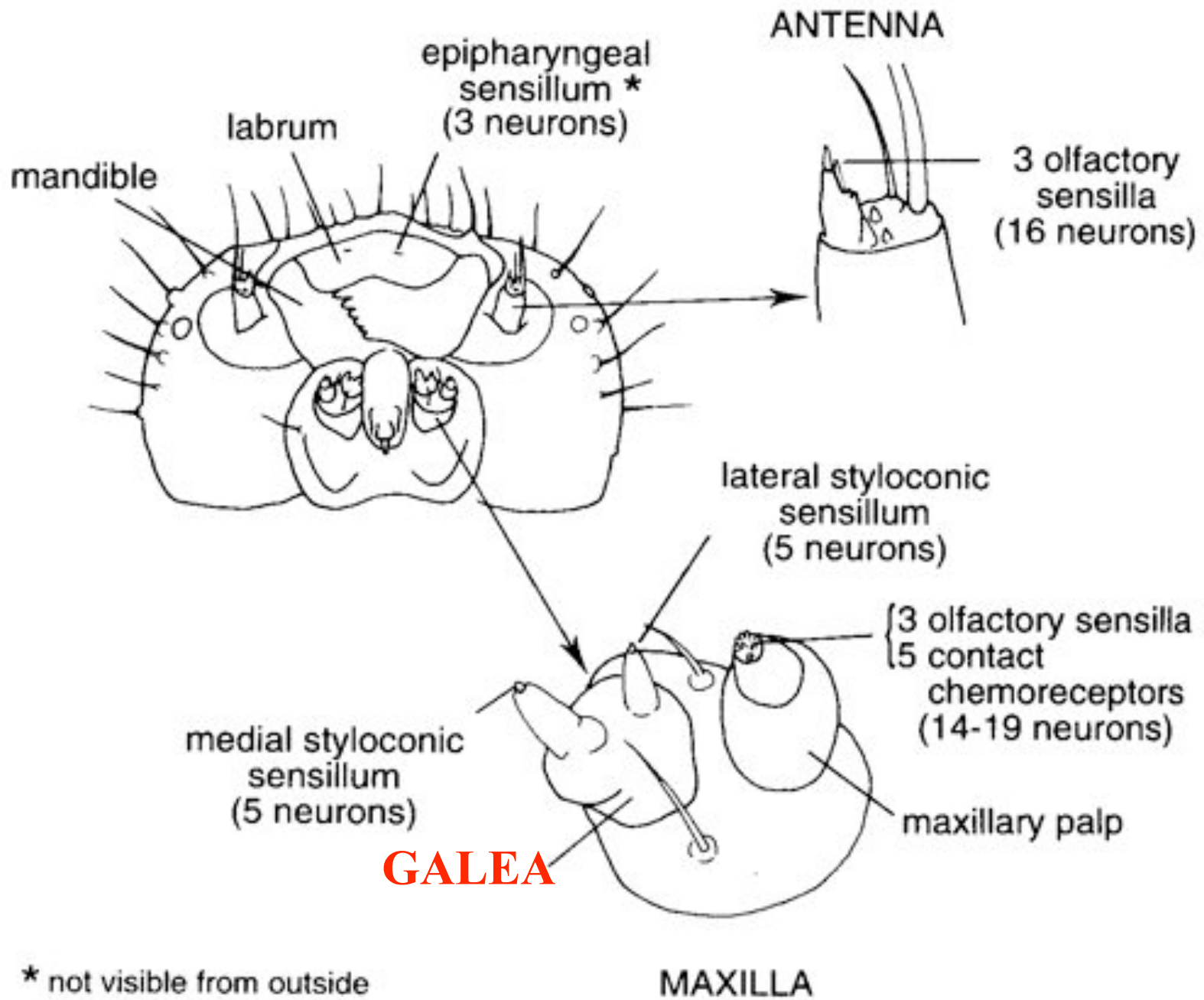


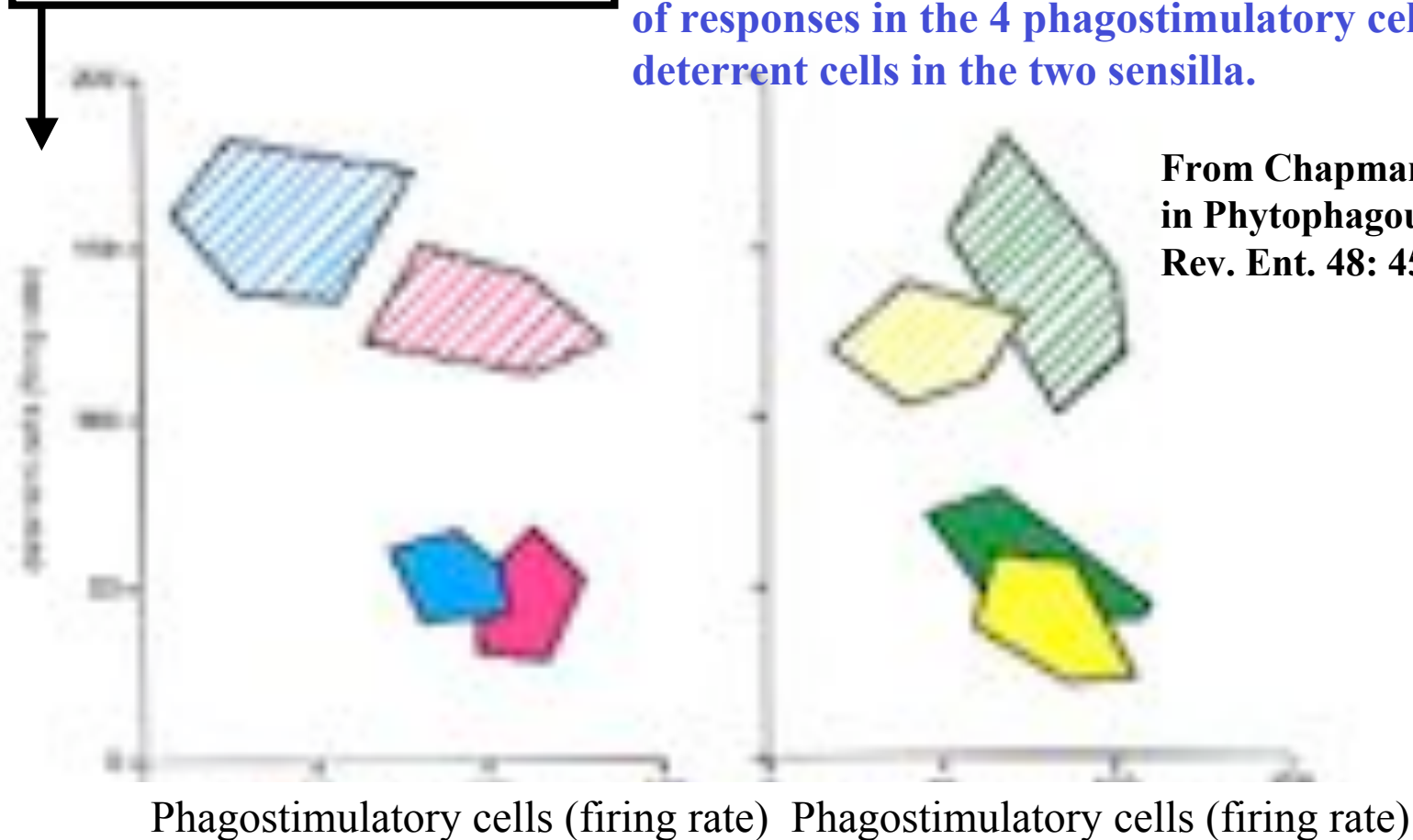
Figure 3.4. Diagram of the head of a caterpillar seen from below

Galeal sensillum



Deterrent cells (firing rate or impulses/unit of time)

Pattern response produced by saps of host and nonhost plants in the galeal sensilla of 4 polyphagous noctuid caterpillars. Each caterpillar was stimulated with saps of 4 plants that were eaten (solid colors) and 4 that were rejected (hatched colors). Each polygon encloses the sums of responses in the 4 phagostimulatory cells and 4 from the deterrent cells in the two sensilla.

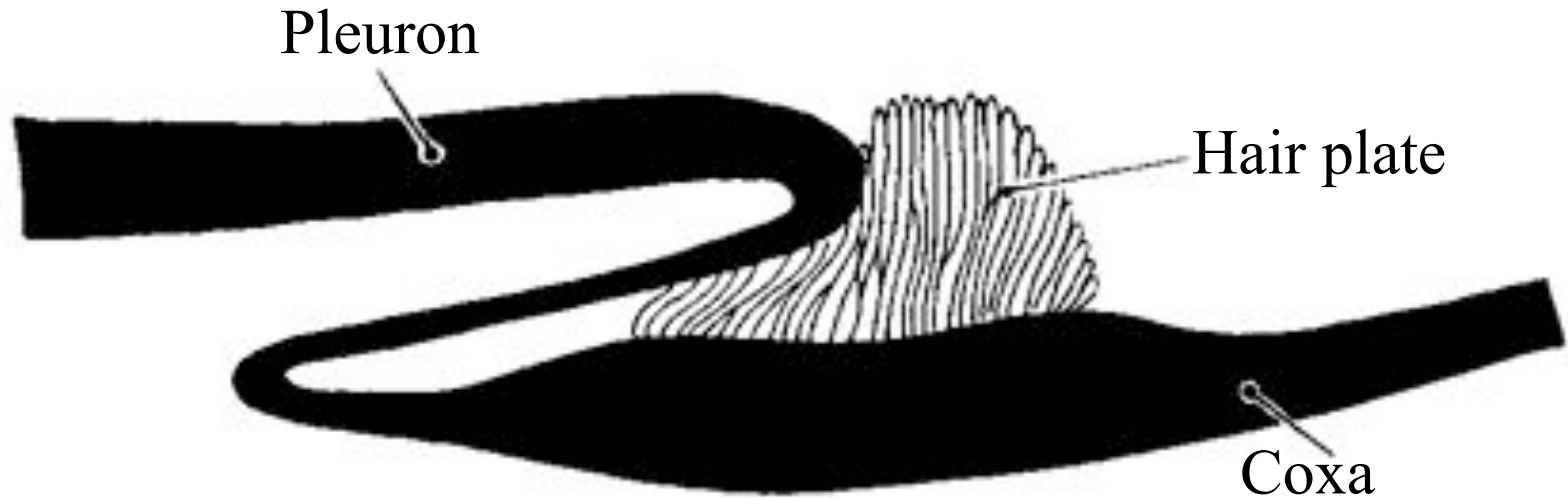


From Chapman 2003. Gustation in Phytophagous insects. Ann. Rev. Ent. 48: 455-84.

 <i>Heliothis virescens</i>	 <i>Spodoptera frugiperda</i>
 <i>Helocoverpa armigera</i>	 <i>Spodoptera littoralis</i>

PROPRIOCEPTORS

Hair plates or position receptors-Hair sensilla that are located in patches. Located in neck region, joints of legs and palps. The hairs are stimulated by folds of the intersegmental membrane or contact with adjoining surfaces as the joints move.



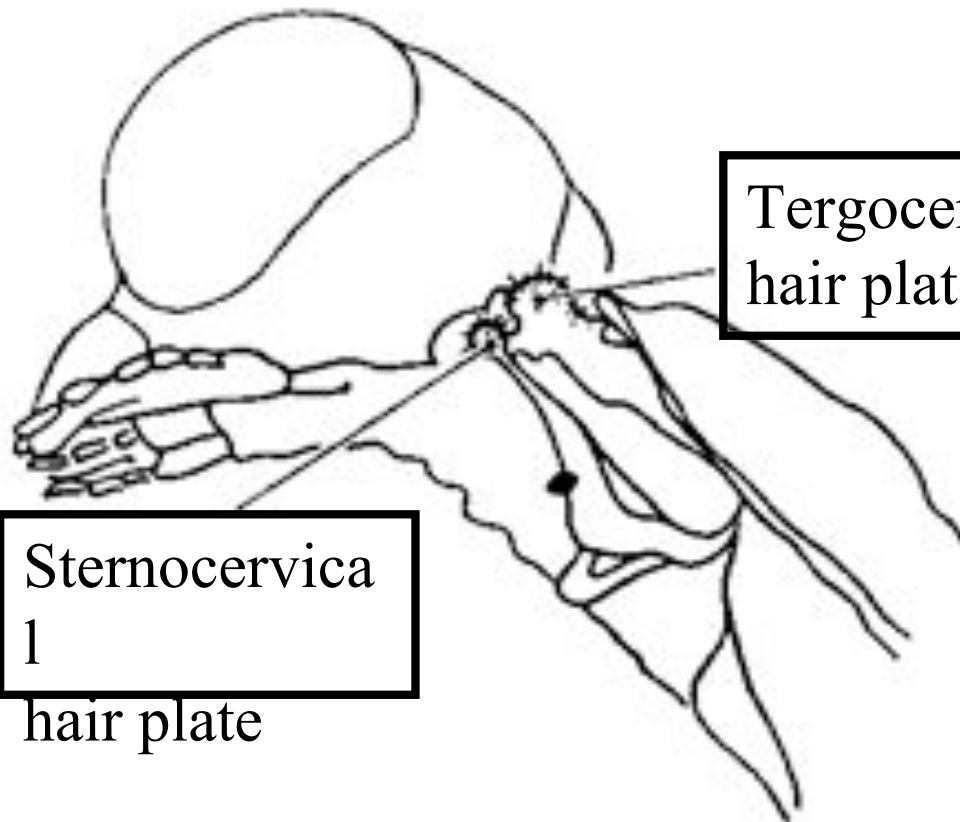
Inner coxal hair plate of *Periplaneta*

HAIR PLATES-In the mantid these hair plates are important in prey capture. Capture of prey necessitates absolute optic localization. Eyes are immovable and the head turns to face the prey. 10-30 millisecond strike with an 85% accuracy. Position of prey is determined by the position of the prey relative to the plane of the prothorax. Two bits of information are important:

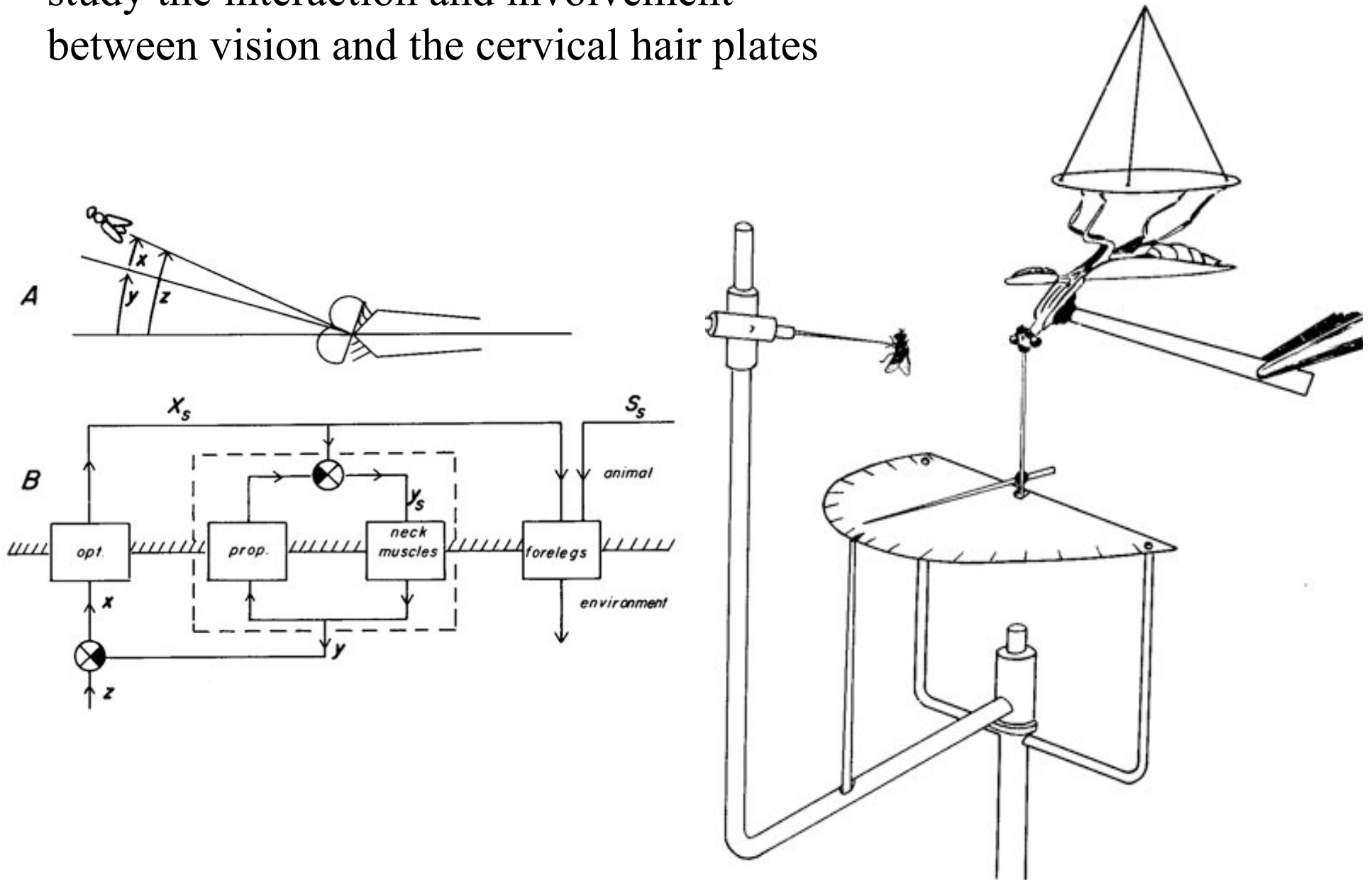
1. Direction of prey relative to the head-determined by the compound eyes
2. Position of head relative to the prothorax-determined by the hair plates in the neck region

How could one study the importance of these hair plates?

By removing the hairs, the accuracy goes from 85% to 20%.



Device used by Mittelstaedt (1957) to study the interaction and involvement between vision and the cervical hair plates



THERMORECEPTORS

Heat reception is used by:

- 1. Hematophagous insects to induce biting**
 - a. Two hairs on tarsi of the forelegs of *Glossina morsitans***
- 2. Heat seeking (smoke and fire) *Melanophila* beetles**
- 3. Find the favored environment for survival**
 - a. On tarsi of *Periplaneta americana* on arolium and pulvilli**

The following website has an excellent presentation concerning heat or infrared reception.

<http://web.neurobio.arizona.edu/gronenberg/nrsc581/powerpoint%20pdfs/infrared.pdf>

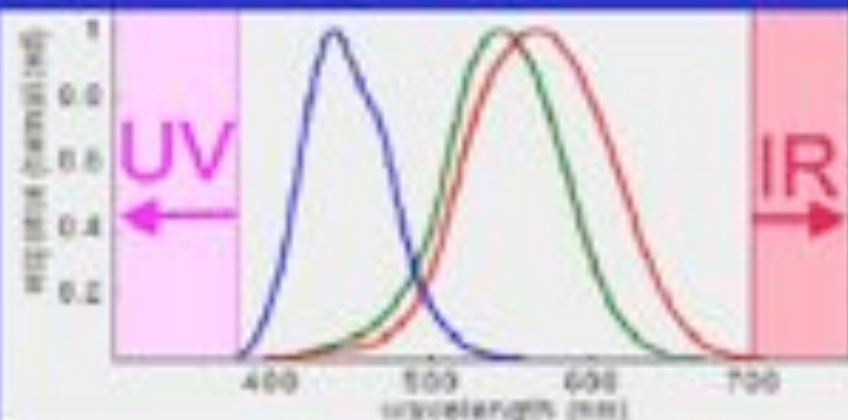
Annals of the Entomological Society of America: Vol. 94, No. 5, pp. 686–694.

Characterization of Beetle *Melanophila acuminata* (Coleoptera: Buprestidae) Infrared Pit Organs by High-Performance Liquid Chromatography/Mass Spectrometry, Scanning Electron Microscope, and Fourier Transform-Infrared Spectroscopy

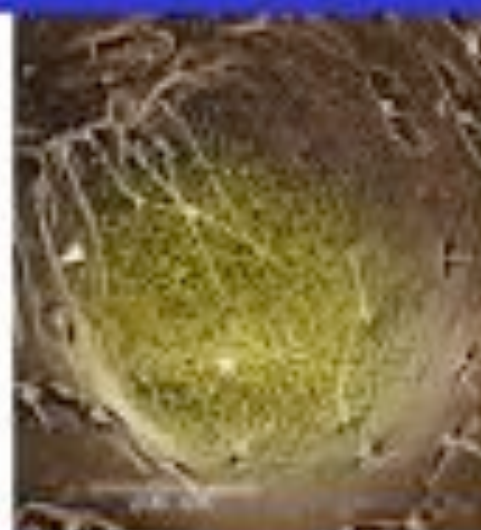
Laura A. Sowards,^{a, e} **Helmut Schmitz,^{b, e} David W. Tomlin,^{c, e} Rajesh R. Naik,^{c, e} and Morley O. Stone^{d, e}**

The beetle *Melanophila acuminata* (De Geer) is able to detect infrared radiation emitted from forest fires with two infrared receptors (pit organs) located on the metathorax next to the coxal cavity of the second set of thoracic legs. Each pit organ houses 70 single IR sensilla, which probably transduce incoming IR radiation into a mechanical event. These pit organs may exhibit chemical differences from the cuticle covering other parts of the beetle, which could account for their enhanced infrared detection. Infrared pit organs and the elytra, the cuticle covering the wings, were subjected to LC/MS analysis by extracting the cuticle with solvents that varied in polarity. The resulting chromatograms and mass spectra were used to identify differences in solute mobility and composition. Energy dispersive spectroscopy and point dwell maps indicated only the presence of carbon, oxygen and nitrogen for the pit organs, wings and elytra. FT-IR transmission spectra were obtained for the pit organs, eye scales, coxal cavities and wings. FT-IR analysis detected chemical bonding for the sensilla of the pit organ, which agreed with the energy dispersive spectroscopy results. Sensilla absorb IR radiation at the maximum emission wavelength of forest fires, and there is no indication of a complex chemical reaction occurring upon IR absorption. Therefore, the degree of expansion of the cuticular apparatus of the IR sensilla seems to be the sole contributing factor for the photomechanical portion of infrared detection.

Like ultraviolet, infrared is 'light' beyond the human's spectral sensitivity range



The Australian 'fire beetle' has an abdominal infrared organ



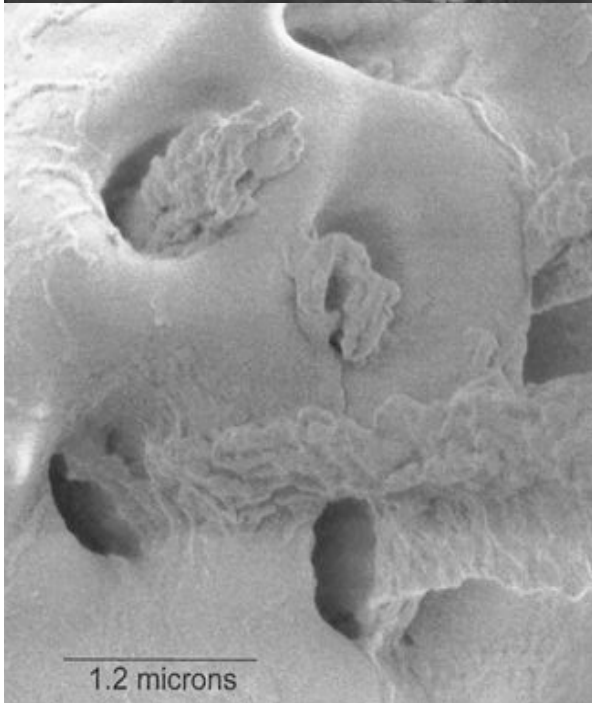
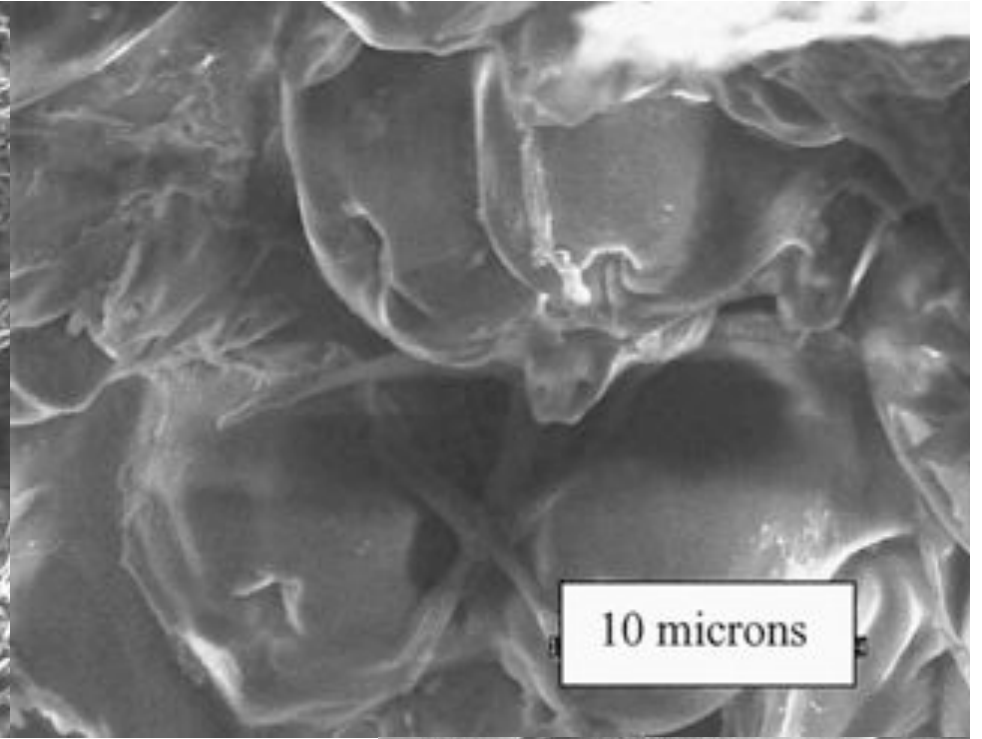
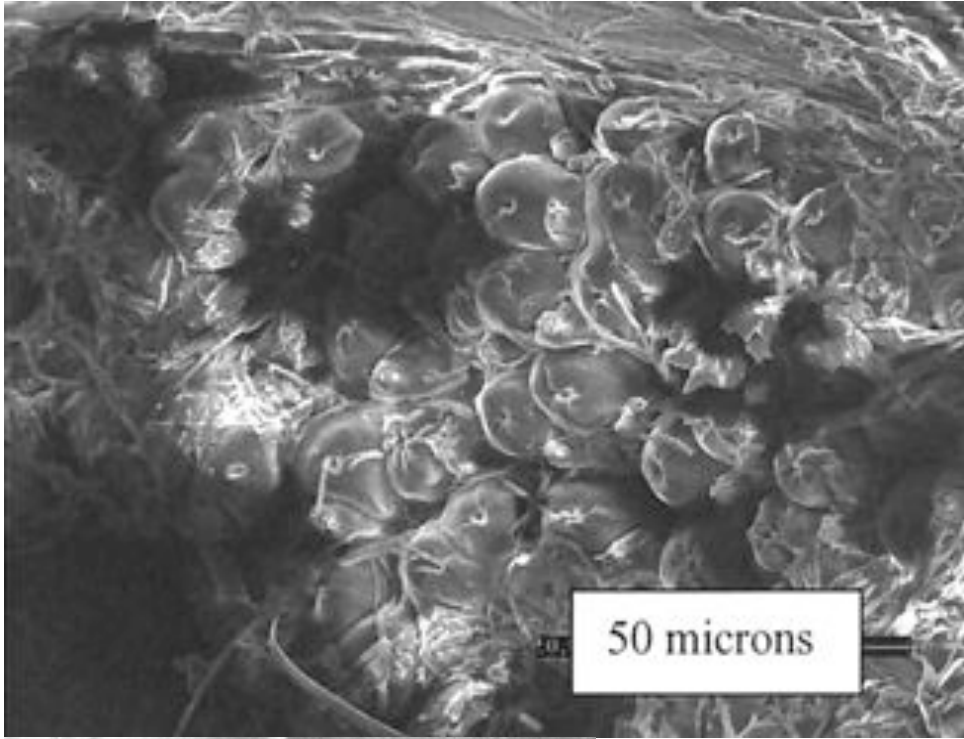
Buprestid *Melanophila* beetles:

- IR sensitive pit organs behind middle legs
- detect and approach forest fires from up to 80 km.
- IR sensilla: 'photomechanic' mechanism (heat-induced strain)



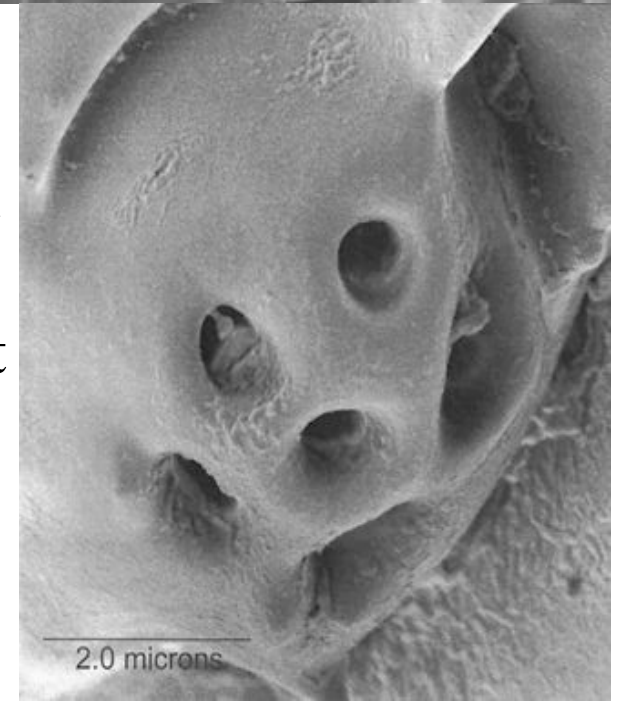
Some beetles can detect forest fires





Pits located in middle coxal cavity (mesothorax). These sensilla are exposed when the beetles are in flight. Wax is extruded out of the pores of these sensilla.

Melanophila acuminata



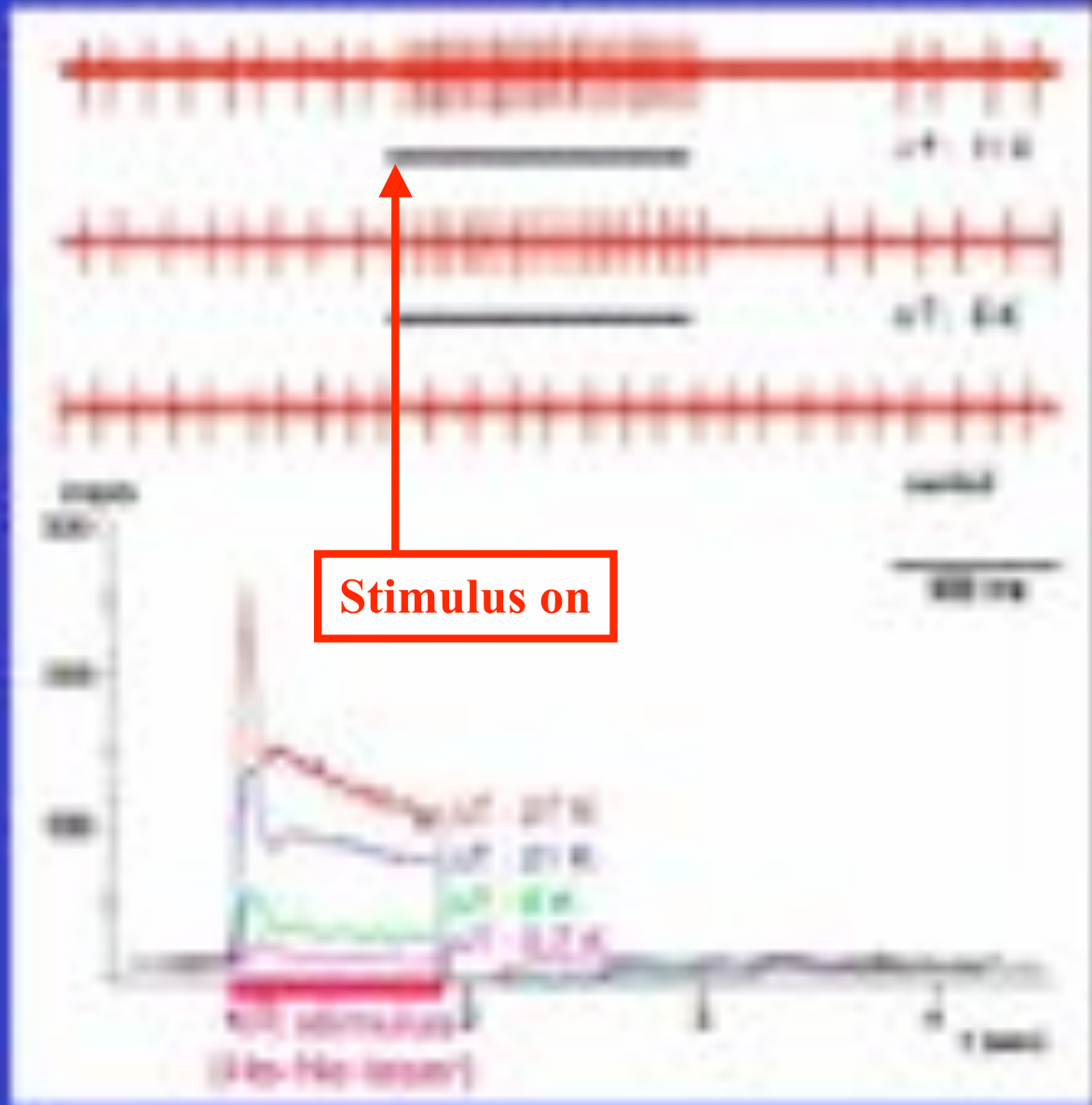
Butterflies may use their IR sensitivity to detect wing patterns or green plants.

(The mesophyll of leaves scatters IR, hence healthy leaves can be detected by their high IR reflection.)

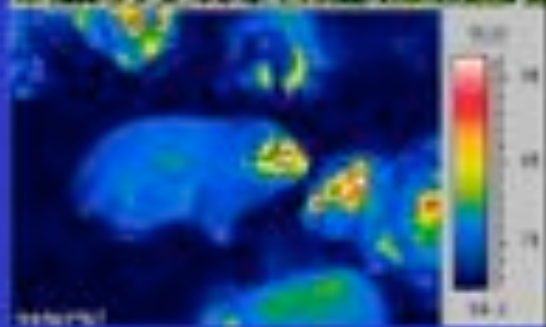


normal and infrared (short-wave) photographs copyright bioresources

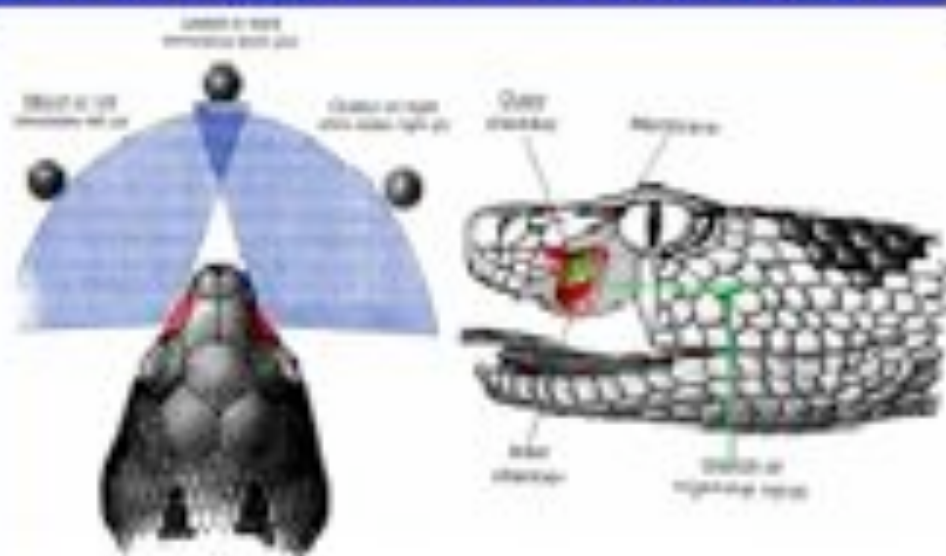
The IR organ of the Australian fire beetle responds to temperature changes (phasic-tonic responses; spontaneous activity)



Warm-blooded animals emit infrared radiation ('heat')



Boas, pythons, and pit vipers (e.g. rattlesnakes) use IR to detect prey. Python max. IR sensitivity: 8-12 μm ; emission maximum of mammalian/bird prey: 10 μm



OSMORECEPTORS-The ability to respond to changes in the osmotic pressure of a fluid

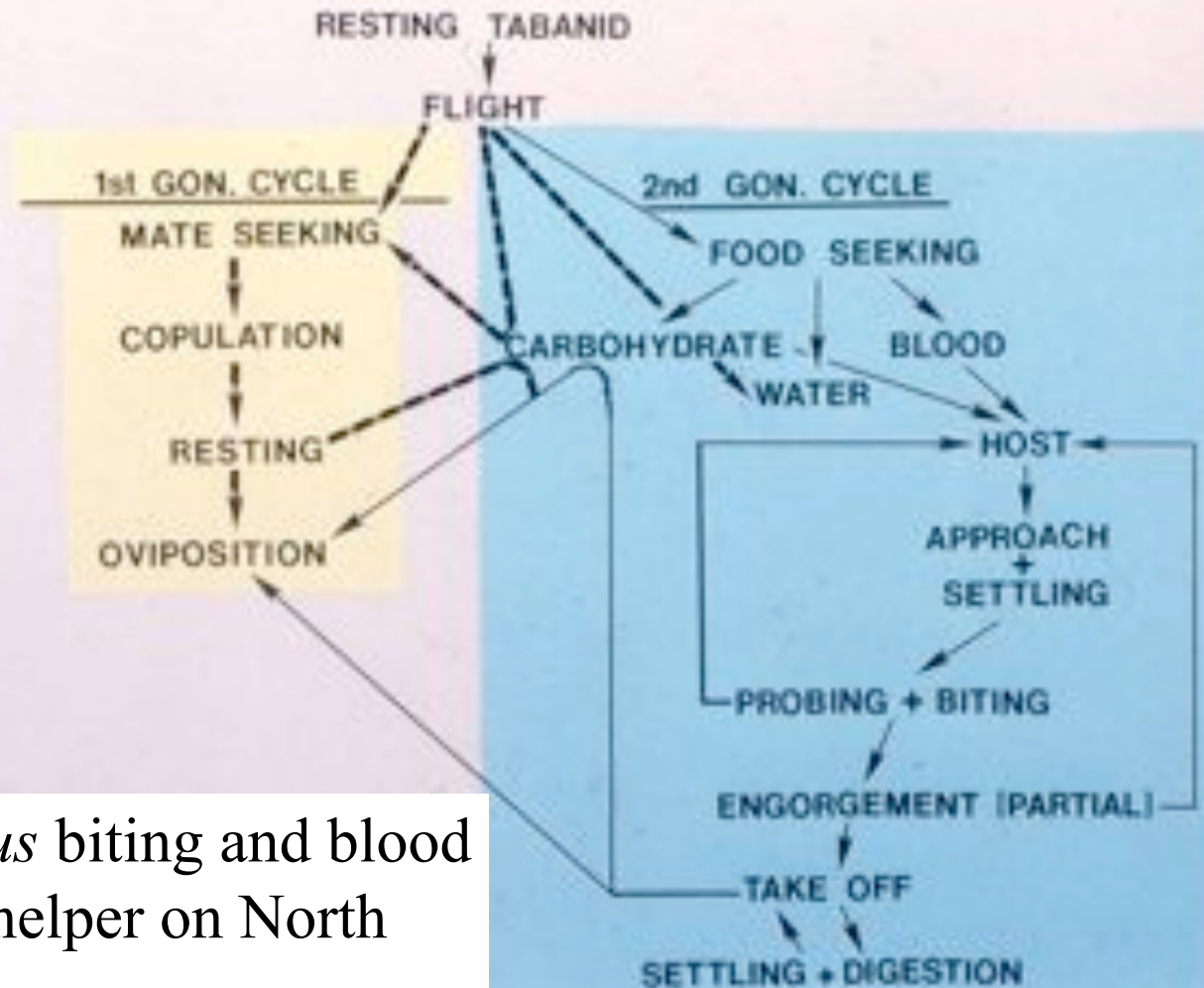
Osmoreceptors have not been well studied in insects

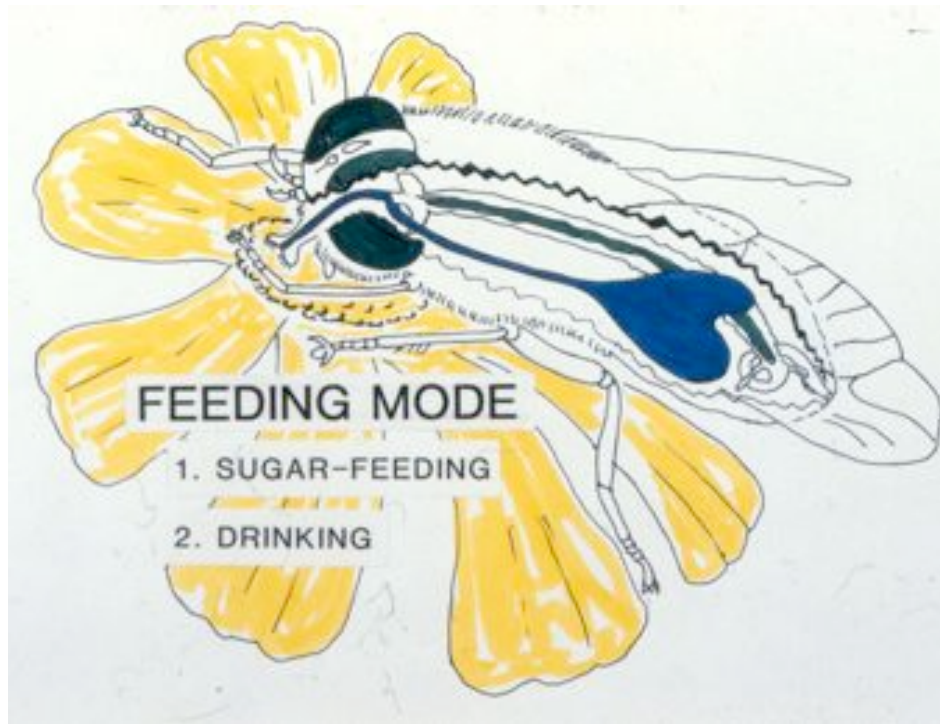
1. Tabanid blood feeding and diversion to the midgut
Friend, W.G. and J. G. Stoffolano, Jr. 1991. Feeding behaviour of the horsefly *Tabanus nigrovittatus* (Diptera: Tabanidae): effects of dissolved solids on ingestion and destination of sucrose or ATP diets. *Physiol. Entomol.* 16: 35-45.

Haustellate or sucking mouthparts of *Tabanus nigrovittatus*



Tabanus nigrovittatus biting and blood feeding on summer helper on North Shore-Pine Island



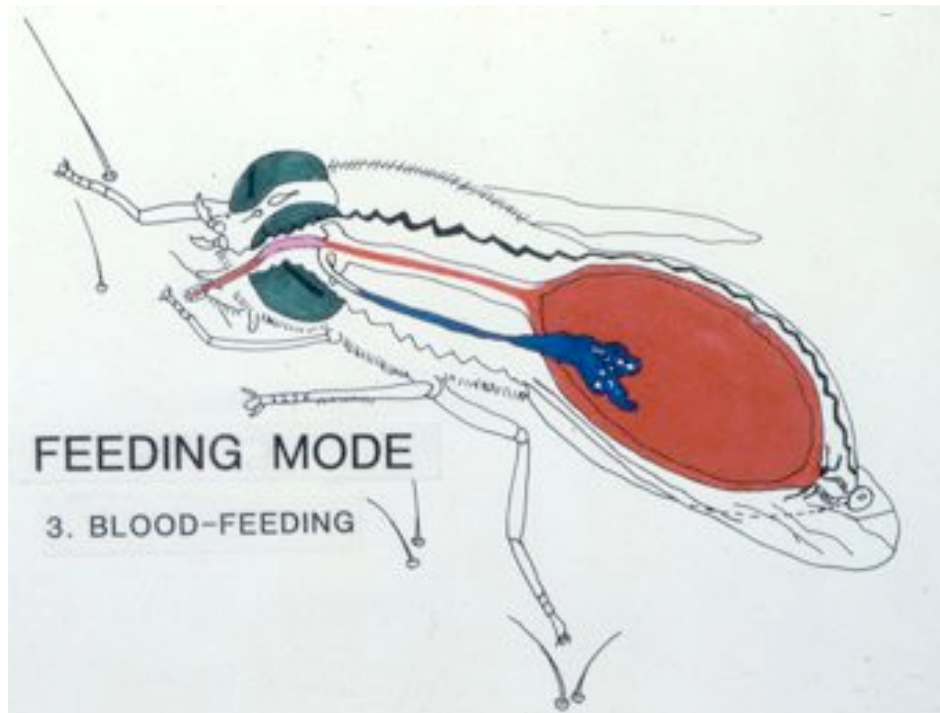


In tabanids, a sugar meal is directed to the crop while a blood meal is sent to the midgut.

What are the controlling mechanisms that regulate where the meal is shunted? **In order to look at this,**

studies were done by changing the osmolarity of both sugar and ATP (which is a phagostimulant) for hematophagous insects.

In the next slide(s) we will present some of this data and also the flow diagrams or models that were generated from these studies.



In these studies we used ATP because it stimulates gorging and in soln. is normally directed to the midgut like blood. We used cellobiose, a chemical that is not detected by the fly's chemoreceptors but, can be used to change the osmolarity of other solutions

Table 1. Osmolarity and viscosity of various concentrations and types of diets tested.

Diet tested	Concentration (M)	Osmolarity (mOsm)	Viscosity (cP)	Diet destination
Sucrose*	1.0	1421	3.19	— All to crop
	0.6	736	1.86	— Large to crop, some to MG
	0.3	336	1.34	— Large to MG, some crop
	0.1	107	1.10	— All to MG
Cellobiose or combinations [†]	1.0	~1400	?	
NaCl*	0.15	277	1.02	
Blood [‡]	—	~300	1.5–3§	↘ Always to midgut
Plasma [‡]	—	293	~1.8	
Water*	—	0	1	— Small amts. to midgut

Note that conc. sucrose always goes to the crop while blood and water always go to the midgut. As the osmolarity of the sugar approaches that of blood (ca. 300 mOsm), it is directed to the midgut, which it normally never enters in large amounts.

Slide to the top right shows the feeding apparatus for feeding blood to tabanids using a parafilm membrane covering the bottom of a cup filled with blood or an ATP solution that has been warmed to human body temperature



Slide to the right shows female tabanids going over to the membrane where the temperature will induce them to probe. If they encounter a phagostimulant then they will engorge and put the blood or ATP into the midgut, not the crop



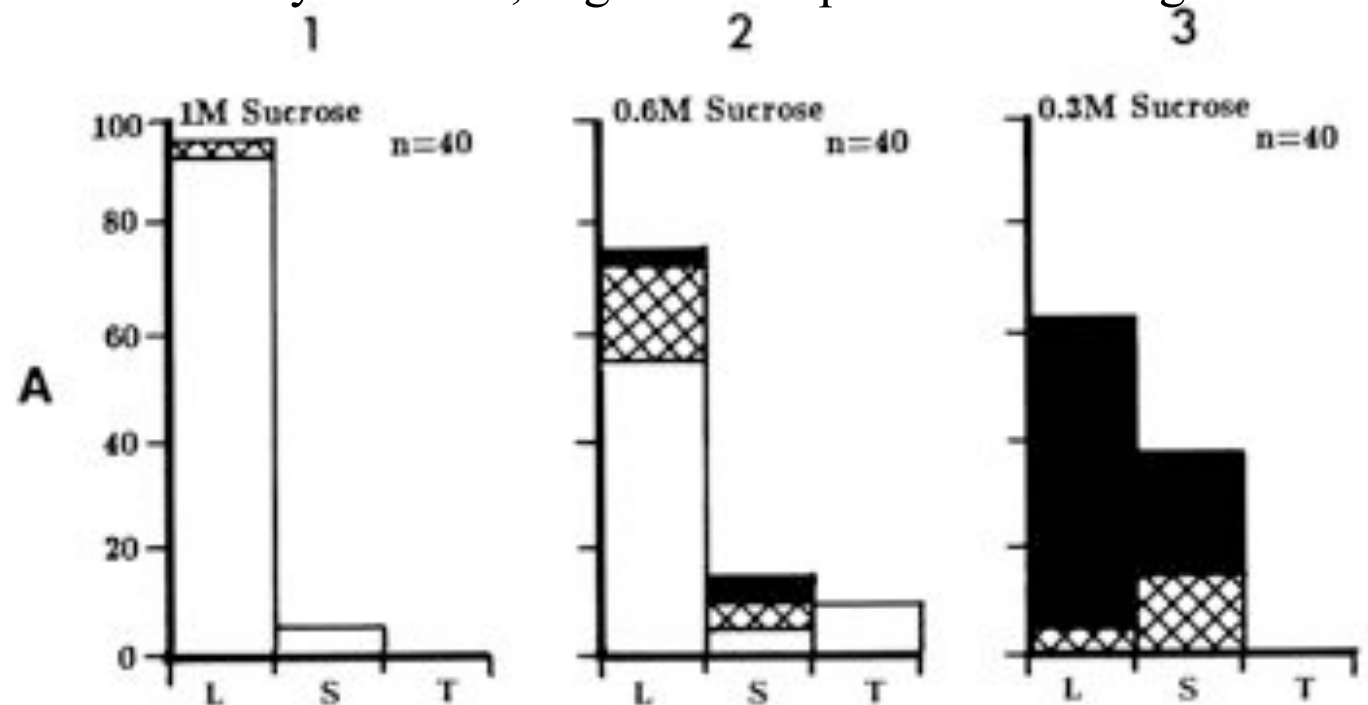
Directing sucrose solution into crop or midgut in *Tabanus nigrovittatus*

Open bar=fluid into crop

Solid bar=fluid into midgut

Hatched bar=both places

1. Normally concentrated sugar solns. from a free surface (nectar) are always put mainly into crop and small amounts into midgut
2. Molarity of 1M sucrose is 1421 mOsm; Blood is 300 mOsm
3. .3M sucrose is 336 mOsm
4. Thus, as approach the osmolarity of blood, sugar is now put into the midgut



L=large amount of fluid; S=small amount of fluid; T=trace amount of fluid

1. In nature, tabanids never put blood into the crop
2. Tabanids fed through a membrane with the solution warmed to body temp. to induce biting. ATP is the phagostimulant causing sucking and imbibing the meal. The 40 μM ATP causes maximum engorgement. With low osmolarity (0.3M Cellobiose), the diet goes always to the midgut but, when its osmolarity at 1M Cellobiose (ca 1400) nears that of 1M sucrose (ca. 1421), the diet now sometimes goes to the crop, which in this insect, blood is never directed to the crop.

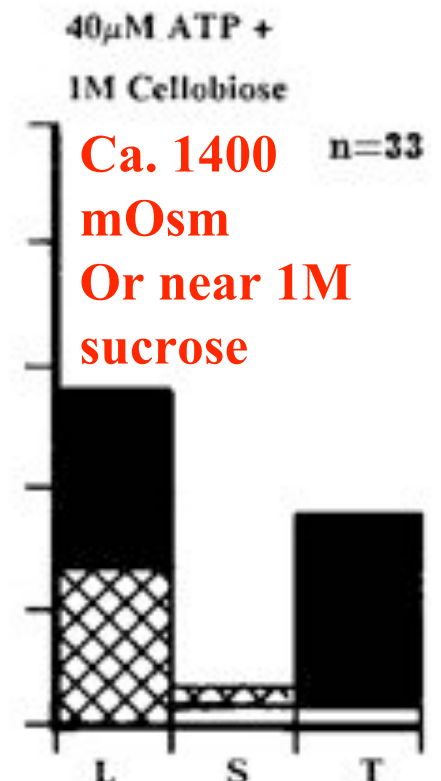
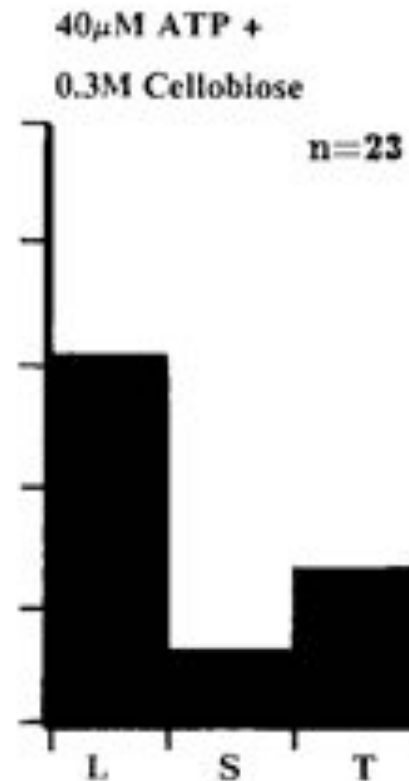
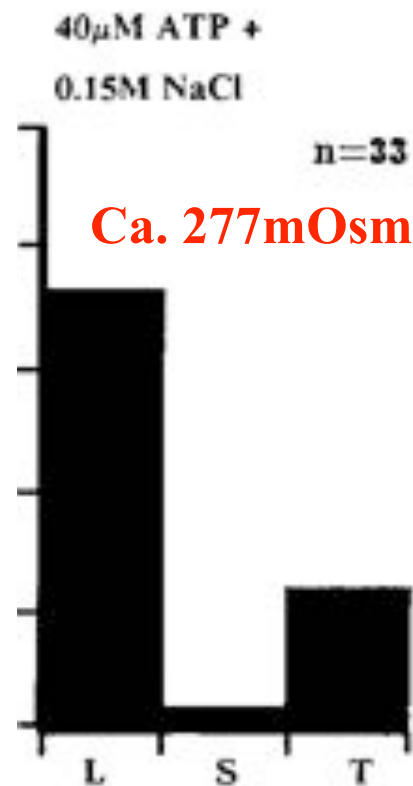
**Blood is ca.
300 mOsm**

Thus it goes to
the midgut

Solid=midgut

White=crop

Hatched=both



NOCICEPTORS

**Nociception is perception of noxious signals (e.g. heat, acid, etc.) that would prove detrimental to the organism, thus an avoidance response is elicited
In humans we call this pain. How does one perceive and interpret pain?**

HUMANS SAY IT IS INTERPRETED IN THE BRAIN

If this is so, how can one measure whether other animals perceive pain?

What makes a neuron nociceptive?

The TRPV ion channel family that is prominent in vertebrate nociception

Tobin, D.M. and C. I. Bargmann. 2004. Invertebrate nociception: Behaviors, neurons and molecules. Published online in Wiley InterScience

Tracey, W.D.J. et. al. 2003. painless, a *Drosophila* gene essential for nociception. Cell 113: 261-218.

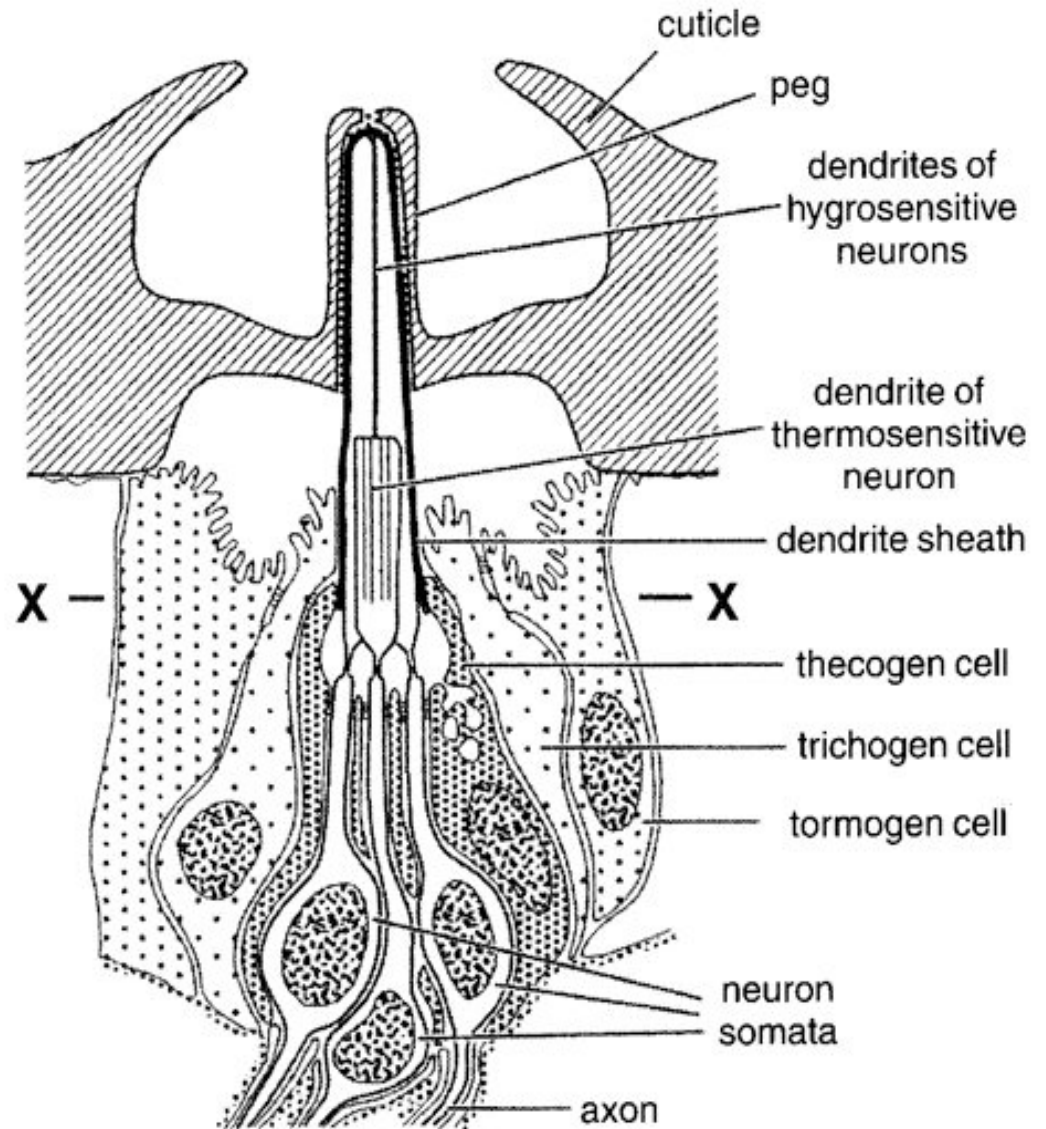
HYGRORECEPTORS-

Sensilla that response to changes in the humidity and are extremely important to insects that need to conserve water loss.

Sense cells responsive to temp. and humidity are usually present in the same sensillum.

Have a short peg and no pore.

All insects studied have these on the antenna.



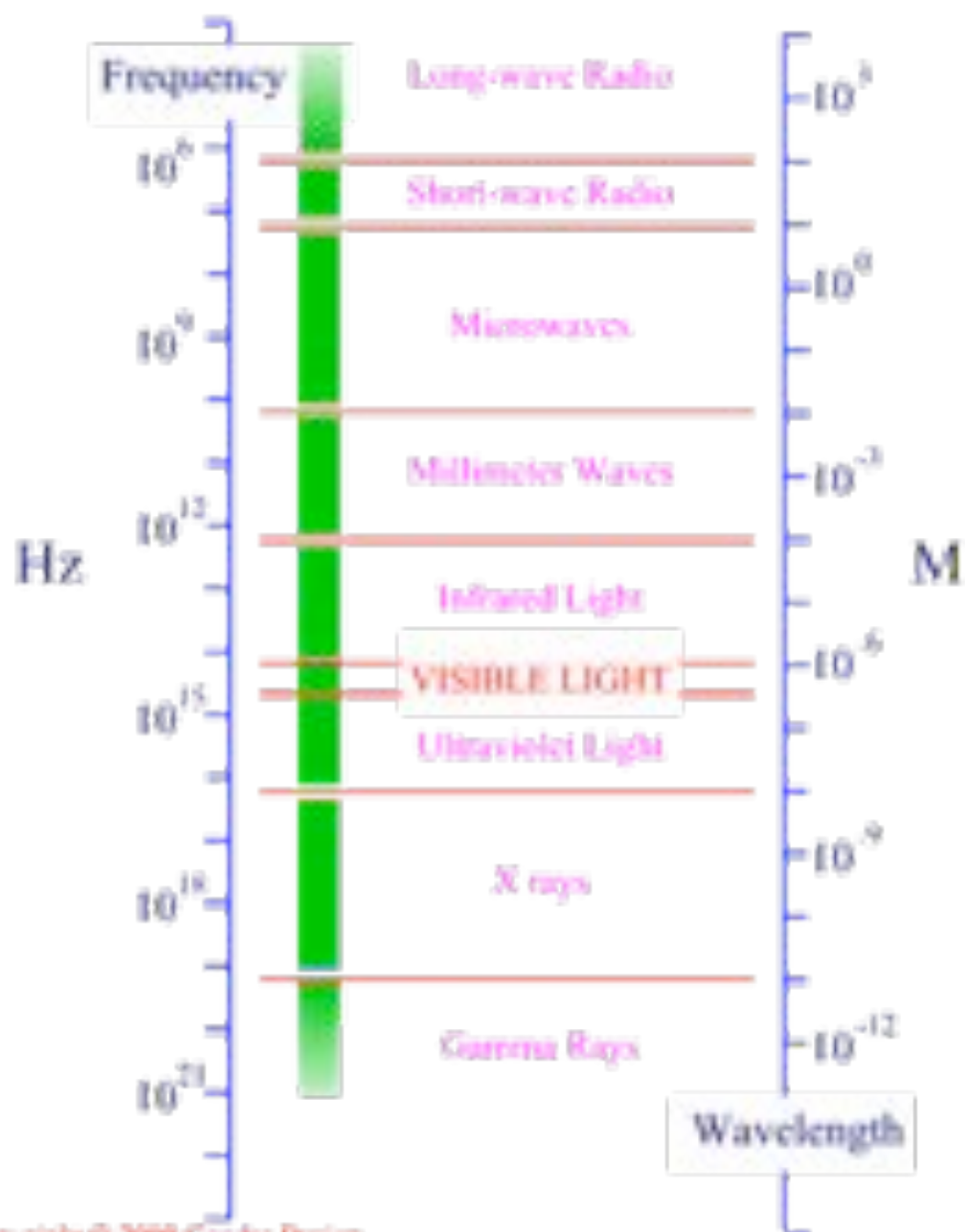
PHOTORECEPTORS

Photoreception is perception to electromagnetic stimuli in the organism's receptor ability to perceive that stimuli or wavelength.

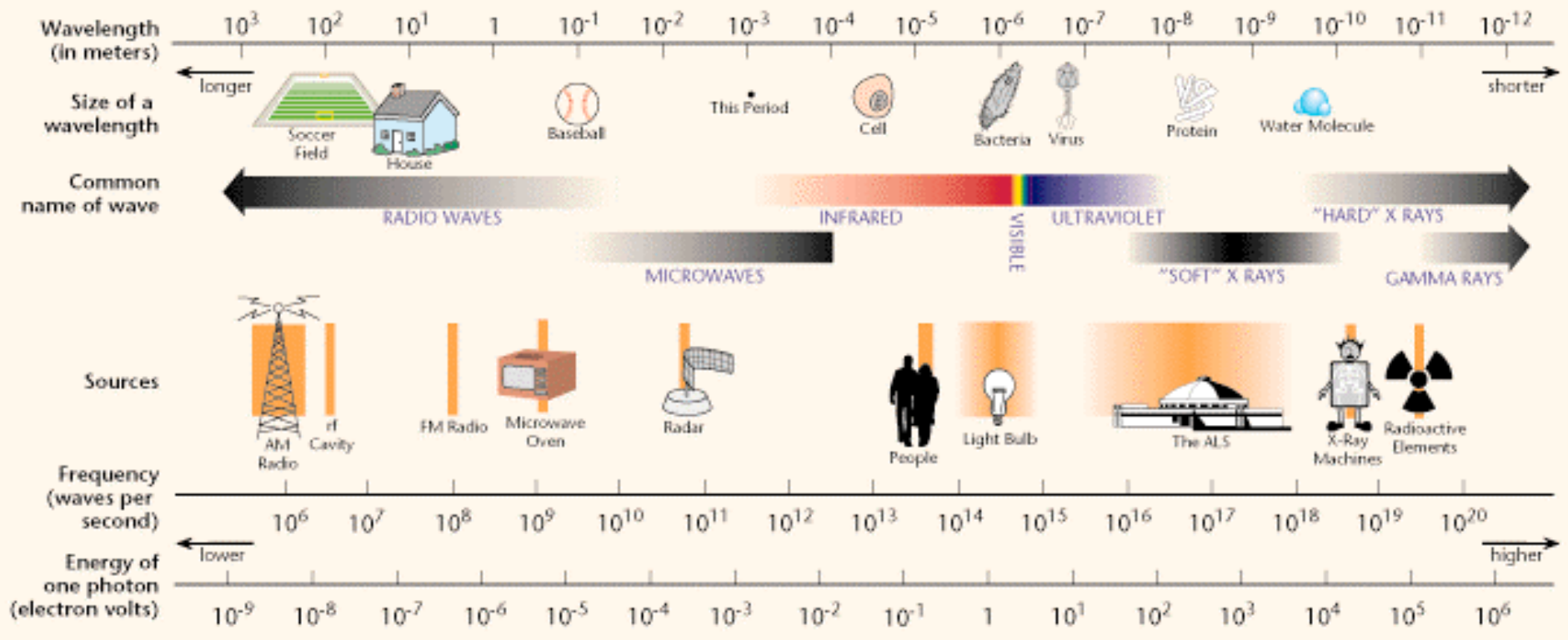
1. Compound eyes
2. Ocelli or simple eyes



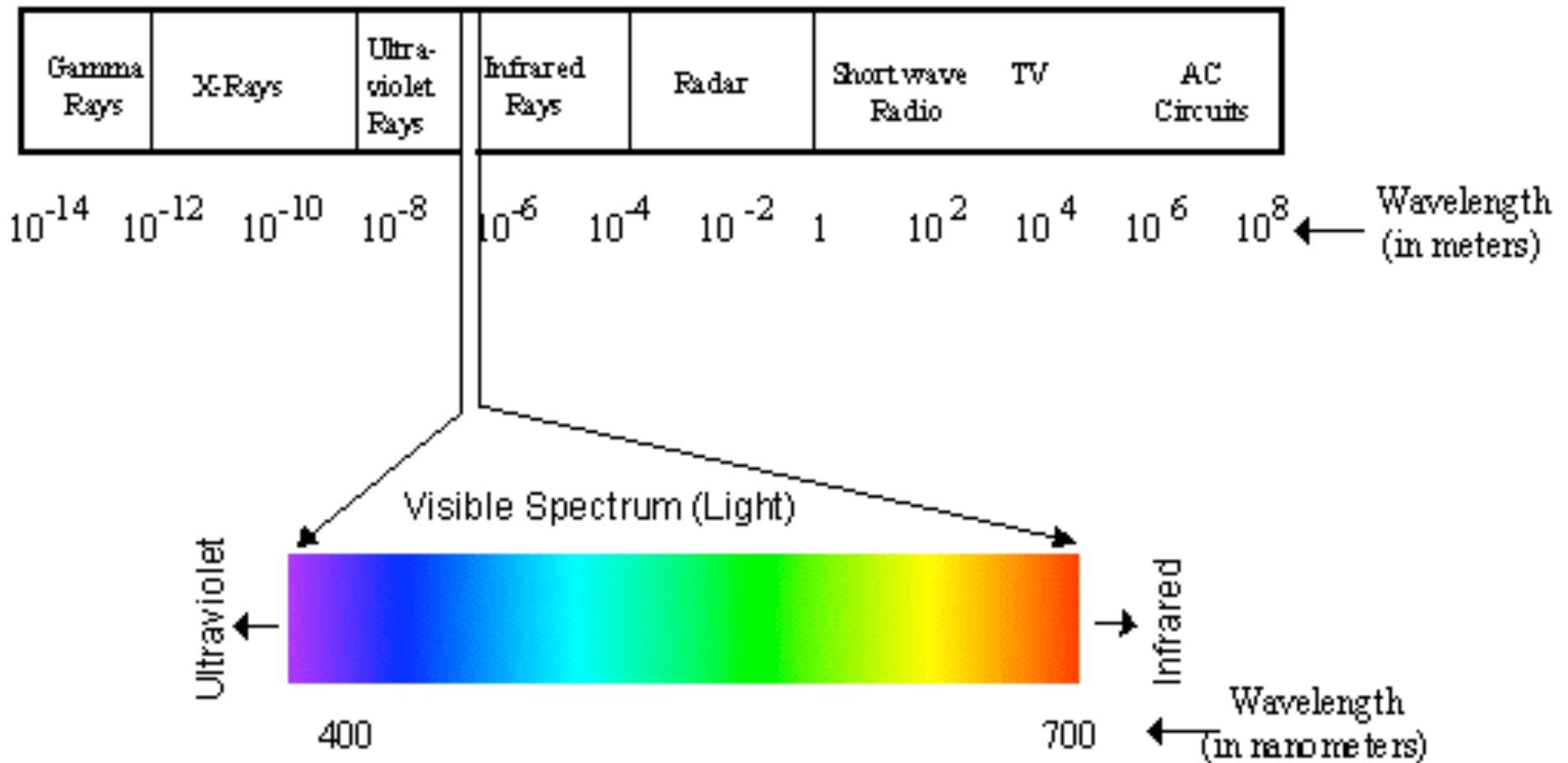
The Electromagnetic Spectrum



THE ELECTROMAGNETIC SPECTRUM



Humans are very visual animals...we use our sense of sight to interpret much of the world around us. What we see is called "light." However, what we see is really only a small part of the entire "electromagnetic spectrum." Humans can see only the wavelengths of electromagnetic radiation between about 380 and 760 nanometers...this is light. Our eyes do not have detectors for wavelengths of energy less than 380 or greater than 760 nanometers, so we cannot "see" other types of energy such as gamma or radio waves. Some insects, however, can detect electromagnetic radiation in the infrared range while the honeybee is able to use UV light emanating from plant flowers to locate honey (called nectar guides).



TRANSDUCTION-The process of changing energy (i.e., a stimulus) from one form to another (i.e., electrical neural input).

STIMULUS

<u>ENERGY</u>	<u>RECEPTOR</u>	<u>ELECTRICAL</u>
---------------	-----------------	-------------------

Light-----	photoreceptors-----	action potentials
------------	---------------------	-------------------

Mechanical---	mechanoreceptors-----	“ “
---------------	-----------------------	-----

sound-----	tympanum-----	“ “
------------	---------------	-----

wing beat-----	Johnston’s organ-----	“ “
----------------	-----------------------	-----

Chemicals

volatiles-----	olfactory sensilla-----	“ “
----------------	-------------------------	-----

contact-----	gustatory, contact sensilla---	“ “
--------------	--------------------------------	-----

Temperature---	thermoreceptors-----	“ “
----------------	----------------------	-----

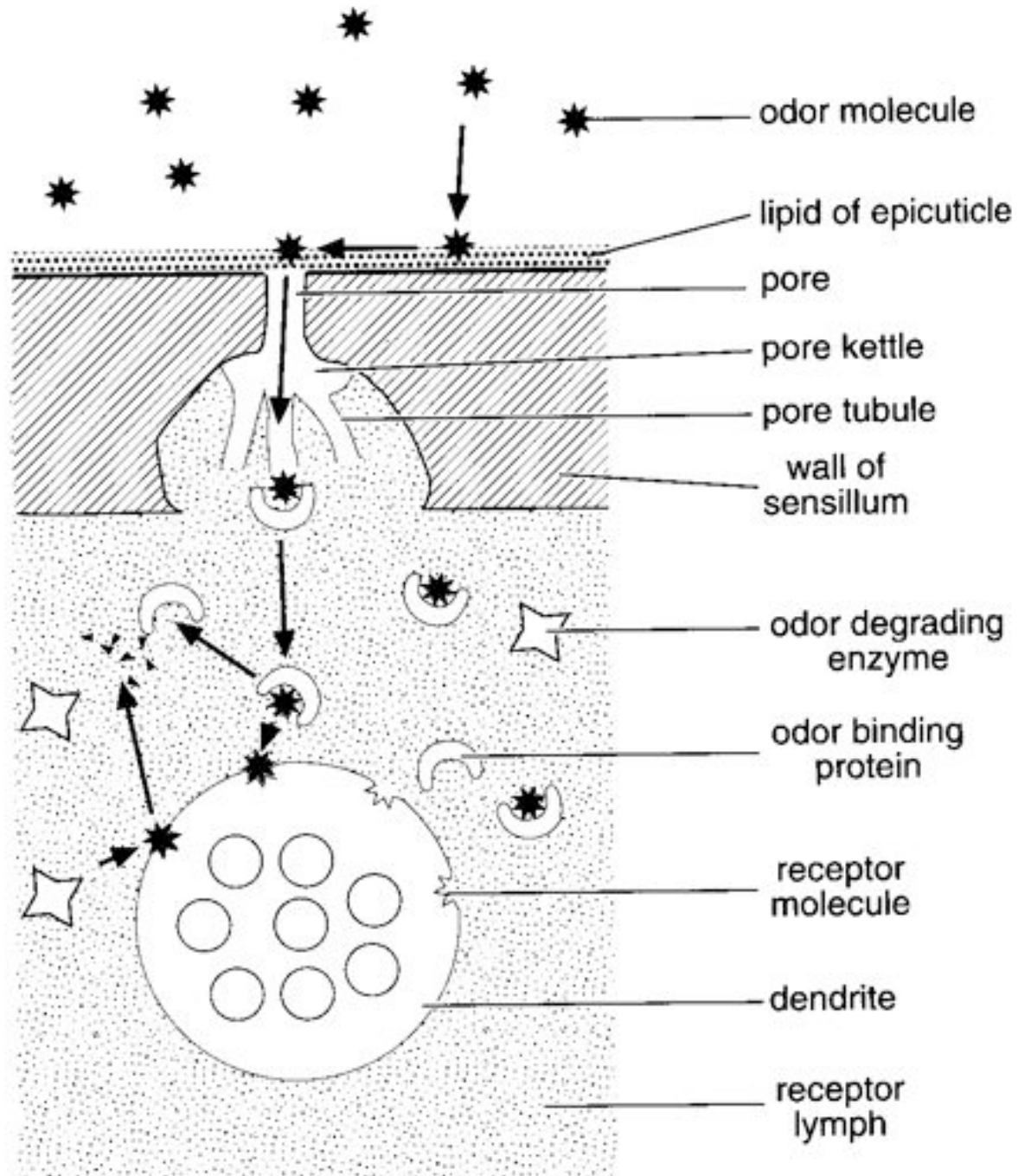
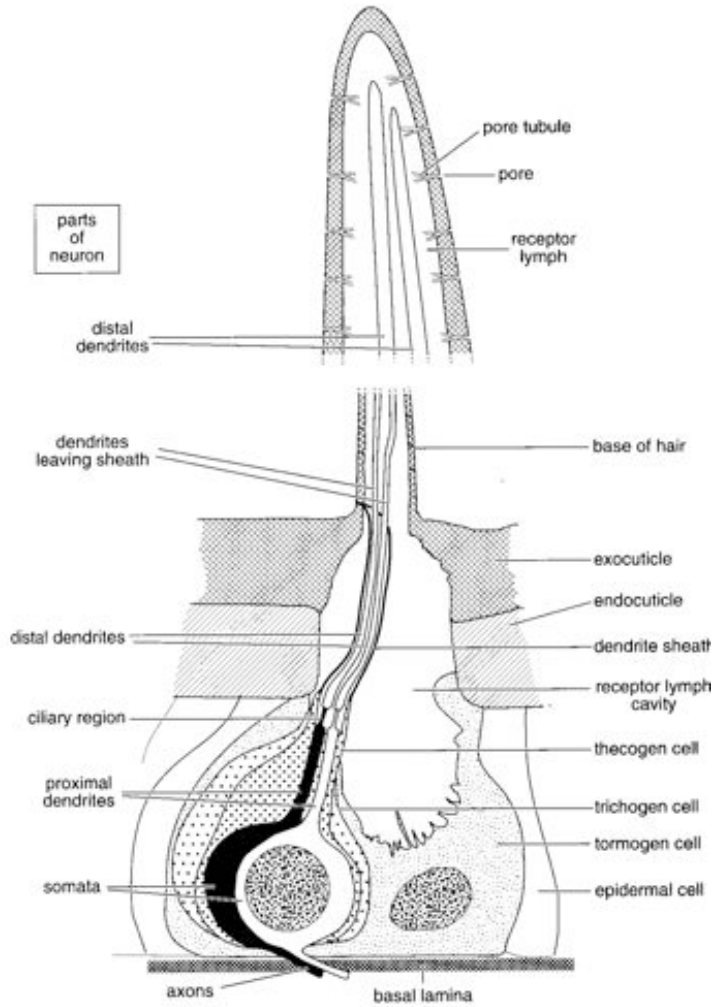
Osmotic-----	osmoreceptors-----	“ “
--------------	--------------------	-----

Moisture-----	hygroreceptors-----	“ “
---------------	---------------------	-----

Noxious-----	nociceptors-----	“ “
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Some principles of sensory physiology

- 1. Transduction mechanisms**
- 2. Central versus peripheral processing**



Transduction in an insect olfactory sensillum

Master gene found for insect smell

The protein encoded by a **single odor receptor molecule gene**, known as Or83B, works in conjunction with almost every odor receptor in fruit flies. When gene is knocked out, flies were unable to smell.

Or83b found in other flies (*Ceratitis capitata*, *Anopheles gambiae*, and *Helicoverpa zea*). Knocked out gene in these flies and flies unable to smell but when put Or83b in they regained smell.

Functional conservation of an insect odorant receptor gene across 250 million years of evolution

Walton D. Jones¹, Thuy-Ai T. Nguyen², Brian Kloss², Kevin J. Lee² and Leslie B. Vosshall¹

Among the 62 *Drosophila* OR genes, there is a single, atypical receptor, *Or83b*, that is co-expressed with the conventional ORs in nearly all olfactory neurons. Recent genetic studies in *Drosophila* have shown that *Or83b* has an important general function in olfaction, and is essential for localizing conventional OR proteins to the sensory dendrite. The absence of ORs in the OSN dendrites, the site of interaction with airborne odorants, eliminates odor-evoked potentials and severely attenuates olfactory-associated behaviors in *Or83b* mutant flies [5].

CENTRAL VERSUS PERIPHERAL PROCESSING

Where is information processed that comes from peripheral sensory input?

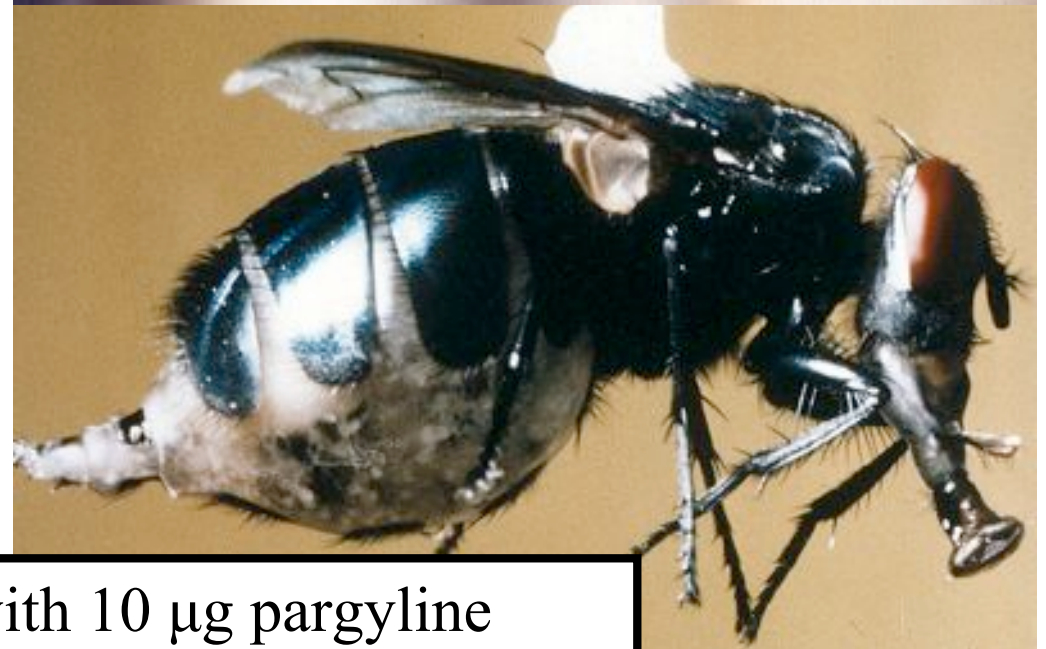
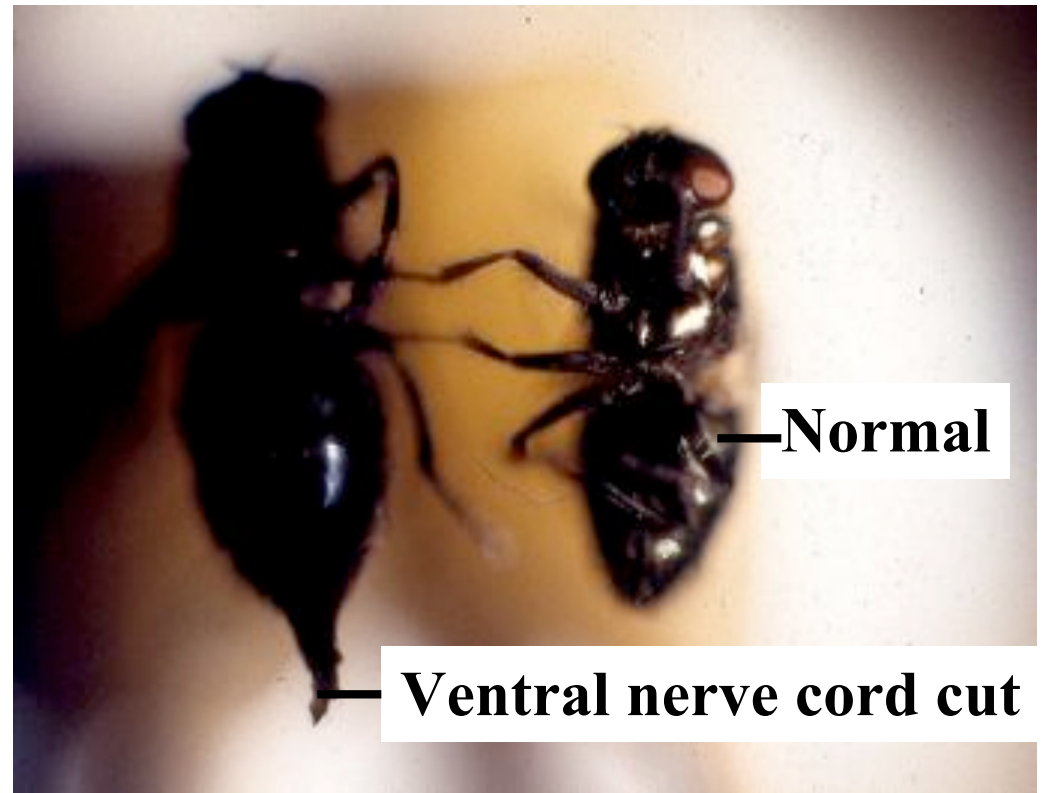
Is it at the peripheral level of the sensillum or sense organ or is it processed centrally?

How can one study this?

Use Murdoch's study with *Phormia regina* and feeding as example

Long, T.F. and L.L. Murdock. 1983. Stimulation of blowfly feeding behavior by octopaminergic drugs. Proc. Natl. Acad. Sci. 80: 4159-4163.

In *Phormia regina*, the model for feeding studies in insects, a normal fly with its ventral nerve cord intact stops feeding when it is full (see fly to the far right). If one cuts the ventral nerve cord, thus the negative feedback causing the fly to cease feeding, the fly becomes hyperphagic and doesn't stop feeding and may eventually burst (see fly nearest on top right with ovipositor extruded). The fly on the lower section has become hyperphagic because of an injection of a drug.



Chemical hyperphagia-injected with 10 μ g pargyline

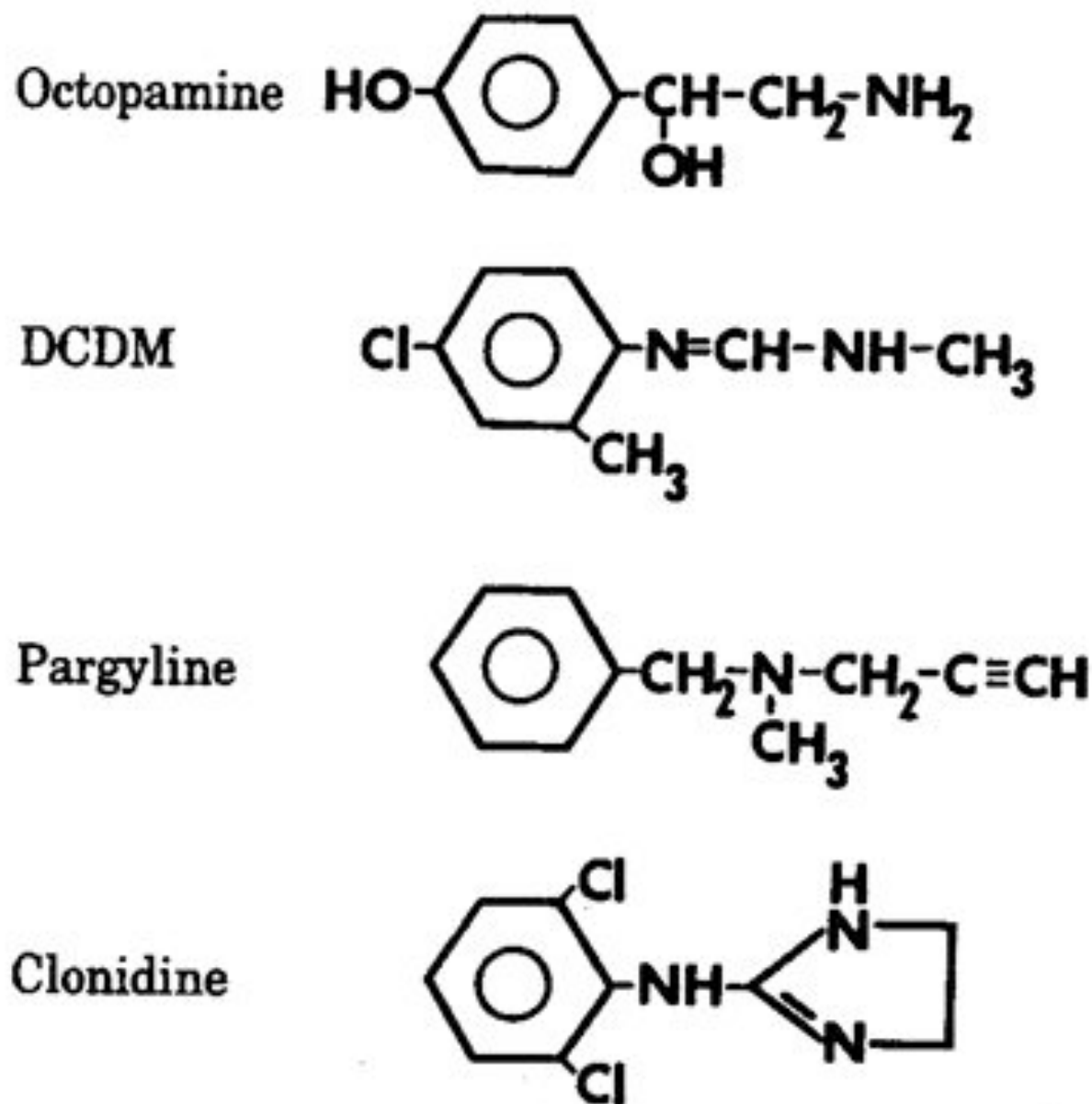


FIG. 1. Drugs that cause hyperphagia and enhanced responsiveness when injected into the hemocoel of adult *P. regina*.

**MORE WILL BE SAID ABOUT THIS
EXPERIMENT WHEN WE GET TO THE
TOPIC OF INSECT PHYSIOLOGY AND
BEHAVIOR**

Central processing of sex pheromone, host odour, and oviposition deterrent information by interneurons in the antennal lobe of female *Spodoptera littoralis* (Lepidoptera: Noctuidae) Sylvia Anton*, Bill S. Hansson. The Journal of Comparative Neurology vol. 350, issue 2, pgs. 199-214.

Physiological and anatomical characteristics of antennal lobe interneurons in female *Spodoptera littoralis* (Boisd.) were investigated using intracellular recording and staining techniques. Responses of local interneurons and projection neurons to female sex pheromone components, host plant odours, and behaviourally active oviposition deterrents were recorded. We found local interneurons and projection neurons that responded specifically to only one or two of the tested odours, but we also found less specific cells, and neurons that responded to most of the tested odourants. These findings show that there are not only specific olfactory pathways in female moths up to the protocerebral level, but also that integration can begin in the antennal lobe. No correlation was found between the degree of specificity of either local interneurons or projection neurons and their respective morphological characteristics. Specialized and unspecialized local interneurons arborized throughout the antennal lobe. Specialized and unspecialized projection neurons had uniglomerular arborizations in the antennal lobe and sent their axons to the calyces of the mushroom body, and to the lateral horn of the protocerebrum. One specific projection neuron had multiglomerular arborizations and projected only to the lateral horn of the protocerebrum. Projection neurons arborizing in the glomeruli closest to the entrance of the antennal nerve always responded to pheromone components. No other correlations were found between the arborization pattern of projection neurons in the antennal lobe or in the protocerebrum and their response characteristics. The sensitivity of local interneurons and projection neurons was in the same range as that of receptor neurons in olfactory sensilla on the antennae, suggesting a much lower convergence in the central nervous system in females than in the pheromone-processing pathway in males.

LIST OF SENSE ORGANS

1. Antennae
2. Compound eyes
3. Ocelli
4. Cerci
5. Palps
6. Tympanum

OTHER SENSORY FIELDS:

1. Ovipositor

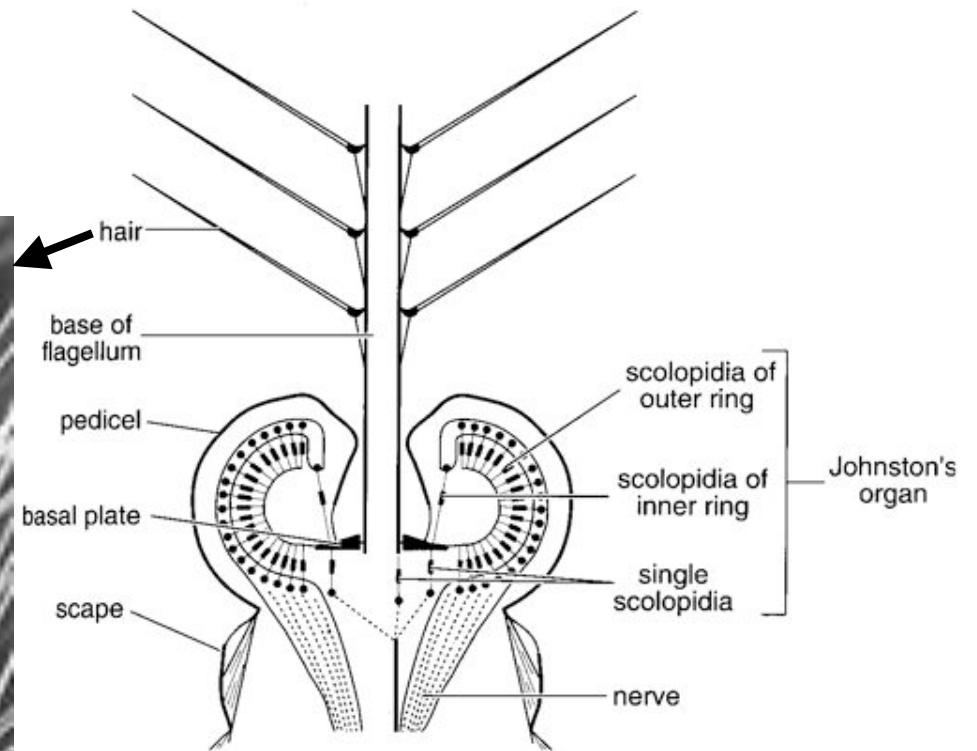
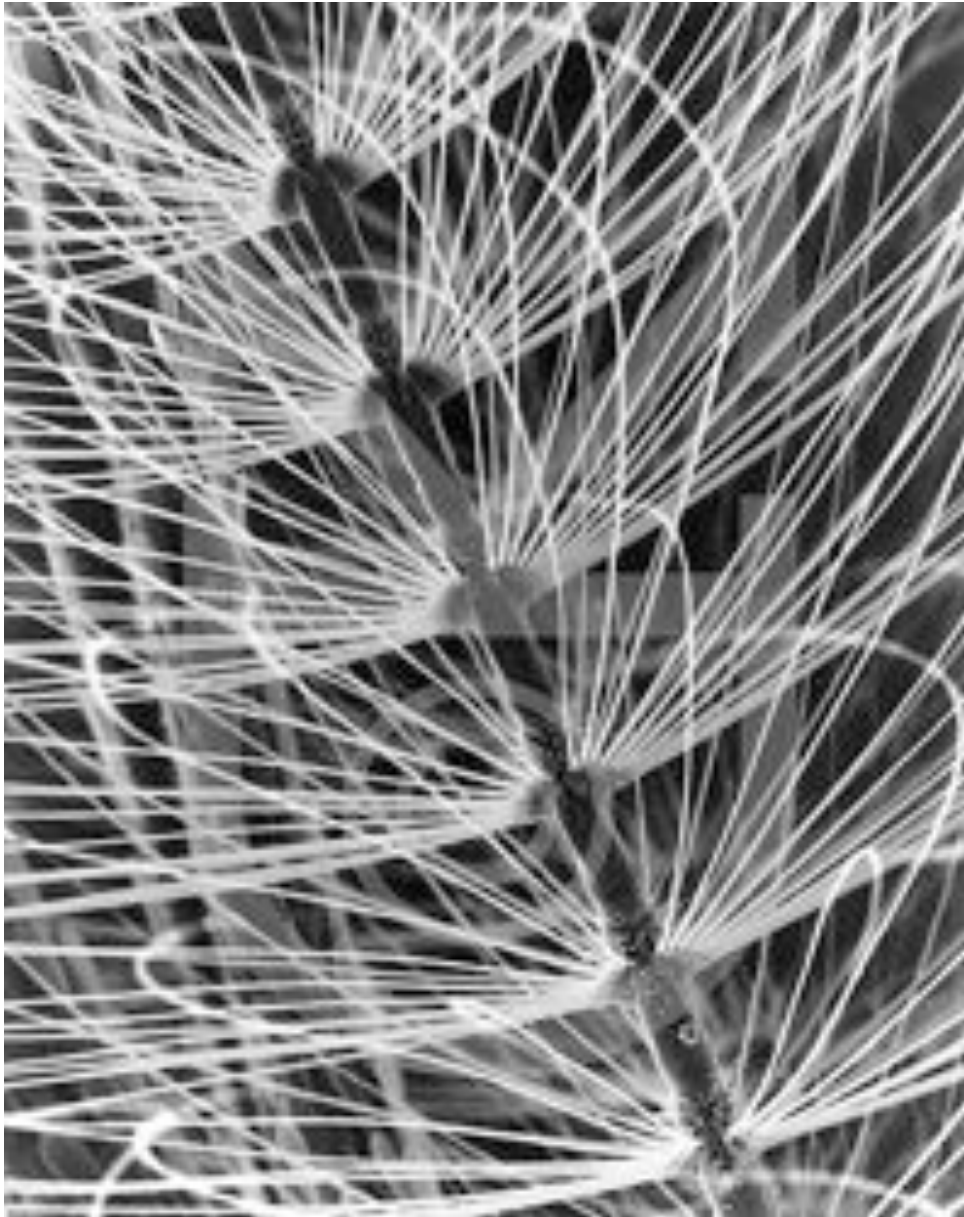
INSECT ANTENNAE + MECHANORECEPTORS

1. Occur in all insects except the Protura
2. Second segment (pedicel) contains a group of sensilla similar to the chordotonal sensilla. In some insects this segment also contains some other sensilla but in the mosquitoes only this one type is found and they are radially arranged in a circular pattern.
3. The Johnston's organ responds to bending of the flagellar segments.

EXAMPLES:

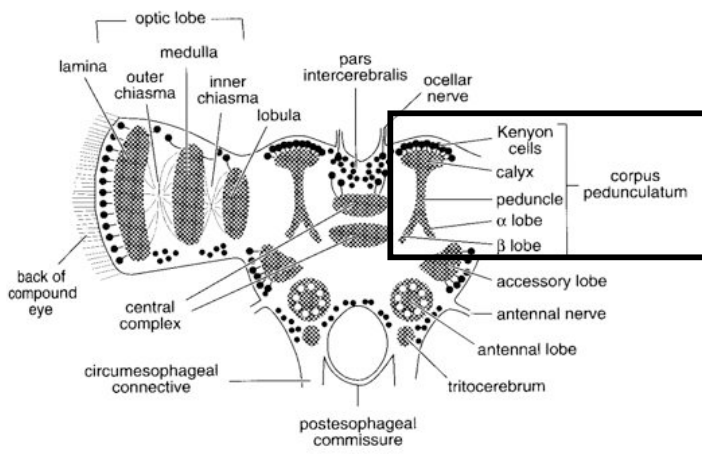
1. Bees measure flight speed by measuring strength of air-stream
2. Male mosquitoes it is the auditory organ
3. Whirligig keeps its antenna on the water surface and may measure vibrations due to waves
4. *Notonecta* and *Corixa* maintain normal swimming posture because of the air trapped between antennae and lower surface of the head
5. In general, it is used in flight to monitor air speed, etc.

Johnston's organ

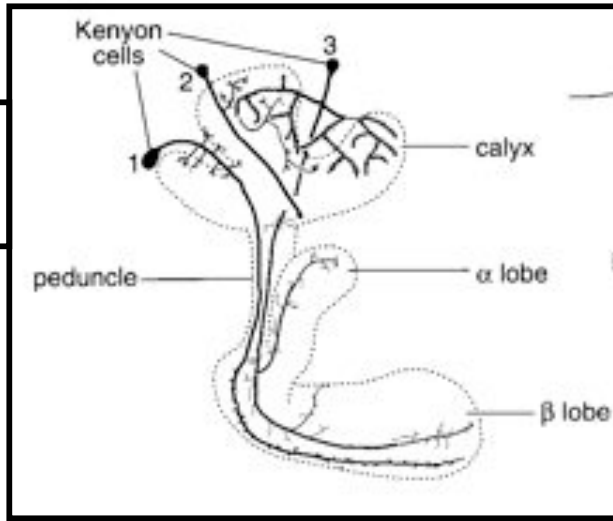


The Johnston's organ in male mosquitoes is extremely important in mating. The male detects the wing beat frequency of the female and is attracted to her. Note in the SEM on the left the tremendous hair arrangement in whorls at each segment that would facilitate antennal vibration and cause the Johnston's organ to be stimulated.

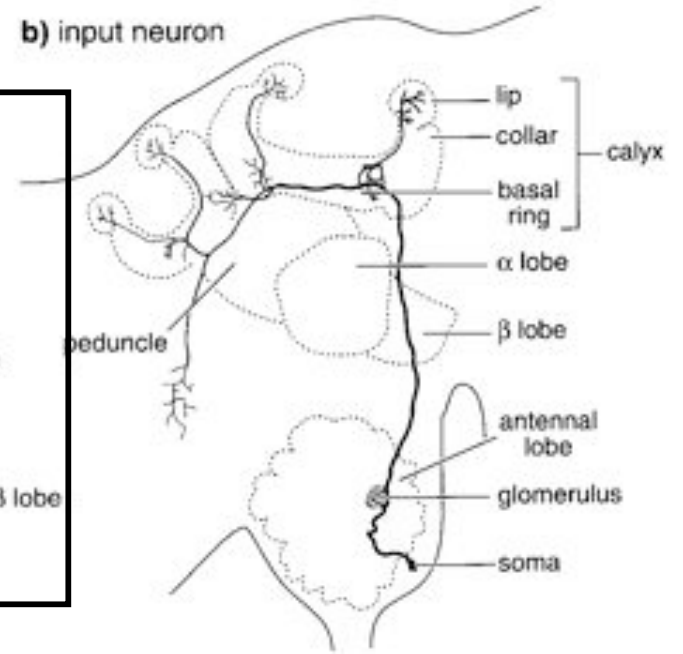
Insect antenna, mushroom bodies and olfaction center



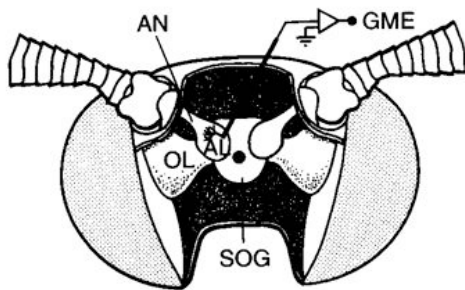
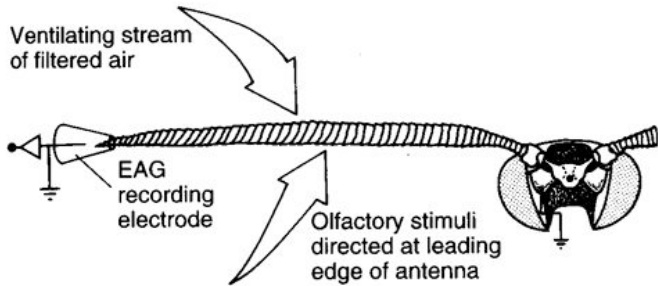
a) intrinsic neurons



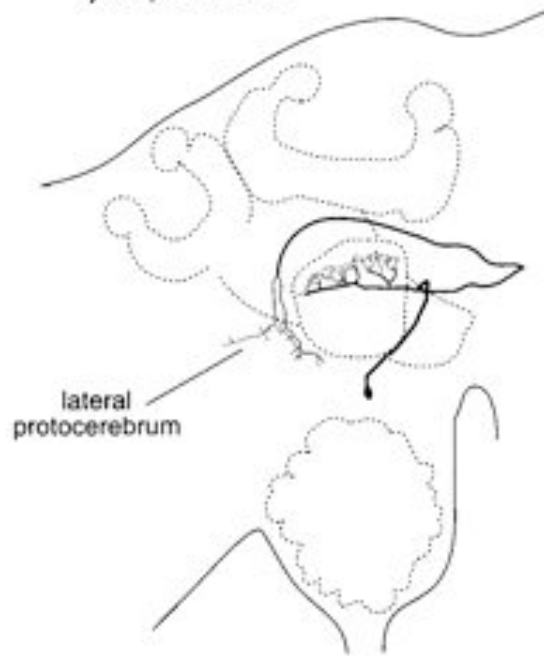
b) input neuron



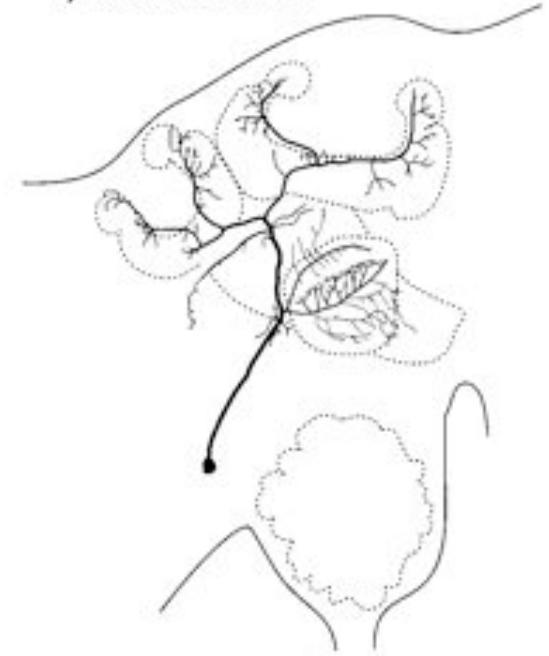
MUSHROOM BODY



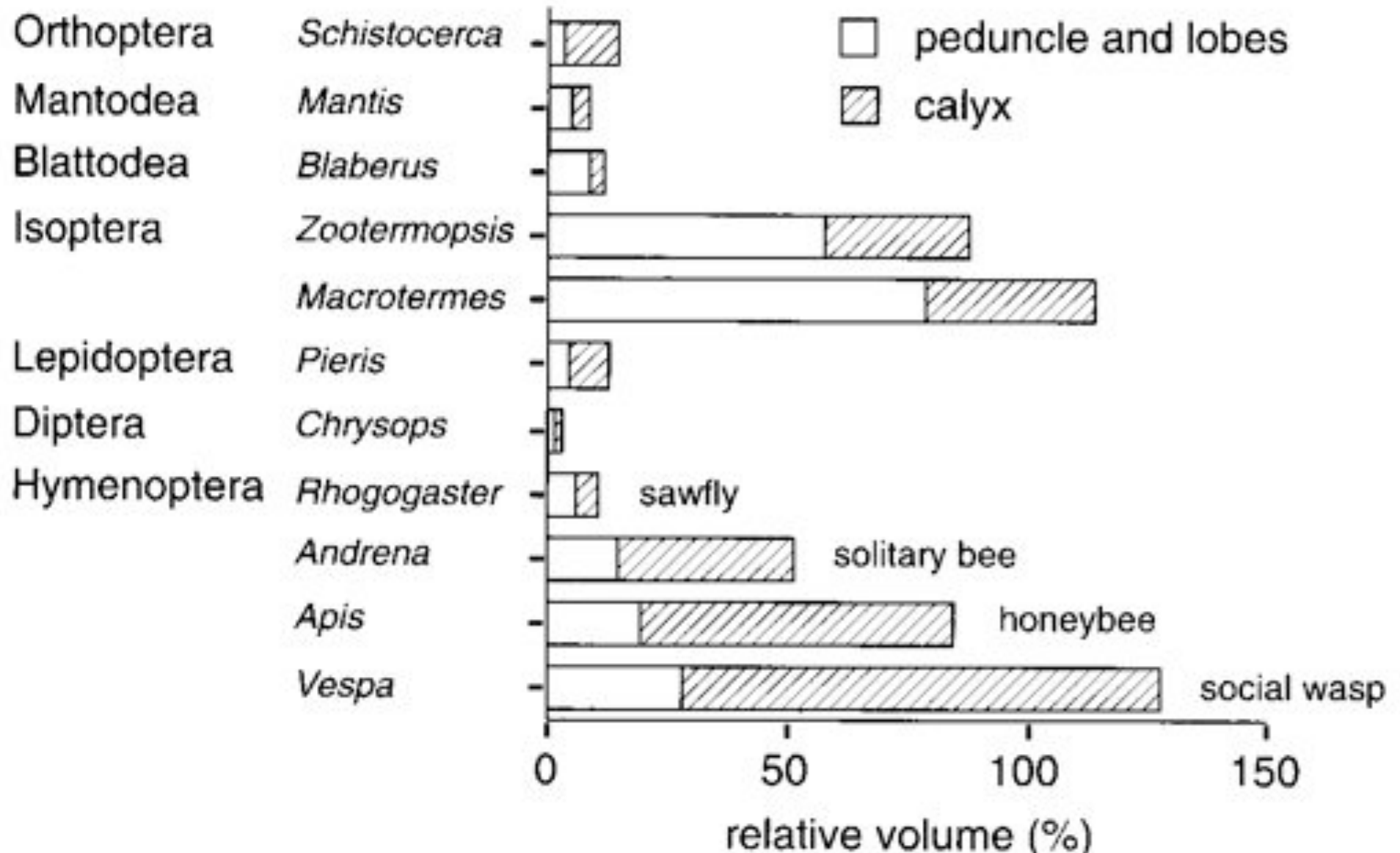
c) output neuron



d) feedback neuron



Volumes of the mushroom bodies in different species of insects expressed relative to the size of the central complex. **What does this chart tell us?**



**COMPOUND EYES, OCELLI,
STEMMATA, and EXTRAOCULAR
VISION**—need some sort of lens system

to focus light onto the photoreceptors

G.A. Horridge (ed.). 1975. The compound eye and vision of Insects. Oxford Press, N.Y. 595pp



OCELLI



**STEMMATA OF
MIDGE LARVA**



COMPOUND EYES



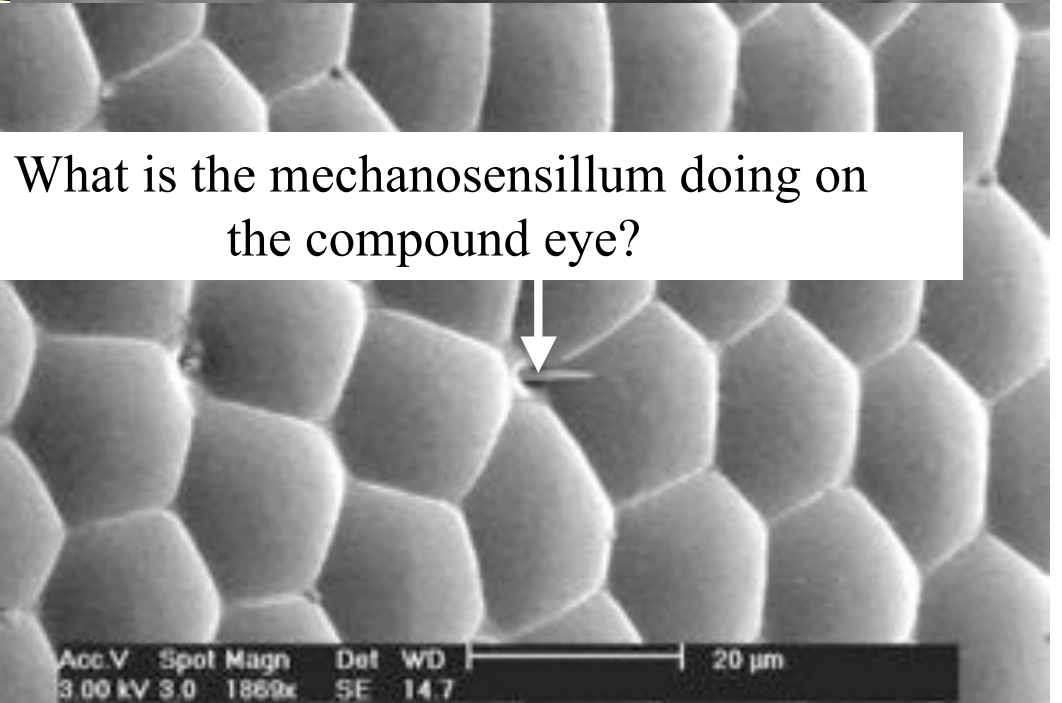
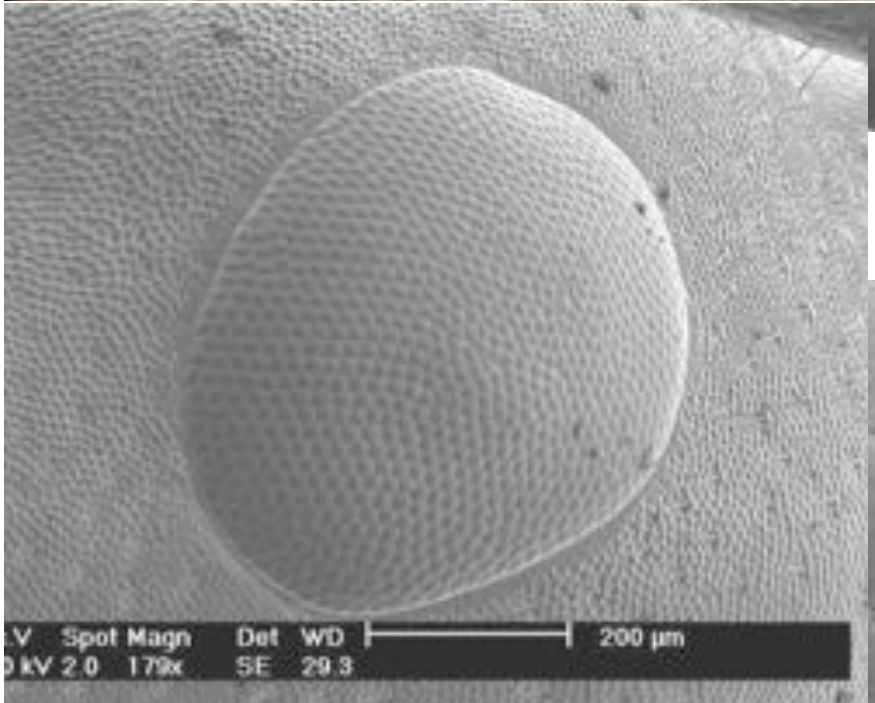
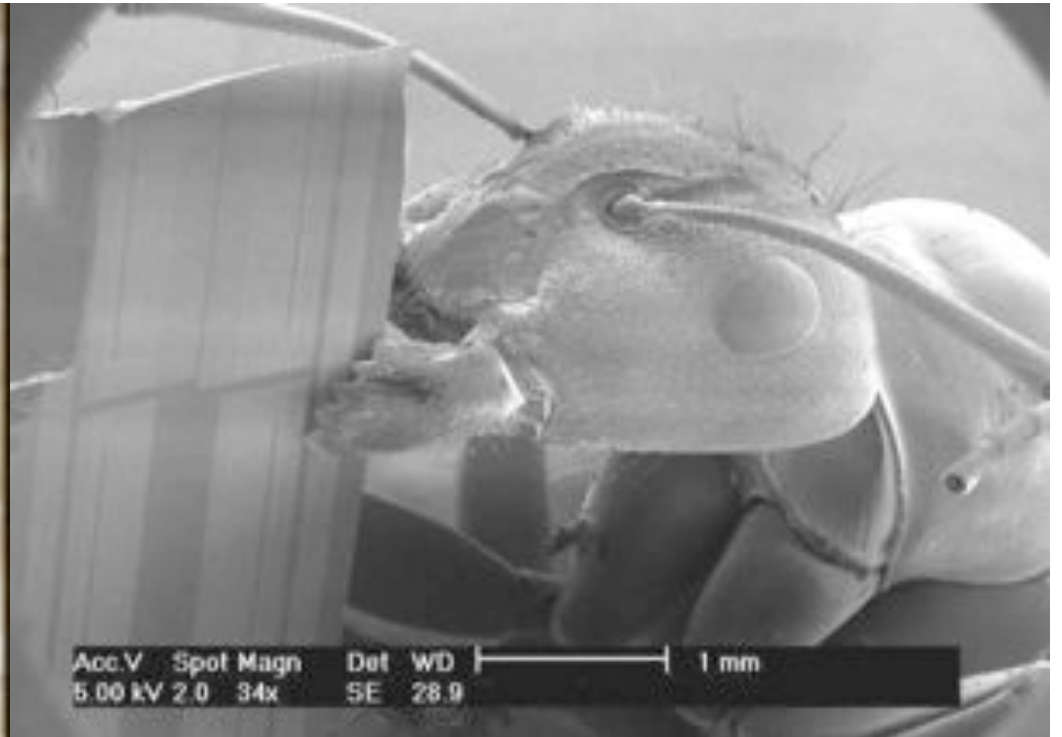
"Wow, this place is really packed—or maybe it's just my compound eyes."

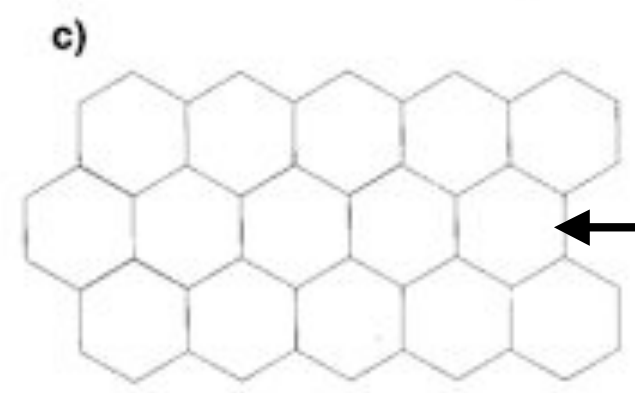
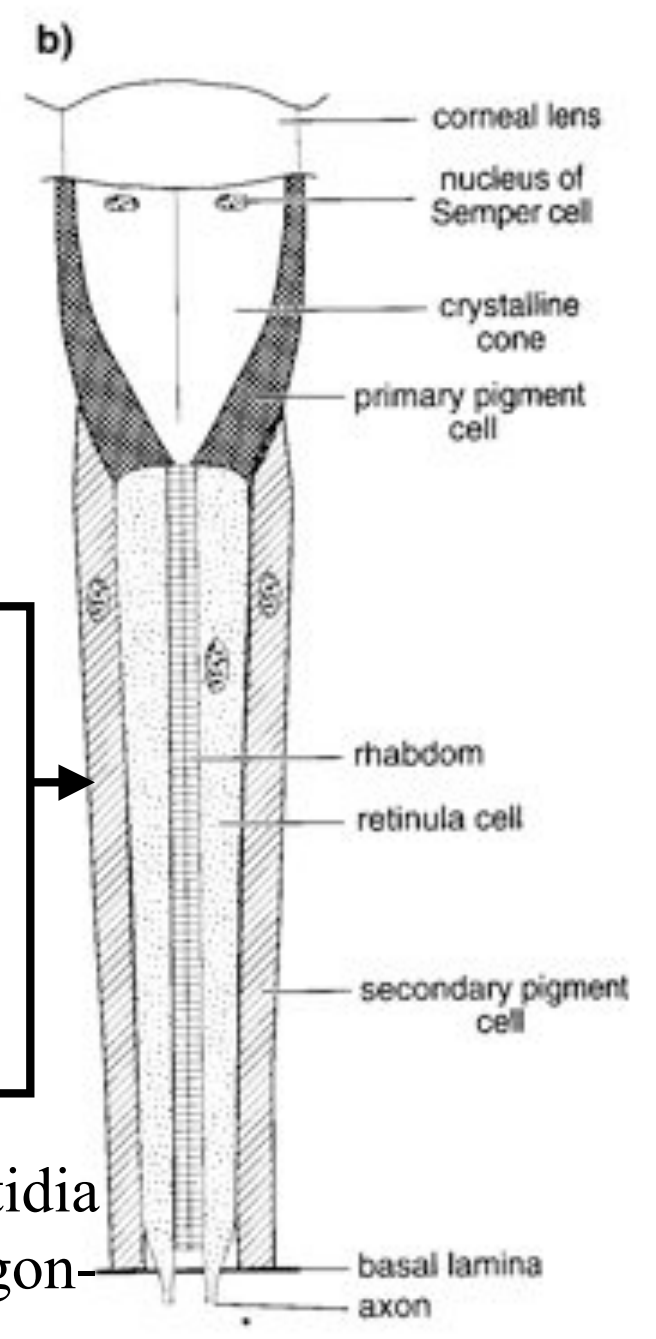
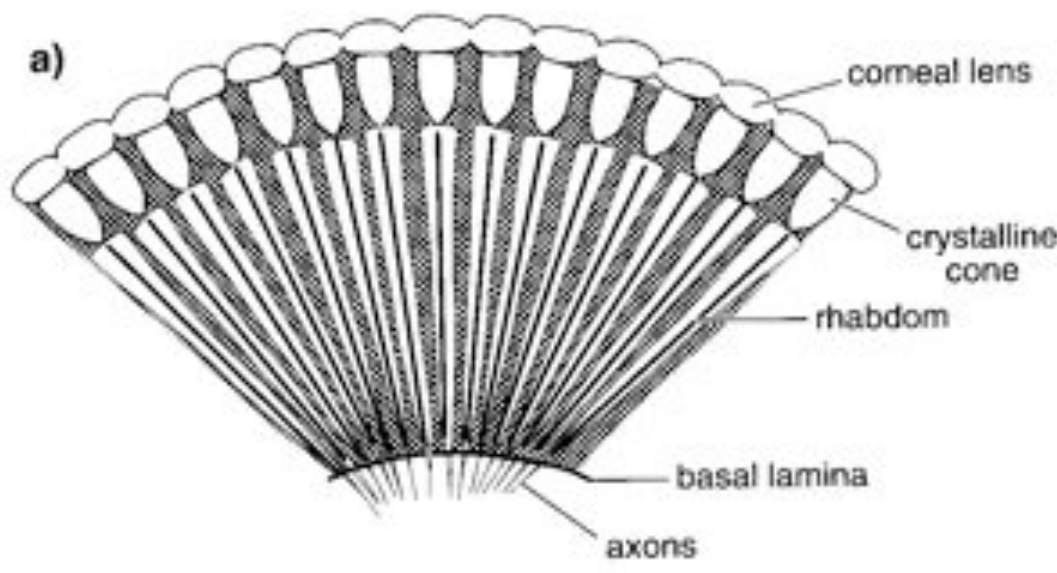
Hemimetabolous insects-adults and larvae have **compound eyes** and 3 single lenses called **ocelli**

Holometabolous insects-adults have **compound eyes** or **ocelli**
immatures have 1 or more single-lens eyes on side of head known as **stemmata**

GROUPS OF HEXAPODS

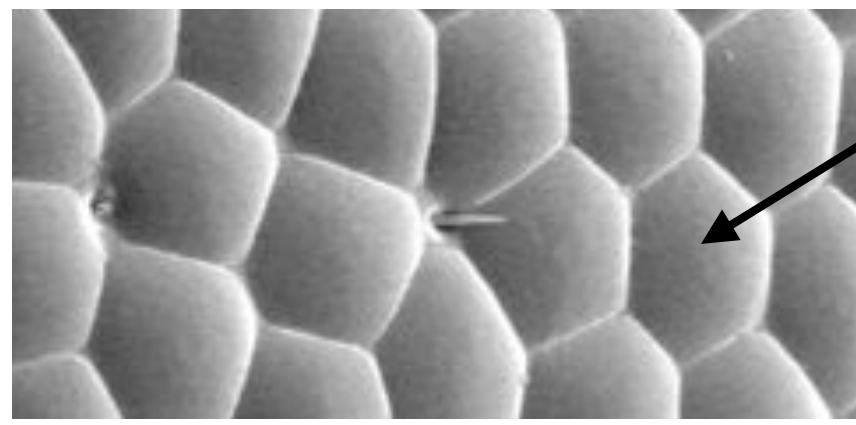
- 1. Protura and Diplura have no light sensing organs**
- 2. Collembola have up to eight ommatidia**
- 3. Cave-dwelling insects eyes can be reduced or absent**



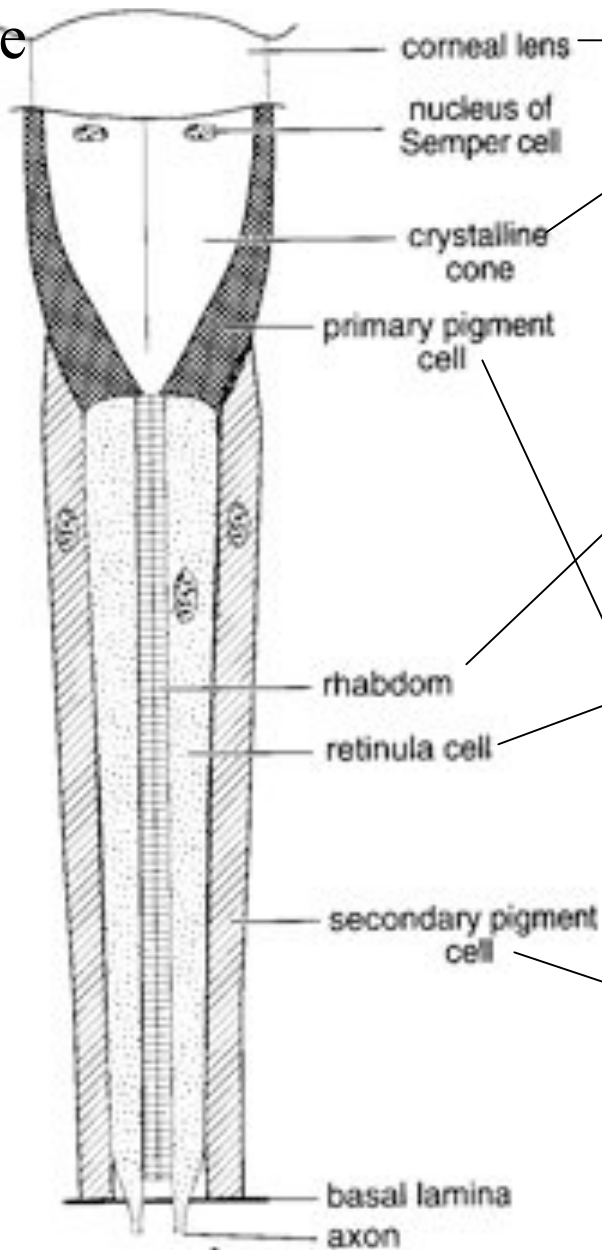


Individual visual units are hexagonal and called ommatidia

10,000 ommatidia in eyes of dragonfly



Ommatidium of compound eye



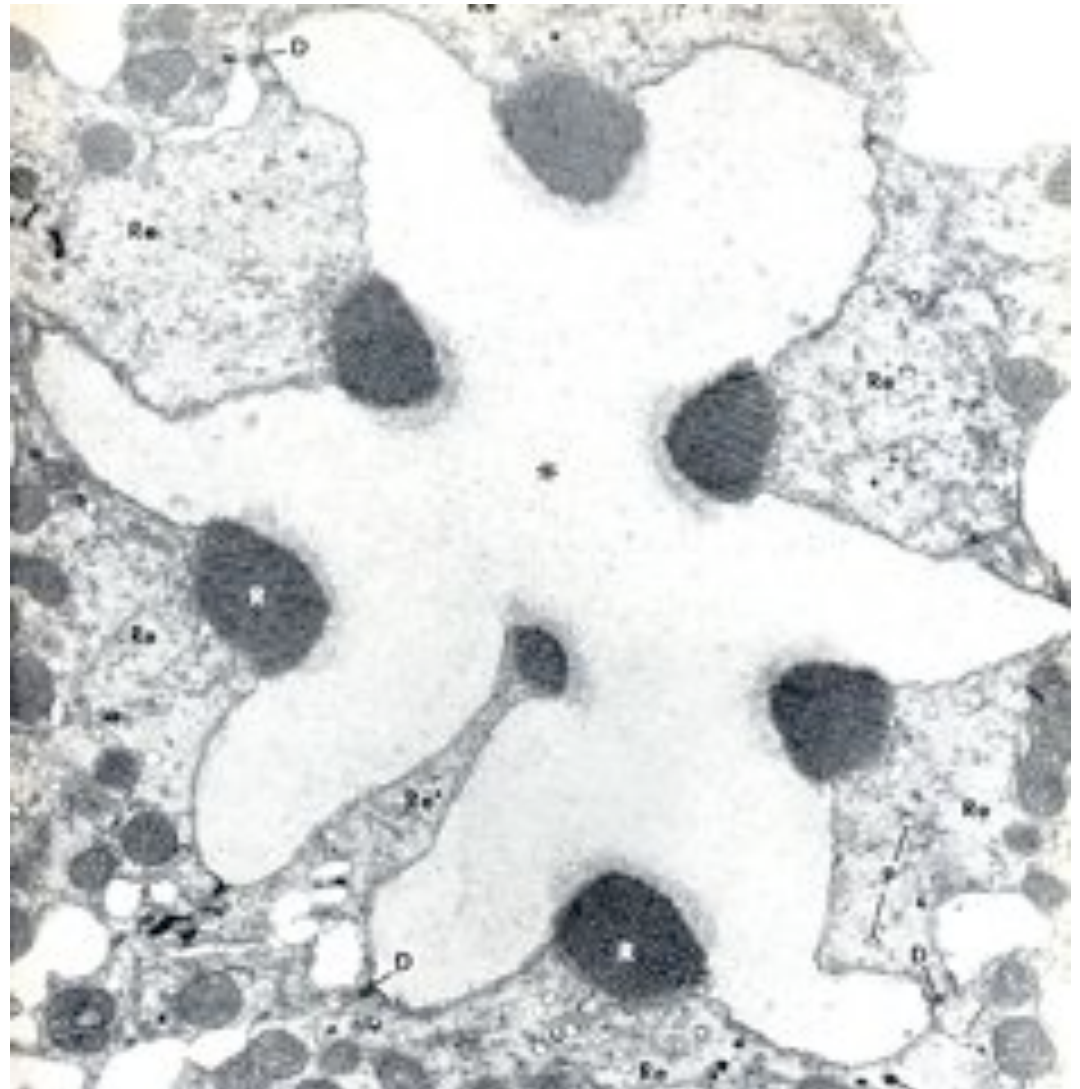
The lens and cones provide the eye with focusing of the light rays that enter the eye. The lenses are cuticular and are secreted by the epidermal cells.

The rhabdom is the photosensitive structure of the eye. It contains the photosensitive pigments.

Retinular cells with sensory areas confined to edge of cell facing inwards towards central axis. Light sensitive faces may touch each other and form a column - rhabdom. Usually 6 or 7 cells (originally 8 but 1 not involved).

The pigment cells (sometimes called the iris) absorb any light that isn't absorbed by the retinula cells and its rhabdom or isn't refractive

Rhabdom (R) - light falling on this causes photochemical reaction. Chromoprotein rhodopsin in presence of light is bleached and dissociates to retinene with altered molecular structure - this leads to production of a nerve impulse. Rhodopsin conjugated with various proteins determines the particular wavelength of light which is absorbed. Rhabdom is part of retinular cells (Re).



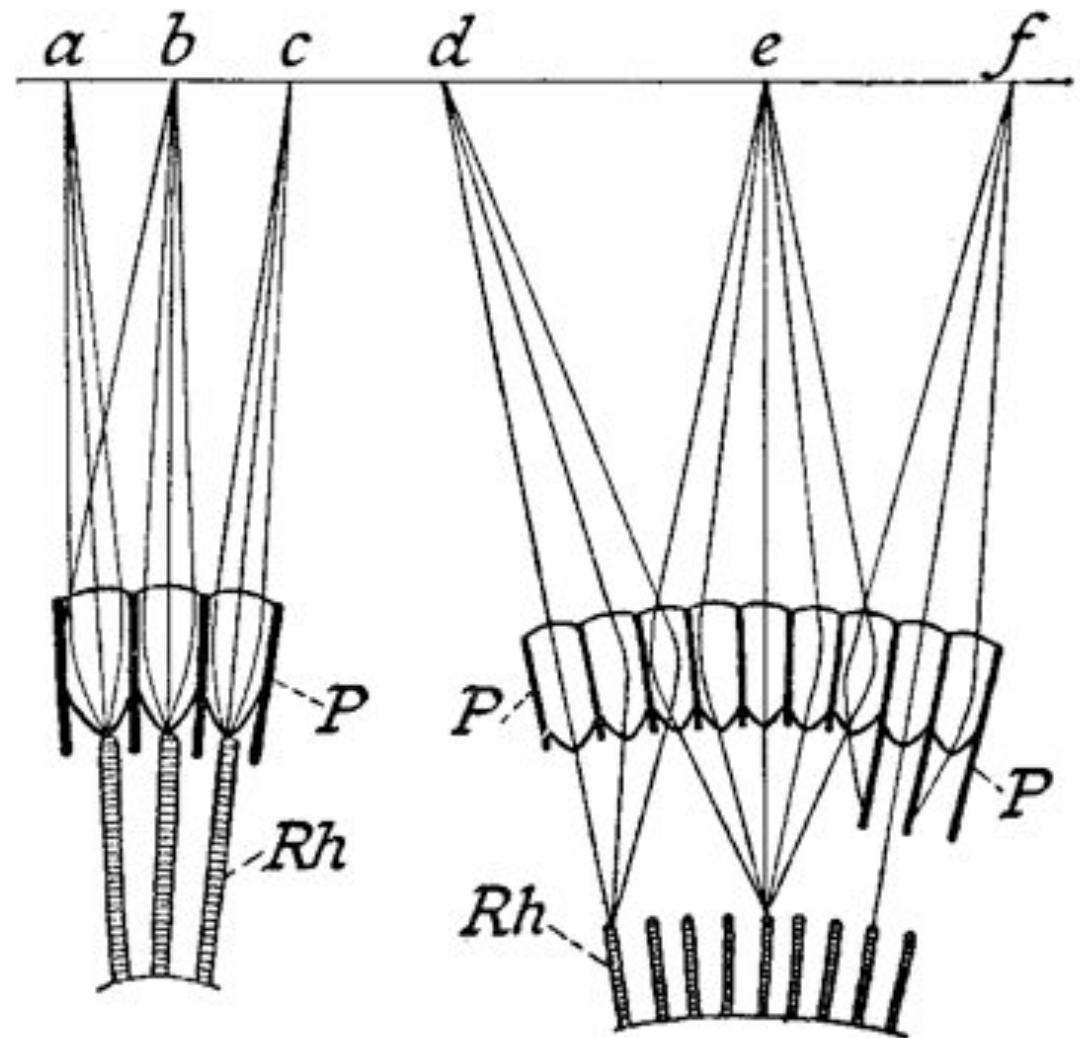
EYES ADAPTED FOR BRIGHT LIGHT CONDITIONS (APOSITION) AND THOSE ADAPATED FOR DIM LIGHT OR NIGHTTIME (SUPERPOSITION)

Iris cell pigments absorb light that isn't refracted. Their structure is the thing that differentiates apposition from superposition type of eye.

Apposition eyes have ommatidia optically isolated and function best under bright light conditions.

Superposition eye, secondary iris cells have mobile pigments which can isolate or expose retinular layer of ommatidium to light from adjacent ommatidia.

Night Shine is some moths-This is similar to that in nocturnal vertebrates except here small trachea at the base of the rhabdom reflect the light back to be used again.



APOSITION

SUPERPOSITION



MOTH

Eyeshine in vertebrates is caused by a structure known as the tapetum lucidum (Latin = bright carpet).

In insects eyeshine is produced by a underbedding of tracheae that reflect the incoming light, thus producing more light for night insects.



JACKEL



RACCOON

Flicker fusion theory – The compound eye is especially good for movement detection and boundary identification through sensing changes in intensity between adjacent ommatidia. May be **very limited in terms of image formation but can produce outline in space and pattern in time.**

Because of their ability to see things that produce a flicker, such as a fluorescent light that is flickering but, which we usually don't see, insects do see it. This is why some labs. only use direct current, rather than alternating current, for the bulbs in their growth chambers or experiments.

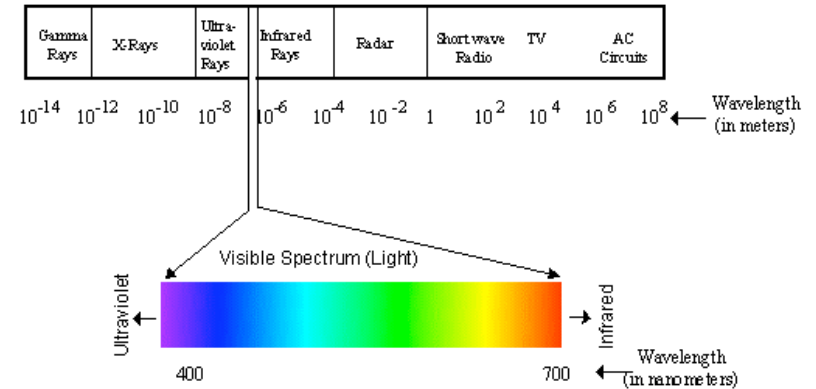
Humans are very visual animals...we use our sense of sight to interpret much of the world around us. What we see is called "light." However, what we see is really only a small part of the entire "electromagnetic spectrum." Humans can see only the wavelengths of electromagnetic radiation between about 380 and 760 nanometers...this is light. Our eyes do not have detectors for wavelengths of energy less than 380 or greater than 760 nanometers, so we cannot "see" other types of energy such as gamma or radio waves. Some insects, however, can detect electromagnetic radiation in the infrared range while the honeybee is able to use UV light emanating from plant flowers to locate honey (called nectar guides).

Spectral range: Man 380 to 760 nm
 Insects 300 to 600 nm

Blow flies have 3 peaks of sensitivity: 350, 480 and 550 nm.

Honey bees can distinguish 6 major categories of color:

yellow	500 - 600	primary
blue-green	480 - 500	
blue	410 - 480	primary
violet	390 - 410	
u-violet	300 - 390	primary



How Can Visual Acuity Be Improved?

- Insects with good vision have large eyes and large numbers of ommatidia (area sampled by each reduced).
 - These eyes tend to be flatter in areas of best acuity; better light gathering.
- Binocular Vision - best developed in predators that need to judge distance. Dragonfly larvae, praying mantis, tiger beetles.

Interference of eyes with other activities.

- Cerambycid beetles have emarginate or divided eyes.
- Gyrinid beetles - compound eyes divided into upper (aerial pair) and ventral (aquatic) pair.

Why do insects have this type of eye?

- space is required for focusing of light, insect head too small to permit focusing.
- muscles needed for focusing, not enough room.
- how complex must a brain be to process image information?

Special eye arrangements-

1. Gyrinidae-Have divided eyes.
Top looks into air; bottom into water.

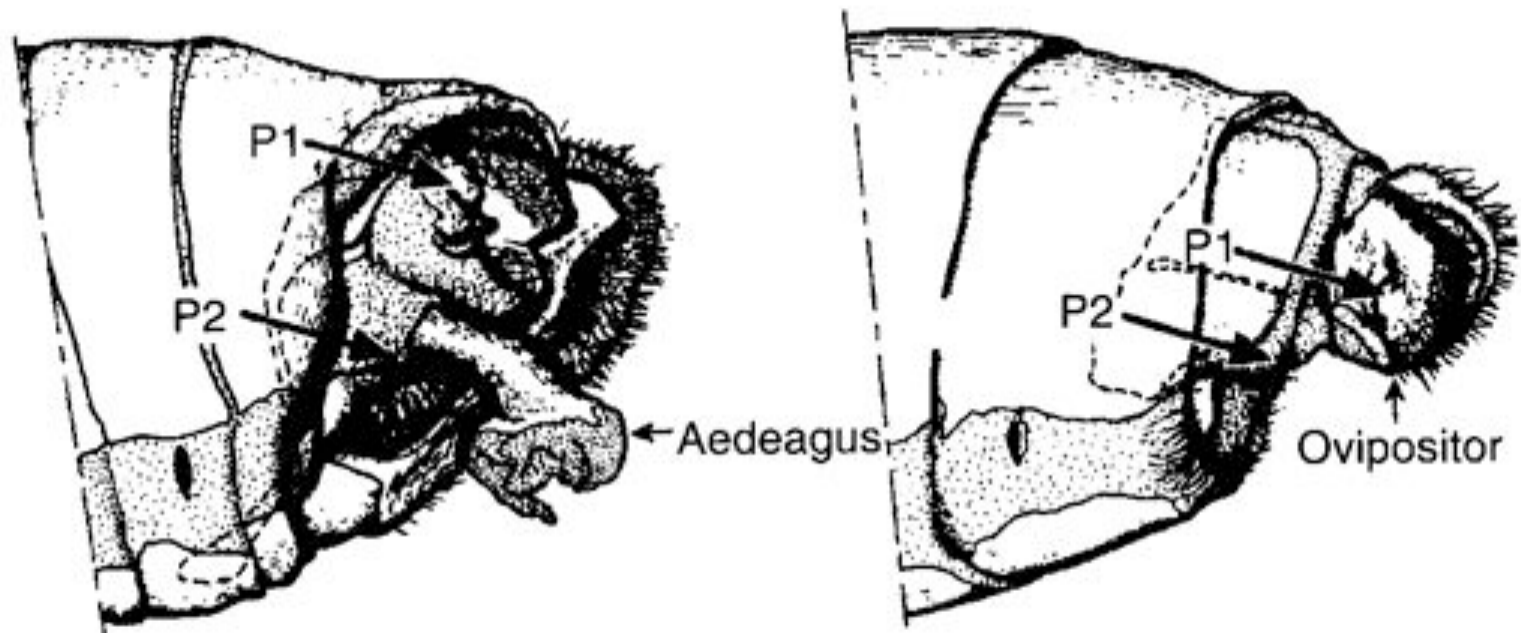


2. Diopsidae-Stalk eyed flies-



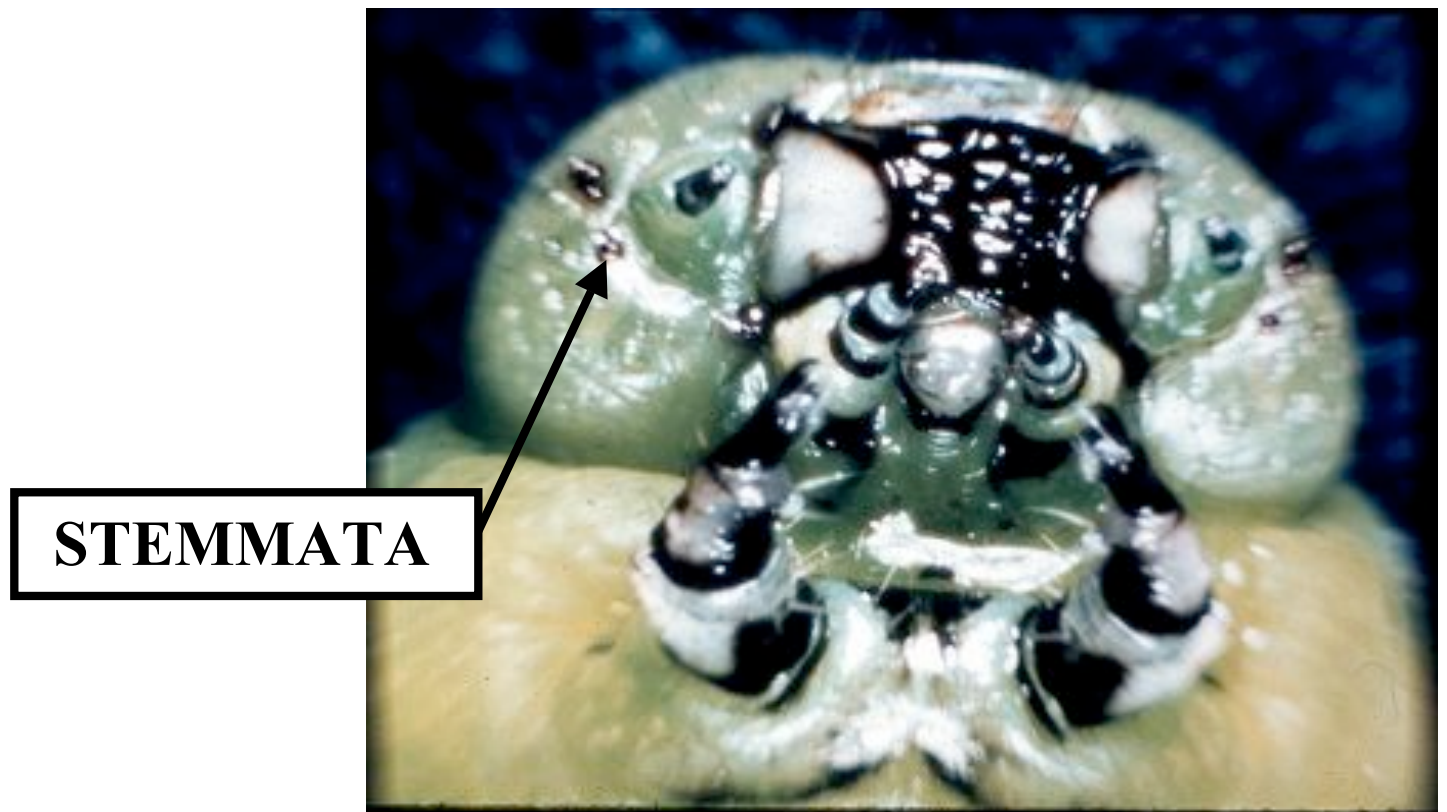
3. Dipteran eyes with larger facets on top and smaller on bottom.
Usually found in those Diptera that mate in a swarm

1. **Extraocular detection**-Some insects can perceive light through the cuticle and have light sensitive cells underneath; however, these have not been identified. Aphids have light sensitive cells in the **brain** that respond to changes in day length. Also, genital photoreceptors (P1, P2) have been identified on the **ovipositor** of some butterflies and probably inform the female when the ovipositor is fully extended. Also believed to play a role in copulation in the male by providing information that the vagina of the female is properly aligned for aedeagus insertion.



2. **Stemmata**-The only visual organs of the larval holometabola and in Apterygote adults. Very poor resolution power. Caterpillars behaviorally scan from side to side using these visual organs. Similar in structure and function to ocelli.

Probably not image forming but sensitive to direction of light, movement and boundaries as each stemma has its own narrow field of view.



3. Ocelli-

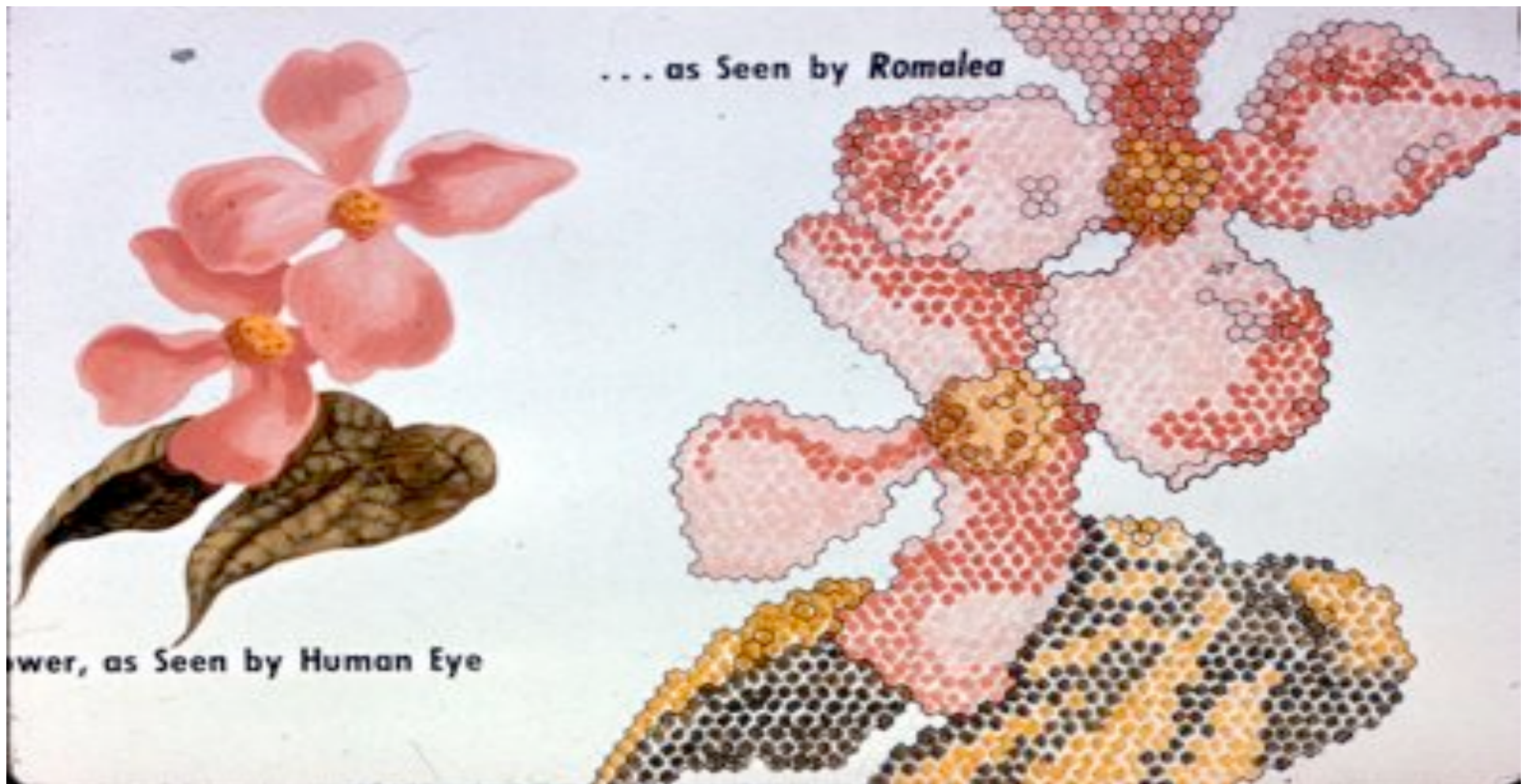
- 1. Lens probably does not produce an image, plane of focus lies below sensitive area of retinular cells.**
- 2. Ocelli very sensitive to low light levels.**
- 3. Ocelli have a role in governing activity of animals. They generally have a stimulatory effect on the nervous system - when exposed to light animal responds more readily to external stimulation.**
- 4. Control function of compound eye - when ocelli are not illuminated compound eye is "switched off" for insect with ocelli darkened does not respond as well to visual stimulation as one with ocelli functional.**
- 5. Role in circadian rhythm, day length responses (eg. diapause).**

Compound eyes

- Provide a very wide field of view, especially in predators (dragonfly, mantid)
- The backswimmer *Notonecta* has a 246° field of view horizontally, and 360° field of view vertically
- Compound eye is an aggregate of subunits called **ommatidia**. Ponerine ants have a single ommatidium/eye whereas some dragonflies have as many as 10,000/eye.
- The external surface is faceted. In species with large numbers of ommatidia, each facet is hexagonal in shape – provides optimal packing per unit area



1. Mosaic theory of Vision in Insects: Each ommatidium perceives a small luminous area corresponding to its projection on the visual field. These zones together form an image of light and darker spots comparable to newspaper photo. Could be more complex as there are 6 - 8 receptors each giving rise to a separate nerve; each rhabdom cell could have different color sensitivity.



Briscoe, A. D. and Chittka, L. (2001). The evolution of color vision in insects. *Annu. Rev. Entomol.* **46**,471 -510. [

Labhart, T. and Meyer, E. P. (1999). Detectors for polarized skylight in insects: a survey of ommatidial specializations in the dorsal rim area of the compound eye. *Microsc. Res. Techniques* **47**,368 –379.

Labhart, T., Meyer, E. P. and Schenker, L. (1992). Specialized ommatidia for polarization vision in the compound eye of cockchafers, *Melolontha melolontha* (Coleoptera, Scarabaeidae). *Cell Tissue Res.* **268**,419 -429.

Labhart, T., Petzold, J. and Hebling, H. (2001). Spatial integration in polarization-sensitive interneurons of crickets: a survey of evidence, mechanisms and benefits. *J. Exp. Biol.* **204**,2423 -2430.

Insects using polarized light

1. Honeybees
2. Desert insects
3. Homing insects like some crickets

Brines, M. L. and Gould, J. L. (1982). Skylight polarization patterns and animal orientation. *J. Exp. Biol.* **96**, 69–91

Fent, K. (1986). Polarized skylight orientation in the desert ant *Cataglyphis*. *J. Comp. Physiol. A* **158**, 145–150.

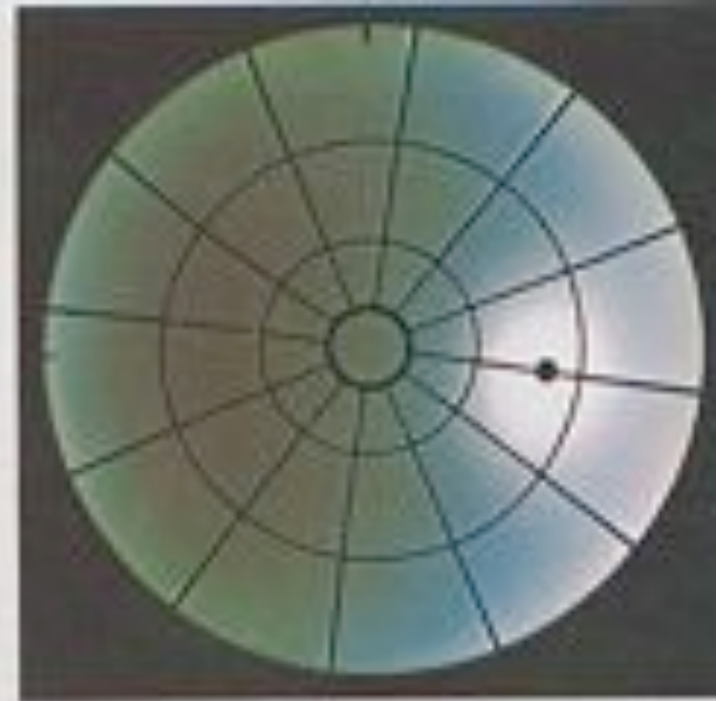
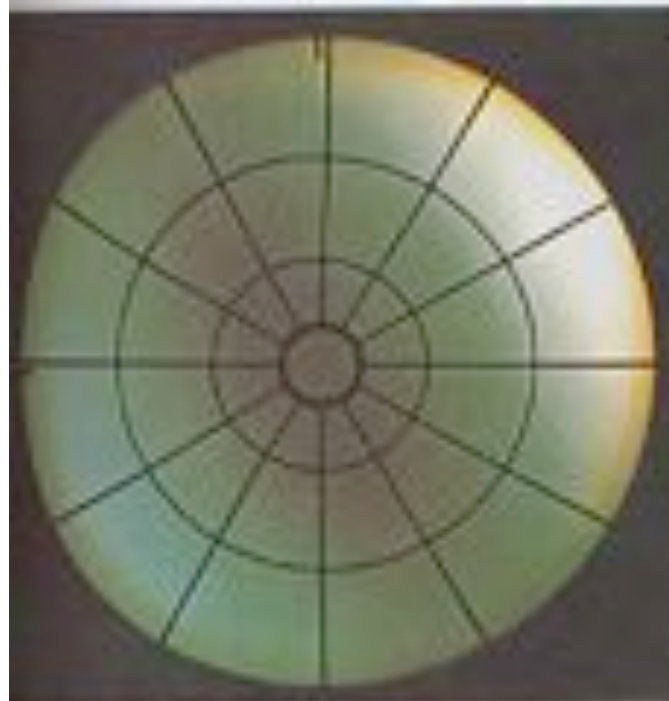
Kriska, G., Horvath, G. and Andrikovics, S. (1998). Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts Ephemeroptera. *J. Exp. Biol.* **201**, 2273–2286.

Rossel, S. and Wehner, R. (1984). How bees analyse the polarization patterns in the sky: experiments and model. *J. Comp. Physiol. A* **154**, 607–615.

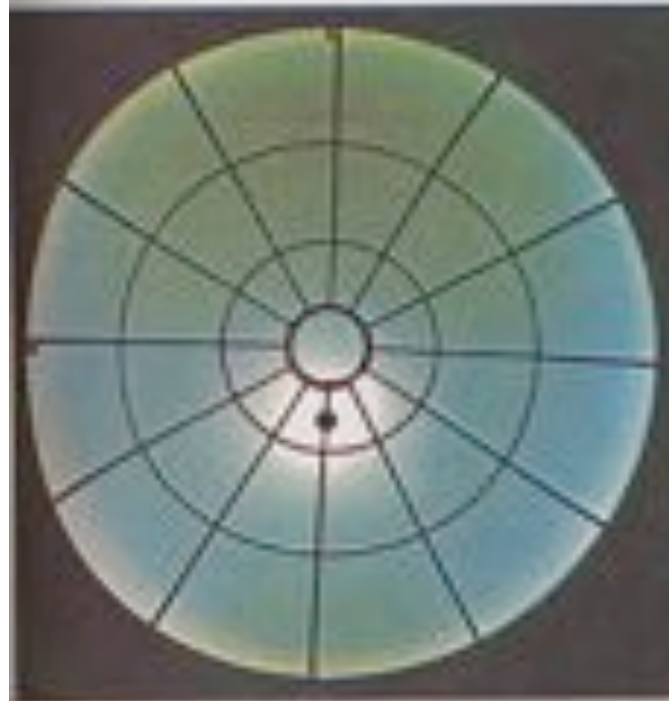
Wehner, R. and Rossel, S. (1985). The bee's celestial compass – a case study in behavioural neurobiology. *Fortschr. Zool.* **31**, 11–53.

Changes in the polarization of the light of the sky at different times of the day.
Kairouan in Tunisia

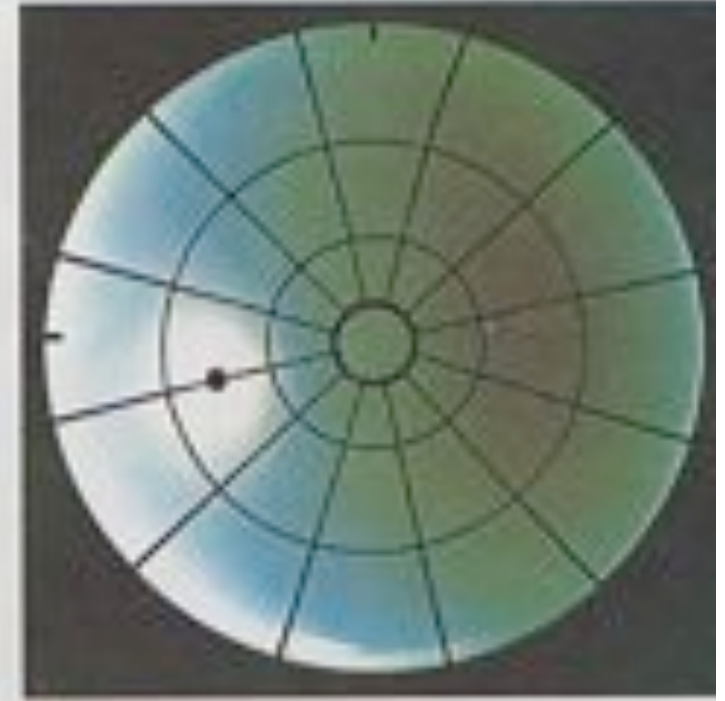
5:15 am top left



9:05 am top right



12:30 pm bottom left



3:40 pm bottom right

How do monarchs find their winter rufugia?



Do monarchs use the earth's magnetic field to migrate?

MONARCH BUTTERFLY MAGNETIC COMPASS PAPER RETRACTED

This is a cautionary tale, an example of how the extraordinary complexity of biological organisms, systems whose operating variables are often unknown, can lead researchers astray. In November 1999 (Proc. Natl. Acad. Sci. US 1999 96:13845), a research team reported that fall migratory monarch butterflies, tested for their directional responses to magnetic cues under three conditions, amagnetic, normal, and reversed magnetic fields, showed three distinct patterns: In the absence of a magnetic field, monarchs lacked directionality as a group; in the normal magnetic field, monarchs oriented to the southwest with a group pattern typical for migrants; when the horizontal component of the magnetic field was reversed, the butterflies oriented to the northeast. In contrast, nonmigratory monarchs lacked directionality in the normal magnetic field. The authors suggested the results were "a direct demonstration of magnetic compass orientation in migratory insects."

Four months later, in March 2000 (Proc. Natl. Acad. Sci. 2000 97:3782), the authors retracted their paper, noting the following: "The positive response to magnetic fields in two experiments cannot be repeated. Further experiments show the false positives in these tests result from a positive [directionality of movement (taxis)] by the butterflies to the light reflected off the clothing of the observers. We therefore retract our report. We regret the inconvenience that publication of this study may have caused."

Proc. Nat. Acad. Sci. <http://www.pnas.org>

ScienceWeek <http://scienceweek.com>

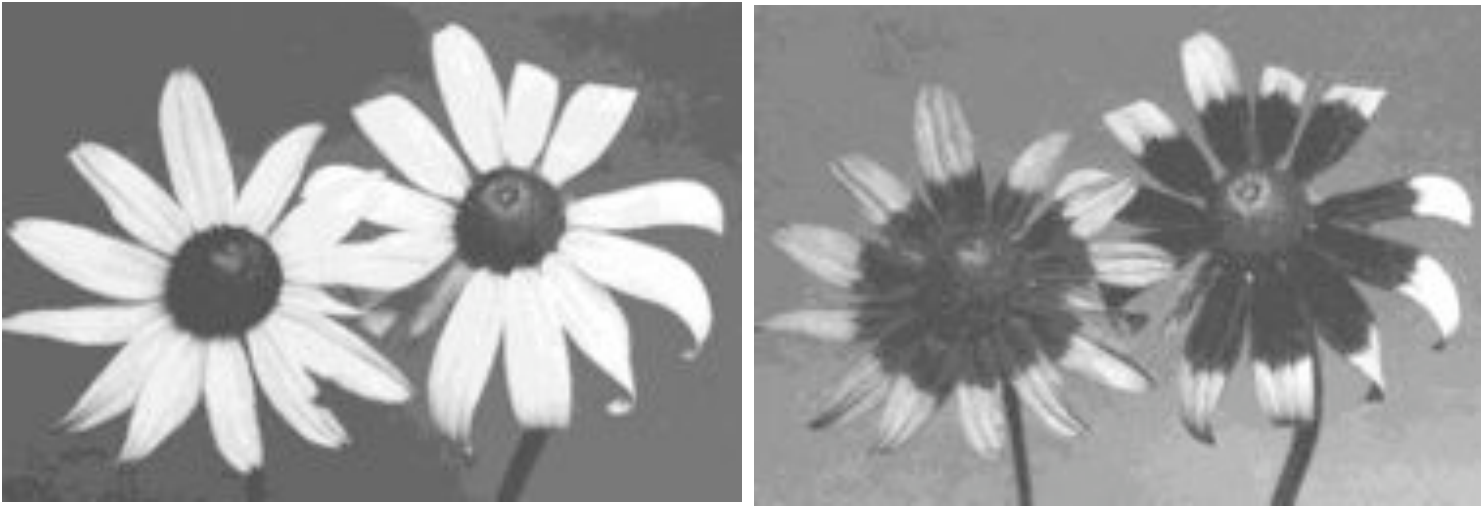
NEUROBIOLOGY: POLARIZED LIGHT AND MONARCH BUTTERFLY NAVIGATION

The following points are made by S.M. Reppert et al (Current Biology 2004 14:155):

- 1) During their spectacular migratory journey in the fall, North American monarch butterflies (*Danaus plexippus*) use a time-compensated sun compass to help them navigate to their overwintering sites in central Mexico [1-3]. One feature of the sun compass mechanism not fully explored in monarchs is the sunlight-dependent parameters used to navigate.
 - 2) Ultraviolet (UV) light is important for the initiation of flight in monarch butterflies [3]. Once flight is attained, however, the relevant features of skylight used for actual compass orientation are unknown. Based largely on studies in honey bees and desert ants, the recognized compass signals visible to insects in the daytime sky consist of the sun itself and polarization and spectral-intensity gradients, which are generated as sunlight scatters through the atmosphere [4-5]. The skylight pattern of polarized light (the e-vector pattern) provides one of the most reliable navigational cues [4,5].
 - 3) The authors provide data suggesting that the angle of polarized skylight (the e-vector) is a relevant orientation parameter. By placing butterflies in a flight simulator outdoors and using a linear polarizing filter, the authors demonstrate that manipulating the e-vector alters predictably the direction of oriented flight. Butterflies studied in either the morning or afternoon showed similar responses to filter rotation. Monarch butterflies possess the anatomical structure needed for polarized skylight detection, as rhabdoms in the dorsal-most row of photoreceptor cells in monarch eye show the organization characteristic of polarized-light receptors. The existence of polarized-light detection could allow migrants to accurately navigate under a variety of atmospheric conditions and reveals a critical input pathway into the sun compass mechanism.
 1. Perez, S.M., Taylor, O.R., and Jander, R. (1997). A sun compass in monarch butterflies. *Nature* 387, 29
 2. Mouritsen, H. and Frost, B.J. (2002). Virtual migration in tethered flying monarch butterflies reveals their orientation mechanisms. *Proc. Natl. Acad. Sci. USA* 99, 10162-10166
 3. Froy, O., Gotter, A.L., Casselman, A.L., and Reppert, S.M. (2003). Illuminating the circadian clock in monarch butterfly migration. *Science* 300, 1303-1305
 4. Frisch, K.v. (1967). *The Dance Language and Orientation of Bees*. (Cambridge: Belknap Press of Harvard University Press)
 5. Waterman, T. (1981). Polarization sensitivity. In *Handbook of Sensory Physiology*. Volume, V. and Autrum, H. eds. (New York: Springer-Verlag), pp. 281-469
Current Biology <http://www.current-biology.com>
-

INSECTS USING ULTRAVIOLET LIGHT

1. Nectar guides for directing pollinator to source of nectar



What dipterans might have UV perception?

“The ability of the dronefly to distinguish UV”. Having a distinct UV receptor provides the dronefly the capability to distinguish color in a region of the spectrum where many flowers show nectar guides. Bishop, L.G. 1974. An ultraviolet photoreceptor in a Dipteran compound eye. J. comp. Physiol. 91: 267-275.

2. Species recognition and mating in butterflies

Butterfly vision simulated



Human Vision



Ultraviolet



HOW TO DEVELOP VISUAL TRAPS BASED ON ENVIRONMENTAL CUES

1. Pattern and shape recognition



2. Motion

3. **Colors-Use spectrophotometer to get the wavelengths of the object one is trying to copy. Then find paints with same wavelengths and make sure that UV light is not part of the problem**

4. ERG-electroretinograms

ERG (electroretinogram of the eye of both male and female *Tabanus nigrovittatus*.



Typical ERG responses of female to 477-nm light flashes. Top=AC recording
Bottom=DC recording



on off
signal



on off
signal



Allan, Stoffolano, Bennett. 1991. Spectral sensitivity of the horse fly *Tabanus nigrovittatus* (Diptera: Tabanidae). Can. J. Zool. 69: 369-374.

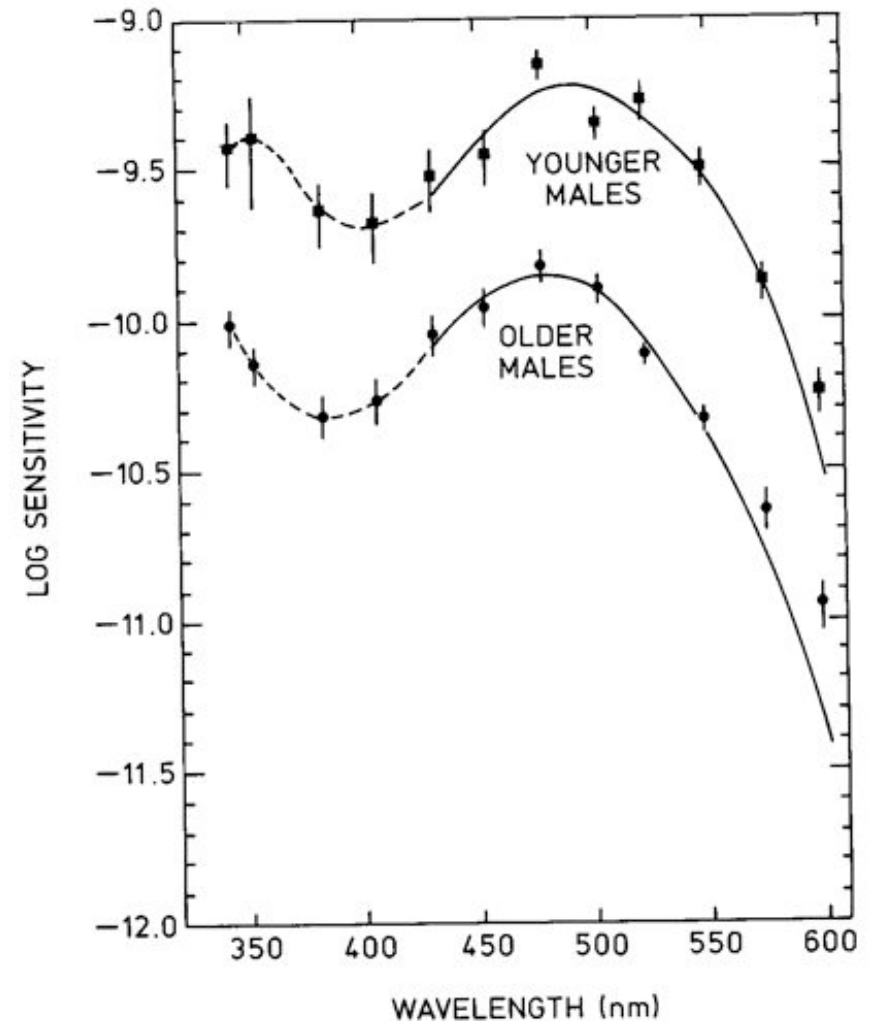
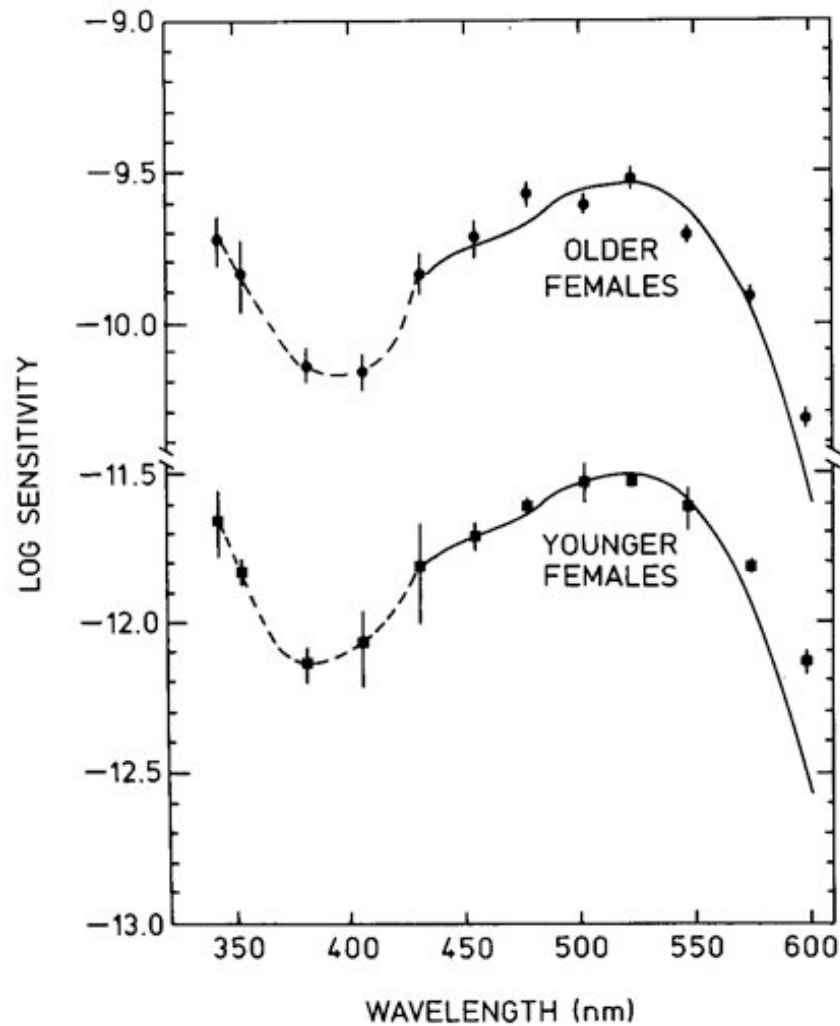


Using panels of different colors to see how male and female tabanids respond to the different colors in the field.

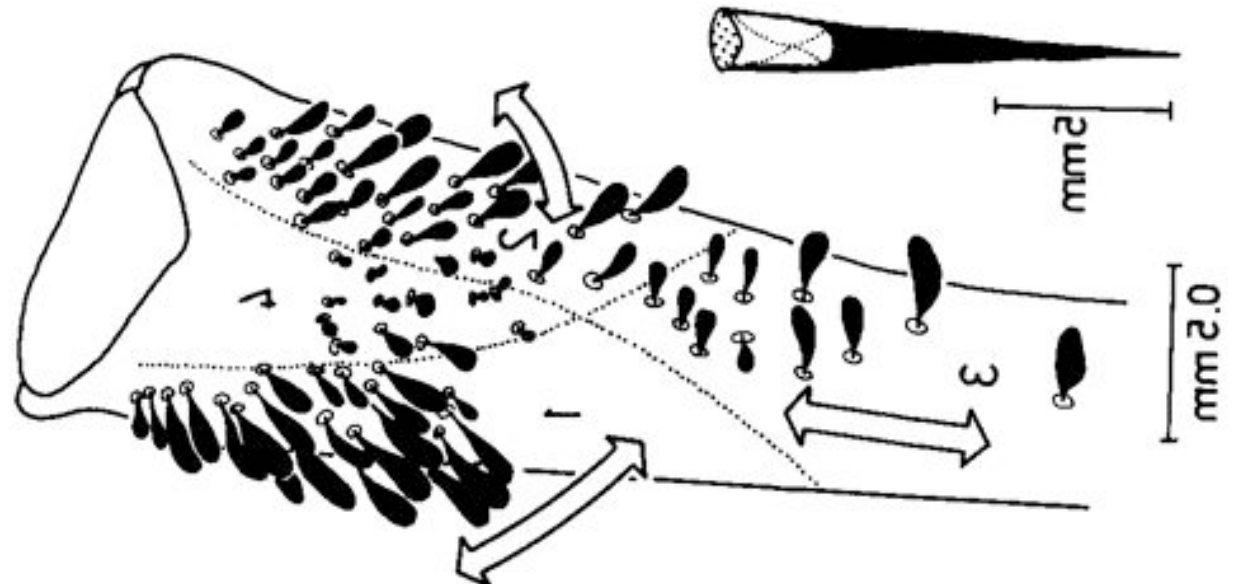
Color	No. of flies collected		
	<u>Males</u>	<u>Females</u>	<u>Total (%)</u>
Blue	10	911	921 (38.5) a
Black	9	634	643 (26.8) b
Red	19	459	478 (19.9) b
White	19	203	222 (9.3) c
Yellow-green	14	115	129 (5.5) c

Only female *Tabanus nigrovittatus* is attracted to mammalian hosts. **Why** does this happen?

How does this happen? Do males and females have different eyes? Is this a case of peripheral or central integration or differences?



CERCI



Club shaped sensilla on the cercus of the cricket are believed to function as gravity receptors.

TYMPANUM AND HEARING



eta from New Zealand

“Ears” in insects:

1. Noctuid moths
2. Lacewings
3. Praying mantids
4. Crickets and katydids
5. Hawkmoths
6. Cicada
7. Grasshoppers



Insect ears that are associated with a tympanum are designed to hear sound vibrations produced by another member of its own species or by a predator. They are an example of a mechanoreceptor.

They have the following characteristics:

1. Tympanic membrane that vibrates
2. Sensilla such as scolopedia attached to pick up the vibration (chordotonal organ)
3. Associated air sacs
4. Associated tracheal trunks

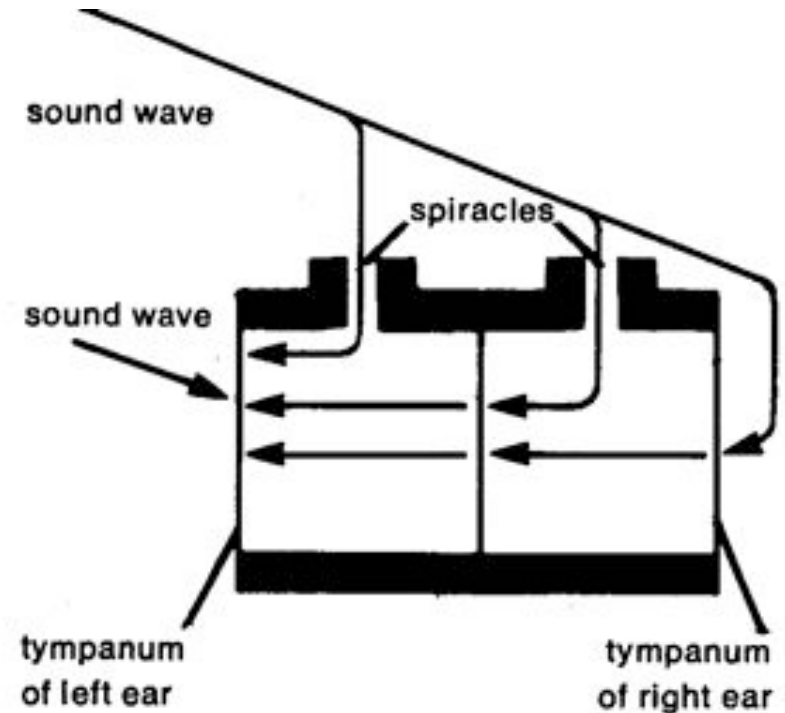
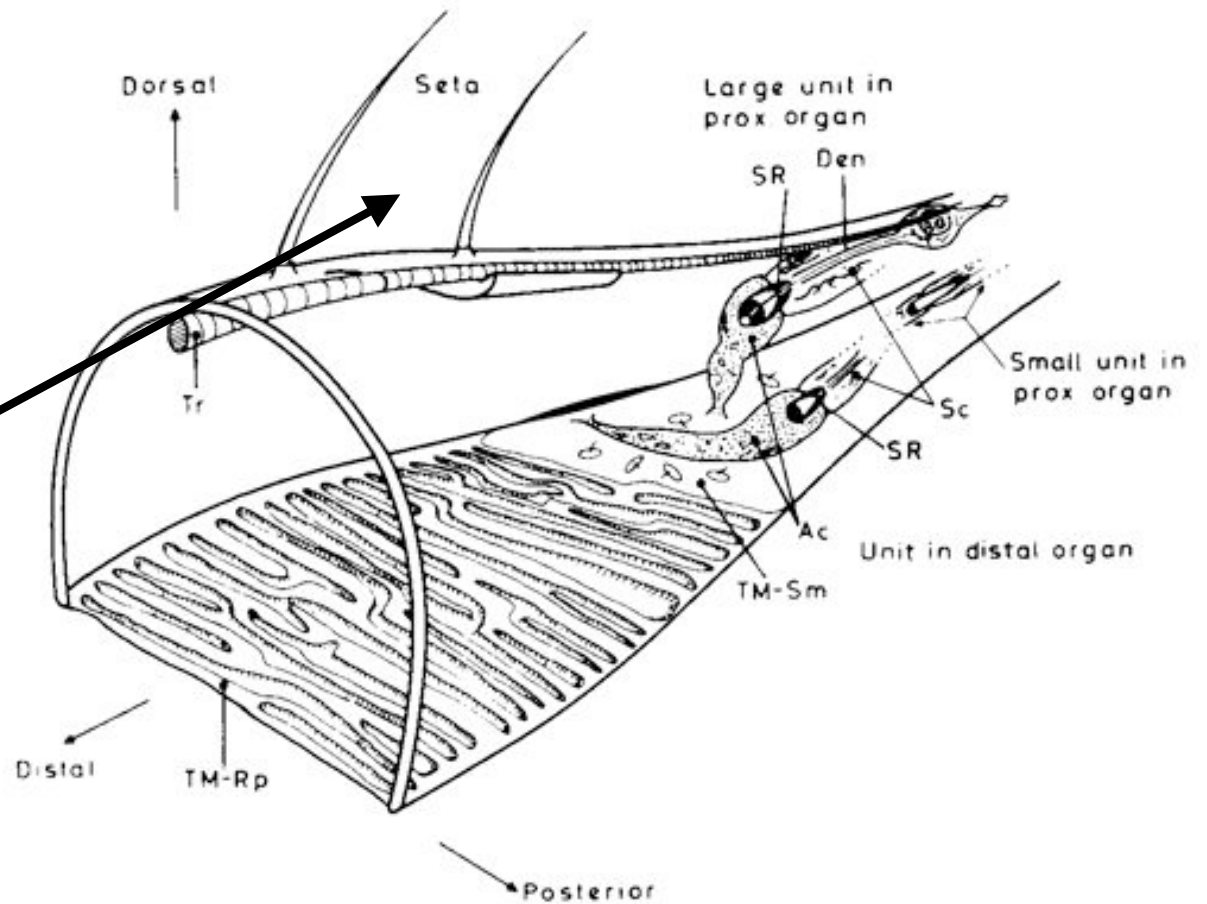
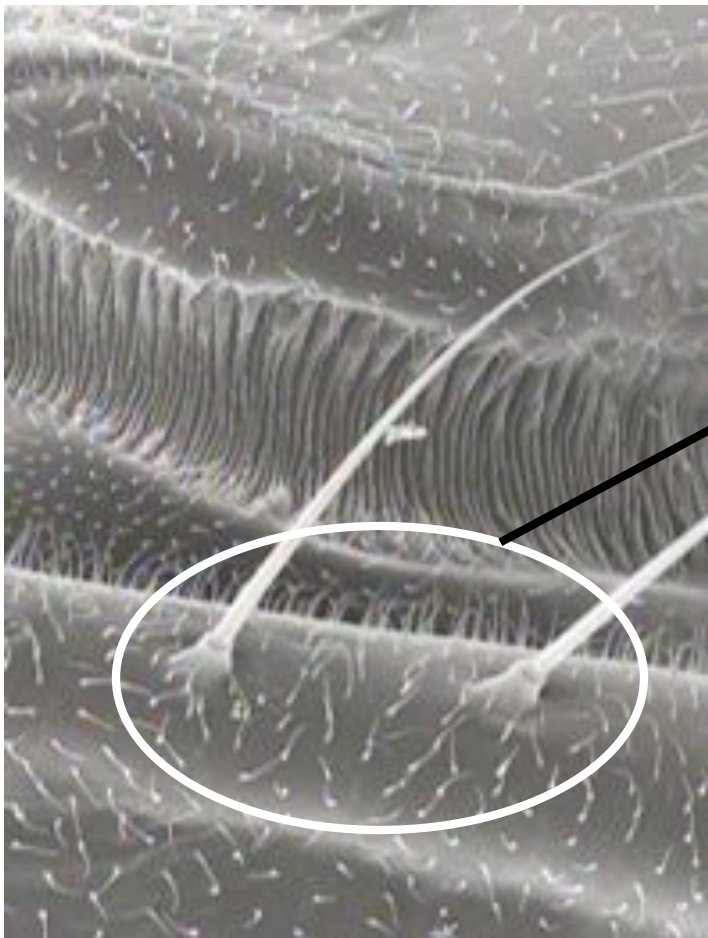


Figure 3. The force which causes the tympanum of the ear to move results from the difference between the pressure acting on the front surface of the tympanum and that acting on the back. The latter is determined by the amount of sound entering the opposite ear or some other input avenue and traveling through the air spaces in the body to reach the back surface. This schematic drawing of the effect of sound waves on the left ear of a cricket shows the several avenues by which these waves reach both the front and the back of the tympanum of the ear in question. In a similar fashion the sound is reaching the tympanum of the other ear. The spiracles of the cricket ear can be opened and closed by lids or valves which are controlled by muscles.

Lacewing ear

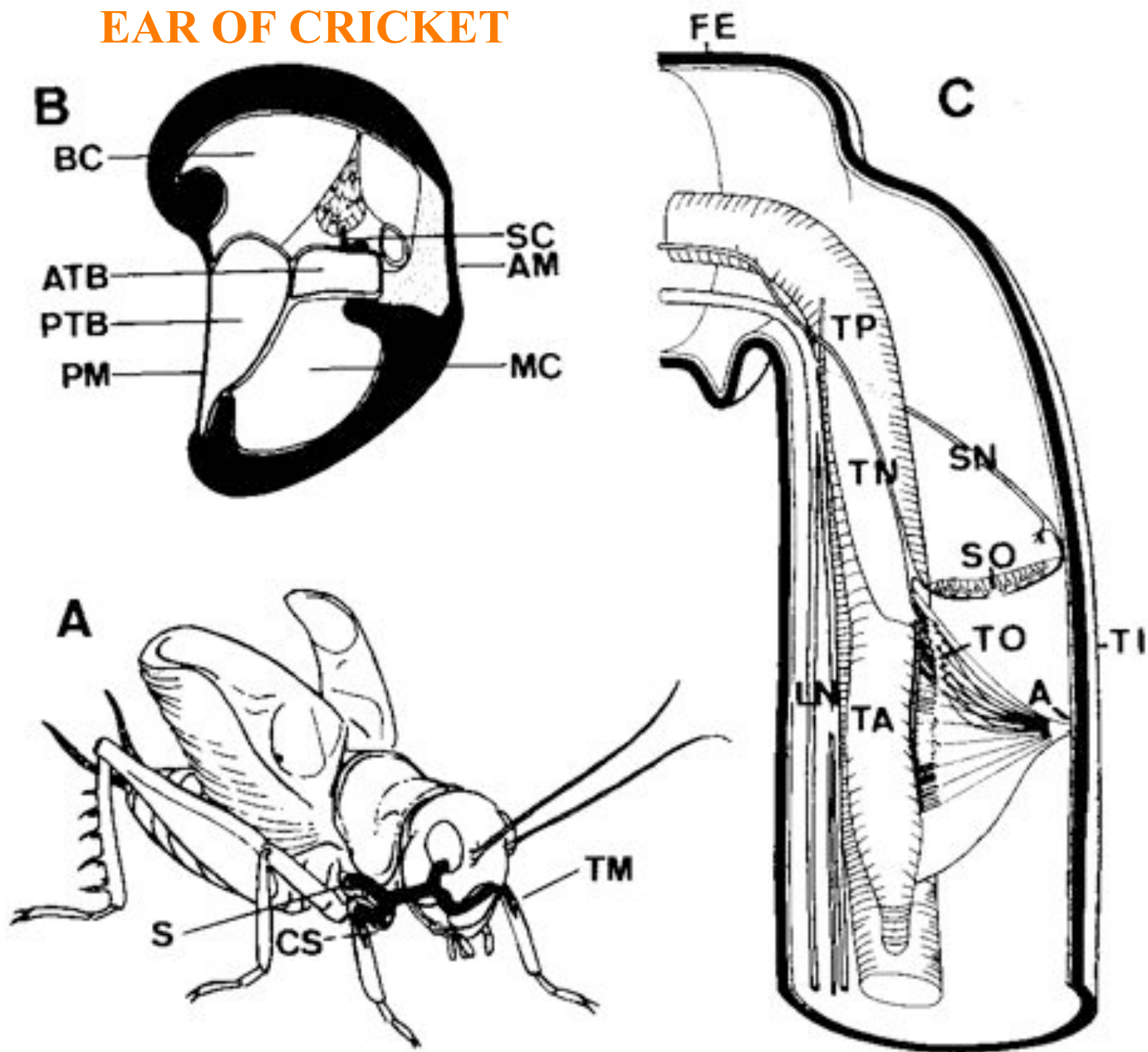
Notice the photo to the right showing a lacewing at night. One of their major predators is the bat. They use the fluid-filled ears located on the radial vein of the forewing to detect bat sonar.



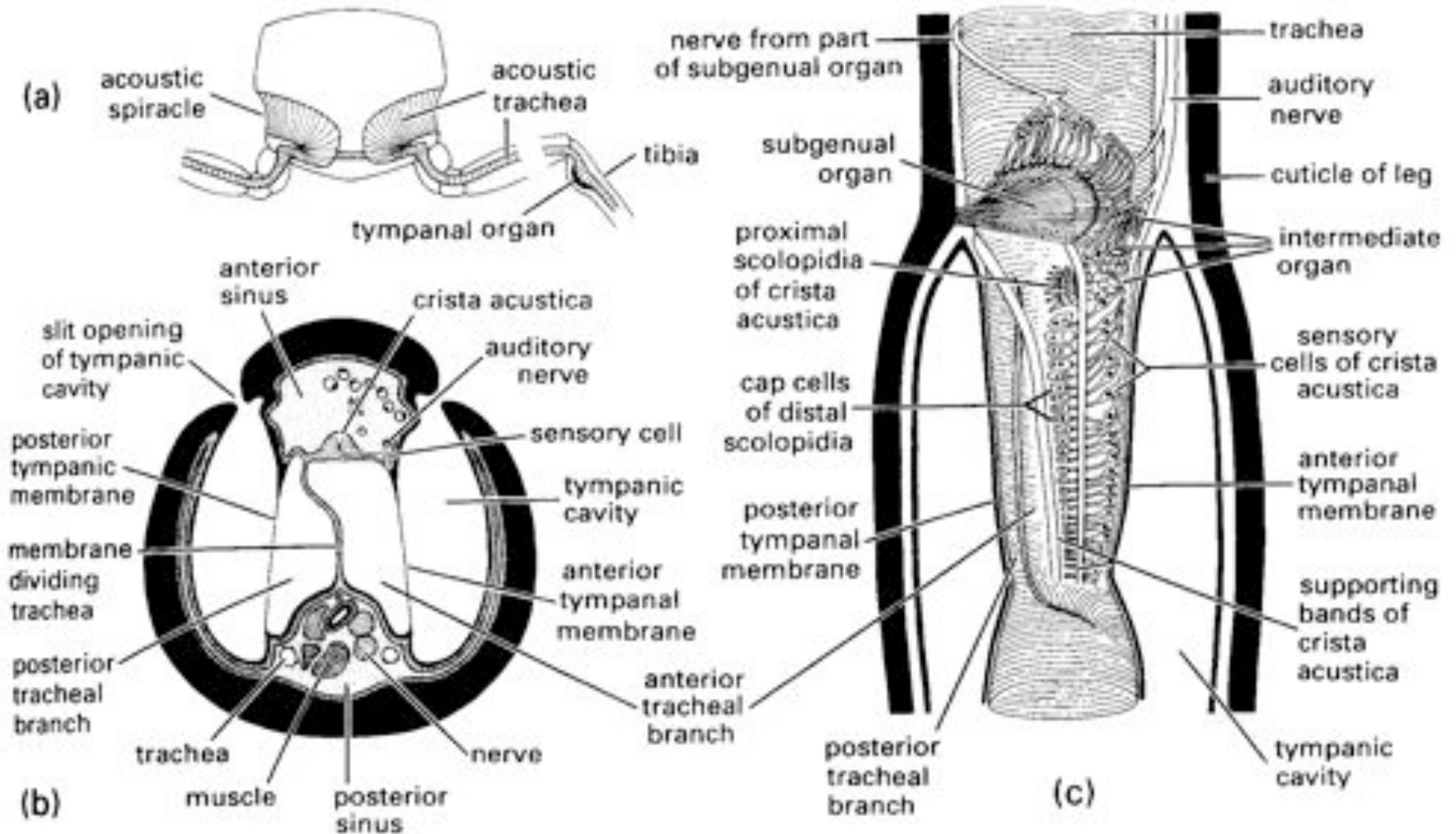
Katydid ear



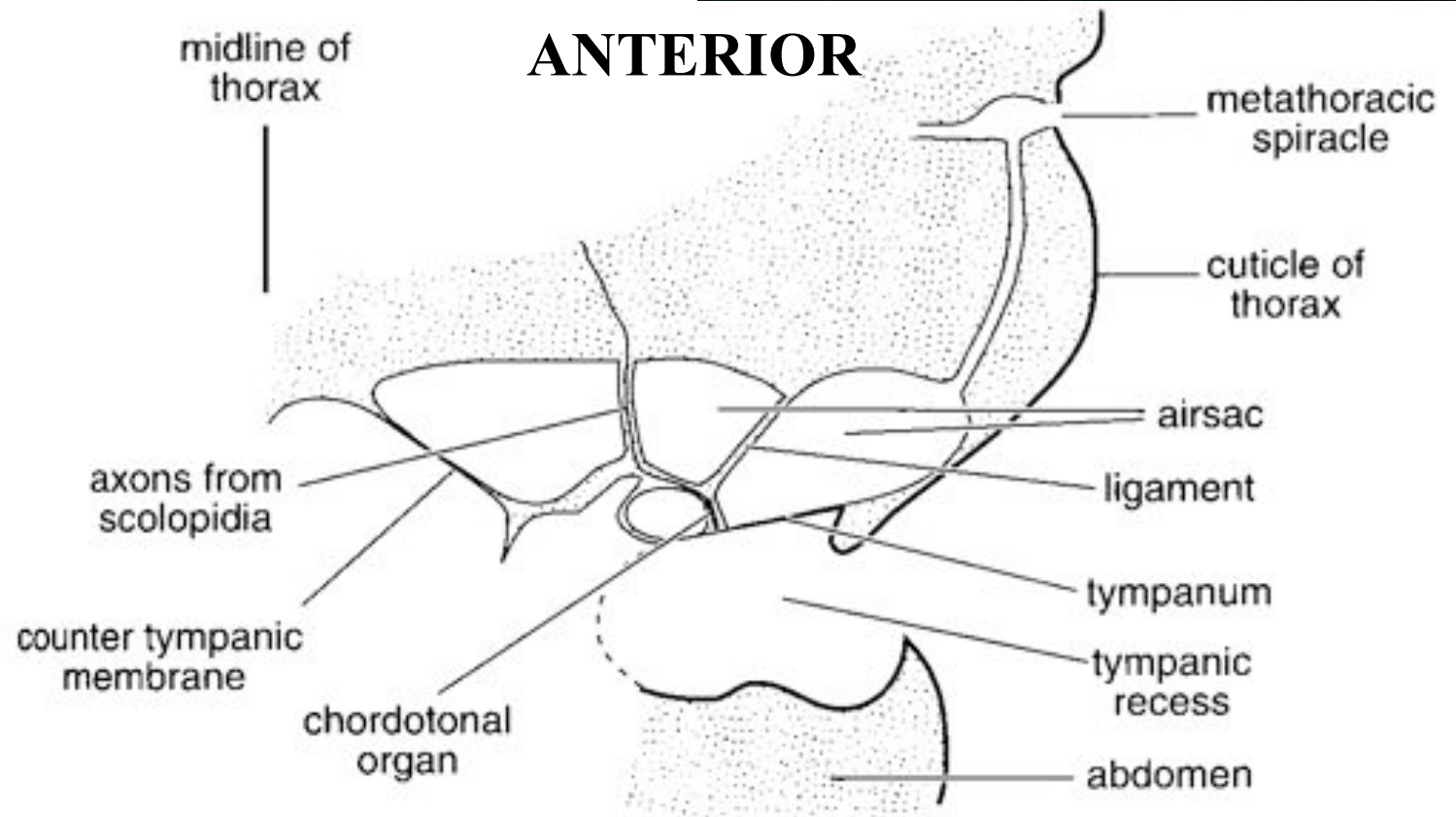
EAR OF CRICKET



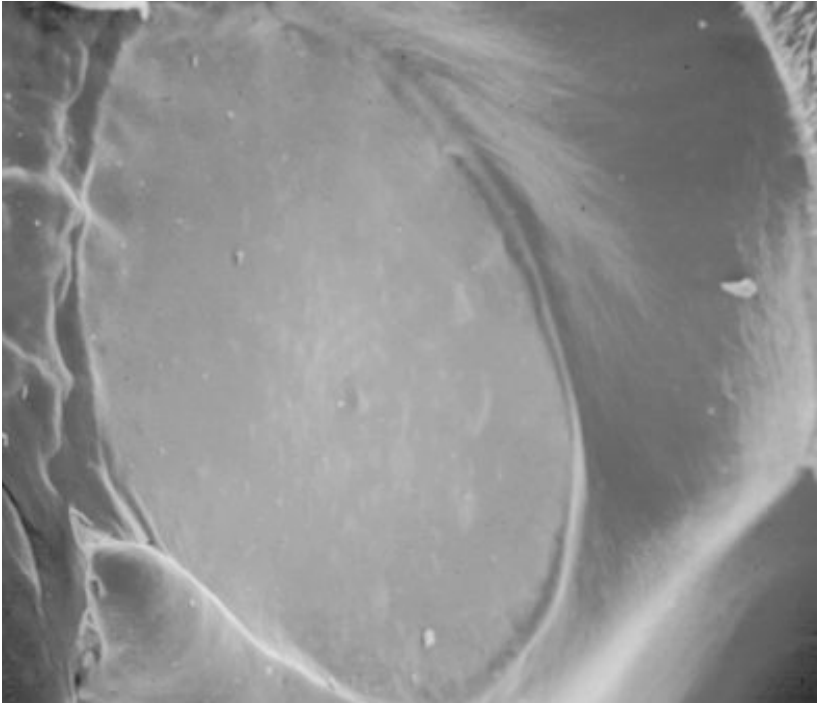
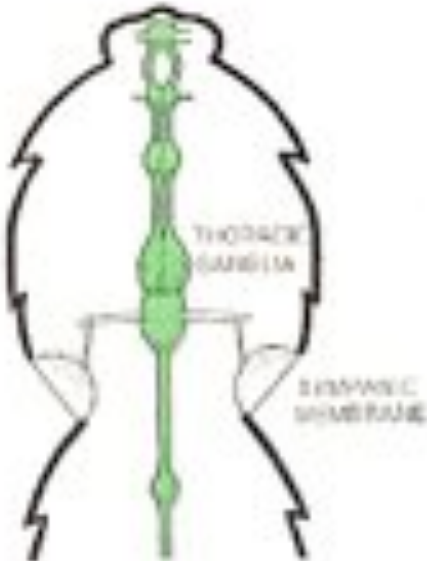
The bush crickets ear is located on its foretibia. Associated with the ear is a large tracheal trunk that opens on the lateral surface of the thorax. This tracheal trunk is also connect to the the one on the opposite side (see Photo a). In bush crickets this spiracle is always open, thus sound waves can enter it and reach the internal surface of the tympanum.



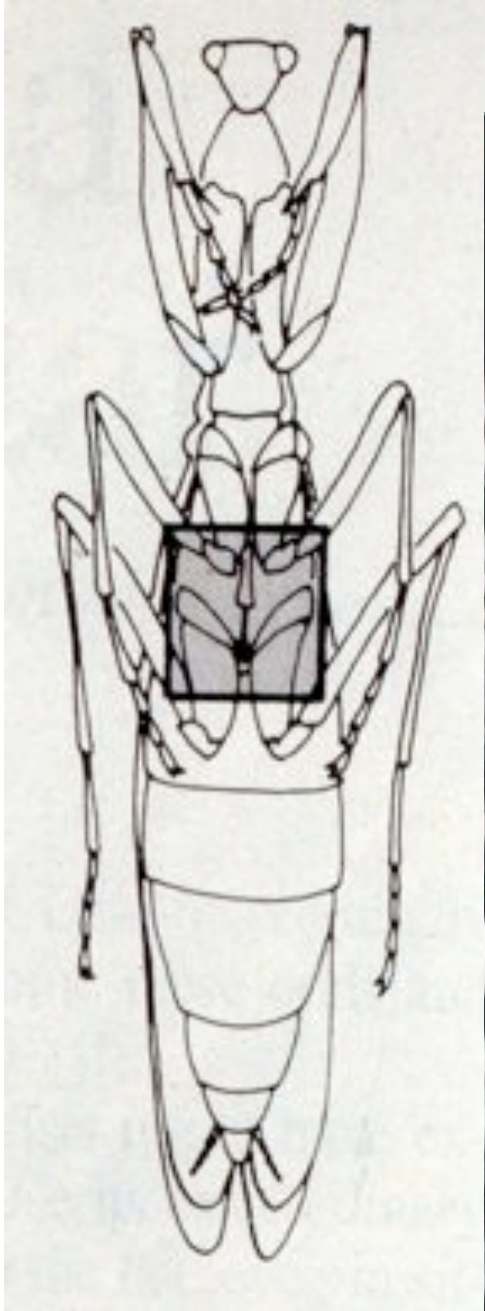
Moth ears look like tiny eardrums. In tiger moths the ears are located on either side of the thorax. They point to the side and to the rear so that a bat cannot sneak up on them



Noctuid moth ear



Praying mantid ear

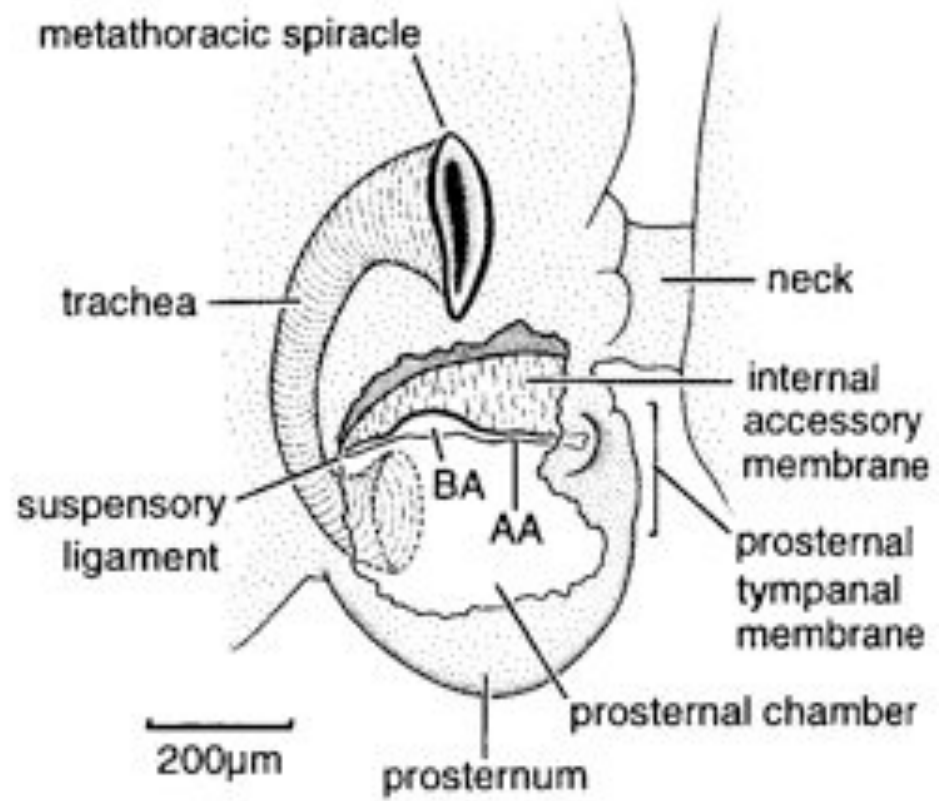
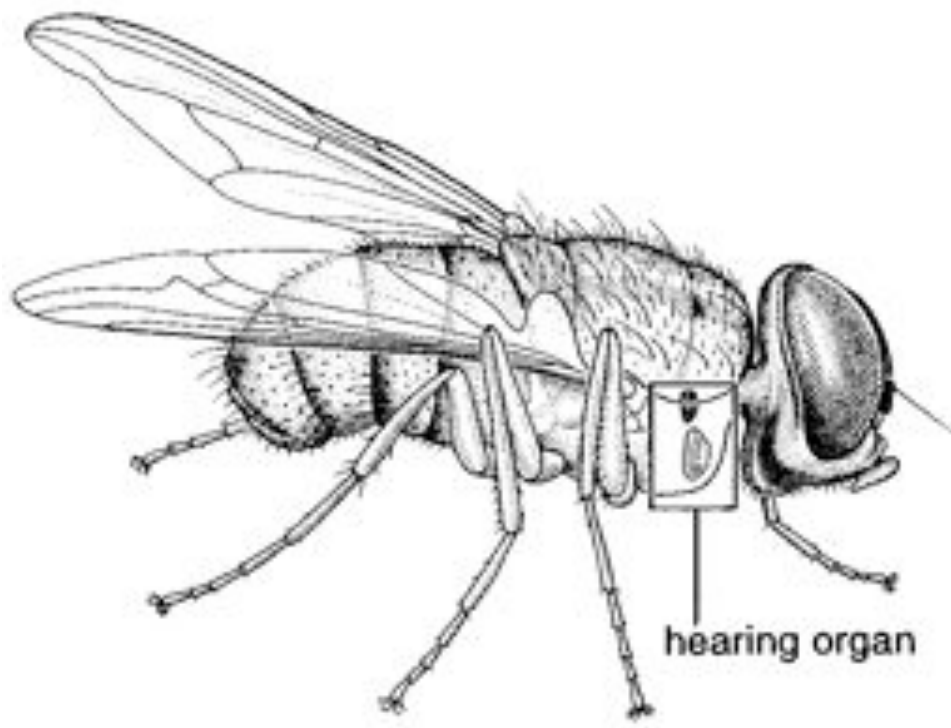


Fly ear-

The tachinid parasitoid locates its cricket host using the sound produced by the male. Once the host is located, the female larviposits one larva. To locate sound is difficult and requires directional hearing, which means the ears must be separated by quite a distance. This is not the case in this insect. In the next slide you will see that the location of the ears in this fly are located on the postsernal area, just behind the neck and point forward. The solution to the directional hearing was discovered to be a cuticular connection that joins the two ears. This flexible lever pivots about a fulcrum and functions to increase the time lag of the sound from one side to the other.



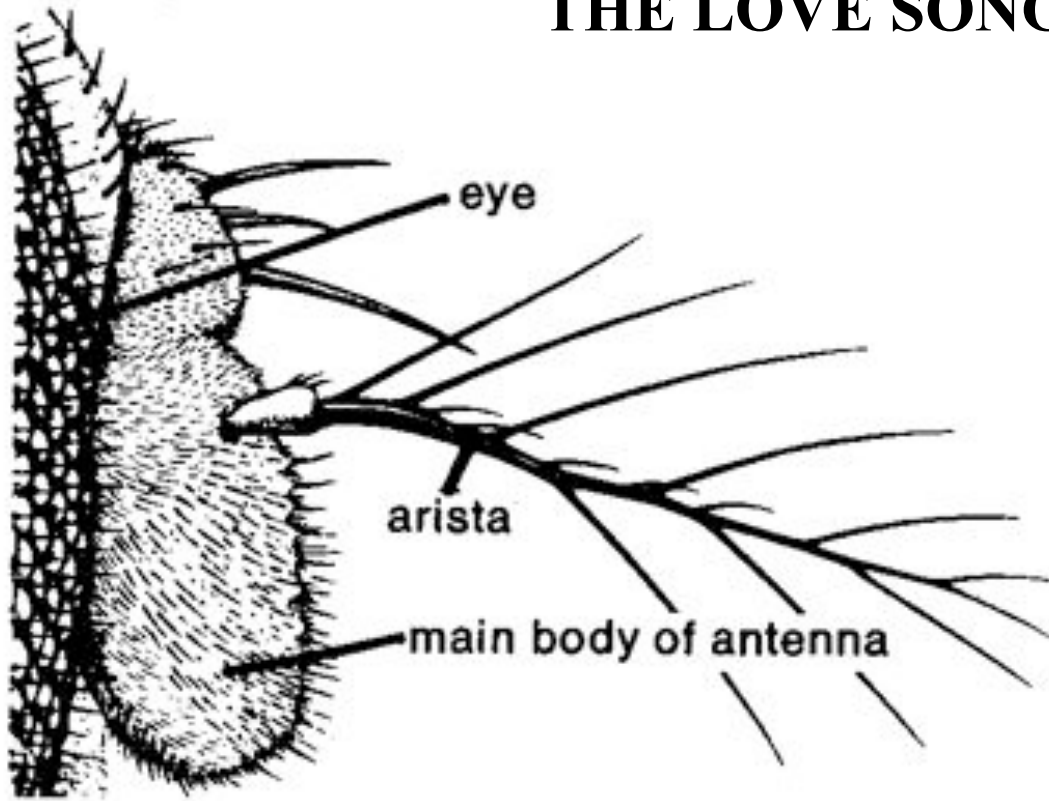
Aural location of host by a parasitoid fly

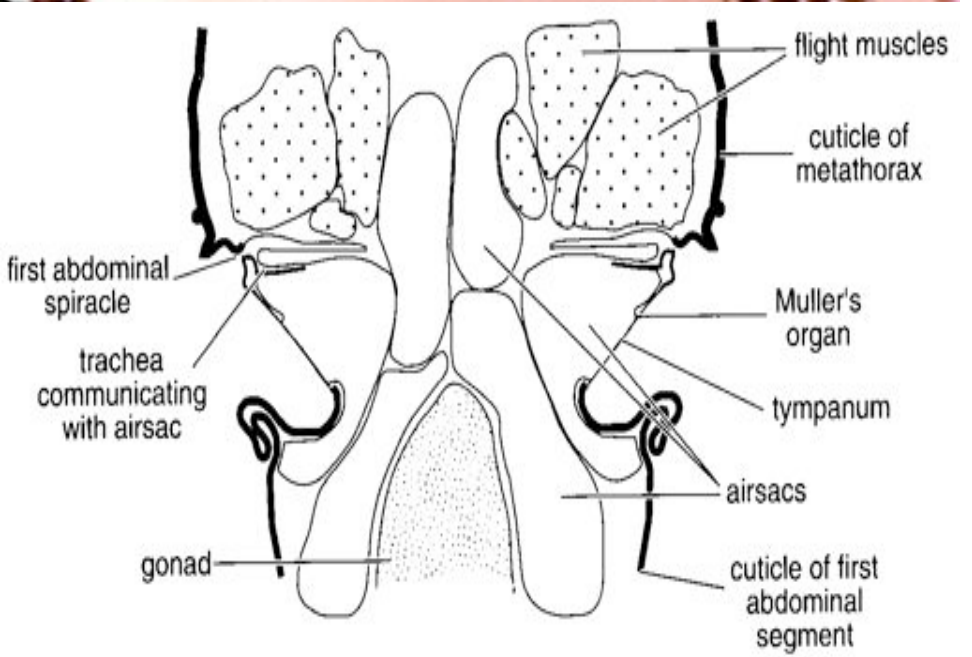
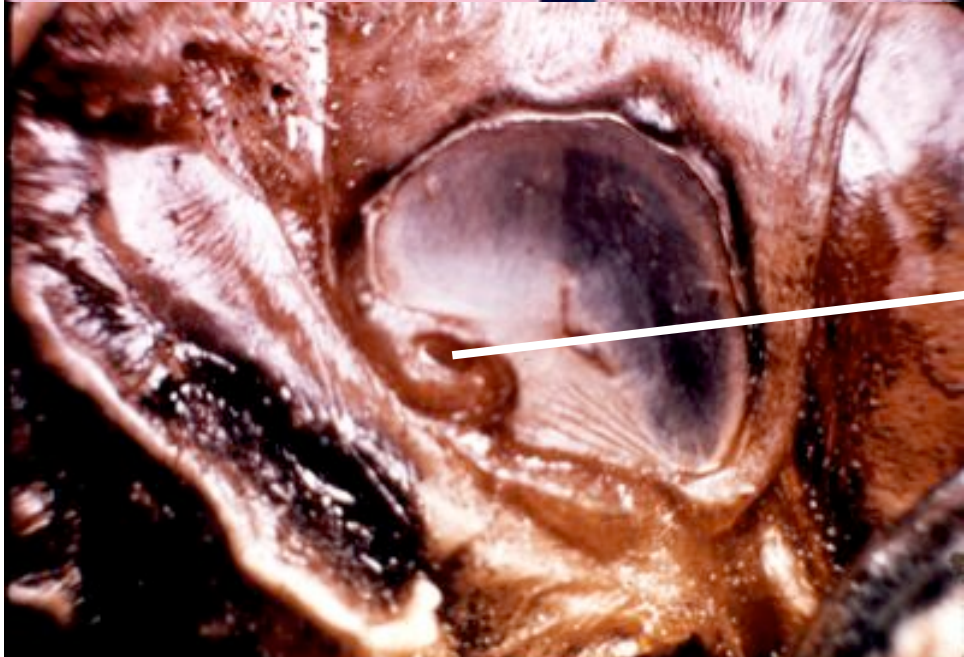
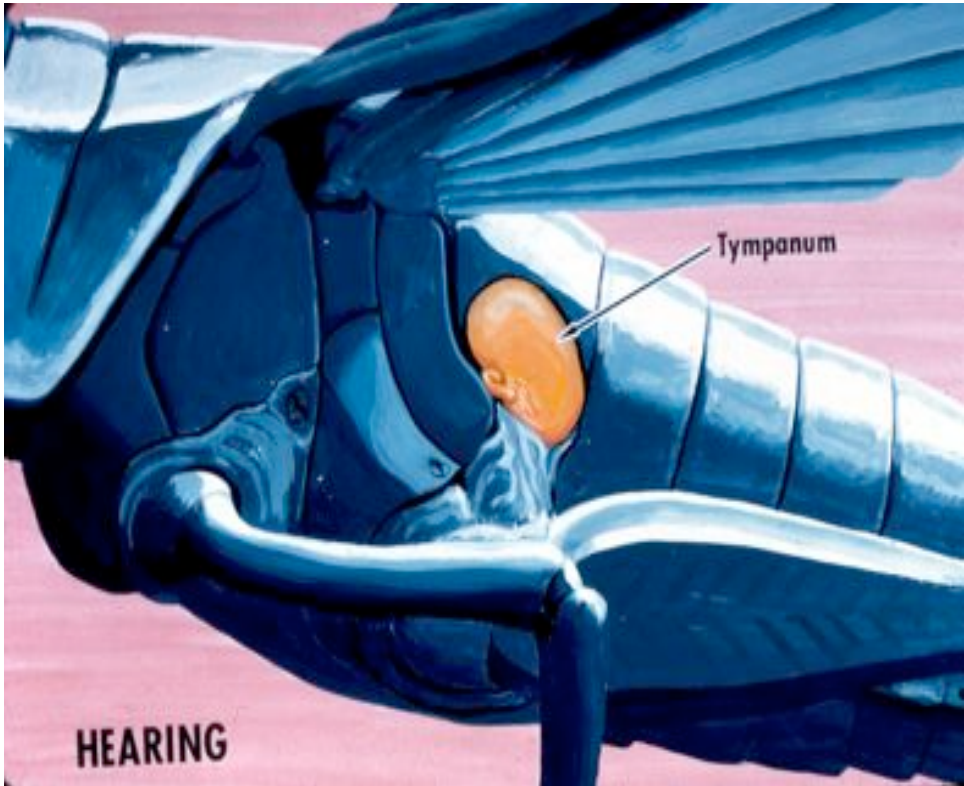


BA = bulbae acusticae
AA = auditory apodeme

Fruit fly

THE LOVE SONG OF THE FRUIT FLY





FEMALE-FEMALE COMPETITION IN KATYDIDS: SEXUAL SELECTION FOR INCREASED SENSITIVITY TO A MALE SIGNAL?

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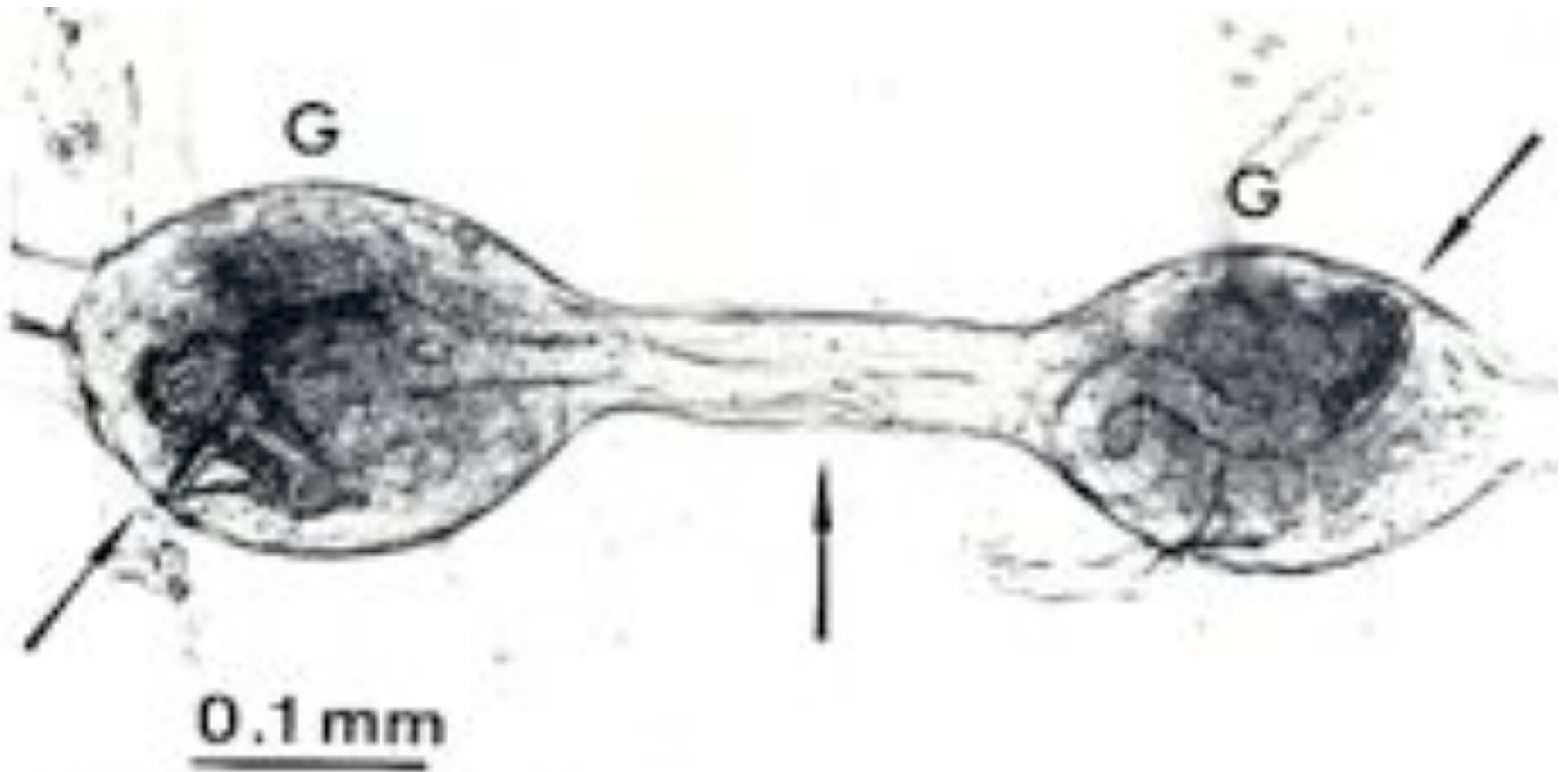
Abstract—In contrast to studies of sex-specific weaponry and other sexually selected traits, there has been no examination of Darwin's (1871, p. 418) suggestion that elaborations or enlargements of "the organs of sense" function to enhance mating success. In certain katydids the size of thoracic spiracles, which are a main input into the hearing system, determines auditory sensitivity of females. Here we present evidence that sexual dimorphism in the spiracle size of a pollen katydid, *Kawanaphila natterii*, is a result of sexual selection on females competing to locate nuptial-gift giving males. In field experiments in which female *K. natterii* were attracted to a calling male, we show a pairing advantage to females with larger auditory spiracles. The spiracle-size advantage was not a correlated result of a larger body size or mass of winners. Finally, there was no spiracle-size advantage or body-mass advantage for mating females in a later stage of competition when experimental females struggled for access to a silent male. We suggest that research on the detection of displays has lagged behind work on the displays themselves; the focus has been on the species specificity of signal perception rather than on the fitness consequences of variation in the ability to detect cues from mates or predators.

IMPORTANCE OF SEXUAL DISPLAYS VERSUS THE ABILITY TO PERCEIVE THEM, THUS FOCUSING ON THE RECEPTOR MECHANISMS

On the top right is the thoracic spiracle of the pollen katydid. In this species, females with larger spiracles were faster at finding the calling males because the larger spiracular opening gave them an advantage when it came to sensitivity to the male's call.



Avoidance of the hemocytic encapsulation response by the nematode *Filipjevimermis leipsandra* (arrows) within the nerve cord of its host, the larva of the cucumber beetle, *Diabrotica undecempunctata*.



BASIC AND APPLIED ASPECTS OF THE NERVOUS SYSTEM

I. Basic

- A. Neuropharmacology
- B. Aging of the nervous system
- C. Sensory integration and coding
- D. Development of the nervous system
- E. Using *Drosophila* as model system

II. Applied

- A. Carbamates and organophosphates-acetylcholinesterase inhibitors
- B. UV lights and electrocutor traps
- C. Feeding baits or repellants
- D. Fly repellents for humans and animals and homes
- E. Pheromone traps
- F. Deterrents of plants