COMPOUND EYES

* Most adult insects have a pair of compound eyes, one on either side of the head, which bulge out to a greater or lesser extent so that they give a wide field of vision in all directions. The compound eyes may, however, be reduced or even absent in some parasitic insects.

* Each compound eye is an aggregation of similar units called **ommatidia**, the number of which varies from one in the worker of the ant *Ponera punctatissima* to over 10,000 in the eyes of dragonflies. When there is only a few ommatidia they tend to be round in shape, whereas when there is a large number they are hexagonal in shape. Usually the two compound eyes are separated (called **dichoptic**), but in some insects, they meet on top of the head (called **holoptic**).

* Each ommatidium consists essentially of an optical, light-gathering part and a sensory part, perceiving the radiation and transforming it into electrical energy. The optical part of the system usually consists of 2 elements, a **corneal lens** and a **crystalline cone**. The **corneal lens** is produced by two epidermal cells, the **corneagen cells**; they later withdraw to the sides and form the **primary pigment cells**. The cuticle covering the eye is transparent and colorless and usually forms a biconvex corneal lens at the outer end of each ommatidium **[SEE OVERHEAD]**. Below the cornea are 4 cells called the **Semper cells** which in most insects produce the crystalline cone. The crystalline cone is a hard, clear intracellular structure bordered laterally by the **primary pigment cells**. Eyes in which the crystalline cone is present are called **eucone eyes**. Immediately behind the crystalline cone in eucone eyes are the sensory elements. These are elongate nerve cells known as **retinula cells** (there are usually eight retinula cells per ommatidia, but there can be seven or nine also). The inner margins of the retinula cells nearest the axis of the ommatidium are differentiated to form the **rhabdomere**. Collectively, the rhabdomeres of each ommatidium form the **rhabdom**. The **rhabdom** may be fused (all rhabdomeres from each retinula cell fused together) of they may be open (fig. in Chapman). On the outside surface of the retinula cells are a number of **secondary pigment cells**. Arising from each cell is a nerve axon which passes out through the basement membrane at the back of the eye into the optic lobe.

* As just mentioned ommatidia in which the Semper cells have produced a crystalline cone are called **eucone eyes**. In some Hemiptera, Coleoptera, and Diptera the Semper cells do not form a crystalline cone, but become transparent and undergo only a little modification. Ommatidia of this type are described as **acone ommatidia**. The acone type may be primitive as many Apterygota also have this type. The Semper cells of most Diptera and some Odonata produce cones which are liquid-filled or gelatinous rather than crystalline. These are called **pseudacone ommatidia**. Finally, in some Coleoptera, the lens is formed from an inward extension of the cornea, not from the Semper cells which form a refractile structure between the cuticle and the retinula cells. This is an **exocone ommatidia**.

* In many insects the rhabdom is very long and extends from the back of the lens almost to the basement membrane. This is called **apposition eyes**. In some insects (some Coleoptera and nocturnal Lepidoptera), the rhabdom is short and separated from the lenses by a space which is crossed by processes of the retinula cells. This is called **superposition eyes**.

OTHER PHOTORECEPTORS

* **Dorsal ocelli** are found in most adult insects and the immatures of hemimetabolous insects. Typically there are three, forming an inverted triangle anterodorsally on the head. Frequently one or more of the ocelli are absent. These are not concerned with form vision, but probably are important in detection of light. They can also detect changes in light intensity.

* In the larval holometabolous insects the only visual organs are the **stemmata**. These are often called ocelli, but since they are somewhat different in structure they should not be called ocelli. These are also probably primarily concerned with light reception.

* In some insects the individuals will still react to light even when all of the known visual receptors have been occluded. Thus it appears that there must be light receptors in the general body surface, but none have been located.

MECHANORECEPTION

* **TRICHOID SENSILLA** - a trichoid sensillum is a hair-like projection of the cuticle articulated with the body wall by a membranous socket so that it is free to move. The hair is produced by a cell, the **trichogen cell**, and the socket by another, the **tormagen cell**. Associated with each hair is one or more nerve cells. Hairs concerned only with mechanoreception have only one neuron, but chemosensory hairs with a number of neurons may also have mechanoreceptor function. The receptor potentials produced may be of 2 types. In most a potential develops only during the movement of the hair, that is a bending or straightening of the hair. This is called a **phasic response**. But in others the potential is maintained all the time the hair is bent, adapting only very slowly. This is known as a **tonic response**. Hairs that show phasic responses function as tactile receptors found primarily on the antennae, tarsi, and wherever the insect touches the substratum. They may also respond to vibrations and so may be involved in sound reception. Hairs that have tonic response are usually concerned with proprioreception and are often associated with joints of legs and between body segments.

* **CHORDOTONAL ORGANS** - **chordotonal, or scolopophorus, organs** consist of single units or groups of similar units called **scolopidia**. They are usually subcuticular and have no external evidence. They generally consist of 3 cells arranged in a linear manner: the **neuron**, the **scolopale cell**, and the **attachment, or cap cell**. These may function as proprioreceptors, but often they may function as sound receptors.

* The **Johnston's organ** is a chordotonal organ lying in the 2nd segment of the antenna with its distal insertion in the articulation between the 2nd and 3rd segments. It occurs in all adult insects except Collembola and Diplura. This organ perceives movements of the antennal flagellum.

* **TYMPANAL ORGANS** - Tympanal organs are specialized chordotonal organs. Each consists of a thin area of cuticle, the **tympanal membrane**, backed by an air-sac so that it is free to vibrate. Attached to the inside of the membrane or adjacent to is a chordotonal organ. Tympanal organs occur on the prothoracic legs in some Orthoptera, on the mesothorax in many aquatic insects, on the metathorax in some Lepidoptera, and on the abdomen in some grasshoppers, Homoptera, and some Lepidoptera. These function in sound reception.

* The **subgenual organ** is a chordotonal organ usually containing between 10 and 40 scolopidia in the proximal part of the tibia. These are concerned with sound reception and the reception of vibrations from the substratum.

* **CAMPANIFORM SENSILLA** - **campaniform sensilla** are areas of thin cuticle, domed and usually oval in shape. These sensilla often occur in groups which probably function as a unit. They occur on all parts of the body subject to stress and are concentrated near the joints as at the base of the wing or the haltere in Diptera. They function as proprioreceptors.

* **STRETCH RECEPTORS** - **Stretch receptors** differ from other insect sensilla in consisting of a multipolar neuron with free nerve endings (called **Type II neurons**), while all others contain a bipolar neuron with a dendrite associated with the cuticle (called **Type I neurons**). Stretch receptors occur in connective tissue or associated with muscles.

CHEMORECEPTION

* **OLFACTORY RECEPTION** - The identification of olfaction receptors is often uncertain, but it is reasonably certain that thin-walled **basiconic pegs** and **coeloconic pegs** are the olfactory receptors.

* **CONTACT CHEMORECEPTION** - This type of reception is usually accomplished by trichoid sensilla, which we have already discussed. Those trichoid sensilla associated with chemoreception usually have 4-6 neurons associated with the hair, one of which is usually involved with mechanoreception.

OTHER RECEPTORS

* There is some slight evidence that a few insects possess **temperature receptors**.

* Some insects also have **humidity receptors**. In some insects it is believe that humidity reception is by the basiconic pegs, while in others it is probably by coeloconic pegs.

SOUND PRODUCTION

* **SOUNDS PRODUCED AS A BY-PRODUCT OF SOME OTHER ACTIVITY** - Many sounds are produced by insects when they are feeding, cleaning, or copulating, but there is no evidence that any of these sounds have any particular significance. Sounds produced in flight, however, may have some significance. The wingbeat frequency is relatively constant within a species but may vary with temperature, age, and sex.

* **SOUNDS PRODUCED BY THE IMPACT OF PART OF THE BODY AGAINST THE SUBSTRATUM** - some insects produce sound by striking the substratum, mostly without any related structural modifications. Some female Psocoptera have a small knob on the ventral surface of the abdomen with which they tap the ground. The death watch beetle produces tapping sounds by bending its head down and banging it against the floor of its burrow. Some grasshoppers drum on the ground with its hind tibia. Some termites bang different parts of their bodies against the substratum.

* **SOUNDS PRODUCED BY FRICTIONAL MECHANISMS** - Many insects produce sounds by rubbing a roughened part of the body against another part. Often it is possible to distinguish a long ridged or roughened **file**, called the **strigil**, from the single scraper, called the **plectrum**. Frictional types of sound are produced by many orders of insects but are particularly associated with Orthoptera, Heteroptera, and Coleoptera.

* In the Orthoptera 2 main methods are used: **elytral** stridulation found in Grylloidea and Tettigonioidea, and **femoro-elytral** stridulation found in Acridoidea.

* In the Heteroptera stridulation is most common in the Pentatomoid groups where 15 different methods have been recorded. The most common mechanisms involve a file on the ventral surface rubbed by a scraper on the leg, or a file on the wing rubbed by a scraper on the dorsal surface. In the Reduvioidea the file is between the front coxae which is rasped by the tip of the rostrum **[SEE OVERHEAD]**.

* In the Coleoptera many different parts of the body are used to stridulate, but most commonly the elytra are involved.

* In some Lepidoptera sound is produced by rubbing veins on the wings together.

* **SOUNDS PRODUCED BY A VIBRATING MEMBRANE** - Sounds produced by the vibration of a membrane driven directly by muscles are common amongst Homoptera and also occurs in some Heteroptera (Pentatomidae) and some Lepidoptera (Arctiidae). This is most studied in the male Cicada. Sound is produced when the **tymbal muscle** contracts, pulling on the **tymbal** so that it buckles inward producing a click as it does. On relaxation of the tymbal muscle the tymbal returns to its normal position due to elasiticity of the surrounding cuticle and so produces a second click. There are often large air sacs below the membrane which help amplify the sound.

* **SOUNDS PRODUCED BY A PULSED STREAM OF AIR** - The only well documented case of a sound produced by a pulsed air stream is the stridulation of *Acherontia* (Lepidoptera). Air is sucked through the proboscis by dilation of the pharynx causing the epipharynx to vibrate and create a pulsed stream of air.