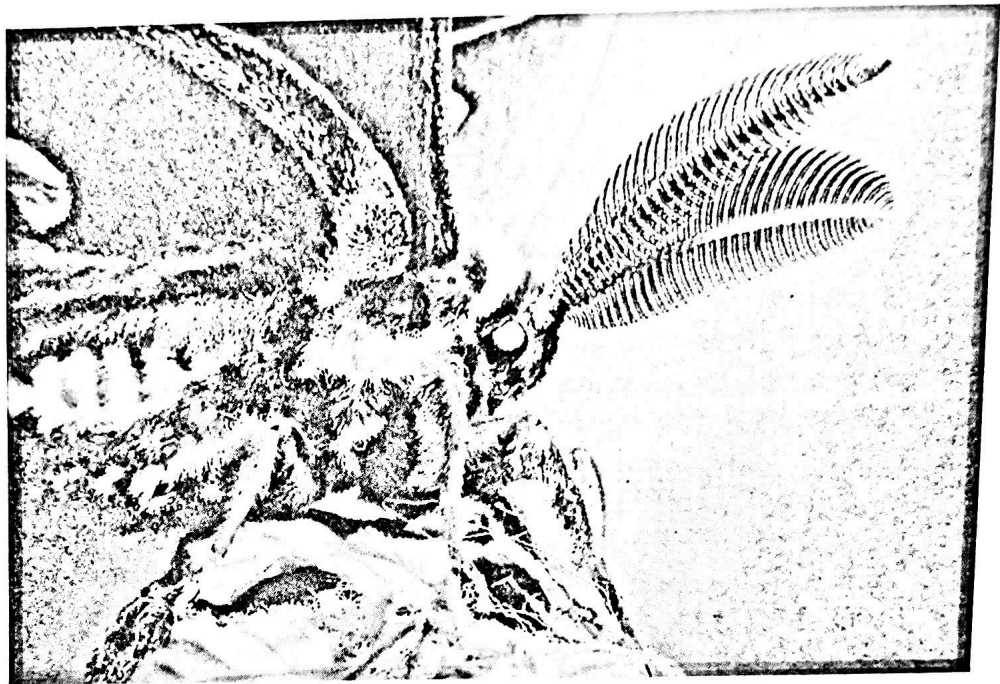


Reception of Stimuli and Integration of Activities



A male western cecropia moth, *Hyalophora euryalis* (Saturniidae), with large plumose antennae that detect minute quantities of airborne sex attractants from the female moth. American physiologist C. M. Williams used *Hyalophora cecropia* for experiments on metamorphosis. The adult males were unexpectedly found to have large amounts of juvenile hormone in the abdomen.

Source: Edward S. Ross.

How does the nervous system enable insects to perceive and relate to their environment? After a brief review of the structure and function of nerve cells, we describe the major sense organs and address how insects respond to internal and external stimuli. After an introduction to the kinds of behavior exhibited by insects, we conclude with a discussion of communication and circadian rhythms.

ORGANIZATION OF THE NERVOUS SYSTEM

Neurons and Neuronal Connections

Nerve cells are either (1) **neurons** that are excitable by chemical or electric signals and rapidly transmit

electric impulses or (2) **glial cells** that support, insulate, and nourish the neurons. The nucleated cell body of a neuron is the **soma**, or perikaryon (Fig. 6.1a). **Axons** are the slender fibers that extend from the soma to connect with other neurons or with muscles or glands.

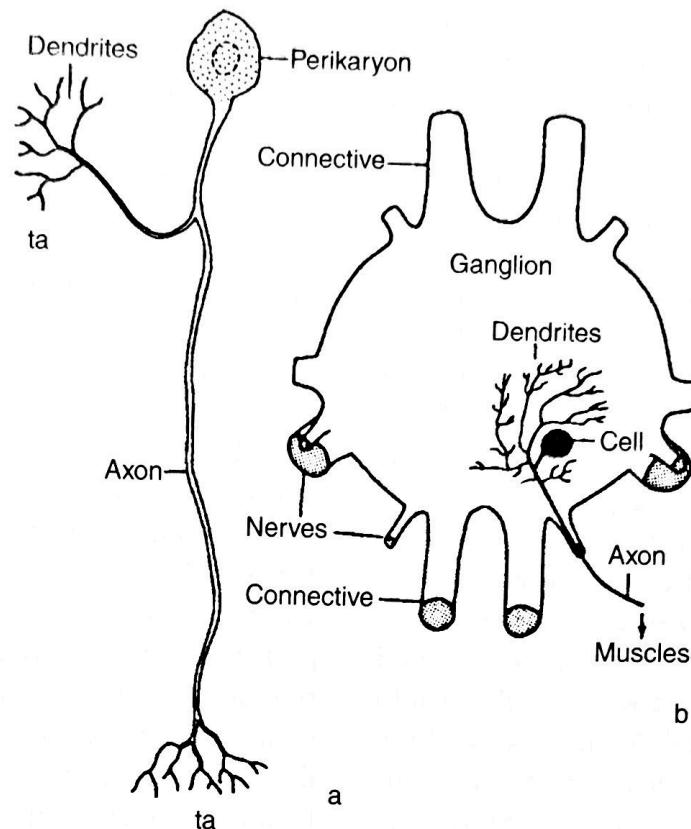


Figure 6.1 Structure of neurons and ganglia: **a**, diagram of a monopolar neuron; **b**, diagram of a monopolar motor neuron inside a thoracic ganglion. ta, terminal arborizations. Source: **a**, Redrawn from R.E. Snodgrass, *The Principles of Insect Morphology* - public domain; **b**, simplified and modified from Altman and Tyrer, 1974.

The **synapse**, or synaptic cleft, is the space between connecting axons or between axons and muscles at the tips of the axons. Most axon tips in insects are finely divided into numerous branches and separated by a gap. Nerve transmission crosses the synapse from the **presynaptic** axon to the **postsynaptic** axon by diffusion of a chemical substance called a **neurotransmitter**. The postsynaptic or receptive axon is also called the **dendrite**. Various types of glial cells wrap tightly around nerve cells.

Monopolar neurons have only one axon issuing from the soma. The single axon is at least forked so that one branch serves as a dendrite. Some monopolar neurons, however, are highly branched and complexly interconnected with other neurons. **Bipolar** neurons have two separate axons extending from the soma. Again, one serves as the dendrite and the other leads to the next neuron. **Multipolar** neurons with more than two axons are

rare in insects (known as stretch receptors, these are discussed later under "Mechanoreceptors").

A nerve cell is basically a tiny battery whose charge is created by membrane-bound ion pumps and ion-specific channels in the nerve cell membrane. A nerve cell at rest has a deficiency of sodium ions (Na^+), which results in a **resting potential** (voltage difference) between the interior and exterior of the cell membrane of about -70 mV. Sodium-potassium pumps that span the nerve cell membrane selectively expel Na^+ and transport potassium ions (K^+) into the cell to create a deficiency of Na^+ within the cell. Ion channels are pores in the nerve membrane that selectively allow passage of certain ions, mainly Na^+ , K^+ , Cl^- , and Ca^{2+} . Pores may be open or "gated"—that is, closed under some conditions and open under other conditions. Open potassium channels create the resting potential by allowing K^+ to diffuse

out of the cell to create an imbalance of Cl^- ions. Voltage-gated sodium channels close in the resting state but open in response to voltage changes. A nerve impulse triggered (fired) by the reception of a neurotransmitter substance at the postsynaptic membrane moves outward as a localized current flow, or **graded response**, to induce the opening of gated sodium channels to allow a surge of Na^+ ions into the cell. This resulting voltage spike, the **action potential**, reverses the voltage difference from about -70 to $+50$ mV. The change in voltage (depolarization) triggers adjacent gated Na^+ channels to open, propagating a wave of depolarization along the axon. Some insecticides, such as plant-derived pyrethrins, are toxic because they cause gated Na^+ channels to remain open and to continue to fire. As the nerve impulse moves along the axon, gated Na^+ channels close and gated K^+ channels open to restore the resting potential. Numerous gated ion channel genes from *Drosophila* have been identified and cloned for use in experiments to help decipher how this system operates in humans and other animals. The most studied of these is the *Shaker* gene (*Sh*), which codes for a transmembrane protein whose conformational changes allow or halt passage of K^+ .

Nerve transmissions across a synapse are slower than the nerve impulses along axons because neurotransmitter substances must be released from vesicles, diffuse across the synapse, and bind to receptor sites. As a consequence, longer axons and nerve cords with fewer interconnecting neurons have evolved to maximize the speed of transmission for rapid reactions to stimuli. Giant axons in the cockroach *Periplaneta americana* (Blattidae, Blattodea) bypass synapses in the abdomen to go directly to ganglia via **giant interneurons** in the thorax to activate legs for escape maneuvers without intervention of the insect brain. In this reflex arc, air movements stimulate sensory hairs on the cerci to trigger nerve impulses that travel directly to the thorax and then on to leg muscles and nerve pattern generators to provoke a movement away from the stimulus without involving the brain. In this case, the increased diameter of the axons also increases the speed of depolarization along the giant axon.

Nerve impulses arriving at an axon tip trigger the opening of Ca^{2+} channels. The resulting higher concentrations of Ca^{2+} within the nerve tip cause vesicles containing neurotransmitters such as acetylcholine to fuse with the presynaptic membrane and release acetylcholine into the synapse. Neurotransmitters that diffuse across the synaptic cleft bind to receptor proteins on postsynaptic membranes of the adjacent dendrite to trigger the opening of a gated sodium channel, which then initiates a nerve impulse. In the case of acetylcholine, enzymes (acetylcholinesterases) then break down this neurotransmitter. Some insecticides such as malathion inhibit cholinesterases by binding strongly to them. As a consequence, acetylcholine is not broken down, and the affected synapses continue to elicit repeated firing of the postsynaptic neuron. Acetylcholine serves as a neurotransmitter at excitatory synapses. The branching of dendrites from a single neuron means that some dendrites may lie opposite axon tips that release inhibiting neurotransmitters such as γ -aminobutyric acid (GABA) that cause hyperpolarization (the opposite of depolarization), and other connecting axons may release activating neurotransmitters. This introduces flexibility and complexity into neural networks. Discovering previously unrecognized neurotransmitters and determining their roles are popular topics for current research in neurobiology. Numerous neuropeptides have been identified as neurotransmitters and often have dual roles as hormones. L-Glutamic acid and L-aspartic acid serve as neurotransmitters for neuron-muscle junctions in insects.

Sensory neurons within sense organs send nerve impulses to the nervous system in response to physical or chemical stimuli. Sensory stimuli to specific parts of the sensory cell may directly alter the permeability of ion channels to trigger a nerve impulse (ionotropic sensory detection), or the stimuli may induce a nerve membrane protein to activate a cascade of molecular intracellular signals that open or close ion channels (metabotropic detection). For example, a sex-attractant molecule (a pheromone, discussed later) that binds to a receptor protein on a sensory neuron of an insect's scent organ triggers the enzymatic activation of a cascade of chemical messengers within the cell that controls

ion channels to fire an action potential. Mechanical stimuli such as stretching and pressure may act directly on ion channels to fire neurons in proprioceptors. Chemosensory receptors detect specific chemicals, photoreceptors detect light, and so on. The sensory soma is usually located just beneath the sense organ and sends nerve impulses along a long fiber to a segmental ganglion. Within the ganglion, the sensory axon transmits impulses either directly by one synapse to a monopolar **motor** neuron or indirectly by two or more synapses involving other monopolar neurons, the interneurons.

The nervous stimulation of muscle fibers in insects differs from that of mammals. In the latter, the axon terminates in a single motor end plate, and the transmitter substance to the muscle is acetylcholine. Motor axons of insects are branched, providing many endings on a muscle fiber, and the neurotransmitter is not acetylcholine. A muscle may receive stimulation from two or three different kinds of motor axons. Stimulation by a **fast axon** produces a "fast" response in the form of a brief, powerful contraction. Each stimulation by a **slow axon** results in a small contraction, but when the stimulation is increased in frequency, a "slow" contraction of increasing force is produced. Slow axons thus give greater control over movements. The transmitter substance for these neuromuscular junctions is glutamate.

Motor programs are neural mechanisms that coordinate repetitive activities, such as ecdysis, wing movements, rhythmic breathing, and walking. Interconnected neurons within the ganglia generate rhythmic bursts of excitatory or inhibitory outputs. These combine with neural feedback from sensory organs to modify the motor activity.

Nerves and Ganglia

On a larger scale, the bundles of sensory and/or motor axons that issue from the segmental ganglia are called **nerves**. A **ganglion** is a mass of nerve tissue (Fig. 6.1b) often including thousands of neurons. The word is used loosely to apply not only to a single large mass but also to smaller masses that may be present inside. Thus, each segmental ganglion is formed by the median fusion of a pair of embryonic ganglia. The central portion is the **neuropile**, consisting entirely of axons and processes

of their associated glial cells. Included are sensory, motor, and connecting axons and their various synaptic junctions. The cell bodies of the neurons and glial cells are located only around the outside of the neuropile. The paired longitudinal connectives between ganglia are bundles of axons plus sensory and motor axons that communicate with other segments.

The ganglia, nerves, and connectives are surrounded by a supportive sheath composed of an outer, noncellular **neural lamella** of connective tissue and an inner **perineurium** of glial cells. The sheath is a "blood-brain barrier," isolating the neurons from the chemical components of the hemolymph and maintaining a chemical environment around the axons that is essential for impulse transmission. The glial cells also pass nutrients to the neurons and probably prevent contact between neurons except at synapses.

The nervous system is divided into four subsystems: (1) **sense organs**, including the light, chemical, temperature, and mechanical receptors; (2) the **peripheral nervous system**, including the sensory and motor neurons that communicate with the integument and muscles (this system is not discussed further); (3) the **central nervous system**, including the brain and the segmental ventral ganglionic chain that generally regulate the bodily activity; and (4) the **stomatogastric nervous system**, including several small ganglia that regulate the foregut, the midgut, and several **endocrine glands**.

CENTRAL NERVOUS SYSTEM

The central nervous system of insects includes the **brain**, situated above the mouth, and the **ventral nerve cord**, beginning behind the mouth. The evolution of the central nervous system was discussed earlier (Fig. 2.4). Recall that the basic structure of the system consists of paired embryonic ganglia connected transversely by commissures and longitudinally by connectives. The insect brain is a marvel, with such a small-sized nervous system enabling many higher functions such as learning and communication. Estimates of the number of neurons in the brain are about 850,000 for a worker honey bee, 1.2 million for a drone honey bee, 330,000 for a house fly, and 360,000 for a locust.

Brain

The brain has three ganglionic masses (Fig. 6.2). Genomic evidence from studies of embryogenesis corroborates that these three major ganglia evolved from individual segments.

The **protocerebrum** is the largest and most complex region. Laterally, it receives the nerves from

the large optic lobes of the compound eyes; dorsally, it receives nerves from the ocelli. Internally, the protocerebrum has a pair of mushroom-shaped neuropiles, the **corpora pedunculata**, which are important centers for the integration of behavior. In most insects, the main sensory input is from the antennal lobes. In social Hymenoptera,

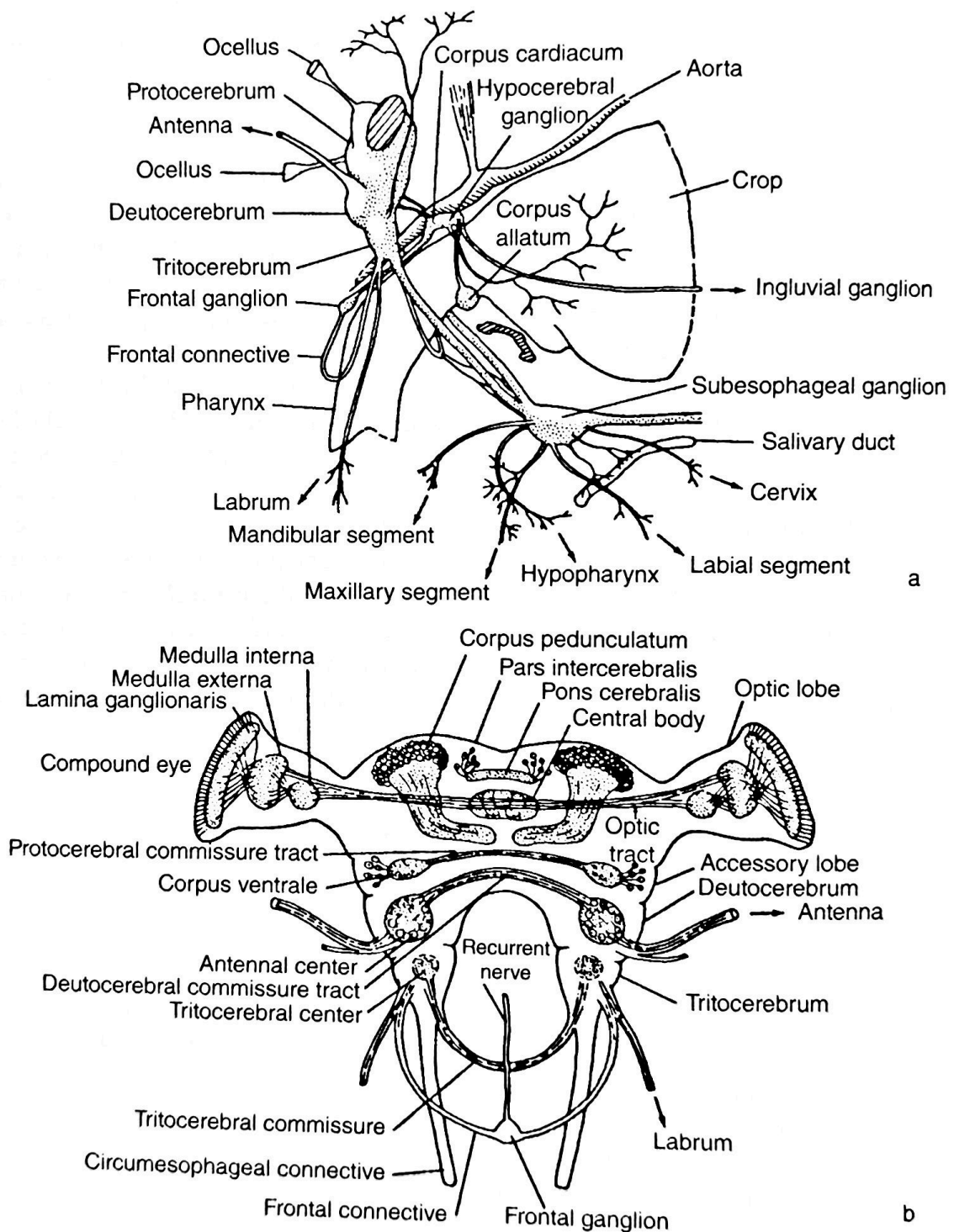


Figure 6.2 Insect brain: **a**, lateral view of nervous system in head of a grasshopper; **b**, diagrammatic cross section of brain showing ganglia and commissures.
Source: Redrawn from R.E. Snodgrass, *The Principles of Insect Morphology* - public domain.

the corpora pedunculata are especially large, suggesting that they are important in the complex behavior of these insects. Medially is the **pars intercerebralis**, a complex cellular mass. Clusters of neurosecretory cells here and elsewhere in the brain communicate by long nerves with the neuroendocrine corpora cardiaca and corpora alata. Three other neuropiles are present in the protocerebrum: the median **protocerebral bridge** encompassing the **central body**, and the ventral, paired **accessory lobes** that are connected by a commissure. The **deutocerebrum** has motor and sensory axons to the antennae. The paired neuropiles, or **antennal lobes**, are connected by a commissure. Recall that both the protocerebrum and deutocerebrum were primitively in front of the mouth.

The **tritocerebrum** has sensory and motor axons to the labrum and to the frontal ganglion of the stomatogastric system. The paired neuropiles, or **tritocerebral centers**, are connected by the **tritocerebral commissure**, which is visible behind the esophagus. The tritocerebrum was primitively

the first ventral ganglion behind the mouth and secondarily became incorporated into the brain.

Ventral Nerve Cord

The ventral nerve cord is a chain of segmental ganglia connected anteriorly with the tritocerebrum by the paired **circumesophageal connectives**. The ganglia of the three gnathal segments are fused into a compound mass named the **subesophageal ganglion**. Motor and sensory nerves extend to the mandibles, maxillae, labium, salivary glands, and cervical muscles. The three ganglia of the thoracic segments serve the legs and flight mechanism and are usually the largest ganglia of the ventral nerve cord. Sensory and motor nerves extend to the various sense organs and muscles. In the abdomen are no more than eight ganglia. The last is a large, compound ganglion serving the eighth and following segments, including the genitalia and cerci.

There is an evolutionary tendency for segmental ganglia to fuse anteriorly into compound ganglia (Fig. 6.3), effectively increasing the speed of nerve

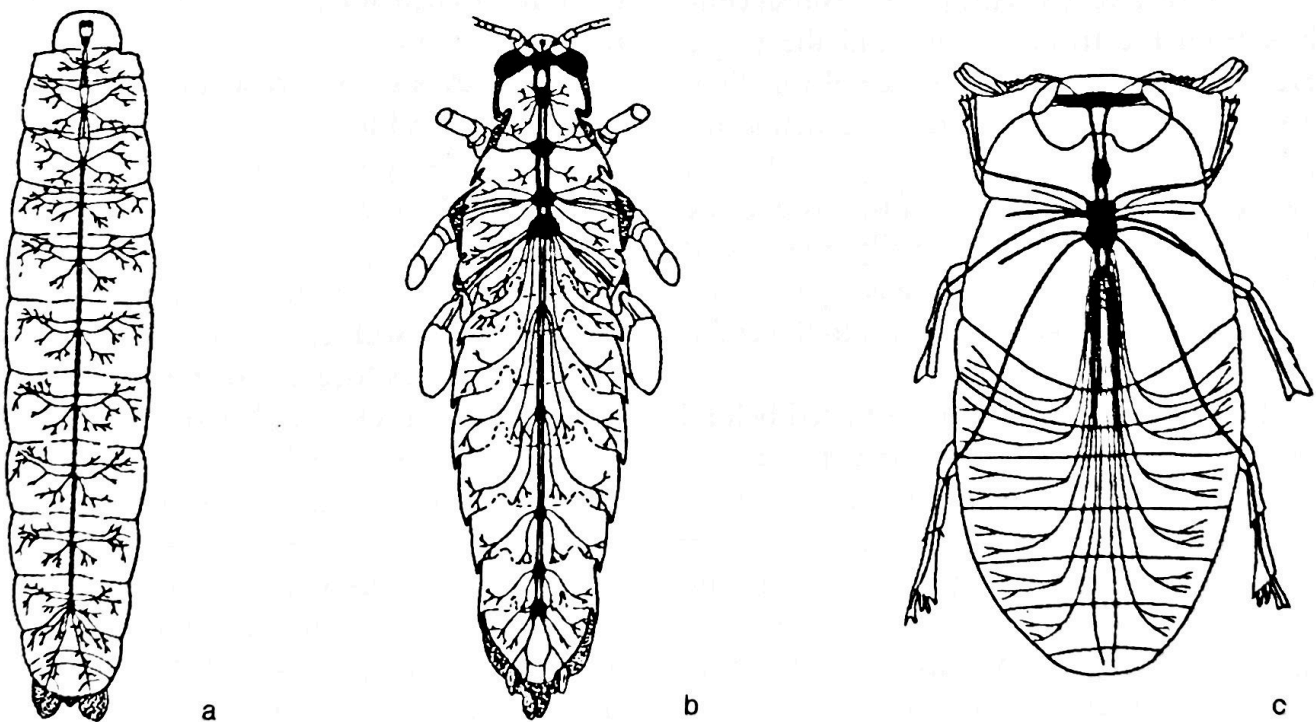


Figure 6.3 Modifications of the ventral nerve chain: **a**, system of a caterpillar, *Malacosoma americana* (Lasiocampidae); **b**, system of a grasshopper, *Dissosteira carolina* (Acrididae); **c**, system of a beetle, *Lachnosterna fusca* (Scarabaeidae).

Source: **a** and **b**, Redrawn from R.E. Snodgrass, *The Principles of Insect Morphology* - public domain; **c**, redrawn from Packard, 1898.

impulse transmission to the thorax and head by reducing the number of ganglia or eliminating interneurons and synapses in the abdomen. In the grasshopper, for example, the first three abdominal ganglia are fused with the metathoracic ganglion. Coleoptera and Diptera have variable amounts of fusion among the ganglia. Nearly all the Hemiptera have all of their ganglia of the thorax and abdomen fused into a single compound ganglion, with nerves extending to the respective segments. During the life history of an insect, a developmental tendency also exists for some separate ganglia in the larva to be fused in the adult. This arrangement presumably permits more rapid communication among the ganglia by reducing the lengths of interconnecting axons.

STOMATOGASTRIC NERVOUS SYSTEM

The stomatogastric nervous system includes two median ganglia connected to the brain and a single ganglion or paired ganglia on the surface of the foregut.

The **frontal ganglion** is situated medially in front of the pharynx, usually just behind the frontoclypeal suture. It receives the paired **frontal connectives** from the tritocerebrum and the single **recurrent nerve** from the hypocerebral ganglion. Some small nerves from the frontal ganglion innervate the foregut and mouth cavity. The frontal ganglion controls the emptying of the crop. If the ganglion is removed experimentally, undigested food accumulates in the crop. The ganglion probably also contributes neurosecretions to the endocrine system.

The **hypocerebral ganglion** is situated behind the brain, between the aorta and foregut. It usually has three major connections: the single recurrent nerve running from the frontal ganglion, either one or two esophageal nerves posteriorly to the ingluvial ganglia on the surface of the foregut, and dorsally to the brain by way of the neuroendocrine corpora cardiaca. The hypocerebral ganglion also sends nerves directly to the wall of the esophagus.

The single or paired **ingluvial ganglia** are located posteriorly on the foregut. They control gut movements through nerves to the foregut wall, proventriculus, and midgut. The neuroendocrine

corpora cardiaca and the corpora allata make the retrocerebral complex and are closely associated with the stomatogastric system.

Often discussed along with the stomatogastric system are two groups of small nerves closely associated with the ventral nerve cord and called the **visceral nervous system**: (1) the unpaired ventral visceral nerves that originate from each ventral ganglion and run caudally to innervate the tracheal system, spiracles, and some somatic muscles and (2) the caudal visceral nerves that originate from the last abdominal ganglion and run to the reproductive organs and hind gut.

SENSE ORGANS

Insect Eyes

Insect eyes are of two types: compound and simple.

Compound eyes (Fig. 6.4a–d) consist of from 8 (Collembola) to over 28,000 (Odonata, Fig. 6.4c) closely packed photoreceptive units, the **ommatidia** (Fig. 6.4b). Each ommatidium has its own corneal lens, which usually forms a hexagonal facet on the eye surface. Compound eyes connect directly to the optic lobes of the brain, minimizing the time needed for nerve impulse transmission from eye to brain.

Simple eyes each have a single round corneal lens with several to many light-sensitive cells beneath. Simple eyes are of two types. (1) **Dorsal ocelli** (Fig. 6.4e) are located on the top of the head in a pair or triangle. They are innervated by the median part of the protocerebrum and commonly occur together with compound eyes in both adult and larval stages (ocelli absent endopterygote larvae). (2) Larval eyes, called **stemmata** or **lateral ocelli**, are located laterally on the head, where usually less than a dozen at each side occur in loose clusters. They are innervated by the optic lobes and commonly occur in endopterygote larvae in the place of compound eyes. Insects do not have devices like eyelids to shield their light-sensitive receptors from direct sunlight.

Compound Eyes and Vision

The general structure of an ommatidium (Fig. 6.4b) includes two lenses, the **corneal lens** and **crystalline cone**, and a set of eight (rarely six, seven, or ten)

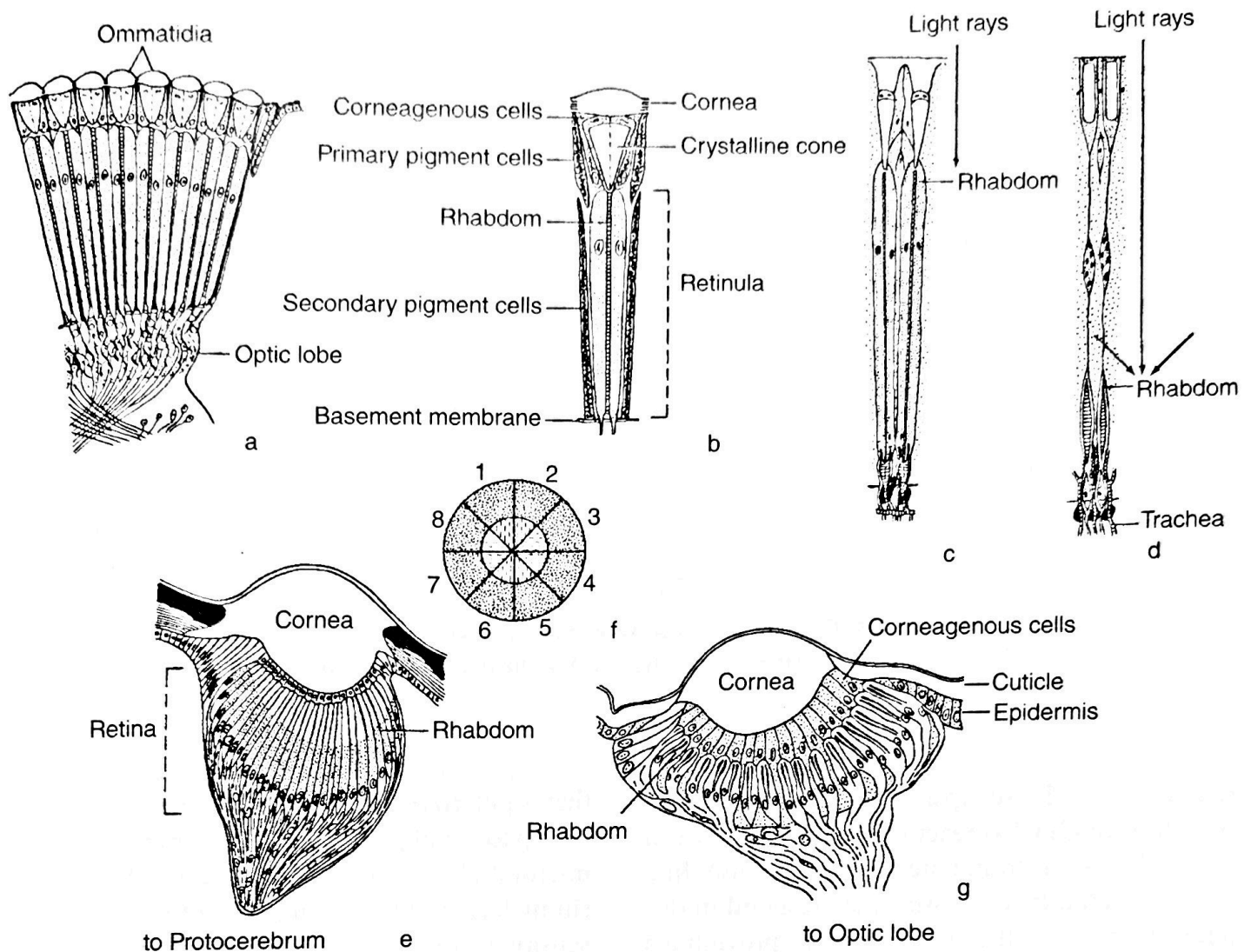


Figure 6.4 Structure of insect eyes: **a**, section of compound eye; **b**, ommatidium; **c**, ommatidium of the apposition type; **d**, dark-adapted ommatidium of the superposition type; **e**, dorsal ocellus; **f**, stemma or lateral ocellus. In **c**, light rays that pass through the cornea of an ommatidium strike only the rhabdom beneath, but in **d**, the light rays pass into adjacent ommatidia and strike other rhabdoms.

Source: **a** and **b**, Redrawn from R.E. Snodgrass, *The Principles of Insect Morphology* - public domain; **c** and **d**, redrawn after Nowikoff, 1931; **e**, redrawn after Caesar, 1913; **f**, redrawn after Corneli, 1924; **g**, Barbara Boole Daly.

sensory, or **retinula**, cells. Surrounding the crystalline cone are **primary pigment cells**, and around the retinula are **secondary pigment cells**. Two modified epidermal cells, the **corneagenous cells**, secrete the biconvex cornea. The cone is composed jointly of four cells, and by their internal structure, light from the cornea is focused on the retinula. The density, and thus the refractive index, of the cone may increase along its longitudinal axis to bend light rays more strongly in focusing. The elongate retinula cells are usually packed together, and each contributes to a central, rod-shaped structure called a

rhabdom. Each cell contribution is a photoreceptive **rhabdomere** of tightly packed microtubules oriented at right angles to the central axis. Microtubules within a rhabdomere are parallel to one another and usually also parallel with those on the opposite side of the axis. In the honey bee, for example, eight retinula cells of each ommatidium are fused pairwise into four compound units. The opposite units have parallel microtubules such that adjacent units have microtubules at right angles (Fig. 6.4f).

Rhodopsins, the visual pigments, are located on the membranes of long, narrow microvilli in the

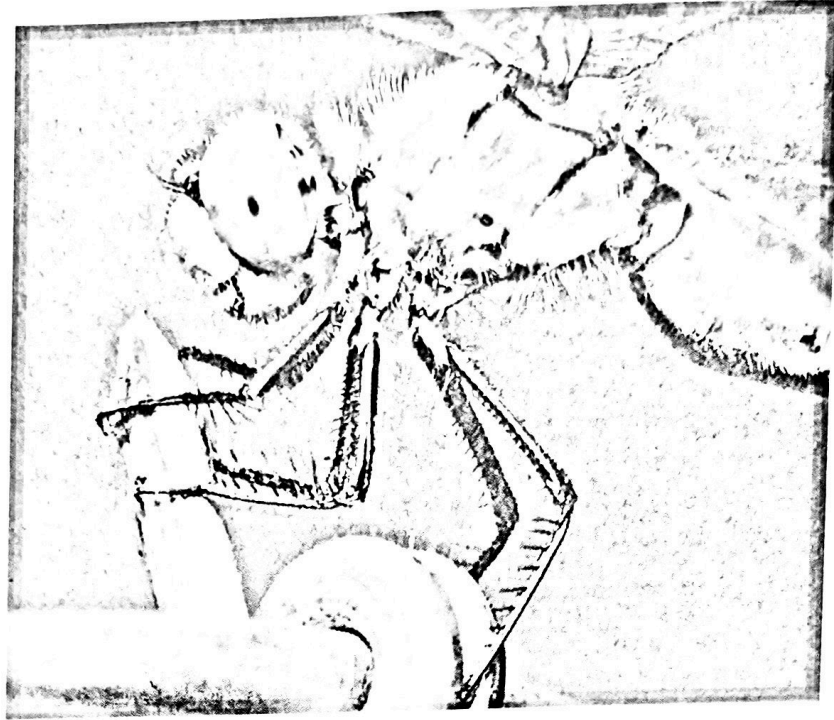


Figure 6.5 Dragonfly head with ommatidia of compound eyes visible. Such aerial predators have a large field of vision for spotting prey.

Source: Edward S. Ross.

rhabdomeres. These opsins (G protein-coupled receptors, or GPCRs) react to light waves between 300 and 700 nm to initiate a nerve impulse. In a single insect, different opsins may respond to different portions of the spectrum, thus providing a mechanism for color vision. Behavioral and electrophysiological experiments have demonstrated that many insects are sensitive to three or four spectral classes: ultraviolet (340–360 nm), violet to blue (420–460 nm), blue-green (490–550 nm), and in butterflies, red (585–610 nm). Although the color vision of insects can be described as a trichromatic system like our own, their visual world is different because the spectrum is shifted toward the shorter wavelengths to include ultraviolet. Except for butterflies, most insects lose the ability to distinguish differences in wavelengths between 550 to 650 nm even though their vision extends into this region.

Some insects are able to discriminate the plane of polarized light coming from the sky and to use this for navigation during walking or flight. Polarized light is light vibrating in a single plane, whereas direct sunlight has planes of vibration in all directions around the line of travel. Depending on atmospheric conditions, the proportion of light

that is polarized increases in certain regions of sky up to about 70%. The regular orientation of microtubules plus the configuration of the rhodopsin molecule provides an inherent mechanism sensitivity to polarized light. Certain ommatidia along the dorsal margin of the eye appear to be specialized for this function in bees, desert ants, and some other insects.

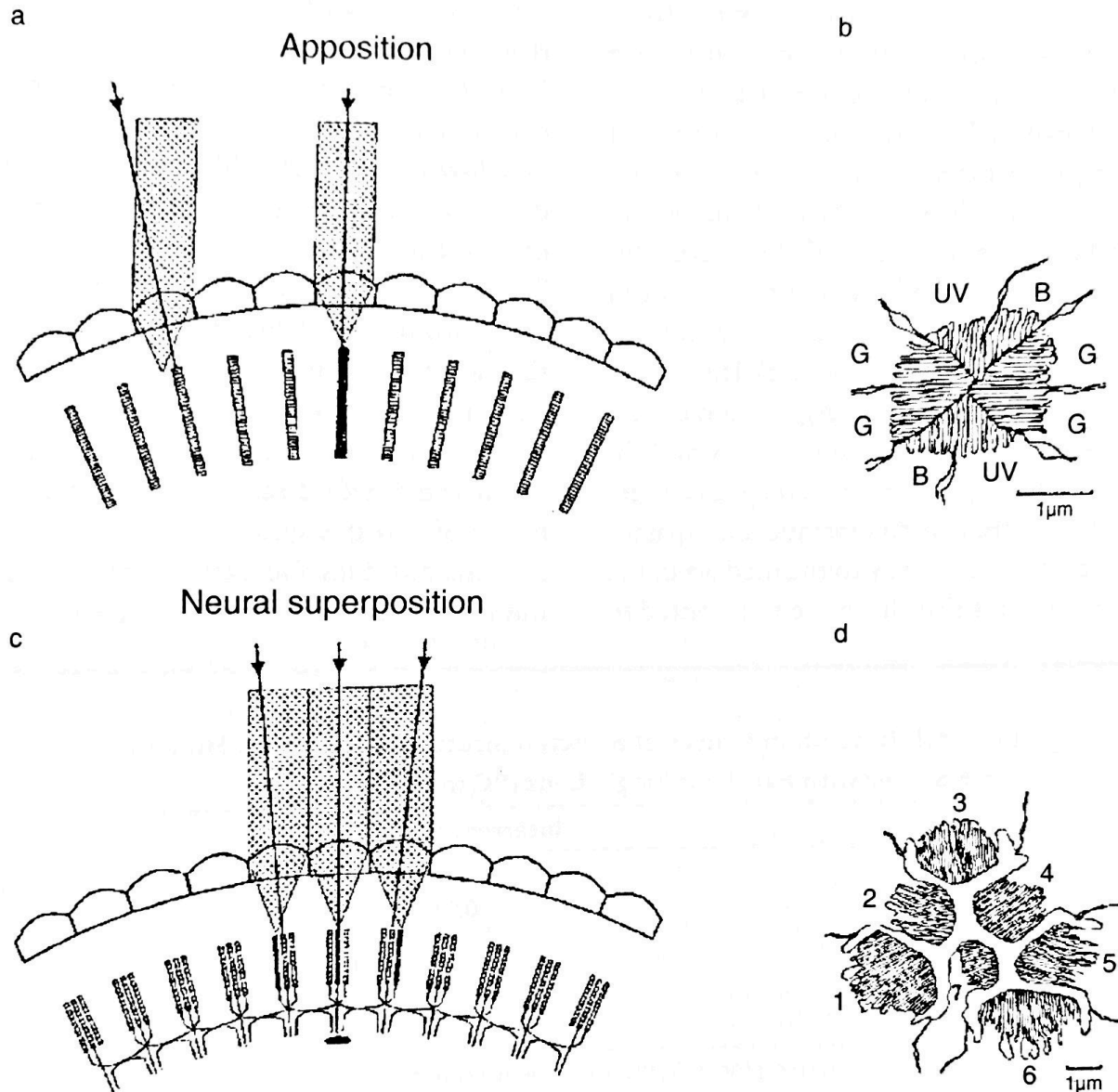
Image Formation in Compound Eyes

What do insects see? Light entering an ommatidium travels down the rhabdom and is reflected within the rhabdom so that all spatial information from light entering a rhabdom is lost. The resulting nervous signal is effectively delivered to the optic nerve as a single “pixel” rather than a crude, 6–10-pixel image from light that enters the ommatidium. Each separate rhabdomere may have distinctive differences in spectral sensitivity, however, so the resulting information transmitted from the ommatidium includes average intensity and duration of the wavelengths received. An exception occurs with flies, in which the tips of seven rhabdomeres within an ommatidium are separated (Box 6.1).

BOX 6.1 Neural Superposition in Compound Eyes

In a normal apposition compound eye such as that of a honey bee, each ommatidium receives light from different directions (Fig. 6.4c; Box Fig. 6.1). The rhab-

dom consists of fused rhabdomeres contributed by the eight retinula cells within the ommatidium (Box Fig. 6.1b,d). The fused rhabdomeres collectively act



Box Figure 6.1 The optics of an apposition eye (a and b) and neural superposition eye (c and d). Each rhabdom in an apposition eye (a) views light from a slightly different direction (arrows), and all eight rhabdoms fuse (b) to act as a single light receptor. However, different rhabdoms in the honey bee (b) may have different sensitivities to light wavelengths such as ultraviolet (UV), green (G), and blue (B). Neural superposition eyes image light from a single direction onto different rhabdomeres (there are eight per rhabdom) in adjacent ommatidia (c). Because the rhabdomeres are separated (d) and the rhabdomeres receiving the same point of light join at the same synapse in the layer beneath the rhabdom, the resulting image transmitted from the synaptic layer has the same structure as an apposition eye (a). The axon from the central rhabdomere (#7, which overlies #8) goes directly to the inset brain rather than the synaptic layer.

Source: From Land and Nilsson, 2002. Reproduced with permission of Oxford University Press.

(Continued)

BOX 6.1 (Continued)

as a single light-sensitive receptor, although different rhabdomeres have different light sensitivities. Flies such as *Drosophila* fruit flies also have apposition eyes but with a neural “twist.” In the fruit fly’s ommatidium, the seven photosensitive tips of the rhabdomeres (Box Fig. 6.1d) do not fuse to form a single rhabdom (an eighth rhabdomere is obscured by the central one above it). The axons from each retinula cell, however, join at the same synapse layer. The optical alignments of the lenses and rhabdomeres and the way in which axons from each rhabdomere connect in the synapse layer result in the same point of vision being viewed by one rhabdomere in each of seven adjacent ommatidia (Box Fig. 6.1c). The “twist” in the arrangement is that the emerging axon bundle reverses direction so that all axons receiving light from the same viewed point share a synaptic connection. One rhabdomere in each ommatidium bypasses the synapse to connect directly to the medulla of the brain. The final result is that the image transmitted to

the synapse layer is the same as a typical apposition eye. This arrangement is called a **neural superposition eye**.

What does this complicated structure and nerve wiring accomplish? The redundant stimulation of rhabdomeres in seven different ommatidia by light from the same point in space makes the neural superposition eye more sensitive in low light levels. If only low numbers of light photons impact the eye, then having multiple photoreceptors for each point of vision increases the chances of detecting some light. This can promote food or mate finding and escaping from natural enemies in low-light conditions such as at dusk. An alternative method of increasing optical sensitivity would be to increase the diameter of the rhabdom in a conventional apposition eye, but this would decrease resolution. This is a likely explanation of why this system evolved. A test of this hypothesis might involve examining the occurrence of this in other insect taxa with nocturnal activity.

Table 6.1 Resolution of Eyes of Selected Insects Compared to Humans and a Spider with Excellent Single Lens (“Camera”) Vision

Organism	Interreceptor Angle
Human	0.0007°
Jumping spider (<i>Portia</i>)	0.04°
Dragonfly (<i>Aeshna</i>)	0.25°
Honey bee (<i>Apis</i>)	0.95°
Vinegar fly (<i>Drosophila</i>)	5°

The smaller the interreceptor angle, the better the ability to distinguish small details (higher resolution).

Source: Data from Land and Nilsson, 2002.

The field of view of a single rhabdom can vary from 1° or 2° to over 20°. This field of view will overlap those of neighboring ommatidia, but the orientations of adjacent ommatidia shift with the curvature of the surface of compound eye.

The resulting image from a compound eye is thus not a mosaic of tiny, identical images in each ommatidium as is so often depicted in science fiction films. Instead, the optic nerve transmits an **apposition image** of **apposed** (literally “side by

side”) dots of varying intensities and colors. Thus, the resulting image must be very coarse. Dragonfly eyes have the greatest known resolving power for insects. They can distinguish angular differences between adjacent points in an image of only 0.25°. The best resolution for a human eye is about 35 times better (Table 6.1). The human eye achieves its higher resolving power by having a larger lens, a longer focal distance, and a larger retina (more photoreceptor cells). For each facet of an ommatidium

to have similar resolution, the compound eye of an insect would be from a little over a meter to numerous meters in width. At the other size extreme for insect eyes, diffraction of light waves blurs the image in very small lens-bearing eyes, limiting how small a functional eye with a lens can be.

Although the visual acuity of insects would seem adequate for seeing objects in some detail, behavioral experiments with honey bees demonstrate that their discrimination of form is poorly developed. The compound eye, however, is well adapted for the detection of movement because successive ommatidia are stimulated as the object sweeps across the visual field. Depth perception is possible when the visual fields of the paired eyes overlap. The position of the object seen by both eyes is thus triangulated. The wide separation of the eyes in predators such as mantids and dragonfly naiads probably improves distance perception.

There are two types of compound eyes: apposition and superposition. In the **apposition type** (photopic) of eye described earlier, the rhabdom is immediately below the crystalline cone, surrounded by a jacket of pigment cells that shields each ommatidium from light outside the ommatidium's field of view or from adjacent ommatidia so that only light from the lens reaches the rhabdom immediately beneath (Fig. 6.4c). An apposition image is most useful for insects that are active in daylight. Day-active predators such as dragonflies and wasps have clusters of anterior ommatidia that subtend smaller angles and have more overlap with adjacent ommatidia, plus have larger corneal facets, all of which increase resolution in the forward field of vision.

The **superposition type** (scotopic) of compound eye does not restrict light reception to individual ommatidia. Instead, light from numerous corneal lenses stimulates a rhabdom layer that forms a retinalike surface beneath a clear zone across which light rays are focused (Fig. 6.4d). Parallel light rays arriving at the surface of the compound eye are refracted (bent) by the lenses so that they emerge as parallel rays toward the central axis of the eye; in the apposition eye, the lenses bend the rays to converge on the photoreceptor cells. The superposition eye is 50- to 100-fold more optically sensitive (detects low light) than apposition eyes of the same

size. Diffraction limits the minimum diameter of the eye facets, just as it does for apposition eyes. Superposition eyes are most useful for nocturnal insects. In the Lepidoptera, butterflies have apposition eyes, and moths and skippers have superposition eyes, as do many beetle groups that are night-active. Butterflies and moths clearly are closely related, but the problem of how these great differences in eye structure between apposition and superposition eyes evolved remains unsolved.

The migration of the secondary pigment cells in some insects permits the eye to form images over a wide range of light intensities. During the day the pigment and to some extent the individual pigment cells move proximally into the clear zone and limit the passage of light from the lenses to single rhabdoms. This is the **day-adapted** eye, and the image is formed by apposition. At dusk, the pigments and secondary pigment cells contract to permit light from adjacent ommatidia to stimulate the rhabdoms. This is the **night-adapted** eye, and the image is formed by superposition. In some moths, a **tapetum** of tracheal tubes between and parallel to the ommatidia aid in reflecting light onto the rhabdoms. Most insects of this type are active at twilight or night. Shining a light directly at the eyes of these insects causes the entire eye to reflect light from the tapetum, giving the appearance of brightly glowing eyes. Superposition eyes have had the reputation of poor resolving power, or even of lacking the ability to resolve images, but day-flying moths (e.g., skippers, Lepidoptera: Hesperidae) have optics that produce observable images of excellent quality.

Ocelli and Stemmata

Simple eyes have a single, biconvex, cuticular lens that transmits light on the rhabdoms of sense cells beneath (Fig. 6.4e,f). This is in principle the camera type of eye found in vertebrates. Insect ocelli, however, focus optical images below the rhabdom layer. The prevailing hypothesis is that this lack of focus helps to determine the position of the horizon because small objects, such as leaves and twigs, are out of focus and so do not interfere with determining the contrast of light above and below the horizon. Monitoring the horizon provides essential guidance information to stabilize flight.

Mechanoreceptors

A variety of simple sense organs, or **sensilla** (sing., sensillum), can detect mechanical distortion of the body. In the usual arrangement, the dendrite of a single bipolar neuron attaches to a movable part of the body, often by a minute cuticular sheath called a **scolopale**. Movements of the body part in response to mechanical stress, touch, wind, or vibrations in air, water, or solid substrates initiate nerve impulses via mechanically activated ion channels. Some sensilla respond to disturbances from the environment as **exteroceptors**, while others respond to the position of one part of the body relative

to another, thus functioning as **proprioceptors**. These are important in maintaining posture and in orienting to gravity.

Two general types of mechanoreceptors are based on morphological structure. Type I receptors are cuticular and ciliated. Type II receptors are multipolar and nonciliated. There are three major groups of Type I mechanoreceptors (Fig. 6.6). **Trichoid** sensilla are hairlike setae with a single dendrite attached at the base. Some project well above the cuticle surface and serve as **tactile**, or touch, organs (Fig. 6.6a). **Campaniform** sensilla are oval, domelike areas of cuticle that rise or lower

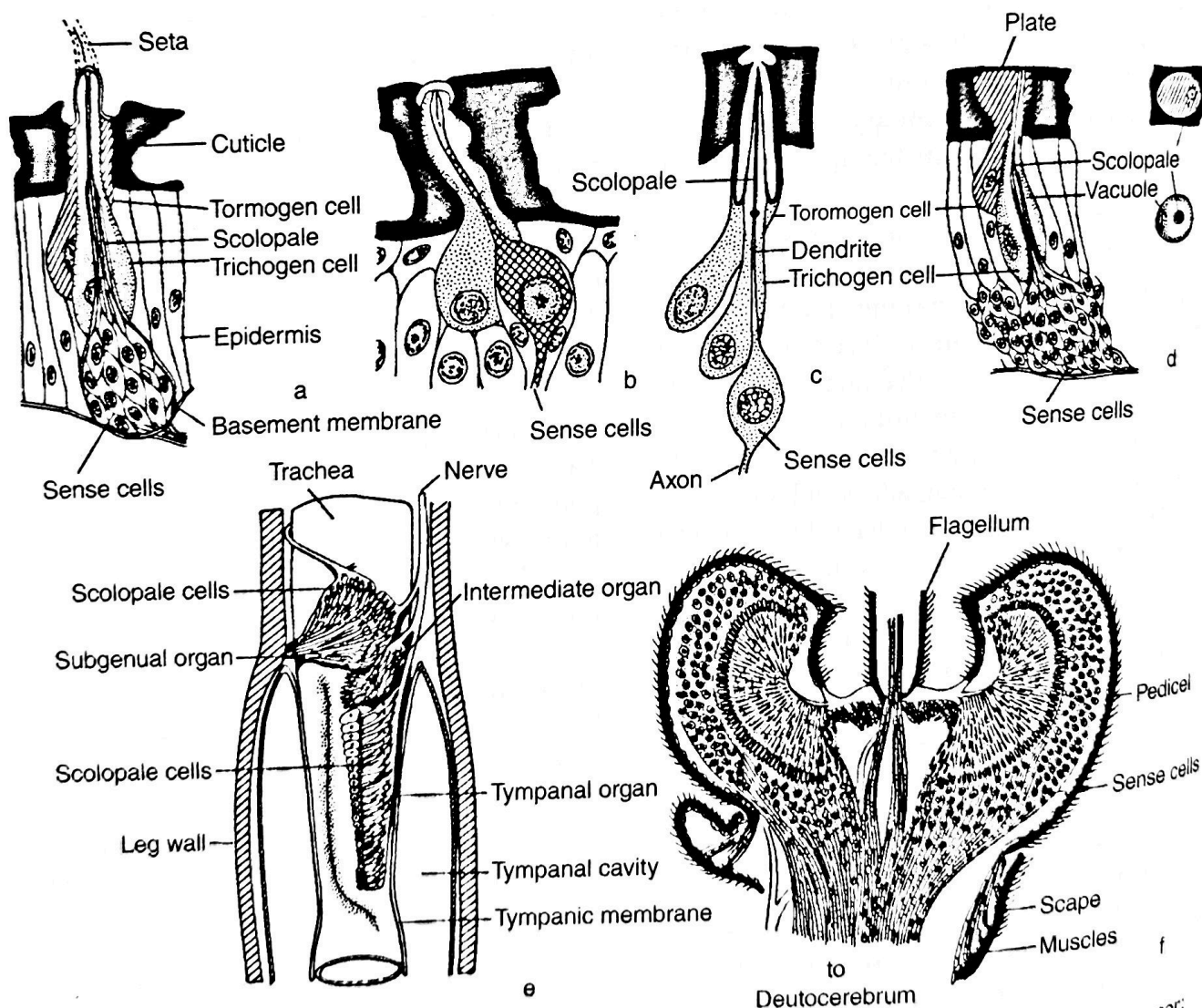


Figure 6.6 Sensilla: **a**, trichoid chemoreceptor; **b**, campaniform mechanoreceptor; **c**, coeloconic chemoreceptor; **d**, plate organ; **e**, chordotonal acoustical organ in tibia of right leg of a tettigoniid; **f**, Johnston's organ in antenna of the fly *Chaoborus*.
Source: **a–c** and **e**, Redrawn from R.E. Snodgrass, *The Principles of Insect Morphology* - public domain; **f**, redrawn after Child, 1894.

as the adjacent exoskeleton is mechanically strained (Fig. 6.6b). The dendrites detect movements of the dome. **Chordotonal** organs (Fig. 6.6e) are internal and formed by **scolopidia** consisting of three cells: a bipolar neuron, a scolopale cell, and an attachment cell. The dendrite sometimes ends inside the scolopale in a process that resembles a cilium. One or more scolopidia cluster into a chordotonal organ and are variously attached to the epidermis. Some are suspended between two points in membranous areas or between leg joints, thus permitting detection of movements between the points of attachment. **Subgenual organs** of the tibia, however, have a single attachment and do not span a joint. They are especially sensitive to vibrations in the substratum. **Johnston's organ** is a chordotonal organ in the antennal pedicel (Fig. 6.6f). By its attachment to the base of the flagellum, movements of the flagellum are detected. **Tympanal organs** are specially designed for the reception of sound (Fig. 6.6e). A chordotonal organ is attached to a thin cuticular membrane or **tympanum** that freely vibrates when struck by sound waves. Type II mechanoreceptors are **stretch** receptors that are attached to connective tissue or muscles, registering the tension of such soft tissues, especially in the abdomen. All four types of sensilla (Types Ia, Ib, Ic, and II) may function as proprioceptors. Groups of trichoid sensilla located at each side behind the head on the **cervical sclerites** register the position of the head with respect to the body. Similar groups at leg joints register the positions of the limbs. Campaniform sensilla are widely scattered over the body surface at points of stress and bending. The halteres of Diptera and insect wings in general are well supplied. Strategically placed chordotonal organs and stretch receptors permit detection of movements of the limbs, segments, and viscera. The positions of the antennae are detected by Johnston's organ.

Vibrations are detected mainly by trichoid sensilla and chordotonal organs. Hairs in the cerci of cockroaches, for example, respond to sound waves of low frequency as well as to wind currents. In male Culicidae and Chironomidae (Diptera), the antennae have fine, long hairs that vibrate in response to the flight tone of the females. This stimulates a mating response. The hair vibrations move

the flagellum, which in turn stimulates Johnston's organ in the pedicel. The same response can be evoked with a tuning fork that vibrates at 100 to 800 Hz.

The special acoustical receptors of insects are the tympanal organs found in various unrelated taxa and in different places on the body. The organs are on the abdomen of grasshoppers (Orthoptera; Fig. 29.2b), cicadas (Hemiptera; see Fig. 6.8a–c), and moths (Lepidoptera; Fig. 45.6e–f); on the tibia of the forelegs in crickets and katydids (Orthoptera; Fig. 29.2a); and on the mesothorax of the bugs *Corixa* (Corixidae, Hemiptera) and *Plea* (Pleidae, Hemiptera) and the metathorax of some moths (Noctuoidea, Lepidoptera; Fig. 45.6e).

The noctuid moths mentioned previously are night-fliers. Their tympanal organs detect approaching bats, the sounds of which can be sensed at about 30 m. The tympanal organs of Orthoptera and Hemiptera are used in courtship behavior. Sounds produced, usually by the male or by both sexes, are detected and serve to bring mates together. In *Plea*, there is only one scolopidium per organ, but in others, the organ may be extremely complex, involving up to 1,500 scolopidia in cicadas. These organs respond to a wide range of sound frequencies, generally less than 20 kilocycles per second. The average upper limit for humans is about 14 kilocycles per second. Insects discriminate poorly, if at all, among the different frequencies; they respond mainly to the intensity and duration of sound and the intervals between sounds. Insects can detect an interval as brief as 0.01 second, whereas the human ear fails to detect intervals of less than 0.1 second.

Chemoreceptors

Insects are famously sensitive to chemical signals for finding food and mates through gustation (taste) and olfaction (smell). Both taste and smell chemosensors require a pathway for the stimulant chemicals to move from the outside environment to contact the membrane or sensory cells beneath a cuticular surface or organ so that receptor proteins (e.g., GPCRs) embedded in the dendrites' membranes can react with specific molecules in the surrounding air or fluid to stimulate a nerve impulse. A water-protein pathway protects the sensory

membrane from drying. Accessory cells supply the concentrations of cations critical to the chemical reactions needed for the stimulus to trigger a signal to the nervous system. Taste (detection of chemicals from a solid or liquid substrate) receptors usually have a single pore filled with liquid. Olfactory receptors have the sensory membranes contained beneath or within a cuticular covering in such a way that gas molecules must pass through narrow

channels or pores to reach the dendritic surface. This tends to restrict chemoreception in olfactory organs to gas molecules.

Four common types of setae are commonly associated with chemoreceptor neurons. (1) **Trichosensilla** may serve both as mechanoreceptors and chemoreceptors (Figs. 6.6a, 6.7). Such hairs on the labella and legs of blowflies (*Calliphoridae*) have a mechanoreceptor attached to the base and the

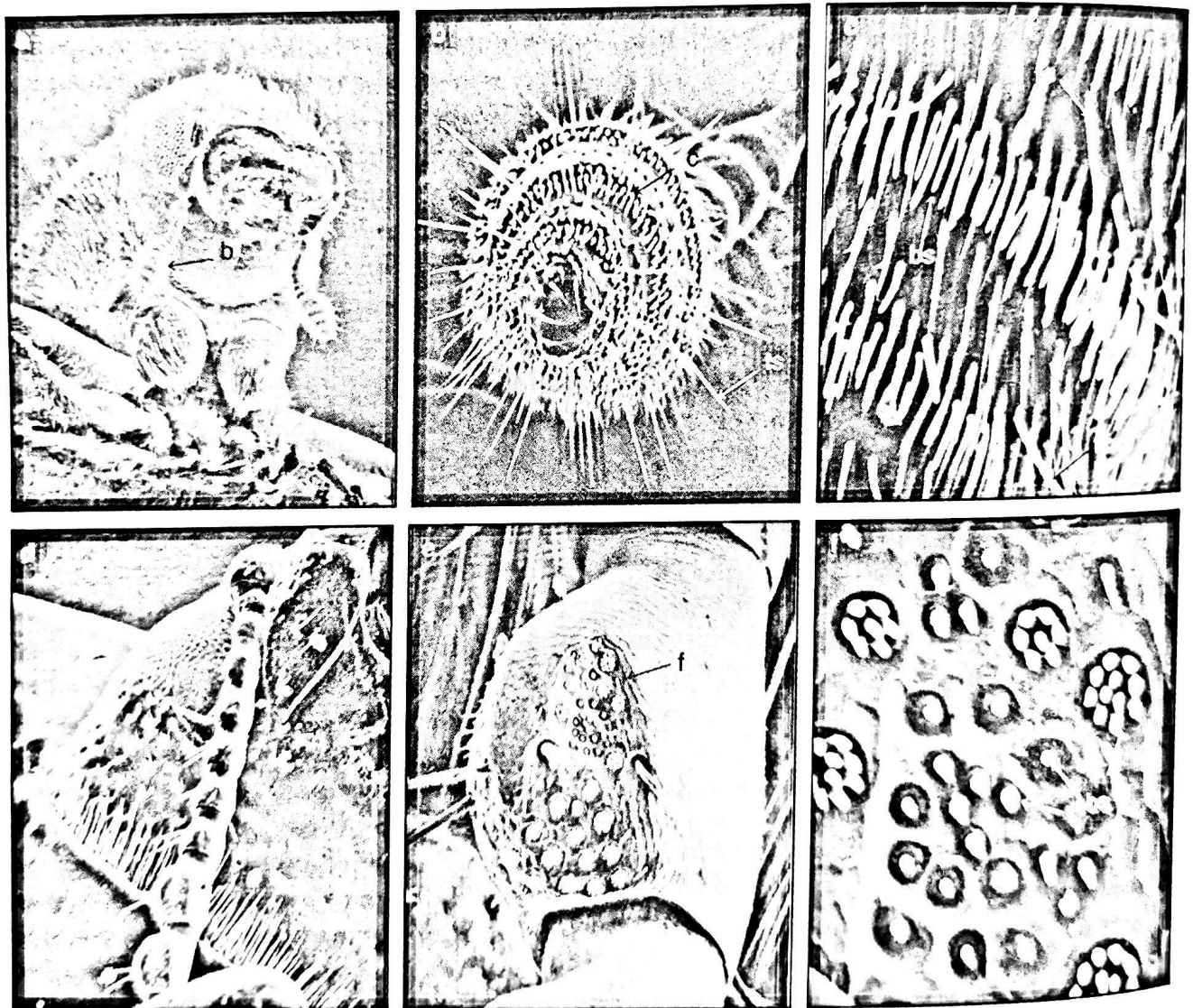


Figure 6.7 Antennal sensilla: **a**, head of the bark beetle *Pseudohylesinus* sp. (Scolytidae), showing antennae (arrow marks position of photo **b**; 37 $\times$); **b**, antennal club of same showing sensory bands (arrow marks position of photo **c**; 304 $\times$); **c**, sensilla of club of same, blunt basiconic sensilla form dense bands (743 $\times$); **d**, head of a male beetle, *Ternochila virescens* (Ostomidae), showing antenna (arrow marks position of photo **e**; 32 $\times$); **e**, ninth antennal segment enlarged (arrow marks position of photo **f**; 169 $\times$); **f**, basiconic sensilla of several types whose functions are unknown (878 $\times$).

Source: Clyde Willson.

dendrites of a few chemoreceptor neurons situated at a single pore at the tip. Trichoid sensilla are commonly taste receptors. (2) **Basiconic** sensilla are peglike and thin-walled, have many pores, and project above the cuticle. They are the most common type of olfactory receptors, typically found on the antennae as well as on the mouthparts and other places on the body. (3) **Coeloconic** sensilla have the sensory peg sunk in a cuticular pit (Figs. 6.6c, 6.7). These are found on the antennae and mouthparts of some insects. (4) **Plate organs** are found on the antennae of aphids and honey bees (Figs. 6.6d, 6.7). Each is a round, flat cuticular plate perforated by pores. (5) **Sensory pits** contain many sensilla in a subcuticular pit. Such pits have been identified on the third antennal segment of Diptera (suborder Cyclorrhapha) and labial palpi of Lepidoptera and Neuroptera. Sensilla that sense odors usually have multiple pores, often opening into a chamber with a network of channels that lead to multibranched dendrites. This arrangement acts to filter larger molecules and particles but allows smaller odor molecules. Taste sensilla most often have a single pore that leads to an interior space where a viscous liquid surrounds the dendrite.

Chemoreceptors are found on the antennae, mouthparts, legs, and ovipositor. They play crucial roles in many activities. The detection of odors, or **olfaction**, is involved in locating food and sites for oviposition and in finding mates through chemical sex attractants. Social insects recognize colony members by odor. The ability of insects to detect minimal concentrations of chemicals varies with the physiological state of the insect and, of course, with the specific chemical compound or mixture of compounds. In tests with honey bees involving many odorous compounds, the general conclusion was that the threshold concentration detected is on average about equal to that of humans. However, bees do sense certain substances important to them at lower concentrations, such as the odors of beeswax and certain glandular secretions.

Certain key compounds that are crucial in the life of an insect may be sensed at unbelievably low concentrations. Calculations for the male silk

moth *Bombyx mori* (Bombycidae, Lepidoptera) indicate that single molecules of the sex attractant bombykol produce impulses in the appropriate antennal chemoreceptors (also GPCRs). The moth responds behaviorally to as few as 200 bombykol-induced impulses per second. This is barely above the theoretical minimum needed to transmit information in a system that already has 1,600 impulses per second of spontaneous nerve activity or "noise" (see Box 6.2).

The taste or **contact chemoreception** of substances in liquid uses the same physiological mechanisms as for olfaction. Behavioral and electrophysiological analyses have shown that insects discriminate among sweet, salt, acid, and bitter compounds in solution and exhibit a sense for water. The minimum taste thresholds are generally lower in insects than in humans. A convenient behavioral response has aided in surveying chemicals at various concentrations. When sugar solutions are applied to the tarsi of flies, butterflies, and honey bees, the insects respond by extending the proboscis. The proboscis is not extended for water or solutions too weak to detect. As a consequence, responses to sugars have been extensively studied.

Of 30 substances that taste sweet to humans, honey bees respond positively to only seven, and marginally to two. Starved bees can detect 0.06 to 0.12 M sucrose in solutions from water with their mouthparts. Their antennae are much more sensitive. With behavioral training, bees respond to sugar solutions applied to their antennae in concentrations as low as 0.0001 M.

The trichoid sensilla on the tarsi and labella of blowflies (Calliphoridae) can be stimulated individually with solutions. Blowflies accept a much greater variety of carbohydrates than honey bees. When it is applied to the tarsi, the acceptance threshold for sucrose in solution is 0.01 M in *Phormia regina* but as low as 0.0006 M in *Calliphora erythrocephala* (Calliphoridae, Diptera). *Pyrameis* butterflies (Nymphalidae, Lepidoptera) respond by tarsal stimulation to 0.00008 M sucrose when starved. The threshold for humans, at 0.02 M, is 250 times poorer by comparison.

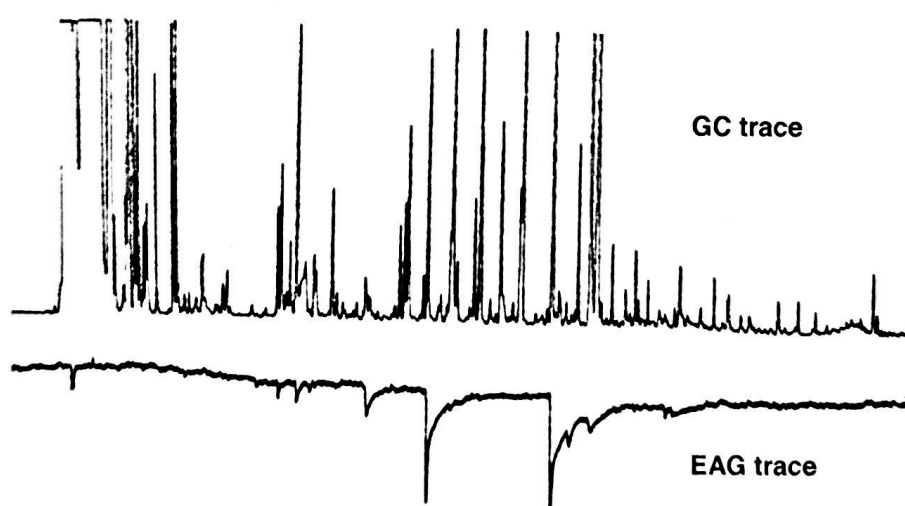
BOX 6.2 How Do We Know This? Electroantennograms

As already noted, insects can be incredibly sensitive in detecting odors from great distances. The attraction of male moths from long distances by caged or tethered female moths was long believed to result from attractant odors (sex pheromones) emitted by the female moths. How does one identify the attractant chemicals? Or prove that an insect responds to a particular chemical?

The electroantennogram (EAG) technique has been used to address these questions by taking advantage of the concentration of olfactory sensory cells in insect antennae and the ability of electrophysiological methods to record nerve impulses as they occur. For a simple example, a freshly detached male moth antenna (a live insect can also be used) can be mounted so as to keep the nerve tissues fresh and biologically active. Fine electrical probes connected either to individual sensory cell output axons or, more often, to larger nerves consisting of many axons are integrated with equipment to amplify and record the electrical signals generated by nerve impulses from the sensory system. Air containing either known volatile chemicals or unknown volatiles from various extracts (e.g., from female pheromone-emitting

glands) is blown across the antenna, and any resulting nerve impulses can be recorded. A sharp increase in nerve transmission from olfactory sensory cells indicates that the sensory system is reacting to specific chemicals.

To identify which chemicals are pheromones that attract mates, chemicals are extracted from biologically attractive sources such as the glands used during "calling" postures taken by female moths. The chemicals in these extracts can be partitioned using a gas chromatograph, a device used to discover the chemical identity of complex mixtures of chemicals or to confirm the chemical composition or purity of chemical preparations. The chromatograph releases volatile chemicals from a stationary liquid phase in a sequence dependent upon the mass and chemical structure of the chemicals, each chemical having a characteristic "retention time" in the stationary phase. The output of volatiles from the chromatograph is recorded graphically (Box Fig. 6.2) as the chemicals are eluted from the device and also blown across the antenna preparation. The detection of a particular chemical by the chromatograph along with a simultaneous sharp increase in antenna



Box Figure 6.2 Diagram of electroantennogram (EAG) set up in conjunction with a gas chromatograph (GC).

Source: Alexander Purcell.

(Continued)

BOX 6.2 (Continued)

nerve transmissions indicates that the chemical is stimulating sensory cells. The chromatograph can also provide quantitative information as to how much of each chemical is eluted during the process. The EAG provides a simple and elegant method for identifying pheromones.

Usually, however, the process is not usually as simple as outlined here because pheromones often

occur as mixtures of two or more chemicals. Indeed, different insect species can have nearly identical pheromones but in different proportions. Behavioral studies with artificial mixtures of compounds tentatively identified as pheromones help to confirm that the molecules identified by EAG are in fact the operative chemicals responsible for driving the behavior of the insects perceiving these compounds.

BEHAVIOR

What an insect does in response to external and internal stimuli depends not only on the nature of the stimulus but also on the insect's physiological state. The response to food may depend on the taste of food, hunger, and hormonal inputs. At the onset of molting, for example, feeding may cease altogether. Thus, both the nervous and endocrine systems control an insect's behavior. Both function to sequence behavior and prevent conflicting behavior to favor the survival of the individual and the propagation of the species. Both communicate directly to various tissues. The nervous system communicates by physical contact and the endocrine system by hormones in the hemolymph. The systems differ in that the nervous system functions instantaneously to integrate specific sensory and motor impulses, while the endocrine system reacts more slowly, with long-term effects in a variety of tissues, including the central nervous system.

The behavior of insects under natural conditions is a complex mixture both of stereotyped responses to stimuli that are controlled and coordinated by the central nervous system and of learning. Segmental ganglia may be largely independent in controlling the responses to certain stimuli. Stepping movements or reflexes of the legs, for example, are controlled directly by the respective thoracic ganglia but are coordinated by the inhibition and stimulation of the brain and other ganglia by neural motor programs. Genetics can program stereotyped responses into the nervous system yet

with considerable flexibility in the timing, coordination, and sequencing of acts, depending on sensory input.

Orientation and Directed Movements

A complex but stereotyped movement that orients the whole body to an environmental stimulus is called a **taxis** (pl, taxes). Commonly, this is an orientation to gravity (**geotaxis**), to light (**phototaxis**), to wind currents (**anemotaxis**), or to sound (**phonotaxis**). An orientation may be either **positive** (toward the stimulus) or **negative** (away from the stimulus). A positive phototaxis, for example, involves orienting the body so that both eyes are equally stimulated in front. The orientation to light may also involve positioning the body so that the light is dorsal or ventral. The **dorsal light reaction** is common among aquatic insects, providing a means to orient to the earth's surface under circumstances where the effect of gravity on proprioceptors is reduced by the buoyancy of water. The backswimmer *Notonecta* (Notonectidae, Hemiptera), so named because it swims upside down (Fig. 8.6d), appropriately has a **ventral light reaction**. Orientation at a fixed angle to sunlight is called the **light compass reaction**. When it is used as a means for navigation to and from a distant point, compensation must be made for the sun's movement. Honey bees, some ants, and a few other insects have such a compensatory mechanism, probably involving their sense of time or circadian rhythm (discussed later). Orientation to a celestial

body combined with compensation for its movement is called an **astrotaxis**.

Although a taxis is a stereotyped behavior, a given taxis is not an invariant response to a given stimulus. Taxes are under the control of the nervous system and can be modified by learning. Depending on the circumstances, a taxis can be quickly switched on or off; the orientation switched from positive to negative, or vice versa; and receptivity to one stimulus replaced by another. Positive geotaxis and negative phototaxis, and each with opposite signs, are widely coupled among insects. In honey bees, gravity and the sun are interchanged as stimuli for orientation.

Using this terminology, an exploratory foraging trip by a worker ant might be described as follows. The ant is negatively geotactic and positively phototactic as she makes her way to the surface from her underground colony. As she walks over the ground, she is oriented at an angle to the sun by astrotaxis. On her return, the astrotaxis is switched 180° , permitting her to navigate back to the nest, and on entering the nest, she becomes positively geotactic and negatively phototactic.

Instincts

Many of the activities of insects are a series of stereotyped behaviors of greater or lesser complexity. Such sequences are loosely called instincts or fixed action patterns. Examples include feeding, migration, mating, oviposition, nest building, cocoon spinning, and movements during ecdysis. Here, the physiological and developmental state of the insect, especially the hormonal milieu, is important in determining whether a stimulus will trigger, or release, a given program of behavior. The program may be complex and flexible, including alternate sequences of behavior depending on the response of the mate, suitability of food, or other circumstances.

Learning

A simple definition of **learning** is a change in behavior as a result of experience. Learning can occur even in the segmental ganglia of insects. Headless cockroaches and grasshoppers can be trained to lift a leg to avoid an electric shock,

demonstrating that learning can occur without a brain. Such elementary forms of learning may prove to be widespread. Nonassociative learning includes habituation, the waning of a response due to repeated stimulation, and sensitization, where repeated exposure to a stimulus enhances a response. More complex associative learning associates a stimulus with another stimulus or a motor pattern. The most important centers for insect learning are the brain's mushroom bodies, or corpora pedunculata. In insects that exhibit complex behavior and learning, the bodies are larger in volume and have more cells and more synapses than insects with simpler and clearly stereotyped behavior. Manipulative experiments have demonstrated spatial learning. For example, moving a rock or twig near a wasp nest in the ground after the mother wasp leaves the nest may make the nest more difficult for the wasp to locate. Spatial learning is critical for foraging insects such as bees and ants or insects that repeatedly return to a nest or food source.

Communication

The behavioral interactions of insects among themselves and with other organisms usually involve some sort of communication. **Communication** occurs when an organism provides a visual, tactile, auditory, and/or chemical signal that influences the physiology or behavior of another organism. The distance over which the communication takes place may be such that only one sense will effectively receive the signal. This is **long-range** communication, in contrast to **short-range** communication, in which more than one sense may be involved.

Instances of communication may be broadly divided into those that occur between members of the same species and those that occur between members of different species. The former, or **intraspecific**, cases of communication are for the purpose of attracting or recognizing mates, aggression or defending territories, assembling or dispersing aggregations, or in social species, various cooperative activities and to control caste development and behavior.

Communication between different species, or **interspecific** communication, may be divided

further into (1) those that benefit the sender, (2) those that benefit the receiver, and (3) those that result in a mutual benefit. In the first relationship, the sender is usually under threat of attack by a predator and produces one or a combination of warning signals to discourage attack (see Chapter 10 for additional details of this strategy). Other instances in which the sender benefits involve signals that confuse the communication of a predator or competitor. High-frequency clicks produced by the tymbals of night-flying Arctiidae moths (discussed later) probably confuse the echolocation system of bats. In the second relationship, the sender may become a victim when some aspect of its activities signals its presence to a predator or parasitoid, or a potential victim may escape after sensing the enemy's presence. The detection of the sounds of bats by the tympanal organs of moths is an example. In either case, the receiver of the signal is the beneficiary. For the third type of relationship, the insect pollination of flowers supplies an example. The flower provides visual, tactile, and chemical signals that attract insects. The insects obtain food, and the flower achieves cross-pollination (see FLOWER VISITING INSECTS in Chapter 9).

As we shall see, communication may become quite complex: a given signal may be sensed both by members of the same species and by members of different species, different species of organisms may produce an identical signal, and the same signal may be used for different purposes by the sender and receiver.

Communication by Sight

Insects that are active by day commonly depend on visual signals. For example, the color patterns, size, and motion of female butterflies are known to attract males of the same species. Male butterflies also respond to visual cues to identify and pursue other males in defending territories during courtship. Visual signals also present the risk of attracting predators and parasitoids.

Lightning bugs or fireflies (Lampyridae, Coleoptera) of both sexes use flashes of light to find each other at night. Males emit flashes while flying that have a species-specific duration and frequency. The females, which are less active or

even wingless and larviform, respond by flashes. Depending on the species, the female's flashes may be emitted after a brief pause of precise duration after the male signal. The luminescent organs consist of large, well-tracheated cells in the abdomen. Light is generated by oxidation of luciferin in the presence of the enzyme luciferase. The reaction is highly efficient; 98% of the energy is released as light. A product of the reaction inhibits luciferase and stops further reaction. Nerve impulses stimulate light production, probably by removing the inhibition of luciferase.

The flash signals of fireflies also may function interspecifically in what is called aggressive mimicry. The females of *Photuris versicolor* and related species are known to flash-respond correctly to mating signals of males of other species and to eat the males that are attracted. *P. versicolor* preys on 11 other species of fireflies.

Communication by Sound

Airborne vibrations so familiar to humans as sound can also be important means of insect communication. Crickets (Orthoptera, Gryllidae) and cicadas (Hemiptera, Cicadidae) are widely recognized examples. Because of the small sizes of most insects, however, vibrations transmitted along liquid or solid substrates are more common than airborne sounds for communication. This is because vibrations of a given energy level travel much farther (and faster) in solid compared to gaseous media. The very low level of vibrational energy expended by small insects requires more sensitive and sophisticated equipment to detect and record. Because of these difficulties, a large realm of insect sounds goes unnoticed, even by professional entomologists.

Insects can create vibrations as a by-product of an activity such as flying to generate communication signals for other purposes. We have already mentioned how the flight tone of female mosquitoes attracts males, thus serving an intraspecific function. Loud buzzing by bees and wasps serves interspecifically as an effective warning signal that is even imitated by other insects. Striking the body against the substratum creates vibrations in wood or soil. The deathwatch beetle *Xestobium* (Anobiidae, Coleoptera) bores in furniture and

wooden houses. At sexual maturity, it strikes its head against the burrow walls, producing a rapping sound that at night influences the behavior of humans as well. Many species of termites drum their heads in response to disturbances of their colonies.

Special devices for creating sound are prevalent in numerous orders but are especially frequent in species of Orthoptera and Hemiptera (Fig. 6.8). Vibrations are generated mostly by one of two mechanisms: movement of roughened surfaces together or vibration of a membrane. In the first type of mechanism, one surface may be modified into a scraper and the other into a file (Fig. 6.8d-f). The

movement of the scraper on the file is called **stridulation**. Some adult as well as immature insects stridulate to produce arrhythmic, rasping warning sounds. These are heard for only a short distance or sensed by contact. The devices are simple and may be formed wherever two parts of the body normally rub together.

In Orthoptera, stridulation by adults can be heard at long range and serves to bring the sexes of the same species together for mating. The devices for sound production and reception are complex, and the sounds of each species have a characteristic frequency, rhythmic spacing, and duration. In

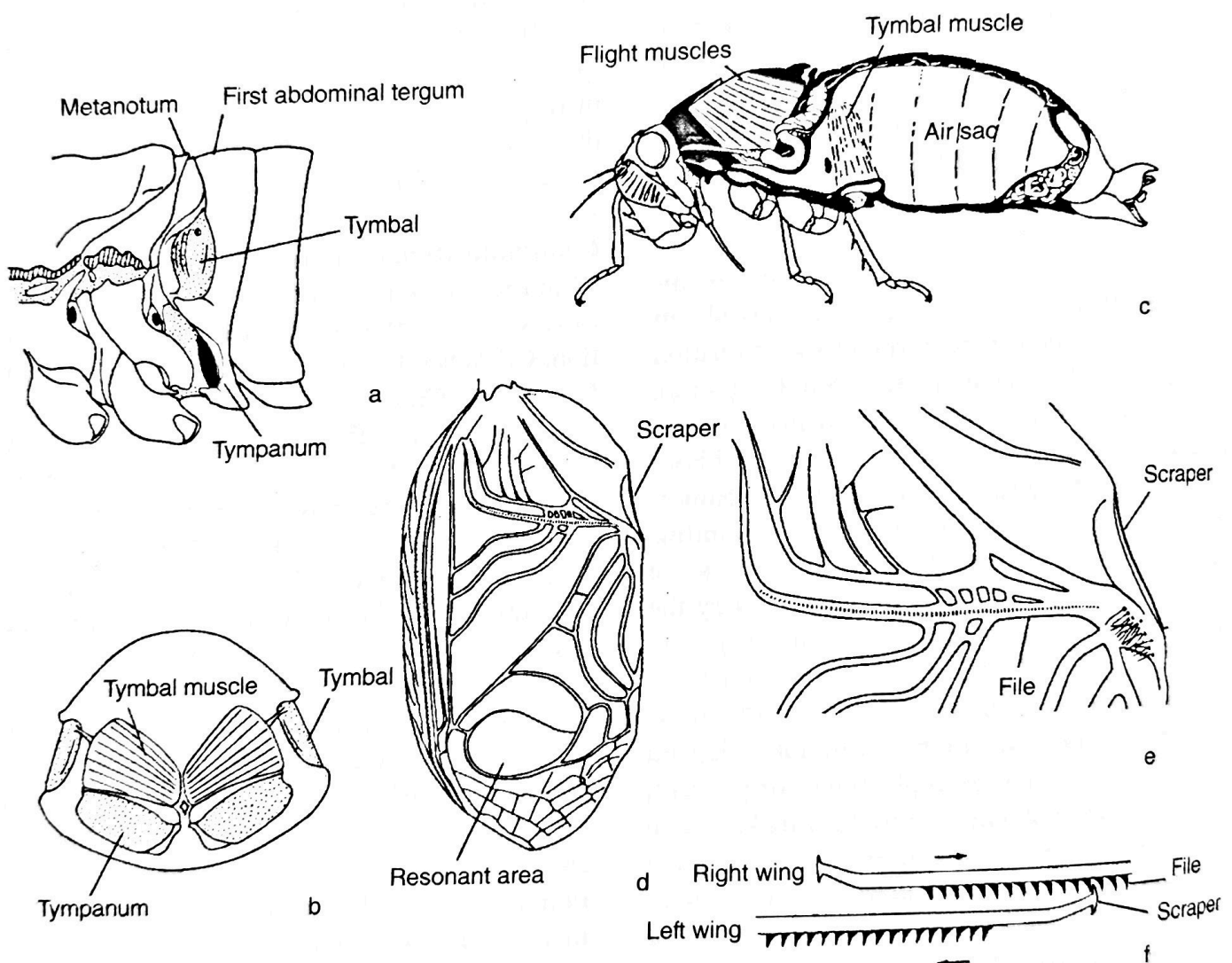


Figure 6.8 Sound-producing organs: **a**, lateral view of anterior abdomen of a male cicada, *Okanagana vanduzeei*, showing sound-producing organ (tymbal) and sound receptor (tympanum); **b**, cross section of same; **c**, longitudinal section of *Magicicada septendecim* (Cicadidae) showing large, resonant air sac; **d**, ventral view of the right wing of the cricket *Acheta assimilis* (Gryllidae); **e**, enlargement of stridulatory organ of same; **f**, diagram of relationship of the right wing and left wing during stridulation.

Source: Redrawn from R.E. Snodgrass, *The Principles of Insect Morphology* - public domain.

crickets (Gryllidae) and katydids (Tettigoniidae), one or both forewings have a resonant area of cuticle that vibrates as the scraper of one wing strikes the teeth of the file on the opposite wing. Tympanal organs of hearing are located in the fore tibiae (Fig. 29.2a). Receptive females orient to the calling songs of the males and are attracted to them. Grasshoppers (Acrididae) rub a row of pegs on the inner side of the hind femur against raised veins of the forewings, causing the wings to vibrate. The tympanal organs are on the first abdominal segment (Fig. 29.2b). Both males and females produce long-range calling songs and approach each other.

Sound-producing membranes called **tymbals** are situated in the metathorax of Arctiidae (Lepidoptera) and in the abdomen of both sexes of cicadas (Cicadidae) and leafhoppers (Cicadellidae) and some shield bugs (Pentatomidae). Tymbals are best developed in male cicadas (Fig. 6.8a-c), in which they produce long-range, airborne calls. In these insects, the tymbal is a thin, resilient area of cuticle situated dorsolaterally on the first abdominal segment. Contraction of an asynchronous fibrillar muscle attached to the center causes the tymbal to click inward. When the muscle relaxes, the elastic cuticle then clicks outward. Large air sacs in the abdomen resonate with the tymbal vibrations to increase sound intensity. The synchronous singing of many individuals forms a "chorus."

The tymbals of the much smaller leafhoppers (Cicadellidae) produce weaker vibrations that are transmitted for longer distances along plants than through the air as sound waves. This communication requires that the insects be on the same or touching plants. Planthoppers (Hemiptera, Fulgoroidea) and lacewings (Neuroptera, Chrysopidae) create vibrations by rapidly drumming their abdomens against a plant surface. Experimentally manipulating various features of recorded insect vibrations and observing the reactions or lack of reactions of responding insects to the altered sounds helps to identify the essential features of the songs.

Communication by Touch

Direct (tactile) physical contact between individuals is a form of communication that is probably

more frequent than the scientific literature acknowledges. As an example of tactile communication, ants exchange not only chemical signaling but touch other nestmates to follow them or determine each other's physical features. Touching can deliver molecules with low volatility for chemical communications. Both males and female of *Macrosteles* spp. leafhoppers (Cicadellidae, Hemiptera) used their legs to stroke each other, first by the female and then by the male immediately before mating. Two closely related *Macrosteles* species failed to mate in short trials, but a few mated and produced hybrid offspring after longer exposure in small cages. Presumably, the very different vibrational communications in these species were not adequate to locate mates, but tactile contact forced by close confinement induced mating.

Communication by Chemicals

Chemical messengers are used for communication throughout the animal kingdom but are especially important for insects. The term **semiochemical** is applied to all chemicals produced by one organism that incite responses in another organism (Matthews and Matthews, 1978). Most semiochemicals of insects are produced by **exocrine glands** of the integument. The chemicals, either single compounds or mixtures, are usually active in minute quantities and are usually species-specific. Nonvolatile chemicals are limited to contact chemoreception. Volatile chemicals function in either short- or long-range communication, but the direction and distance may be limited by wind.

Semiochemicals that function intraspecifically are called **pheromones**. These are often blends of several compounds and, at least in social insects, may have more than one effect on the behavior and physiology of the recipient. Pheromones are the dominant mode of communication for insects. They may be grouped broadly into **primer** pheromones, which have a long-term effect on the physiology and development of the receiver that is mediated by hormones but may not have an immediate effect on behavior, and **releaser** pheromones, which have immediate, reversible effects on the receiver's behavior. Among insects, primer pheromones are well known in social species, where they

are involved in caste determination and the inhibition of reproduction by workers (see Chapter 7). In other insects, especially those that aggregate, primer pheromones function to bring adults into reproductive synchrony. For example, the presence of mature males of the locust *Schistocerca gregaria* (Acrididae, Orthoptera) increases the rate of sexual maturation of immature males. Experimental evidence indicates that the pheromone responsible for promoting maturation is transmitted by air and by contact to the young adults and affects their corpora allata (see Chapter 4).

Releaser pheromones are greatly varied in function and widespread taxonomically. The best known are the sex attractants, or **sex pheromones**, which bring the sexes together. In the most common situation, odors are emitted at a certain time of day or night by the female as a long-range signal to advertise her receptivity to mating. The odors are carried away from her by wind currents, forming an odor trail that becomes wider and less concentrated with increasing distance. A male downwind that perceives the odor with chemoreceptors on his antennae becomes active and flies against the direction of the wind, oriented by a positive anemotaxis. The flight is a zigzag pattern toward the female as the male turns back and forth to remain in the odor trail. In the vicinity of

the female, where the odor concentration is high, the male arrests his forward flight and searches for the female by other senses, especially sight. Courtship and copulation are then stimulated by close-range communication involving visual, tactile, or auditory signals, alone or together with pheromones. The long-range sex attractant released by the female may continue to excite the male, and the male, on close contact, may produce his own releaser pheromone or aphrodisiac that makes the female more receptive.

The foregoing sequence of sex attraction is not universal. In some insects, males produce long-range sex attractants; in some, the females produce aphrodisiacs; and in some, one sex produces pheromones or **aggregating scents** that attract both sexes to a common place (see the behavior of bark beetles in Box 6.3).

The active compounds in the sex pheromones of a number of insects have been isolated, identified, and synthesized. Sex pheromones are extremely useful in pest management (see Chapter 13).

Intraspecific pheromones also have nonsexual functions. In some insects, the aggregations of immatures or of females at oviposition sites are probably assembled and maintained by chemical releasers. Rapid dispersal from an assemblage may likewise be signaled by chemicals, in this case by

BOX 6.3 How Do Bark Beetles Use Pheromones?

A complex system of semiochemicals coordinates the mass attacks on living trees by the bark beetles *Ips*, *Dendroctonus*, and *Scolytus* (Curculionidae, Coleoptera) (Wood, 1982; Raffa et al., 1993). Coniferous trees resist attack by expelling or drowning ("pitching out") boring insects in sticky resin (Box Fig. 6.3). Bark beetles preferentially attack trees weakened by drought or disease and by simultaneously attacking in large numbers and introducing a fungus that interrupts the water-conducting system of the tree. "Pio-

neer" beetles (males of *Ips*; females of *Dendroctonus*) initiate attacks to feed. They excavate galleries in and under the bark of host trees, probably as a direct result of chemical feeding stimuli in the bark and/or phloem. During this initial boring activity, beetles emit an aggregation pheromone or a species-specific mixture of such pheromones by de novo biosynthesis (Seybold et al., 1995) and by conversion of host terpenes (Hendry et al., 1980) at some unknown site inside the insect and liberated with the feces. These

(Continued)

BOX 6.3 (Continued)



Box Figure 6.3 A bark beetle, *Dendroctonus brevicornis* (Scolytidae) trapped in a pitch tube on a pine tree.

Source: Photo courtesy of and with permission of Clyde Willson.

compounds may be derived from bacterial, fungal, and/or insect biosynthetic pathways. Some fungi are closely associated with the beetles as symbionts in the gut or gallery (see Chapter 11). The waste, or frass, from the borings is made attractive at a long range to other beetles. Thus, the pioneers attract more beetles of both sexes. By their boring activity, the aggregation pheromone concentration increases. In some cases, certain volatile compounds from the host tree itself also contribute to the overall attractiveness of the tree—for example, myrcene for *Dendroctonus brevicornis* and α -cubebene for *Scolytus multistriatus*. The total aggregation pheromone now consists of products from the beetle's gut and from the weakened tree.

Both sound and odor provide signals to locate mates. *Ips* females are attracted to frass marked with a male pheromone, and they stridulate before being permitted entry into the gallery occupied by a male. Frass marked pheromones produced by female *Dendroctonus pseudotsugae* attract males, and they also stridulate at the entrance to her gallery before entering. Birch and Wood (1975) discovered that *Ips pini* and *I. paraconfusus* both attack *Pinus jeffreyi* and *P. ponderosa* at the same season in the Sierra Nevada of California,

but not at the same individual trees. The volatile compounds produced by male *I. paraconfusus* inhibit the response of *I. pini* to its own pheromone, and vice versa. Thus, the first males to arrive at a tree effectively prevent colonization by the other species. The pheromone components simultaneously act as intraspecific attractants and as an allomone against a competitor.

Bark beetle aggregations attract a large number of other insects that feed on the beetles, or on other insects, or on the weakened host tree. One or more of the constituents of the aggregation pheromones specifically attract certain of the predators and parasitoids of bark beetles. In this situation, the pheromone components function simultaneously as kairomones (Borden, 1982; Wood, 1982; Raffa et al., 1993). Studies indicate that fungi inoculated into trees during host colonization may attract parasitoids, which generally arrive on the tree when the new bark beetle broods have developed to late-stage larvae (Stephen et al., 1993). Beetle aggregation on suitable trees, mate finding, and inhibiting competing beetle species thus rely on a complex of diverse chemical signals from the targeted trees, fungi carried in the **mycangia** of the beetles, and from both sexes of the beetles.

alarm pheromones. When disturbed, the aphid *Myzus persicae* (Aphididae, Hemiptera) discharges a secretion that disperses nearby aphids.

Social insects, especially ants, employ an array of chemical signals for aggregation, alarm, and other communications among colony members. Odor trails that recruit and guide foragers to food are known in certain ants, termites, and stingless bees (*Trigona*, Apidae, Hymenoptera). On returning to the nest after discovering a food source, a forager ant lays down a minute trace of a volatile, species-specific chemical, or a trail pheromone. Other ants are stimulated to follow the odor trail from the nest to the food and on their return add their own trail pheromone. A rich food source is soon visited by an increasing number of foragers. When the food becomes covered by ants or diminishes in size or quality, some ants return without contributing to the trail. Unless renewed by successful foragers, the trail declines in attractiveness because the odor is rapidly dissipated to a level below the ant's threshold of perception. Thus, the foragers readily shift in appropriate numbers to exploit new food sources.

Territorial marking with scents is widely recognized for mammals, and insects have some similar behaviors with respect to food sources. For example, fruit flies (Tephritidae, Diptera) that lay their eggs in fruits drag the ovipositor across the fruit surface to mark the fruit with a pheromone that inhibits other females from laying eggs in the same fruit. Wasps that parasitize other insects by inserting eggs into the host insect they attack avoid attacking hosts that have already been parasitized by the same species.

Semiochemicals involved in **interspecific** communication are called **allelochemicals** and are divided according to the effect on the sender or receiver as follows: (1) **allomones** are substances released by the sender that evoke a response in the receiver that is beneficial to the sender; (2) **kairomones** are substances that, when transmitted, benefit the receiver; and (3) **synomones** are substances that are mutually beneficial to the sender and receiver. Theoretically, the same allelochemical compound can be an allomone, kairomone, or synomone, depending on the context in which it is transmitted.

Allomones include the venoms injected by the sting of female aculeate Hymenoptera, defensive secretions of nasute termites and various beetles and true bugs, and toxic chemicals in the body, such as cardiac glycosides in the monarch butterfly, that discourage ingestion by vertebrate predators (see Chapter 12). Plants also produce allomones, such as the secondary metabolites, juvenile hormone mimics, and phytoecdysteroids that protect against plant-feeding insects.

Kairomones include odors or tastes that attract and stimulate attack, be it an insect victim or a plant host. Sex pheromones become kairomones when predators or parasitoids are attracted to feed on the mating insects. Secondary plant compounds can serve as kairomones for insects that tolerate the toxic compounds and attack the plant. When specific plant odors attract insect parasitoids or predators, they benefit both the natural enemies and the plants.

Odors of flowers that attract pollinating insects are synomones; both plant and insect benefit because the plant is cross-pollinated and the insect obtains food (see Chapter 9). Here, again, the same odors may be kairomones by attracting flower-feeding insects that destroy the flowers and seeds.

Learning and Communication in Honey Bees

The ancient Greek philosopher Aristotle noticed that a bee forages on one species of flower on each foraging trip and is attended by other bees on her return to the hive. These simple observations describe aspects of what has proved to be a remarkable ability for learning and communication in the honey bee *Apis mellifera* (Apidae, Hymenoptera). Much of our knowledge has resulted from the investigations of the late Professor Karl von Frisch in Germany. For his efforts, he shared a 1973 Nobel Prize in Physiology (see von Frisch, 1974).

After about 3 weeks spent as an adult in the hive, a worker honey bee begins the last phase of its life foraging for pollen and nectar in flowers. In an extensive series of experiments that began prior to 1914, von Frisch demonstrated that bees could be trained to seek a sugar solution and to associate specific stimuli with this food source.

The following experiment for color discrimination is typical. A table was placed near a hive. A blue square of cardboard was placed flat on the table and surrounded by gray cards of different shades. On each square was placed a glass dish. The dish on the blue card was then filled with sugar solution. After a few hours during which the bees foraged on the food, the cards and dishes were removed and replaced by clean cards and empty dishes arranged in a different pattern. The bees returned and landed on the blue card, demonstrating that they discriminated the blue color from all shades of gray. This indicated that they have true color vision and that they had learned to associate the color with food.

In similar experiments, von Frisch (1971) trained bees to one or a combination of odors, flavors, geometric figures, and colors within their range of discrimination. He also trained bees to visit a feeding station at a specific time. Some bees were even trained to seek food at three to five separate times of day, thus demonstrating a time sense in bees.

The most famous of von Frisch's discoveries was the complex signaling system that communicates the distance and direction to food sources up to about 14 km from the hive. On returning to the hive from a rich food source 100 m or more away, the worker inside the dark hive moves excitedly in a **waggle dance** on the vertical comb (Fig. 6.9c). After performing the dance, she may move to a different area on the comb and repeat the dance. Although it is dark, some bees follow the dance with their antennae, and they detect the flower odor on the waxy surface of the forager's body. The forager may also offer some of the nectar she has collected and carries in her crop. A rich concentration of sugar is highly attractive and stimulating to other bees. In experiments with feeding stations located at various distances and directions from the hive, von Frisch demonstrated that bees recruited by the dancer search in a certain direction and at a certain distance for food of the same odor and nectar flavor as that collected by the dancer. After successful foraging trips, these newly recruited bees begin to dance too. More bees are recruited, and the number of foragers rapidly increases. When

the food supply diminishes, the frequency of dancing declines.

During part of the waggle dance, the bee makes a straight run, vigorously wiggling her abdomen and emitting sound pulses at a rate of about 32 per second. This is called the waggle run of the waggle dance. Then, she circles back to the starting point and repeats a waggle run of the same duration. The time spent during each run and the total number of pulses is directly proportional to the distance traveled to the food source. For a flight of 100 m, the time of a single waggle run is about 0.25 second, and for a 1,200-m flight, the time is 2 seconds. Thus, the waggle runs take longer with increasing distance, and fewer runs are completed within a given period.

The direction the bee moves during the waggle run on the vertical comb has a consistent orientation with respect to gravity (Fig. 6.9d-g). This is related to the direction from the hive to the food with respect to the compass direction of the sun when it is more than about 2° from the zenith position. Recall that positive phototaxis and negative geotaxis are commonly linked. For example, if the forager flew toward the compass direction of the sun en route to the food, her waggle run is oriented vertically up the comb, and her head points up during the run. If she flew at an angle to the right of the sun, the run is oriented at the same angle to the right of vertical.

As the food site is moved closer to the hive at distances of about 100 m or less, the dance shifts from the waggle dance to a transition form (Fig. 6.9b) and then to the **round dance** (Fig. 6.9a). The waggle runs become less conspicuous, but as the bee moves on the comb in a direction appropriate for the direction of the food, she still emits sounds (Kirchner et al., 1988). It is likely that bees following a round dance obtain information about the direction of food quite close to the hive. However, the duration of the sound is too variable to indicate different distances to food less than 100 m from the hive.

The dance is important in initially recruiting new foragers to a new, distant food source. By following the dance, the recruit learns the distance, direction, flower odor on the dancer's body, and

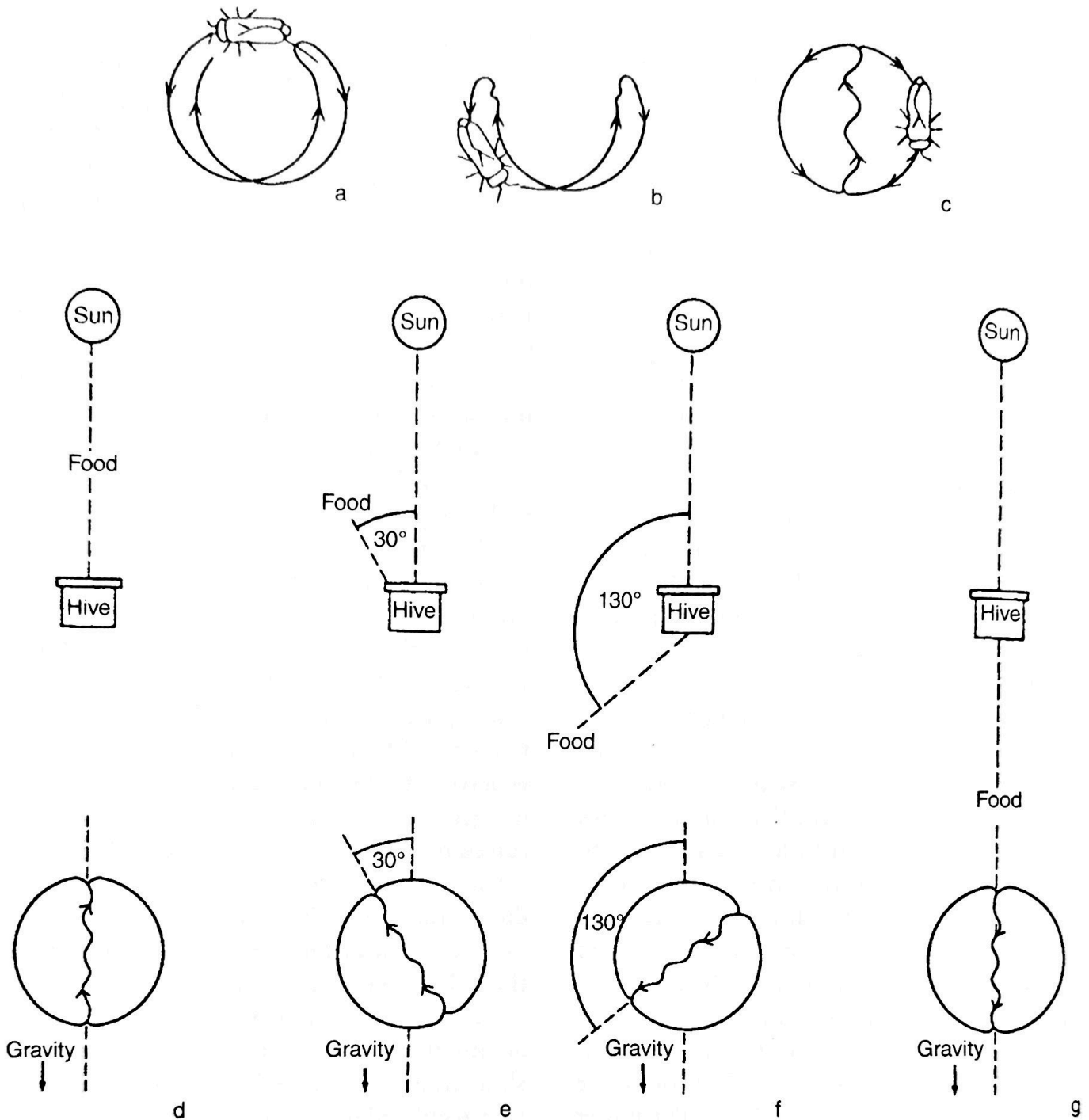


Figure 6.9 Dance communication of the honey bee: **a**, round dance; **b**, transition between round and wag-tail dance; **c**, wag-tail dance; **d–g**, diagrams of wag-tail run (on vertical surface of comb in dark hive) in relation to the direction of food from the hive and the compass direction of the sun.

Source: Barbara Boole Daly.

nectar flavor from samples given by the dancer, but not the color or shape of the flower or the landmarks and obstacles en route. Once they have made the trip, foragers are able to return to the food by their memory of landmarks, obstacles, and various odors encountered along the way; distance and the compass direction with reference to

the sun's position; and color pattern and shape of the flower. For orientation to the sun, they utilize an astrotaxis and compensate for the sun's movement with an internal clock. Cells connected to the nervous system in the abdomen contain magnetite and are believed to function in magnetic orientation.

BOX 6.4 Challenges to the Conventional Explanations of Honey Bee Dance Communication

There were counterclaims that behaviors other than bee dances better explained how bees communicated food sources. Wenner and associates (1971, 1990) criticized the design of previous experiments on bee dance communication and argued that their own experiments indicated that odor (specific food odor, Nasonoff gland scent, and overall odor of the food area) was the main stimulus both for recruitment and for the finding of food at some distance from the hive. These criticisms stimulated others to look more closely at the behavior of the dancers and recruits.

By ingenious experiments, Gould (1975) demonstrated that distance and directional information is indeed passed from the dancer to other bees. He was able to have a forager send recruits to a food site that the forager had never visited and, consequently, could not have the odor of the food site on her body. How did Gould do it? When bees dance on the comb in a light beam of sufficient brightness, they will orient to the light instead of to gravity. The bees that follow the dancer also orient to the light and correctly interpret the direction to the food source. If, however, the ocelli of the dancer are covered by paint, she becomes much less sensitive to light, and a much brighter light is required to stimulate her to reorient to it. In Gould's experiments, the light was adjusted not to affect the ocelli-covered dancer but to cause reorientation of the recruits to the light. The wag-tail run of her dance vertically upward

indicates a food station directly toward the sun. If the light beam is directed from the left at 90° from the vertical, or horizontally, then the recruits with normal ocelli will orient to the light and interpret the direction of the food station to be 90° to the right of the sun. If they rely only on her odor, the recruits should appear at the dancer's station, but if they rely on their interpretation of her dance, they should be "misdirected" to other stations situated at 90° to the right of the sun. Gould found that normal recruits were "misdirected" according to the dance information of an ocelli-covered dancer. The light could be placed at various angles, and the recruits appeared at the predicted stations with an error of about 11.9° , or 31 m at 150 m, and 4.2° , or 29 m at 400 m. The reasons why the more distant stations are indicated with less error are unknown.

Kirchner, Michelsen, and their associates (Kirchner and Towne, 1994) carried the analysis further with the construction of a computer-controlled, mechanical model bee that danced with waggle runs, vibrated, and dispensed sucrose to recruits. The researchers were able to show that both the waggle run and the pulsed vibrations of the dancer's wings were required for successfully directing a recruit to the food site. Honey bees were thought to be deaf to airborne sounds, but they demonstrated that Johnston's organ in the antennal pedicel was responsive to the movement of air particles in the vicinity of the dancer's wings.

On returning to the hive, foragers unload the liquid carried in their crop to nest bees. The rate at which the nest bees accept the liquid regulates how quickly the forager can depart for another trip. When the hive is overheated and water is used for evaporative cooling, the nest bees readily take water or dilute nectar rather than concentrated nectar from the returning foragers. This stimulates the foragers to collect water or dilute nectar on their next trip rather than concentrated nectar.

When the hive temperature is normal, nest bees favor foragers with concentrated nectar over those with dilute nectar. At times, the amount of incoming nectar may exceed the capacity of the nest bees. When delayed in unloading concentrated nectar, a forager performs a **tremble dance**, a distinctive shaking motion, plus a vibration against the comb called a stop signal. This signals to nest bees to increase the reception of nectar and inhibits other foragers from dancing (Nieh, 1993; Seeley, 1992).

Rhythmic Activity and Sunlight

Sunlight has a key role in the orientation of insects in their environment and in the timing of events in their life cycles. Momentary responses to light, perception of images, color vision, and behavioral reaction to light and polarized light were discussed earlier in this chapter. Of interest here is the influence of the natural alternation of light and darkness in the rhythmic activity of insects.

The regular tilting of the earth during its annual orbit of the sun causes sunlight intensity and duration per day to gradually increase or decrease from day to day depending on the season. Many insects in polar or temperate zones respond to decreasing day lengths in late summer to time many important life history actions, such as diapause in a particular developmental stage, wing formation in adults, or the appearance of males in aphids that normally only females for most of the spring and summer months. In equatorial regions, day lengths change very little, but insects still use this to time important development and reproductive events to a specific time of year. In some cases,

rainfall or plant phenology affect the timing of such events.

The daily activities of insects usually take place during specific periods of the 24-hour cycle. Such synchronization, for example, permits the sexes to find each other, limits the search for food to periods of peak abundance, and allows insects to avoid enemies or to take advantage of a favorably high humidity for ecdysis or oviposition. Insects usually spend a part of each day inactive. For example, at night some bees and wasps (Fig. 6.10) clasp leaves or the stems of plants with their mandibles or crawl into flowers and seem to "sleep." During their regular rest period at night, honey bees exhibit behavioral and physiological changes comparable to sleep in birds and mammals.

An activity during the day is termed **diurnal**; at dawn or dusk, **crepuscular**; at night, **nocturnal**; and at dawn only, **matinal**. These terms should be used in reference to specific activities or events rather than loosely to describe overall activity: the emergence of adult *Drosophila pseudoobscura* (Drosophilidae, Diptera) from pupae is **matinal**.



Figure 6.10 Gripping with their mandibles, these male eucerine bees (Anthophoridae) in Peru cling to the underside of a leaf. They may remain together during midday heat or all night. Such sleeping aggregations of male wasps and bees often assemble at dusk.

Source: Photo courtesy of and with permission of Clyde Willson.

attraction to food baits, mating, and oviposition are crepuscular; and pupation is mainly crepuscular or nocturnal.

One might interpret a daily rhythm in activity as simply a response to a certain level of light or other physical factor that occurs regularly each day. In other words, the insect's activity is a response to **exogenous** factors. This is true for oviposition behavior in the walkingstick *Carausius morosus* (Phasmatidae, Phasmatodea). Most eggs are laid at or near dusk, or at the time the lights are switched off in laboratory experiments. After *C. morosus* has been kept only a day in constant light or darkness, the laying of eggs no longer occurs at 24-hour intervals but is distributed over the 24-hour period. A direct response to an environmental signal may also be delayed a specific interval as if timed by a "sand hourglass."

Circadian Rhythms

Activity in insects and other organisms that occur regularly about the same time each 24 hours and have a physiological basis are called **circadian rhythms** (from the Latin *circa diem* for "approximately daily"). Because of such circadian rhythms, humans experience "jet lag" in their patterns of sleepiness after long flights. In a light/dark cycle of 12:12 hours, mature male crickets, *Teleogryllus commodus* (Gryllidae, Orthoptera), begin to stridulate their mating song 1 to 2 hours before the onset of darkness. Singing continues during darkness and is terminated 2 to 3 hours before the lights switch on. When these crickets are placed in constant darkness, singing begins at intervals of about 23.5 hours and lasts the normal period. In constant light, singing occurs at intervals of about 25.3 hours (Fig. 6.11, days 1–12). A return to the 12:12-hour cycle

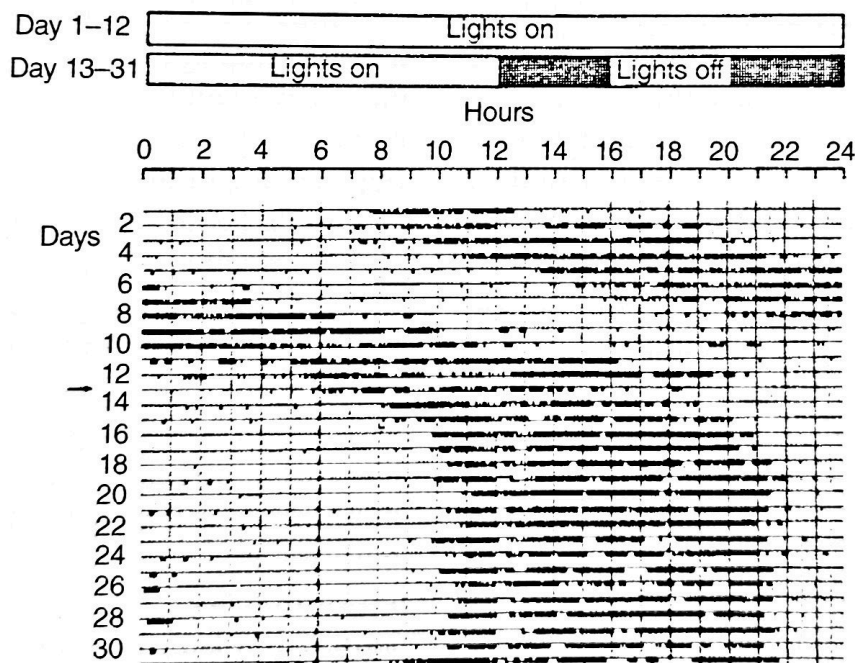


Figure 6.11 Circadian rhythm of stridulation in a male cricket, *Teleogryllus commodus* (Gryllidae). Marks in rows are tic marks from automatic recorder that is actuated by sound of stridulation. Each row records stridulation during 1 day. When the record began, the cricket had been in constant light and the stridulation rhythm was free-running. On day 13 the lights were switched off at 12:00 and remained off for 12 hours. Thereafter, the cricket was exposed to 12 hours of light and 12 hours of dark. Note that stridulation is temporarily interrupted when the lights are switched off at 12:00 each day.
Source: Authors (data courtesy of Werner Loher).

of light/dark results in a return to the 24-hour rhythm, beginning 2 hours before darkness (Fig. 6.11, days 13–31).

When a given activity or event can be demonstrated experimentally to recur at about 24-hour intervals after all environmental signals have been excluded, the circadian time interval under constant conditions is nearly always slightly more or less than 24 hours, resulting in a progressive drift each day in the time of initiation (Fig. 6.11, days 1–12). The presence of the drift is evidence that other possible signals with 24-hour periodicities are not influencing the insect. Cosmic radiation and geomagnetic forces, for example, fluctuate on an exact 24-hour cycle with the earth's rotation. Individual cells exhibit rhythmic changes in nuclear volume and protein synthesis. Specific organs function cyclically; for example, endocrine glands synthesize hormones cyclically. Susceptibility to insecticide poisoning is rhythmic, as is general oxygen consumption. Clearly, rhythms are evident in a variety of physiological processes.

The physiological basis for circadian rhythms has been a subject of intense and prolonged study. The fruit fly *Drosophila melanogaster* is an important model system for circadian rhythm studies. Mutants of *D. melanogaster* that have drastically altered circadian rhythms led to the identification of numerous genes (*per* (period), *tim* (timeless), *cyc* (cycle), *clk* (clock)) that influence rhythmicity. The rhythm itself, however, is not determined by the metabolic rate of the process. Unlike nearly all physiological processes, circadian rhythms are largely independent of temperature within normal limits of tolerance.

The underlying mechanism is conceptualized as a "biological clock" or an "oscillator." The clocks of circadian rhythms are reset daily or entrained by brief environmental signals. The most common cues are dawn or dusk, when light intensity varies rapidly. The location of the photoreceptors varies with the species. The homology of proteins identified as critical molecules for circadian rhythms in *Drosophila* (e.g., "period" and "timeless") with proteins found in mammals suggests that the

underlying mechanisms evolved early and should be widely applicable to many animals.

An entrained circadian rhythm is called a **diel** rhythm. It is possible that more than one clock controls the different rhythms of cells, development, general physiology, and behavior. The clock or clocks serve to coordinate life processes within the insect while at the same time scheduling the insect's activity in a changing environment. Locomotor activity, feeding, mating, and the insect's varying responsiveness to stimuli are programmed to take place at opportune times in the daily cycle.

A different type of diel rhythm involves populations and "once-in-a-lifetime" events. If *Drosophila melanogaster* (Drosophilidae, Diptera) is reared in constant darkness, the adults emerge from pupae at any time. When the pupae are given as little as 1 minute of exposure to light, emergence becomes synchronized to occur during one period each 24 hours. The period of emergence has been compared to a developmental "gate" that opens or closes. If the open gate is missed by an individual, then its emergence is delayed 24 hours. Gated phenomena are known for egg hatching in the pink bollworm *Pectinophora gossypiella* (Gelechiidae, Lepidoptera), pupation of the mosquito *Aedes taeniorhynchus* (Culicidae, Diptera), and emergence of the intertidal midge *Clunio marinus* (Chironomidae, Diptera) in Europe.

The genetic basis of circadian rhythms is illustrated by the mating behavior of moths. Most moths have specific periods for mating activity, but certain closely related species have identical sex pheromones. Consequently, the males can be attracted to females of different species. Some of these species are allopatric (do not occur in the same place) or mate at different seasons. In the sympatric species (occur in the same place), mating is at different times of day under circadian control, thus preventing cross-attraction. Another is the timing of mosquito feeding, which may be timed to when their animal or human hosts are easiest to locate and feed upon.

SELECTED REFERENCES**General Structure and Function of the Nervous System**

Chapman, 1982, 1991; Homberg et al., 1989 (deutocerebrum); Kerkut and Gilbert, 1985 (vols. 5 and 6); Nation, 2008.

Sense Organs

Gilbert, 1994 (stemmata); Land and Nilsson, 2002 (vision); Mitchell, 2003; Nation, 2008; Payne et al., 1989 (olfaction); Roelofs, 1984 (electroantennograms); Zacharuk and Shields, 1991 (sensilla).

Behavior

Atkins, 1980 (general text); Kerkut and Gilbert, 1985 (vol. 9); Matthews and Matthews, 1978 (general text); Papaj and Lewis, 1993 (learning); Wehner, 1984 (astronavigation).

Communication

Aldrich, 1988 (Heteroptera semiochemicals); Blum, 1987 (exocrine compounds); Byers, 1991 (locust maturation); Claridge, 1985a,b (acoustic signals of Auchenorrhyncha); David and Birch, 1989 (pheromones and behavior); Drosopoulos and Claridge, 2006 (sound communication); Lewis, 1984 (general); Lloyd, 1971, 1983, 1984 (bioluminescence and Lampyridae); Pickett et al., 1992 (aphid semiochemicals); Schneider, 1992 (pheromones of Lepidoptera); Stowe et al., 1995 (kairomones used by predators and parasitoids).

Host Selection by Bark Beetles

Birch and Wood, 1975; Borden, 1984; Schowalter and Filip, 1993; Seybold et al., 1995; Wood, 1982.

Sensory Physiology, Behavior, and Communication

Frisch, 1967 (classic reference), 1971, 1974; Gould, 1975; Hsu and Li, 1994; Kaiser and Steiner-Kaiser,

1987 (sleep); Kirchner, 1993; Kirchner and Towne, 1994; Kirchner et al., 1988 (round dance); Landgraf et al., 2008 (bee robots), 2011; Nieh, 1993; Purcell and Loher, 1976; Seeley, 1992; Wenner, 1971, 1990 (role of dance questioned).

Circadian Rhythms

Lavialle and Dumortier, 1975 (*Carausius* behavior); Loher, 1972 (*Teleogryllus* behavior).

See Also

Discussions of behavior elsewhere: reproductive and ecdysis behavior (Chapter 4); cold hardiness (Chapter 5); social behavior (Chapter 7); feeding behavior by phytophagous insects (Chapter 10); behavior of predators and parasitoids (Chapter 11); and cryptic and aposematic behavior (Chapter 12).

Web Search Terms (special interest in parentheses)

Nerve cell anatomy (images)
 Insect brain
 Insect eyes (images)
 Insect ocelli (images)
 Insect apposition eye
 Insect supposition eye
 Bee vision
 Master hunter dragonflies
 Dragonfly
 Insect proprioceptors
 Insect tympanum (images)
 Cicada tymbal
 Insect chemoreceptors
 Insect pheromones
 Insect communication (videos)
 Fireflies/lightning bugs communication
 Insect pheromones
 Bee dance robot (videos)
 Circadian rhythms