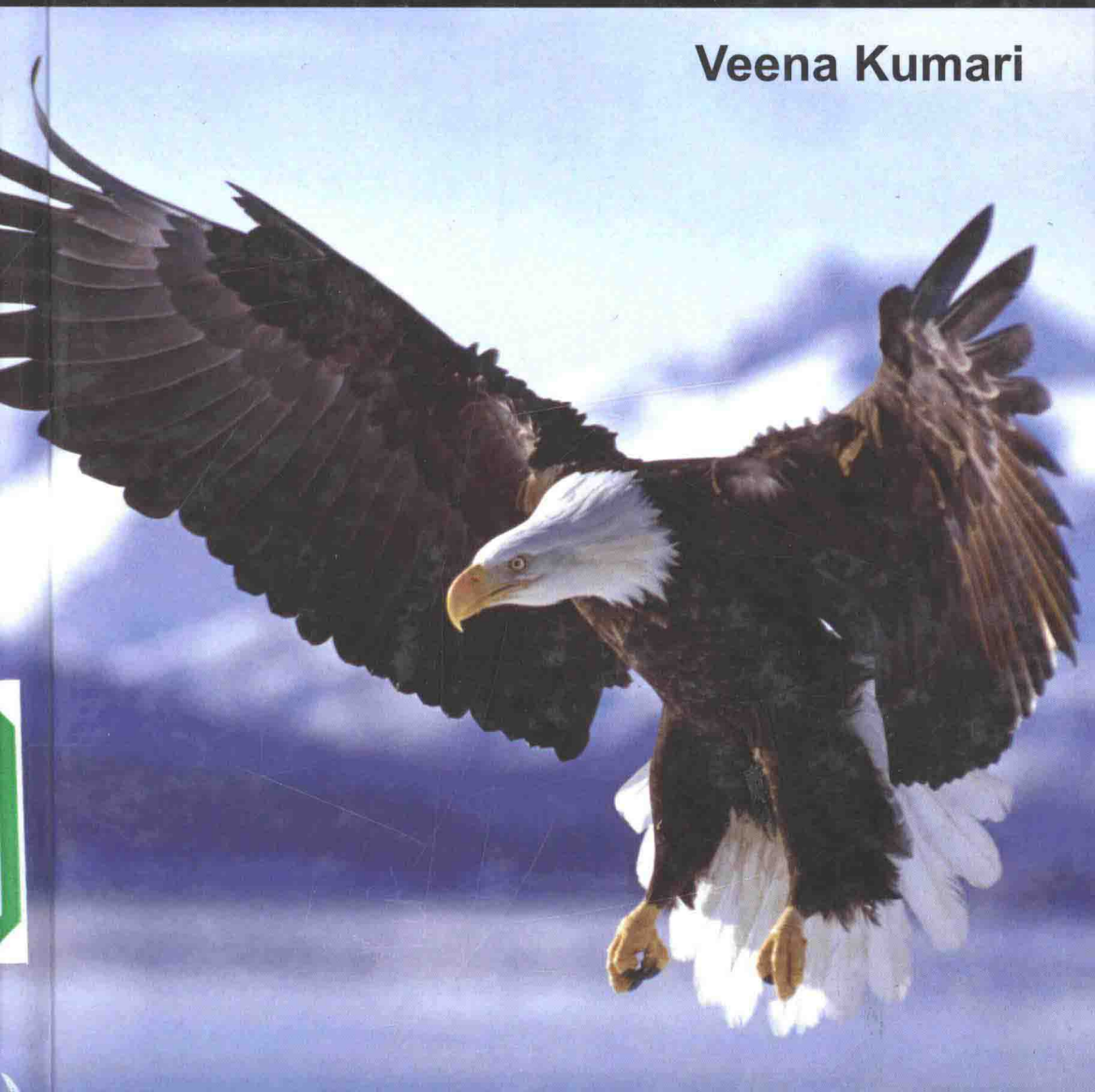
CONCEPTS IN

Animal Physiology

Veena Kumari



CONCEPTS IN ANIMAL PHYSIOLOGY

Dr. Veena Kumari

ANMOL PUBLICATIONS PVT. LTD.
NEW DELHI-110 002 (INDIA)

ANMOL PUBLICATIONS PVT. LTD.
Regd. Office: 4360/4, Ansari Road, Daryaganj,
New Delhi-110002 (India)
Tel.: 23278000, 23261597, 23286875, 23255577
Fax: 91-11-23280289
Email: anmolpub@gmail.com
Visit us at: www.anmolpublications.com

Branch Office: No. 1015, Ist Main Road, BSK IIIrd Stage
IIIrd Phase, IIIrd Block, Bengaluru-560 085 (India)
Tel.: 080-41723429 • Fax: 080-26723604
Email: anmolpublicationsbangalore@gmail.com

Concepts in Animal Physiology

First Edition, 2013

ISBN: 978-81-261-5361-9

PRINTED IN INDIA

CONCEPTS IN ANIMAL PHYSIOLOGY

Preface

Physiology is the science of the *function* of living systems. This includes how organisms, organ systems, organs, cells, and biomolecules carry out the chemical or physical functions that exist in a living system. The ABO blood group system is the most important blood type system (or blood group system) in human blood transfusion. The associated anti-A antibodies and anti-B antibodies are usually IgM antibodies, which are usually produced in the first years of life by sensitization to environmental substances such as food, bacteria, and viruses. ABO blood types are also present in some other animals, for example apes such as chimpanzees, bonobos, andgorillas. The gene encodes a monomeric single-pass type I membrane glycoprotein found on erythrocytes, leukocytes, glomerular podocytes, and splenic follicular dendritic cells. The Knops blood group system is a system of antigens located on this protein. The protein mediates cellular binding to particles and immune complexes that have activated complement. Decreases in expression of this protein and/or mutations in its gene have been associated with gallbladder carcinomas, mesangiocapillary glomerulonephritis, systemic lupus erythematosus and sarcoidosis. Mutations in this gene have also been associated with a reduction in *Plasmodium falciparum* rosetting, conferring protection against severe malaria. Alternate allele-specific splice variants, encoding different isoforms, have been characterized. Additional allele specific isoforms, including a secreted form, have been described but have not been fully characterized.

In primates, CR1 serves as the main system for processing and clearance of complement opsonized immune complexes. It has been shown that CR1 can act as a negative regulator of the complement cascade, mediate immune adherence and phagocytosis and inhibit both the classic and alternative pathways.

The number of CR1 molecules decreases with aging of erythrocytes in normal individuals and is also decreased in pathological conditions such as systemic lupus erythematosus (SLE), HIV infection, some haemolytic anaemias and other conditions featuringimmune complexes. In mice, CR1 is an alternatively spliced variant of the complement receptor 2 (CR2) gene.

Certain alleles of this gene have been statistically associated with an increased risk of developing late-onset Alzheimer's Disease. DAF is used as a receptor by some coxsackieviruses and other enteroviruses. Recombinant soluble DAF-Fc has been tested in mice as an anti-enterovirus therapy for heart damage; however, the human enterovirus that was tested binds much more strongly to human DAF than tomouse or rat DAF. Echoviruses and coxsackie B viruses that use human decay-accelerating factor (DAF) as a receptor do not bind the rodent analogues of DAF. and DAF-Fc has yet to be tested in humans.

The book helps the student in overall self assessment and prompts him to practice and review the gap areas in his learning process.

—Editor

Contents

1

Physiology of Animals

Central Nervous System

Unlike vertebrates, in which a single, relatively large brain is encased in a skull, central nervous systems of insects are composed of variously distributed ganglia. The major association centre is called the brain. The other important ganglia are subesophageal ganglion, frontal ganglion, up to three thoracic ganglia and up to eight abdominal ganglia. Three major regions of brains are recognized: protocerebrum, deutocerebrum and tritocerebrum. The protocerebrum is the most complex part of insect brains; it has two lobes, and is continuous with the optic lobes. The deutocerebrum contains antennal lobes, from which project both afferent and efferent neurons.

The tritocerebrum is a small, bilobed ganglion. Major nerve tracts connect the tritocerebrum to other ganglia. The tritocerebrum is linked to subesophageal ganglion by circumesophageal connectives and to the frontal ganglion by frontal commisure. This part of the brain has efferent and afferent connectives to certain mouthparts. The subesophageal ganglion is the first ganglion in the ventral nerve cord. This ganglion has motor and sensory connections to salivary glands, mouthparts, and neck. Most insects have three thoracic ganglia, each with connectives to muscles and sensilla. Abdominal ganglia have connections to muscles, though usually fewer than thoracic ganglia. Numbers of ganglia vary among groups of insects. The thoracic and abdominal ganglia are fused into a single compound ganglion in houseflies. This is an example of extreme fusion. The least fusion is shown in a thysanuran. The last abdominal ganglion is always a

compound structure, derived from the ganglia of the last four segments. The structure of a ganglion. The central nervous system is completely invested in what is called the nerve sheath, the most outer part of which is a non-cellular neural lamella and the inner part of which is called perineurium, composed of a single layer of cells. The perineurium is thought to produce and secrete the mucoprotein and mucopoly-*saccharide neural lamella. The perineurium serves as a blood-brain barrier, and as such it regulates the chemical environment of nerve cells and transports nutrients and other materials between hemolymph and nerve cells.

The centres of ganglia are made up of axons and fibres of afferent, efferent and interneurones. These centres specifically do not contain cell bodies, and they are called neuropile. Within neuropiles, some axons and fibres are orientated such that they form fibre tracts. Cell bodies, or perikarya, are found around the periphery of ganglia. The inter ganglionic connectives are similarly arranged, with neural lamella and perineurium forming a sheath around the tracts and giant fibres running along in the middle. Within neuropiles and connectives, each neuron is surrounded by glial cells which form a protective barrier around nerve cells. Glial cells can have a number of arrangements, and are often folded around axons, in which case they are called mesaxon. Glial cells probably insulate nerve processes from each other to reduce uncontrolled electrical noise or "cross-talk" from one nerve to another. Glial folds do not occur around synapses.

Transmission

The important features include presynaptic vesicles, many filled with transmitter substance, usually acetylcholine in nerve-nerve synapses, and L-glutamate in nerve-muscle junctions. Gamma-aminobutyric acid (GABA) is the usual transmitter chemical in inhibitory junctions. Other features are presynaptic membrane, and postsynaptic membranes. Finally two proteins are important, acetylcholine esterase and acetylcholine receptor sites. This drawing shows the synaptic cleft, which separates pre- and postsynaptic membranes by 200 to 500 angstrom units.

Contemporary wisdom holds that depolarization of presynaptic membrane leads to fusion of presynaptic vesicles with membrane, and release of acetylcholine by a process of exocytosis. Vesicles contain on the order of a few thousand

molecules of transmitter; each depolarization causes about 100 or so vesicles fuse with presynaptic membranes and release their molecules. Acetylcholine molecules move randomly as in free solution within synaptic clefts, and it is about equally possible for any given molecule to meet acetylcholine esterase or acetylcholine receptor sites. The enzyme hydrolyzes acetylcholine to acetate and choline. The acetylcholine molecules that bind to their receptor sites eventually cause a depolarization of the postsynaptic membrane called excitatory postsynaptic potential (EPSP), which is transmitted to the axon. Axon depolarizations and continuation of the nerve impulse follow.

Insect Vision

Vision is the perception of light. Insects perceive light through three classes of sensory organs. Most adult insects have a single pair of compound eyes. Larvae of hemimetabolous insects and most adults have usually three simple eyes called ocelli. These are typically located on the dorsum of the head capsule, and they are sometimes called dorsal ocelli. Larvae of holometabolous insects do not have compound eyes. These insects perceive forms, to a limited extent through stemmata located on either side of the head.

Compound Eyes

The compound eyes are prominent features of adult insects. The eyes occupy a fairly large portion of the surface of insect heads, and they facilitate a rather wide field of vision. Compounds eyes are not present in all insects. They are reduced or absent in parasitic forms, many soil insects, and in some species that live in very dark places, such as caves. The basic unit of compound eyes is the ommatidium (singular of ommatidia). Ommatidia vary in size and number among insect groups. At one extreme, dragonflies have thousands of ommatidia in each compound eye; many insects have far fewer, and at the other extreme, the workers of the ant species *Pomera punctatissima* have only one ommatidium in each eye.

The sizes of ommatidia vary from about 5 to 40 microns in diameter. Sizes vary among species and even within a single compound eye. In some dragonflies, for example, the dorsal units are considerably larger than the ventral ones.

The structure of a single ommatidium. The ommatidium rests on a basement membrane. The height of the eye comes from the long retinula cells and secondary pigment cells. The corneagen cells (sometimes called primary pigment cells) rests atop the long retinula and secondary pigment cells. The crystalline cone lies within the corneagen cells. The surface of the ommatidium is covered with the corneal lens. The corneal lens is a specialized part of insect cuticle. It is secreted by the corneagen cells, which are specialized epidermal cells. The crystalline cone is a clear, intracellular structure synthesized within Sempter cells. The primary pigment cells surround the Sempter cells. Not all compounds eyes feature a crystalline cone; those that do are called eucone eyes. The corneal lens and crystalline cone make up the optical part of ommatidia. The sensory elements are just under the optical apparatus. The retinula cells are long neurons. Part of each retinula cell is a specialized area known as a rhabdomere. A nerve axon from each retinula cell projects through the basement membrane into the optic nerve. Ommatidia are functionally isolated because the retinula cells are surrounded by the secondary pigment cells.

Compound eyes are commonly categorized as either apposition eyes or superposition eyes. There is no separation between the corneal layer and the photoreceptors in apposition eyes. There is a clear space between the two units in superpositions eyes. Some authors use the expression "clear zone eyes" for the superposition eyes. Superposition eyes are generally found in crepuscular and nocturnal insects, while apposition eyes occur in diurnal insects. The crystalline cone couples the lens and photoreceptors in apposition eyes. Some higher Diptera have pseudocone eyes.

Crystalline cones do not occur in pseudocone eyes, and optical coupling is by means of a gelatinous substance that is contained in a two-celled structure. Still another arrangement is found in some apposition eyes that lack solid cones or gelatinous pseudocones. In these acone eyes four flat transparent cells are found in place of the cones. In superposition eyes the space between the corneal lines and the photoreceptors is traversed by crystalline tracts. These are thought to act as wave-guides that direct light to the photoreceptors. Tracheal tapeta are known from several Lepidoptera. Small tracheae run parallel with the

longer cells of the ommatidia. It has been suggested that these structures function as interference reflector filters.

Light sensitivity of insect eyes varies according to the state of light- adaptation or dark-adaptation of the eyes. In bright light, the eye is less sensitive to light, and the eye is regarded as light-adapted. Maximum sensitivity occurs in darker conditions, when the eye is fully dark-adapted. Some insect eyes can change light sensitivity by about three orders of magnitude within a few minutes of changing light conditions. There are a number of mechanisms of adaptation to light and dark conditions. One mechanism relates to the biochemistry of vision. The visual pigment is broken down by interaction with light. In daylight the breakdown rate can equal or exceed the replacement rate. This leads to decreased light sensitivity, and partly explains light adaptation. In the dark, the visual pigment accumulates, and the insect becomes dark adapted.

A second mechanism of adaptation is the movement of screening pigments. Screening pigments are located in the retinula cells. In light-adapted eyes granules of screening pigments surround the rhabdom. These pigments absorb light, and they have the effect of optically isolating individual ommatidia. The endoplasmic reticulum of dark-adapted eyes forms large, clear vesicles. This forms a clear space around the rhabdom, so that a greater amount of light falls upon the rhabdom. Vision involves the transduction of light energy into a bioelectric signal within the nervous system. The first events in this process take place in the retinula cells. The fine structure of rhabdomeres consists of thousands of closely packed tubules. These tubules are about 500 A in diameter and one micron long. They are aligned at right angles to the long axis of the rhabdom. The visual pigments occur mainly in these rhabdomeric microvilli. It has been suggested that the small diameter of each microvillus inhibits free rotation of visual pigments. This specific orientation may be the molecular basis of insects' sensitivity to polarized light.

Photobiological processes occur in a narrow band of the electromagnetic spectrum between 300 and 700 nm. Photons in this region of the spectrum have enough energy for photochemical interactions, but not enough energy to disrupt macromolecules. Visual pigments initiate vision by absorbing light in this region.

These pigments are a class of membrane bound proteins known as opsins that are conjugated with a chromophore. Visual pigments whose chromophore is retinal are called rhodopsins. The visual pigments of all invertebrates, including insects, crustaceans and squids, are all rhodopsins. There are a number of geometric isomers of retinal. The 11-cis isomer is the chromophore of native rhodopsin. Free retinal absorbs light strongly at about 380 nm. When 11-cis-retinal is linked to opsin to form rhodopsin, the main absorption peak is shifted. The maximum absorption values of different rhodopsins range from about 345 nm (ultraviolet) to as high as 610 nm (red).

The absorbing properties of any given rhodopsin is related to the disposition of charged opsin groups around the chromophore. These interactions between the side-groups of the amino acids within the opsins and the chromophores are thought to modify the p electron orbital of the chromophores, and thereby modify the absorbance spectra of rhodopsins. When the chromophore of rhodopsin absorbs a photon, the chromophore undergoes an isomerization from the 11-cis to the all-trans configuration.

The rhodopsins of insects and other invertebrates differ from vertebrate rhodopsins on the point of the chemical events that follow the isomerization step. Vertebrate rhodopsins go through a series of spectrally distinct intermediates. The process is called bleaching because the absorption shifts from visible to ultraviolet wavelengths, which we can not see. The vertebrate process can lead to hydrolysis of the opsin and chromophore. Invertebrate rhodopsins generally do not bleach. Light transforms the rhodopsins to a stable intermediate. The isomerized 11-cis chromophore stays in place in the microvilli. The stable intermediates have spectral properties similar to metarhodopsin I of vertebrates, which has earned them the term metarhodopsins.

The mechanism of transducing light-induced chemical changes in rhodopsins into electrical signals remains the major unresolved issue in understanding the physiology of light receptors. Several milliseconds are required before the absorption of light can be recorded as electrical activity in the receptor cell membrane. Certainly, the phototransduction event occurs during the transition from rhodopsin to metarhodopsin. We can not say much more

about the detailed mechanisms of transducing light into bioelectrical signals. A key requirement in the chemistry of vision is that metarhodopsin, or the bleached pigment of vertebrates, must be reconverted to rhodopsins. In the eyes of vertebrates, this regeneration is the product of a complex biochemical pathway. The pathway involves isomerization back to the 11-cis configuration and assembly with the opsins. Again, invertebrates differ from vertebrates on this aspect of photochemistry. Light is absorbed by rhodopsin and metarhodopsin in invertebrates.

Absorption of light transforms metarhodopsin back to rhodopsin. The pigments exist in two stable conformations, and light causes them to switch back and fro from one state to the other. This regeneration is essential because conformational changes in rhodopsin, but not in metarhopsin, leads to phototransduction.

Experiments on insect behaviour indicate that many insect species can distinguish colours. Colour vision depends on the ability to discriminate between light of different wavelengths. Such discrimination is possible because compound eyes have photopigments with differing spectral properties. Many insects have two rhodopsins, one with maximum absorption in ultraviolet wavelengths and one with maximum absorption in green wavelengths. Some species have a third pigment that absorbs maximally in the blue region. A few Lepidoptera have four visual pigments.

Dorsal ocelli

Dorsal ocelli occur in larvae of hemimetabolous insects and in nearly all adults. Here is the structure of a dorsal ocellus. Although there are variations in structure, a typical ocellus has a single lens that is usually rather thickened. Most ocelli feature a large number, often hundreds, of retinula cells. Rhabdomeres of several cells combine to form a number of rhabdoms. Axons project from the retinula cells through the basement membrane and they end in a synaptic plexus behind the eye. Light causes a sustained depolarization of the retinula cells, however, the biological roles of ocelli remain unknown. It is generally agreed that ocelli allow only poor, if any, perception of form. In some orthopterans the ocelli are active in orientation to a light source.

Stemmata

The larvae of holometabolous insects have stemmata on the sides of the head capsule. Many larvae have a single stemma (singular of stemmata) on either side, but the number can be as many as six on a side. Here is a sketch of a section through a stemma. Each stemma has a cuticular lens and a crystalline cone distal to the sense cells. Stemmata generally do not produce clear images, but most caterpillars can discriminate some shapes and they can orientate themselves with respect to boundaries.

Biochemistry of Insect Body

Homeostatic Mechanism

Homeostatic mechanisms maintains stable conditions with respect to any given physiological parameter. Consider homeostasis of thoracic temperature during flight; of hemolymph energy metabolite concentrations; of water balance in terrestrial insects; of osmotic balance; of symbiotic organisms. Two aspects of physiology are implied in discussions of homeostatic mechanisms: first, organisms can register changes in an homeostatic parameter, and second, features of the parameter can be adjusted. In homeostasis of thoracic temperature, it is clear that thoracic temperature is monitored during flight (even if we do not understand the measuring system), and it is clear hemolymph circulation patterns are adjusted in response to changes in thoracic temperature.We introduce a discussion of the insect fat body in terms of homeostasis for a couple of reasons.

In most insects the fat body serves as a storage depot for food reserves, and sometimes for storage excretion. Lipid reserves are often accumulated in massive quantities in this organ, so that it looks like a body, or organ, of fat. The term fat body was coined during early days of studying insect morphology, and it derives from the fatty appearance of the tissue. This term is deeply entrenched in the literature of our field, so much so that it would be a futile exercise to try working towards a more descriptive expression for this organ. The alternative is to expand our conception of what the term fat body represents. In addition to its important roles as a storage depot, the fat body of insects functions as a key centre of metabolism and biochemistry. As a metabolic and biochemical centre, the biological significance of

fat body is its ability to maintain a balance between resources and requirements during the many phases of an insect's life. On one side of the balance, during times of feeding fat bodies biosynthesize and accumulate not only lipid reserves, but also carbohydrates, amino acids, proteins and other metabolites.

On the other side, fat bodies respond to physiological and biochemical needs in a number of ways, including very high rates of protein biosynthesis, formation and release of trehalose, release of lipids, detoxification of nitrogenous waste products, and biosynthesis of hormones. Many of the responses to physiological needs occur on a relatively large scale, and they can have substantial impact on insect biology. Very often fat body metabolic functions are regulated by various endocrinological mechanisms.

Structures of Fat Bodies

The morphology of fat bodies varies considerably in various insect groups. In many species it is a loose aggregation of cells that may be unevenly distributed among all body segments, including the brain case. Fat body cells often surround the major organ systems in insects, including reproductive tissues, alimentary canals, thoracic muscles, and elements of central nervous systems. This close association of fat body cells and other tissues may facilitate exchanges of macromolecules. Fat bodies may also protect organs from physical damage by providing packing. In other species fat bodies are compact cell masses invested in a membranous covering such that they easily can be removed from the insect intact.

Structures of fat bodies may vary according to life stage, sex and reproductive status. Fat bodies can have different functions between sexes, and functions also can differ among life stages. In some species they undergo histological breakdown and reformation during papal stages, though in most species they do not appear to do so. Fat bodies of all insects are in intimate contact with circulating hemolymph, which is consistent with movements of molecules between the two compartments. The vast majority of the cells in fat bodies are called trophocytes, and it is in these cells that most fat body functions are carried out. Trophocytes are very similar to some hemocytes; the two cell types may be quite closely related. In the homopteran Aleyrodes, for example, fat body cells float individually in hemolymph and can not be clearly

distinguished from hemocytes. Other fat body cell types include urate cells. These cells are associated with storage excretion, in which uric acid crystals are accumulated rather than excreted. Fat bodies of most insect species do not include urate cells. For the sake of complexity, uric acid is stored in trophocytes of some species. Fat bodies of many species also contain mycetocytes, which are involved in housing symbiotic micro-organisms. Many of these symbiants play crucial roles in insect nutrition by providing certain vitamins and other essential nutrients to insects that are not able to acquire these nutrients in the diet.

Protein Biosynthesis in Fat Body

Many of the proteins that are crucial in the lives of insects are biosynthesized in fat bodies. Protein synthesis is often under control of juvenile hormone (JH). One of the most well-studied examples of endocrine regulated protein synthesis in fat bodies is the formation of vitellogenins by adult females. Vitellogenins are the yolk proteins that are accumulated during egg maturation. Fat bodies biosynthesize many other proteins as well, including virtually all of the major proteins found in the hemolymph of larval insects. There are also many examples of specialized proteins in insects. Larvae of the midge *Chironomus* biosynthesize hemoglobins, heme-containing proteins important in storage of oxygen. Hemoglobins can make up more than 80 per cent of the hemolymph proteins in these larvae. The lipoproteins that function in hemolymph transport of diacylglycerol are synthesized in fat bodies. There are many other examples, all bearing on the point that protein synthesis in fat bodies is a central issue in insect biology.

We review the biochemistry of protein synthesis by way of appreciating the importance of this topic. First we recall the expression originally put forth by Francis Crick, and later articulated by Charlie Brown as the central dogma of molecular biology: DNA Makes RNA Makes Protein. As an aside, a group of my biochemical colleagues at the University of Nevada, Reno and myself once entered a biochemical T-shirt logo contest. We added the expression makes lipids to the expression of the central dogma of molecular biology. We did not win. The transcription process produces a special form of RNA called messenger RNA, or mRNA. Messengers go places, and in this case mRNA makes