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Department of Zoology.

II M.Sc., Zoology

Elective paper III. General Entomology

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Unit. IV.

Insect Muscular System, Skeletal Muscles, Visceral Muscles, Energetic's Of Muscle Contraction,

Insect Muscle

- Muscles power all the movements, external and internal, in insects.
- All insect muscles are striated, like vertebrate cardiac and skeletal muscle.
- Insect muscles show high levels of homology to these vertebrate muscles in their structure, protein content, contractility and regulation.
- Insect muscles are mostly translucent, colourless or grey, though the flight muscles often show a yellowish or brown tinge.
- In most skeletel muscles, especially those of the appendages, one end of the muscle is attached to a movable part.
- Cuticular invaginations or apodemes, in the form of cords, bands or plate like structures, may provide the true sites of attachment.

➢ FUNCTIONS OF THE MUSCULAR SYSTEM

1. Support of the body.

2. Helps maintain posture.

3. Movement of the limbs, including ovipositor.

4. Movement of the wings-insects are the only invertebrates that fly.

5. Movement of the viscera.

6. Locomotion.

7. Closure of spiracles.

8. Operation of various pumps such as cibarial pump and the pumping of the poison glands.

➢ TYPES OF MUSCLES BASED ON MORPHOLOGY

1. Cardiac muscles :- not found in insects.
2. Smooth muscles :- not found in insects.
3. **Striated muscles :- found in insects.**

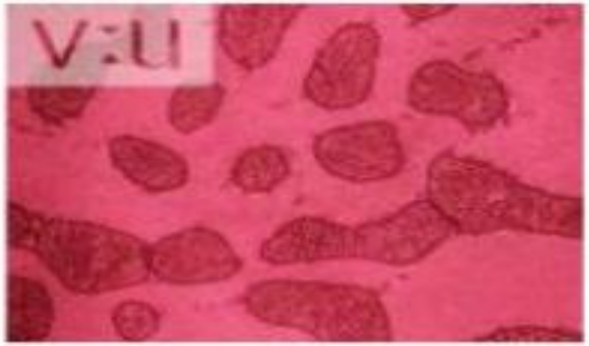

Fig :- Cardiac Muscle

The only muscle type found in insects is striated muscle. Insects do not have cardiac or smooth muscle types.

Fig :- Smooth Muscle

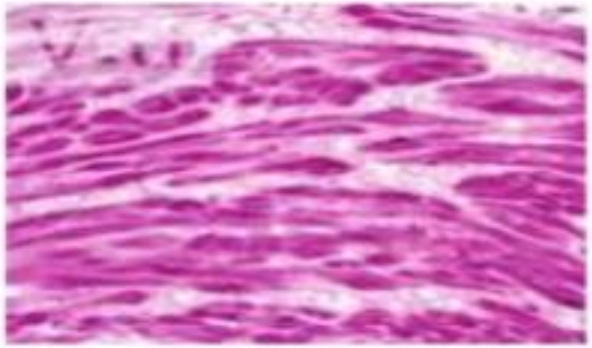

Fig :- Striated Muscle

➢ TYPES OF MUSCLES BASED ON LOCATION

1. Skeletal muscles :

a. Cephalic Muscles
b. Thoracic Muscles
c. Muscles of Flight
d. Abdominal muscles

2. Visceral muscles :

a. Alary muscle
b. Dorsal blood vessel
c. Accessory pulsatile organs and various diaphragms
d. Alimentary canal, including the crop
e. Reproductive organs and ducts
f. Venom glands
g. Repugnatorial glands
h. Organs of defense
i. Malpighian tubules

3. Cardiac Muscles :

➢ Histology Of The Muscles

➢Each muscle is made up of a number of fibers, which are long, usually multinucleate cells running the length of the muscle.

➢The characteristic feature of muscle fibres is the presence of myofibrils.

➢These are embedded in the cytoplasm i.e Sarcoplasm and extend continuously from one end of the fibre to the other.

➢The fibrils are long serial arrays of contractile units known as Sarcomeres.

➢Each sarcomere is composed of interdigitated molecular filaments, consisting mainly of two proteins : Myosin and Actin.

➢These proteins through their cyclical, ATP dependent interactions generate the contractile forces and movements.

➢Each sarcomere is bounded by electron-dense Z-discs which connect neighbouring sarcomeres.

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- From either side of each Z-disc (also called Z-line), so called "thin filaments" extend toward, but do not reach, the center of the sarcomere.

- Each sarcomere comprises of an anisotropic region (the A-band) and two half isotropic regions (I-bands) containing the proximal parts of the thin filaments.

- The dense A-band is further transversed by a lighter H-bands.

- An array of thin I-band actin filaments (each some 5 nm in diameter) extends from the Z-disc to the edge of the H-band.

- While thicker myosin filaments (each about 15 nm in diameter) run throughout the A-band.
- Actin and myosin filaments are linked by temporary cross-bridges, each myosin filament usually being surrounded by 6 actin filaments.

- According to theory of Huxley and Hanson, contraction of the fibril is due to the sliding of the actin and myosin filaments relative to each other

- The actin filaments move further into the A-disk while the myosin filaments thus approach the Z-disks.

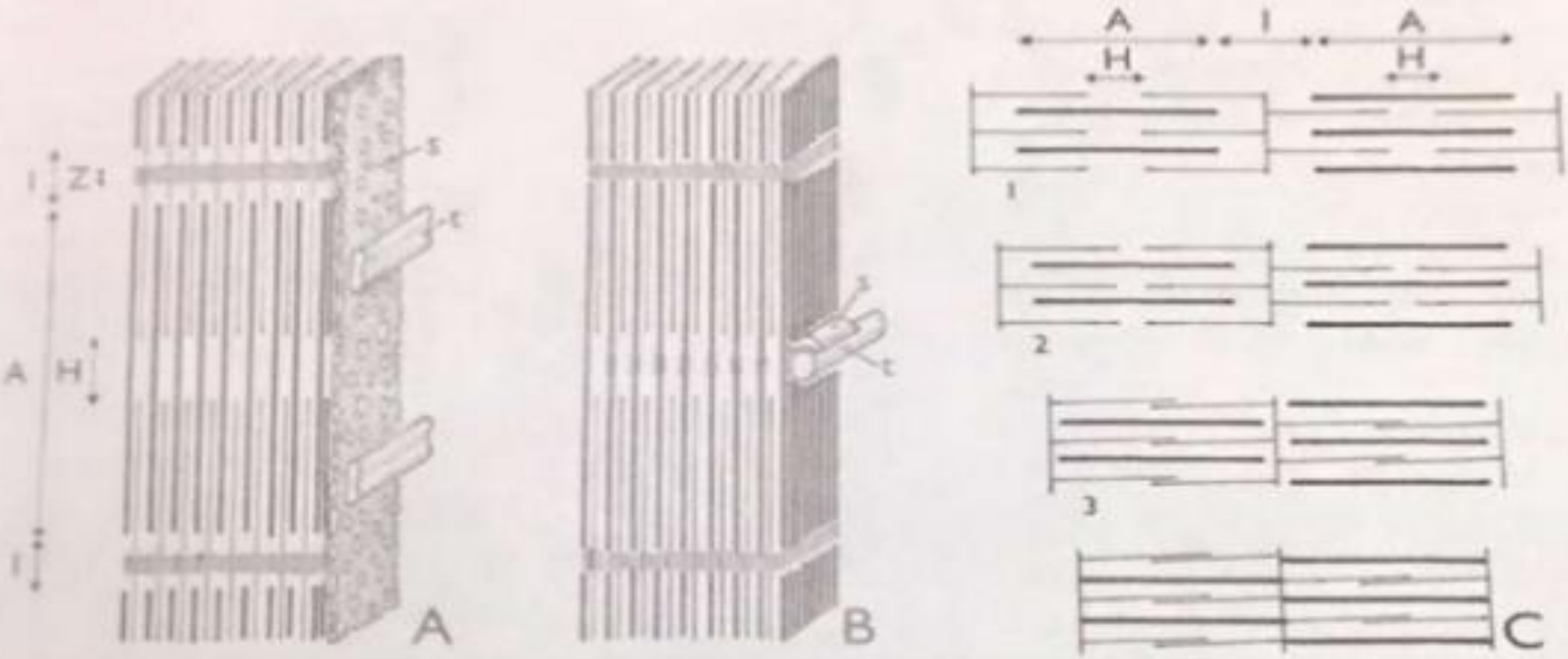

FIG. 53 Ultrastructure of insect muscle (*after* Smith and Huxley). A, synchronous muscle fibril showing extensive sarcoplasmic reticulum and wide I-band. B, asynchronous fibril showing reduced sarcoplasmic reticulum and narrow I-band. C, schematic representation of successive stages in the contraction of two sarcomeres, illustrating changes in the relative positions of the thick and thin filaments (respectively of myosin and actin)

s, sarcoplasmic reticulum; *t*, transverse membrane system (T-system). The relationships of the A, I, H and Z bands to the ultrastructural and molecular constitution of the fibril are indicated at the left and top right.

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- The skeletal muscles of insects have a complex structure, which have :

i. The fibrous contractile system
ii. The mitochondria
iii. The tracheal and nervous supply
iv. The membrane systems

- Variations in the histology and ultrastructure of these components are associated with functional differences between different groups of muscles.
- The mitochondria of insect muscle vary greatly in size, shape and distribution. Most extensively developed in the flight muscles, because of high metabolic rate of these contracting structures.
- They may be scattered randomly throughout the sarcoplasm or arranged between fibrils opposite to z-disks.
- The tracheal supply also varies with their activity, visceral muscles being poorly supplied while flight muscles are much more richly tracheated with intracellular tracheoles penetrating the fibrils
- Visceral muscle fibres occur singly or in groups around the gonads, their ducts, diaphragms (in the heart) and gut wall.
- Visceral muscles differ from skeletal muscles having smaller fibers linked by desmosomes (absent in skeletal muscles), poor tracheolar supply, few mitochondria and a poorly developed T- system and sarcoplasmic reticulm.

Contd……

c) The Anterior Labral Muscles (Retractors) :- Run from the anterior margin of the labral base to the wall of the head.

d) The Dorsal Abductors :- Originate on the upper lateral part of the epicranium and insert each on an apodeme connected with the inner, basal region of the mandible.

e) The Ventral Abductors :- Present only in the Apterygotes and some lower Pterygotes.

f) Dorsal Basal Muscles :- Arising on the dorsal part of the head and forming the anterior and posterior rotators of the cardo and the cranial flexure of the lacinia.

g) Ventral Basal Muscles :- Inserted on the cardo and stipes and originate on the tentorium in most pterygotes and on the tentorial apodemes in the apterygotes.

i) Stipital Muscles :- Originate on the stipes and include the levator and depressor of the palp, flexor of the galea and the stipital flexor of the lacinia.

j) Extrinsic Labial Muscles :- Arise on the tentorium or cranial wall and insert on the prementum. They correspond to the ventral basal muscles of the maxilla.

k) Median Labial Muscles :- Run from the back of the prementum to the postmentum and have no homologues in the maxilla.

l) Labial Salivary Muscles :- Usually two pairs, arising on the prementum and converging on the labial wall of the salivarium near the opening of the salivary duct.

m) Musles of the endites and palps :- From the prementum there run the levator and depressor muscles of the palps and a flexor of each glossa and paraglossa.

Contd......

n) Intrinsic Palp Muscles :-Inserted on the suspensorium of the hypopharynx.

3. Muscles of Antennae :- Classified as follows :

a) Extrinsic antennal muscles :- A levator and usually two depressors are inserted on the base of the scape.

b) Intrinsic antennal muscles :- Pair of muscles arising in the scape and inserted on the base of the pedicel.

B. Thoracic Muscles

✓ The principal Thoracic Muscles may be divided as follows :-

a) Longitudenal :- Divisible into tergal and sternal groups, the former being important indirect flight muscles.
b) Dorsoventral :- Two main groups here are : tergosternal muscles : principal levators of wing (acting antagonistically to the longitudenal tergals and tergocoxal muscles : act as the tergal promoters and remotors of the leg.
c) Pleural :- Three main groups here are : tergopleural muscles : variable in development and include the axillary muscles, pleurosternal muscles : short fibres linking the pleural and sternal apophyses, pleurocoxal muscles : act as abductors of the coxae.

Contd.....

d) Sternal :- Includes two muscle groups : sternocoxals : are sternal promotors and remotors of the leg, lateral intersegmental : runs from sternum to the pleuron or tergum of the succedding segment and is best developed in larval forms.
e) Intrinsic Leg Muscles :- Lying within the segments of the legs. They include levator and depressor of the trochanter, tibia and tarsus and the levator of the pretarsus.

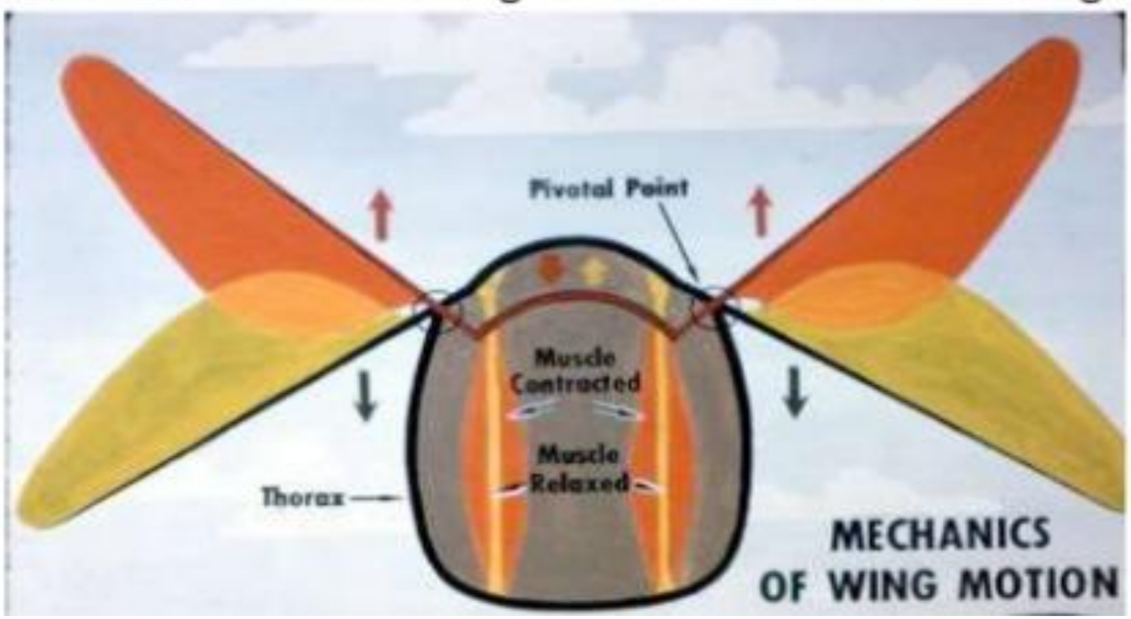
C. The Abdominal Muscles

a) Longitudenal :- Divided into (a) tergal and (b) sternal longitudenal muscles. In each case they run between the intersegmental folds or antecostae of successive segments. Acting together the groups act as retractors by telescoping the abdomen. Acting alone , the sternal muscles curve the abdomen downwards and the tergals straighten it or bend it upwards.
b) Lateral :- Typically run dorsoventrally and are both inter and intrasegmental in position. They are usually tergosternals, but when distinct pleurites are present there may also be tergopleural and sternopleural muscles. By contraction they tend to compress the segment and are therefore important in respiratory movements.
c) Transverse :- Better known as the muscles of the dorsal and ventral diaphragms.

- In addition there are special muscles concerned with movements of the genitalia, cerci and spiracles.

D. Muscles Of Flight

The flight movements are caused by three sets of muscles , the indirect, direct and accessory indirect flight muscles. The indirect muscles are usually the largest in the body and are attached to the thorax and not to the wing base. Wing movement, and most of flight, is controlled by indirect flight muscles. They are called this because the longitudinal and dorsoventral muscles do not connect directly to the wing but, control flight by affecting the dorsal surface of the thorax. When the dorsoventral muscles contract, it causes a depression of the tergum, causing the wings to go up. Contraction of the longitudinal muscles causes an arching of the notum and the wings go down. It is a pivotal movement based on the arrangement of the cuticle and wings.



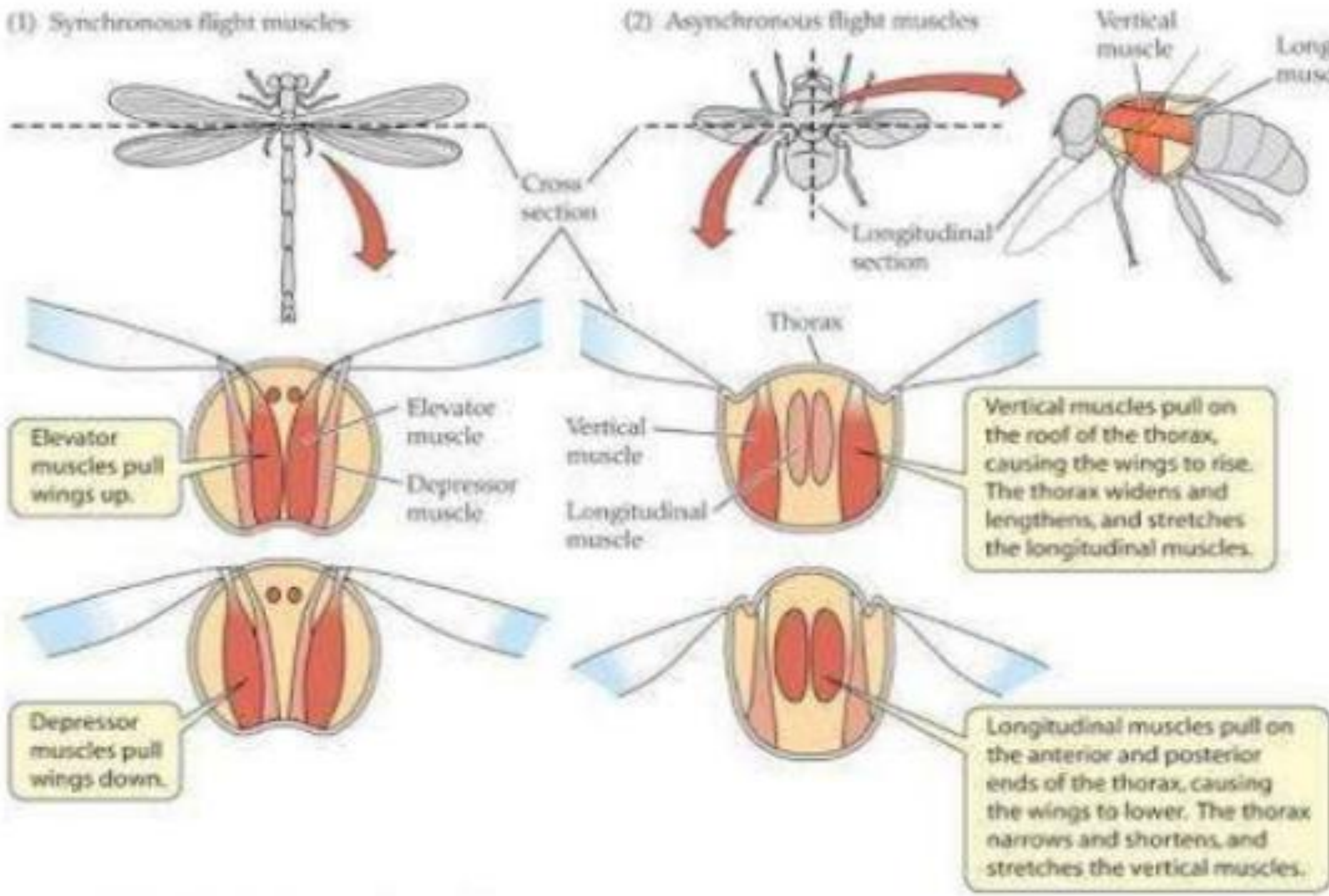


Fig :- Mechanism of working of Flight Muscles

➢ Visceral Muscles

✓ These muscles differ in structure from skeletal muscles in severe respects.

✓ Adjacent fibers are held together by desmosomes, which are absent from skeletal muscle.

✓ The sacroplasmic reticulm is poorly developed, mitochondria are small and often few in number.

✓ All insect muscles are striated, s visceral muscle resembles skeletal muscle in contrast to the smooth visceral muscle of vertebrates.

✓ Visceral muscles may be innervated from the stomodeal nervous system or from the ganglia of the ventral nerve cord, but are sometimes without innervation as in the heart of *Anopheles spp* larvae.

➢ Cardiac Muscles

✓The insect heart usually consists of a simple tube that contains a layer of contractile myocardial cells.

✓ These are usually mononucleate cells with straited longitudinal and circular myofibrils.

✓ Heart rate is influenced by nerves that innervates the heart in most insects.

➢ Physiology Of Insect Muscles

✓ Properties of insect skeletal muscles such as absolute muscular power and simple contraction do not differ greatly from those of vertebrates.

✓Unlike vertebrates, insect muscles contain relatively few fibres and to achieve smooth contractions they are supplied by multiple nerve endings.

✓ The neuromuscular transmitter substances of insect is probably L-glutamate.

✓ The muscles of legs and abdomen and most flight muscles respond synchronously to the nervous impulses.

✓ In Diptera, Hymenoptera, Coleoptera and Hemiptera there evolved the characteristics fibrillar type of asynchronous indirect flight muscles.

✓ Here the frequency of contraction is not determined by the central nervous system but is directly controlled by the loading on the muscles.

➢ Metabolism of Insect Muscles

- ✓ The oxygen consumption of an insect may rise a hundred fold when flight begins and if it is to continue for long periods a reserve of oxidizable respiratory material is needed.

- ✓ In Diptera and Hymenoptera a respiratory quotient of unity during flight indicates that carbohydrates are the main substrate.

- ✓ In Lepidoptera, Homoptera and Orthoptera on the other hand, R.Q. values of about 0.7 occur and fat reserves are depleted.

- ✓ Some spp such as locusts and aphids, use glycogen and the disaccharide depletes first then consume fat during prolonged flight.

- ✓ There are important biochemical differences in the metabolism of different muscles e.g in locust flight muscles lactic dehydrogenase is virtually absent and lectic acid is not an end product of glycolysis, whereas in the leg muscle lactic acid accumulates and is slowly removed by oxidation and conversion to glycogen.

➢ Degeneration of Musculature

- ✓ Degeneration of the flight muscles occur after sexual maturity in many spp.
- ✓ In queen ants and termites due to degeneration of flight muscles reproduction is promoted by releasing amino acids that can be used in egg formation.
- ✓ The alate forms of aphids also undergo flight muscles histolysis after settling on their host plants.
- ✓ These changes and accompanying hypertrophy of the fat body and resumption of embroy development in the ovaries are caused by hormonal changes.
- ✓ Degeneration of the indirect flight muscles also occurs in adult females of *Dysdercus spp* where it coincides with oocytes growth and is under endocrine control.
- ✓ Interesting changes take place in the segmental muscles of the abdomen of *Rhodnius spp* which undergo periodic regressive and regenerative changes associated with the moulting cycle.

- The muscular system of insects ranges from a few hundred muscles to a few thousand. Unlike vertebrates that have both smooth and striated muscles, insects have only striated muscles. Muscle cells are amassed into muscle fibers and then into the functional unit, the muscle.[6 Muscles are attached to the body wall, with attachment fibers running through the cuticle and to the epicuticle, where they can move different parts of the body including appendages such as wings.The muscle fiber has many cells with a plasma membrane and outer sheath or sarcolemma.

- The sarcolemma is invaginated and can make contact with the tracheole carrying oxygen to the muscle fiber. Arranged in sheets or cylindrically, contractile myofibrils run the length of the muscle fiber. Myofibrils comprising a fine actin filament enclosed between a thick pair of myosin filaments slide past each other instigated by nerve impulses.

- **Visceral**: these muscles surround the tubes and ducts and produce peristalsis as demonstrated in the digestive system.
- **Segmental**: causing telescoping of muscle segments required for moulting, increase in body pressure and locomotion in legless larvae.
- **Appendicular**: originating from either the sternum or the tergum and inserted on the coxae these muscles move appendages as one unit.[These are arranged segmentally and usually in antagonistic pairs. Appendage parts of some insects, e.g. the galea and the lacinia of the maxillae, only have flexor muscles. Extension of these structures is by haemolymph pressure and cuticle elasticity.

- **Flight**: Flight muscles are the most specialised category of muscle and are capable of rapid contractions. Nerve impulses are required to initiate muscle contractions and therefore flight. These muscles are also known as neurogenic or synchronous muscles. This is because there is a one-to-one correspondence between action potentials and muscle contractions. In insects with higher wing stroke frequencies the muscles contract more frequently than at the rate that the nerve impulse reaches them and are known as asynchronous muscles.

- Flight has allowed the insect to disperse, escape from enemies and environmental harm, and colonise new habitats.One of the insect's key adaptations is flight, the mechanics of which differ from those of other flying animals because their wings are not modified appendages. Fully developed and functional wings occur only in adult insects. To fly, gravity and drag (air resistance to movement) have to be overcome

- Most insects fly by beating their wings and to power their flight they have either direct flight muscles attached to the wings, or an indirect system where there is no muscle-to-wing connection and instead they are attached to a highly flexible box-like thorax.
- Direct flight muscles generate the upward stroke by the contraction of the muscles attached to the base of the wing inside the pivotal point. Outside the pivotal point the downward stroke is generated through contraction of muscles that extend from the sternum to the wing. Indirect flight muscles are attached to the tergum and sternum. Contraction makes the tergum and base of the wing pull down. In turn this movement lever the outer or main part of the wing in strokes upward. Contraction of the second set of muscles, which run from the back to the front of the thorax, powers the downbeat. This deforms the box and lifts the tergum.

- Insect muscles are mostly translucent, colourless or grey, though the flight-muscles often show a yellowish or brown tinge. Both skeletal and visceral muscle fibres are cross-striated and some older reports of unstriated visceral muscles need reinvestigation. Insect muscles differ fundamentally from those of Annelids, both in histological structure and in not being incorporated into the body-wall to form a dermo-muscular tube.

- In most skeletal muscles, especially those of the appendages, one end of the muscle (its *origin*) is attached to a fixed skeletal region while the other end (its *insertion*) is attached to a movable part. Cuticular invaginations or apodemes, in the form of cords, bands or plate-like structures, may provide the true sites of attachment and therefore intervene between the muscle and the main structure

The skeletal muscles

- The skeletal muscles of insects have a complex structure, in which one may distinguish (i) the fibrous contractile system, (ii) the mitochondria, (iii) the tracheal and nervous supply, and (iv) the membrane systems
- Variations in the histology and ultrastructure of these components are associated with important functional differences between different groups of muscles. Essentially, however, a muscle is composed of a number of long fibres, each measuring from a few to a few hundred (Lm in diameter.

- Each of these is in turn subdivided into separate, smaller fibrils which are themselves composed of a highly organized array of myofilaments made up of the proteins actin and myosin (Fig. 53). The fibre is surrounded by an outer membrane, the sarcolemma, which encloses the nucleated sarcoplasm in which the fibrIls are embedded. Each fibril is typically composed of alternating isotropic (1) and anisotropic (A) regions which, under appropriate microscopical illumination, appear as light and dark bands or disks.

- Because these appear at about the same level in adjacent fibrils they give to the whole fibre its characteristic cross-striated appearance. Crossing each isotropic region is a partition, the Z-disk, which thus divides the fibril into short units or sarcomeres, each comprising an anisotropic region (the A-band) and two half I-bands. The dense A-band is further traversed hy a lighter H-band. These features, easily seen by light-microscopy, reflect the submicroscopic organization of the myofibrils.

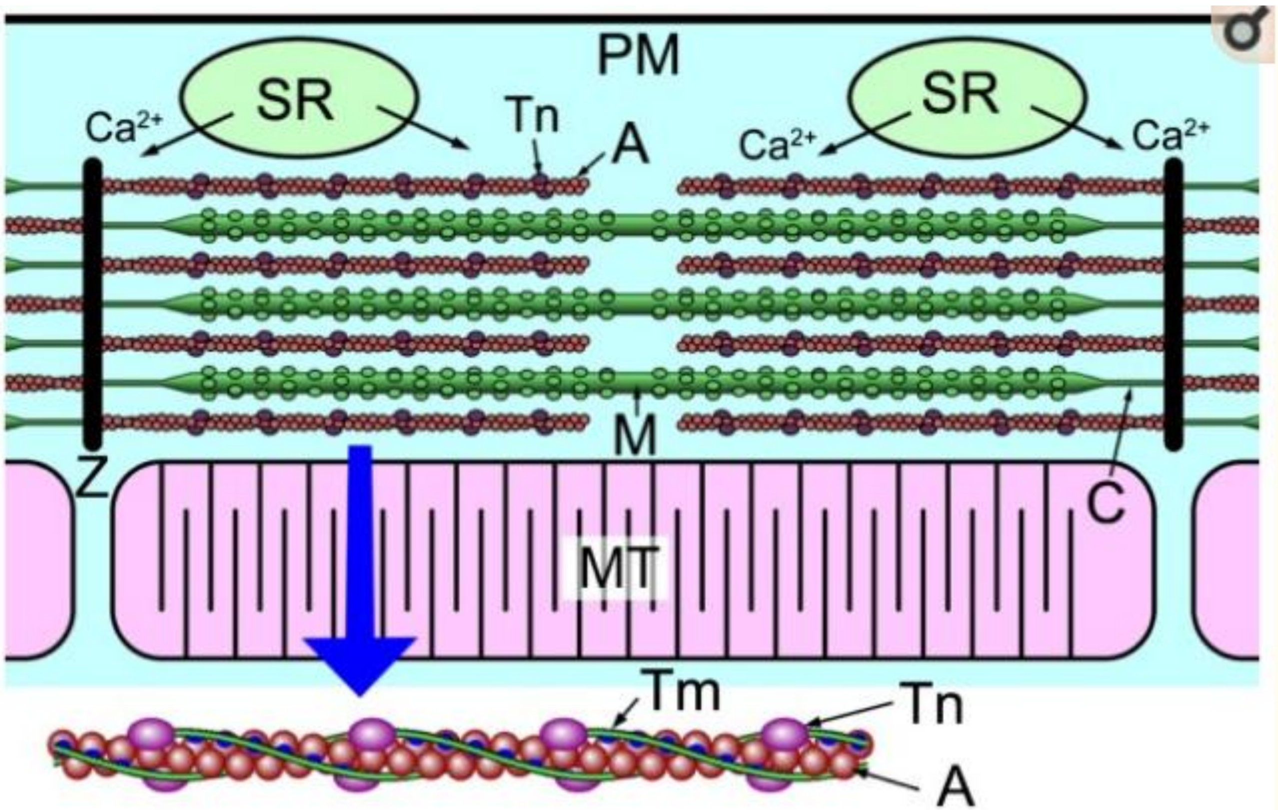
- An array of thin I-band actin filaments (each some 5 nm in diameter) extends from the Z-disk to the edge of the H-band in a relaxed fibre, while thicker myosin filaments (each about IS nm in diameter) run throughout the A-band. Actin and myosin filaments are linked by temporary cross-bridges, each myosin filament usually being surrounded by 6 actin filaments (Garamvolgyi, 1965; Hagopian, 1966). According to the well-established theory of Huxley and Hanson, contraction of the fibril is due to the sliding of the actin and myosin filaments relative to each other (Hanson, 1956; Pringle, 1966; Osborne, 1967); the actin filaments move further into the A-disk while the myosin filaments thus approach the Z-disks

- The mitochondria of insect muscle vary greatly in size, shape and distribution, being most extensively developed in the flight-muscles, as one would expect from the extremely high metabolic rate of these actively contracting structures. They may be scattered randomly throughout the sarcoplasm or arranged between fibrils opposite the Z-disks; in the flight-muscles of the Odonata they form large slab-like structures and in the powerful fibrillar indirect flight-muscles of Hymenoptera and Diptera the giant mitochondria form conspicuous 'sarcosomes'.

- The tracheal supply of insect muscles also varies with their activity, visceral muscles being poorly supplied while flight-muscles are much more richly tracheated, with intracellular tracheoles penetrating the fibrils. Of considerable physiological importance are the membrane systems revealed by electron microscopy. The sarcolemma, about 7"5 nm thick, is a unit-membrane like that investing other cells. Transverse tubular invaginations from it form the so-called T-system, while close to these are the longitudinally arranged cisternae of a separate membrane system, the sarcoplasmic reticulum.

'visceral' fibres.

- In anatomical considerations of the insect body, the muscular systems are commonly divided into two general categories: 'skeletal' and 'visceral' fibres. The former act upon the articulated exoskeleton, while the latter invest the various regions of the intestinal tract and other internal organs within the body cavity. Whereas many of the skeletal muscles, notably those concerned with flight and locomotion, may contract rapidly and often at high frequency, the visceral fibres, like their analogues in the vertebrate body, generally exhibit a slower peristaltic or irregular activity.



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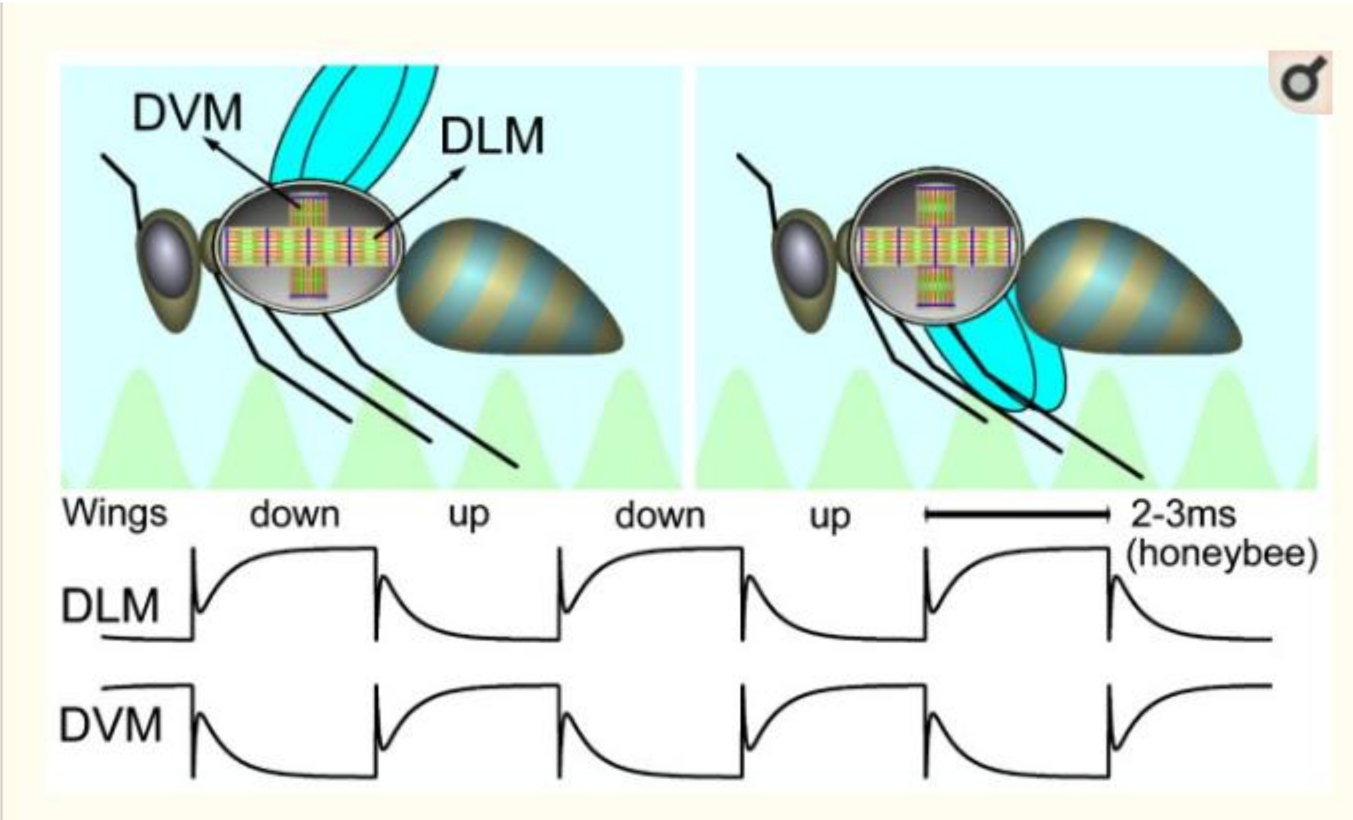
DVM
DLM
Wings
down
up
down
up
2-3ms
(honeybee)
DLM
DVM

Role of regulatory proteins on stretch activation

- The troponin complex, the calcium sensor on the thin filament, consists of three components: Troponin-C (TnC) which binds calcium ions, troponin-I (TnI) which inhibits actin-myosin interaction, and troponin-T (TnT) which anchors the whole complex to tropomyosin. TnC is a calmodulin- like dumbbell-shaped molecule, and it typically has four binding sites for divalent cations (two in the N-terminal end and two in the C-terminal end). In the vertebrate skeletal muscle isoform, the 1st and 2nd binding sites from the N-terminus play a regulatory role, while the 3rd and 4th binding sites bind magnesium ions rather than calcium, and are considered to play a structural role

Summary of structure, function and constituent proteins in insect muscle

	asynchronous IFM	asynchronous IFM (Diptera)	synchronous IFM	non-IFM muscles
beat frequency	>>100 Hz in small species	>>100Hz in small species3	<100Hz even in small species4	—
sarcomere	near-crystalline17,18	near-crystalline23	non-crystalline23	non-crystalline
myofibril	single giant protein crystal9	single giant protein crystal9	non-crystalline9	non-crystalline9
myosin	faster kinetics in faster-beating species20	faster kinetics in faster-beating species20,21	not studied	not studied
actin	unique structural change23	unique structural change23, IFM-specific (Act88F in *Drosophila*)22	unique structural change23	various isoforms (*Drosophila*)22
tropomyosin	normal MW	heavy MW with Pro-Ala-rich extension (TmH)25	normal MW	normal MW
troponin C	IFM-specific, 2 or more isoforms13,28	IFM-specific, 2 or more isoforms28	single isoform?	general-expression isoforms28
troponin I	heavy MW with Pro-Ala-rich extension (TnH)24	normal MW	heavy MW with Pro-Ala-rich extension (TnH)	normal MW
projectin	connects thick filament and Z-line29	connects thick filament and Z-line29	localized in A-band	localized in A-band29

- The IFM of the giant waterbug (*Lethocerus*, Hemiptera) is known to have two TnC isoforms (F1 and F2). F1 has only one functional calcium binding site at the 4th position, and F2 has two calcium binding sites at the 2nd and 4th positions. F1 and F2 are expressed in *Lethocerus* IFM with a molar ratio of 7:1–10:11. From the result of TnC-exchange experiments, Bullard and colleagues1 postulate that F1 causes SA by sensing stretch rather than calcium binding, while F2 is responsible for eliciting steady-state isometric force as the vertebrate skeletal muscle isoform. The 3-D structure of the F1 molecules is almost identical to that of other TnC isoforms, so that it is unlikely that F1 directly senses stretch. In this respect, Bullard and colleagues propose that the stretch sensor resides in TnI1. The TnI of IFM has a long Pro-Ala-rich extension, and is called TnH (H is for heavy) because of its heavier molecular weight.

- The extension is postulated to reach the thick filament, and to detect the relative sliding between the thick and thin filaments. However, the extension is also found in insects with synchronous IFM (which hardly exhibits SA), and the reduced expression of this extension in mutant fruitflies has been reported to have unexpectedly light effects. Therefore, one should carefully draw conclusions about the role of the Pro-Ala-rich extension.

- This implies that the higher the wing-beat frequency, the faster is the attachment/detachment. Currently no experimental evidence has been reported for multiple attachment/detachment events within a single ATP hydrolysis cycle, and actually IFM myosins from faster-beating insects are shown to exhibit higher ATPase activities. A detailed kinetic study has been made for myosin isoforms in *Drosophila*, which beat at 200Hz . There is only a single gene for muscle myosin (myosin II) in *Drosophila*, and all isoforms, including the IFM-specific one, are expressed from this gene through alternative splicing. In the case of the IFM-specific isoform, the rate constant for dissociation from actin (usually regarded as an index for the 'speed' of myosin) is unusually high (3,698 s^{-1} as opposed to 200–500 s^{-1} in vertebrate skeletal muscle).

- Thus, the IFM myosin from *Drosophila* is called the fastest myosin II, but the rate constants may be greater in faster-beating insects. It detaches from actin quickly because the step of ADP release (usually the rate-limiting step for actin-activated ATPase reaction) is accelerated. As a result of this acceleration, the affinity for ATP is also reduced ($K = 0.2\text{mM}^{-1}$ as opposed to $0.8–9\text{mM}^{-1}$ in vertebrate). The authors of the paper expect that *Drosophila* IFM may operate at a high intracellular ATP level, but the results in the literature or our own measurement show that the intracellular ATP levels in asynchronous IFM are not much greater than in other muscles. It is possible that, unlike in vertebrate muscle, IFM myosin may operate at substantially sub-saturating levels of ATP.

Actin

- It is well known that *Drosophila* has an IFM-specific actin gene (Act88F). Actin is a conservative protein, and there are 27 differences in amino-acid (a.a.) residues between Act88F and other actin isoforms. The function of IFM is little affected after replacement of a few of these 27 residues by those of other isoforms, but the flight ability is lost after replacement of 18 residues2. Therefore, Act88F may have acquired specialized functions by the replacement of these residues.
- It is unknown whether other insects express IFM-specific actin isoforms as well. However, an X-ray diffraction study on various insect species has shown that calcium activation of IFM causes actin to change its structure in a manner different from that in vertebrate skeletal muscle2. This structural change is also observed in synchronous IFM of dragonflies (Odonata), and is therefore not restricted to asynchronous IFM.

Troponin and Tropomyosin

- The most peculiar of IFM proteins are troponin and tropomyosin. Among the 3 components of troponin, TnI(TnH) has the most striking feature because of the Pro-Ala-rich 200 a.a. residues-long extension at its C-terminus as stated earlier. Because of its size, the troponin complex of IFM can be clearly recognized in electron micrographs. Initially, TnH was expected to explain the SA mechanism of asynchronous IFM, but it is now clear that TnH is ubiquitously distributed among all winged insect orders (although it is still IFM-specific). Interestingly, TnH does not exist in Diptera. In the IFM of these insects, TnI has ordinary molecular weights. Instead, the Pro-Ala-rich extension is associated with tropomyosin. In *Drosophila*, two high-molecular- weight tropomyosin isoforms (~80 kDa) are expressed besides the ordinary isoform (35 kDa).

- These high-molecular-weight isoforms were first described by Mogami et al. as IFM-specific proteins 33 and 34 (note that these isoforms are called TnH in some literature). Diptera is a monophyletic group of insects, and is considered to have arisen from a common ancestor. Probably the high-molecular-weight tropomyosin isoforms were created by gene transfer in an early stage of evolution. In any event, the fact that the long extension is preserved in all winged insects implies that it has some functional significance. For example, the extension is known to bind glutathione-S-transferase (GST. GST is an enzyme that detoxifies various noxious substances, and is known to render pesticide-resistance to malaria-transmitting tropical mosquitoes2. In human bodies the liver is the organ for detoxification, but in insects, the IFM is the most voluminous organ, and it is not surprising if the IFM takes the role for the liver.

- As for TnC, the F1 isoform of *Lethocerus* IFM has only one functional calcium-binding site at the 4th position, and it is important for SA according to Bullard's hypothesis, as described earlier. However, according to Marco et al., who examined in detail the evolution of the TnC gene groups, the F1 type is ubiquitously expressed in the body and it is the F2 type, which has two binding sites at the 2nd and 4th positions, that is the IFM-specific species that emerged with the development of flight muscle functions2. According to them, the F2 type further generated its subtypes by gene duplication. The number of its copies is one in *Lethocerus* that beats at 30 Hz, two in *Drosophila* and *Apis* (honeybee) that beat at 200Hz, and four in *Anopheles* (mosquito) that beat at 500Hz. The F2 types of *Apis* IFM have evolved from an ancestral gene different from that of Dipterans, and therefore the similarities of the F2 type molecules in these insects are the result of convergence.

- As we have reviewed, the current understanding of the TnC isoforms in IFM is still in its early stage. The largest problem would be the difficulty in identifying which of the TnC isoforms of those holometabolous insects are the true homologs of the F1 or F2 isoform of *Lethocerus*. The difficulty is simply because hemimetabolous *Lethocerus* and holometabolous insects are phylogenetically remote to each other. The functionality of each divalent cation binding site has not been determined experimentally, but is only inferred from its a.a. sequence. Clearly more studies are needed to clarify the identity and the role of each TnC isoform.

Projectin

- Projectin is one of so-called modular proteins, consisting of many immunoglobulin- and fibronectin-like domains connected in series. Projectin is a homolog of connectin (titin) in vertebrate, and is expressed by sls gene through alternative splicing2. In asynchronous IFM, it is a component of the C-filament as described earlier, and anchors the thick filament to the Z-line. Projectin is also found in non-IFM (leg) muscles, but its intracellular localization is different, and it seems to run along the thick filament as connectin in vertebrate skeletal muscle. Projectin is probably an elastic protein commonly distributed among protostomes, and may have been diverted for specialized purposes with the development of asynchronous IFM, and localized around the Z-line.

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THE INSECT NERVOUS SYSTEM

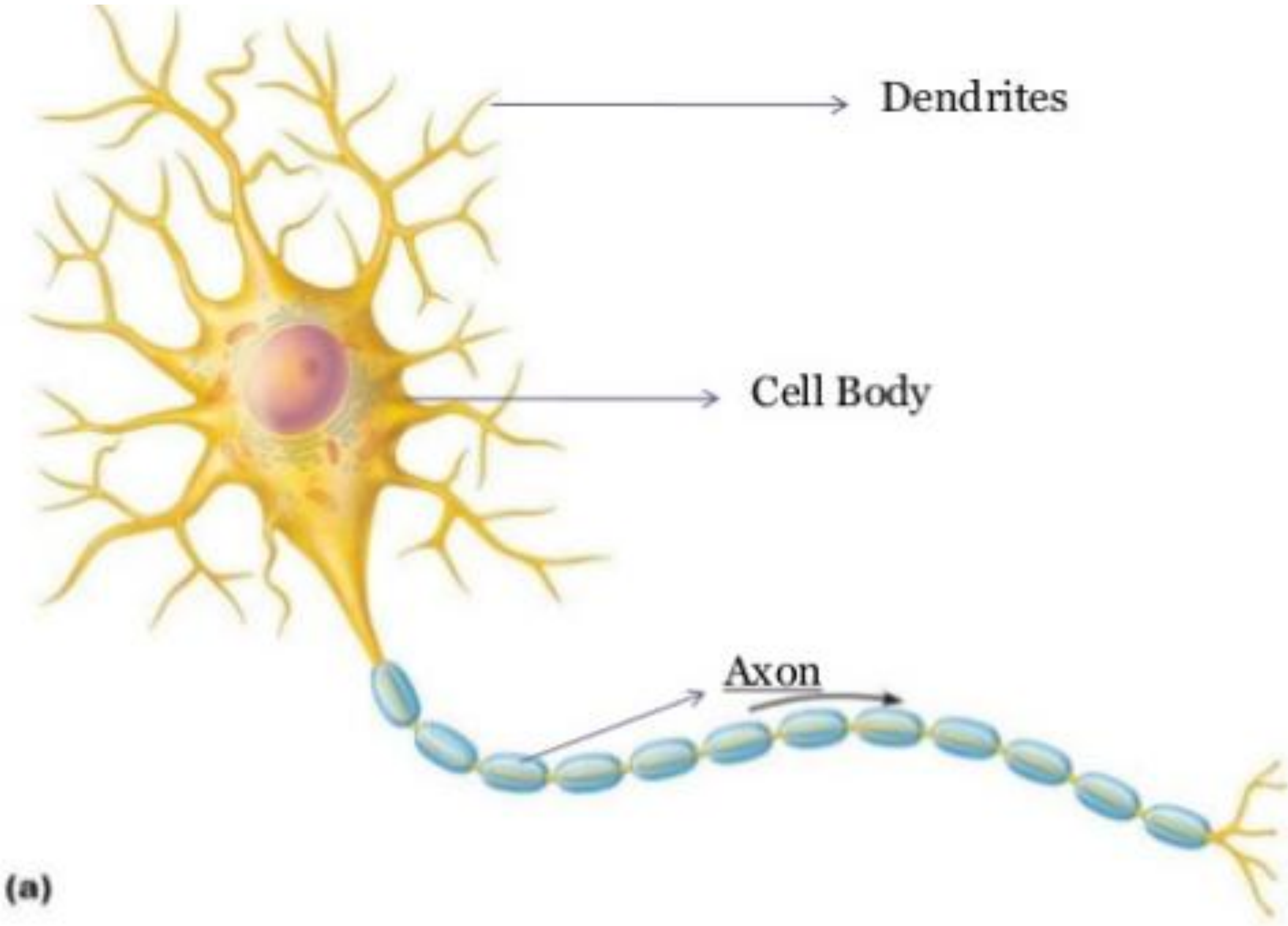
Neuron

The basic unit of nervous system that functions in nerve impulse transmission is the nerve cell or neuron.

A neuron is composed of:

- A cell body where nucleus is found
- One or more receptor fibrils=Dendrites
- An axon that branches at the tip

THE INSECT NERVOUS SYSTEM



THE INSECT NERVOUS SYSTEM

- An insect's nervous system is a network of specialized cells called **neurons** that serve as an "information highway" within the body.

- The nervous system of insect functions to generate and transport electrical impulses, to integrate information received and to stimulate muscles for movement.

THE INSECT NERVOUS SYSTEM

Nervous system

Clip slide

✓The basic component in the nervous system is the nerve cell or **neuron**, composed of a cell body with two projections (fibers) the **dendrites** that receive stimuli and the **axon** that transmits information, either to another neuron or to an effector organ such as a muscle.

✓ Axon may have lateral branches called Collateral and terminal arborization and synapse.

✓ Insect neurons release a variety of chemicals at synapses either to stimulate or to inhibit effector neurons or muscles. Acetylcholine and catecholamines such as **dopamine** are the important neurotransmitters involved in the impulse conduction. Neurons are of following types based on structure and function.

THE INSECT NERVOUS SYSTEM

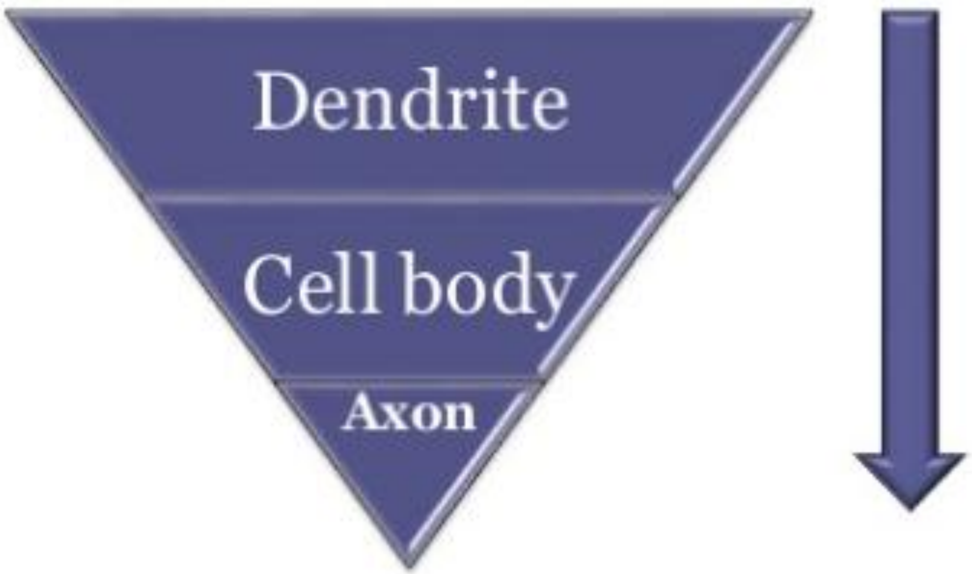
- Nerve cells are typically found grouped in bundles. A **nerve** is simply a bundle of dendrites or axons that serve the same part of the body.

- A **ganglion** is a dense cluster of interconnected nerves that process sensory information or control motor outputs.

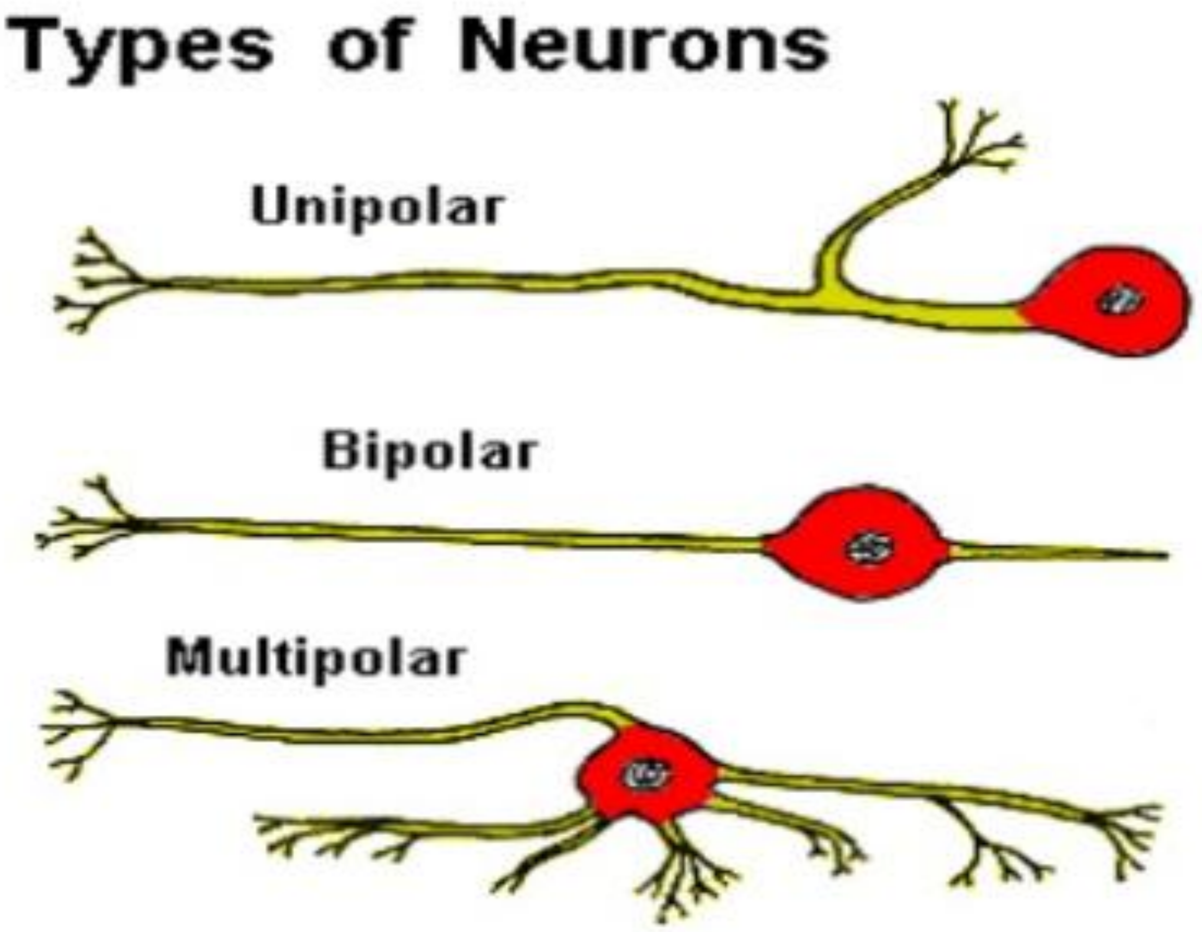
THE INSECT NERVOUS SYSTEM

Signal transmission

- Signal transmission is always unidirectional, moving toward the nerve cell body along a dendrite and away from the nerve cell body along an axon.



THE INSECT NERVOUS SYSTEM



THE INSECT NERVOUS SYSTEM

- Neurons are usually divided into three categories, depending on their function within the nervous system:

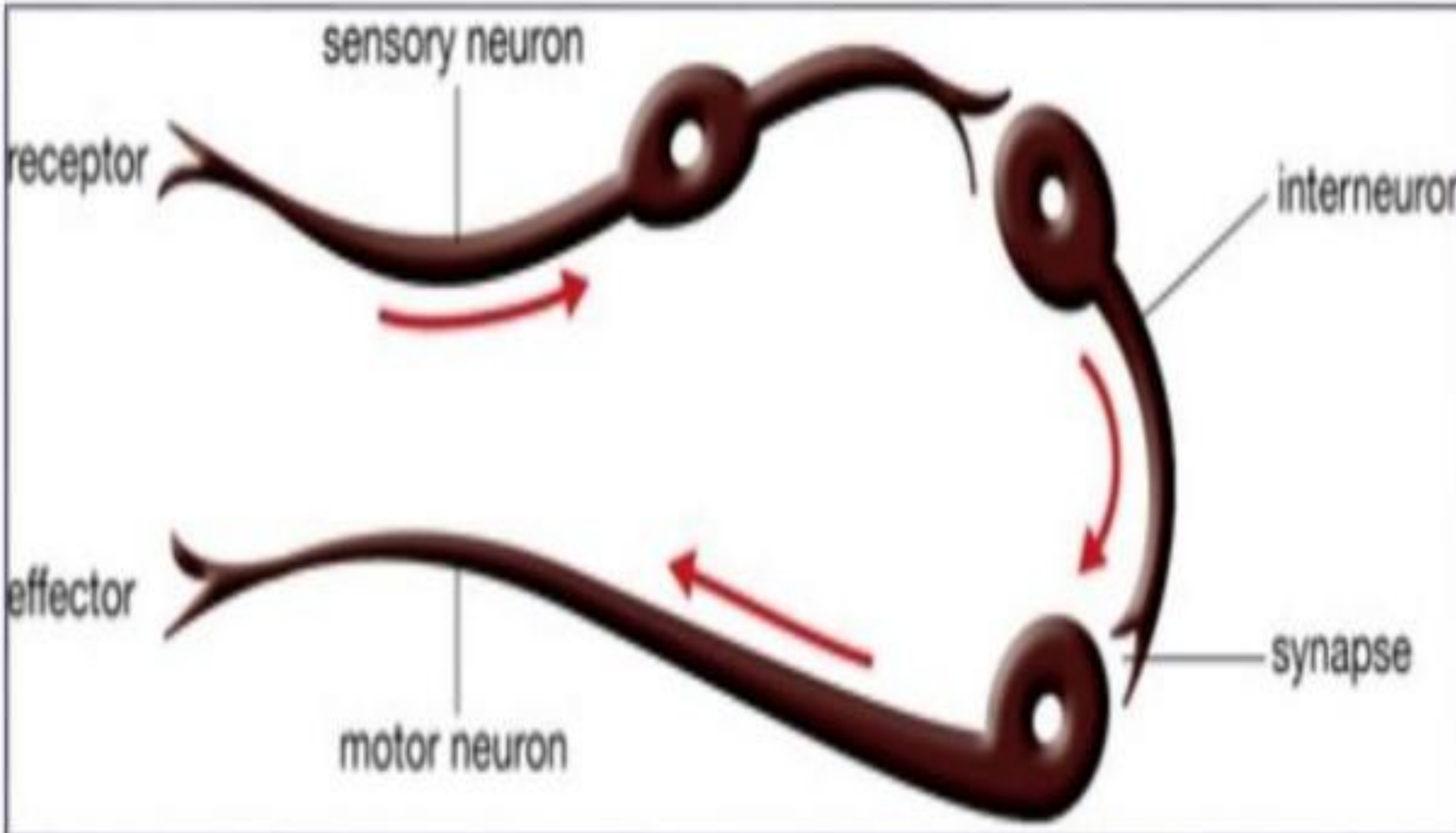
1. **SENSORY NEURONS:** These bipolar or multipolar cells have dendrites that are associated with sense organs . They always carry information toward the central nervous system.

THE INSECT NERVOUS SYSTEM

- **MOTOR NEURONS :** These uni polar cells that conduct signals away from the central nervous system and stimulate responses in muscles and glands.

- **INTERNEURON (ASSOCIATION) NEURONS:** These neurons connect sensory and motor neurons that conduct signals within the central nervous system.

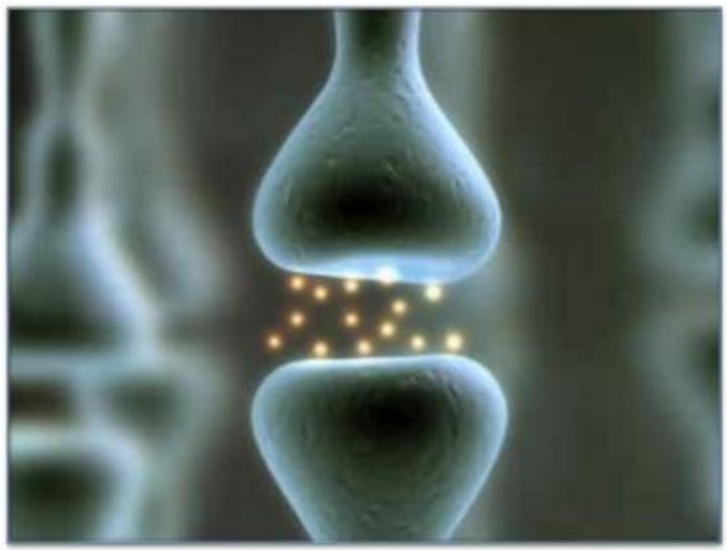
THE INSECT NERVOUS SYSTEM



THE INSECT NERVOUS SYSTEM

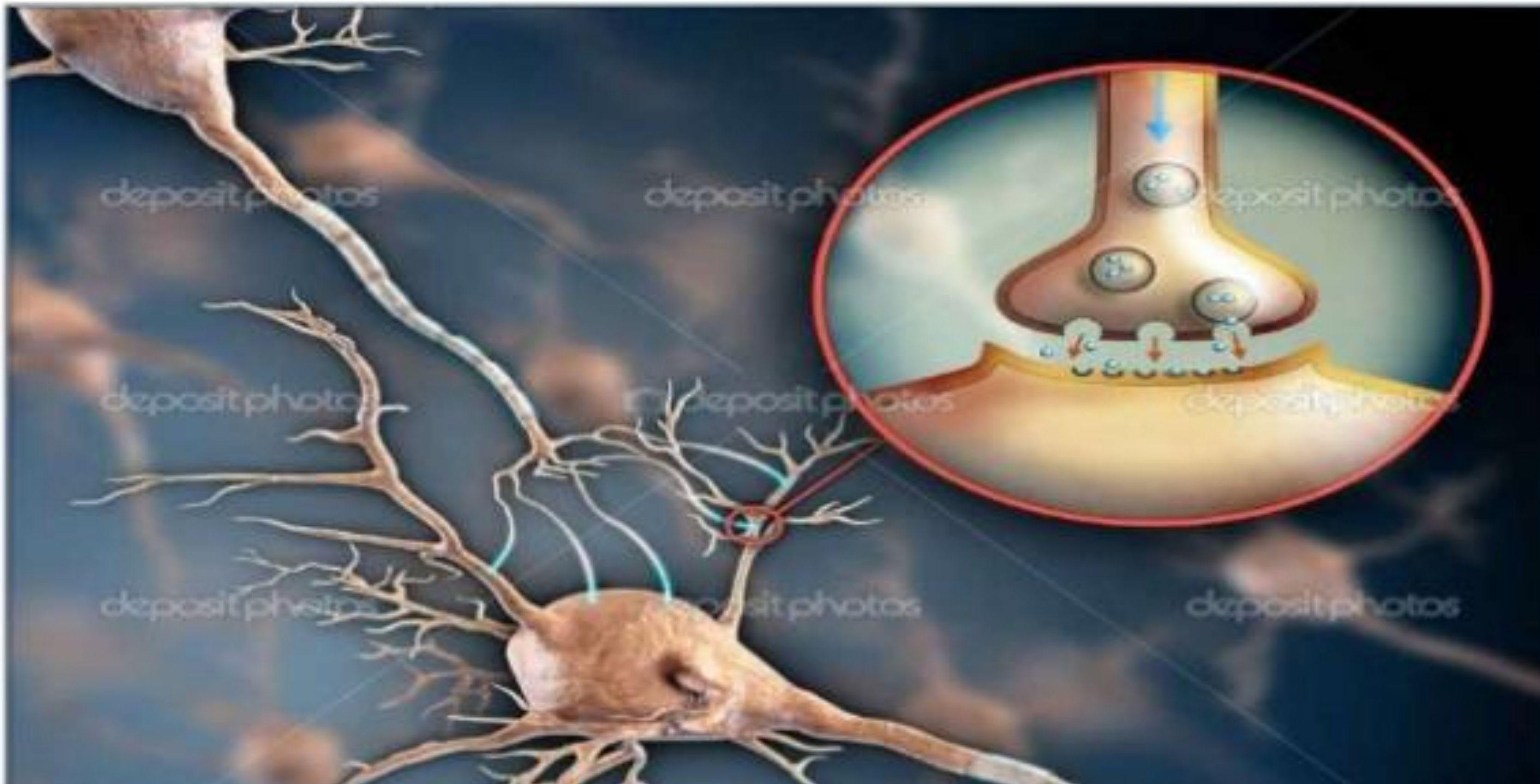
- Individual nerve cells connect with one another throug s.

- Individual nerve cells connect with one another
through special junctions, called **synapses**.



THE INSECT NERVOUS SYSTEM

- Acetylcholine, 5-hydroxytryptamine, dopamine, and adrenaline are examples of neurotransmitters found in both vertebrate and invertebrate nervous systems.



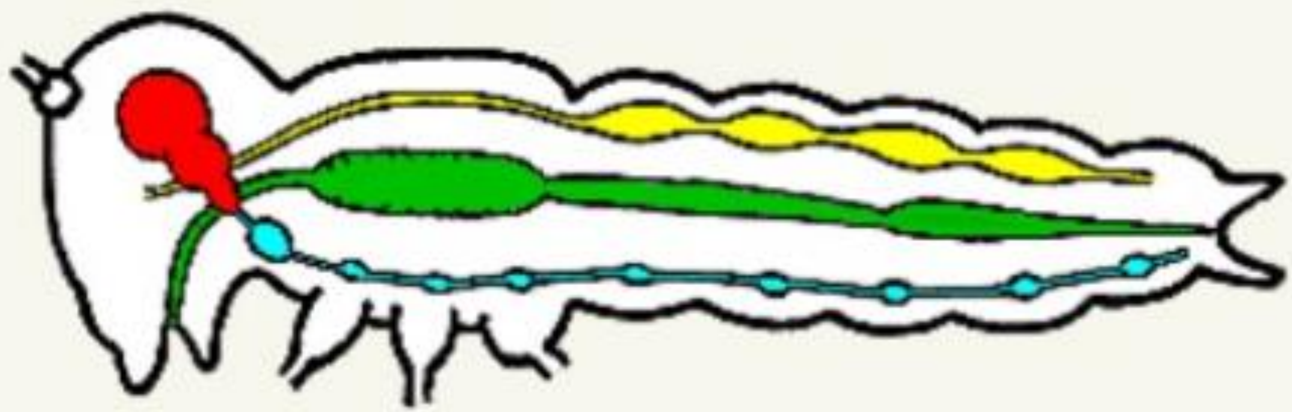
THE INSECT NERVOUS SYSTEM

The Central Nervous System

- Like most other arthropods, insects have a relatively simple central nervous system with a dorsal brain linked to a ventral nerve cord that consists of paired **segmental ganglia** running along the ventral midline of the thorax and abdomen.

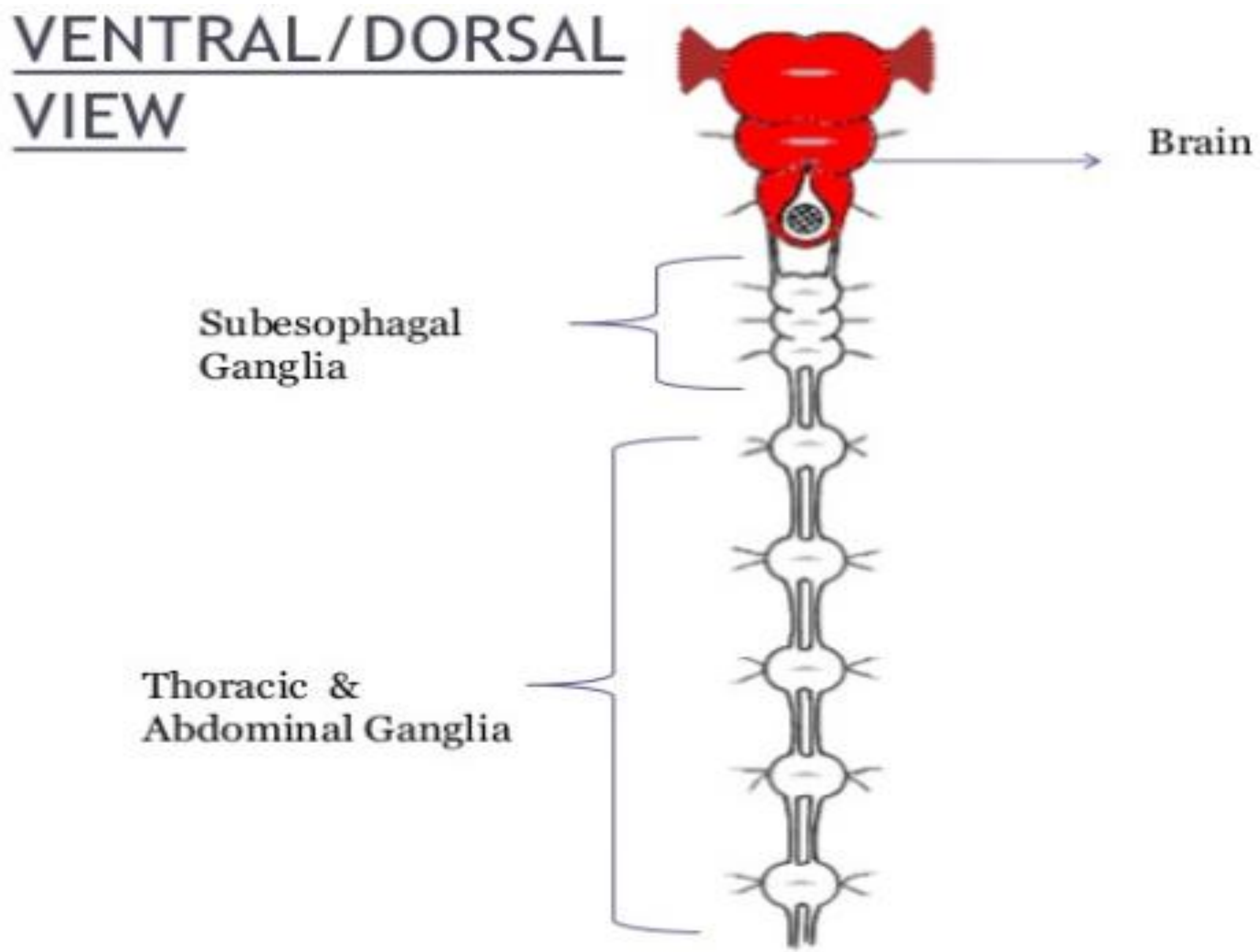
THE INSECT NERVOUS SYSTEM

LATERAL VIEW



Side view of body showing relative position of circulatory (yellow), digestive (green), and nervous (blue) systems. Brain (Red)

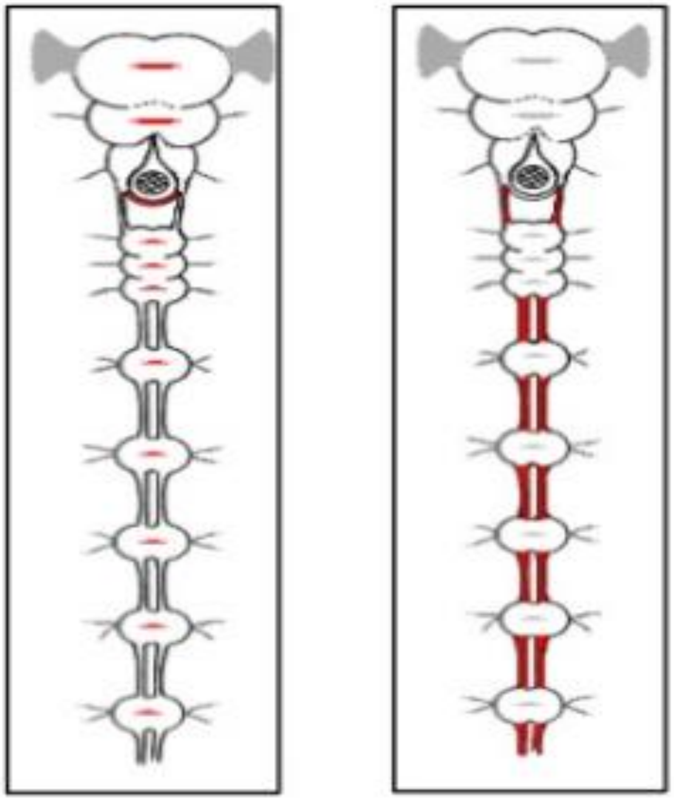
THE INSECT NERVOUS SYSTEM



THE INSECT NERVOUS SYSTEM

- Ganglia within each segment are linked to one another by a short medial nerve (commissure) and also joined by intersegmental connectives to ganglia in adjacent body segments.

Commissure nerves in red



Intersegmental connectives

THE INSECT NERVOUS SYSTEM

BRAIN

- An insect's **brain** is a complex of six fused ganglia (three pairs) located dorsally within the head capsule.

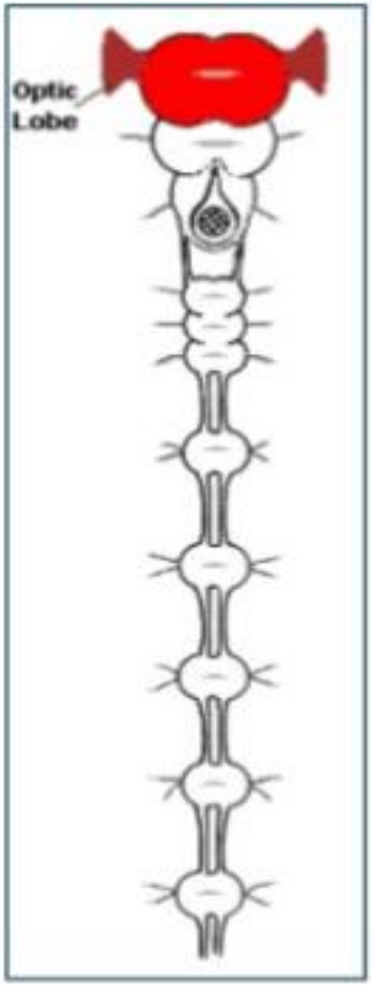
- Each part of the brain controls (innervates:supply) a limited spectrum of activities in the insect's body:

1. Protocerebrum
2. Deutocerebrum
3. Tritocerebrum

THE INSECT NERVOUS SYSTEM

Protocerebrum

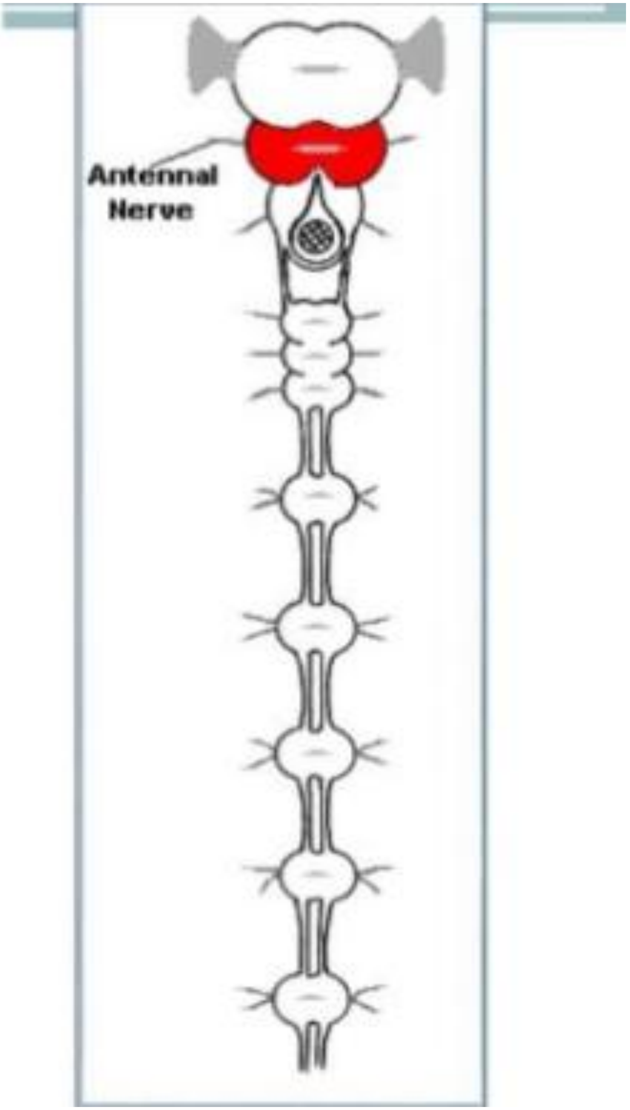
- The first pair of ganglia are largely associated with vision; they innervate the compound eyes and ocelli.



THE INSECT NERVOUS SYSTEM

Deutocerebrum:

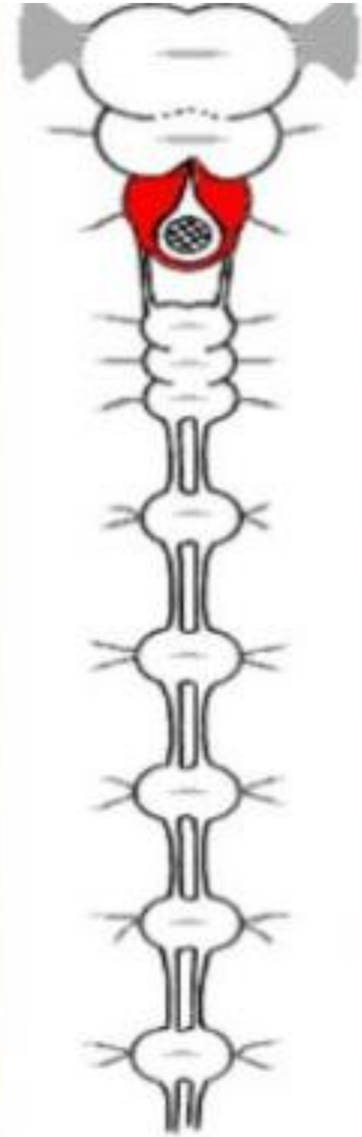
- The second pair of ganglia process sensory information collected by the antennae.



THE INSECT NERVOUS SYSTEM

Tritocerebrum:

- The third pair of ganglia innervate the labrum and integrate sensory inputs from proto- and deutocerebrums.
- They also link the brain with the rest of the ventral nerve cord and the **stomodaeal nervous system**, that controls the internal organs.
- The commissure for the tritocerebrum loops around the digestive system.



THE INSECT NERVOUS SYSTEM

SUBESOPHAGEAL GANGLION

- Located ventrally in the head capsule (just below the brain and esophagus) is another complex of fused ganglia (jointly called the subesophageal ganglion).
- The subesophageal ganglion innervates not only mandibles, maxillae, and labium, but also the hypopharynx, salivary glands, and neck muscles.

THE INSECT NERVOUS SYSTEM

VENTRAL NERVE CORD

- In the thorax, three pairs of thoracic ganglia (sometimes fused) control locomotion by innervating the legs and wings.

- Thoracic muscles and sensory receptors are also associated with these ganglia.

THE INSECT NERVOUS SYSTEM

- Similarly, abdominal ganglia control movements of abdominal muscles.
- Spiracles in both the thorax and abdomen are controlled by a pair of lateral nerves that arise from each segmental ganglion.
- A pair of abdominal ganglia usually fused to form a large **caudal ganglion**, innervates the excretory system, reproductive organs, and sensory receptors (such as cerci) located on the insect's back end.

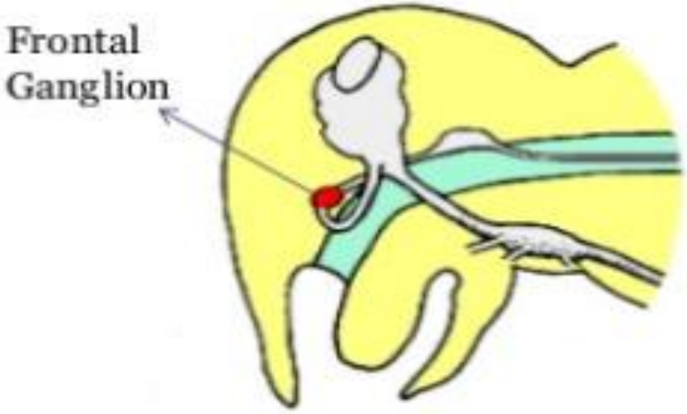
THE INSECT NERVOUS SYSTEM

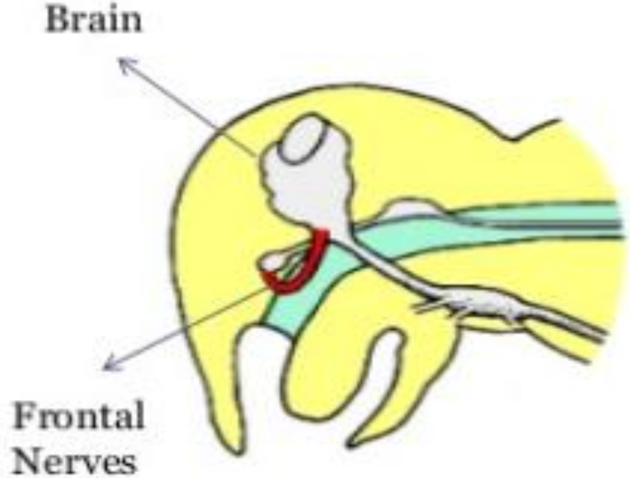
THE STOMODAEAL NERVOUS SYSTEM

- An insect's internal organs are largely innervated by a stomodeal (or stomatogastric) nervous system.
- The stomodeal nervous system controls activities of the gut and circulatory system

THE INSECT NERVOUS SYSTEM

- A pair of frontal nerves arising near the base of the tritocerebrum link the brain with a frontal ganglion(unpaired).





- This ganglion innervates the pharynx and muscles associated with swallowing.

THE INSECT NERVOUS SYSTEM

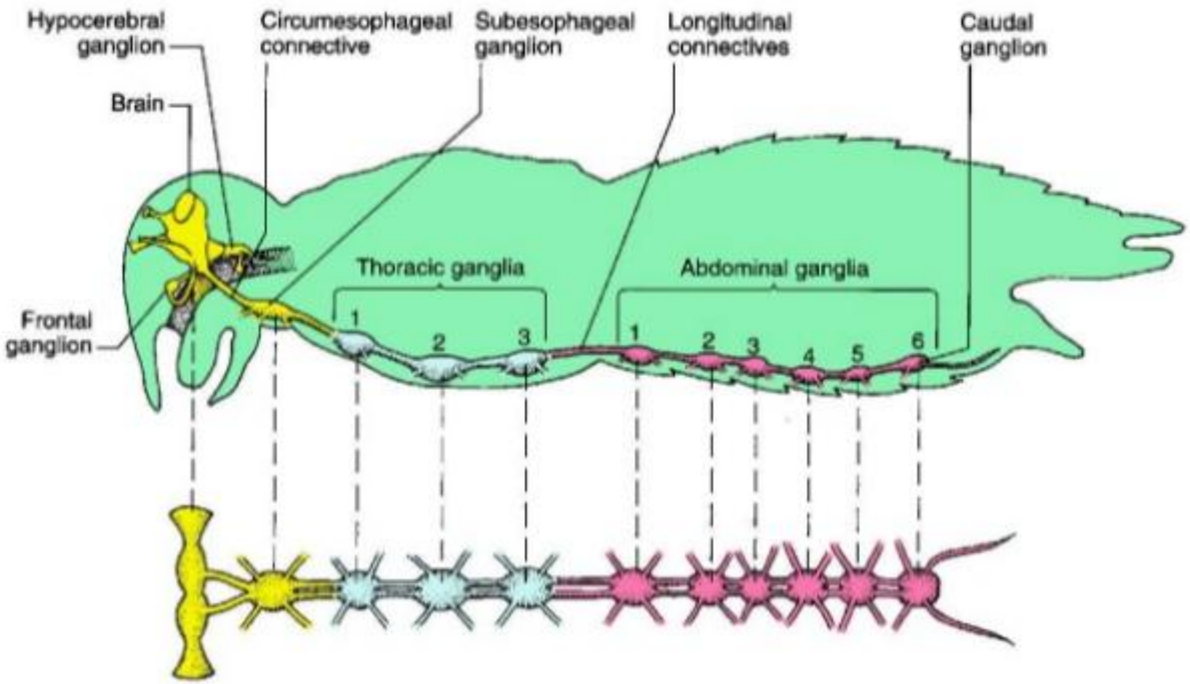
- In comparison to vertebrates, an insect's nervous system is far more de-centralized.
- Most overt behavior (*e.g*. feeding, locomotion, mating, etc.) is integrated and controlled by segmental ganglia instead of the brain.

THE INSECT NERVOUS SYSTEM

- In some cases, the brain may stimulate or inhibit activity in segmental ganglia but these signals are not essential for survival.

- Indeed, a headless insect may survive for days or weeks (until it dies of starvation or dehydration) as long as the neck is sealed to prevent loss of blood!

THE INSECT NERVOUS SYSTEM



THE INSECT NERVOUS SYSTEM

A. On structural basis

i. **Monopolar**: neuron with a single axon

ii. **Bipolar**: neuron with a proximal axon and a long distal dendrite.

iii. **Multipolar**: neuron with a proximal axon and many distal dendrites.

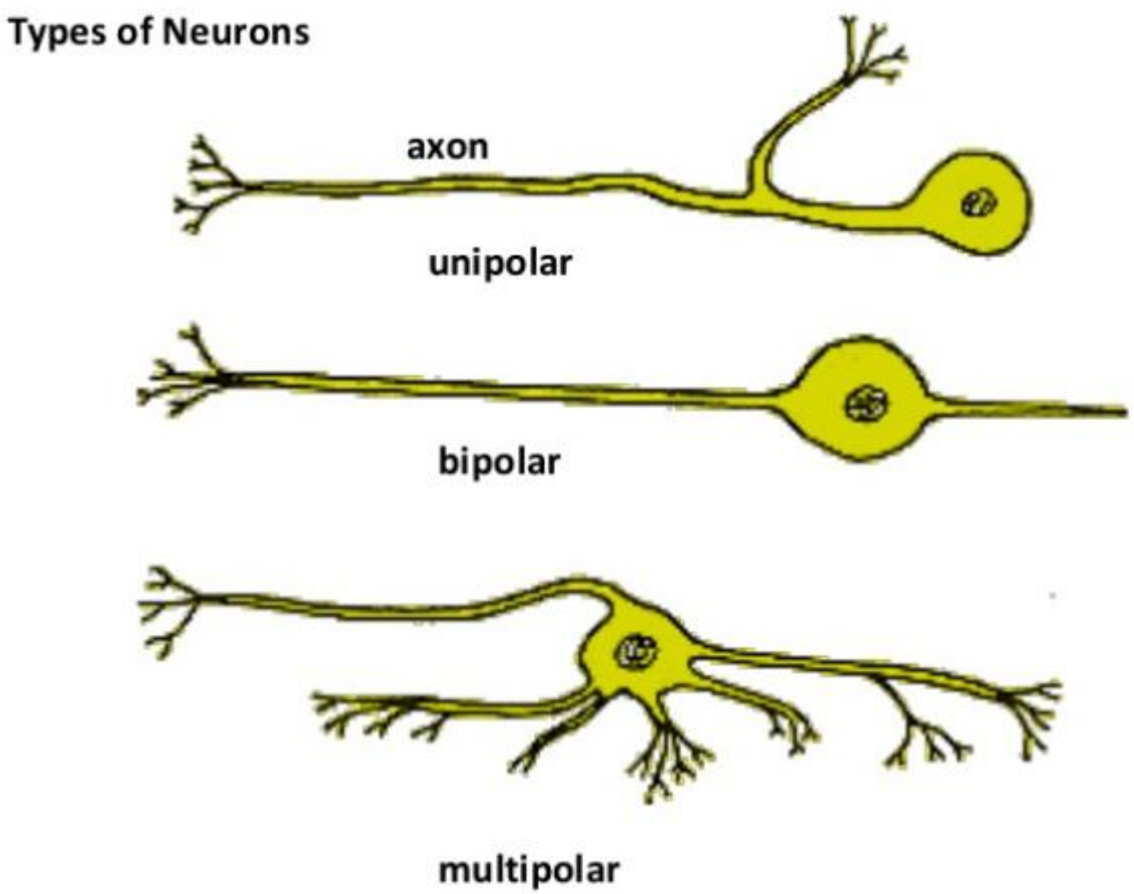
B. Functional basis

i. **Sensory neuron**: It conducts impulse from sense organs to central nervous system (CNS).

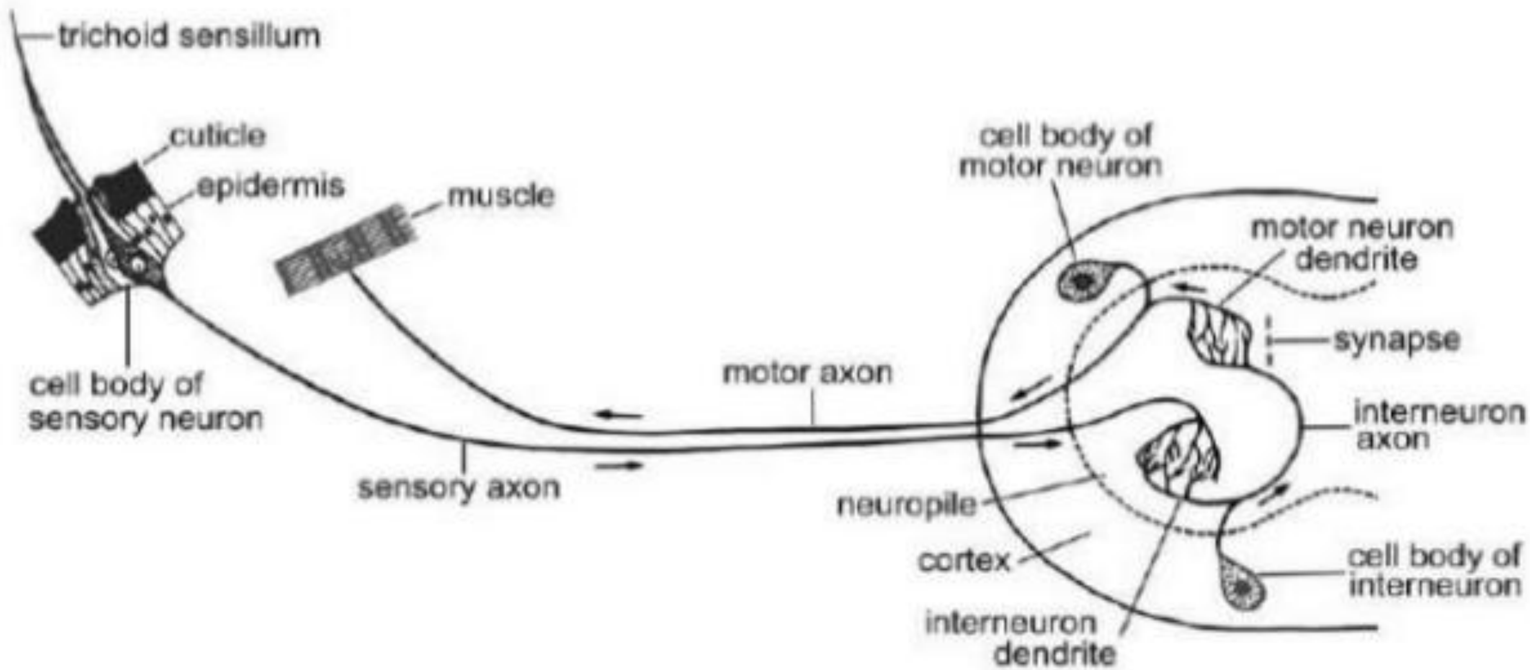
ii. **Motor neuron**: It conducts impulse from CNS to effector organs

iii. **Inter neuron** (association neuron): It inter-links sensory and motor neurons. The cell bodies of inter neurons and motor neurons are aggregated with the fibers inter connecting all types of nerve cells to form nerve centers called **ganglia.**

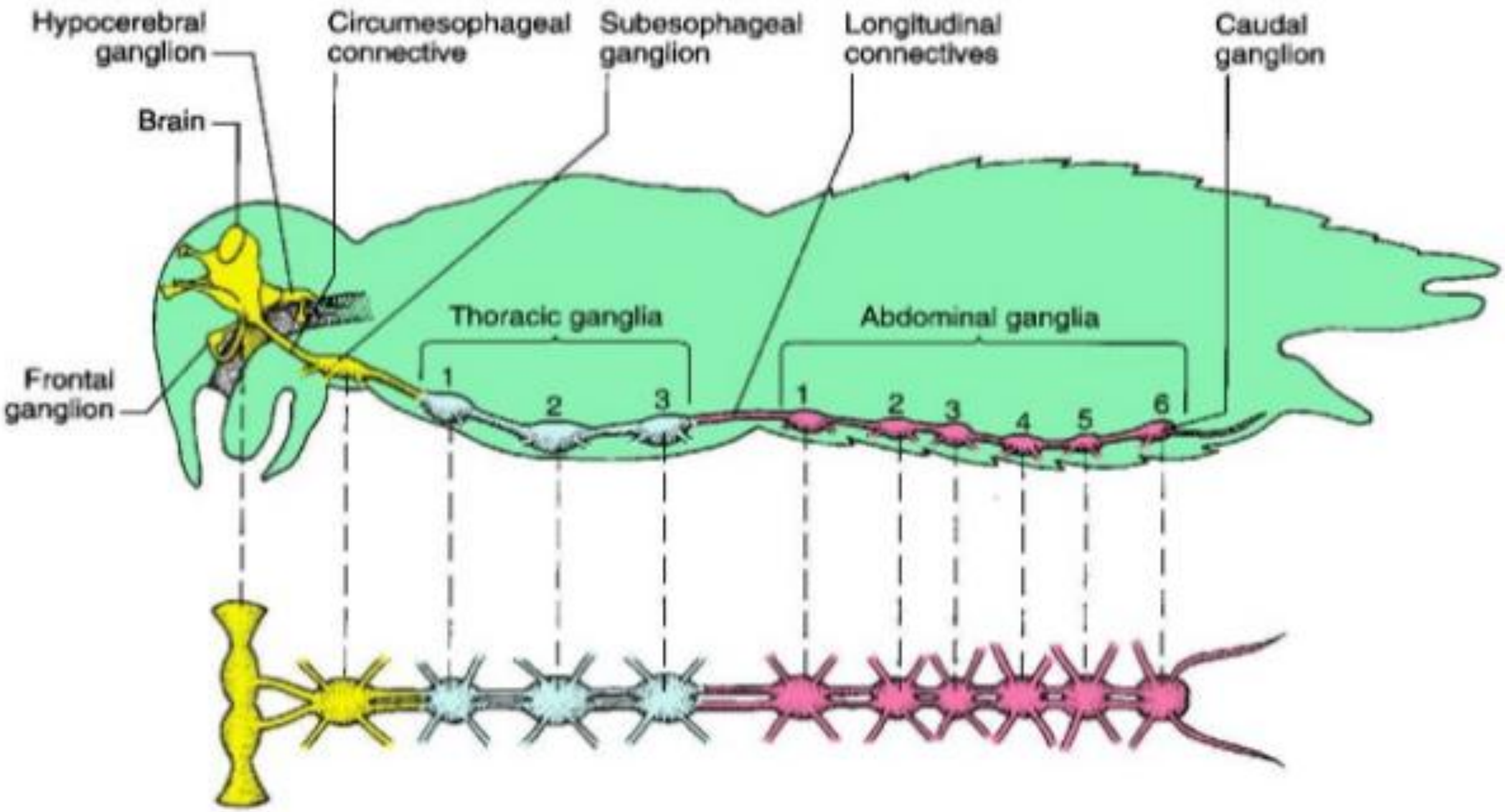
THE INSECT NERVOUS SYSTEM



THE INSECT NERVOUS SYSTEM



THE INSECT NERVOUS SYSTEM



THE INSECT NERVOUS SYSTEM

Mechanism of impulse conduction: Impulses are conducted by the neurons by two means.

1) **Axonic conduction**: Ionic composition varies between inside and outside of axon resulting in excitable conditions, which leads to impulse conduction as electrical response.

2) **Synaptic conduction**: Neurochemical transmitters are involved in the impulse conduction through the synaptic gap. Neurotransmitters and the type of reactions helping in the impulse conduction are as follows.

THE INSECT NERVOUS SYSTEM

Nervous system can be divided in to three major sub-systems as

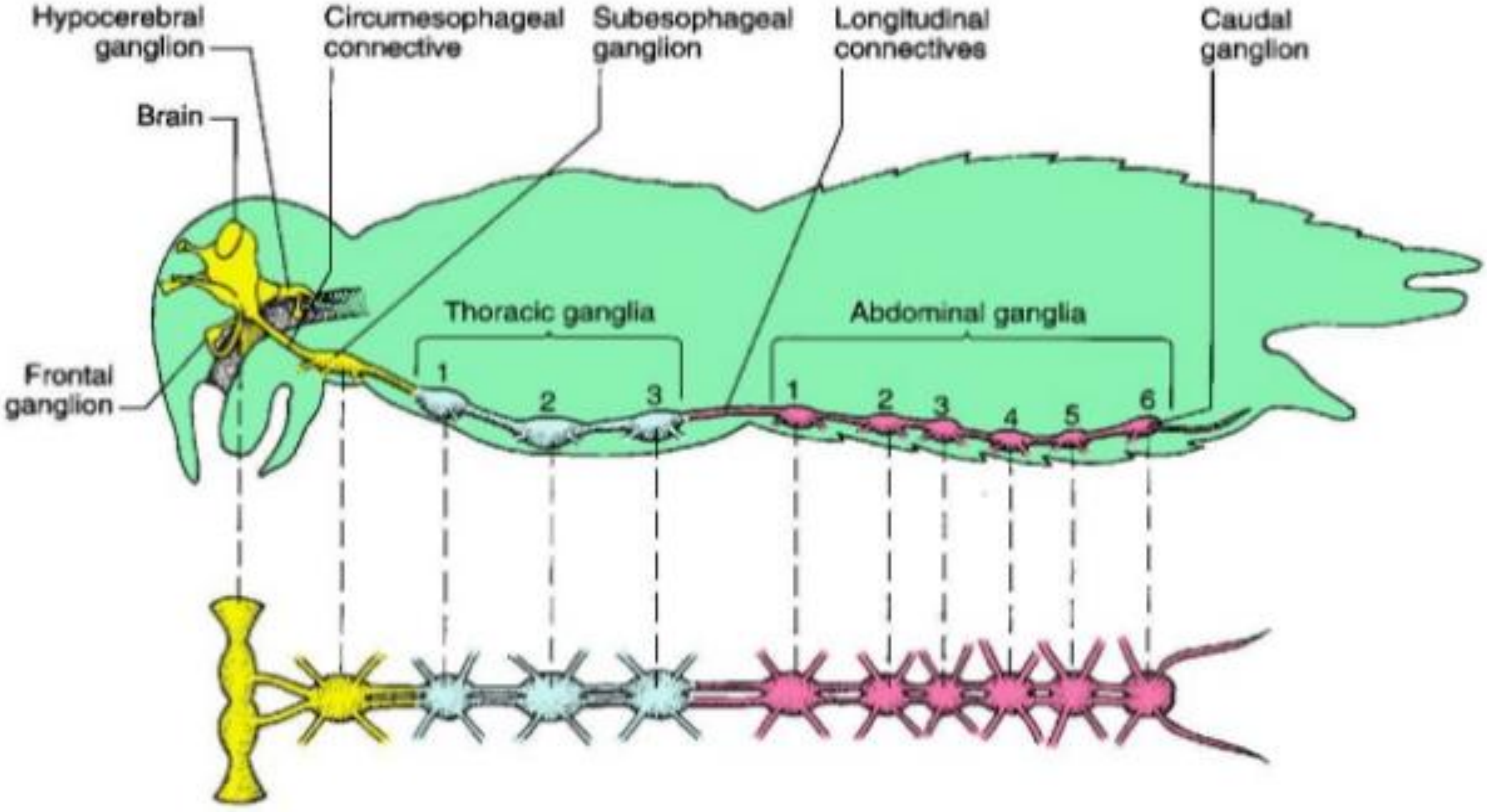
i. Central nervous system (CNS)

ii. Visceral nervous system (VNS)

iii. Peripheral nervous system (PNS)

I. **Central nervous system**: It contains double series of nerve centers (ganglia). These ganglia are connected by longitudinal tracts of nerve fibers called **connectives** and transverse tracts of nerve fibers called **commissures**. Central nervous system includes the following.

THE INSECT NERVOUS SYSTEM



THE INSECT NERVOUS SYSTEM

a. Brain: Formed by the fusion of first three cephalic neuromeres.

1)Protocerebrum: Large, innervate compound eyes and ocelli.

2)Deutocerebrum: Found beneath protocerebrum, innervate antennae.

3)Tritocerebrum: Bilobed, innervate labrum.

Brain is the main sensory centre controlling insect behaviour.

b. Ventral nerve cord: Median chain of segmental ganglia beneath oesophagus.

c. Sub esophageal ganglia: Formed by the last three cephalic neuromeres which innervate mandible, maxillae and labium.

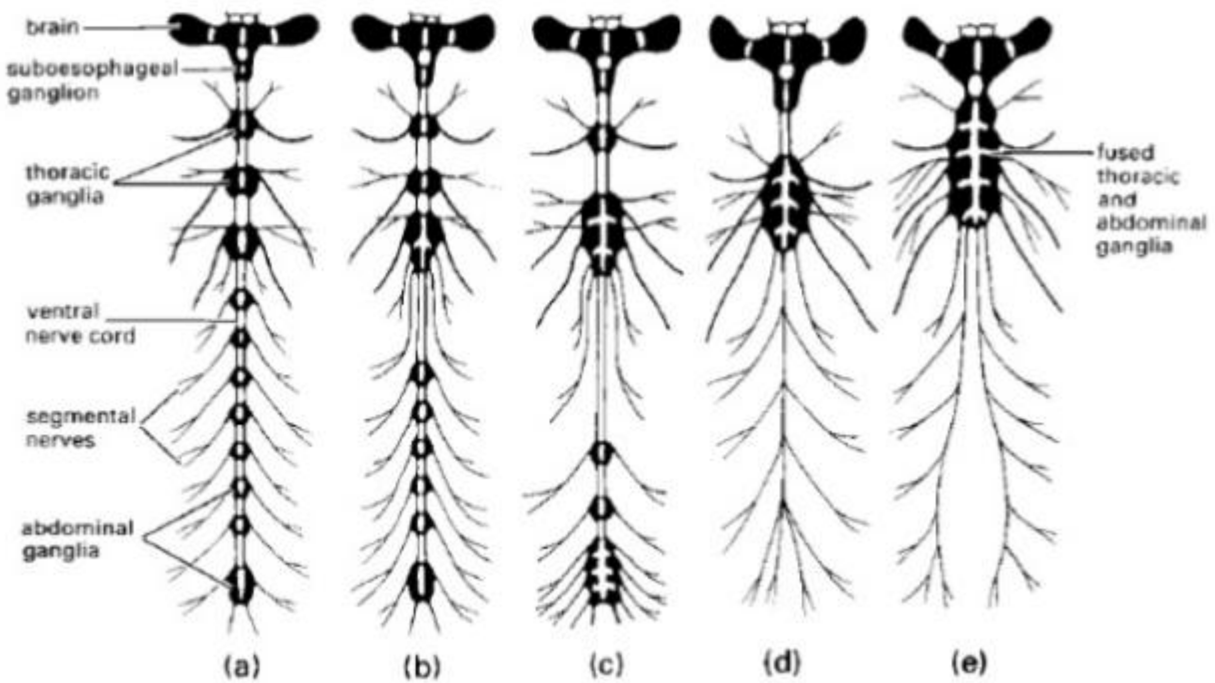
THE INSECT NERVOUS SYSTEM

d. Thoracic ganglia: Three pairs found in the respective thoracic segments, largest ganglia, innervate legs and muscles.

e. Abdominal ganglia: Maximum eight pairs will present and number varies due to fusion of ganglia. Innervate spiracles.

f. Thoracico abdominal ganglia : Thoracic and abdominal ganglia are fused to form a single compound ganglia. Innervate genital organs and cerci.

THE INSECT NERVOUS SYSTEM



THE INSECT NERVOUS SYSTEM

II. **Visceral nervous system**: The visceral (sympathetic) nervous system consists of three separate systems as follows:

(1) stomodeal/stomatogastric which includes the frontal ganglion and associated with the brain, aorta and foregut;

(2) Ventral visceral, associated with the ventral nerve cord; and

(3) Caudal visceral, associated with the posterior segments of abdomen. Together the nerves and ganglia of these subsystems innervate the anterior and posterior gut, several endocrine organs (Corpora cardiaca and Corpora allata), the reproductive organs, and the tracheal system including the spiracles.

THE INSECT NERVOUS SYSTEM

Nervous system can be divided in to three major sub-systems as

i. Central nervous system (CNS)

ii. Visceral nervous system (VNS)

iii. Peripheral nervous system (PNS)

I. **Central nervous system**: It contains double series of nerve centers (ganglia). These ganglia are connected by longitudinal tracts of nerve fibers called **connectives** and transverse tracts of nerve fibers called **commissures**. Central nervous system includes the following.

THE INSECT NERVOUS SYSTEM

IV. **Peripheral nervous system**: The peripheral nervous system consists of all the motor neuron axons that radiate to the muscles from the ganglia of the CNS and visceral nervous system plus the sensory neurons of the cuticular sensory structures (the sense organs) that receive mechanical, chemical, thermal or visual stimuli from an environment.