Control of ventilation

- Ventilatory movements initiated by the accumulation of carbon dioxide and, to a lesser extent, the lack of oxygen in the tracheal system.
- This will act directly on centers in the ganglia of the central nervous system.
- Each abdominal ganglion produce rhythmical sequences of activity controlling movements.

- In normal ventilation by *Schistocerca*, involving only dorso-ventral movements sclerites, expiration is produced by tergosternal muscles innervated by motor neurons from the ganglion of the corresponding segment.
- Inspiration is produced by muscles inserted low on the tergum and innervated by axons in branches from the median ventral nerve .
- Alternation of inspiratory and expiratory movements is controlled from different ganglia.

- Coordination is achieved by an interneurone, one in each ventral connective (cell 2 in Fig. 356), which originates in the metathoracic ganglion and extends to the last abdominal ganglion.
- Action potentials in the interneurone activate the segmental local interneurone (cell 3) and probably have a weak inhibitory effect on the inspiratory motorneurones (cell 5 in Fig. 356).

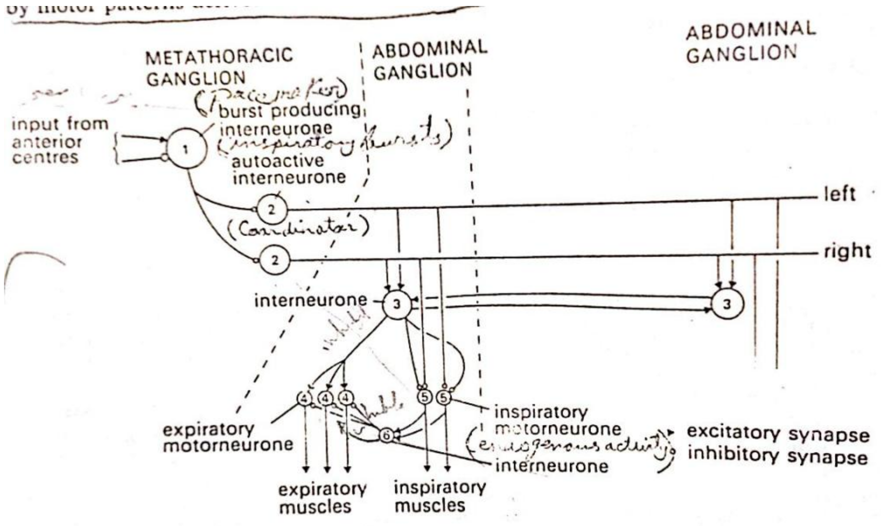

Fig. 356 Diagram of the connections between neurones in the central nervous system involved in the control of ventilation in a locust (after Lewis *et al.*, 1973)

- The local interneuron excites the expiratory motor neurons (cell 4) and strongly inhibits the inspiratory motor neuron (cell 5).
- Inspiration occurs when the intersegmental interneurons are silent and the ispiratory motor neurons become spontaneously active, at the same time inhibiting the expiratory motor neurons via another local interneuron (cell 6)
- Hence inspiration only occurs when the interneurones (cell 2) are inhibited, so that the inspiratory motor-neurones fire as a result of their endogenous activity and inhibit the expiratory motorneurones via a small interneurone (cell 6).

- The rate of ventilation is altered by reducing the interval between inspiratory bursts and is affected by sensory input form various sources.
- Centres sensitive to carbon dioxide are present in the head and thorax of *Schistocerca* and these modify the activity of the pacemaker, while the output is also modified by high temperature and nervous excitation generally.
- The coordination of the spiracles with the ventilatory movements is brought about by motor patterns derived from the ventilator centers.

Control of spiracle opening

- The spiracles are normally open for the shortest necessary for efficient respiration in order to keep water from the tracheal system to a minimum.
- Spiracle closure results from the sustained of the closer muscle, while opening commonly results from the elasticity of the surrounding cuticle when the closer muscle is relaxed.

- The muscle is controlled by the central nervous system, but may also respond to local chemical stimuli which internal control.
- The frequency of motor impulses to the opener muscle is also affected by the water balance of the insect, possibly acting through the concentration of a particular ion.
- If the insect is desiccated the impulse frequency rises and the spiracles remain closed longer; with excess hydration the converse is true and so that rate of water loss is increased.

- Slowly, in the course of the interburst period, carbon dioxide accumulates.
- Most of it is in the tissues, and in the pupa of agapema (Lepidoptera) 90 % of the carbon dioxide produced during the interburst is retained in the tissues.
- Nevertheless the concept reaction in the tracheal system rises and ultimately it reaches a level which promotes spiracle opening.
- In Hyalophora this occurs when the gas in the tracheae contains more than 6% carbon dioxide then the spiracles open wide, releasing a burst of carbon dioxide.

- The bulk inward movement of air, while preventing the outward flow of carbon dioxide and carrying in oxygen also carries in a large volume of nitrogen and the inflow of this gas must be matched by its outward diffusion .
- The cyclic release of carbon dioxide may not , in itself , be important, but the prolonged periods of closure of the spiracles are important because they result in the restriction of water loss from the tracheal system.
- Kanwisher (1966) suggests that as a result of this mechanism water loss from the pupa of Hyalophora dose not greatly exceed the production of metabolic water and the pupa only loses 5% of its weight over a four-month period.
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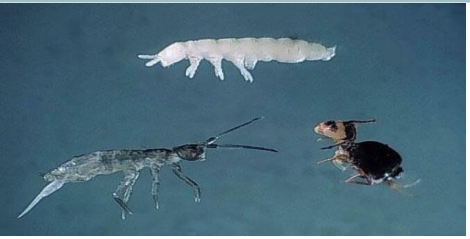

Cutaneous respiration

- Some gaseous exchange takes place through the cuticle of most insects, but this does not usually amount to more than a few percent of the total movement of gas.
- On the other hand, Protura and most collembola have no tracheal system and must depend on cutaneous respiration together with transport from the body surface to the tissues by the haemolymph.

- Cutaneous respiration is also important in eggs , aquatic insects, coupled with an apneustic tracheal system , and endoparasitic insects.
- Cutaneous respiration without an associated apneustic tracheal system can only suffice for very small insects with a large surface/volume ratio.
- The impermeability of most insect to oxygen arises from the epicuticle, but not from the wax layer which renders the cuticle impermeable to water.
- The permeability to carbon dioxide may be rather greater and the loss of this gas through the intersegmental membranes may be appreciable.

Other functions of the tracheal system

- Apart from respiration the tracheal system has a number of other functions. The whole system, and in particular the air-sacs, lowers the specific gravity of the insect in aquatic insects. It gives some degree of buoyancy.
- The tracheal system in some insects has a major role in hemolymph circulation.
- Air-sacs, being collapsible, allow for the growth of organs within the body without any marked changes in body form.

- Thus at the beginning of an instar the tracheal system of Locusta (Orthoptera) occupies 42% of the body volume. By the end of the instar it only occupies 3.8% , due to the growth of the other organs causing compression of the air-sacs.
- The air-sacs also permit changes in gut volume as a result of feeding. In Locusta the increase in crop volume following a meal is accompanied by a corresponding decrease in the volume of the thoracic air-sacs (Bernays and Chapman, 1973).

- In some noctuids (Lepidoptera), trachea form a reflecting tapetum beneath the eye, and tympanal membranes are usually backed by an airsac which, being open to the outside air, allows the tympanum to vibrate freely with a minimum damping.
- Expansion of the tracheal system may also assist when an insect inflated itself after molt. Thus in dragonflies, spiracle closure , preventing the escape of gas from the tracheae, accompanies each muscular effort of the abdomen during expansion of the wings .
- The airsacs of some isnects insulate the thorax, and therefore the flight muscles, from the abdomen. This makes it possible for thorax and abdomen to have significantly different tempratures and gives the insects the capacity to regulate thoracic temprature.

- An important general function of trachea and tracheal cells is in acting as connective tissue, binding other organs together.

- Finally, the tracheal system may be involved in defense (forcibly expelled from the second abdominal spiracle, *Gromphadorrhina* (Blattodea) sounds are produced forcing air out through the spiracles.