A DECADE OF DRAGONFLY NEUROBIOLOGY

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During the past ten years there have been about 200 papers written on various aspects of dragonfly neurobiology; these can be divided into several topics - central nervous system, stomodeal nervous system, sensory and motor neurons, mechanoreceptors, chemoreceptors, visual receptors, muscles, ventilation, swimming, prey capture and flight - which are discussed below. Neurosecretion and the physical aspects of vision are not considered here.

CENTRAL NERVOUS SYSTEM

The basic arrangement of a brain and sub-oesophageal, three thoracic and up to eight abdominal ganglia is well established. The first abdominal is fused with the metathoracic ganglion in late instar aeshnid larvae at least. Apart from the lateral segmental nerves, most segments have an associated unpaired median nerve, the motor axons of which divide to send one branch to each side (TILLYARD, 1917; WHEDON, 1919; ZAWARZIN, 1924; MILL, 1964, 1965; MATHUR, 1972a). There are few recent papers on the structure of the odonate brain (e.g. GOODMAN, 1974) but there are three reviews on insect brain structure (HOWSE, 1974, 1975; STRAUS-FELD, 1976). Possible neurotransmitter substances have been described in last-instar larvae of *Aeshna viridis*, where catecholamines (dopamine and noradrenaline) and an indolamine (5-hydroxytryptamine) have been located in the optic lobes (ELOFSSON & KLEMM, 1972; see also KLEMM, 1974, 1979).

STOMODEAL NERVOUS SYSTEM

The presence of a stomodeal nervous system has been known for

a long time, but has recently been described in *Crocothemis servilia erythraea* (MATHUR, 1972b), *Bradinopyga geminata* and *Orthetrum chrysis* (VARMA, 1972), and *Pantala flavescens* (NANDCHAHAL & RATHORE, 1979). The brain has connections with a small frontal ganglion and a pair of small, posteriorly fused corpora cardiaca, and the latter are connected to a small hypocerebral ganglion and to the paired corpora allata. Posteriorly the hypocerebral ganglion gives rise to a median gastric nerve which in *C. s. erythraea* and *P. flavescens* terminates in an ingluvial ganglion, from which nerves arise to innervate the anterior region of the gut. In *B. geminata* and *O. chrysis,* however, there is no ingluvial ganglion and the gastric nerve divides into a pair of ingluvial nerves. The corpora allata are large, but variable in position. They may lie anterior to the brain (*C. s. erythraea*), posterior to the brain and sub-oesophageal ganglion (*P. flavescens*) or ventral to the nerve cord (*B. geminata* and *O. chrysis*).

SENSORY AND MOTOR NEURONS

In a mid-abdominal segment of a late instar larva of *Anax imperator* the 1st segmental nerve contains about 2,000 axons, some 26 of which are motor, the 2nd nerve contains about 1,250 axons (including about seven motor), and the 3rd nerve is entirely motor and contains about eight axons. Thus there are about 41 pairs of motor neurons per segment. In addition there is a pair of axons in the median nerve, arising from two unpaired, median somata. The 43 motor axons on each side innervate 19 pairs of muscles (ZAWARZIN, 1924; Mill & Whittles, in preparation).

MECHANORECEPTORS

The work on proprioceptors in insects up to about 1975 has been reviewed by FINLAYSON (1976) — abdominal and thoracic receptors; LAVERACK (1976) — external receptors; MOULINS (1976) — ultrastructure of chordotonal organs; WALES (1976) — receptors of the mouthparts and gut; and WRIGHT (1976) — limb and wing receptors. There is also a general review on mechanoreceptors in some of the more primitive insect orders (FUDALEWICZ-NIEMCZYK *et al.,* 1978). The following account is largely restricted to those papers pertaining to the Odonata which have been published since 1971.
The structure of antennal sensilla, including Johnston's organ, has been studied in larval *Coenagrion* and *Aeshna* (IVANOV, 1978 a, b). A variety of sensilla have been described on the mouthparts of

Libellula depressa and *L. quadrimaculata*; some are presumably mechanoreceptors, others are probably chemoreceptors (PETRY-SZAK, 1977).

Leg receptors include the spines which have recently been redescribed by PILL & MILL (1979), and the internal joint receptors. Of the latter, recent attention has been given to the two coxal organs (LOMBARDO, 1973) and the tarso-pretarsal (TP) organs of *Anax imperator* (MILL & PILL, 1981). The latter contains about eight sensory cells embedded in a connective tissue strand, and a brief physiological study indicated that flexion-sensitive movement units predominate. Most abdominal segments contain two pairs of dorsal stretch receptors and a pair of lateral chordotonal organs (for earlier references see FINLAYSON, 1976). The latter each contain three sensory cells and their fine structure has been described in *Anax imperator*, *Aeshna cyanea* and *Libellula depressa*. Recordings from virtually intact larvae confirmed that the two stretch receptors (one longitudinal and one vertical) on each side behave antagonistically to each other during rhythmic ventilation, and that the chordotonal organs may be active during expiration (PILL & MILL, 1981).

CHEMORECEPTORS

Insect antennal chemoreceptors have been reviewed by CALLA-HAN (1975), but there appears to be comparatively little recent information on odonates, with the exception of a survey by SLIFER & SEKHON (1972) which covered six species of Zygoptera and 11 species of Anisoptera. They described simple and compound pit pegs (sensilla coeloconica) on the antennal flagella, more abundant in anisopterans than in zygopterans. Single-pore sensilla have been described on the maxillary palps of *Coenagrion puella* and *Ischnura elegans*. There are four on each palp, innervated either by two (A-sensilla) or five (B-sensilla) sensory cells (BASSEMIR & HANSEN, 1980).

VISUAL RECEPTORS

As well as a pair of compound eyes, dragonflies possess a median and two lateral ocelli. The compound eyes provide visual acuity and also fine resolution to define the position of the horizon during flight whereas the ocelli monitor rapid changes in the position of the horizon, information which is important for correcting altitude during flight (STANGE & HOWARD, 1979). There is an extensive literature on visual receptors, with recent reviews on various aspects by MAZ-OKHIN-PORSHNYAKOV (1971), LAUGHLIN (1976c), BURK-

HARDT (1977), CHAPPELL (1979), JARVILEHTO (1979), MEN-ZEL (1979), MILLER (1979) and SNYDER (1979) (see also HOR-RIDGE, 1975); also a very recent annotated bibliography (LAVOIE *et al.*, 1981). The following account excludes information on various aspects of the visual system such as development, pseudopupils, visual fields, binocular vision, resolving power, acceptance angle of the ommatidia, and the arrangement of the facets in the compound eyes.
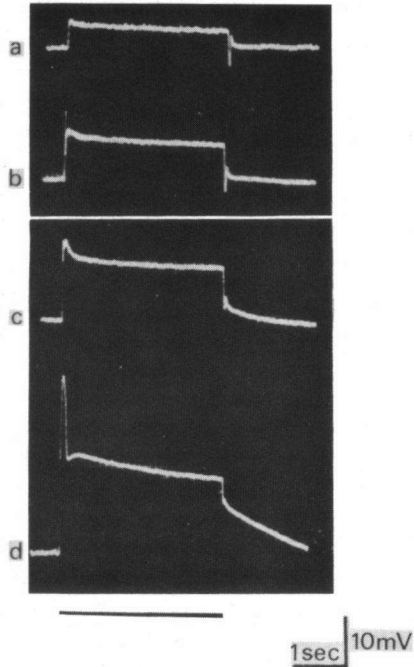

Fig. 1. Ocellar receptor-cell responses to 3 sec light flashes (indicated by the horizontal lines). Intensity increases from (a) to (d). Upwards indicates depolarization. (From CHAP-PEL & DOWLING, 1972.)

O c e l l i. − The median ocellus consists of two lateral halves, in which pigment movements (dispersal and retraction) are independent (STAVENGA *et al.*, 1979). The light response in the photoreceptor cells consists of a depolarizing 'on' transient followed by a graded depolarization. At the end of the light flash there is a hyperpolarizing 'off' transient followed, notably at higher intensities, by a slow decay of the remaining depolarization (Fig. 1). After a latency of 5-20 ms there is a response in the post-synaptic, second-order neurons in the ocellar nerve, which consists of a large hyperpolarizing 'on'
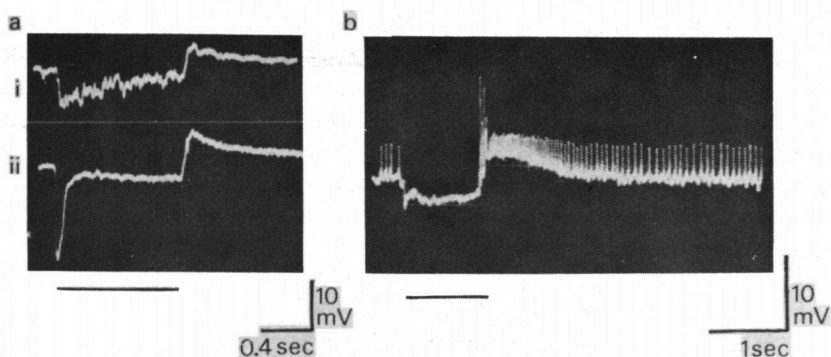
Fig. 2. Ocellar second-order neuron responses to 1 sec light flashes (indicated by the horizontal lines): (a) shows the more usual type of response, in which there is no impulse activity. (ii) is at a higher intensity than (i). In (b) the neuron is spontaneously active before and after stimulation. Upwards indicates depolarization. (From CHAPPEL & DOWLING, 1972.)

transient with a smaller maintained hyperpolarization and a depolarizing 'off' transient (Fig. 2) (CHAPPELL & DOWLING, 1972; KLINGMAN, 1976).

There is ultrastructural evidence that reciprocal (feedback) and serial synapses occur, both between adjacent photoreceptor cells and between the receptor cells and the second-order neurons (DOW - LING & CHAPPELL, 1972), and the latter is supported by physiological studies (STORE & CHAPPELL, 1979). DOWLING & CHAP - PELL (1972) suggested that the lateral and feedback synapses help to enhance the transients in the post-synaptic responses in the second order neurons.

In *Anax junius, Aeshna tuberculifera* and *Libellula pulchella* all cells of the median ocelli have peak sensitivities at 360nm and 500 nm, but in *A. junius* a third peak was present at 440nm (CHAPPELL & DEVOE, 1975).

There are indications that the neurotransmitter at the receptor cell-ocellar nerve neuron junctions may be acetylcholine acting as an inhibitor, while the neurotransmitter acting at the feedback synapses from the ocellar nerve dendrites onto the receptor cells may be GABA (excitatory) (KLINGMAN, 1976; KLINGMAN & CHAPPELL, 1978).

The lateral ocellar nerves at least contain both afferent and efferent neurons (ROSSER, 1974). A large efferent neuron is activated by illumination of the eyes and by wing movements. The latter also elicit activity in a large afferent fibre which is inhibited by illumination

(KONDO, 1978).

C o m p o u n d   E y e s. – The arrangement of the ommatidia in the compound eyes is similar in larvae and in adults. The eye grows by adding rows of new ommatidia, particularly at the last ecdysis, but there is some reorganization of the optic lamina prior to the adult ecdysis (MINELLI & PAVAN, 1974; LAVOIE *et al.*, 1978b; PAULUS, 1979). The structure of the adult eye of *Enallagma boreale* is described by LAVOIE *et al.*(1975) and, in this species, the crystalline cone is longer and narrower in the larva than in the adult (LAVOIE *et al.*, 1978a). Growth and differentiation of the eyes are independent of the optic lobes, however, interaction occurs between them which affects the structure of the ommatidia and the growth of the optic lobes (MOUZE, 1971, 1974, 1976, 1978, 1979, 1980).
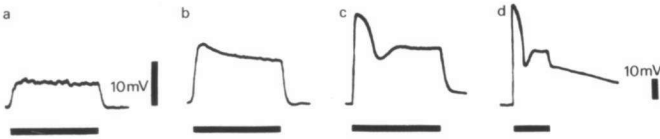

Fig. 3. Compound-eye retinula-cell responses to 0.5 sec light flashes (indicated by the horizontal lines). Intensity increases from (a) to (d). (From LAUGHLIN, 1973.)

Each compound eye comprises a crystalline cone of four cone cells, below which lie eight retinula cells. The rhabdom is of the closed type and is formed by fused or tiered rhabdomeres. In the dorsal region of the eye of *Aeshna* there are seven normal cells (5 distal and 2 proximal), each of which bears a rhabdomere and hence contributes to the central rhabdom, and one small (vestigial) cell which does not possess a rhabdomere. There are also three sublayers in *Crocothemis servilia*. In ommatidia of the dorsal retina of *Hemicordulia tau* there are four normal cells and four vestigial cells, the latter making virtually no contribution to the rhabdom. In the ventral retina of this species there are seven normal and one vestigial cell in each ommatidium. Different dorsal and ventral regions of the retina occur typically in insects that need to detect objects against the background of the sky (EGUCHI, 1971; PAIK *et al.*, 1972; LAUGHLIN & McGINNESS, 1978). The fused rhabdom acts as a single, integrated unit and is associated with high absolute sensitivity combined with colour vision and acuity. The partitioning or tiering (in zygopterans) may be to enhance the polarization sensitivity of the retinular cells (SNYDER, 1973a,b).

The dark-adapted retinula cells show graded depolarizations in

response to light flashes. At low levels of illumination the response is monophasic, but at higher levels there is an initial transient 'on' response followed by a maintained depolarization. After the 'on' transient there is fairly rapid adaptation (100 ms) at first, followed by a slower phase, lasting up to 60 s. At the end of the light flash there is a decrease in the depolarization which is initially fairly rapid. At low light intensities some cells show a short (25 ms) hyperpolarizing afterpotential, but in others (and in all cells at higher intensities) the afterpotential consists of an exponential decay of the depolarization (Fig. 3) (AUTRUM & KOLB, 1972; LAUGHLIN, 1973; LAUGHLIN & HARDIE, 1978).

Fig. 4. Compound-eye second-order neuron (LMC) responses to 0.5 msec light flashes (indicated by the horizontal lines). Intensity increases from (a) to (d). (From LAUGHLIN, 1973.)

After a latency of about 2 ms a post-synaptic response occurs in second-order neurons called 'large monopolar cells' (LMCs), which receive input from several retinula cells. These show graded hyperpolarizations to light flashes. At low light intensities the response is monophasic, but at higher intensities there is a rapid 'on' transient, which decays in about 200 ms to a sustained plateau, and a small, depolarizing 'off' transient. At very high intensities some hyperpolarization remains after the 'off' transient and this decays slowly (Fig. 4). It appears that the amplitude of the visual signal is amplified at the retinula cell-LMC synapses. Furthermore, lateral inhibition between the retinula cells narrows the visual fields of the LMCs and thus angular sensitivity is increased. Hence the LMCs retain the retinal acuity and provide a high-sensitivity, low-noise detection system which is ideal for high-acuity movement perception (LAUGHLIN, 1973, 1974a, b, 1976a, c; LAUGHLIN & HARDIE, 1978). The electroretinogram has an initial positive spike followed by a slow direct current component (YONEKUBO et al., 1971).

In the larva of A cyanea higher-order interneurons in the optic lobes and protocerebrum show considerable variation in the size and shape of their receptive fields (one ommatidium to the whole field of vision), and direction of motion and target size are unimportant (MOKRUSHOV & FRANTSEVICH, 1973). High-velocity movement

detecting units (Jittery movement fibres) occur in the optic lobes of aeshnid larvae. They respond at a frequency of 150-250 impulses/second to movement of a single target and have a large receptive field. The response increases with target size. Uniform rate of movement elicits high-frequency volleys separated by pauses, and repetitive movements along the same path produce habituation. Movement of a complex pattern inhibits the response to movement of a single target in the field up to 30° on either side of the habituated zone (spreading inhibition) (FRANTSEVICH & MOKRUSHOV, 1974a,b, 1977). FRANTSEVICH & MOKRUSHOV (1974b) noted that optical stimuli which strongly excite these neurons also cause avoidance and retreat reactions by the larvae.

Direction-sensitive units have been described in the connectives of the adults of a variety of species (FRANTSEVICH et al., 1978). Most visual descending interneurons in the connectives react only to movement of small objects (angle size of 0.3° - 15.0°), but there are some which respond to any visual stimulus (ZENKIN & PIGAREV, 1971). In the thorax of adult *Anax junius* there are descending direction-sensitive unimodal and multimodal visual units. The former respond only to movement of relatively small contrasting objects, while the multimodal units respond best to large vertical patterns (background units) and are directionally sensitive to mechanical stimulation of various types as well (OLBERG, 1979). In adults of *Sympetrum* spp. some visual interneurons in the thorax have contralateral receptive fields and are selectively sensitive to rapid upward movements (MOKRUSHOV & FRANTSEVICH, 1976).

The retinula cells in *Sympetrum rubicundulum* project to a single cartridge in the lamina. Six of the processes (short visual fibres) terminate here, but the other two (long visual fibres) pass through to the medulla. Each lamina cartridge also contains the axons of monopolar cells (ARMETT-KIBEL et al., 1977; see also MEINERTZHAGEN et al., 1980).

There are three types of 'single pigment' receptor cells in adult anisopterans: ultra-violet with a maximum spectral sensitivity of about 350 nm, blue (440 nm) and green (510 nm). In the dorsal region the u-v and blue receptors are usually more frequent, and indeed in *Aeshna* and *Anax* are the only ones present, whereas green receptors, are more frequent in the frontal and, in *Aeshna*, ventral regions (MENZEL, 1979). EGUCHI (1971) suggested that the distal retinula cells are the green receptors the proximal cells the u-v receptors. In *Hemicordulia tau* there is a fourth type of receptor cell, a 'linked pigment' cell which contains at least three photopigments,

and hence has a broad spectral sensitivity, but which is insensitive to polarized light (LAUGHLIN, 1976b). LAUGHLIN (1976b) suggested that, in the ventral region of the retina, the retinula cells are divided into colour-sensitive, polarization-sensitive and contrast-coding types. The larvae generally have only u-v and blue receptors, but green and red receptors have been reported (AUTRUM & KOLB, 1968). The spectral sensitivity of the LMCs is dependent on intensity and not on wavelength. Furthermore they have no polarization sensitivity in the green region of the spectrum and only low sensitivity in the ultra-violet (LAUGHLIN, 1976a).

MUSCLES

Most of the work on odonate muscle structure is prior to 1972 and hence only a brief description will be given for completeness. For a review of insect muscles see USHERWOOD (1975). All insect muscles are cross-striated and can be divided into various types (MILL & LOWE, 1971). The flight muscles of dragonflies are radial, *i.e.* the fibrils are arranged radially. They have a sarcomere length of 4-6 μm, there is a circle of 6-8 actin filaments around each myosin filament, both the sarcoplasmic reticulum and the T-system are well developed and there are numerous large mitochondria. They have been described in *Aeshna* (SMITH, 1961; AUBER, 1967), in *Sympe-trum* and *Enallagma* (SMITH, 1966) and in *Celithemis eponina* (SMITH & ALDRICH, 1971), and their development in *Anax imper-ator* has been described by VALVASSORI *et al.*,(1978). Notably the T-system develops from longitudinal grooves in the surface of the muscle fibre juxtaposed to vesicles of the sarcoplasmic reticulum. Al-so the ratio of thin to thick filaments is initially as high as 4.5:1, rapidly decreasing to 3:1.

The dorso-ventral muscles of *Anax imperator* have sarcomeres 5--6.5 μm long and possess a well-developed T-system. The expiratory dorso-ventral muscles have 9-10 actins around each myosin filament and the mitochondria are arranged fairly regularly on either side of the Z-line. However, in the anterior and posterior dorso-ventral mus-cles 10-12 actins encircle each myosin filament and there are rather few mitochondria. Furthermore, the sarcoplasmic reticulum is better developed in the anterior and posterior dorso-ventral muscles, while glycogen is more abundant in the expiratory dorso-ventral muscles. The expiratory dorso-ventral muscles are also very heavily tracheated (MILL & LOWE, 1971).

In the myocardial cells the sarcomere length is 3.3-6.1 μm, there

are 9-12 actins surrounding each myosin filament, the T-system and the sarcoplasmic reticulum are well-developed, and, in *Sympetrum danae* at least, the mitochrondria are fairly regularly arranged on either side of the Z-line. In *Aeshna juncea* the fibres are capable of supercontraction (MYKLEBUST, 1975; JENSEN, 1976).

At metamorphosis aeshnid dragonflies undergo a marked change in the shape of their abdomen and, during the teneral stage, there is a considerable amount of muscle degeneration. Most of the longitudinal, dorso-ventral and oblique musculature disappears, leaving four pairs of short longitudinal muscles at the posterior end of each segment and two pairs of dorso-ventral muscles. In addition a closer muscle for each spiracle becomes functional (opening is by skeletal elasticity). An analysis of the abdominal musculature and its innervation in larval (WHEDON, 1919; MILL, 1965), teneral (Mill & Whittles, in preparation) and adult (WHEDON, 1919; Mill & Whittles, in preparation) specimens indicates that the adult muscles probably correspond to the anterior tergo-pleural, posterior dorso-ventral, one of the longitudinal sternal, the oblique tergo-pleural, the inferior longitudinal tergal (lt_5) and one of the superior longitudinal tergal muscles of the larva.
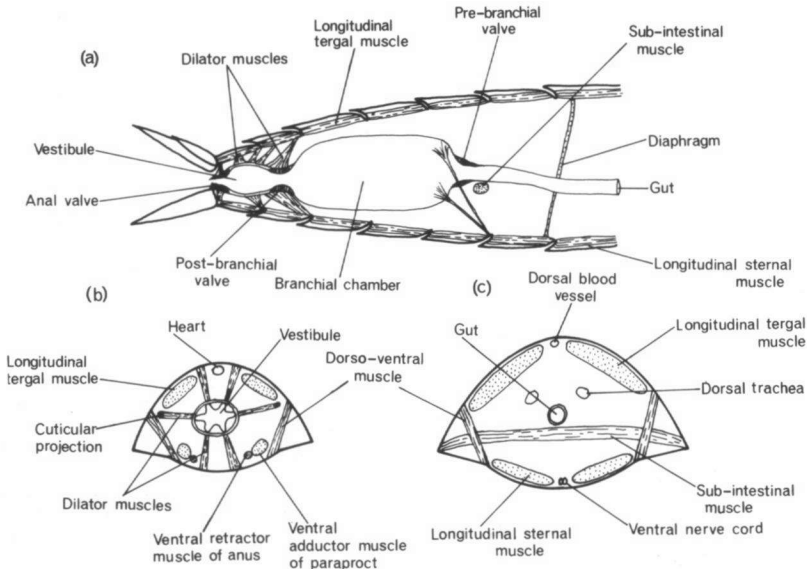

Fig. 5. Diagram of the ventilatory system of an aeshnid dragonfly larva: (a) longitudinal section; −(b, c) transverse sections through the vestibule (b) and the sub-intestinal muscle (c) regions. (From MILL, 1977.)

VENTILATION

In anisopteran larvae there is a closed tracheal system and respiratory exchange occurs over the surface of gills contained within a modified region of the hind gut — the branchial chamber (Fig. 5). The mechanics and physiology of this system have been studied in aeshnids. The normal rest position is in the fully inspired state and
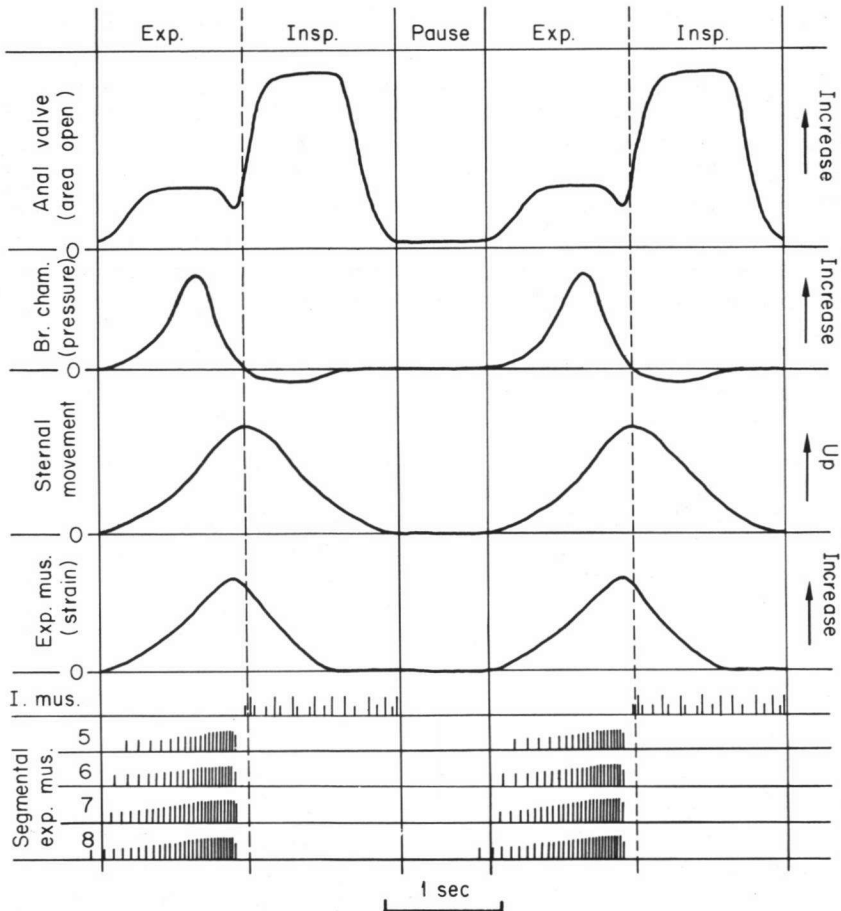

Fig. 6. Summary diagram to show the sequence of events which occurs during normal, rhythmic ventilation in an aeshnid larva. Br. cham., branchial chamber; Exp. mus., expiratory dorso-ventral muscle; I. mus., sub-intestinal transverse muscle. (From MILL, 1972; after MILL & PICKARD, 1972b.)

the first phase of ventilation is thus expiration. This is effected by contraction of the segmental expiratory (respiratory) dorso-ventral muscles, which causes an increase in pressure in the abdominal cavity and hence in the branchial chamber (up to about 4 cm H_2O), and water is thus ejected through the partially open anal valve. There are no segmental inspiratory muscles; inspiration is effected instead by two transverse muscles, the diaphragm and the sub-intestinal transverse muscle. These lie respectively between the fourth and fifth, and between the fifth and sixth abdominal segments; their contraction lowers the floor of the abdomen and is probably accompanied by contraction of the dilator muscles of the vestibule (a small muscular chamber lying between the branchial chamber and the anus). The net effect is to cause a slight negative pressure in the branchial chamber and water is drawn in through the fully open anal valve (Fig. 6) (HUGHES & MILL, 1966; MILL & HUGHES, 1966; MILL & PICK-ARD, 1972b; PICKARD & MILL, 1972, 1974).
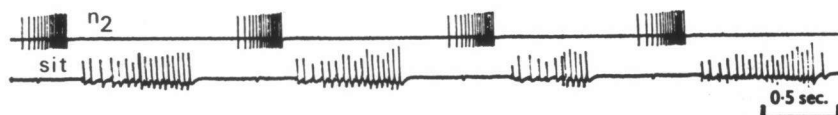

Fig. 7. Alternating expiratory and inspiratory bursts in larval *Aeshna*, recorded from a second lateral nerve (n_2) and the subintestinal transverse muscle (sit) respectively. (From MILL, 1970.)

Fig. 8. A single expiratory burst recorded simultaneously in a second lateral nerve (n_2) and the corresponding expiratory dorso-ventral muscle (rdv) in *Anax imperator*. (From MILL, 1970.)

Alternating expiratory and inspiratory bursts of activity are seen when recording from the appropriate nerves or muscles (Fig. 7). Each expiratory dorso-ventral muscle is innervated by about three axons in the second segmental nerve, but only one of these is active during expiration (Figs 7 & 8). At lower ventilatory rates this expiratory motor neuron shows an increase in frequency during the expiratory burst and this increase is accompanied by facilitation of the muscle potentials (Fig. 8). With increase in frequency and depth of ventilation the duration of the bursts becomes shorter and there is an increase in the intra-burst firing frequency of the neuron; at higher fir-

ing frequencies it tends to fire more uniformly (Fig. 9). (Uniform firing is typical of the corresponding motor neuron in *Libellula quad-rimaculata*, which has a higher overall ventilatory frequency). There is a posterior-anterior expiratory rhythm, with the expiratory motor neuron in successively anterior ganglia being delayed by 100-150 msec per segment. However, they all cease to fire at about the same time. A pair of inspiratory neurons in each of the appropriate median unpaired nerves innervate the transverse muscles, each neuron sending a branch to each side of the muscle. These fire fairly regularly throughout the inspiratory burst (Fig. 7). The results obtained from chronic preparations appear virtually identical with those from dissected preparations (HUGHES & MILL, 1966; MILL & HUGHES, 1966; MILL, 1965, 1970; PICKARD & MILL, 1972, 1975).

Fig. 9. Recordings from an expiratory dorsoventral muscle ($IRDV_7$) of a larval aeshnid during slower (a) and faster (b) ventilatory rates. (From PICKARD & MILL, 1975.)

During expiration there is often activity in motor neurons innervating the anterior, but not the posterior, dorso-ventral muscles; this probably occurs during deeper ventilation. There are also expiratory bursts in the first segmental nerves, with activity in motor neurons innervating the longitudinal tergal and sternal muscles, and this is thought to be to prevent elongation of the abdomen due to the increase in abdominal pressure during expiration (MILL, 1970, 1977; PICKARD & MILL, 1975). Stimulation of the 1st segmental nerve of one of the more posterior ganglia during the interval between expiratory bursts may elicit an expiratory burst in the 2nd segmental nerves and so reset the respiratory rhythm. Indeed, over short periods at least, it is possible to entrain the rhythm to a stimulation frequency slightly greater than the existing normal ventilatory frequency (MILL & HUGHES, 1966; MILL, 1970; KOMATSU & KUSACHI, 1979; KOMATSU, 1980a).

Spontaneous, bursting activity has been shown to occur in the isolated nerve cords of larval *Libellula* and, after passing carbon dioxide over the preparation, of *Aeshna* and *Anax*, although it is uncer-

tain whether this activity is associated with ventilation (MILL & HUGHES, 1966). Recently Komatsu (in press) has recorded alternate expiratory and inspiratory bursts of action potentials in the second segmental and median nerves respectively of the isolated abdominal nerve cord of *Anax parthenope*, which are similar to those recorded in dissected preparations. In most cases in which these rhythmic bursts were seen they were either from the last ganglion alone or from the nerve cord connected to the last ganglion; in a few cases the nerve cord separated from the last ganglion was capable of maintaining the rhythm. It seems likely that the last ganglion contains the main oscillator, but that others are present more anteriorly (KO-MATSU, in press; see also MILL, 1977).

Inspiratory motor neurons and at least some of the expiratory motor neurons apparently receive both excitatory and inhibitory inputs (KOMATSU & KUSACHI, 1979; KOMATSU, 1980a,b). Furthermore, ascending expiratory (AE) and inspiratory (AI) interneurons have been recorded in *A. parthenope*. The AE has its cell body in the eighth abdominal ganglion. It fires in bursts, each burst preceding activity in the expiratory motor neurons in the 2nd segmental nerves. Stimulation of the 4th segmental nerve of the eighth ganglion resets the rhythm in both the AE and the expiratory motor neurons, but directly evoked bursts in the AE do not reset the rhythm. Bursts in the AI have been evoked by rebound excitation (following a hyperpolarizing current pulse) and elicit an inspiratory burst in the median nerve of the 6th ganglion at least, followed by an expiratory burst in the 2nd segmental nerves (KOMATSU, 1982, and pers. comm.).

After metamorphosis the spiracles become functional, but dorso-ventral movements of the abdominal floor continue and, by rhythmically increasing and decreasing the abdominal pressure, serve to force air out of and in through the spiracles. Of particular significance from the point of view of ventilation is that the larval expiratory dorso-ventral muscles have disappeared (see 'Muscles'). Nevertheless, ventilation still comprises raising (expiration) and lowering (inspiration) of the sterna (with associated spiracular movements). Bursts of impulses associated with expiration occur in both the 2nd and 3rd segmental nerves, but the firing frequency remains fairly regular throughout the bursts. There is also activity in the 1st segmental nerves associated with inspiration and often also with expiration, and activity in the median nerves is presumably associated with spiracular movements, since these nerves appear to innervate the spiracular closer muscles in tenerals and adults (Mill & Whittles, in preparation).

MILLER (1962) described spiracle activity in several species of ani-sopterans at rest, in flight and during recovery from flight. At rest the pattern of opening and closing varies in different species. Some spiracles are synchronized with either expiration or inspiration, but many remain closed, especially in crepuscular species. However, at the start of flight spiracles 1-3 immediately open, probably as a result of a central inhibitory reflex, and remain open throughout flight, while spiracles 4-9 open during inspiration.

SWIMMING

The jet-propulsive escape mechanism comprises an exaggerated expiratory movement. The burst to the expiratory dorso-ventral muscles is of shorter duration than a normal expiratory burst, the firing within the burst is of higher frequency and more than one unit appears to be firing (Fig. 10). There is synchronous activity in both anterior and posterior dorso-ventral muscles as well as in the motor neurons to the longitudinal tergal and sternal muscles, the latter eliciting a longitudinal contraction concurrent with sternal lifting. The overall effect is to produce a much higher pressure within the branchial chamber — up to 25-30 cm water — than during normal expiration. This results in a strong jet of water being ejected from the anus and a rapid forward movement of the animal. This is usually repeated several times before normal ventilation is resumed. During jet-propulsive swimming the legs are held back against the body (HUGHES, 1958; MILL & PICKARD, 1972a, 1975).
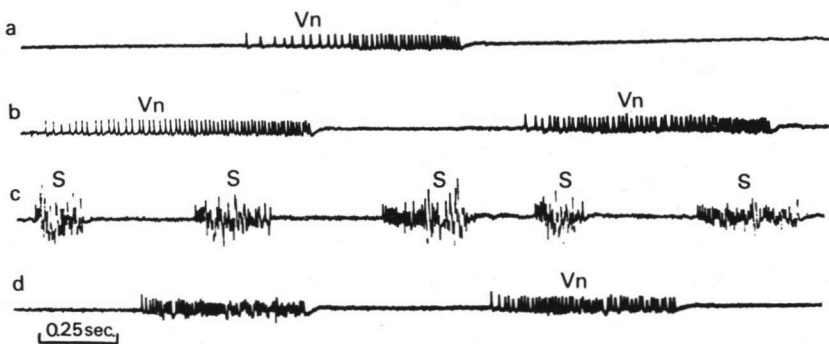

Fig. 10. Recordings from an expiratory dorsoventral muscle of an aeshnid larva during ventilation (V_n) and jet-propulsive swimming (S). (From MILL & PICKARD, 1972a.)

FLIGHT

The muscles involved in flight have been described in *Hemianax papuensis* and *Aeshna brevistyla*. Each wing is moved by five major muscles, three for wing elevation and two for wing depression, and their innervation is shown in Figure 11. The cell bodies of the pool
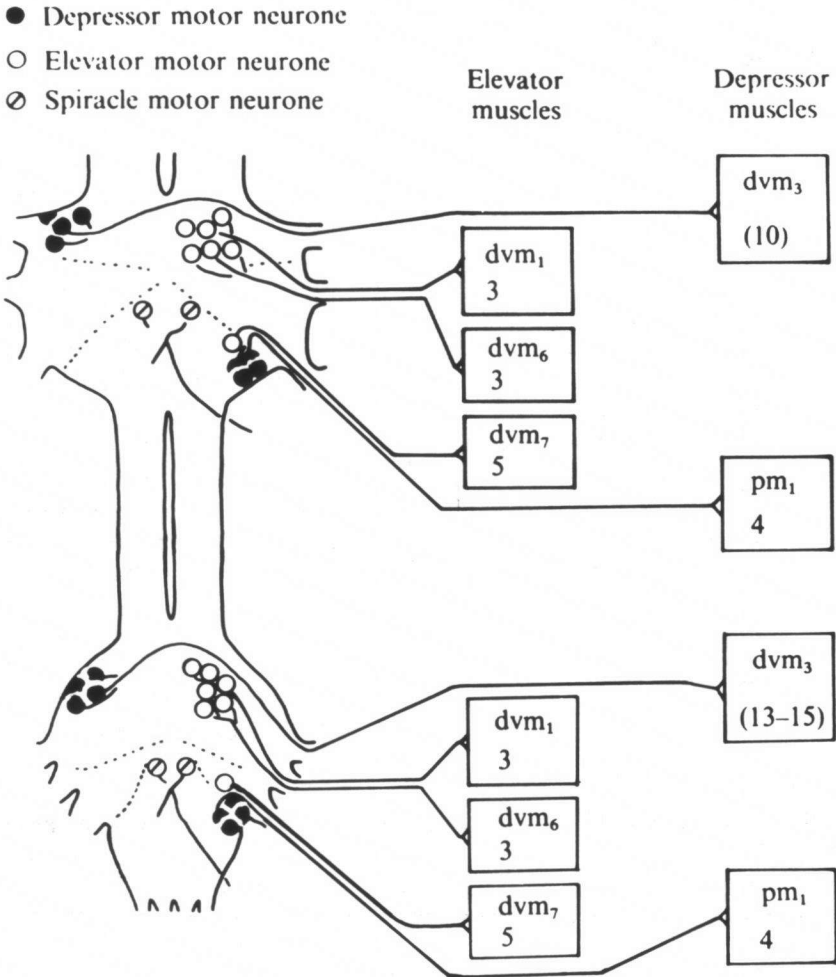

Fig. 11. Diagram showing the arrangement of the elevator and depressor motor neurons in the mesothoracic and metathoracic ganglia of *Hemianax papuensis*. (From SIMMONS, 1977a.)

of motor neurons which innervate any one muscle are clustered to-
gether in the same region of the ganglion, and their dendritic branch-
ing patterns are similar to each other. The motor neurons innervating
one of the depressor muscles are contralateral; all of the others are
ipsilateral (SIMMONS, 1977a). There are, in addition, four other
muscles associated with flight, one with elevation and three with de-
pression. Of the latter, two supinate the wing.

Fig. 12. Alternating elevator and depressor activity in wing motor neurons of *Hemianax
papuensis* recorded from second (N2) and first (N1) lateral nerves respectively in the meta-
thorax. (From SIMMONS, 1977b.)

In *Aeshna* spp. there is a pre-flight 'warm up' period in which
wing vibrations occur (POND, 1973), whereas in some libellulids (*e.g.*
Trithemis spp.) the wings are held in an extremely depressed position
by tonic contractions of the depressor muscles (MILLER, 1974).
During flight in *H. papuensis* alternate bursts of activity occur in the
axons of the motor neurons innervating the elevator and depressor
muscles respectively (Fig. 12). The 1st segmental nerve innervates de-
pressor muscles exclusively, the 2nd innervates elevator muscles ex-
clusively, while the 3rd innervates both (Fig. 11). Large, rhythmical
fluctuations occur in the membrane potential of both elevator and
depressor motor neurons, probably as a result of presynaptic input
from interneurons, and, during depolarization, action potentials may
occur. There is evidence that each motor neuron receives input from
a separate set of interneurons; also that the motor neurons have in-
put onto interneurons (SIMMONS, 1977b).

In adult *Orthetrum cancellatum* antennal receptors stimulated by
the flow of air over the animal during flight apparently provide in-
formation about the velocity of the air current, and their input has
an effect on the dorsal wing stroke cycle (GEWECKE *et al.*, 1974).
Similarly, trichoid sensilla on the head of *Aeshna grandis* are stim-
ulated by wind and provide information on the onset, velocity and
duration of the air current during flight, and their input serves to
maintain flight (SVESHNIKOV, 1972). There are also four groups
of receptors (crevice organs) on each wing of aeshnids which are well
situated to detect strains during wing movements (SIMMONS, 1978).

PREY CAPTURE

Dragonfly larvae catch their prey by a rapid forward extension of their labial mask. The labial muscles are incapable of producing this action on their own and an extension is effected by an increase in internal body pressure produced by rapid contraction of the abdominal dorso-ventral and longitudinal muscles in much the same way as for jet-propulsion (see above) (although there are some differences in the abdominal muscle activity in the two behaviours), and OLESEN (1979) recorded intra-thoracic pressures of 50-100 cm H_2O. If the labium is released from its 'locked' position it will extend; conversely if the anal valve is opened, jet-propulsion will ensue. The two behaviours appear to be mutually exclusive (OLESEN, 1972, 1979). PRITCHARD (1976) has shown that the thoracic muscles are also involved; also that the flexor muscles of the prementum are probably contracted during the early part of the pressure build up, their release contributing to the force of the strike. He also pointed out that the elastic properties of the T-shaped hypopharyngeal apodeme are responsible for the return of the postmentum after the strike. Antennal and prothoracic tarsal receptors are involved in prey detection in *Calopteryx splendens*; in *Cordulegaster boltoni* tactile information is augmented by visual clues (CAILLERE,1976).

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