TRANSMISSION THROUGH THE LAST ABDOMINAL GANGLION OF THE DRAGONFLY NYMPH, 
ANAX IMPERATOR

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INTRODUCTION

Mechanical stimulation of the abdomen or anal appendages of a dragonfly nymph generally elicits a characteristic escape response. The legs are drawn into the side of the body, water is rapidly ejected from the rectal chamber and the animal is propelled forwards (Tonner, 1936; Snodgrass, 1954; Hughes, 1958). The movement is analogous to that of the evasion response of the cockroach and suggests a similar approach to the problem in terms of transmission in the abdominal cord and through the last abdominal ganglion (Pumphrey & Rawdon-Smith, 1937; Roeder, 1948).

Synaptic transmission in insects has received relatively little consideration in comparison with the crustacea, and the dragonfly nymph provides several advantages for such a study. It is a large aquatic insect and the histology of both the central and peripheral nervous system has been studied in some detail (Zawarzin, 1924; Rogosina, 1928). Hughes (1953) showed that the fibres of the ventral nerve cord of late instar nymphs of Anax imperator range up to 16 μ in diameter and are comparable to the giant fibres of the cockroach or locust (Roeder, 1948; Cook, 1951). He further demonstrated that stimulation of the anal appendages is followed by bursts of activity in which large spikes are prominent in the nerve cord. The present paper is a more detailed analysis of the escape response with particular emphasis on the peripheral connexions of the ‘giant’ fibres and the characteristics of transmission through the last abdominal ganglion. The properties of the latter are shown to be of more general interest in demonstrating the existence of a simple segmental reflex in an invertebrate ganglion.

MATERIAL AND METHODS

Last instar nymphs of Anax imperator were kept in aerated tanks at a temperature of 10–15°C. They were fed regularly on blowfly larvae but starved just prior to an experiment. Intact nymphs were pinned in a wax dissecting dish containing insect Ringer (7.5 g. NaCl, 0.1 g. KCl, 0.2 g. CaCl, 0.2 g. NaHCO, distilled H₂O 1000 ml.). A minimum of exoskeleton was removed in order to expose the ventral nerve cord and care was taken to ensure that the tracheal system to the ganglia remained intact. It was rarely necessary to remove any muscles except when dissecting the
paraproct nerves for electrical stimulation. Breathing continued for 2–3 hr. and aeration was aided by injecting aerated water into the rectal chamber with a fine pipette. Preparations remained viable for 5 hr. or more.

The twin-channel recording system consisted of Tektronix Type 112 and Grass P4 preamplifiers and a Cossor double-beam oscilloscope. Two pairs of tapered silver/silver chloride electrodes were used for leading off activity. Stimulating electrodes were also of silver/silver chloride and pulses were provided by a rectangular pulse generator. Fine-trimmed paint brushes and tapered needles were used for mechanical stimulation of the abdomen and anal appendages.

RESULTS

Innervation of the terminal abdominal segments

The ventral nerve cord of the dragonfly nymph comprises three thoracic and seven abdominal ganglia. Zawarzin's (1924) classical studies on *Aeshna* are largely concerned with the organization of the second thoracic and fourth abdominal ganglia. Similarly the work of Rogosina (1928) is restricted to the distribution of nerves from the sixth abdominal ganglion and there is little reference to the seventh. It is therefore relevant, as a background to the physiology involved, briefly to describe the innervation of the terminal abdominal segments and anal appendages from the last abdominal ganglion. For this purpose animals were dissected *in vivo* and the nervous system stained with Rongalit methylene blue.

The seventh ganglion is larger than those of the other abdominal segments, innervates a greater area and possesses five pairs of lateral nerves (N1–N5, Fig. 1). Three pairs run laterally, innervate segment 8 and are comparable in their distribution to the abdominal roots of *Aeshna* (Rogosina, 1928). The remaining two pairs (N4, N5) are stout nerves running posteriorly to innervate segments 9 and 10 and the anal appendages. Physiologically it was shown that roots N1, N2, N4 and N5 are mixed nerves but N3 contains motor fibres only, an observation that is supported by Zawarzin's histological study of the fourth ganglion.

The general distribution of nerves from the seventh ganglion is shown in Fig. 1; considerable variability occurs in the terminal branches. N1 is a stout nerve with motor branches to the longitudinal sternal muscles, dorso-ventral oblique segmental muscles and the longitudinal tergal muscles (nomenclature from Whedon, 1918). It receives sensory fibres from the anterior part of the sternite, the pleurite, including lateral spine, and the tergite. Fibres from the stretch receptors have been demonstrated oscillographically in this first nerve which therefore resembles those of the other abdominal ganglia (Finlayson & Lowenstein, 1958). N2 is a smaller nerve and appears to be composed of a larger proportion of sensory fibres than N1. It branches freely ventrally and supplies the longitudinal sternal muscles and dorso-ventral segmental muscles. Sensory fibres from most of the sternite and part of the tergite run in this second root. N3 is a very fine nerve running at first caudally, then turning laterally to supply the longitudinal sternal muscles, dorso-ventral oblique and segmental muscles.
The fourth nerve, N₄, innervates segment 9 and appears to be rather similar in its distribution to N₁. It supplies the longitudinal sternal muscles, dorso-ventral oblique segmental muscle and longitudinal tergal muscles. An additional branch sends motor fibres to the dorso-ventral segmental muscles. N₄ receives sensory fibres from the sternite, pleurite and tergite of segment 9 and from stretch receptors. N₅ is the largest root and as shown by sections (Holmes silver, iron haematoxylin) contains the greatest number of fibres, which is correlated with its distribution to part of segment 9, segment 10, the anal appendages and respiratory chamber. It runs parallel to N₄ for some distance and often in the same sheath, then divides.
Ganglionic transmission in dragonfly nymph

into two branches which pass over and under the longitudinal muscles and fuse at the anterior edge of segment 10 (a and b, Fig. 1). In segment 10 longitudinal sternal and tergal muscles, dorso-ventral oblique muscles, abductors of the paraprocts, retractor muscles of the anus, rectal and sphincter muscles are all supplied by motor fibres in branches of N 5. Large branches also run to the respiratory chamber extending as far forward as segment 5; these appear to be purely motor in function. N 5 receives sensory fibres from the sternite of segment 9, sternite, pleurite and tergite of segment 10, paraprocts, lateral and median spines.

It can be seen from this brief description that the last abdominal ganglion of Anax is concerned with the reception and distribution of information from a relatively large area of the body. In this respect the distribution of its paired roots is more extensive than that of the last ganglion of the cockroach or locust (Roeder, 1948; Cook, 1951). Recording from the peripheral ends of nerves of the seventh ganglion showed that the sensory representation deduced physiologically supports the anatomical evidence. Similar peripheral distribution was shown to occur in nerves of the other abdominal ganglia, where responses were obtained from stimulation of the same segment but not adjacent segments.

Responses to mechanical stimulation

Responses recorded from the ventral nerve cord of the dragonfly nymph have to be studied against a background of spontaneous activity and breathing discharges. The latter appeared to be of two different patterns accompanying the two types of breathing (Tonner, 1936). Shallow breathing was often characterized by rhythmic bursts from repetitively firing fibres, whilst in gulping breathing expiration was typically accompanied by a prominent burst of higher frequency in many more fibres. Gulping breathing and the response to mechanical stimulation of the paraprocts appeared to be due to a very similar sequence of movements of the abdomen, paraprocts and anal sphincter. These movements are the same as those involved in swimming and have been described by Hughes (1958). Briefly stimulation of tactile hairs on the inner surface of the paraprocts or of the anal sphincter elicited a rapid contraction of the abdominal muscles and of the intrinsic gut muscles, opening of the anal sphincter, divergence of the paraprocts and ejection of water from the rectal chamber. Simultaneously all six legs were drawn into the side of the body. This evasive response was not always seen on stimulation and was sometimes observed on touching other parts of the body.

Electrodes placed on a connective between ganglia 6 and 7 and the ipsilateral N 5 showed that the pattern of nervous activity associated with gulping breathing and the escape response had similar characteristics (Fig. 2). Both pre- and post-ganglionic recordings showed a large burst of activity in which large spikes were prominent. In the cord the response typically began in large fibres which rapidly increased in frequency as more units became active and often ended in a slow discharge. The burst sometimes lasted as long as 0.5-1.0 sec. The present results confirmed those of Hughes (1953) in showing that the large spikes accompanying stimulation of the anal appendages travelled through the abdominal and thoracic
ganglia without synapsing. The ascending barrage excited efferents in all the abdominal and thoracic roots, as recording from the central ends of the segmental nerves showed that motor discharges accompanied gulping breathing or the events associated with mechanical stimulation. Stimulation of the head gave fewer large spikes many of which did not traverse the length of the cord. An attempt was made to simplify the post-ganglionic response from the last ganglion by fine dissection following de-sheathing of the connectives. This has so far not been successful owing to poor survival of the preparations.

Fig. 2. Records of the nervous activity arising from mechanical stimulation of the paraprotect in *Anax* nymph. (a) Large spikes recorded between ganglia 6 and 7 (upper trace) and thoracic ganglia 2 and 3 (lower trace). (b) Synchronous firing of units in the ipsilateral N5 (upper trace) and ipsilateral connective (lower trace). (c) Efferent spikes in the ipsilateral N5 (upper trace) and the cut proximal end of the contralateral N5 (lower trace). Time scale 0.5 sec.

Recording from N5 showed that the large burst of activity on stimulation was correlated with the abrupt opening of the anal sphincter, suggesting that part of the activity was in efferent neurons. This was shown to be the case by placing the other pair of electrodes on the cut central end of the contralateral N5, when large discharge occurred in both nerves on stimulation of the anal appendages (Fig. 2). Contraction of the sphincter was asymmetrical under these conditions. Comparison of the two recordings showed that most of the activity in the ipsilateral N5 was efferent and that the afferent spikes were in small fibres only. Recording from the peripheral end of N5 supported this observation, as the sensory inflow from
Ganglionic transmission in dragonfly nymph

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tactile receptors was seen to be only a relatively small response. The large efferent bursts were unaltered by severing all inputs to the ganglion and appeared as a much more definite and predictable reflex than that described in the crayfish caudal ganglion (Fielden, 1960). Mechanical stimulation of the paraprocts therefore gives rise to a small afferent inflow to the last ganglion which excites efferent neurons in both ipsi- and contralateral N5's. Recording from other nerves showed that this inflow also excited interneurons in ipsi- and contralateral N1, N2, N3 and N4 and the unpaired nerves. Occasionally the response in N5 and a connective showed a 1:1 relationship of large spikes on either side of the ganglion, which was therefore due to synchronous firing of efferent fibres in the segmental nerves and interneurons in the connective (Fig. 2). Similar synchronous firing was sometimes noted in the efferent spikes in the two N5's or from N5 and the ipsilateral N4 and in gulping breathing. It seems that the latter is due to the excitation of the same groups of neurons by some small afferent source as in mechanical stimulation.

It was impossible to decide from recording the nervous activity due to mechanical stimulation whether fibres pass through the last ganglion from receptors in the terminal abdominal segments, or whether afferents always synapse with ascending fibres in the ganglion. Electrical stimulation was therefore used to clarify this point and to study the segmental reflex in more detail.

Responses to electrical stimulation

Motor responses. The results confirmed the previous observations (Hughes, 1953) that stimulation of the abdominal nerve cord produces a precisely similar response to that seen on touching the paraprocts. The characteristic leg movement has a strict frequency dependence—the legs are drawn into the side of the body only at frequencies above 20–30/sec., but some movement of the abdominal muscles, intrinsic gut muscles and paraprocts occurs in a 1:1 manner on stimulation. It has now been established that stimulation of N5 of the last abdominal ganglion also elicits the evasive response and movement of both contra- and ipsilateral legs at frequencies of 20–30/sec. Stimulation of N4 produced a similar response, but this was less predictable and often not shown by the contralateral legs. Movement of the rectal chamber was seen only if N5 remained intact.

A markedly different response was seen on stimulation of the ventral nerve cord anterior to the prothoracic ganglion. The legs in this case were bent in the grasping position, the response being similar to that seen on seizing the head. These responses immediately suggest a study of the transmission involved to the segmental nerves of the thoracic and abdominal ganglia.

Neuronal pathways in the last ganglion

The results of tracing pathways using electrical stimulation are summarized in Table 1. They illustrate still further the diffuse nature of the neuronal connexions in the ganglion. Diffuse connexions appear to be a characteristic property of the dragonfly nervous system as similar responses were obtained from the other
Table 1. *Results of tracing neuronal connexions in the last abdominal ganglion of Anax nymph*

<table>
<thead>
<tr>
<th>Stimulation</th>
<th>N1</th>
<th>N2</th>
<th>N3</th>
<th>N4</th>
<th>N5</th>
<th>unp. conn.</th>
<th>N1</th>
<th>N2</th>
<th>N3</th>
<th>N4</th>
<th>N5</th>
<th>conn.</th>
</tr>
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<tbody>
<tr>
<td>Ni</td>
<td>+</td>
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<td></td>
<td>+</td>
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<td>N2</td>
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<td>+</td>
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<td>N4</td>
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<td>+</td>
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<td>+</td>
<td>+</td>
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<td>+</td>
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<td>N5</td>
<td></td>
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<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
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<td>+</td>
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<tr>
<td>conn.</td>
<td>+</td>
<td>+</td>
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</tr>
</tbody>
</table>

+ response on stimulation; - no response; N1–N5 segmental nerves; conn. connective; unp. unpaired nerve.

abdominal ganglia. Their existence is supported by Zawarzin's (1924) histological work on the fourth ganglion of *Aeshna*. Some of the pathways showed distinct synaptic properties in terms of thresholds, delays and transmission frequencies, while others indicated that ‘through’ fibres were present. In many preparations the same group of neurons could be recognized in a barrage excited by stimulation of several different inputs to the ganglion. For example, in one rather clear experiment as far as could be identified an identical group of efferent fibres in N4 were excited by stimulation of the ipsilateral connective, Ni, N2 and N5, and the contralateral connective, N1, N4 and N5.

*Stimulation of the segmental nerves of the last ganglion*

Stimulation of N5 and recording from electrodes proximally on N5 and on the ipsilateral connective clearly showed the two-component nature of the response seen on mechanical stimulation. Fig. 3c illustrates a typical result. Stimulation at position 1 gave an afferent burst, recorded at 2, which excited two post-ganglionic responses: one in the connective recorded at 3 and the other in the same N5 recorded at 2. These post-synaptic responses possessed different thresholds, delays and frequency relationships. The effects of increasing intensity of stimulation are shown in the series 3a–c and resulted in the following pattern of response.

(a) At lowest intensity afferent fibres only were excited. These conducted at a velocity of 1·5–2·5 m/sec. and the spikes appeared to be in small fibres.

(b) Slightly raising the intensity increased the afferent volley and elicited a post-ganglionic response in the connective. This showed a ganglionic delay that was relatively constant in a given preparation but ranged from 2·0 to 4·5 msec. in different preparations. The response in the connective was difficult to characterize as it was composed of a large number of often compound spikes of similar size and threshold. The larger spikes, excited at low intensity and with a short delay, travelled the length of the cord at a velocity of 3·8–4·5 m./sec. apparently without synapsing.
A further increase in intensity excited the efferent neurons of N5. It also resulted in stimulation of units with a longer delay in the connectives and often shortened the delay for some of the larger spikes by as much as 0.8 msec. The post-synaptic response in N5 is of particular interest as it demonstrates the existence of a segmental reflex in the seventh ganglion. The motor neurons invariably possessed a higher threshold and longer, more variable delays (3.5–8.0 msec.) than did the units responding in the connectives. The spikes travelled at a velocity of 2.5–3.0 m./sec. in the paraproct nerves and were larger than those in the sensory fibres. Several of the units appeared to fire repetitively to a single afferent shock in some preparations even when all inputs to the ganglion were severed. Repetitive
firing was also seen in large units in the connectives similar to those occurring on mechanical stimulation.

Increasing the frequency of stimulation resulted in the post-synaptic units of N5 dropping out at frequencies of 30–40/sec. The majority of units in the connectives were blocked at similar frequencies, but some of the larger spikes persisted to 50–70/sec. and occasionally higher. The repetitive spikes in the paraproct nerves and connectives ceased at frequencies of 5–10/sec. On the basis of these observations it is concluded that afferent fibres from the anal appendages synapse with several large fibres which ascend the cord. No evidence was found for afferent fibres entering the last ganglion from the paraproct nerves without synapsing, and the preparation therefore resembled that of the cockroach (Roeder, 1948; Hess, 1958). A comparison of transmission with that through the last abdominal ganglion of the cockroach gave no evidence for the adapted state described for the giant-fibre synapses by Pumphrey & Rawdon-Smith (1937).

The response in the contralateral connective on stimulation of N5 is shown in Fig. 3d. It appeared similar to that in the ipsilateral connective and in this respect differed from that of the cockroach (Roeder, 1948). It showed the same threshold, delay and frequency relationships and included spikes which travelled throughout the cord. Crossing of both ascending and descending barrages was shown to occur in the other abdominal and thoracic ganglia, where a difference in threshold and delay distinguished these synapsing contralateral fibres from the ‘through’ fibres of the ipsilateral side.

Observations on the other roots of the seventh ganglion showed that stimulation in all cases elicited a response in the connectives except for N3 which is purely motor in function. Stimulation of N4 excited a smaller barrage than did stimulation of N5, but this included large spikes which were conducted straight through the other abdominal ganglia. Stimulation of N1 revealed an interesting feature in that afferent fibres appeared to pass through the ganglion to the ipsilateral connective without interruption by a synapse. Spikes with a short delay (0.2–0.4 msec.) and following frequencies of more than 160/sec. were recorded in the connective. Similar responses were seen in the anterior connective following stimulation of a first nerve of the other abdominal ganglia. Histological evidence (Zawarzin, 1924) supports the conclusion that these are in ‘through’ afferent fibres comparable to those described in the roots of the crayfish abdominal ganglia (Hughes & Wiersma, 1960).

Stimulation of the connectives

Stimulation of a connective gave rise to responses in contra- and ipsilateral nerves of the last ganglion (Fig. 3e), and movements of the paraprocts and sphincter comparable to those seen on direct stimulation of N5. These efferent synapses proved to be of particular interest as they showed a definite temporal summation or facilitation effect of increased frequency that was not seen at the afferent: ascending fibre synapses. With an intensity just subthreshold an increase of frequency produced an efferent burst in the fourth and fifth nerves in particular. At threshold intensity an increase in frequency to 10–30/sec. also excited more efferent units.
These effects were most obvious in older preparations, as they are in the 'adapted' state in the cockroach. Similar facilitation or summation was seen in the segmental nerves of the other abdominal ganglia, and was especially prominent in the thoracic nerves where a response was rarely seen at frequencies below 5/sec. even in fresh preparations. The first roots again showed a compound spike with a very short delay which is interpreted as due to antidromic excitation of direct afferent fibres. Responses in N_4 and N_5 often included units which fired repetitively to a single afferent shock (Fig. 3e).

**DISCUSSION**

The evasion response of the dragonfly nymph depends on neuronal pathways and connexions very similar to those of the cockroach. In the last abdominal ganglion afferent fibres from tactile receptors on the paraprocts synapse with large fibres which ascend the length of the cord and synapse with efferents in the thoracic and abdominal ganglia. Closer investigation of the thoracic ganglia may reveal synapses between the large fibres in the connectives entering and leaving the ganglia, but this seems unlikely on histological and physiological grounds. As in the cockroach, the degree and duration of the evasion response is dependent not only on the intensity of stimulation but on the characteristics of the synaptic junctions between (a) sensory neurons and ascending fibres, and (b) these fibres and efferents in the segmental nerves. There is evidence in the dragonfly that these two types of junction possess different properties comparable to those of the cockroach, which is the only insect in which synaptic transmission has yet been studied in any detail.

It is of interest to compare the 'giant' fibres system and its peripheral connexions in the dragonfly, cockroach and locust (Table 2). Although the systems appear very similar the functional significance of the pathway in the locust is not very obvious as the evasion response is absent (Cook, 1951). The response is of evident survival value in the cockroach and dragonfly. These are believed to differ, however, in the presence of more widespread afferent connexions to the 'giant' fibres in the dragonfly. In the latter the last abdominal ganglion appears to be of more localized importance than in the cockroach in view of its large motor output to the muscles of the posterior abdomen and rectum. Zawarzin (1924) has suggested that this ganglion is a composite of four which may be correlated with the large area supplied by the ganglion and the extremely diffuse connexions between its roots.

Transmission through the last ganglion and abdominal nerve cord is very similar in general pattern. There is evidence that many tactile afferents transmit to relatively few large fibres and a synapse exists in all cases. The shorter delays found by Roeder (1948) in the cockroach may be due to the comparatively larger size of the ascending giant fibres, or may indicate a monosynaptic pathway in comparison with a polysynaptic one in the dragonfly. The properties of the latter do not preclude the possibility that interneurons are present between afferents and ascending 'giants', but this seems unlikely. Comparative evidence from the crayfish caudal ganglion supports the suggestion that the larger fibre synapses have shorter delays (Fielden, 1960). Delays in both the dragonfly and cockroach shorten
Table 2. Comparison of the 'giant' fibre system and its peripheral connexions in Anax nymph, Periplaneta and Locusta

<table>
<thead>
<tr>
<th></th>
<th>Anax nymph</th>
<th>Periplaneta</th>
<th>Locusta</th>
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</thead>
<tbody>
<tr>
<td>Size 'giant' fibres</td>
<td>12-16 μ*</td>
<td>20-45 μ†</td>
<td>8-15 μ‡</td>
</tr>
<tr>
<td>Number 'giant' fibres</td>
<td>6-7*</td>
<td>6-8†</td>
<td>4†</td>
</tr>
<tr>
<td>Cond. velocity 'giants'</td>
<td>3.5-4.5 m./sec.</td>
<td>6-7 m./sec.†</td>
<td>3-4 m./sec.§</td>
</tr>
<tr>
<td>Connexions in last ganglion</td>
<td>Synapse with efferents from paraprocts</td>
<td>Each synapse with several afferents from cercae†</td>
<td>Synapse with afferents from cercae§</td>
</tr>
</tbody>
</table>

Properties of afferent synapse with 'giant' fibre

(a) Delay 2.0-4.5 msec. 1.4-1.9 msec.† 2-3 msec.§
(b) Transmission frequency 50-60/sec. 70-100/sec.‖ 70-80/sec.§
(c) Facilitation temporal summation – + ‖ – †?

Properties of synapse between 'giants' and efferents in thoracic nerves

Labile, fatigues, facilitation or temporal summation important†

* Hughes, 1953; † Roeder, 1948; ‡ Cook, 1951; § Fielden, unpublished observations; ‖ Pumphrey & Rawdon-Smith, 1937.

on increasing the intensity of stimulation. Similar shortening has been observed for single units in the crayfish ganglion where it has been suggested that the post-fibre has a graded longitudinal threshold for the several afferents synapsing on it (Preston & Kennedy, 1960).

The major physiological control of the evasion response in the cockroach appears to occur largely at the labile synapses between ascending fibres and motor efferents in the thoracic ganglia (Roeder, 1948). The same feature is seen in the dragonfly where the efferent responses, particularly in the thoracic nerves, are very frequency-dependent. Whether this frequency effect is one of facilitation or temporal summation or both was impossible to decide on the gross scale of the current recordings, and it is hoped that future work at the unit level will throw some light on this problem. A clear distinction between facilitation and temporal summation is not always made in the literature, but it seems that temporal summation does not occur at the sensory: giant synapses of the cockroach last ganglion (Roeder, 1948). Facilitation is seen at these synapses in the 'adapted' state, but was not observed in the dragonfly ganglion under the conditions of this study. A further property requiring analysis at the unit level is that of repetitive discharges from large cells in the connectives and roots. The only arthropod where this has been shown to occur at a 1:1 junction is that of efferents in the roots of the crayfish abdominal ganglia which fire repetitively to one shock in a single giant fibre (Wiersma, 1952). After-discharges have been described in the cockroach (Roeder, 1953), but here, as in the dragonfly, they may be due to multiple connexions with variable delays or the firing of several afferents on a single efferent or interneuron, and it would be of interest to find a junction in the insect analogous to that in the crayfish.
Ganglionic transmission in dragonfly nymph

The reflex stimulation of motoneurons in the fifth roots of the *Anax* last abdominal ganglion has not been studied in any comparable preparation in the cockroach. Indeed information on the relationship between sensory and motor nerves is very meagre in insects and restricted almost entirely to the highly specialized giants. Segmental reflexes concerned with respiratory, locomotory and sexual activities have been described in many insects largely through observations on behavioural changes after removal of portions of the central nervous system. Pringle (1940) describes a locomotory reflex in the cockroach in which he was able to show the effects of changes in afferent activity on tonus and contraction in different leg muscles. But there has not yet been a detailed study using controlled electrical stimuli of the connexions between afferent and efferent fibres and the dragonfly isolated ganglion, and a fifth root therefore provides a preparation analogous to that of the vertebrate spinal cord. Zawarzin noted this in his histological work and drew a comparison between the dorsal and ventral roots of the dragonfly and the vertebrate. The present results seem to indicate that delays in the dragonfly reflex are more comparable to those of the mammalian polysynaptic pathway (Alvord & Fuortes, 1954), but transmission frequencies are lower (Eccles, 1957). Further work on this preparation should give information on such problems as facilitation, inhibition and summation in the insect central nervous system.

**SUMMARY**

1. In the last abdominal ganglion of the dragonfly nymph afferent fibres from tactile endings on the paraprocts synapse with large ascending fibres in the ventral nerve cord. The latter run the length of the cord and synapse with efferent fibres in the segmental nerves of the thoracic and abdominal ganglia. The evasion response is mediated by this pathway and can be elicited by electrical stimulation of the nerves from the paraprocts.

2. The synapses between tactile afferents and ascending fibres show delays of 2-0-4-5 msec. and transmit synchronously to frequencies of 50–60/sec. There is no evidence for facilitation at these synapses, but facilitation and/or temporal summation is of importance at the efferent synapses which appear more labile in their properties.

3. Stimulation of the paraprocst nerves shows the existence of a reflex connexion between afferents and efferents of the same nerve comparable to that of the vertebrate spinal cord. This provides a preparation for a study of the relationship between sensory and motor neurons in the insect nervous system.

4. Transmission through the last abdominal ganglion and cord is compared with that in the cockroach and locust.

I wish to thank Dr G. M. Hughes for suggesting this problem and for his help and advice during the course of the work and the preparation of this manuscript. I am also grateful to the Medical Research Council under whose auspices the work was carried out.
REFERENCES


