

LOCAL INTERNEURONES AND LOCAL INTERACTIONS IN ARTHROPODS

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SUMMARY

As their name implies, local interneurones arborize within anatomically restricted regions of a nervous system, and the connections that they make establish local circuits. In arthropods, they may arborize wholly within a segmental ganglion, or within a specialized region of the brain. Local interneurones can be divided into two physiological types: spiking and non-spiking. In segmental ganglia, spiking local interneurones are largely responsible for the local processing of primary sensory inputs, whereas non-spiking ones play a major role in the control and coordination of motor neurone activity at the segmental level. By contrast, in the brain, primary visual inputs are processed mainly by non-spiking interneurones.

Local interactions between neurones may occur in three ways: by the graded release of transmitter, by the presynaptic modulation of spike-evoked PSPs and by the 'conventional' mechanism where spike frequency is translated across a synapse as the summed amplitude of discrete spike-evoked PSPs. Although graded synaptic transmission is the only mechanism so far described for the local interactions of non-spiking interneurones, it is not limited to them. It may occur also in non-spiking neurones specialized to transmit graded signals over long distances, or in local, intraganglionic regions of motor neurones or long interneurones. The ability of spiking neurones to exert graded effects may depend upon input and output synapses being intermingled on their fine branches, at sites relatively distant from the region of spike initiation. Since these synapses are widely distributed over the neurones, local intraganglionic interactions can be seen as the summed effect of many, yet more restricted local interactions. Restricted local interactions also may occur within parts of non-spiking interneurones, but this is a conjecture, based on modelling studies, and upon considerable EM evidence for serial and reciprocal synapses in most other types of arthropod neurones.

Local interneurones are found in animals of many invertebrate phyla, including molluscs, annelids, coelenterates and arthropods (Pearson, 1979). However, only in studies on arthropods has there been a concerted effort to investigate their electrophysiological properties, to discover how they are organized into local circuits, and to describe how their activities may be related to the behaviour of the animal. As a result, we know that local interneurones are central neuronal elements in the processing of

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sensory inputs, and in the control and coordination of motor outputs. In addition, studies on arthropod nervous systems have revealed that regions of long interneurons or motor neurones may participate in local, intraganglionic interactions.

This review is divided into two sections. The first will describe the ways that local interneurons act as parts of local circuits, to process sensory inputs and to control motor output. It will concentrate on those local interneurons about which we have the most physiological information, rather than attempting to catalogue all local interneurons that have been described in arthropods. The second section will consider how local interactions occur. It will discuss the physiology of graded synaptic transmission, how graded and spike-mediated transmission may be effected together in the same neurones, the morphological constraints upon local synaptic interactions and how spiking interneurons may function in local circuits.

For the purposes of this review, local interneurons are considered to be those that branch exclusively in a limited, anatomically defined region of the nervous system. For example, they may branch within one of the segmental ganglia, or within a specialized neuropilar region of the brain, such as an antennal lobe. By contrast, long interneurons (or 'principal' or 'projection' neurones; Rakić, 1975) are considered, for example, to be those in the brain with wide neuropilar fields, or those in the ventral nerve cord that have interganglionic axons.

WHAT LOCAL INTERNEURONES DO

Spiking local interneurons as integrators of primary sensory inputs

In the locust metathoracic ganglion, which controls the hind legs and hind wings, there are at least two large populations of spiking local interneurons in each half ganglion (Burrows & Siegler, 1982, 1984; Siegler & Burrows, 1984). They have extensive branches within half of the ganglion (Fig. 1) and respond to sensory stimuli to the hind leg of the same side. Many of these are second order neurones, receiving direct inputs from afferents of hairs and campaniform sensilla (Siegler & Burrows, 1983). When hairs on the surface of a leg are touched, these interneurons depolarize, and spike (Fig. 2A, B), with different interneurons responding to hairs on different regions of a leg (Burrows & Siegler, 1982, 1984). The hairs, and the campaniform sensilla, are each innervated by single sensory neurones, and can be stimulated individually (Fig. 2C). Thus, it is possible to show that each spike in a single sensory neurone produces an EPSP in a postsynaptic, spiking local interneurone (Fig. 2B, C). These EPSPs follow sensory spikes at a high frequency, with a latency consistent with a monosynaptic connection (Siegler & Burrows, 1983). Several hairs from an area on a hind leg converge on a given interneurone (Fig. 2C), and each hair may synapse on several interneurons (Siegler & Burrows, 1983). Thus the interneurons may have different, but overlapping receptive fields of hair inputs (Burrows & Siegler, 1983, 1984). In addition, local interneurons in the same populations may respond to proprioceptive inputs, for example, those arising from imposed movements of joints of a leg (Burrows & Siegler, 1982, 1984), although the possibility that these other inputs connect directly to the spiking interneurons has not been tested.

In the terminal abdominal ganglion of the crayfish, several spiking local interneurons have also been described anatomically and physiologically and some

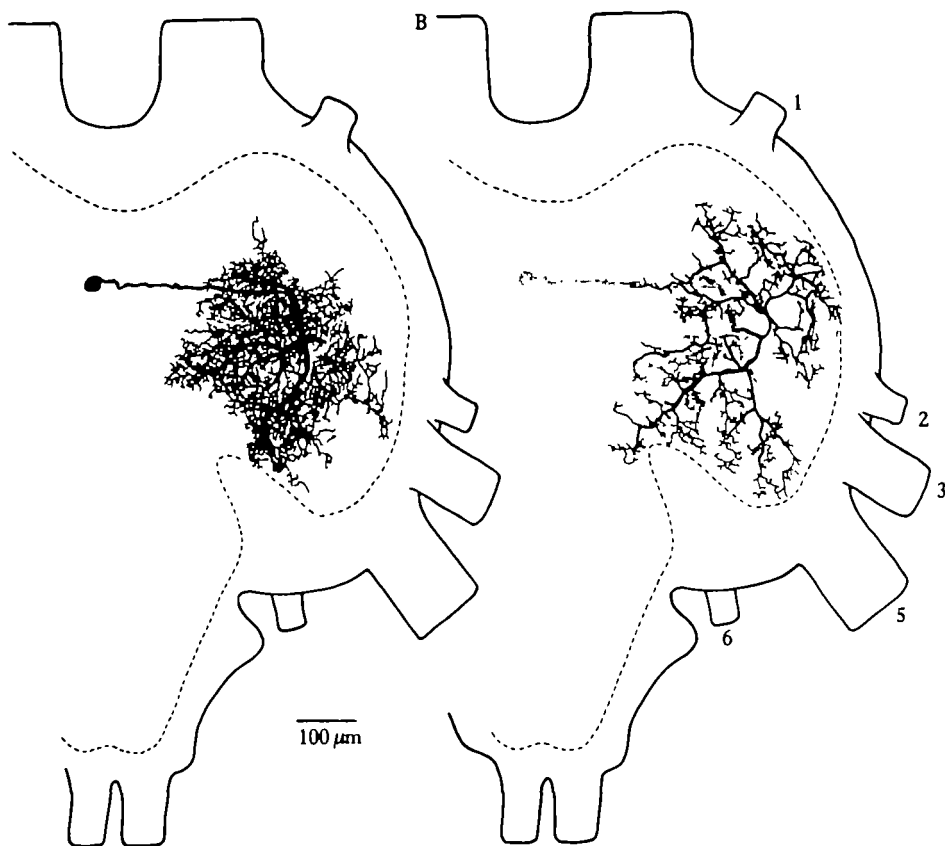


Fig. 1. Morphology of a spiking local interneurone in the metathoracic ganglion of the locust. The interneurone spiked when hairs on a region of the right hind leg were touched. The interneurone has two distinct regions of branching, drawn separately in A and B. The interneurone was injected with Co^{2+} , which was then precipitated as CoS , and subsequently intensified with silver. The dashed line shows the outline of the neuropile. Lateral nerves 1, 2, 3, 5 and 6 are numbered. (A) Drawing of the right half of the ganglion, showing the cell body, the primary neurite and the more ventrally originating branches of the interneurone. (B) Drawing of the more dorsal neuropilar branches, which arise from a single dorsoventral process. The cell body and larger ventral neuropilar processes from A are stippled. (From Siegler & Burrows, 1983.)

evidence suggests that, like the interneurons in the locust, these integrate primary sensory inputs (Reichert *et al.* 1982). All of these have small, clearly defined receptive fields on the tailfan (uropods and telson), and are readily excited by sudden water movements, by light touches to the tailfan or by imposed movements of its parts. In some of the interneurons, electrical stimulation of particular peripheral roots evokes EPSPs with short latencies, suggesting a direct input from the afferent population.

In the cricket, two types of prothoracic auditory interneurons are local: the omega-shaped ON1 and ON2 (Wohlers & Huber, 1982). Both produce EPSPs and spikes in response to tone pulses, but respond maximally to different frequencies, and have different directional sensitivities. ON1 is considered to receive direct sensory inputs (Wohlers & Huber, 1978). However, the evidence for this is indirect, namely that it has branches in the same neuropilar region as do the primary auditory fibres (Popov, Markovitch & Andjan, 1978) and 'latency measurements do not rule out the possibility

of monosynaptic connections' (Wohlers & Huber, 1982). Since latencies from sound pulses to the onset of EPSPs in ON1 are some 20 ms, this idea needs to be tested more rigorously, by recording from the afferents and the interneurons simultaneously.

Spiking local interneurons in the brain may also integrate primary sensory inputs. In the tobacco hornworm moth *Manduca*, the bilaterally paired antennal lobes of the

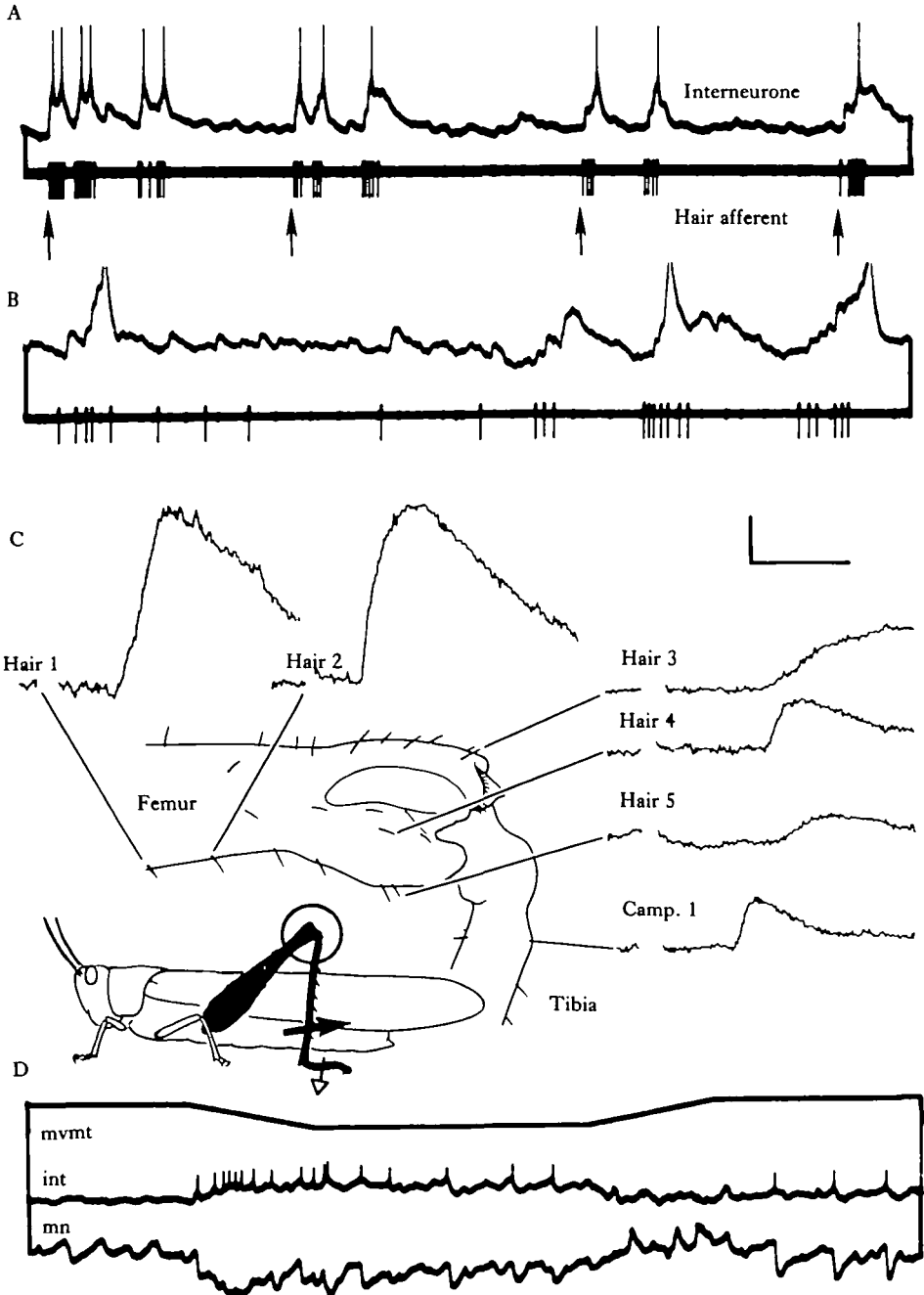


Fig. 2

adult consist of many discrete glomeruli. These are composed of central terminals of afferents from an antenna and processes of local and long interneurons. The local interneurons can be divided into four types, according to their morphology and the odours to which they respond (Matsumoto & Hildebrand, 1981). At least one type, (Ib) is thought to be directly postsynaptic to primary afferent receptors from an antenna. These, found in males and females, are radially symmetrical, and with the exception of the male-specific macroglomerulus, have elaborate branches in most, if not all, of the antennal glomeruli (Matsumoto & Hildebrand, 1981). These type Ib interneurons respond with EPSPs and a burst of spikes when odours are applied to the ipsilateral antenna, but do not respond to stimulation of the contralateral antenna (Matsumoto & Hildebrand, 1981; Tolbert, Matsumoto & Hildebrand, 1983). EPSPs can also be evoked in type Ib interneurons by electrical stimulation to the ipsilateral antennal nerve (Tolbert *et al.* 1983). These occur with a short and constant latency. This suggests a monosynaptic connection between some afferents and the interneurons. Other types of local interneurons, and the output interneurons, have more complex responses and their connections are unknown.

In the spiking local interneurons of cricket, crayfish and locust, anatomical and physiological evidence suggests that different parts may be specialized as regions of input or output. In the cricket auditory interneurone, ON1, branches within the two halves of the prothoracic ganglion appear markedly different from each other in stained whole mounts (Popov *et al.* 1978). Furthermore, on the presumed input side, the EPSPs evoked by sound are large. The spikes are small, and passively decremented. On the presumed output side, however, the EPSPs are small and spikes large (Wohlers & Huber, 1978). In the crayfish, bilaterally branched spiking local interneurons show a similar physiological division (Reichert *et al.* 1982). In the spiking local interneurons of the locust metathoracic ganglion, there is anatomical evidence for a division of function in different parts of the interneurons. The interneurons, which branch mainly or exclusively within one half of a ganglion, have two regions of branching. One is more ventral than the other, and branches in the two regions are of markedly different appearance (Fig. 1; Siegler & Burrows, 1984). Only the branches in the ventral region (Fig. 1A) overlap with terminals of presynaptic sensory afferents, whereas only the branches in the dorsal region (Fig. 1B) overlap with those

Fig. 2. Responses of spiking local interneurons in locust to sensory stimuli. (A) Repeatedly touching a single hair on the hind leg (arrows) consistently evokes a depolarization, and spikes in the interneurone. Spikes of the hair afferent are recorded extracellularly from a leg nerve. (B) Small deflections of a hair elicit a low frequency of afferent spikes. These evoke one-to-one EPSPs in the interneurone. Peaks of spikes in the interneurone are not shown. (C) A schematic drawing of the femoral-tibial joint of a hind leg, and the responses of a spiking local interneurone to hair, and campaniform sensilla (Camp.), stimulated electrically. In the inset drawing of a locust, the femoral-tibial joint is circled. Each record is an average of the responses to 128 stimuli, which elicit EPSPs in the interneurons. (D) Local reflex mediated by a spiking local interneurone. The tibia of one hind leg is forcibly extended from a femoral-tibial angle of 90° to 140°, held there, and then returned to 90° (mvmt). Solid arrow on inset of locust indicates extension of the tibia. Extension elicits a series of spikes, recorded in the cell body of a local interneurone (int). Spikes are followed one-to-one by IPSPs in the tarsal levator motor neurone (mn). In response to extension of the tibia to 140°, the tarsus is depressed (open arrow on inset); in response to flexion to 90°, the tarsus is levated. Calibration. Vertical: A, 7 mV; B, D, 3.5 mV; C, 0.5 mV. Horizontal: A, B, 200 ms; C, 32 ms; D, 400 ms. (A–C from Siegler & Burrows, 1983; D after Burrows & Siegler, 1982.)

of postsynaptic leg motor neurones. Thus one region may be specialized for sensory input, and the other for motor output.

In the local interneurons of the antennal lobes of *Manduca*, a different physiological division is proposed (Matsumoto & Hildebrand, 1981). Spikes of different sizes may be recorded intracellularly, which apparently arise from the same neurone. Smaller 'dendritic' spikes give rise to larger 'neurite' spikes. The frequency of these spikes can be altered independently, in response to different odours. From this physiological evidence it is proposed that spikes arise separately in different regions of an interneurone, each region integrating inputs from different primary afferents. Regions of a local interneurone would thus participate independently in more restricted local circuits.

Other functions for spiking local interneurons

In addition to processing sensory information, spiking local interneurons may also effect motor outputs. In the locust, a few spiking local interneurons are known to make monosynaptic inhibitory connections with leg motor neurones. The interneurons are excited by touching or moving parts of a leg, and participate in local reflexes (Fig. 2D; Burrows & Siegler, 1982; Siegler & Burrows, 1984). Such spiking local interneurons are the central element in a three neurone pathway, consisting of sensory afferent, interneurone and motor neurone. Their connections with leg motor neurones seem restricted, however, by comparison with those of non-spiking interneurons: all spiking local interneurons found so far affect only a single motor neurone, whereas the non-spiking local interneurons may affect several (Burrows & Siegler, 1982; see below). In the crayfish, a few of the types of local spiking interneurone that respond to sensory inputs also have motor effects. When depolarized they cause an increase in the frequency of spiking in efferents (presumably motor neurones) to the tailfan (Reichert, Plummer & Wine, 1983).

Spiking local interneurons may also integrate inputs from long interneurons. In the locust, some long interneurons that descend from the brain spike at the offset of light to the ocelli (Rowell & Pearson, 1983). Spikes in the long ocellar interneurons are followed by EPSPs that occur at short, apparently monosynaptic latencies, in several spiking local interneurons in the mesothoracic ganglion. A few of the spiking local interneurons discharge in rhythm with the wing depressor motor neurones during simulated flight, but their outputs are unknown.

Another large group of interneurons that integrate sensory inputs are the giant interneurons in the lobula plates of flies. The interneurons respond selectively to movements in the visual field, with different ones responding maximally to stimuli of different directionalities (for a review, see Hausen, 1981). Unlike the other spiking interneurons discussed so far, the lobula plate interneurons are separated from sensory neurones by an unknown, but possibly large number of synapses. They are mentioned here for two reasons. The first is the problem of defining 'local' interneurons in the brain. Though the processes of the giant interneurons occur largely in the lobula plate, some have processes extending into other parts of the brain. Thus, depending upon how wide or narrow a definition one favours, they may be considered local or long interneurons. The second reason is that there has been some debate about whether they normally support spikes. Hengstenberg (1977) demonstrated that

Some of the interneurons, previously regarded as non-spiking, could be induced to spike in response to visual stimuli, by imposing a sustained intracellular hyperpolarization. It was argued, therefore, that normally the neurones generated spikes, and the absence of them indicated an abnormal state, perhaps due to anoxia in the brain. This demonstration reinforced the suspicions of some that 'non-spiking' interneurons described elsewhere in arthropods behaved in this way only because of insults they had received at the hands of experimenters. In more recent studies, however, Hausen (1981) has demonstrated that the responses of the same lobula plate neurones change with repeated movements in the visual field. At first, the interneurons generate spikes. With prolonged stimulation, these gradually diminish in amplitude, so that finally only graded potentials are conducted electrotonically. However, the normal visually guided behaviour of the animal is still elicited, and continues for at least a day after the tracheae overlying the lobula plate are removed. Thus it is postulated that the interneurons normally function with both spikes and graded potentials (Hausen, 1981). By contrast, imposed hyperpolarization of non-spiking local interneurons in locust ganglia does not reveal spikes (Burrows & Siegler, 1978). This, and considerable other evidence indicates that normally these interneurons function solely with graded potentials (Pearson & Fourtner, 1975; Burrows & Siegler, 1978).

Non-spiking local interneurons controlling motor output

Non-spiking local interneurons that control motor outputs have been described in the ventral ganglia of cockroach, locust, crayfish and crab. Studies have focused on the role of the interneurons either in the graded recruitment and the coordination of motor neurones, or as part of central rhythm generators.

The graded control of movement and posture

In the cockroach metathoracic ganglion, non-spiking local interneurons have been described that recruit leg motor neurones in a graded way (Pearson & Fourtner, 1975; Meyer & Walcott, 1979). The interneurons are depolarized in phase with leg movements, and may be part of the central rhythm generator for walking (Pearson & Fourtner, 1975), as will be discussed below. In the metathoracic ganglion of the locust, recordings have been made simultaneously from non-spiking local interneurons and leg motor neurones, to establish that the graded effects of the local interneurons are due to chemical synaptic transmission (Burrows & Siegler, 1976, 1978). Small depolarizations of an interneurone from its 'resting' membrane potential are sufficient to effect transmitter release (Fig. 3A–D; Burrows & Siegler, 1978), with EPSPs of only some 2 mV evoking discrete IPSPs in motor neurones (Burrows, 1979a). The non-spiking interneurons branch mainly, or wholly within one half of the ganglion, and act on motor neurones of the ipsilateral leg (Fig. 4; Siegler & Burrows, 1979). When depolarized, a non-spiking interneurone can excite or inhibit several postsynaptic motor neurones, and cause vigorous and well-coordinated movements of a leg (Burrows, 1980). Some non-spiking interneurons inhibit others, possibly to prevent antagonistic motor neurones from being activated together (Burrows, 1979b). Thus, non-spiking interneurons appear to be crucial elements in the initiation and coordination of leg movement. In a quiescent animal, the non-spiking

interneurons may be sufficiently depolarized to release transmitter continuously (Fig. 3D), suggesting that they normally act also to maintain the posture of a leg (Burrows & Siegler, 1978; Wilson & Phillips, 1982). In addition, sustained changes in membrane potential, imposed by the injection of current, can alter the strength of proprioceptive reflexes of a leg (Fig. 3E; Siegler, 1981b).

Non-spiking interneurons in locust receive considerable sensory influence, primarily from the leg whose motor neurones they affect (Burrows & Siegler, 1978; Burrows, 1979a,b; Siegler, 1981a). Sustained or phasic changes in membrane potential can be evoked, for example, by imposed movements of the joints of a leg (Fig. 3F),

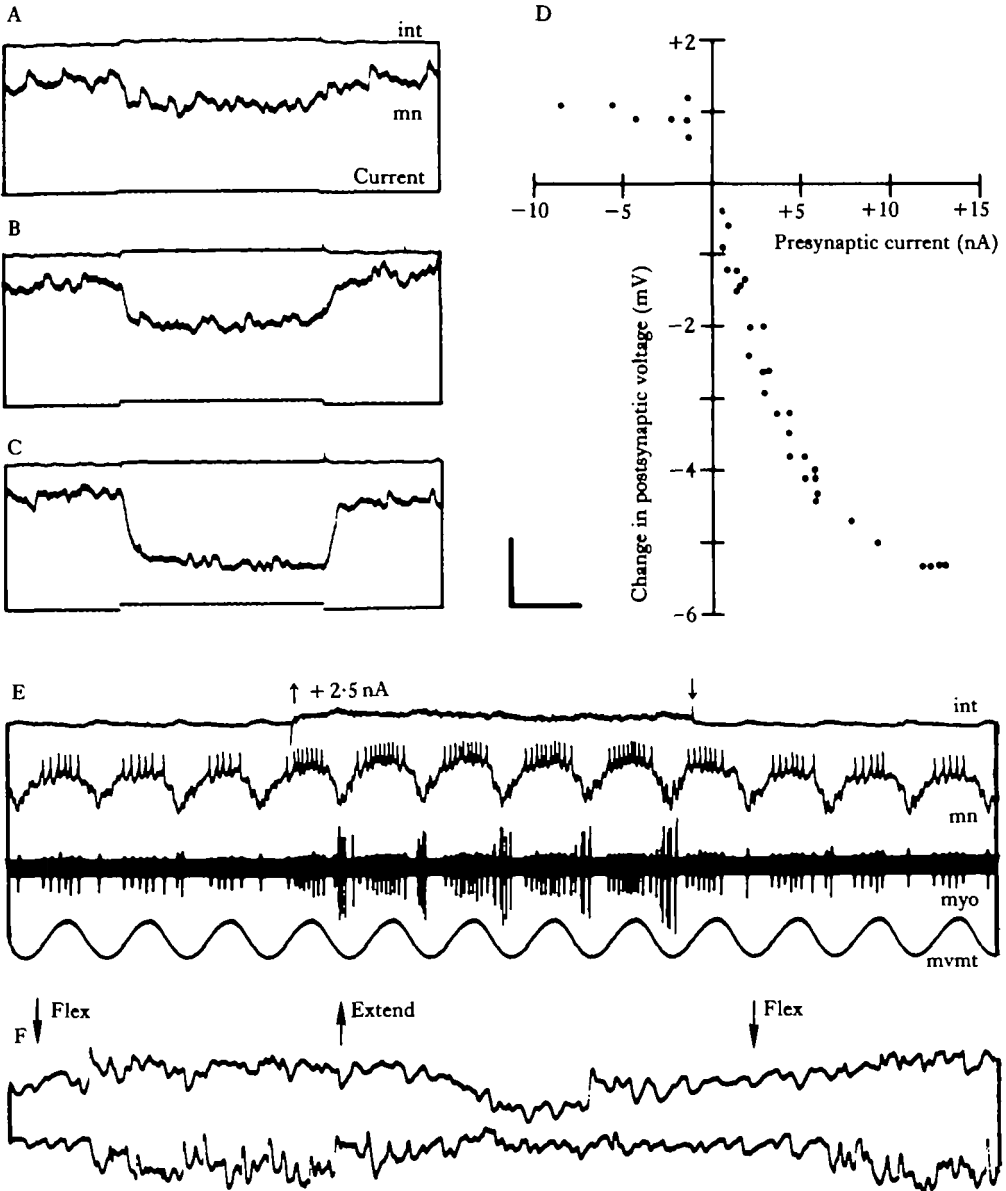


Fig. 3

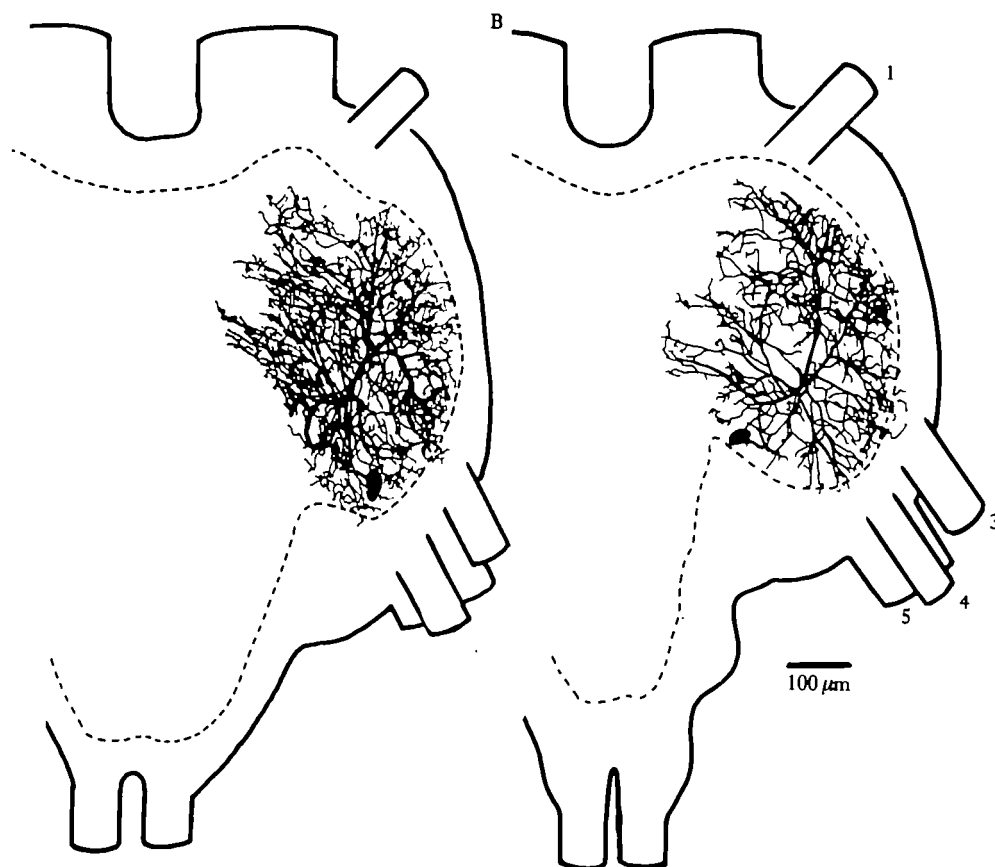


Fig. 4. Morphology of two non-spiking local interneurons in the metathoracic ganglion of locust. Both interneurons, when depolarized with intracellularly injected current, excite the slow extensor tibiae motor neurone of the right hind leg. The interneurons were stained as for Fig. 1. The ganglia are viewed dorsally, and lateral nerves 1, 3, 4 and 5 are numbered. The dotted lines indicate the outline of the neuropile. (From Siegler & Burrows, 1979.)

Fig. 3. Physiology of non-spiking local interneurons in the metathoracic ganglion of locust. (A–D) Graded inhibitory synaptic transmission between a non-spiking interneurone (int) and a motor neurone (mn) is elicited by depolarizing the interneurone with steps of current. Current is injected into a neuropilar process of the interneurone *via* a bridge circuit; response of motor neurone is recorded in its cell body. As the current is increased in A–C, the hyperpolarization of the motor neurone also increases. (D) plots the relationship between presynaptic current, and the change in postsynaptic voltage. Hyperpolarizing current results in a depolarization of the motor neurone, indicating that at rest, the interneurone holds the motor neurone continuously hyperpolarized. (E) Sustained depolarization of a non-spiking interneurone (int) enhances reflexes of tarsal motor neurones. A tarsal depressor motor neurone (mn), recorded intracellularly, is depolarized and spikes, each time the tibia is extended about the femur (upwards on the movement trace, mvmt). When the interneurone is depolarized (between arrows) firing of the depressor motor neurone increases, as does that of the alternately active tarsal levator motor neurone (larger spikes in myogram, myo). (F) Imposed flexion and extension of the femoral-tibial joint of a hind leg cause complex changes in the patterns of synaptic inputs to non-spiking local interneurons. When depolarized with injected current (not shown) the two interneurons have the opposite effect on motor neurones of the same hind leg. One (first trace) excites flexor tibiae motor neurones, whilst the other (second trace) excites extensor tibiae motor neurones. Calibration. Vertical: A–C, int, 42 mV; mn, 4 mV; current, 37 nA; E, int, 40 mV; mn, 6 mV; F, 8 mV. Horizontal: A–C, 245 ms; E, 1 s; F, 100 ms. (A–D from Burrows & Siegler, 1978; E from Siegler, 1981b; F from Burrows, 1979b.)

or by tactile stimuli to cuticular receptors. Each non-spiking interneurone responds to a much wider variety of inputs than does a spiking local interneurone, and does not appear to integrate primary sensory inputs. In the locust, afferents from tactile hairs on the legs have not been found to synapse upon non-spiking local interneurons, as they do upon spiking local interneurons (Siegler & Burrows, 1983). In the cockroach, however, stimulation of hair plate sensilla on the coxa evokes EPSPs in some unidentified non-spiking interneurons (Pearson, Wong & Fournier, 1976). In the locust, indirect evidence suggests that the local non-spiking interneurons may receive inputs from the spiking local interneurons (Siegler & Burrows, 1983). These sensory inputs can influence the efficacy of transmission between non-spiking interneurons and motor neurones (Siegler, 1981*b*).

Local non-spiking interneurons that recruit motor neurones in a graded way occur also in the terminal abdominal ganglion of crayfish (Takahata, Nagayama & Hisada, 1981; Reichert *et al.* 1982). When depolarized, they may excite, or inhibit the spiking of motor neurones (recorded extracellularly) to different parts of the tailfan. The non-spiking local interneurons respond to many of the same sensory inputs that affect the spiking local interneurons in the same ganglion, including water movement, and touch or pressure to the tailfan, but do so in a less specific way (Reichert *et al.* 1982). Thus, there is some similarity to the differing responses of spiking and non-spiking local interneurons in the metathoracic ganglion of the locust (Burrows & Siegler, 1982), with non-spiking interneurons responding to a wider array of sensory inputs than do the spiking local interneurons.

In these non-spiking interneurons of crayfish and locusts, the branches throughout the neuropile are of generally uniform appearance, as compared with those of spiking local interneurons (Reichert *et al.* 1982; Siegler & Burrows, 1979, 1984). As yet there is no physiological evidence that different regions of non-spiking interneurons are specialized for receiving inputs, or effecting outputs.

Pattern generation

In the cockroach metathoracic ganglion, one non-spiking interneurone is considered to be part of the oscillator that drives the walking rhythm (Pearson & Fournier, 1975). This conclusion is based largely on an experiment where the rhythm of leg movements was reset by injecting current into the interneurone. The possibility remains, however, that resetting could have occurred indirectly, by sensory feedback from altered leg movements. There is considerable sensory feedback to non-spiking interneurons that control leg motor neurones in the locust, as discussed above, and sensory inputs can influence the walking rhythm in the cockroach (Pearson, 1972). Although a role in rhythm generation is not excluded, it is important to stress that studies on the locust show the widespread and diverse nature of the interactions between non-spiking interneurons and motor neurones. This evidence suggests that the non-spiking interneurons are likely to recruit motor neurones in any behaviour that involves postural adjustments or coordinated movements of the legs. Thus, it now seems inappropriate to label them as 'oscillator' neurones.

In crustaceans, studies of non-spiking local interneurons in motor control have focused on their role in generation of the ventilatory rhythm in crabs and lobsters (Mendelson, 1971; Simmers & Bush, 1980; Simmers, 1981), or of the swimmeret

Rhythm in crayfish (Heitler & Pearson, 1980). The usual approach has been to record non-spiking interneurons intracellularly, and to observe the effects they have on the rhythmical alternation of spike activity in antagonistic groups of motor neurons, recorded extracellularly. These motor neurons are classified, for the ventilatory rhythm, into levators and depressors of the scaphognathites, or gill bailers, and for the swimmeret rhythm, into swimmeret power stroke and return stroke motor neurons.

In ventilation, two types of non-spiking neurons have been described physiologically, both of which are considered to be part of the central rhythm generator. One type, when depolarized with current pulses of long duration, evokes sustained firing in depressor motor neurons, and suppression of firing in levators; in addition, injected current of either polarity resets the rhythm (Mendelson, 1971; Simmers & Bush, 1980). The other type modulates the frequency of the rhythm in a graded way, according to the intensity and polarity of intracellularly injected current (Simmers & Bush, 1980; Simmers, 1981). Intracellular staining of neurons with these physiological properties reveals local interneurons (DiCaprio & Fournier, 1981).

A wider variety of types of non-spiking neurons have been shown to influence the activity of swimmeret motor neurons in the crayfish (Heitler & Pearson, 1980; D. Paul & B. Mulloney, in preparation). Some, considered to be part of the central rhythm generator, could, when depolarized or hyperpolarized with injected current, alter the strength or timing of the swimmeret rhythm. One interneuron, for example, could reset the rhythm and alter the relative strength of power stroke and return stroke bursts (Heitler & Pearson, 1980). Another, could, when hyperpolarized, initiate the rhythm in a quiescent nerve cord, and when depolarized, slow or stop a rhythm and reset it (D. Paul & B. Mulloney, in preparation). Others, which were not considered to have a role in rhythm generation, had sustained effects and could interrupt the swimmeret rhythm, by exciting return stroke motor neurons, and/or inhibiting power stroke motor neurons (D. Paul & B. Mulloney, in preparation). Thus, as in insects, the non-spiking interneurons function other than as a part of a central rhythm generator.

The connections that underlie generation of the ventilatory and swimmeret rhythms are as yet unknown, but probably involve motor neurons as well as non-spiking interneurons. Motor neurons are considered to be part of the rhythm generating networks, for when injected with current, they may reset the rhythm or alter its frequency (Heitler, 1978; Simmers & Bush, 1983).

Local non-spiking interneurons in sensory processing

A local sensory interneuron in crayfish

So far, it has been shown that, in segmental ganglia, spiking local interneurons are involved in the processing of primary sensory inputs and that non-spiking ones are involved in the coordination of motor output. Exceptions to this are the non-spiking local, directionally-selective (LDS) interneurons in the terminal abdominal ganglion of crayfish (Reichert *et al.* 1982, 1983). The LDS interneurons respond selectively to water currents of a particular directionality. There is perhaps only a single pair of LDS interneurons in the ganglion, by contrast with the larger number of non-spiking interneurons that affect motor neurons (Reichert *et al.* 1982). In the LDS interneurons, large EPSPs occasionally give rise to graded, active transients, similar to

those recorded in the 'nonimpulsive' stretch receptors of crabs (Reichert *et al.* 1983; Bush, 1981). This contrasts with the passive responses of the premotor non-spiking interneurons in the same ganglion, and of those in the ventral ganglia of insects.

The LDS interneurons receive inputs directly from mechanosensory hairs on the tailfan, with EPSPs occurring in phase with oscillatory water movements (Reichert *et al.* 1983). They have extensive bilateral arborizations, with branches of different appearance in the two halves of the ganglion. This, and physiological evidence suggests that the interneurons are divided into input and output regions (Reichert *et al.* 1983). Branches in one half of the ganglion are thought to receive monosynaptic inputs from mechanosensory hairs, and branches in the other to effect direct outputs to some long, ascending interneurons. Synaptic transmission by LDS interneurons onto the long interneurons is graded, inhibitory and chemically mediated. When an LDS interneurone and one of the long interneurons are penetrated simultaneously, depolarization of the LDS interneurone with current hyperpolarizes the long interneurone. Furthermore, graded EPSPs in the LDS interneurone, evoked by electrical stimulation of a nerve root of the tailfan, in turn cause graded IPSPs in the long interneurone. When the LDS interneurone is gradually hyperpolarized with injected current, the IPSP in the long interneurone is gradually diminished, then abolished, indicating that the LDS interneurone was mediating the IPSP. If the spiking local interneurons in the ganglion are also second order neurones (Reichert *et al.* 1982), then these and the LDS interneurons may process some sensory inputs in parallel.

Arthropod visual systems

In the visual systems of insects and crustaceans, graded, passively propagated signals and non-spiking transmission underlie integration at the most peripheral synapses (for reviews see Shaw, 1979, 1981; Chase, 1975; Stuart & Oertel, 1978). What is particularly interesting in the context of local and long interneurons, is that although the responses to light at the first few stages of visual processing for barnacle ocelli, locust ocelli and insect compound eyes are remarkably similar, the morphology of the cells involved differs considerably.

Fig. 5. Physiology and morphology of neurones in arthropod visual pathways. (A) Responses to light of photoreceptor (PR), second order cell (I-cell), and third order cell (A-cell) of barnacle median ocellus. Light pulse is given to dark adapted cells. Each recording is taken from a separate experiment, and that of the A-cell from a preparation bathed in TTX. (From Oertel & Stuart, 1981). (B) Five responses of photoreceptor in compound eye of fly *Calliphora*, recorded in the axon of the photoreceptor, to square wave light pulses. The 200 ms stimulus is indicated by the horizontal bar. From top to bottom of column, light intensity decreases. (From Zettler & Järvilehto, 1973.) (C) Four responses of a second order L neurone, and a third order descending interneurone in the ocellar pathway of the locust *Schistocerca* to light pulses. Recordings are made simultaneously from the axon of the second order neurone, and cell body of the third order neurone. From top to bottom of column, light intensity decreases. Solid bar is light pulse. At 'light off', the third order neurone spikes for the three highest intensities, whilst the second order neurone spikes only at the highest intensity. (From Simmons, 1981.) (D) Left: morphology of a second order I-cell in barnacle, injected with HRP and drawn from a whole mount. Right: diagram to show the position of the I-cell (arrow) in the supraoesophageal ganglion (SEG). Its arborizations are in the same region as those of photoreceptors projecting from the median ocellus (MO). AN, antennal nerve; CEC, circumoesophageal connectives. (From Oertel & Stuart, 1981.) (E) Morphology of ocellar L-neurone, revealed by intracellular injection of Co^{2+} , and intensification of CoS with silver. The extensive arborizations occur in the subocellar neuropile, (OC) and a process extends in the ocellar nerve (ON) to the protocerebral (PC) area of the brain, where the neurone cell body is located. (From Mizunami, Yamashita & Tateda, 1982.)

The photoreceptors respond to a light pulse with a depolarizing increase in membrane conductance, which is graded with light intensity (Fig. 5A, B). The signal spreads passively to the axon terminals, with little decrement, even in a barnacle photoreceptor, which has an axon up to 1 cm in length (Shaw, 1972). Depolarization of the photoreceptor causes the release of a transmitter that hyperpolarizes second order neurones (Fig. 5A, C). This hyperpolarizing signal is graded with light intensity (Fig. 5C), and is also conducted passively within the neurones, with little decrement

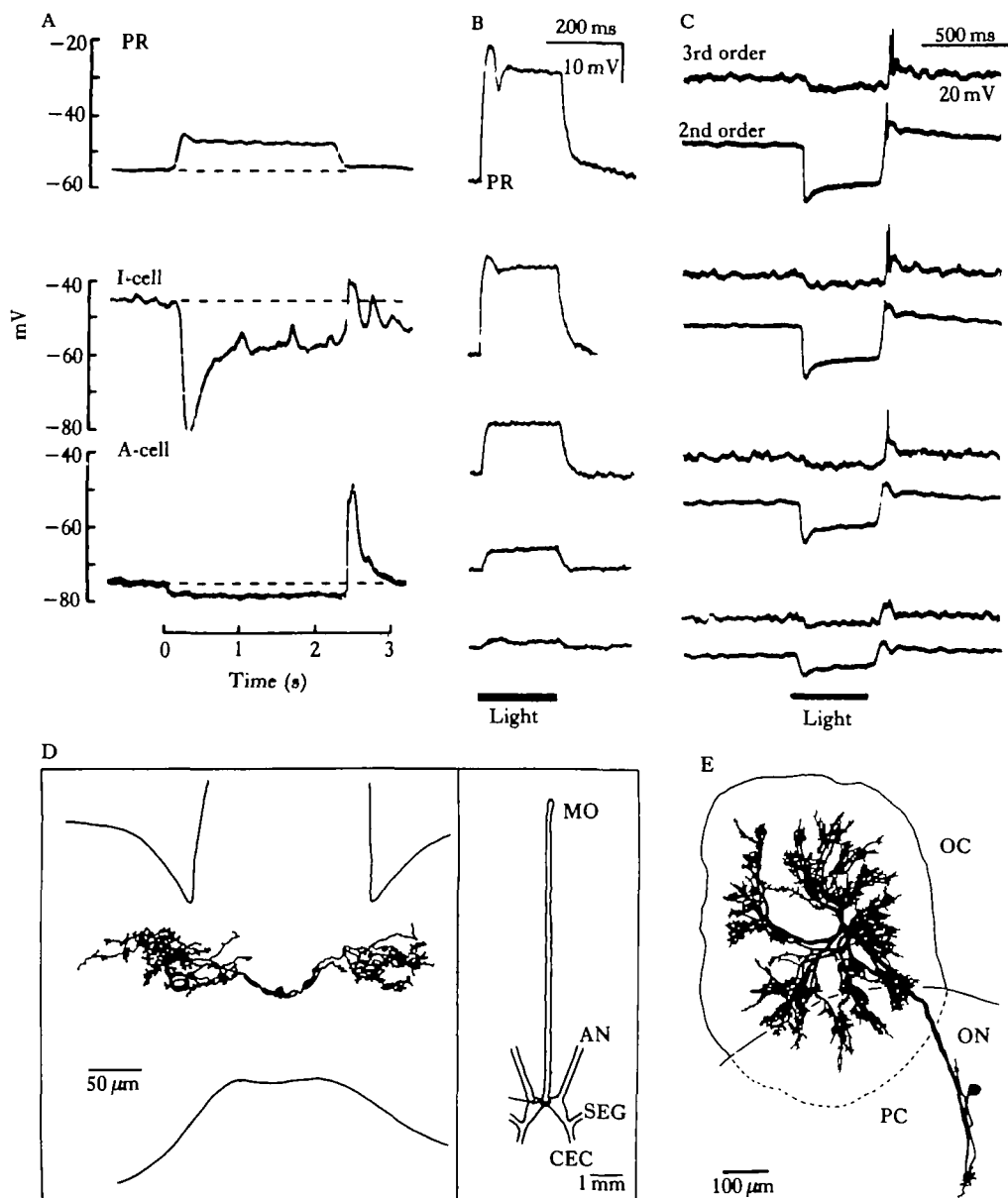


Fig. 5

(Wilson, 1978; Shaw, 1979, 1981). At 'light-off' the second order neurones depolarize, to overshoot their resting membrane potential (Fig. 5A, C). The responses of third order neurones have been recorded only in locust and barnacle (Simmons, 1981; Stuart & Oertel, 1978; Oertel & Stuart, 1981). During a light pulse, the third order cells are slightly hyperpolarized (2–5 mV) (Fig. 5A, C) and their membrane conductance is decreased. This occurs because the second order neurones continually release excitatory transmitter at a low level (Fig. 6C), and during a light pulse, when they are hyperpolarized, this release is turned off. At 'light-off', when the second order neurones depolarize, the third order neurones also depolarize, and may give rise to regenerative, actively propagated spikes (Fig. 5C). The third order ocellar neurones have axons that project caudally from the brain, and presumably, the 'conventional' spikes are associated with their long axons.

In the compound eyes of insects, the photoreceptors and the second order neurones are confined to one neuropilar region of the optic lobe, and thus may be considered local neurones. In locust ocelli, the photoreceptors are also confined locally, to the subocellar neuropile, but the second order neurones send their processes over 1 mm in the ocellar nerve to enter the brain (Fig. 5E). There they contact the third order neurones. By contrast, in the barnacle, the photoreceptors themselves project the greater distance, up to 1 cm in the ocellar nerve, to enter the supraoesophageal ganglion (SEG) (Fig. 5D). The second order neurones are local interneurones, which branch only within the SEG. In visual processing, then, it seems that it is the ability of the neurones to conduct graded responses with little decrement and to effect transmitter release in a graded way, that is primary, rather than their morphological identities as local or long interneurones.

HOW LOCAL INTERACTIONS OCCUR

Transmitter release mediated by graded presynaptic signals

The graded release of transmitter is the only mechanism described thus far for synaptic actions of non-spiking local interneurones, but it is not restricted to them. Thus, it may occur in some neurones that are specialized to transmit graded signals over long distances, such as the crab stretch receptor, and the barnacle photoreceptor, and in long interneurones or motor neurones, such as those of the lobster stomatogastric ganglion. The latter neurones may have some regions where graded interactions occur, and others, where 'conventional' spikes are actively propagated.

Graded postsynaptic effects

Two excitatory synapses where graded transmitter release has been studied in detail illustrate its general features. One synapse is between a 'nonimpulsive' stretch receptor and a coxal motor neurone in the crab (Blight & Llinás, 1980; Fig. 6A, B). The other is between a second order, L (large) neurone, and a third order interneurone in the ocellar pathway of the locust (Simmons, 1981; Fig. 6C, D).

In studies of the crab stretch receptor synapse, the relationship between pre- and postsynaptic potential was tested by superimposing depolarizing voltage steps of varying amplitude on a holding potential of -80 mV (Fig. 6A). (Resting potential of

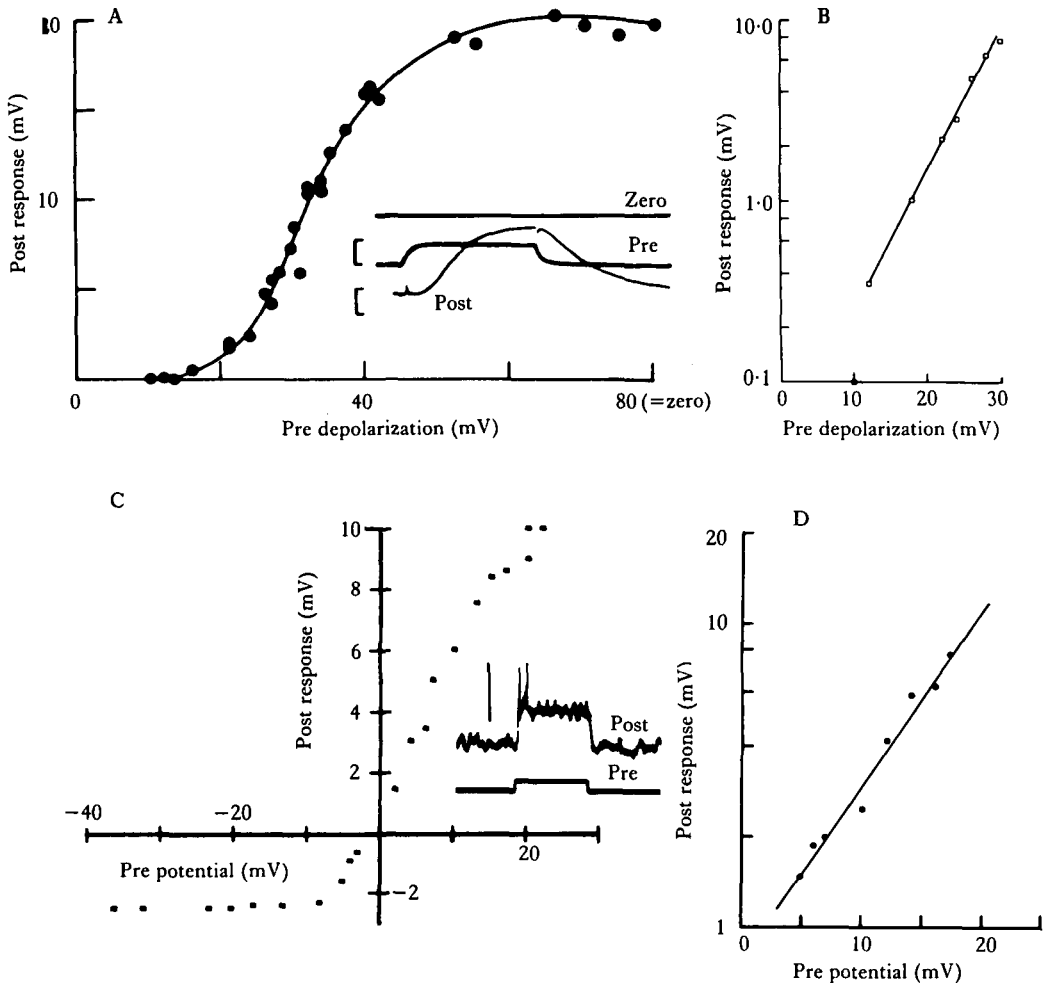


Fig. 6. Transfer characteristics of graded synaptic transmission at two synapses. (A) Stretch receptor T fibre to promotor motor neurone synapse in crab *Callinectes*. Relationship between peak amplitude of postsynaptic potential in motor neurone, and depolarization of the T fibre from an imposed membrane potential of -80 mV; inset shows sample response to 100 ms current pulse. Voltage: pre, 50 mV; post, 5 mV. (From Blight & Llinás, 1980.) (B) Lower portion of relation shown in A, plotted semilogarithmically. (C) L neurone to third order neurone synapse in locust ocellar system. Relationship between steady amplitude of postsynaptic potential in third order neurone, and depolarization or hyperpolarization of the presynaptic L neurone from its resting potential of about -32 mV in dim light; inset shows sample response to 500 ms current pulse. Voltage: pre, 50 mV; post, 10 mV. (From Simmons, 1981.) (D) Lower portion of relation shown in C, replotted semilogarithmically. Values for pre- and postsynaptic changes in voltage are measured relative to the plateau of the hyperpolarizing response of the third order neurone, which is evident when the presynaptic L neurone is hyperpolarized from rest by potential changes of -8 mV or greater (see C).

a stretch receptor in a dissected preparation is normally -60 to -70 mV; Bush, 1981.) The smallest presynaptic depolarizations produce no change in postsynaptic potential. Then, as the presynaptic depolarization is further increased, there is a region of rapidly increasing sensitivity, (threshold for transmitter release, around -60 mV), a region where the relationship is roughly linear, and finally, a region of decreasing sensitivity, as the postsynaptic response begins to reach a plateau.

At the locust synapse, the relationship between presynaptic and postsynaptic potential is roughly similar in shape to that of the crab (Fig. 6C). It has a different position relative to the axes, however, because the normal membrane potential of the presynaptic L neurone (around -32 mV) is more depolarized than the threshold for transmitter release (around -40 mV). Thus, when the L neurone is hyperpolarized from its 'resting' membrane potential, the release of excitatory transmitter is diminished and the postsynaptic neurone is hyperpolarized.

Despite the differences in 'resting' membrane potential, and in threshold for transmitter release, the crab and locust presynaptic neurones both have a range of about 20 mV over which they are most effective in altering the postsynaptic potential: from -60 to -40 mV for the crab stretch receptor, and -35 to -15 mV for the locust L neurone (Fig. 6A, C). In addition, the two synapses are of similar sensitivity, as measured when the voltage relationships are plotted semi-logarithmically (Fig. 6B, D). At the crab synapse, a presynaptic change of some 12.5 mV is needed to effect a ten-fold change in postsynaptic potential, and at the locust synapse some 16 mV is needed. These values are in the range recorded at the squid giant synapse, where Katz & Miledi (1967) considered a 9 mV/ten-fold change to be a representative value. However, they recorded mean values of 16–3.7 mV, for a ten-fold change, finding the highest values when the presynaptic recording electrode was farthest from the synapse. Rough calculations from data published on other central neurones in arthropods where graded transmission occurs suggest that presynaptic changes of some 10–20 mV are needed to effect a ten-fold change in postsynaptic voltage (e.g. lobster stomatogastric interneurones and motor neurones: Graubard, 1978; Graubard, Raper & Hartline, 1980; locust L neurone to L neurone: Simmons, 1982; locust non-spiking interneurones: Burrows & Siegler, 1978; Burrows, 1979b). These are an order of magnitude less sensitive than the synapses made by photoreceptors in the locust compound eye, where a presynaptic change of only 0.8 mV is needed to effect a ten-fold change in postsynaptic potential (Laughlin, 1973; see also Shaw, 1981 for discussion). Whereas Llinás (1979) considers the squid synapse to be a low gain one, Blight & Llinás (1980) consider the crab synapse to be a high gain one. The basis for this distinction is that in the squid, the presynaptic neurone needs to be depolarized considerably from rest to effect transmitter release, but in the crab, only small depolarizations from rest are needed. This, however, would seem to say more about the resting potential of the neurone, relative to the transmitter release threshold, than about the synaptic gain.

Membrane potential and the threshold for transmitter release

The proximity of the resting potential to the threshold for transmitter release (and to the threshold for spike generation, if it occurs) are, of course, important in determining how effective small, graded signals will be in evoking the release of transmitter. Many non-spiking interneurones have relatively low 'resting' potentials. They include non-spiking local interneurones in segmental ganglia of cockroach (Pearson & Fourtner, 1975), locust (Burrows & Siegler, 1978) and crayfish (Reichert *et al.* 1982; Takahata *et al.* 1981), and second order neurones in the ocellar systems of barnacle (Stuart & Oertel, 1978) and locust (Simmons, 1981). All have 'resting' membrane potentials that are some 10–20 mV more depolarized than those of surrounding spiking

neurons (e.g. locust non-spiking interneurons, average -48 mV; spiking neurons, average -64 mV). Furthermore, the 'resting' potential is close to, or more depolarized than the threshold for transmitter release [e.g. ocellar interneurons, the release threshold is around -45 to -50 mV, compared with resting potentials of -42 mV (barnacle) and -32 mV (locust)]. By contrast, relatively high (-60 to -70 mV) resting potentials are found in barnacle photoreceptors (Stuart & Oertel, 1978), crab stretch receptors (Bush, 1981) and LDS interneurons in crayfish (Reichert *et al.* 1982, 1983); none of these are significantly different from those of surrounding spiking neurons. In the barnacle photoreceptor and crab stretch receptor, however, the threshold for transmitter release is also at a more hyperpolarized membrane potential, around -60 mV. Thus it seems to be generally true that non-spiking neurons have 'resting' membrane potentials close to the threshold for transmitter release, though not necessarily low in comparison with those of surrounding neurons. This would have the obvious advantage that small changes in membrane potential could be effective in releasing transmitter.

How sustained is graded transmission?

Studies of synaptic transmission in the absence of spikes in the presynaptic neurone have demonstrated unequivocally that postsynaptic voltage can be finely graded, as a function of presynaptic voltage or current. The effectiveness of transmission may also vary with time, to different degrees for different synapses. At one extreme are synapses such as those of the locust ocellar L neurones. Postsynaptic effects are sustained without decrement for at least 5 min during imposed presynaptic depolarization at the synapse between an L neurone and a third order neurone (Simmons, 1981), and at excitatory synapses between the L neurones (Simmons, 1982). The L neurones, the second order ocellar neurones of barnacle, and some non-spiking interneurons in locust thoracic ganglia are normally depolarized above their threshold for transmitter release (Simmons, 1981; Oertel & Stuart, 1981; Burrows & Siegler, 1978), implying that release can be sustained indefinitely, at least at the 'resting' membrane potential. However, in the barnacle second order ocellar neurones, and also at the crab stretch receptor synapse, large presynaptic depolarizations, imposed by injected current, result in a diminution of the postsynaptic response with time (Oertel & Stuart, 1981; Blight & Llinás, 1980). Even with small presynaptic depolarizations, non-spiking regions of long interneurons and motor neurons in the lobster stomatogastric ganglion evoke postsynaptic responses with a pronounced peak-plateau waveform (Fig. 7D; Graubard, 1978; Graubard *et al.* 1980, 1983). In effect, the sensitivity of the synapse declines markedly over time. Another, and extreme, example of this are the L neurones of locust ocelli. In addition to having sustained excitatory effects on third order neurones, some L neurones inhibit other L neurones (Simmons, 1982). In these inhibitory interactions, sustained presynaptic depolarizations elicit only a transient IPSP. This IPSP is extremely labile, and can be evoked only about once a second. It is not known why transmission declines at this, or at any of the other synapses, though at the crab stretch receptor synapse, a slow depletion of transmitter is thought to be the most likely explanation (Blight & Llinás, 1980). Other possibilities are the inactivation of Ca^{2+} entry, a decline in the presynaptic voltage during a steady current, the desensitization of postsynaptic receptors and

the activation of postsynaptic conductances that would oppose the initial postsynaptic response.

The apparent limitations on some synapses to sustain graded synaptic transmission, in response to experimentally imposed changes in membrane potential, may simply reflect the size or duration of the normal presynaptic signal. At synapses of the crab stretch receptor, or of the barnacle second order neurone, the postsynaptic responses may decline only when the imposed presynaptic voltage is larger than that which normally occurs. At synapses of stomatogastric motor neurones in lobster, the peak postsynaptic responses are comparable in duration to the oscillations in membrane potential that occur during the stomatogastric rhythm (cf. Fig. 7B and D). Thus the decline to a plateau, prominent when longer duration presynaptic voltages are imposed, would probably not limit transmission under normal circumstances.

Graded and spike-mediated transmission occurring in the same neurone

The stomatogastric ganglion of the lobster provides the most completely studied example of local interactions amongst spiking neurones in an arthropod. Physiological studies have shown the nature and significance of the graded local interactions between motor neurones, ultrastructural studies have shown the morphological basis for these interactions, and modelling studies have shown the contribution made by the electrotonic properties of the neurones.

In the stomatogastric ganglion some 30 motor neurones interact to generate a pyloric and a gastric rhythm (Selverston, Miller & Waldepuhl, 1983). Generation of the pyloric rhythm depends upon inhibitory synaptic interactions amongst the motor neurones (Fig. 7A), and upon the ability of some motor neurones to generate graded depolarizing plateau potentials (Russell & Hartline, 1978). Recordings from the cell bodies of pyloric motor neurones reveal bursts of action potentials 10–20 mV in amplitude (Fig. 7B, C). These arise from 15–25 mV oscillations in membrane potential, and, during the hyperpolarizing part, discrete IPSPs sum with a smoother hyperpolarization (Fig. 7B). It has long been known that the discrete IPSPs are mediated by spikes in presynaptic motor neurones, but only more recently has it been appreciated that the smoother hyperpolarizations are due to the graded release of transmitter from the same neurones (Raper, 1979). Maynard & Walton (1975) first demonstrated that imposed depolarization below the spike threshold of one pyloric motor neurone could decrease the frequency of spiking in another, *via* a chemical inhibitory synapse. Subsequently, Raper (1979) showed that the pyloric rhythm could continue when spikes in the motor neurones were blocked by tetrodotoxin (TTX), provided that spikes in descending excitatory axons were not blocked, or that dopamine was added to the bath (Fig. 7C). Thus, graded synaptic interactions within the ganglion can bring about the correct phasing of activity in pyloric motor neurones, although spikes are necessary for transmission to the periphery. Graded synaptic interactions are now known to be widespread within the ganglion, occurring between all pairs of motor neurones previously shown to interact by spike-evoked PSPs (Fig. 7D; Graubard *et al.* 1980, 1983). Spike-mediated and graded transmission share common features, suggesting that the transmitter and ionic mechanisms underlying the two are the same (Graubard *et al.* 1983). The postsynaptic potentials have similar reversal potentials, involve increased

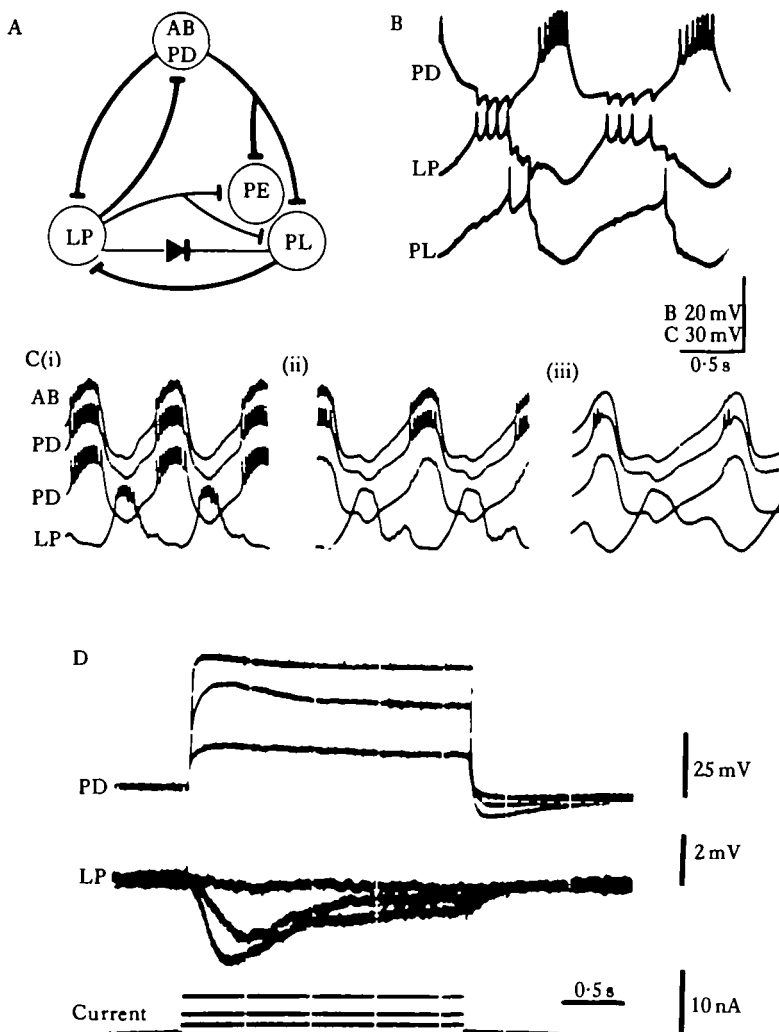


Fig. 7. Graded local interactions in stomatogastric ganglion of lobster. (A) Summary of connections between classes of pyloric motor neurones. Inhibitory chemical connections are shown as T symbols; rectifying electrotonic connections by diode symbol. AB, anterior burster; LP, lateral pyloric; PE, 'early' pyloric; PD, pyloric dilator; PL, 'late' pyloric. (B) Intracellular recordings made simultaneously from the cell bodies of three pyloric motor neurones, in an isolated stomatogastric ganglion, during the pyloric rhythm. (C) Effect of TTX on pyloric rhythm, recorded intracellularly from four pyloric motor neurones. As TTX is applied locally, near spike initiating sites of a PD motor neurone, spike are blocked, but the rhythm continues. (i) Before superfusion. (ii) Seven minutes after start of TTX application. (iii) Ten minutes after start. Descending inputs from oesophageal and commissural ganglia were intact, providing a higher level of excitatory input than to isolated ganglion in B. (D) A graded series of depolarizing currents injected into the cell body of a PD motor neurone evokes a graded series of hyperpolarizing responses in an LP motor neurone. The stomatogastric ganglion is bathed in saline containing TTX, which blocks spikes and endogenous slow wave oscillations in the motor neurones. Note that the peaks of the postsynaptic responses are of similar duration or longer than the depolarizations of the motor neurones during the stomatogastric rhythm shown in B and C. (A, B, D from Graubard, Raper & Hartline, 1983; C from Raper, 1979.)

conductances and are similarly sensitive to low Ca^{2+} , high Mg^{2+} and picrotoxin.

The ability of the stomatogastric motor neurones to interact with graded as well as spike-mediated transmission seems to depend upon their shape, and upon how their input and output synapses are situated relative to each other and to the site of spike initiation. Synapses between the monopolar motor neurones occur in the neuropile, on the relatively thinner and more distal parts of second order branches (King, 1976a). Hundreds, or perhaps thousands of synaptic contacts, distributed over many secondary branches, underlie the interaction between a given pair of neurones (King, 1976a,b). Although input synapses are near output ones, they are relatively distant from the cell body and from the axon, where spikes are initiated. This, and the fact that all-or-none spikes are not actively propagated back into the neuropile, seems to account for the ability of the intraganglionic regions of the neurones to release transmitter in a graded way. Modelling studies are consistent with such an interpretation and indicate that PSPs arising from input synapses on the finer branches would be relatively large, and thus very effective in altering the release of transmitter from output synapses nearby (Graubard & Calvin, 1979). They would decrement severely as they spread proximally towards the axon, however, and thus be less effective in altering spike frequency or the level of transmitter released from synapses on other fine branches of the neurone.

Restricted local interactions

Since input and output synapses are intermingled, but widely distributed, in the stomatogastric ganglion, the local, intraganglionic interactions between any two motor neurones can be seen as the summed effect of many, yet more restricted, local interactions. Many other neurones in arthropods likewise have input and output synapses intermingled on the same branches, implying that they too support restricted local interactions (Pearson, 1979; Watson & Pflüger, 1984). For example, identified motor neurones and long interneurones in locust thoracic ganglia have branches that support complex synaptic arrangements (Fig. 8; Watson & Burrows, 1981, 1982, 1983). Serial EM reconstructions of branches of horseradish peroxidase (HRP) stained neurones have revealed serial synapses, where the stained interneurone or motor neurone is presynaptic to one neurone, and postsynaptic to another, and reciprocal synapses, where the stained neurone is both pre- and postsynaptic to another neurone. Although the lengths of these reconstructed regions are large compared to the thickness of a single EM thin section, they are small compared with the total anatomical extent of a neurone's branches within a ganglion. (A reconstructed length of some $15\text{ }\mu\text{m}$ compares with that of some $3000\text{ }\mu\text{m}$, a conservative estimate of the total length of branches of a local, non-spiking interneurone in the locust

Fig. 8. Serial and reciprocal synapses in motor neurone and long interneurone of locust. (A) Tracings of selected EM sections from a series cut through an HRP-labelled neurite (shaded) of the fast extensor tibiae motor neurone in the metathoracic ganglion. Input and output synapses are indicated by arrows. Unlabelled profiles that could be traced through the series are numbered from 1 to 7. In sections (ii) and (iii) the motor neurone synapses upon a glial cell (g). (From Watson & Burrows, 1982.) (B) Three-dimensional reconstruction from serial EM sections of HRP-labelled neurite ($16\text{ }\mu\text{m}$ region) of a long, intersegmental interneurone in the mesothoracic ganglion. Input (●) and output (▲) synapses are indicated. (From Watson & Burrows, 1983.)

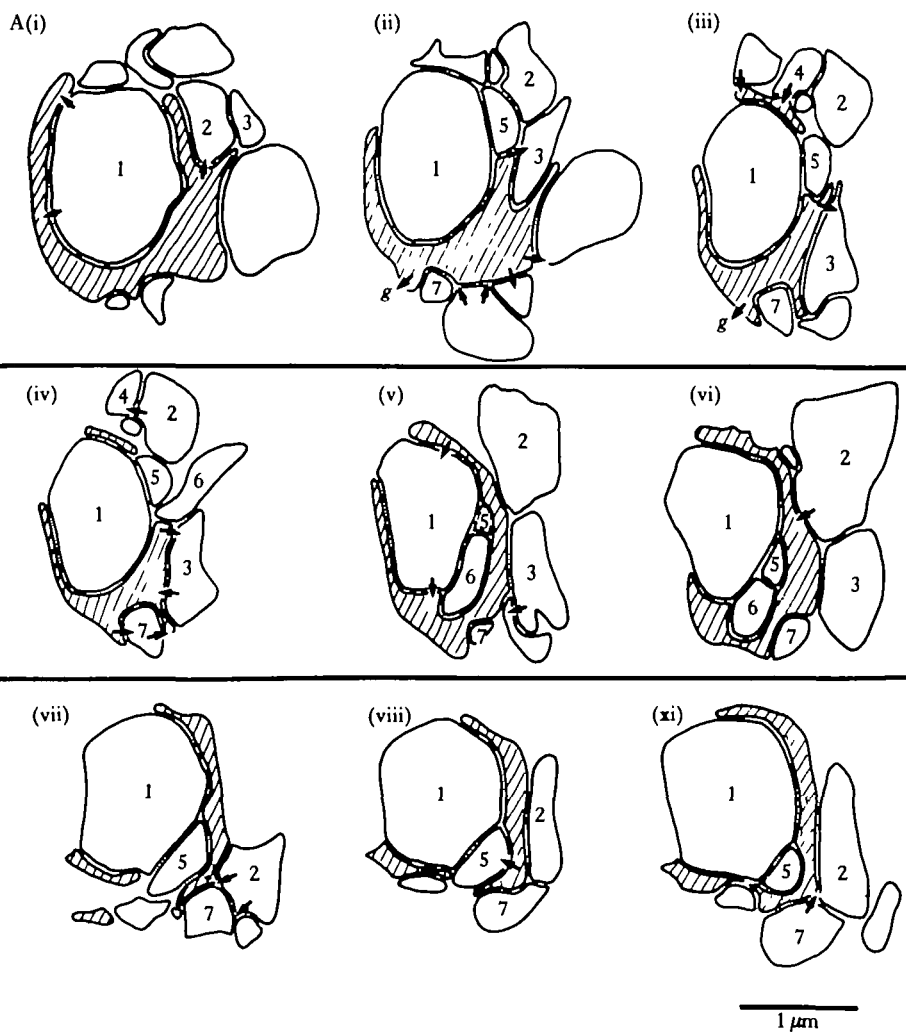


Fig. 8

metathoracic ganglion.) Therefore, as in the lobster neurones, anatomical findings imply that a single neurone can participate in numerous more restricted local interactions.

Whether these restricted local interactions do occur will depend upon the geometry, and the electrotonic properties of the neurones involved. This can be appreciated by considering a model (Fig. 9C; Rall, 1981) of a non-spiking interneurone in the locust, based on anatomical studies (Fig. 9A, B; Siegler & Burrows, 1979). Rall calculated

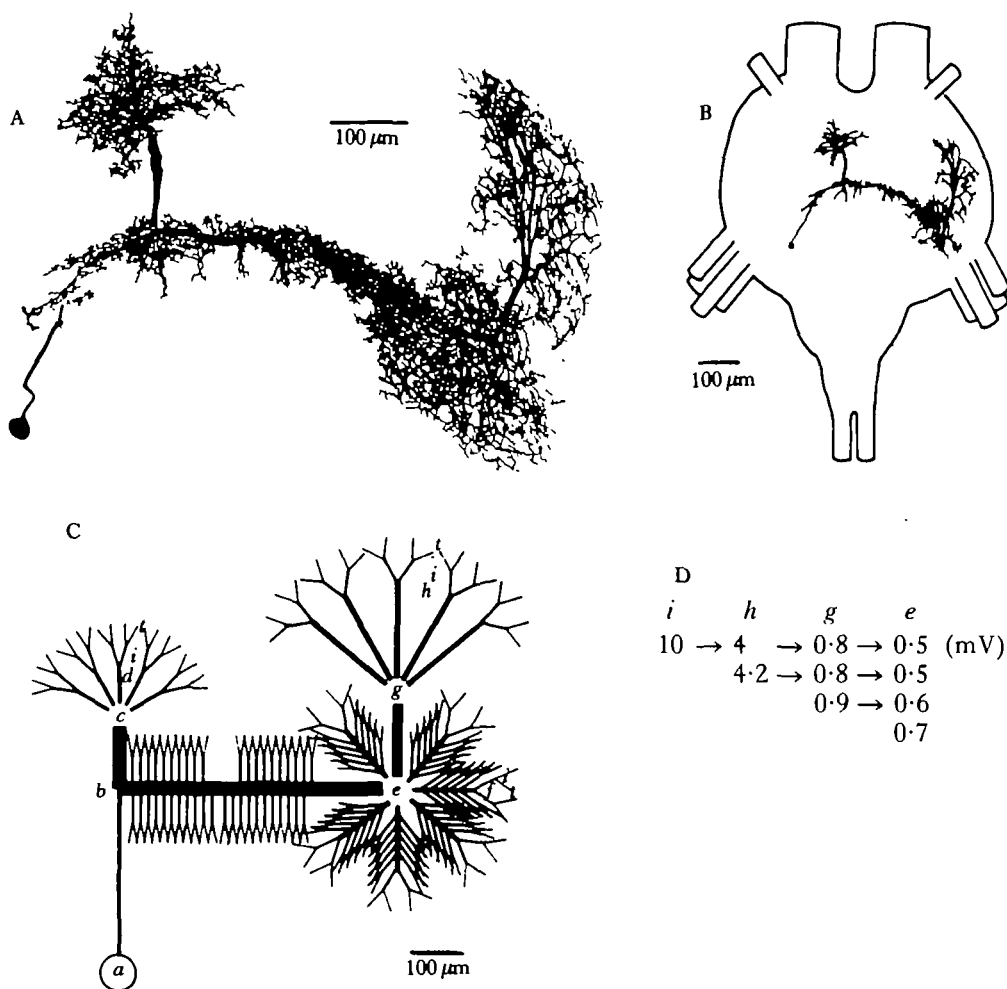


Fig. 9. Non-spiking local interneurone from locust metathoracic ganglion. (A) Drawing of interneurone from whole mount. Interneurone was stained as described in legend to Fig. 1. (B) Drawing of metathoracic ganglion, containing simplified outline of interneurone. (C) Schematic abstraction of interneurone morphology. Branch dimensions (diameter, μm \times length, μm) are: *ti*, 0.5×50 ; *ih*, 1×50 ; *hg*, 2.5×200 ; *ge*, 3×150 . Input resistances ($\text{M}\Omega$) at branch points are: *i*, 90; *h*, 38; *g*, 8.5; *e*, 6.1. For further details see Rall (1981). (D) Decrement of steady state voltage from peripheral to central parts of the interneurone. Each column indicates a branch point. Each line shows the successive decrement of potential from branch point to branch point, in the direction of the arrows. For each line, a similar current is injected, at a different branch point. The initial voltages produced are calculated from the values for input resistance given in C. (A, B from Siegler & Burrows, 1979; C from Rall, 1981.)

steady state attenuation factors along the branches of the schematized interneurone (Fig. 9C), and the input resistance that would be measured at the branch points. Although there is little independent evidence about the membrane and intracellular resistivity on which these calculations are based, the resulting values of input resistance and voltage decrement agree well with the physiological evidence we have (Burrows & Siegler, 1978; Rall, 1981). Rall's calculations indicate how steady voltage changes might be evoked, and decremented in a part of the interneuronal tree (Fig. 9D). There are two points of interest. Firstly, voltages spreading centrally from thin to thick branches will decrement considerably. For example, a 10 mV change imposed at *i* will decrement to 0.5 mV at *e*. Secondly, the higher input resistance at a thin, distal branch means that a given synaptic current would be much more effective in altering the membrane potential there, than at a central, thicker branch (Graubard & Calvin, 1979). Thus, a current sufficient to evoke a 10 mV change at *i* will evoke only a 0.7 mV change at *e*.

Ultrastructural evidence suggests that input and output synapses of non-spiking interneurons do occur primarily on thin, higher order branches (Wilson & Phillips, 1982), though relative positions of the input and output synapses have not been described. From the Rall model, it is clear that output synapses on fine branches will be largely influenced from input synapses nearby. Whether these fine branches do operate independently will thus depend partly upon whether inputs from particular presynaptic neurones are widely distributed, as they are in the stomatogastric motor neurones, or are localized to thin branches.

Other considerations include the regionalization of active and passive membrane, the threshold for transmitter release compared with the resting potential or the spike threshold in different parts of a neurone, and the sustained or transient nature of postsynaptic effects. These and many other possibilities are reviewed by Calvin & Graubard (1979).

Presynaptic modulation – another mechanism for local interactions?

In spiking neurones, graded local inputs may also alter the amplitude of discrete PSPs that are evoked in postsynaptic neurones. Such presynaptic modulation has been described briefly for lobster stomatogastric motor neurones, where spike-evoked IPSPs increase in size with presynaptic depolarization, and decrease with hyperpolarization (Maynard & Walton, 1975). A similar phenomenon has been investigated more thoroughly in central neurones of leech (Thompson & Stent, 1976; Nicholls & Wallace, 1978a) and *Aplysia* (Shimahara & Tauc, 1975; Shimahara & Peretz, 1978; Shapiro, Castellucci & Kandel, 1980).

In the leech, presynaptic modulation of spike-evoked PSPs occurs normally during interactions between heart interneurons (HNs) and heart excitor motor neurones (HEs), and has a role in phasing the activity of motor neurones during the heart rhythm (Thompson & Stent, 1976). The IPSPs evoked in HEs by HNs increase in size with successive spikes during a burst of activity, or during an imposed depolarization (Fig. 10A; Thompson & Stent, 1976). This increase results from the gradual depolarization of the presynaptic HN terminals, rather than from the increasing frequency of HN spikes (Thompson & Stent, 1976; Nicholls & Wallace, 1978a). Thus, individual spikes evoked during a prolonged depolarization of HN produce

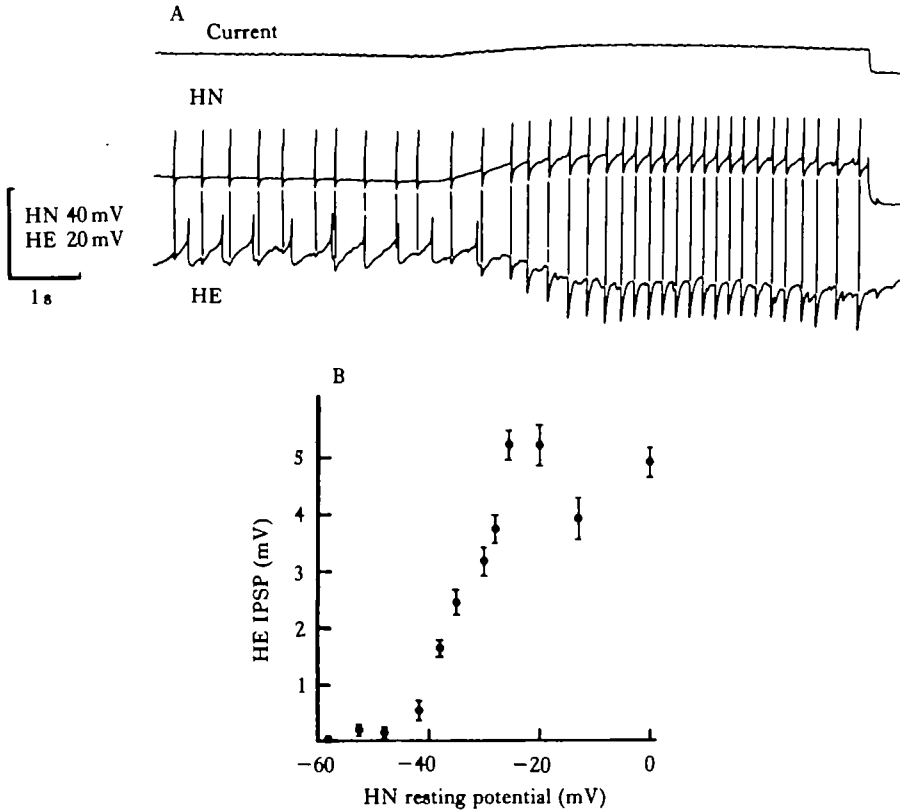


Fig. 10. Presynaptic modulation of spike-evoked PSPs. (A) Effect of graded depolarization of heart interneurone (HN) on postsynaptic heart excitator motor neurone (HE) in the third segmental ganglion of leech. Lines connect spikes in HN with IPSPs they evoke in HE. As HN is depolarized with intracellularly-injected current, spikes in it increase in frequency, IPSPs evoked in HE increase in amplitude and HE is gradually hyperpolarized. Recordings are from the cell bodies of HN and HE. (From Thompson & Stent, 1976.) (B) Dependence of IPSP amplitude in HE on the membrane potential of HN. The resting membrane potential of HN (abscissa) is adjusted to various levels by passing steady currents via the recording microelectrode, and spikes are evoked in HN by brief depolarizing current pulses. The amplitude of the IPSP evoked in HE (ordinate) increases as HN is depolarized. The normal resting potential of HN is about -40 mV. (From Nicholls & Wallace, 1978a.)

larger IPSPs in HEs than do spikes evoked during a prolonged hyperpolarization (Fig. 10B; Nicholls & Wallace, 1978a). The modulation of transmission results from changes in the mean number of quanta released by each spike, but the underlying mechanism is unknown (Nicholls & Wallace, 1978b).

In *Aplysia* neurones, two mechanisms contribute to the increase in spike-evoked PSPs when the presynaptic neurone is depolarized (Shapiro *et al.* 1980). Firstly, imposed depolarization inactivates some K^+ channels; this accounts for an increased amplitude and duration of the spikes that are evoked from more depolarized presynaptic potentials. Consequently, the transient Ca^{2+} current would be increased, and transmitter release augmented. Secondly, imposed depolarization activates a steady state inward Ca^{2+} current. This is proposed to interact with the transient Ca^{2+} current, again to augment the release of transmitter.

In the leech neurones, as in lobster stomatogastric neurones, sustained presynaptic

Depolarizations can also cause the graded release of transmitter locally, from branches in the ganglion where the depolarization is imposed (Fig. 10A; Thompson & Stent, 1976; Nicholls & Wallace, 1978a). The question arises, therefore, as to whether the presynaptic modulation of spike-evoked PSPs has a mechanism separate from that governing the graded release of transmitter. Imposed depolarization could simply shift the presynaptic neurone into a more sensitive region of its input-output curve for transmitter release (cf. Fig. 6), possibly by increasing a maintained Ca^{2+} current, as occurs in *Aplysia* neurones. Thus, spikes of a similar size could evoke larger PSPs.

The presynaptic modulation of spike-evoked PSPs undoubtedly deserves further investigation as a mechanism for local interactions of arthropod neurones. Contrary to the interpretation of Shimahara & Peretz (1978), however, there is as yet no evidence that such a modulation of transmitter release occurs in the non-spiking interneurones of locust (Burrows & Siegler, 1976, 1978), or in those of other species. Rather, presynaptic changes in voltage (from EPSPs, IPSPs or current injected at a neuropilar process) sum directly to alter the level of transmitter release, without the intervention of spikes.

Local spiking interneurones and local interactions

When non-spiking interneurones were first described in arthropod ganglia, and graded transmission was becoming recognized as their normal mechanism of synaptic function, it was suggested that local interactions occurred largely by graded, electrotonically-spreading potentials (Schmitt, 1979). This was a corollary of the idea that spikes were a specialization for transmission over longer distances, between the separated local circuit regions of a nervous system. Studies on arthropod neurones have now shown that local interactions may be mediated by spiking as well as non-spiking local interneurones, and that the same ganglia may contain both types of local interneurones (Burrows & Siegler, 1982; Reichert *et al.* 1982). Thus, we must consider spike-mediated transmission as a normal and important part of local circuit function.

Only in the locust metathoracic ganglion, however, have recordings been made simultaneously from a spiking local interneurone and a postsynaptic motor neurone (Burrows & Siegler, 1982). Here, the local interneurones appear to operate in a 'conventional' way, with graded analogue inputs being translated into a digital output, spike frequency. Spikes in an interneurone evoke discrete IPSPs in the postsynaptic motor neurone; these sum, causing sustained hyperpolarization. The question was not specifically addressed, however, as to whether graded inputs to the spiking interneurone might also cause the graded release of transmitter, or a presynaptic modulation of the spike-evoked IPSPs, so these possibilities remain.

CONCLUSION

Considering all of the neurones discussed, it is clear that there is a continuum of physiological properties in the neurones involved in local interactions. The neurones range from non-spiking local ones that exert their postsynaptic effects solely *via* the graded release of transmitter, to interneurones or motor neurones that give rise to

'conventional' spikes. In some long interneurons or motor neurones, spikes are graded local changes in membrane potential both may initiate the release of transmitter. The graded local changes may also modulate, presynaptically, the efficacy of spike-evoked transmitter release. Local spiking interneurons are the only type of spiking neurone described here, not so far shown also to exert graded transmission; but in principle there is no reason why they could not, given an appropriate geometry of input and output synapses.

Studies on vertebrate nervous systems provide evidence that the kinds of local interactions occurring in arthropod neurones occur also in those of vertebrates. Many classes of retinal neurones operate without spikes (for review see Fain, 1981), and olfactory bulb spiking neurones may also mediate graded postsynaptic effects (for review, see Shepherd, 1981). The advantage, of course, in studying invertebrate neurones is that their interactions can be investigated directly, by recording simultaneously from identifiable and often unique pre- and postsynaptic neurones.

A division into local, and long interneurons has been justified, insofar as it has focused experimental attention on a large group of neurones about which we know comparatively little (for reviews, see Rakić, 1975; Pearson, 1979; Burrows, 1981). Nonetheless, it is now abundantly clear that not all local neurones are non-spiking, and not all non-spiking neurones are local ones. Thus, such an anatomical classification does not coincide with the physiological classification, into non-spiking and spiking neurones. It is tempting, of course, to try to fit the physiological observations to some anatomical scheme, for with the advent of selective intracellular staining techniques, it has become easier to reveal the shape of a neurone than it is to discover all of its physiological properties. From an integrative point of view, however the physiological properties of a neurone must be considered more important. It is the information conveyed in sustained and graded postsynaptic effects, or in discrete, spike-evoked postsynaptic effects, that is of functional significance, not whether a particular neurone is a local or a long one.

What the significance of the two modes of signalling may be remains elusive, although several suggestions have been made as to the advantages of graded, rather than spike-mediated transmission. These include: the ability of single presynaptic neurones to exert finer control over postsynaptic neurones with graded rather than discrete PSPs; isolation of function within different parts of a neurone; sensitivity to very small signals (Pearson, 1976); increased speed of transmission over short distances; temporal accuracy; and reduced ambiguity from 'noise' (Shaw, 1981). In some measure, all of these factors may be important, perhaps to different degrees for different neurones, and as we learn more about the local interactions of neurones, a consensus may emerge.

In 1959, Bullock argued that much of the normal functioning in a nervous system might be carried out 'without all-or-none propagated spikes, but by means of graded and decrementally spreading activity'. It was some time before the physiological and anatomical techniques were available to give this idea the experimental attention it deserved. Now we have reached the stage where variations on this functional theme are being described with rapidly increasing frequency. Indeed, it may some decades hence be difficult to find a neurone that operates in a way once considered 'conventional'.

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