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# Idiosyncratic Computational Units Generating Innate Motor Patterns: Neurones and Circuits in the Locust Flight System

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## Summary

To what extent do general models of neural networks reflect the operation of real circuits of neurones? A consideration of the central neuronal circuitry underlying the generation of the deafferented flight rhythm in the locust reveals that, in this system, the individual computational units (identified neurones) and the ways in which they are organized and interact are highly idiosyncratic. The unique character of this system results from its evolutionary and developmental history as well as from pure, functionally adaptive constraints. Many details of operation may be suboptimal and/or baroque and these may simply be the unavoidable burden of an individual history. This implies that detailed models of systems with different histories, while very important for generating and testing hypotheses specific to the particular systems, are likely not to be transferrable to other systems. Circuits that are unique in their organization and operation demand unique models if such models are to be useful. Nevertheless, assuming that general principles of network operation exist, generalized modelling with idealized units is a valid approach as a means of determining such principles. However, most of the general network models which are currently available do not address the issue of innate motor patterning. The principle of operation in the locust flight system is likely to be largely independent of many of the fine details of the way in which the system actually operates.

## 14.1 Introduction

Can the essence of the computing neurone, the neurone as a computational unit, be distilled? That is to say, is it possible to define those characteristics that are necessary and sufficient to enable neuronal networks to perform similar computations? Neurones exist in an almost infinite variety of shapes and sizes within an organism and between species. This variability in morphology alone is able to affect physiology, but neurones also possess, in different proportions, a

plethora of intrinsic biochemical and membrane properties to increase still further the diversity in the ways that they operate (Bullock, 1980). In addition, there is a variety of ways in which neurones can interact to form operating circuits. Finally, the situation is complicated when one recognizes that the current make-up of nervous systems, like that of other biological systems, reflects their evolutionary and developmental histories and thus not all of the features and characteristics of a neuronal circuit are necessarily adaptive for the particular function under investigation (Dumont & Robertson, 1986). One result of all this variety is that any definable output of a circuit, i.e. the end result of the 'computation' of the neuronal assemblage, might be produced by any of a number of different theoretical systems (i.e. the hardware), and the algorithms might be different. In order to recognize general computational strategies that could be used by biological neural networks it is therefore necessary to document the different characteristics of specific networks and try to determine the relevance, if any, of these differences to network function and computing ability.

One class of neuronal circuit which has been comparatively well studied in recent years includes the circuits that are responsible for patterning the motor activity underlying simple behaviours in invertebrates (see e.g. Kristan *et al.*, Chapter 10; Selverston & Mazzoni, Chapter 11). The motor patterns are generated and controlled by central (Delcomyn, 1980) and peripheral (Pearson, 1985b) nervous mechanisms. Whatever the relative contribution of the two to the final motor output in different systems, it is indisputable that circuits of interneurones in central nervous systems repeatably produce measurable patterns of output. The central circuits controlling simple invertebrate behaviours are composed of relatively few neurones most of which can be uniquely identified on the basis of an idiosyncratic set of morphological and physiological characteristics (e.g. Hoyle, 1977; Bullock, 1980). These systems are highly represented in the literature because of the persuasive argument that such systems are inherently more tractable due to the ability to characterize the individual components. However, in spite of impressive advances in the knowledge of the cellular and network processes underlying specific systems, few general principles of organization and function have emerged (Burrows, 1984; Pearson, 1985a; Dumont & Robertson, 1986). Such systems are characterized by much complexity within them and diversity between them. This is in sharp contrast to the computational 'neural' networks which are the subject of other chapters in this volume. In these artificial systems the neurone-like units are simple, the operational rules are straightforward and there is much general similarity between different systems. Modification of such networks according to certain learning rules during a training period can greatly diversify the interactions between the units (e.g. Rumelhart *et al.*, 1986). Furthermore, the systems are clearly very powerful and they can perform the same sorts of tasks as nervous tissue. However the question remains whether the artificial systems are true models of neuronal systems, operating on the same principles, or simply very good mimics. It is only with a detailed knowledge of the functional organization and mode of operation of different biological systems that it will be possible to answer this question.

## 14.2 The locust flight system

Locust flight is a behaviour which has received a lot of attention in the past and much is known about many aspects of its control. Much of this need not concern us here and I will concentrate on the neural mechanisms underlying the rhythmical beating of the wings. There are two pairs of wings and two homologous sets of wing muscles and their motoneurons. The motor pattern during straight and steady flight is simply described (Wilson & Weis-Fogh, 1962). There is currently some controversy over the role of peripheral sense organs in generating the motor pattern (Pearson, 1985b; Pearson & Wolf, 1987; Stevenson & Kutsch, 1987; Wolf & Pearson, 1987a), however this is not an issue I wish to pursue here. Suffice it to say that the deafferented thoracic nervous system produces a rhythmical motor output which is obviously related to flight (Wilson, 1961) and which indicates the existence of an important central component of the control mechanism, comprising circuits of interneurons and motoneurons. Many flight interneurons have now been described (Robertson & Pearson, 1983; Pearson & Robertson, 1987; Reye & Pearson, 1987; Ramirez & Pearson, 1988) and the individual and network properties of many of these neurons have been described (Robertson & Pearson, 1985a; Robertson & Reye, 1988; Robertson & Wisniewski, 1988). My intention is to review the properties of locust flight interneurons and their circuits in order to illustrate the general point that features of organization and operation contributing to the complexity in the system are not necessarily related to adaptive function. A negative consequence of this observation is that systems of this sort are likely to be composed of idiosyncratic computational units, to be unique in the details of their operation, and to be generally unpredictable. A positive consequence is that for the formulation of general models many of the fine details could be ignored as they are likely to have little functional relevance.

## 14.3 General properties of flight interneurons and circuits

Fixing functional labels to particular interneurons is a dangerous business, first because of the fact that in the majority of cases the data on the interneuron have been accumulated under experimental rather than natural conditions, and second because of the possibility that an interneuron is involved in more than one behaviour. The term 'flight interneuron' indicates at the very least that the membrane potential of the interneuron shows pronounced oscillations in phase with the flight motor pattern, but it does not preclude the interneuron having another, possibly more important, functional role. For most of the interneurons that have been described as being involved in flight the evidence is more substantial (Figure 14.1). These neurons show sharply-defined bursts of spikes at a high intraburst frequency (200 - 400 impulses per second) riding upon large (15 - 25 mV) membrane potential oscillations; depolarizing stimulation of some of these neurons is capable of inducing rhythmical activity in the system at rest. Short

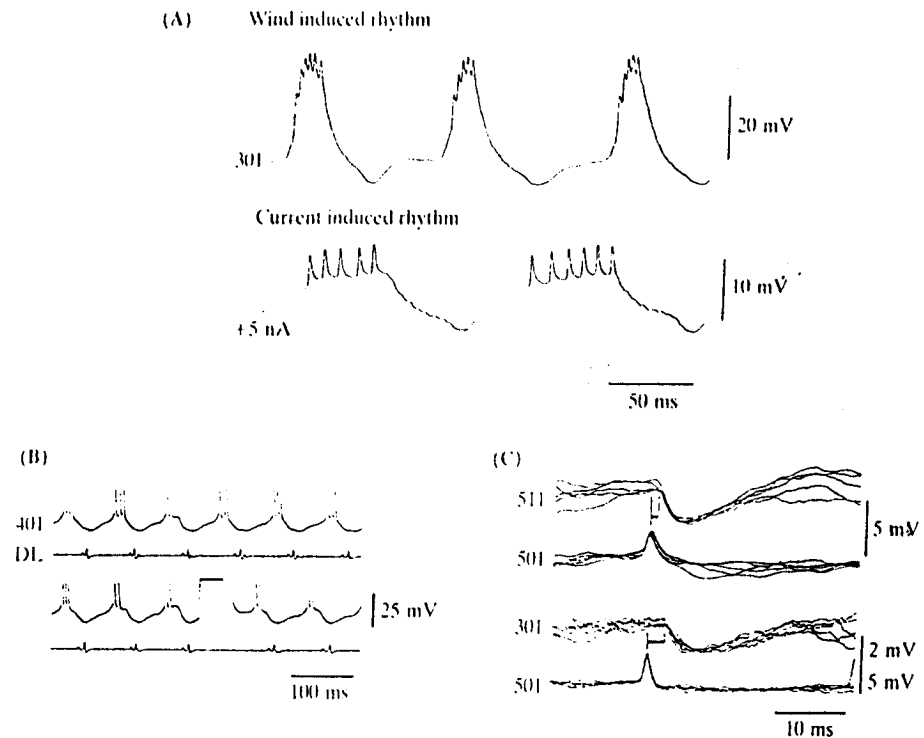


Figure 14.1 Criteria to determine the participation of interneurons in the generation of the flight rhythm. Intracellular recordings are taken from the neuropil segments of selected interneurons in the thoracic ganglia using glass microelectrodes. A. Ability to generate rhythmical activity related to flight. Interneuron 301 fires bursts during the elevator phase of the flight rhythm induced by a wind stimulus to the preparation (upper trace). Moderate depolarization of this interneuron with +5 nA of tonic current injection induces rhythmical activity in the system (lower trace). Note the rhythmical synaptic input evident in the membrane potential waveform indicating that other interneurons are rhythmically active. This stimulus also induces rhythmical activity of wing muscle motoneurons and flight-like phase relationships are maintained (not shown). B. Ability to reset the flight rhythm. Interneuron 401 fires bursts during the elevator phase (upper pair of traces). The time of depression is indicated by the electromyographic monitor of the activity of a dorsal longitudinal (DL) wing depressor muscle. Stimulation of this interneuron with a short duration pulse of depolarizing current (indicated by bar above lower pair of traces) resets the flight rhythm by increasing the duration of the cycle (indicated by successive bursts of DL activity) in which the stimulus occurs. C. Direct synaptic connections to wing muscle motoneurons (not shown) or with other flight interneurons. Successive sweeps of the oscilloscope triggered off the rising phase of the spike recorded from 501 show that each 501 spike is followed after a short and constant latency by an IPSP in interneuron 511 (upper pair of traces), and in interneuron 301 (lower pair of traces). The shortness and constancy of the latencies (indicated by bars) show that the connections are probably monosynaptic. 501 and 511 are in the same ganglion (metathoracic) and the latency is around 1 ms. 301 is in the next anterior ganglion (mesothoracic) and the increase in latency (of around 1.3 ms) is consistent with it simply being due to an increase in conduction path length of the 501 spike. (Robertson & Pearson, 1985a; Robertson, unpublished)

pulses of current delivered to some of these neurones during the expression of the flight rhythm can reset the timing of the rhythm by delaying or advancing the occurrence of the subsequent cycle; and some can be shown to be important in generating the wingbeat by virtue of their synaptic connections either directly or indirectly to the motoneurons of the wing muscles.

The flight interneurons that have been described to date are, for the most part, large intersegmental interneurons in the meso- and metathoracic ganglia. This raises the question of whether there is a sampling bias such that smaller local interneurons have been neglected due to technical limitations. This is certainly possible but, in my opinion, it is unlikely that we have missed a large population of small, important neurones. Stable recordings can be made from small local interneurons. Moreover, all of the intracellular recordings are taken from the branches of the interneurons in the neuropil rather than from the neuronal somata, and at this level the disparity in size between intersegmental and local interneurons is much reduced. A more likely possibility is that, for one reason or another, particular regions of the thoracic ganglia have not been submitted to detailed scrutiny. Almost invariably the dendritic and axonal branching is confined to the most dorsal layer of the neuropil just under the ganglionic sheath. Interneurons that can be segregated according to the motor pattern with which they are active, can also be segregated according to the location of their branching in the neuropil with the branching of flight interneurons occupying the dorsal rind of neuropil (Ramirez & Pearson, 1988). Excluding serial homologues (see below) and the contralateral partner of a bilaterally symmetrical pair, most flight interneurons are strikingly unique in their structure (Figure 14.2). Each has an idiosyncratic morphology which suggests an idiosyncratic set of input and output connections.

Undoubtedly as a consequence of its idiosyncratic set of input connections, each interneurone has unique membrane potential waveforms during expression of the flight rhythm. It is usually possible to identify individual interneurons solely on the basis of their physiology (rate and extent of depolarization and hyperpolarization, number and magnitude of different phases of synaptic input, number and frequency of spikes/burst). To date there is no evidence for endogenous membrane properties contributing to membrane potential oscillations - the rhythm is generated via synaptic interactions in a network of interneurons. Three types of synaptic interaction have been described: chemically-mediated excitatory connections which result in excitatory post-synaptic potentials (EPSPs) of 2 - 5 mV following each pre-synaptic spike; similar inhibitory connections to give inhibitory post-synaptic potentials (IPSPs) which are likely to be the result of a gamma-aminobutyric acid (GABA) mediated increase in conductance to chloride ions; and a delayed excitatory connection which is probably the result of disinaptic disinhibition with tonic release of inhibitory transmitter at least at the second synapse (Robertson & Pearson, 1985a). A local, subthreshold interaction between flight interneurons has been described (Robertson & Reye, 1988) but the functional relevance of this is still unclear (see below). Each functional synaptic connection is likely to be the summed effect of several hundred ultrastructurally

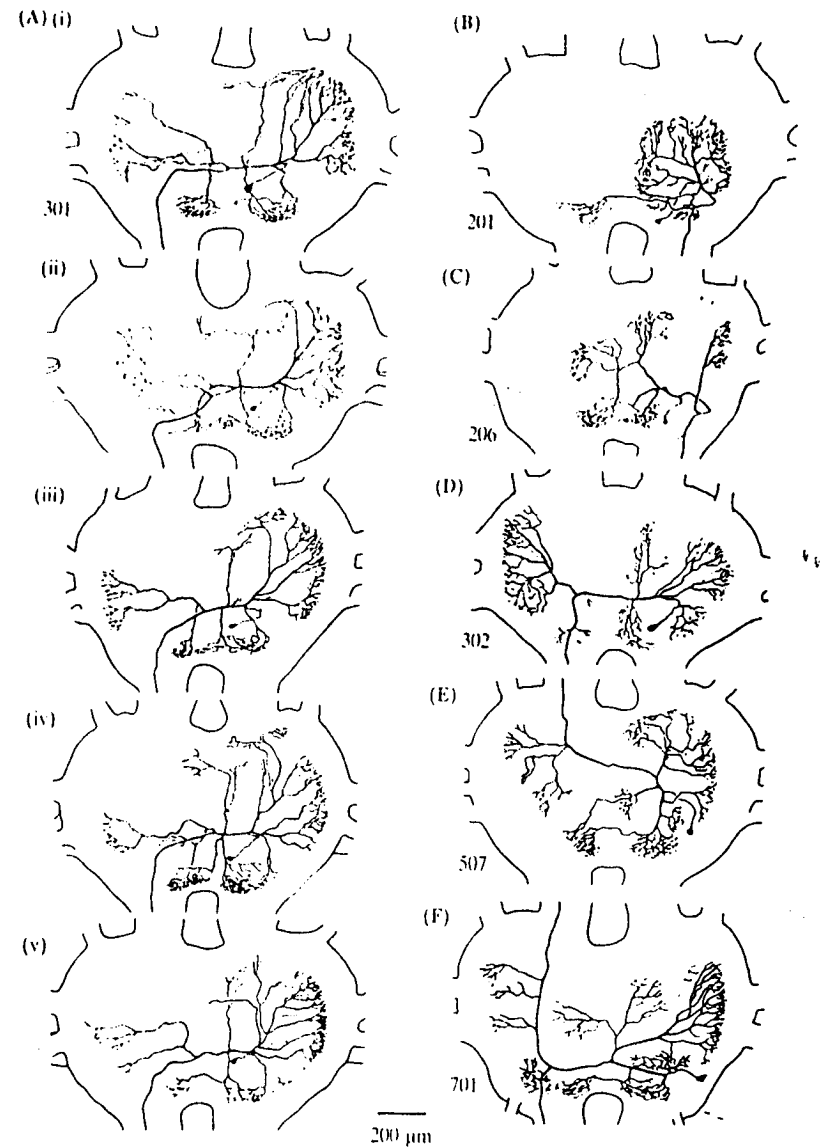


Figure 14.2 Idiosyncratic morphology of flight interneurons. A (i-v): Drawings of the right 301 in the mesothoracic ganglion of five different individuals to illustrate the range within which the morphology of an identified neurone can vary. B-F. Drawings of five different identified flight interneurons with cell somata in the right mesothoracic hemiganglion to illustrate the idiosyncratic nature of an identified neurone's morphology. (Robertson & Pearson, 1983; Robertson, unpublished)

distinct synaptic contacts (Watson & Burrows, 1983; Killmann & Schurmann, 1985; Peters *et al.*, 1985).

It is evident that most units involved in generating the output pattern in this system have unique, characteristic sets of properties. In the course of investigating the system it has not yet been possible to predict neuronal or circuit properties by extrapolation from an emerging pattern of organization. Some prediction has been possible (Pearson & Robertson, 1987) but in this case the similarity is likely to be a result of common developmental origins rather than reflecting functional adaptation. An early proposal that it may be possible to segregate flight interneurons into functional classes (Robertson & Pearson, 1983) was proved to be premature (Robertson & Pearson, 1985a). Nevertheless it has been possible to determine some of the interneuronal circuitry in the system and relate this to features of the output pattern.

#### 14.4 Features contributing to the output pattern

The deafferented flight motor pattern can be characterized as follows: the pattern repeats with a frequency of around 12 Hz; elevator motoneurons alternate their activity with that of depressor motoneurons; equivalent motoneurons on the right and left sides are active in synchrony; and hindwing motoneurons are active in advance of equivalent forewing motoneurons by 5 - 10 ms. Different aspects of the central circuitry contributing to the generation of this output pattern have been relatively recently reviewed (Robertson & Pearson, 1985b; Robertson, 1985, 1986, 1987) and to do so again in detail is unnecessary. My purpose here is to provide an update to these reviews based on recent findings and to comment in more general terms on the circuitry in the system.

Based on observations of the organization of flight interneurons it was proposed that the central pattern generating system is a unit distributed throughout the prothoracic ganglia (Robertson & Pearson, 1983, 1984). Recent experiments support this proposal (Wolf & Pearson, 1987b). The neuronal basis for rhythm generation in this system is unknown. Certain elements of the known circuitry could certainly contribute to burst generation and under conditions of tonic excitation can produce rhythmical output. Circuits of reciprocal inhibition (Robertson, 1987) and delayed excitation with feedback inhibition have been described (Robertson & Pearson, 1985a). Models of similar circuits have been shown to be capable of generating rhythmical activity (Perkel & Mulloney, 1974; Stetting, 1983). Although it is possible to identify candidate circuits for rhythm generation it is unlikely that it will be possible to identify a single source or a unique mechanism for the underlying oscillation. Stimulation of different single interneurons produces rhythms with different characteristics and with a different time subset of the flight interneurone population (Robertson, 1987). It seems that to generate alternating activity is a trivial problem for nervous tissue whereas the special task is co-ordinating the activity of rudimentary oscillators and organizing appropriate timing of such activity.

Elements of the described circuitry do contribute to the co-ordination of the timing of different components of the output. A relatively constant latency from elevator motoneurone activation to depressor motoneurone activation in deafferented preparations has been described as occurring either usually (Hedwig & Pearson, 1984; Pearson & Wolf, 1987) or occasionally (Stevenson & Kutsch, 1987). A circuit which could underlie this observation has been described (Robertson & Pearson, 1985a). Separate synaptic pathways exist from a single interneurone to both elevator motoneurons and depressor motoneurons. The pathway to the elevator motoneurons is direct, whereas that to the depressor motoneurons is indirect through a cascade of synapses. In this instance the mechanism controlling the timing of alternate activation of elevator and depressor motoneurons is that of an increased delay to the depressor motoneurons via a greater number of synapses in the pathway. Interestingly, a proposal for the mechanism controlling the timing of the lag between activation of the hindwing and forewing depressor motoneurons is that of an increased conduction delay, because of a greater path length to the forewing motoneurons, even though the number of synapses in the pathway to the depressor motoneurons is the same (Robertson & Pearson, 1985b). Finally there is a high degree of synchronous firing of the two members of pairs of bilaterally symmetrical interneurons (Robertson, in preparation). In some cases the synchrony is such that single spikes occur within 1 ms of each other in the two interneurons (Figure 14.3). To date, any direct excitatory interaction between the interneurons has been found to be small (<1 mV) and unable to account for the synchrony. Rather, it appears that synchronous firing of bilateral homologues is a result of a large amount of common synaptic input and that it is dependent upon activation of a sufficient proportion of the flight circuitry - rhythmical activity can be obtained by partial activation of the system but the activity shows inappropriate timing.

The point of this section is to demonstrate that circuit analysis in this system is possible and that functional roles can be assigned to many features of the circuit. However, and in spite of this ability, it has not been possible to recognize any coherent pattern to the organization of the circuit. Individual components of the system resemble components of other invertebrate pattern generating networks, but the selection and assembly of these components appear idiosyncratic to the locust flight system and seem almost arbitrary when viewed from a functional perspective.

#### 14.5 Features apparently unrelated to the output pattern

The hypothesis that a feature of organization and operation in a neuronal circuit is sub-optimal or not adaptive is hazardous to make. The counter claim, that we have merely not provided the system with the appropriate context to reveal the importance of the feature, is irrefutable. The original hypothesis is therefore justifiable only with the existence of a convincing, non-adaptive explanation for the presence of the feature. Moreover the hypothesis does not imply that the feature is

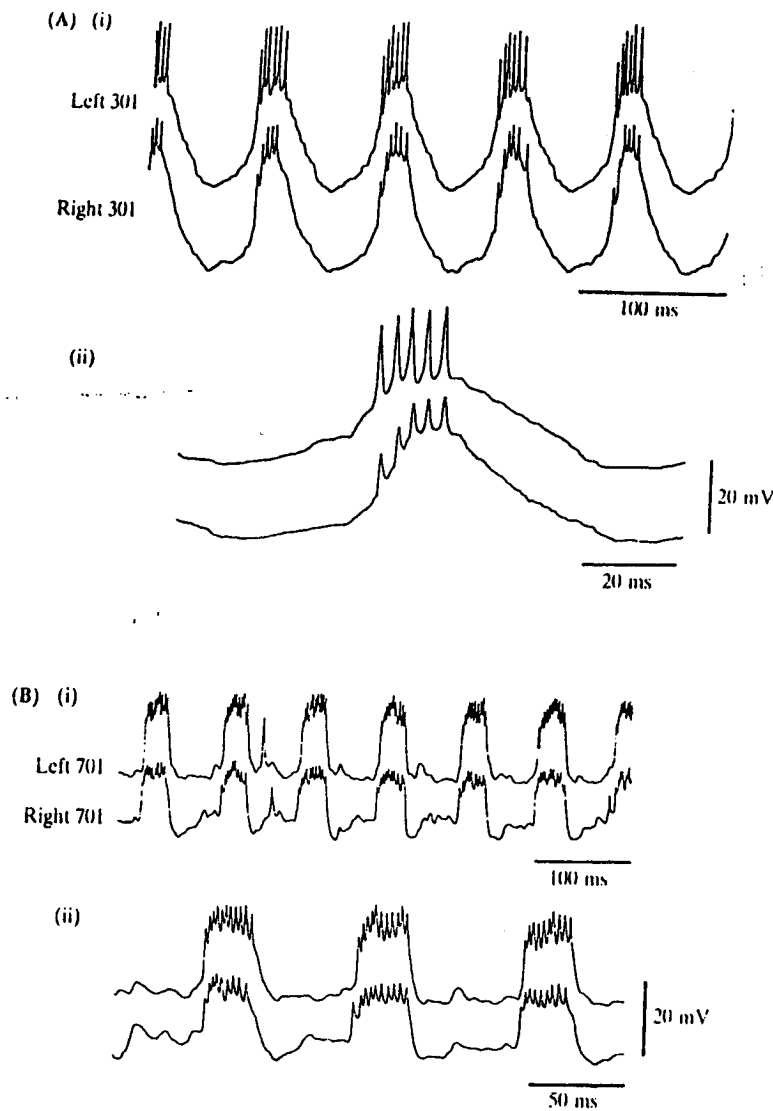


Figure 14.3 Synchronous activity of bilaterally symmetrical interneurons during expression of a flight rhythm. A (i). Simultaneous intracellular recordings from the left 301 and from the right 301 show highly synchronous bursts. (ii). A single burst from a flight sequence demonstrates that spikes in one neurone occur within 1 ms of spikes in the other. B (i), (ii). Other flight interneurons (e.g. 701) show highly synchronous bursts but without intraburst synchrony of single spikes. (Robertson, unpublished)

non-functional, or unnecessary, but it does follow that the system in which it occurs is unpredictable from purely functional principles.

The effect of evolution on neuronal interactions is obvious at a gross level. Different taxa use different sets of components to construct their circuits. For example electrical connections are rare in insects (Robertson, 1987) but more common in molluscs and crustacea; the multi-component synapses of the *Tritonia* escape circuit (Getting, 1981), which figure prominently in an associative neural network model for pattern generation (Kleinfeld & Sompolinsky, 1988), have not yet been reported in other biological pattern generating systems. More subtle effects of evolution can be observed. An early finding in the investigation of the locust flight system was of sets of serially homologous interneurons in the four fused neuromeres of the metathoracic ganglionic mass (Robertson *et al.*, 1982). Each interneurone in a set has similar morphological features and, as far as has been determined, similar physiology. Furthermore they all have important roles to play in generating the rhythm and driving wing muscle motoneurons. This peculiar arrangement has no obvious adaptive benefit for the control of flight and it has been argued in detail elsewhere (Robertson *et al.*, 1982; Dumont & Robertson, 1986) that this organizational feature reflects a prior stage in the evolution of the flight system and is sub-optimal in its design as flight circuitry. A similar lack of optimal design is evident in the escape circuitry of the crayfish (Dumont & Wine, 1987) and in the characteristics of certain midbrain neurones of electric fish (Rose *et al.*, 1987).

A further point is that the evolution of biological systems is a continuing, dynamic process. It would therefore be expected that our investigations at one particular stage in this process will reveal features that are in the process of being eradicated by selection, and other features which are the substrate of future elaborations or at least have not reached their full potential. Many of the weak synaptic connections whose effects on the spiking activity of post-synaptic neurones are negligible, could be considered candidates for such features. Thus the evolutionary histories of different systems have constrained their current organizations with the result that their organizations are not predictable from general modelling principles.

The developmental history of the system may also result in features which increase its complexity in ways not adapted to its function. As illustrated in the example above, serially homologous interneurons with similar morphology and physiology can be recognized. By observing the embryonic development of interneurons in the segmental ganglia it is possible to identify serial homologues which have diverged during evolution (Pearson *et al.*, 1985). In spite of differing in certain aspects of their phenotype such homologous interneurons retain a common ground plan of organization which reflects their common developmental origins (Bastiani *et al.*, 1984). Moreover, as the large intersegmental interneurons enlarge and extend their processes during development they become transiently dye-coupled both to neurones originating from the same neuroblast and to unrelated neurones in their early environment (Raper & Goodman, 1982; Raper *et al.*, 1983). Such dye-coupling suggests the existence of gap junctions and electrical interaction, i.e. the

existence of electrical synapses between the neurons. These interactions are thus related to pathfinding rather than to the generation of appropriate patterns of nervous activity. It has been suggested that some ultrastructurally defined gap junctions in adult locusts may be relics of developmental history (Killmann & Schurmann, 1985). Indeed, the only example of an electrical connection in the locust thoracic nervous system is that between a leg muscle motoneurone and its supernumerary partner (Sieglar, 1982) - a developmental anomaly rather than a functional necessity. A further example can be seen in the transmitter type of inhibitory flight interneurons. GABA is often assumed to be the central inhibitory transmitter in invertebrates. Indeed most of the inhibitory flight interneurons that have been examined show a positive GABA-like immunoreactivity indicating that these neurones are probably GABA-ergic (Robertson & Wisniewski, 1988). However at least one inhibitory interneurone does not show GABA-like immunoreactivity. This particular interneurone is different in other ways (Pearson & Robertson, 1987) and it is a reasonable assumption that it is different as a result of its different developmental history. There are two ways to view this observation: either the use of a different inhibitory transmitter is necessary to allow the interneurone to fulfil the detailed requirements of its functional role; or the nature of the transmitter is not germane to a consideration of its functional role. Given that the known physiological characteristics of the IPSPs caused by activity in this interneurone do not seem measurably different to the IPSPs from GABA-ergic interneurons, and in the continuing absence of contradictory evidence, then the conclusion that the identity of the inhibitory transmitter of this interneurone is not crucial to the operation of the system is valid. It is clear from the above examples that the full complement of adult characteristics of interneurons and circuits contains traces which link neurones with their origins and with the developmental pathways from those origins.

Finally, a problem arises in consideration of the reductionist way in which most circuits are investigated. How much of the detailed information that can be experimentally determined about a system ought to be incorporated into any model? It is an unavoidable consequence of physical, pharmacological, or other dissection of a system that many features will be altered in ways that are difficult to determine. Thus it is more than likely that the dissected system has features which are either relics, or transformations, of the real phenomena underlying the operation of the system. Another danger is that phenomena which can be characterized are reified and assume a significance that they do not really warrant. For example, Figure 14.4 shows a plateau-like potential recorded in a flight interneurone as a result of a short duration pulse of current elsewhere in the neurone. The basis for this is thought to be a disinaptic, disinhibitory, feedback circuit from the neurone to itself operating beneath the threshold for spike generation (Robertson & Reye, 1988). The important point is that the findings indicate a role for subthreshold and local interactions in the operation of the flight system. It is quite possible that the plateau-like potential has limited significance, as a phenomenon in its own right, for the generation of the flight rhythm. Much apparent complexity and diversity in different

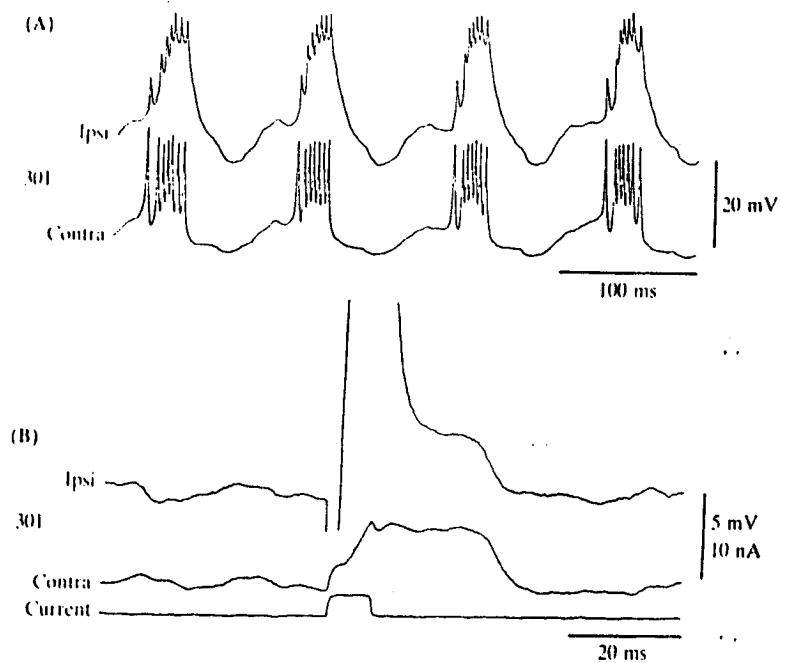


Figure 14.4 Subthreshold activation of a membrane potential event whose duration exceeds that of the stimulus. A. Simultaneous intracellular recordings from two sites in a single 301. Ipsi and contra indicate electrode positions in the neuropil segment on either side of the midline ipsilateral and contralateral to the cell soma respectively. The relative sizes of the spikes and membrane potential oscillations alter as a consequence of the relative electrotonic distance from the sites of action potential generation and synaptic input. B. A short pulse of subthreshold depolarizing current delivered to the neurone through the ipsilateral electrode induces a depolarizing potential which is maintained longer than the stimulus. This, with other evidence (not shown), is evidence for the subthreshold activation of local synaptic circuitry in the flight system. (Robertson & Reye, 1988)

systems may arise as the result of restricted viewpoints, and thus may be irrelevant for modelling these systems.

## Conclusions

A picture is emerging of the locust flight system as a complex and idiosyncratic mix of different neuronal processes. Its unique character results from a combination of adaptive and non-adaptive constraints in the course of its evolution. Similar systems, i.e. small networks of identified neurones controlling innate behaviours, are likely to be similarly idiosyncratic. It is conceivable that the allure of the identified neurone has focussed interest on idiosyncratic systems and hindered

the discovery of more general strategies for control. In my concluding remarks I should like to consider briefly the implications of these ideas in the context of this volume - neuronal network modelling.

Models of neurones and networks exist in at least two general classes - models of how systems actually work, and models of the principles by which they work. The first class includes models that are very specific to particular systems and these provide a useful means of generating and testing hypotheses relevant to those systems. These models necessarily have to be very detailed and include all the described features of a system, whatever their origins, in order to be as realistic as possible. Several of the ideas of how different components of the locust flight circuitry operate, could and should be tested more rigorously with such specific models. Unfortunately, if circuits are unique in the details of their organization and operation then models of this sort have little value as exemplars of general solutions. For the same reason any general network model incorporating simplified neurone-like elements is unlikely to be able to serve as an accurate, or even useful, representation of, for example, how the locust flight system operates.

Nevertheless, if there is any hope of extracting some general principles of functional organization which are applicable to different neuronal systems throughout the phyla, then general computational modelling, to produce models within the second class mentioned above, is a valid and worthwhile approach. The operating principles of the locust flight system remain to be determined but, when discovered, they will undoubtedly be formulated without reference to the mass of detail actually present in the system. Much of the detail simply represents the burden of the flight system's history. Examining the current collection of network and associative models there is little that I find particularly relevant to locust flight, or systems like it. Possibly the computational unit of these models should not be mapped to the neurone in systems comprised of few, identified neurones, but to some other definable unit. The models are arguably more relevant to the large arrays of similar neurones in vertebrate brains (e.g. Rolls, Chapter 8). In these cases the features that seem to have been selected include the general ones of increased computational potential, capacity and flexibility, and ability to make associations, rather than any specific computational task. In addition, many of the motor patterns tend to be constructed by association with sensory feedback and learned post-embryonically rather than being innate. It is not surprising therefore if network models applicable to such systems are much less applicable to the locust flight system, which is innate and which has been selected for one specific computational task - the generation of the flight motor pattern. I look forward to future generations of network models with the hope that they have more to say about neuronal computation in invertebrate motor systems.

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