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INTEGRATION OF WING PROPRIOCEPTIVE AND DESCENDING EXTEROCEPTIVE SENSORY INPUTS BY THORACIC INTERNEURONES OF THE LOCUST

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SUMMARY

1. The campaniform sensilla on the wings of the locust are strain-sensitive mechanoreceptors that provide proprioceptive feedback about wing forces, particularly aerodynamic lift, experienced during flight. They can be excited by imposed deformations of the wing, including those caused by imposed wing twisting. The afferents of the single subcostal group of sensilla on the hindwing had the same directional selectivity for supinating twist and shared the properties of a dynamic sensitivity and adaptation. A group of strain-sensitive mechanoreceptors with similar properties, presumably campaniform sensilla, is also found in the forewings.

2. Four types of thoracic interneurones influenced by these factors were recorded and stained intracellularly. The response of interneurone 5AA to imposed deformations of the hindwing ipsilateral to its soma is determined by excitatory chemical synaptic input from the campaniform sensilla. Interneurone and sensilla have a common directional selectivity and optimal stimulus, and similar qualitative dynamics of response. Each spike of individual afferents is followed at short, constant latency by an excitatory postsynaptic potential (EPSP) in the interneurone, even at instantaneous frequencies of about 90 Hz. Physiological evidence is consistent with direct, chemically mediated synaptic inputs from campaniform sensilla afferents.

3. Interneurone 5AA is also excited by a short-latency, chemical synaptic input from the ocelli when lights are turned off. EPSPs could be elicited by light-off stimuli to the median and contralateral, but not the ipsilateral, ocelli. In addition, the interneurone is excited when the head is moved relative to the thorax.

4. The other three interneurones respond to strains in more than one wing. Inputs are derived from specific combinations of wings, with the sign of response depending on the neurone and the particular wing. Interneurones 3AA and 1AA are also phasically excited by light-off stimuli. In 1AA this response was shown to originate from the ocelli. Median and contralateral, but not ipsilateral, ocelli could evoke EPSPs. This neurone was also excited by imposed head movements.

5. It is argued that the interneurones described here at suited to monitor lift production in particular wings and its pattern among several wings. Convergence of

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ocellar and head-motion inputs implies a function in the exteroceptive detection and correction of flight instability. It is inferred that these thoracic interneurones may act as the nexus for several different feedback pathways, proprioceptive and exteroceptive, which modulate flight motor output.

INTRODUCTION

Sensory information has a powerful influence upon the neural control of posture and locomotion. This information comprises feedback from proprioceptors, which monitor the state and performance of effectors, and feedback from equilibrium receptors (where present) and exteroceptors, which can register the animal's position and movement in space or relative to the environment. Integration of these signals is vital for the production of appropriate motor responses if stability is to be maintained and deviations from the intended course corrected. The need for such integration is clearly seen in swimming or flying animals, where defective motor performance, or turbulence in the medium, will cause instability if not detected and corrected. Locust flight is a relatively simple locomotor behaviour that is under these constraints. As locusts possess no specialized inertial organs, information about position and movement in space is provided entirely by exteroceptors. The modification of flight motor activity by both proprio- and exteroception is well documented in behavioural studies (e.g. Weis-Fogh, 1949; Goodman, 1965; D. M. Wilson, 1968; Wendler, 1974; Pearson, Reye & Robertson, 1983; for reviews see Wendler, 1983; Reichert, 1985). Its stereotyped motor pattern and identifiable central neurones make this system an advantageous subject for physiological analysis (reviewed by Burrows, 1976*a*, 1977). Recent studies have elucidated some aspects of the interneuronal organization of the flight pattern generator (Robertson & Pearson, 1982, 1983, 1985), so that it is now feasible to ask how sensory feedback is processed by interneurones that may be involved with flight activity.

Proprioceptors on the wings of a flying locust must register the forces which act in the wing during flight. In particular they must monitor the aerodynamic force experienced by the wing. This force provides the flying animal with vertical lift and forward thrust. Registration of this force is important, as any fluctuations in its generation by one wing, or the pattern of its generation amongst different wings, may quickly lead to instability. The wing campaniform sensilla are the probable sensors (Gettrup & Wilson, 1964; Gettrup, 1965, 1966; Wilson, 1964; Pringle, 1976). A campaniform sensillum is a mechanoreceptor which detects strains in the exoskeletal cuticle through deformations of its cuticular cap, which in turn excite the single underlying sensory neurone (Pringle, 1938*a*,*b*; Moran, Chapman & Ellis, 1971). In flight, the sensilla react to forces encountered at each wingbeat, and can register the lift produced by their wing. Behavioural studies have shown that they are essential for the active regulation of lift during flight (Gettrup & Wilson, 1964; Gettrup, 1966). However, interneurones that process feedback from these receptors have not been studied.

Exteroceptive feedback is also important in flight stabilization. Deviations from straight flight can be detected by reference to the relative wind, or to the image of the surroundings (see Reichert, 1985), as provided by the compound eyes and ocelli (simple eyes) (Goodman, 1965; M. Wilson, 1978; Taylor, 1981*a*). The three ocelli (one located medially on the head, the other two laterally and on opposite sides) are luminance detectors that are suited for rapid detection of apparent movements of the horizon; pitching down and rolling are signalled by dimming of the median and a lateral ocellus, respectively (Wilson, 1978; Stange & Howard, 1979). The exteroreceptive signal is conveyed by large, descending 'deviation detector neurones' (Reichert, Rowell & Griss, 1985) to the thorax. Here the descending neurones synapse in specific combinations on thoracic interneurones which may modulate the flight motor output to produce appropriate compensatory changes in wingbeat (Simmons, 1980; Taylor, 1981*a*,*b*; Rowell & Pearson, 1983; Reichert & Rowell, 1985; Reichert *et al.* 1985). A second control route involves an initial corrective repositioning of the head following a course deviation. Deviation causes a misalignment of head and thorax that is detected by proprioceptors of the neck, which then elicit a flight compensation by the wings that restores the alignment (Goodman, 1959, 1965; Taylor, 1981*a*,*b*). However, it is not known how exteroceptive feedback is integrated with proprioception from the wings.

In this paper I report an analysis of the responses of four types of thoracic interneurone that receive potent input from the wing campaniform sensilla. This provides a first characterization of interneurones which integrate inputs from these important receptors. One type is shown to be a first-order sensory interneurone for campaniform afferents from a hindwing. The results allow an insight into how interneurones may register the forces experienced by the two pairs of wings. I also show that ocellar and possibly neck inputs can converge on these same interneurones. The pattern of convergence of specific proprioceptive and exteroceptive inputs is described, and its possible functional significance discussed in terms of the control of flight stability.

MATERIALS AND METHODS

Adult locusts, *Schistocerca gregaria* (Forskål), were obtained from a crowded culture at the Department of Zoology, Cambridge.

Electrophysiological techniques

Two types of acute preparation were used to record from, and stain, neurones of the meso- and metathoracic ganglia. In the first, locusts were mounted ventral surface uppermost with the legs firmly restrained but the wings outspread. The sternum was removed and the pleura spread slightly. This preparation was used to record from the soma of interneurone 5AA. In the second, locusts were restrained dorsal surface uppermost with wings spread. The body cavity was opened by a dorsal midline cut from the third abdominal segment to just behind the head. This type of preparation was used for neuropilar recordings from the other interneurones. In both

preparations the posterior edge of the pronotum was trimmed to allow the forewings to unfold freely; the hindwings were prevented from passive refolding by restraining pins.

Touching or brushing the wings can be an auditory stimulus. Therefore, care was taken to distinguish wing proprioceptive responses from auditory reactions, and in some experiments metathoracic nerves 6 (carrying the auditory afferents) were cut bilaterally. Similarly, in some experiments meso- and metathoracic nerves 1D2 (sometimes the whole nerve 1D) were cut bilaterally to eliminate input from the proprioceptors of the wing hinge, and the tegulae of all four wings were cauterized or excised, leaving intact the afferents of sensilla located on or in the wing, running in nerve 1C.

The meso- and metathoracic ganglia were stabilized upon a wax-coated platinum platform, which also acted as the reference electrode. The tracheal supply was left intact and the thorax perfused continuously with locust saline (Usherwood & Grundfest, 1965) at room temperature. The ganglionic sheath was softened by applying protease (Sigma type XIV, approximately 1 % w/v in saline) for 2–5 min. Glass microelectrodes had resistances, measured in saline, of 40–80 MΩ when filled with 2 mol l^{-1} potassium acetate, or 100–200 MΩ when filled with 0·1 mol l^{-1} hexamminecobalt (III) chloride (Brogan & Pitman, 1981) for intracellular staining. Neurones were filled using positive current pulses of 3–10 nA, 500 ms long, at 1 Hz for between 5 and 30 min. After injection, the cobalt was allowed to diffuse for 30–60 min before precipitation with ammonium sulphide and intensification with silver (Bacon & Altman, 1977). Drawings of neurones in whole-mounts were made using a *camera lucida*.

Spikes of sensory neurones were recorded by one of two methods: in the ventral preparation the tips of a pair of electrolytically sharpened tungsten pin electrodes were placed in the subcostal vein of the hindwing, near the campaniform sensilla. This technique seems to give recordings of only a fraction of the sensilla, presumably those sensory neurones near to the electrodes. These electrodes were also used to stimulate the campaniform sensilla electrically. In other preparations, hook electrodes were placed under nerve 1C.

Sensory stimulation

Mechanical stimuli were applied to the wings manually, using a fine paintbrush or a glass probe, or by a servomotor that twisted the wing about its longitudinal axis (see Fig. 1A). Head movements were produced by pushing with a probe.

Simple light-off and light-on responses were evoked by the movement of a bar of shadow across the eyes and ocelli. Whole-field changes in illumination were effected by a small torch bulb located about 5 cm in front of the locust in a darkened laboratory. Changes in light emission were monitored by an apposed photosensitive diode. Light-on and light-off stimuli were also applied to individual ocelli, using high brightness, green light-emitting diodes (LEDs) whose light was delivered *via* plastic light piping (Dupont 'Crofon', diameter 0·5 mm), or apposed miniature green LEDs whose aperture was restricted to 2 mm. Voltage pulses produced light pulses,

rectangular in time course of intensity, whose onset and offset followed those of the voltage at latencies of less than 0·04 ms. The peak emission wavelength was 565 nm (the spectral sensitivity of ocellar receptors contains a broad secondary peak whose maximum occurs at 515 nm; Wilson, 1978).

All experiments were carried out at room temperature (17–25 °C). The results are based on 20 impalements of interneurone 5AA, including five dye-fills; one impalement and fill of 3AA; four of 1AA, including two fills; and one impalement and fill of 1AB.

RESULTS

Response of campaniform sensilla to deformation of the wing

Campaniform sensilla are concentrated in one group of 60–70 receptors on the ventral posterior face of the subcostal vein at the base of the hindwing (Fig. 1Ai). The forewing has two groups on the subcosta, a distal group homologous in organization and position to the one on the hindwing and a more proximal group of about 20 sensilla, and also some sensilla on the most anterior costal vein (Gettrup, 1966). The following account refers only to the hindwing group, but a group of afferents from the forewing, presumably those of the homologous subcostal campaniform sensilla, responded very similarly (R. C. Elson, in preparation).

The hindwing sensilla spiked in response to *bending* the hindwing (deflecting the tip upwards or downwards relative to the base) and to *twisting* the wing (specifically, its anterior, more rigid section) about its longitudinal axis (Fig. 1Aii). Twisting the wing so that its leading edge was elevated (*supination*) evoked an increase in the rate of spiking (Fig. 1B, Sup.), whereas twisting in the opposite direction (*pronation*) caused a decrease (Fig. 1B, Pro.) These stimuli elicited qualitatively similar responses in many campaniform afferents, recorded in the wing sensory nerve (nerve 1C), although estimates of the number of active units were difficult. Favourable recordings allowed the discrimination of units by spike amplitude, and showed that units with small spikes discharged at smaller amplitudes of twist, compared with larger ones (Fig. 1C, arrowheads). Units of all sizes showed adaptation by spiking at higher frequencies during a supinating twist movement than during the subsequent maintained twist in ramp-hold stimulation (Fig. 1D). The frequency of spikes in single small units initially adapted rapidly during steady deformation, but then progressively more slowly (Fig. 1E). Larger units spiked in response to twisting movement but fired at much lower frequency during steady twist (Fig. 1D).

Twisting stimuli were used extensively in this study since, in addition to the intrinsic interest of the twist response, this form of deformation is readily applied and controlled and is relatively selective in action: no other receptors associated with the wing showed this sensitive, directionally selective response to supination [although the stretch receptor of the wing-hinge can be excited by twisting (see Pfau, 1983) it discharged only a few spikes during this stimulation].

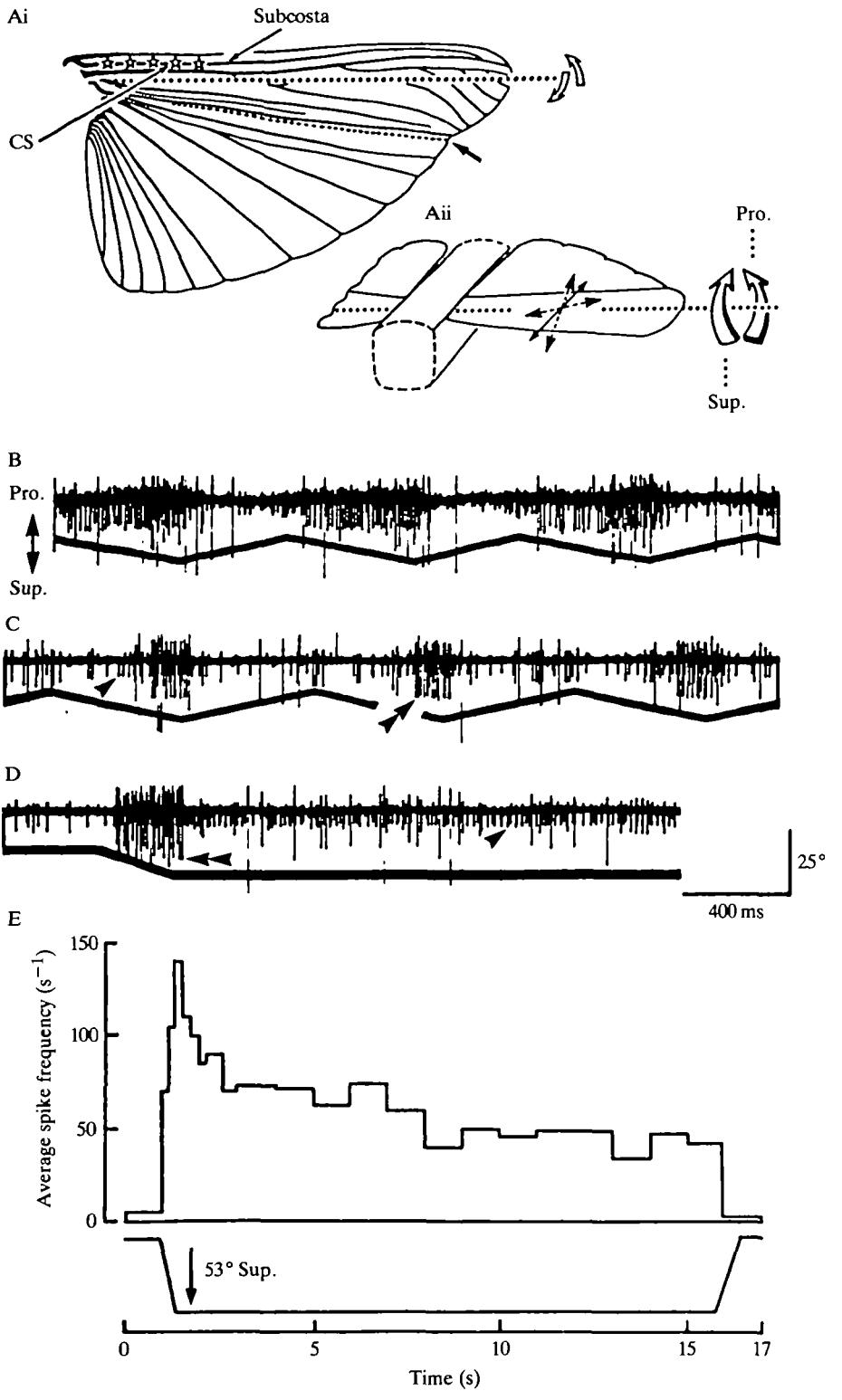

Ai
Subcosta
CS
Aii
Pro.
Sup.
B
Pro.
Sup.
C
D
25°
400 ms
E
Average spike frequency (s⁻¹)
150
100
50
0
53° Sup.
0
5
10
15
17
Time (s)

Fig. 1

Thoracic interneurones sensitive to wing strains: morphology and criteria for selection

The morphologies of four types of thoracic interneurone that responded sensitively to imposed wing strains, particularly imposed wing twist, are shown in Fig. 2. These neurones were selected on the basis of their reactions to wing deformation, and were characterized by: (i) *specific, low-threshold sensory responses* – changes in synaptic or spike activity were evoked by small deformations of specific wings (care was taken to ensure that responses were not secondary effects of motor reactions triggered by the stimulus); and (ii) *consistent, non-habituating responses* (in interneurone 5AA, up to stimulus repetition rates of at least 10 Hz – data not shown). Three of these interneurone types, however, responded also to sensory stimuli of other modalities (see below).

In order to name these cells without functional bias, a modified version of Robertson & Pearson's (1983) nomenclature for thoracic interneurones was provisionally adopted. Interneurones were given a three-character designation, in which the first digit signifies the presence or absence of an axon and its course relative to the soma, while the remaining characters specify the neurone within its class (see Robertson & Pearson, 1983, for more detail). To avoid unintentional overlaps with the designations of interneurones found by other workers, the final two characters of the provisional names given here are alphabetical, not numerical.

It is not possible to say unequivocally that any of these four cell types is a unique individual. However, dye-fills of interneurone 5AA (Fig. 2A) in five preparations revealed a neurone with very consistent morphology, indicating the occurrence of either a single identified cell or a small cluster of equivalent cells. Microelectrode searches for the soma of 5AA revealed that it was surrounded by the somata of

Fig. 1. Qualitative characteristics of the response of campaniform sensilla afferents to imposed twisting deformations of the hindwing. (Ai) Dorsal aspect of a right hindwing. The location of the row of campaniform sensilla (CS) on the posterior ventral surface of the subcosta (the second most anterior wing vein) is indicated by the row of stars. Also shown is the longitudinal axis (dotted line) about which the anterior part of the wing was twisted by rotation applied distally (curved arrows), and the vannal fold (broken line, arrowed) about which the anterior part articulated with the posterior. (Aii) A schematic view, from anterior and above, of a right hindwing. Curved arrows show the directions of twisting: Sup., supination, Pro., pronation. Double-headed arrows mark the cross-section of the wing midway along its length, showing how it is rotated relative to the base during twisting. (B–D) The spikes of campaniform sensilla afferents from the hindwing, recorded in nerve 1C (upper traces). Lower traces show the angle of wing twisting, imposed at the distal end. (B) Directional selectivity. Afferents spike during supinating twist, but are silenced by pronating twist. (C) Different units, distinguished by spike amplitude, have different sensory thresholds. A small unit (single arrowhead) is excited to spike at a smaller degree of twisting than a larger unit (double arrowhead). (D) Adapting responses. Spike frequencies of afferents are higher during twisting movement (ramp) than during subsequent maintained twist. The same units are arrowed as in C. (E) Time course of adaptation of a small unit. Average spike frequency in successive 1-s bins (except initial 2 s of stimulus, where bins are 200 ms) during a ramp-hold–release twist stimulus. Adaptation is initially rapid but becomes progressively slower.

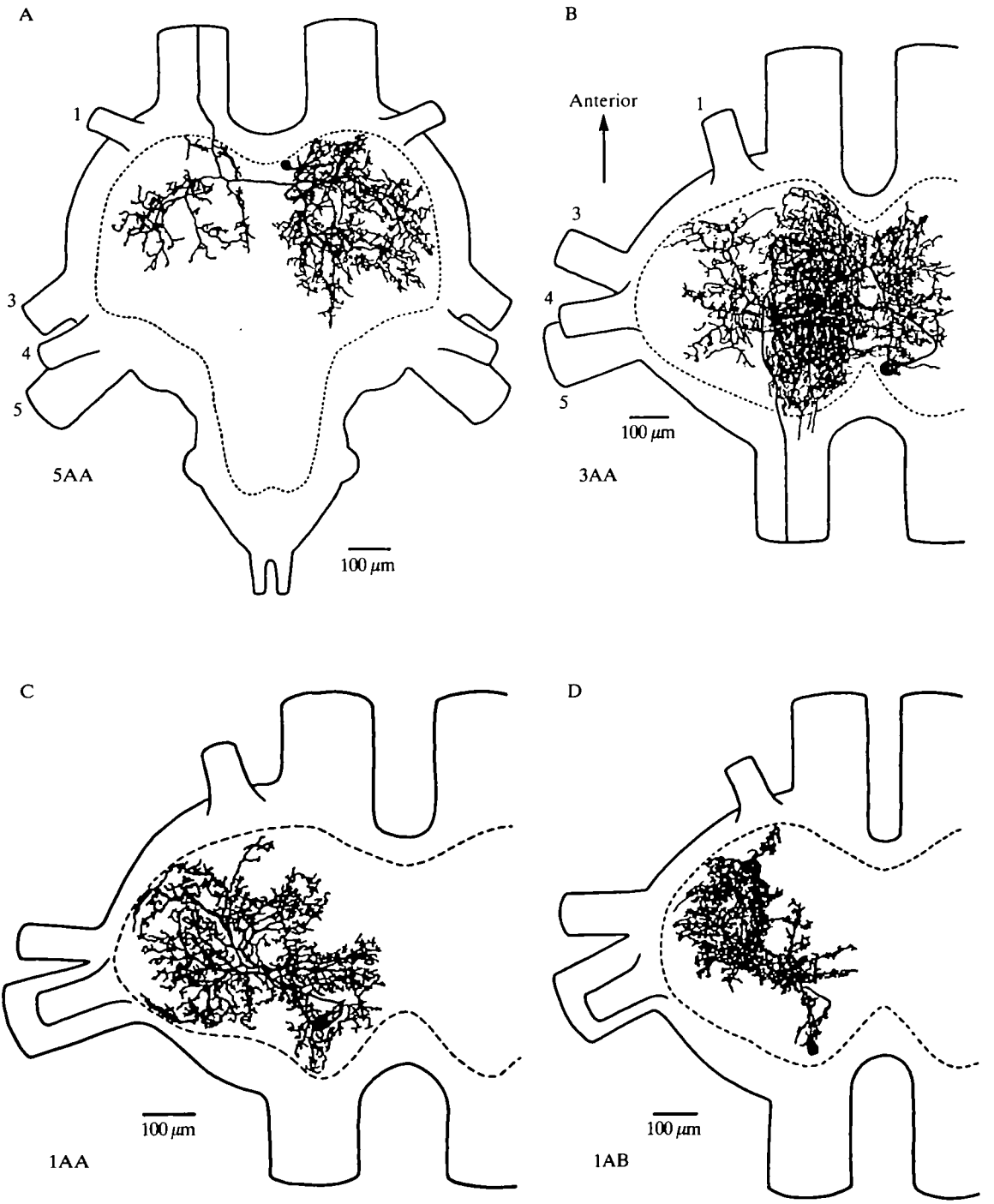

A
1
3
4
5
5AA
100 μm
B
Anterior
1
3
4
5
100 μm
3AA
C
100 μm
1AA
D
100 μm
1AB

Fig. 2

different interneurones, so that the number of cells in such a cluster must be very small, and may be only one.

In the dorsoventral dimension of the ganglia, the somata are located ventrally, but the arborization of all four types is confined almost exclusively within the dorsal half of the neuropile. Lateral branching (particularly the axon collaterals of 5AA and 3AA) runs just below the dorsal ganglionic sheath. In other respects the cells, morphologies are diverse. 5AA is an ascending interganglionic interneurone, originating in the metathoracic ganglion and having axon collaterals in the contralateral neuropiles of the meta- and mesothoracic ganglia (Fig. 2A; mesothoracic projection not shown). 3AA (Fig. 2B) is also interganglionic with contralateral axon collaterals, but originates in the mesothoracic ganglion and descends (metathoracic projection not known). 1AA (Fig. 2C) and 1AB (Fig. 2D) are both unilateral local interneurones.

Proprioceptive input to interneurone 5AA from hindwing campaniform sensilla

Interneurone 5AA responded to imposed deformations of the hindwing ipsilateral to its soma (Fig. 3). No response was evoked by mechanical stimuli applied to the other wings. *Movement* of the whole ipsilateral hindwing, e.g. elevation or depression, evoked no synaptic input or changes in spike frequency unless it secondarily distorted the wing cuticle, whereas deformations were still effective when the wing was immobilized at the wing-hinge. Effective deformations included bending the wing and twisting it about its longitudinal axis. The response to twisting was directionally selective. *Supination* caused the neurone to depolarize and spike (Fig. 3A), while twisting in the *pronating* direction caused a decrease in the rate of spiking (Fig. 3A,C, end of stimuli). Alternatively supinating and pronating the wing therefore evoked a clear directionally selective response, and revealed the occurrence of increased depolarizing input in the supinating phase compared with the pronating phase (Fig. 3D).

Ramp-hold stimuli revealed a phasic-tonic reaction to supinating twist (Fig. 3A). The frequency of spikes during the ramp equalled or exceeded that at the start of the steady twist, and during the maintained twist the spike frequency slowly declined. Adaptation in response to steady twist was initially rapid but became progressively slower (Fig. 3E). Hyperpolarizing the neurone by injected negative current abolished spiking and revealed a barrage of EPSPs whose envelope paralleled the time course of the spiking response to the same stimulus (Fig. 3B). Injection of depolarizing current failed to reveal any inhibitory postsynaptic potentials (IPSPs) associated with the stimulus, including the pronating ramp at the end (Fig. 3C). Thus cessation of spiking at the end of the supination, as also during pronation stimuli

Fig. 2. The morphology of (A) interneurone 5AA; (B) interneurone 3AA; (C) interneurone 1AA; and (D) interneurone 1AB. 5AA (A) is situated in the metathoracic ganglion, the other three cells (B–D) in the mesothoracic ganglion. Interneurones were stained by intracellular cobalt injection, followed by silver intensification, and drawn in whole-mount from the dorsal aspect. The dashed lines indicate the border of the neuropile. Lateral nerves 1, 3, 4 and 5 are labelled.

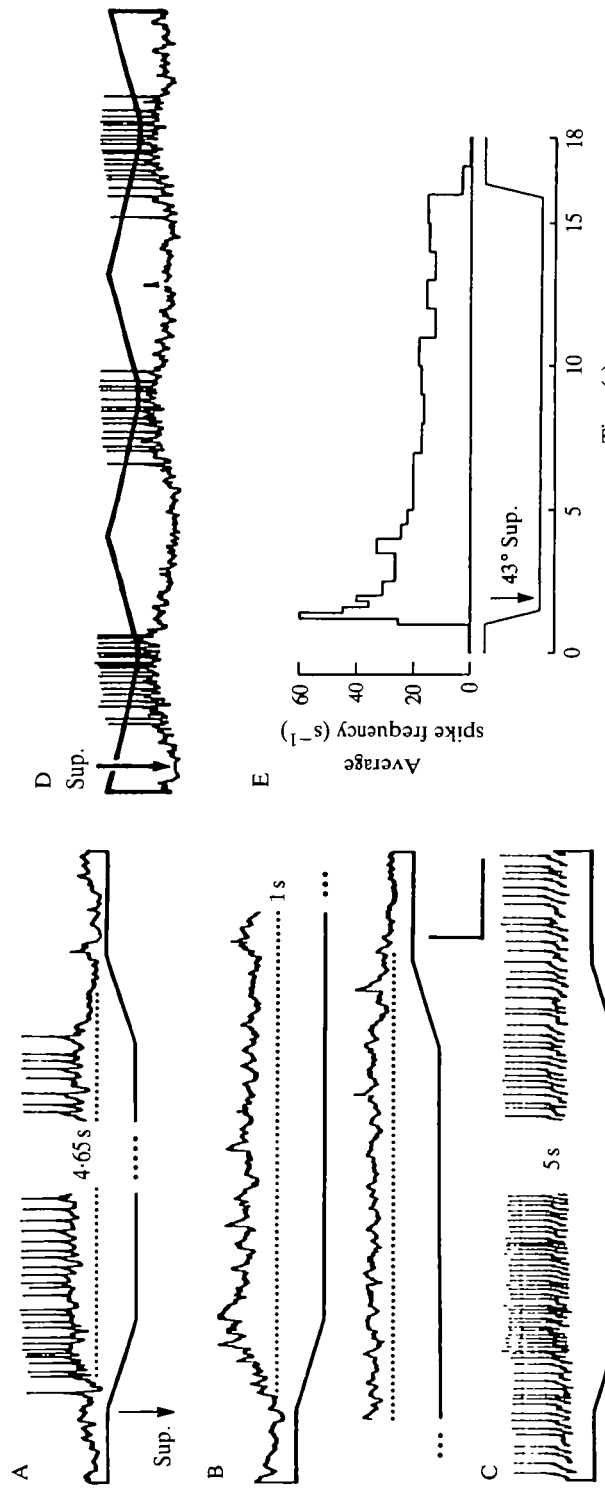


Fig. 3. Mechanosensory responses of interneurone 5AA, recorded intracellularly in its soma, to twisting of the ipsilateral hindwing. (A–C) Phasic-tonic responses to supination (Sup.) and the determining role of excitatory synaptic input. Three identical ramp-hold–release stimuli are given. Lower traces monitor angle of twist, as in Fig. 1. (A) The response when no polarizing current is passed through the electrode. (B) The interneurone is hyperpolarized by 1 nA of negative current. Dotted lines indicate the pre-stimulus membrane potential. (C) 1 nA of depolarizing current. See text for analysis of these results. The durations of the portions omitted from the records are indicated. (D) Directional selectivity, shown in response to periodic twisting. (E) Time course of adaptation of spiking. Average spike frequency in successive 1-s bins (except: initial 1 s of stimulus in 200-ms bins, and subsequent 3 s in 500-ms bins). Calibrations: 8 mV, 50°; 400 ms (D, 800 ms).

(data not illustrated), was due to withdrawal of excitatory synaptic input. Hyperpolarizing current augmented, while depolarizing current diminished, the amplitude of the summed synaptic input underlying responses to identical supinating stimuli (Fig. 3B,C), implying that the input was predominantly chemical in nature.

This excitatory input was derived from the hindwing campaniform sensilla. Thus simultaneous recordings from 5AA and hindwing campaniform sensilla showed that deforming stimuli which excited the interneurone also excited the campaniform sensilla (Fig. 4A,C). Small deformations of the wing elicited brief bursts of spikes in the afferents that were followed by depolarizing synaptic potentials in the interneurone (Fig. 4A). As these potentials elicited spiking, they were evidently EPSPs.

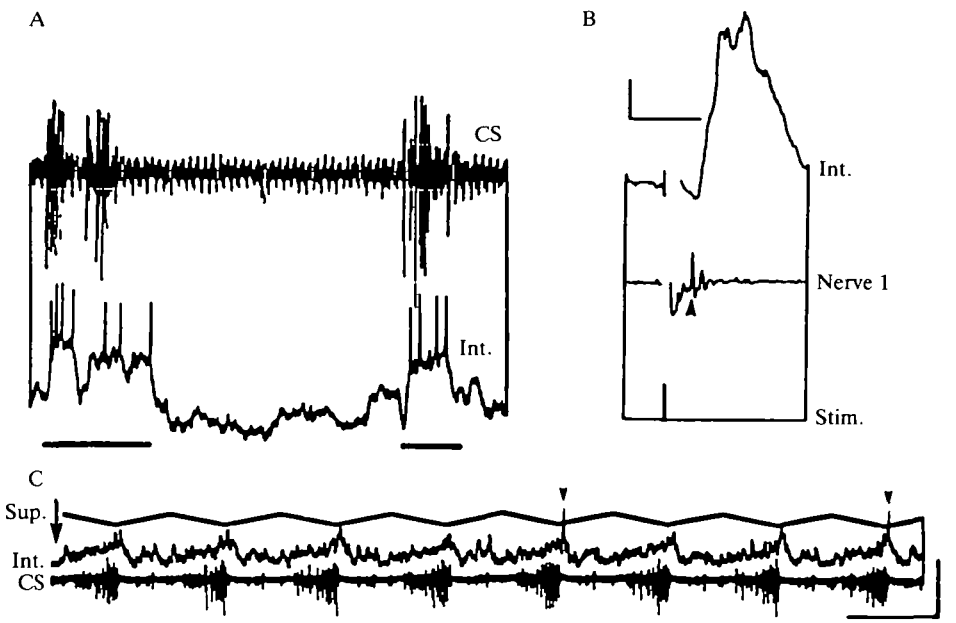


Fig. 4. Discharge of campaniform sensilla afferents (CS) is correlated with depolarizing, spiking responses in 5AA (Int). The campaniform sensilla in the ipsilateral hindwing are recorded (A,C) or stimulated (B) *via* pin electrodes implanted in the subcostal vein (also used in Fig. 5; not all the sensilla are recorded – see Materials and Methods). (A) Small transient deflections of the wing's leading edge (marked by the bars) elicit three brief, high-frequency bursts of spikes in some recorded afferent units that are followed at short latency by depolarization and spikes in 5AA. The continuing excitation after the second afferent burst may represent input from other, unrecorded afferents. (B) Electrical stimulation of the hindwing campaniform sensilla (Stim.) evokes synaptic potentials in 5AA (Int). The depolarizing potential in 5AA was averaged from 128 events. The sensory volley attributed to the campaniform afferents (arrowhead) was subsequently recorded in nerve 1 about 1 mm from the metathoracic ganglion, and the two recordings combined, using the monitor of the stimulus pulse (60 V, 0·5 ms) as a time marker. (C) Correlated directionally selective responses in the afferents and the interneurone (which is d.c. hyperpolarized). Upper trace shows the angle of wing twist (Sup., supination). The interneurone spikes twice (arrowheads). Calibrations: vertical, A, 6 mV; C, 20 mV, 500°; B (separate calibration bars), 0·1 mV; time, A, 250 ms; C, 800 ms; B (separate), 40 ms.

Deformations of the wing base that strongly excited the interneurone also caused the campaniform sensilla, which are located in that region, to spike at high frequencies (not illustrated). Compound depolarizing potentials could also be evoked when the campaniform sensilla were stimulated electrically (e.g. Fig. 4B). Potentials followed stimulus pulses at constant latency and without decrement at frequencies up to 10 Hz (the highest frequency tested). These results are consistent with the common responses of afferents and interneurone to controlled twisting stimuli. Thus, the time course of adaptation was qualitatively similar in both (cf. Figs 1E, 3E). Periodic twisting of the wing showed common directional sensitivity. Excitatory synaptic input to the interneurone during the supinating phase correlated with the occurrence of activity in the afferents in the same phase (Fig. 4C).

Short-latency connections of campaniform sensilla afferents to 5AA

Usually the response of the campaniform sensilla to imposed deformations, recorded in the wing vein, consisted of many units. In some favourable preparations, however, individual afferents could be distinguished by the amplitude and shape of their spike. In one such preparation, depolarizing postsynaptic potentials (PSPs) followed each spike of seven of the eight identifiable afferent units recorded at that site in the subcosta, without failure and at a constant latency of approximately 10 ms. Examples are shown for two units in Fig. 5A,B. These individual potentials were EPSPs, capable of exciting the interneurone to spike (Fig. 5A, starred). A second unit spiked at high frequencies, and was consistently followed by an EPSP even at instantaneous frequencies of about 90 Hz (afferent 2, Fig. 5B,C). The EPSPs associated with all seven afferents had similar amplitudes, about 2 mV as recorded in the soma (interneurone tonically hyperpolarized by about 1–2 nA). The amplitude was apparently augmented by increasing hyperpolarization, consistent with the summed synaptic responses shown in Fig. 3.

The EPSPs associated with single afferents showed fluctuations in amplitude due to their occurrence in a background of continuing synaptic input from other afferents and other, unrecorded, sources (e.g. Fig. 5C). Signal averaging provided a clearer picture of the time course of an EPSP. This is illustrated in Fig. 5D, taken from a second preparation. A depolarizing PSP, about 25 ms in duration, followed the spike of an individual large unit after a delay of about 9 ms. The sharp onset of the averaged potential indicated a constant latency. Signal-averaging showed depolarizing PSPs following the spikes of other size classes of large afferents, again at latencies of about 9 ms.

Estimates of central synaptic delay were obtained in a different preparation from electrical stimulation of the campaniform sensilla, which presumably elicited a synchronous spike in many afferents. Each stimulus pulse elicited a sensory volley in the wing nerve and a depolarizing potential at constant latency (signal averaged in Fig. 4B). The measured conduction velocity of the sensory volley was $0{\cdot}7\,m\,s^{-1}$, leaving a central delay of 1·7 ms from arrival at the ganglion to evoking the PSP. Of this delay, at least 0·7 ms must be subtracted for conduction over some 500–600 μm to the probable synaptic sites (anatomical data not illustrated; R. C. Elson, in

preparation). This yields an estimated central synaptic delay of 1 ms (error range at least ± 0·3 ms), comparable to that reported for monosynaptic connections between another flight afferent and motor neurones in the locust (Burrows, 1975). Taken together, these data are therefore consistent with an interpretation that some, at least, of the campaniform sensilla afferents make monosynaptic connections with 5AA.

Exteroceptive and other inputs to 5AA

In addition to receiving input from the campaniform sensilla of the ipsilateral hindwing, 5AA also responded to specific sensory stimuli of other modalities.

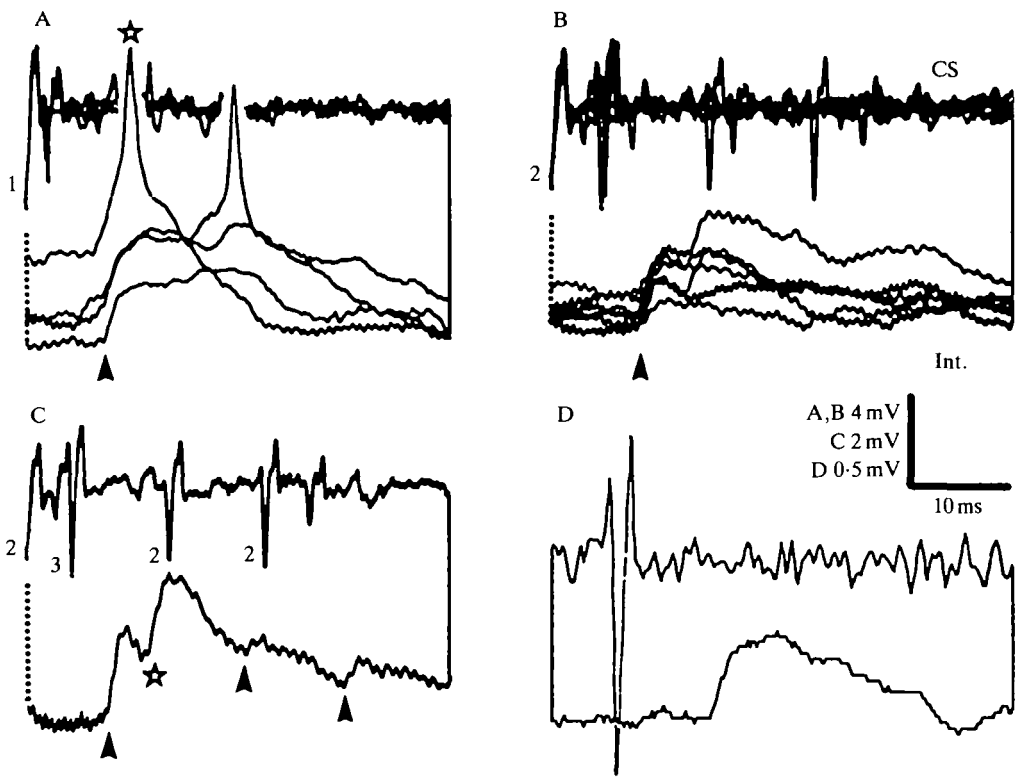


Fig. 5. Connections between individual campaniform afferents (CS, extracellular spikes, upper traces) and interneurone 5AA (Int., intracellular, lower traces). (A–C) The sweep is triggered by the spikes of selected individual afferents, from the same preparation. (A) Each spike of a single unit, termed afferent 1, is followed by an EPSP (arrowhead) at a constant latency. One EPSP triggers a spike in the interneurone (star). (B) An EPSP (arrowhead) follows the spike of afferent 2 at a constant latency. (C) Each spike of afferent 2 is followed by an EPSP (arrowheads), even at high instantaneous frequency. Another unit, afferent 3, is also followed by an EPSP (star) in this example. Changes in the amplitude of the EPSP of afferent 2 are probably due to changes in postsynaptic membrane potential and conductance. (D) In another preparation, signal averaging (64 events) reveals a small depolarizing potential following the spike of an individual large afferent.

Ocellar stimulation

Light-off evoked a reliable, phasic burst of EPSPs and high-frequency spikes in 5AA (Fig. 6A). Gradual light-off sets revealed many small EPSPs in the response

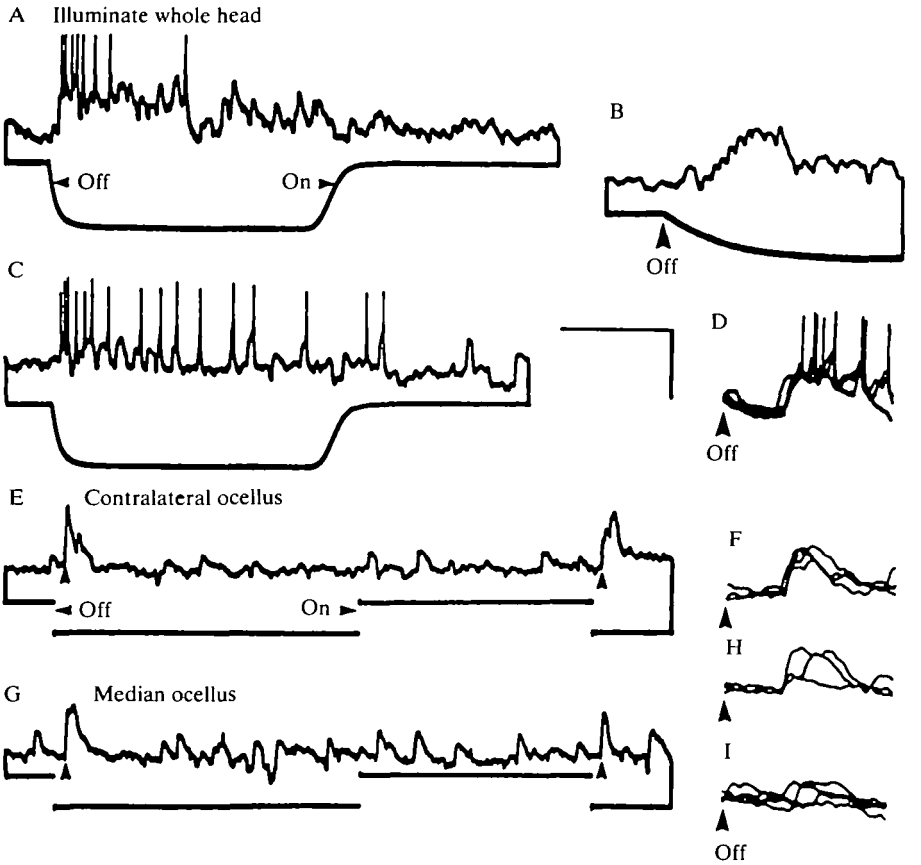


Fig. 6. Exteroceptive input to 5AA: responses to light-on and light-off. (A–D) Responses to changes in the intensity of light incident on the whole head (monitored by a photosensitive diode, whose output is displayed in lower traces of A, B and C). (A) Phasic depolarization and spiking in response to light-off. (B) The light-off response comprises several summating EPSPs. (C) Tonic depolarizing current injected into the interneurone reduces the amplitude of the synaptic input at light-off, suggesting that it is chemically mediated. (D) Triggering the oscilloscope sweep from rapid light-off stimuli (as in A) reveals that the depolarizing synaptic input occurs at a constant latency (several traces overlaid). (E–I) Stimulation of individual ocelli. (E) Light-off at the ocellus on the side contralateral to the soma elicits depolarizing potentials (vertical arrowheads). There is no response to light-on. (F) These potentials follow the light-off stimulus (at arrowhead) at a constant latency. Several sweeps are overlaid. (G) Depolarizing potentials (arrowheads) evoked by light-off stimuli to the median ocellus. (H) These potentials also follow light-off (at arrowhead) at a constant latency. (I) In contrast, no such potentials are evoked by light-off stimuli (at arrowhead) to the ipsilateral ocellus (a higher frequency of EPSPs occurs in the background synaptic activity of this record; these are not correlated with the stimulus, and probably derive from the hindwing sensilla). All records except B are from the same experiment. Calibrations: voltage, 8 mV (except B, 10 mV); time, A,C,E,G, 400 ms; B, 200 ms; D,F,H,I, 67 ms).

(Fig. 6B). These potentials were apparently conventional chemical EPSPs, as d.c. depolarization of the interneurone reduced the amplitude of the summed synaptic input at light-off (Fig. 6C). For a given light pulse, the latency from light-off to the initial depolarizing response was constant (Fig. 6D). Light-offsets from bright light gave latencies as short as 35 ms, but latency increased as the size and steepness of the light-offset was decreased. Light-on elicited no consistent response, but could terminate a train of EPSPs triggered by a closely preceding light-off stimulus (Fig. 6A). The movement of black or white spots or stripes, against plain white backgrounds or the contrast-rich background of the laboratory, also evoked no response. These results do not preclude the possibility of a visual input from the compound eyes in response to an appropriate stimulus. However, simple light-off stimuli to either compound eye, delivered by a light-emitting diode (see Materials and Methods), evoked no response in the interneurone.

Stimulation of individual ocelli contralateral (Fig. 6E) and medial (Fig. 6G) to the soma could elicit one or two EPSPs at short, constant latency of about 35 ms for each light-off (contralateral, Fig. 6F; median, Fig. 6H), i.e. at the same latency as the whole-field off response (Fig. 6D). In contrast, stimulation of the ipsilateral ocellus elicited no such PSPs (Fig. 6I).

Head movement

Interneurone 5AA was also powerfully excited by imposed displacements of the head relative to the thorax. Small (2–3 mm) brief tilting movements elicited a phasic burst of spikes (Fig. 7A), and sudden head deflections to a new position evoked an adapting train of spikes (Fig. 7B). Imposed rolling movements of the head were also excitatory, but directional responses were not studied. The spikes were underlain by discernible EPSPs, showing that the excitatory input was received in the meta-thoracic ganglion and not in anterior ganglia, to which 5AA projects. These

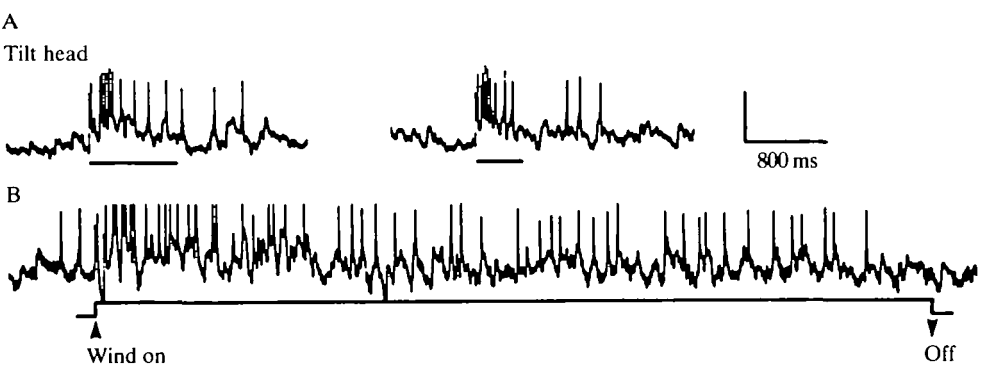


Fig. 7. Interneurone 5AA is excited by movement of the locust's head relative to the thorax (which was fixed). (A) Brisk spiking responses to imposed downward tilting of the head (stimuli marked by bars). (B) Evidence for a phasic-tonic reaction. A sudden head deflection is produced by a strong frontal airstream whose duration is shown schematically in the lower trace (the response is unlikely to be due primarily to wind: the antennae were amputated and the cephalic wind-hairs covered by Vaseline; and weaker wind stimuli did not elicit this response). Voltage calibration: A, 8 mV; B, 4 mV.

responses were not related to touching any particular head structure and could be elicited by other stimuli, for example, by deflections of the head caused by a wind jet (where the cephalic wind-hairs were covered by Vaseline and the antennae amputated, thus greatly attenuating any response to the air movement itself; here, however, thoracic wind-hairs might also have been stimulated). The responses persisted undiminished in darkness (tested immediately after darkening, so that little dark adaptation would be expected). This suggests that a large part of this reaction was not visual, but proprioceptive, e.g. from mechanoreceptors of the neck region. Responses were apparently not mediated by receptors on the cervical sclerites (Goodman, 1959), as touching these structures with a probe in one experiment elicited no response.

Other inputs

Interneurone 5AA received a weak auditory input. Loud claps elicited small depolarizing potentials. Lightly touching the tarsi or femorotibial joints of the ipsilateral legs also evoked depolarizing potentials and spikes.

Other interneurones

Multimodal responses were also detected in 3AA (Fig. 2B) and 1AA (Fig. 2C). Interneurone 3AA depolarized and spiked at high frequency in response to imposed twisting (supination) of the forewing ipsilateral to the axon (Fig. 8A). A weaker excitatory response was evoked by supinating the opposite forewing (Fig. 8B). Hindwing responses were not tested. Light-off stimuli produced strong excitation (Fig. 8C).

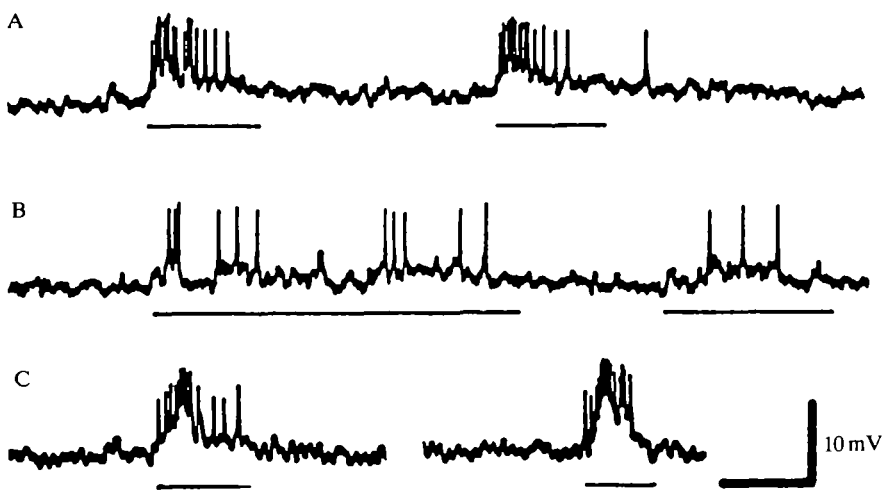


Fig. 8. Interneurone 3AA responds to wing strains and light-off. Bars indicate timing of stimuli. (A) Supinating the forewing ipsilateral to the axon causes depolarization and spiking. (B) Excitatory response to supination of the other forewing. (C) Depolarization and spikes elicited by a bar of shadow passed over the ocellar region of the head. This response is very similar to that evoked in 5AA by the same stimulus. Time calibration: A,B, 400 ms; C, 200 ms.

Interneurone 1AA gave specific excitatory and inhibitory responses to imposed deformations of all four wings, was excited by ocellar stimulation and head movement, and was inhibited by auditory stimulation. The spontaneous spike discharge of this interneurone was also modulated in the absence of applied stimuli, by rhythmic input or inputs in time with ventilation (Fig. 9A). This modulation could therefore interfere with the wing responses (cf. Fig. 9B,F). Its source was not identified, but sensory detection of stresses caused in the restrained wings by the animal's ventilatory movements cannot be excluded.

Supination of the ipsilateral (Fig. 9B) or contralateral (Fig. 9C) forewings, or the ipsilateral hindwing (Fig. 9D), evoked hyperpolarizing potentials and inhibition of spiking. The inhibitory responses were phasic and, where tested, directionally selective for supinating twist (Fig. 9B). In contrast, supination of the contralateral hindwing evoked depolarization and an increased rate of spiking (Fig. 9E). This excitatory response was underlain by a train of apparently unitary EPSPs (Fig. 9F). The frequency of these EPSPs increased with increasing stimulus amplitude (not illustrated), showed sensitivity to twisting movement and adapted during maintained twist (Fig. 9F). This excitatory input was selective for supination, being terminated by pronating movement.

In response to light-off, 1AA phasically depolarized and gave a burst of spikes. Light-on elicited no reaction. Light-off responses could be evoked by stimulation of the median (Fig. 9G,H) or contralateral (Fig. 9I) ocelli, at constant latencies of about 40 ms. Stimulation of the ipsilateral ocellus, however, elicited no response.

Interneurone 1AB (Fig. 2D) was excited by supinating twist applied to the ipsilateral forewing and received weaker excitatory input from the contralateral forewing. Responses to light-on and light-off stimuli and head movements were not obvious in the single penetration of this interneurone.

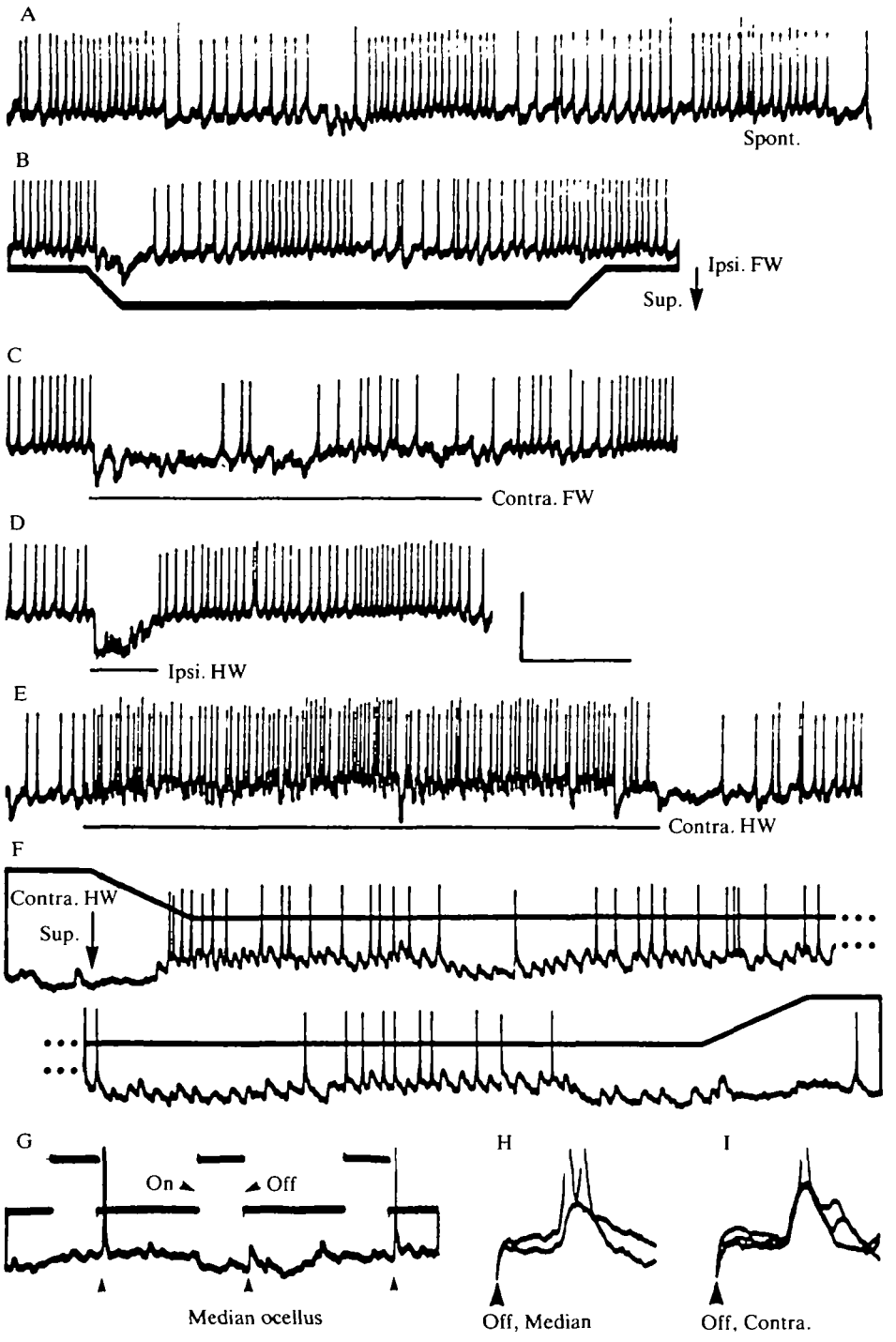
DISCUSSION

Wing sensory inputs to the interneurones

Nature of inputs

This paper reports the discovery of several thoracic interneurones that respond to wing strains. They may derive input from strains in one wing or a combination of wings, and may be either excited or inhibited by these inputs. The response of interneurone 5AA is mediated by wing campaniform sensilla. The nature of stimulation used (wing twisting and bending), the characteristics of response (adapting, directionally selective) and the elimination of wing-hinge receptors together indicate that campaniform sensilla probably also drive the responses of the other interneurones.

Interneurone 5AA is the first identified type of interneurone found to receive monosynaptic inputs from wing campaniform sensilla. The evidence for such connections is physiological: unitary EPSPs follow the spikes of individual afferents,


A
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Contra. HW
Sup.
G
On
Off
Median ocellus
H
Off, Median
I
Off, Contra.

Fig. 9

1:1, at short, constant latency and at high instantaneous frequencies. This behaviour would not be expected if spiking neurones were interposed. Non-spiking neurones might possibly be interposed, but none have yet been found to receive direct inputs from mechanosensory afferents in the locust (Siegler & Burrows, 1983). The estimated central synaptic delay is brief, about 1 ms. Anatomical evidence from the light microscope is also consistent with direct connectivity: the afferent projection occupies the same localized, identified regions of neuropile as parts of the interneurone's arborization (R. C. Elson, in preparation).

Monosynaptic inputs to interganglionic interneurones from another flight proprioceptor, the wing-hinge stretch receptor, were reported recently by Pearson *et al.* (1983). This and other evidence (e.g. Callec, Guillet, Pichon & Boistel, 1971; Bacon & Murphey, 1984; Hustert, 1985; this paper) indicates that mechanosensory afferents of insects can connect directly to interganglionic interneurones, as well as to spiking local interneurones (Siegler & Burrows, 1983). In comparison, the existence of monosynaptic connections from mechanoreceptor afferents to intersegmental interneurones in the crayfish, is well established (Calabrese, 1976; Zucker, 1972).

For the other interneurones described, there are no physiological data concerning the directness of afferent input. However, anatomy precludes direct input from certain wings. The afferents of the campaniform sensilla do not ascend or project contralaterally (Tyrer & Altman, 1974), so that the hindwing responses in 1AA, and the contralateral wing responses in 1AA and 1AB, must be mediated by other, intercalated interneurones. Interestingly, the contralateral hindwing input to 1AA is derived from a presynaptic neurone that has 5AA-like response properties (see Fig. 9F). 1AA's ipsilateral inhibitory input is also probably indirect, as no mechanosensory afferents are yet known to produce monosynaptic inhibition in central neurones (Calabrese, 1976; Siegler & Burrows, 1983).

It cannot be excluded that other, unidentified, strain-detecting receptors might contribute inputs to these interneurones as well. One such class could be the small-axoned multipolar sensilla dispersed within the wing cuticle (Knyazeva, 1970).

Fig. 9. Responses of 1AA to deformations of all four wings and to ocellar stimulation. (Ipsi., ipsilateral; Contra., contralateral; FW, forewing; HW, hindwing). (A) In the absence of sensory stimulation there is a slow, spontaneous (Spont.) rhythm of spikes apparently in time with ventilation. (B) Supination (Sup.) of the ipsilateral forewing (angle of twisting monitored in the lower trace) evokes a transient inhibition. Note IPSPs during the twisting movement. (C–E) Stimulation by a hand-held probe. Bars show the duration of imposed stimuli. (C) Supinating the contralateral forewing evokes IPSPs. (D) IPSPs are also evoked by deforming the ipsilateral hindwing. (E) Supinating the contralateral hindwing excites the interneurone. (F) Apparently unitary EPSPs in the response to contralateral hindwing supination (Sup., angle of twist in upper trace). The duration of the omitted portion is 3·8 s. (G–I) Stimulation of individual ocelli. (G) Light-on and light-off stimuli (monitored in upper trace) to the median ocellus elicit phasic EPSPs and spikes at off, but no response at on. (H) EPSPs follow the off stimulus (at arrowhead) to the median ocellus at a constant latency. (I) as H, but for the contralateral ocellus. Initial deflection is an artefact of the pulse offset. Calibrations: vertical, A,E–G, 8 mV; B–D, 10 mV; H,I, 4 mV; B, 100°; F, 50°; time, 800 ms (except F, 400 ms; H,I, 67 ms).

Functional significance

The possible functioning of the interneurones in flight must be inferred from their response properties and those of the sensory neurones which drive them. In the flying animal the mechanical stimulation of the campaniform sensilla results from the forces acting on and in the wing. Behavioural studies indicate that a principal stimulus for these receptors is the aerodynamic force (lift and thrust) generated by their wing (Gettrup & Wilson, 1964; Gettrup, 1965, 1966; Pringle, 1976). The proprioceptive response of the interneurones may therefore be largely determined by this force. A neurone with excitatory input from just one wing (e.g. 5AA) will progressively depolarize and spike at higher frequency as the intensity of activity in the campaniform sensilla increases. In flight it would provide a simple monitor of the resultant strain perceived by the campaniform sensilla, and thus the aerodynamic force, in that wing. A neurone deriving excitatory input from the sensilla of more than one wing (e.g. 3AA) would allow an interneurone to monitor the sum of the force experienced by those wings. Where an interneurone derives a combination of excitatory and inhibitory inputs, from the sensilla of several wings (e.g. 1AA), the net excitation will depend on the balance of these inputs. Here the interneurone could monitor the pattern of strains among the wings, and therefore their relative aerodynamic contributions. The development of an imbalance of forces could also be detected. A comparable monitoring of the pattern of proprioceptive inputs from several appendages occurs in decapod crustaceans. Joint proprioceptors in each leg detect the movements caused by body displacements relative to the substrate. The direction of displacement is abstracted from the pattern of movement among the legs and determines the direction of an equilibrium reflex. Some sensory interneurones with opposite bilateral inputs from leg proprioceptors, which could detect components of these displacements, have been found in lobsters (Schöne, Neil, Stein & Carlstead, 1976; Priest, 1983; Neil *et al.* 1984).

Although the cells described here probably represent only a fraction of the total number of interneurones with sensitive reactions to wing strains, they do indicate the types of proprioceptive responses which can occur, and how they could function in flight.

Exteroceptive input to the interneurones

The synaptic responses evoked in interneurones 5AA and 1AA by ocellar stimulation resemble those seen in a small population of thoracic interneurones, described by Rowell and co-workers (Rowell & Pearson, 1983; Reichert & Rowell, 1985), that are postsynaptic to ocellar units that descend the nerve cord from the brain, and occur at comparable latencies. The descending interneurones respond to light-off stimulation of specific ocelli by firing one or two rapidly conducted spikes at constant latencies (Patterson & Goodman, 1974; Simmons, 1980; Rowell & Pearson, 1983; Reichert *et al.* 1985; Rowell & Reichert, 1986). The thoracic interneurones described here, therefore, probably also derive their ocellar inputs from these descending units, and may similarly receive direct connections; if the input is not direct, it

must be mediated *via* non-spiking neurones, or neurones which themselves are caused to spike at consistent latencies. The response of 3AA to light-off stimuli is very similar to those of 5AA and 1AA, and may also be ocellar, though this was not tested.

Interneurones 5AA and 1AA also resemble the thoracic interneurones described above in the asymmetry of ocellar input (EPSPs from the medial and one lateral ocellus). In the thoracic interneurones of Rowell & Pearson (1983) and Reichert & Rowell (1985), the asymmetric input patterns derive from particular combinations of presynaptic descending units, and have functional significance for the detection of flight instability. Lateral ocelli can detect rolling, the medial ocellus, pitching. The ocelli mediate compensatory reactions which would correct the perceived deviation from straight, stable flight (Wilson, 1978; Stange & Howard, 1979; Taylor, 1981*a*,*b*). The pattern of ocellar input to 5AA and 1AA, as to the thoracic interneurones above, implies that they will respond optimally to particular rotations in the rolling and pitching planes. Modulation of activity in the thoracic interneurones, some of which are premotor, is thought to underlie compensatory changes in flight motor output (Reichert & Rowell, 1985; Reichert *et al.* 1985). These cells have therefore been termed 'steering interneurones' (Reichert, 1985). The asymmetric ocellar inputs to 5AA and 1AA are suggestive of some function in steering reactions for those neurones also.

Interneurones 5AA, 3AA and 1AA resemble steering interneurones in two further respects: first, in morphology – both types arborize in the most dorsal regions of neuropile (Rowell & Pearson, 1983; R. C. Elson, in preparation; note especially the close structural resemblance of 1AA to Rowell & Pearson's thoracic interneurone 116, and 3AA to their 315); second, in other sensory responses – both types have multimodal reactions, including tactile and auditory inputs (Reichert & Rowell, 1985). All these similarities suggest that the interneurones of this paper and previously described steering interneurones are overlapping categories and may be sampled from the same population. The results then have two implications. First, as the descending interneurones and steering cells also respond to appropriate compound eye, wind-hair and antennal stimuli that would signal flight deviations (Reichert *et al.* 1985), these types of response should be looked for in the type of neurones reported here. (The lack of a clear wind response in 5AA – see legend of Fig. 7 – may reflect the relative insensitivity of the descending neurones to weak wind stimuli and the inhibition of their wind response during bright illumination, as often used in the preparations described here: cf. Rowell & Reichert, 1986.) Second, proprioceptive inputs from wing campaniform sensilla may also occur in previously described steering interneurones, and this type of convergence should be studied further.

Some of the same interneurones, described here, that receive ocellar input can also be excited by imposed movements of the locust's head. In 5AA (and probably also in 1AA) a major part of this response is probably proprioceptive, and detects head motion rather than specifically touch or pressure on the head. Detection of head misalignment with the thorax, resulting from corrective repositioning of the

head, elicits compensatory flight reactions in a second pathway for exteroceptive responses to course deviations (see Introduction). It is tempting to ascribe such a function to the responses in 5AA and 1AA. The receptors underlying these responses and the reaction of the interneurones to active head movements must receive study, however, before behavioural function can be inferred.

Specific convergence of proprioceptive and exteroceptive inputs

The convergence of specific proprioceptive and exteroceptive inputs suggests that the same interneurones that could be active during the exteroceptive adjustment of flight could also participate when adjustments are signalled by proprioceptive feedback. Proprioceptive input from the wings is involved in the coordination of the movements of individual wings and the ensemble of four wings (Burrows, 1976*b*; Möhl, 1985*a*,*b*,*c*). This coordination is important for the maintenance of flight stability, as each wing has its own set of motor neurones and is capable of independent fluctuations in performance. In flying locusts where exteroceptive feedback has been disabled, this coordination appears as correlations in the activity of motor neurones of different wings. Correlation patterns commonly link activity in contralateral and heterosegmental wings (Möhl, 1985*a*). The interneurones described here project contralaterally and intersegmentally, or have bilateral and heterosegmental wing inputs. In this way the feedback they derive about force (lift and thrust) generation in various wings (which, if irregular or unbalanced, will cause instability) could be used in the coordination of compensatory motor changes among the wings, leading to correction of the instability.

Interneurones of this type could therefore be used by several feedback pathways in the production of appropriate flight adjustments. Different sensory inputs that require a common motor response may converge (see Olberg, 1981). For instance, the ocellar inputs to 5AA (excitation at dimming the median and contralateral ocelli) would signal downward pitch and contralateral roll (i.e. rolling downwards on the contralateral side, upwards on the ipsilateral side). The interneurone can also detect ipsilateral roll of the head (i.e. rolling downwards on the ipsilateral side), a mismatch with the thorax that might occur during repositioning of the head following a contralateral roll by the whole locust. Similarly, 5AA would detect an increase in lift generation by the ipsilateral hindwing, which, if uncompensated, would cause downward pitching and contralateral rolling. In each case the appropriate flight compensation, which the interneurone might signal, would be the generation of a restoring torque that included upward pitching and ipsilateral rolling components.

Similar convergence of modalities occurs in the equilibrium reactions of other arthropods and of vertebrates. Unintended body movements are detected by equilibrium receptors (functional analogues of the exteroceptors used by the flying locust) and by limb proprioceptors. The two sensory systems commonly interact in the control of posture. These interactions seem to involve integration at a segmental (spinal) level, analogous to the suggested role of the interneurones described here. In decapod crustaceans, feedback signals from statocyst and leg proprioceptors (see

above) interact in the production of appropriate righting responses and compensatory eye movements, suggesting that they converge in appropriate patterns (Schöne *et al.* 1976; Schöne, Neil, Scapini & Dreissman, 1983; Neil *et al.* 1984; Hisada & Neil, 1985). The convergence is thought to occur at segmental, premotor interneurones, as yet unidentified (Hisada & Neil, 1985). In vertebrates there is a continual interaction between vestibular inputs and those from proprioceptors and cutaneous afferents. The lateral vestibulospinal tract excites limb extensor motor neurones and flexor Ia inhibitory interneurones, spinal neurones which are also excited by the extensor Ia afferents (Grillner, Hongo & Lund, 1970; Hultborn, Illert & Santini, 1976).

To understand more fully the functions of the types of interneurone described here, we need to know more about the range of sensory inputs to individual neurones, and what outputs they have. Some reflex effects of wing campaniform sensilla on flight motor neurones are known (Wendler, 1978; Horsmann, 1981; R. C. Elson, in preparation) in which these cells might participate, but the particular motor effects of single interneurones remain unknown. It is clear, however, that single thoracic interneurones can receive both ocellar and head-motion signals (implicating them in exteroceptive flight control), and combine these with proprioceptive feedback about wing forces. These multimodal flight interneurones and, by inference, analogous steering interneurones, may be the nexus of several parallel feedback loops (see Rowell & Pearson, 1983) which converge in specific patterns. This utilization of single interneurones by different pathways reflects the economy of design in the locust's nervous system.

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