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WIND-EVOKED ESCAPE RUNNING OF THE CRICKET *GRYLLUS BIMACULATUS*

II. NEUROPHYSIOLOGICAL ANALYSIS

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Summary

Following the description of some typical variables of escape running in the cricket *Gryllus bimaculatus* in a companion paper, this study gives an account of the physiological characteristics of identified interganglionic cell types recorded during normal and wind-evoked walking.

1. Intracellular recording and staining of axons in the prothoracic ganglion revealed a group of intersegmental wind-sensitive neurones with large axons in the laterodorsal tract and somata in the pro- or mesothoracic ganglion. These interneurones rapidly conduct signals to their projections in the thoracic and cephalic ganglia. Wind pulses evoke strong, non-habituating spike reactions, which tend to summate during repeated stimulation.

2. During walking, the sensory response to wind stimulation is suppressed in a velocity-dependent manner in all ascending interneurones tested (N=40). During slow walking, the sensory responsiveness is merely reduced, whereas it is completely blocked during fast escape running bouts. Conversely, during pauses occurring during wind-evoked escape behaviour, the sensory responsiveness in ascending cells is significantly enhanced.

3. One type of interneurone that descends from the suboesophageal ganglion and projects to the thorax and abdominal connectives has been identified. In the resting animal, this neurone fires in the rhythm of abdominal ventilatory contractions. During walking, the rhythmic spike discharges disappear and, as in ascending interneurones, velocity-dependent spike suppression is observed.

4. In contrast to all other types of interneurones, which uniformly showed reduced spike activity during walking, cells descending from the brain were tonically excited during walking. Brain cells (N=21) have been classified according to whether their spike activity during walking was correlated with forward speed or with the intended walking direction.

5. Mechanisms underlying the observed gating of sensory responsiveness are discussed in terms of their possible functional significance. Modulated spike activity in ascending cells during walking suggests a role in tuning the thoracic motor centres for a central walking command. It is proposed that descending

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interneurones from the suboesophageal ganglion coordinate different behavioural rhythms. Possible functions of different types of brain neurones in the control of specific variables of walking behaviour are discussed.

Introduction

Escape reactions suitable for predator evasion can be regarded as the most vital behaviour beside feeding and reproduction in many animals. In the preceding paper (Gras and Hörner, 1992) we described some characteristic aspects of the escape behaviour of the cricket *Gryllus bimaculatus*. This rapid running behaviour can readily be evoked by mild wind stimuli directed at the cerci, abdominal sense organs specialized for the detection of air turbulence. The aim of the present paper is to describe the neurophysiological properties of identifiable neurones involved in the control of this behaviour.

The neural pathway underlying the wind-evoked escape behaviour has been studied in detail in orthopterans at both the behavioural and neuronal levels (Murphey and Palka, 1974; Camhi and Tom, 1978; Ritzmann, 1984; Camhi and Levy, 1988; Boyan and Ball, 1990). The transmission of cercal inputs to the giant fibres, which conduct sensory information to the thoracic motor centres and the brain, have been thoroughly investigated (Edwards and Palka, 1974; Tobias and Murphey, 1979; Palka *et al.* 1977; Kämper, 1984). Because of their directional, low-threshold reaction to wind stimuli and their high conduction velocities, the giant fibres are crucial for triggering the rapid escape reaction.

In the thorax, the excitatory giant interneurone-to-motor pathway, first thought to be direct (Ritzmann and Camhi, 1978), now appears to be organized polysynaptically (Ritzmann, 1984). In the cockroach, Ritzmann and Pollack (1986, 1988, 1990) and Westin *et al.* (1988) identified thoracic interneurones which receive input from giant interneurones and excite leg motor neurones. These interneurones are, therefore, likely candidates to pass giant fibre activity to thoracic motor centres, and may be important for the release of oriented escape behaviour (Ritzmann *et al.* 1991).

However, the functional role of wind-sensitive thoracic interneurones has not been directly addressed since the neural activity of the elements has not been investigated during behaviour. The present investigation is, therefore, focused on the identification of wind-sensitive interneurones in the thorax of the cricket *Gryllus bimaculatus*. For this purpose, the neural activity of these elements was monitored by intracellular recordings during behaviour. The simultaneous measurement of neurophysiological and behavioural events with high resolution (Gras and Hörner, 1992) allowed a direct correlation of variables suitable for an analysis of the functional role of different neurone types in the behaviour pattern.

Such an approach seems to be of particular interest since it has been demonstrated in crickets (Murphey and Palka, 1974) and cockroaches (Daley and Delcomyn, 1980*a*,*b*) that the giant fibre activity, which represents the main input from the wind-sensitive cerci in the thorax, is substantially modulated during

walking behaviour. Since the observed effects in giant interneurones were, at least partially, due to activity changes in central cells, interneurones other than giant fibres or thoracic cells are also likely to participate in motor control. Brain interneurones reacting to wind stimuli and possibly mediating spike modulations have been identified in the cricket and cockroach (Schildberger, 1984; Hörner and Gras, 1985; Burdohan and Comer, 1990). An array of several interneurones, including descending and ascending elements of the head and thoracic ganglia, therefore seems to be involved in the control of walking behaviour.

Analysis of the time course of the running and standing phases that typically occur during wind-evoked behaviour in crickets has shown that the duration of the running bouts is strictly fixed and is independent of the actual wind stimulus (Hörner and Gras, 1988; Gras and Hörner, 1992). This reflex-like organization led to the hypothesis of a possible 'behaviour-gated' sensory information transfer in the central nervous system (CNS) of the cricket (Hörner *et al.* 1989).

In the search for neural correlates of such a gating mechanism, the sensory responsiveness of different neurone types was tested systematically during normal and wind-evoked walking. The finding of suppressed spike activity in ascending interneurones and a simultaneous increased excitation in descending brain cells indicates a temporal separation of periods of major sensory input from those of motor output activity during wind-evoked escape behaviour in crickets.

Preliminary accounts of parts of this work have been published in abstract form (Hörner and Gras, 1987, 1988, 1989).

Materials and methods

Animals

Adult male and female specimens of *Gryllus bimaculatus* de Geer were used for electrophysiological experiments as described in the companion paper (Gras and Hörner, 1992), which gives a detailed methodological description of the apparatus used for measurement of the intended walking behaviour and the stimulation techniques.

Electrophysiology and preparation

To demonstrate the location of large intersegmental cells probably responsive to wind stimuli, the neck connectives were backfilled with $CoCl_2$ (Bacon and Altman, 1977). The position of the labelled axons with respect to the pattern of the main tracheae on the dorsal surface of the prothoracic ganglion (PTG) was documented and used subsequently to localize the recording electrode in an appropriate position. To measure the direction and velocity of spike propagation in intersegmental fibres, simultaneous recordings were made using extracellular suction electrodes placed at the dorsal surface of the neck connectives. Off-line identification of the extracellular correlate of the signal recorded intracellularly in the PTG allowed determination of conduction direction and velocity.

The morphology of Lucifer-Yellow-stained neurones was revealed by *camera lucida* reconstructions. To determine the position of dendrites and axonal arborizations, the whole-mount preparations were serially sectioned and examined in the light microscope (neuroanatomical terminology according to Wohlers and Huber, 1985).

Intracellular recording during walking

Intracellular recordings were made from more than 180 wind-sensitive neurones in the PTG. Quantitative analysis of electrophysiological data is based on 80 recordings which were stable for at least 15 min, obtained from animals readily performing the typical running reaction. Recordings of action potentials were fed to window discriminators, the output of which, together with the measurement of the intended walking behaviour, was sampled by a computer for analysis. Alternatively, recordings were replayed from FM tape (Racal store 7DS) and passed to a computer (Gras and Hörner, 1985) for off-line analysis with respect to appropriate behavioural measurements.

To elucidate possible modulations of the sensory responsiveness in wind-sensitive cells during behaviour, the neuronal reaction spectra in different behavioural contexts (i.e. spontaneous or wind-evoked locomotion) were analysed and compared separately. To estimate the coincidence of a neuronal event with a specific phase in behaviour, histograms of the distribution of translational and rotational speed were calculated for consecutive time intervals. The occurrence of spikes in these intervals was plotted below the corresponding histogram bins to illustrate the activity during behaviour (for further details see Gras and Hörner, 1992).

Results

Ascending interneurones

Ascending cells identified so far (N=40) share some common features such as a dorsal posterior soma located contralateral to a prominent axon within the lateral dorsal tract (LDT). Medioventral projections in the centre of the ganglion are separated from dorsolateral axon collaterals. In the following paragraphs three examples of single-cell recordings are presented and discussed with respect to the characteristics of other neurones of the same type.

Ascending interneurones with somata in the mesothoracic ganglion

Morphology. Two types of intersegmental neurones with somata in the mesothoracic ganglion (MSG) have been identified by recording from their axons in the PTG. The morphology of a neurone with a dorsal soma in the MSG is shown in Fig. 1A. The primary neurite connects the soma with a U-shaped structure positioned medioventrally within the ganglion. The axon bifurcates into descending and ascending branches (T-fibre; diameter, 12 μm), which run inside the LDT.

Dorsolateral axon collaterals are restricted to the hemiganglion contralateral to the soma. In the brain, fibre terminals project to the lateral protocerebrum and tritocerebrum. The staining posterior to the MSG was not traced.

Physiology. Except for some occasional single spikes, no spontaneous activity is present in this T-fibre in the resting animal. The velocity of spike conduction in the anterior direction is $1.48\pm0.1\,m\,s^{-1}$ (mean±S.E.M.; $N=4$; Fig. 1C). The neurone spikes in response to wind and sound stimuli. Although the response to sound stimuli is weak, wind stimuli directed at the cerci evoke a biphasic (on/off) reaction (Fig. 1B). A train of wind pulses causes an initial decrease in the response level, but the neuronal reaction then remains constant without further habituation. The response is direction-specific, since identical wind pulses directed to the cercus ipsilateral to the soma position elicit stronger reactions than contralateral wind pulses. In addition, the reactions to repetitive wind pulses tend to summate with increasing stimulus frequency (Fig. 1D). Fig. 1E shows that the number of spikes per wind pulse increases significantly ($P<0.0001$; two-tailed U-test) with increasing stimulus repetition rates from 2 to 10 Hz (except for 7 and 10 Hz stimulation from the axon-contralateral direction).

The sensory responsiveness of this neurone to wind stimuli is modulated during walking (not shown) and running (Fig. 2). The observed modulations are correlated with the walking speed as can be deduced from the distribution of the translational walking speed plotted in relation to spike activity (Fig. 3A). A velocity-dependent reduction in spike activity is visible, causing total spike suppression during running phases above 60–80 $mm\,s^{-1}$ of mean forward speed. In contrast, no correlation between the intended rotational speed and the magnitude of spike suppression seems to exist, since even during fast rotations spiking persists in this neurone (Fig. 3B).

During wind-evoked behaviour, the neural activity reflects the walking rhythm (Fig. 2). Because of the velocity-dependence of spike suppression, no spikes are recorded during the fast running bouts occurring during wind-evoked running. Data evaluation using enhanced temporal resolution revealed that the spike suppression started about 30 ms prior to the visible initiation of walking and lasted until the end of a running phase. In contrast, in the standing phases during wind-evoked behaviour, spike bursts with higher spike frequencies than those in the resting animal occurred (Fig. 2). In these phases, the neuronal background activity is tonically increased and the sensory responsiveness to the standard wind pulses is enhanced. This can be seen by comparing post-stimulus-time histograms of the neural response during standing phases (Fig. 3C): one histogram is calculated from data obtained from a resting animal, the other from an animal engaged in escape running. Another example of an ascending fibre with a different morphology is given in the next paragraph.

Morphology. The reconstruction of another ascending T-fibre with a dorsal soma in the MSG is shown in Fig. 4A. A medioventral U-shaped arc, similar to that of the previously described type of T-fibre is again present. The axon (diameter, 15 μm) runs in the soma-contralateral LDT. In contrast to the example

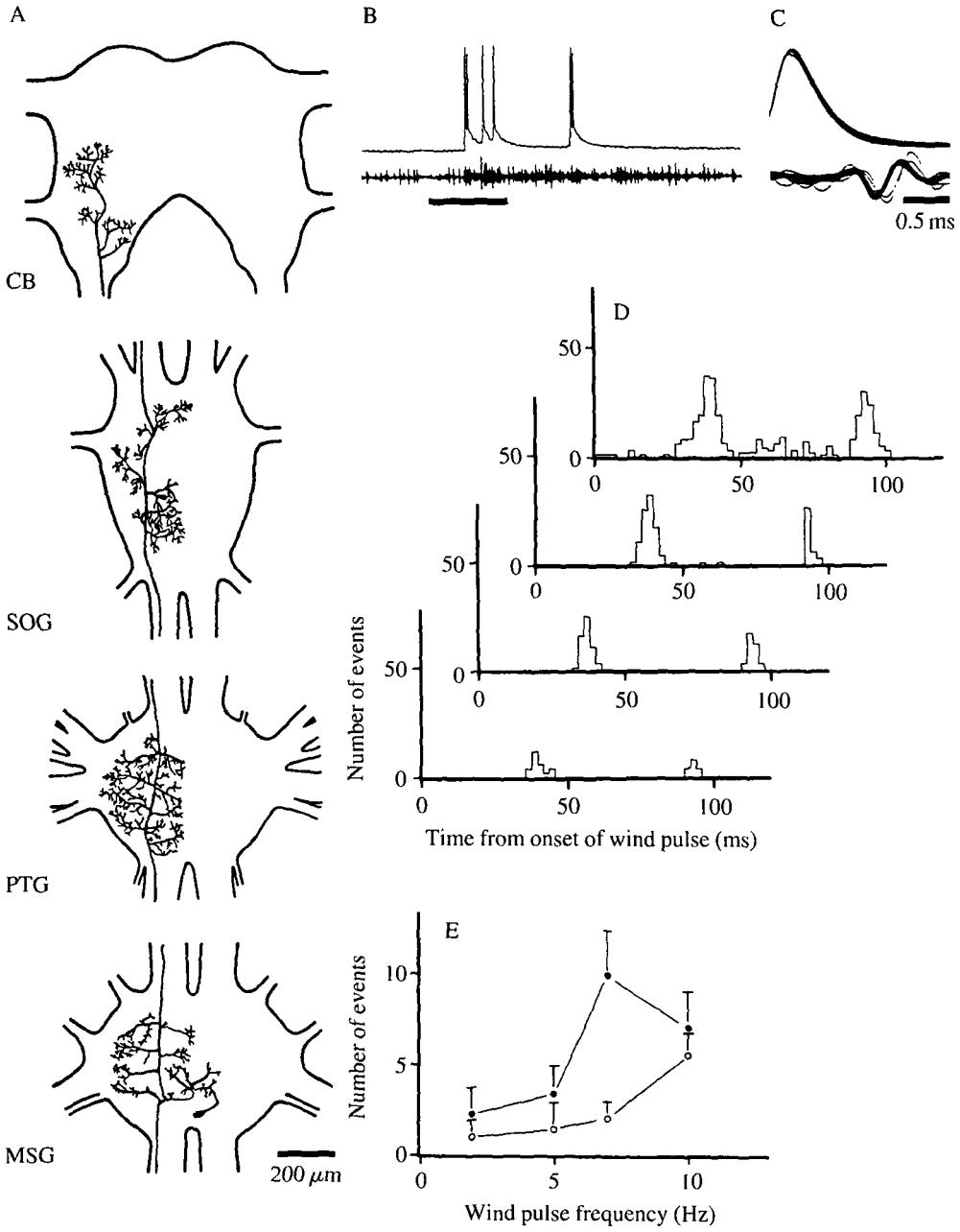

Fig. 1. For legend see p. 222.

mentioned above, axon collaterals penetrate the ventral intermediate tract in all thoracic ganglia and the suboesophageal ganglion (SOG). In the brain, there are two distinct fields of arborizations in the tritocerebrum and lateral protocerebrum.

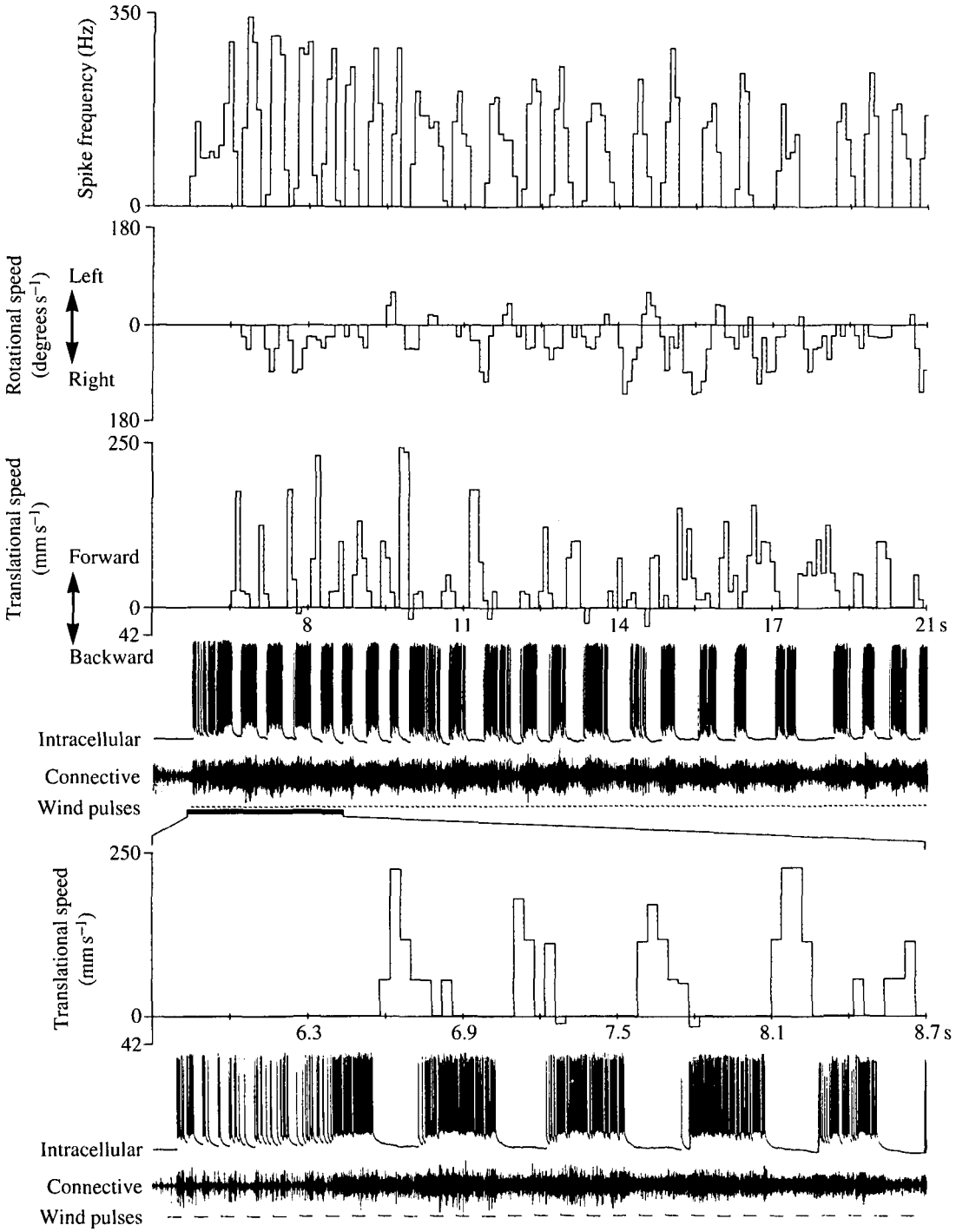

Fig. 2. For legend see p. 222.

Fig. 1. Morphology and physiology of an intersegmental interneurone with its soma in the mesothoracic ganglion. (A) *Camera lucida* reconstruction of this neurone in the mesothoracic (MSG), prothoracic (PTG), suboesophageal (SOG) and cerebral (CB) ganglia after intracellular Lucifer-Yellow staining. (B) Response to wind stimulation. Intracellular recording (top trace: spike amplitude, 80 mV) from the axon within the PTG and recording of extracellular activity (middle trace) from the left neck connective (bottom trace: stimulus marker for a 50 ms wind pulse; wind velocity $0.5\,m\,s^{-1}$). (C) One-to-one correlation between the intracellular (top trace: spike amplitude, 80 mV) and extracellular spikes (bar, 0.5 ms); multiple oscilloscope sweeps superimposed. The temporal relationship demonstrates spike propagation towards the head ganglia. (D) On/off-responses to wind pulses given with different frequencies to the left (axon-ipsilateral) cercus. Each post-stimulus-time histogram was calculated for 60 wind pulses (2, 5, 7 and 10 Hz stimulus frequency, respectively, bottom to top; wind pulse duration, 50 ms; wind velocity, $0.5\,m\,s^{-1}$). (E) Relationship between frequency of wind pulses (abscissa) and number of spikes per stimulus (ordinate; open circles, stimulation of axon-ipsilateral cercus; filled circles, stimulation of axon-contralateral cercus; bars, standard deviations; $N=50$).

Fig. 2. Intracellular recording from the neurone shown in Fig. 1 during wind-evoked running. Neurophysiological and behavioural variables are plotted on a common time axis (bin width upper part, 80 ms; bin width lower part, 40 ms). The time segment marked below the upper spike recording (intracellular spike amplitude, 80 mV) is shown expanded in the bottom traces (top trace, spike frequency; second trace, rotational speed, upward deflections represent a turning tendency to the left side, downward to the right side; third and seventh traces, translational speed; fourth and eighth traces, intracellular recordings; fifth and ninth traces, extracellular recordings from the left neck connective; sixth and bottom traces, stimulus marker; wind pulses directed to the left cercus; 50 ms; 10 Hz; $0.5\,m\,s^{-1}$).

Physiology. The neurone shows irregular spontaneous spike activity in the range 2–5 Hz. The conduction velocity in the anterior direction is $1.38\pm0.1\,m\,s^{-1}$ ($N=7$; Fig. 4C). Wind stimuli evoke a phasic on/off-response (Fig. 4B). After an initial decline in responsiveness, there is little further habituation of the neuronal response to wind pulse trains, even during long-lasting series with high repetition rates. Like the other neurone described in the MSG, this cell also shows an augmented spike response to increasing wind pulse frequencies (Fig. 4D,E). There were no significant differences between responses to stimulation of the axon-ipsilateral or axon-contralateral cercus ($P>0.05$, two-tailed U-test). During spontaneous walking, the background activity and sensory responsiveness to wind stimuli are markedly reduced in this neurone. Again, the strength of spike suppression correlates with the walking speed but seems to be independent of the speed of intended rotation (see Fig. 6A,B).

During wind-evoked behaviour, spikes are completely suppressed during running. Spike suppression begins about 20–30 ms prior to the start of running, whereas in the standing phases strong spike discharges are observed (Fig. 5). Therefore, the timing of the spike discharge pattern resembles the timing of the behaviour. Although firing in this neurone is suppressed during running, the

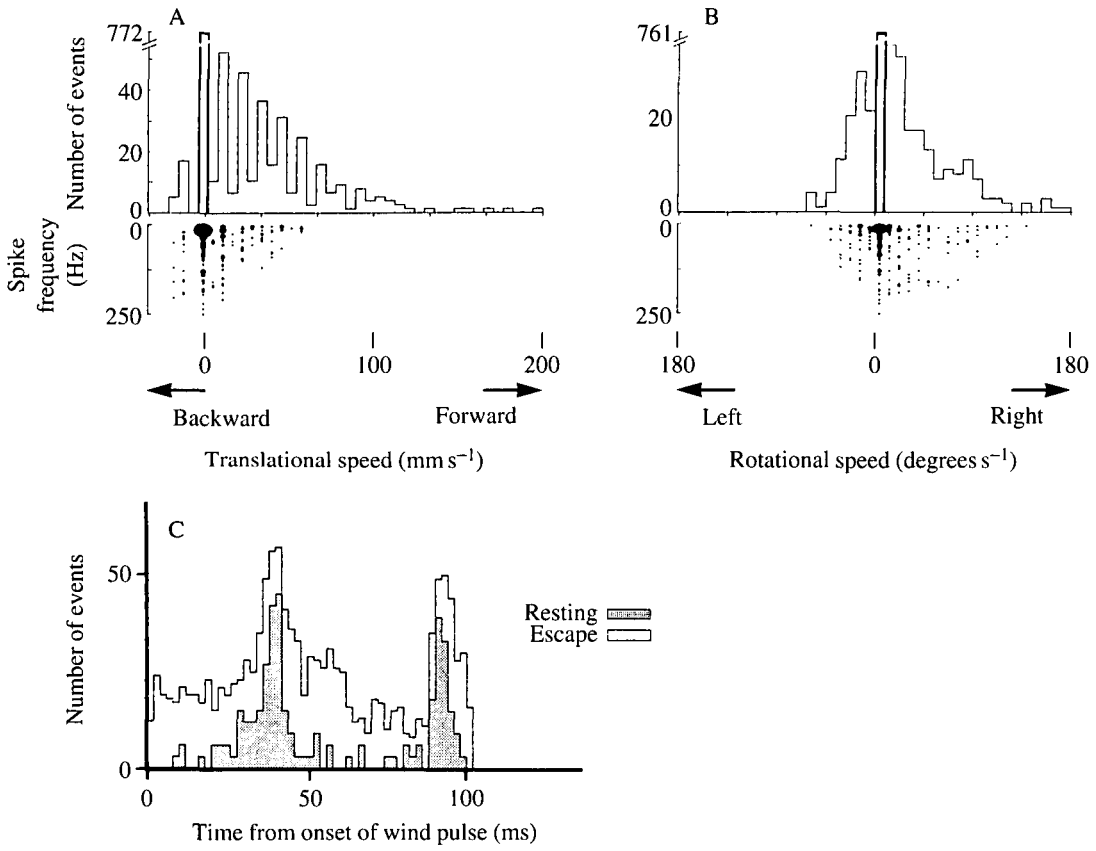

Fig. 3. Correlation between neuronal activity and walking behaviour for the neurone shown in Fig. 1. (A) Histogram of translational walking speed calculated from 210 s of spontaneous and wind-evoked locomotion and pauses (bin width, 200 ms). The discontinuous form of the histogram is caused by interference between the discrete linear resolution of the optical detector and the temporal measuring interval (see Gras and Hörner, 1992). The dots below the histogram indicate the spike frequency during a 200 ms interval of a given speed. The size of the dots corresponds to the number of occurrences of the same spike frequency in a given velocity class. During about two-thirds of the analysed period the animal stands still (the zero bin of the histogram); the occurrence of high spike frequencies in this histogram class is caused by reactions to wind stimuli. Above a translational walking speed of about 60 mm s^{-1} spike discharge is blocked. (B) Histogram of angular velocity and spike frequency displayed as in A. Spike discharge is maintained throughout the range of occurring angular velocities. (C) Comparison of sensory responsiveness to wind pulses (50 ms; 10 Hz; 0.5 m s^{-1}) during different behavioural conditions. The shaded bars show the neuronal response to wind stimulation in a resting animal (60 wind pulses) while the open bars (60 wind pulses with the same parameters) represent the responsiveness during pauses in wind-evoked walking behaviour. Note broken ordinate in A and B.

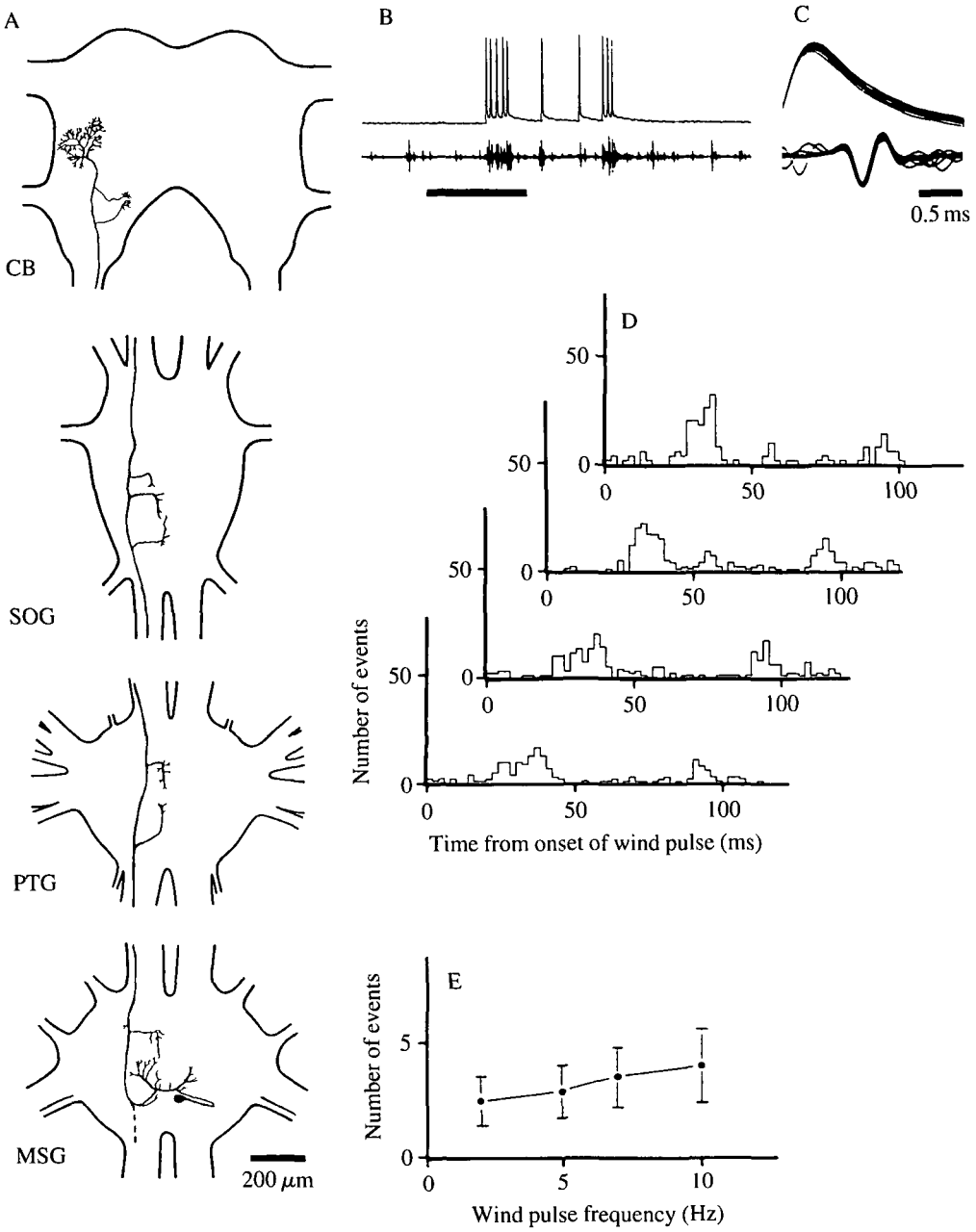

Fig. 4. Morphology and physiology of another intersegmental interneurone with its soma in the mesothoracic ganglion (for arrangement and further explanations, see Fig. 1). (A) *Camera lucida* reconstruction of this neurone in the thoracic and brain ganglia. (B) Response to wind stimulation (spike amplitude, 80 mV). (C) One-to-one correlation of the intracellular and extracellular spikes (bar, 0.5 ms). (D) On/off-responses to wind pulses given with different frequencies to the left (axon-ipsilateral) cercus. (E) Relationship between frequency of wind pulses (abscissa) and number of spikes (ordinate) per stimulus (bars, standard deviations, $N=60$).

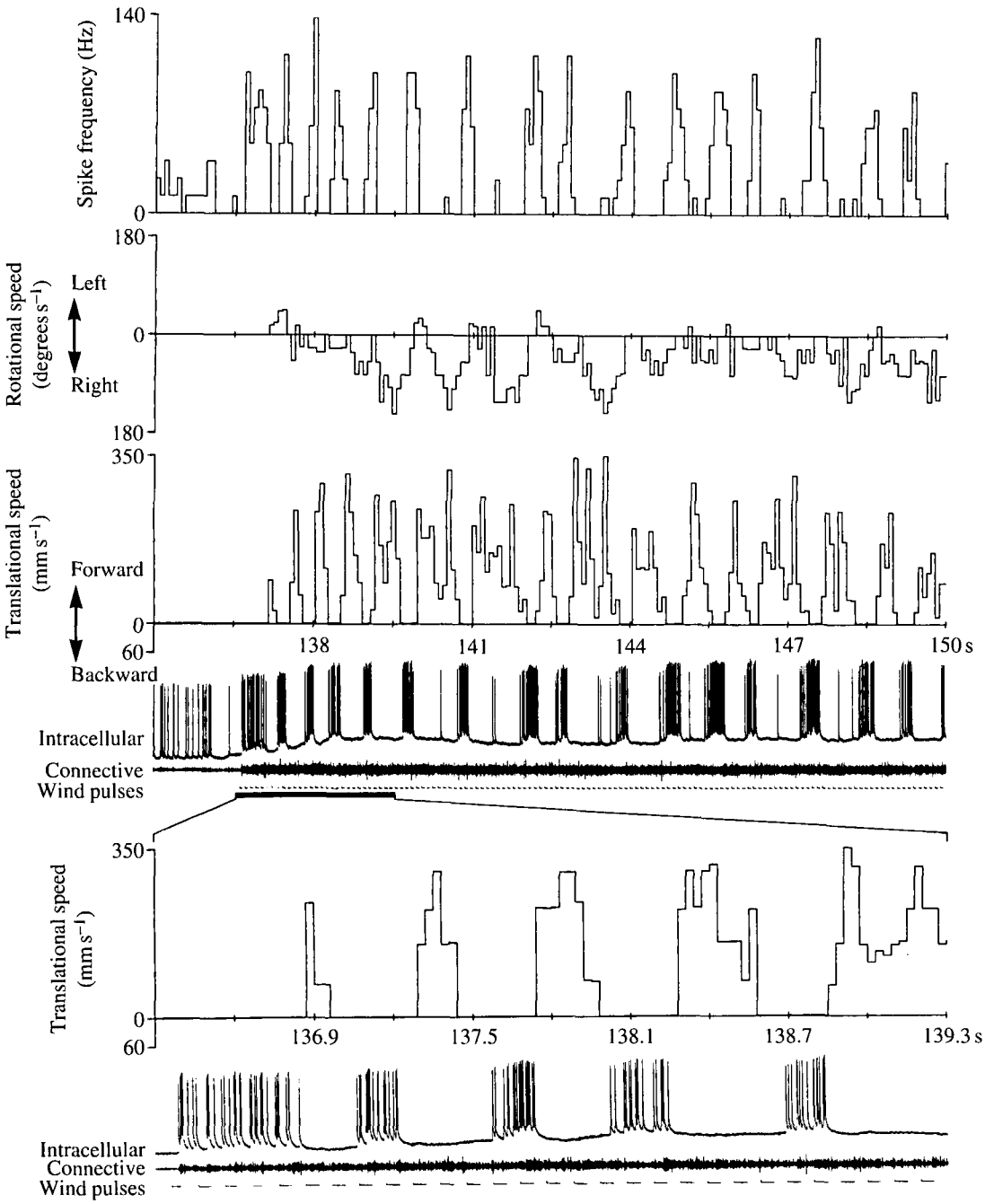

Fig. 5. Analysis of the response of the neurone shown in Fig. 4 during wind-evoked running, illustrating non-habituating high-frequency discharges during standing phases of wind-evoked escape behaviour (for arrangement and further explanation, see Fig. 2; amplitude of intracellular spikes, 80 mV; wind pulses directed to the left cercus; 50 ms; 10 Hz; 0.5 m s^{-1}).

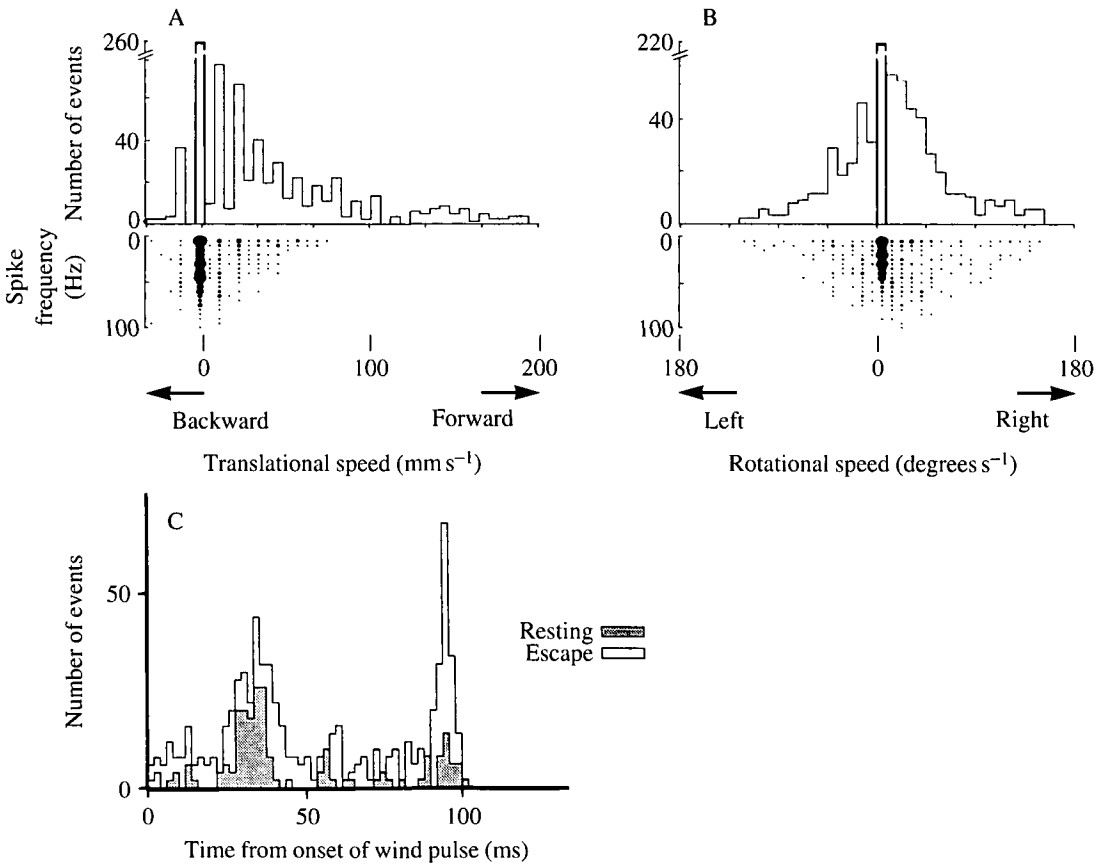

Fig. 6. Correlation between neuronal activity and walking behaviour for the neurone illustrated in Fig. 4 (for arrangement and further explanation, see Fig. 3). (A) Histogram of translational walking speed calculated from 140 s of spontaneous and wind-evoked locomotion and pauses (bin width, 200 ms). During about one-third of the analysed period the animal stands still (the zero bin of the histogram); the occurrence of high spike frequencies in this histogram class is caused by reactions to wind stimuli. Above a translational walking speed of about 60 mm s^{-1} spike discharge is blocked. (B) Histogram of angular velocity and spike frequency displayed as in A. (C) Comparison of sensory responsiveness to wind pulses (50 ms; 10 Hz; 0.5 m s^{-1}) during different behavioural conditions. The shaded bars show the neuronal response in a resting animal (70 wind pulses) while the open bars (70 wind pulses with same parameters) represent the responsiveness during standing phases of wind-evoked behaviour.

sensory responsiveness is enhanced during standing (Fig. 6C). As described above, the level of background activity is also increased in these standing phases.

Ascending interneurones with somata in the prothoracic ganglion

Morphology. Six wind-sensitive interneurones have been identified in the PTG. One example is shown in Fig. 7A. The dorsal soma is situated in the most posterior

region of the ganglion contralateral to its ascending axon in the LDT. Projections in the centre of the ganglion in the medioventral position are separated from the dorsolateral axonal collaterals.

Physiology. In this interneurone (Fig. 7A) no spontaneous activity is seen in the resting animal except for some occasional single spikes. The conduction velocity in the anterior direction is $1.1\,m\,s^{-1}$ (Fig. 7C). This interneurone shows a phasic–tonic reaction to wind stimulation (Figs 7B, 8C). Habituation of sensory responsiveness is slight, even during high-frequency stimulation.

During wind-evoked running, the neuronal activity reflects the time course of behaviour, with rhythmic spike suppression during fast running and high-frequency discharges during the standing phases (Fig. 7D). Spike suppression appears not to be correlated with the speed of rotation, because discharges also occur during intended turns of high velocity (Fig. 8A,B). Sensory responsiveness is markedly enhanced within the standing phases, as can be seen in the spike histograms. A comparison of the wind-evoked spike responses in the resting animal with those recorded during behaviour (Fig. 8C) reveals an increased reaction during the standing phases. Even after the termination of wind stimulation, spike discharges occur during pauses in walking, indicating that the spike-initiating mechanism does not depend exclusively on the external stimulation (Fig. 7D).

Descending interneurones

Because of incomplete stainings, brain cells could not be classified according to their soma position (see Williams, 1975). Unequivocal separation of brain and SOG neurones was nonetheless possible by tracing the stainings up to the connectives anterior to the SOG. Fibres conducting spikes posteriorly and passing through the SOG with no soma stained within the SOG or a thoracic ganglion were regarded as cells descending from the brain.

Descending interneurones with somata in the suboesophageal ganglion

Morphology. One type of SOG descending neurone with a ventral soma has been repeatedly recorded and stained (Fig. 9A). Two distinct projection fields are present in dorsolateral regions of the SOG. The axon (diameter, $8\,\mu m$) descends within the LDT to the thoracic ganglia, where it projects in the dorsal and ventral neuropiles. The axon leaves the metathoracic ganglion and travels to the abdominal ganglia at least, but it was not traced further.

Physiology. This neurone shows a rhythmic discharge pattern (0.7–0.9 Hz burst repetition rate) in the resting animal (Fig. 10A). To reveal the direction and speed of spike propagation, the recordings were replayed backwards since the extracellular spikes in the neck connective precede the intracellular spikes recorded in the PTG, which were used to trigger the oscilloscope. The conduction velocity is $0.72\pm0.08\,m\,s^{-1}$ ($N=5$; Fig. 9C). From visual inspection, the spike activity appears to be blocked in phase with ventilatory abdominal contractions (i.e. compression and lifting of the whole abdomen). This SOG neurone receives

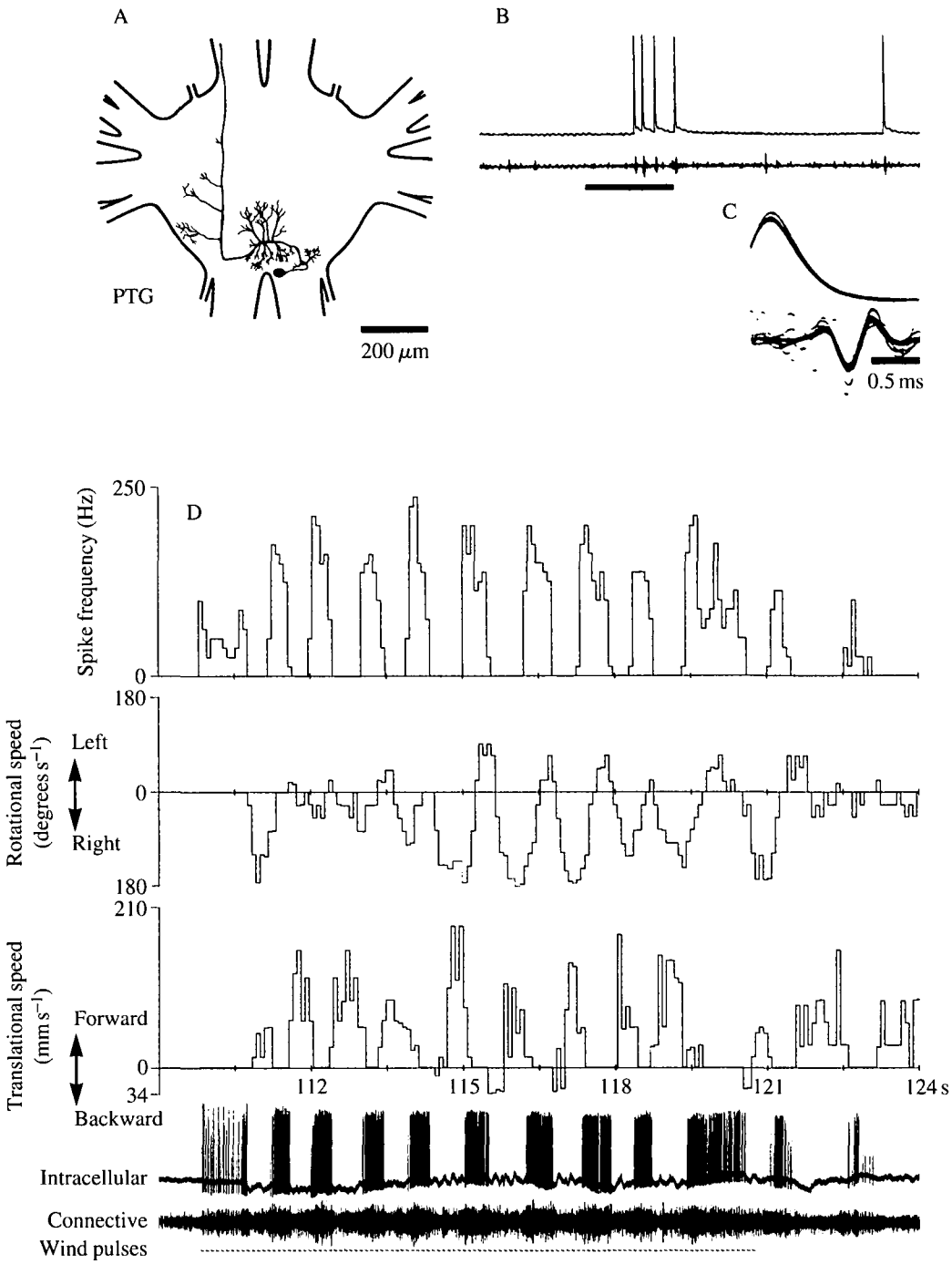
A
B
C
PTG
200 μm
0.5 ms
D
Spike frequency (Hz)
250
0
Rotational speed (degrees s⁻¹)
180
Left
0
Right
180
Translational speed (mm s⁻¹)
210
Forward
0
34
Backward
112
115
118
121
124 s
Intracellular
Connective
Wind pulses

Fig. 7

Fig. 7. Morphology and physiology of an intersegmental interneurone with its soma in the prothoracic ganglion. (A) *Camera lucida* reconstruction of this neurone. (B) Response to wind stimulation (top trace, intracellular recording; spike amplitude, 60 mV; middle trace, extracellular recording from the left neck connective; bottom trace, stimulus marker for a 50 ms wind pulse; 0.5 m s^{-1}). (C) One-to-one correlation between the intracellular (top trace) and extracellular spikes (bar, 0.5 ms). (D) Analysis of intracellular recording made during wind-evoked running (top trace, spike frequency; bin width, 80 ms; second trace, rotational speed; third trace, translational speed; fourth trace, intracellular recording; spike amplitude, 60 mV; fifth trace, extracellular recording from the left neck connective; bottom trace, stimulus marker; wind pulses directed to the left cercus; 50 ms; 10 Hz; 0.5 m s^{-1}).

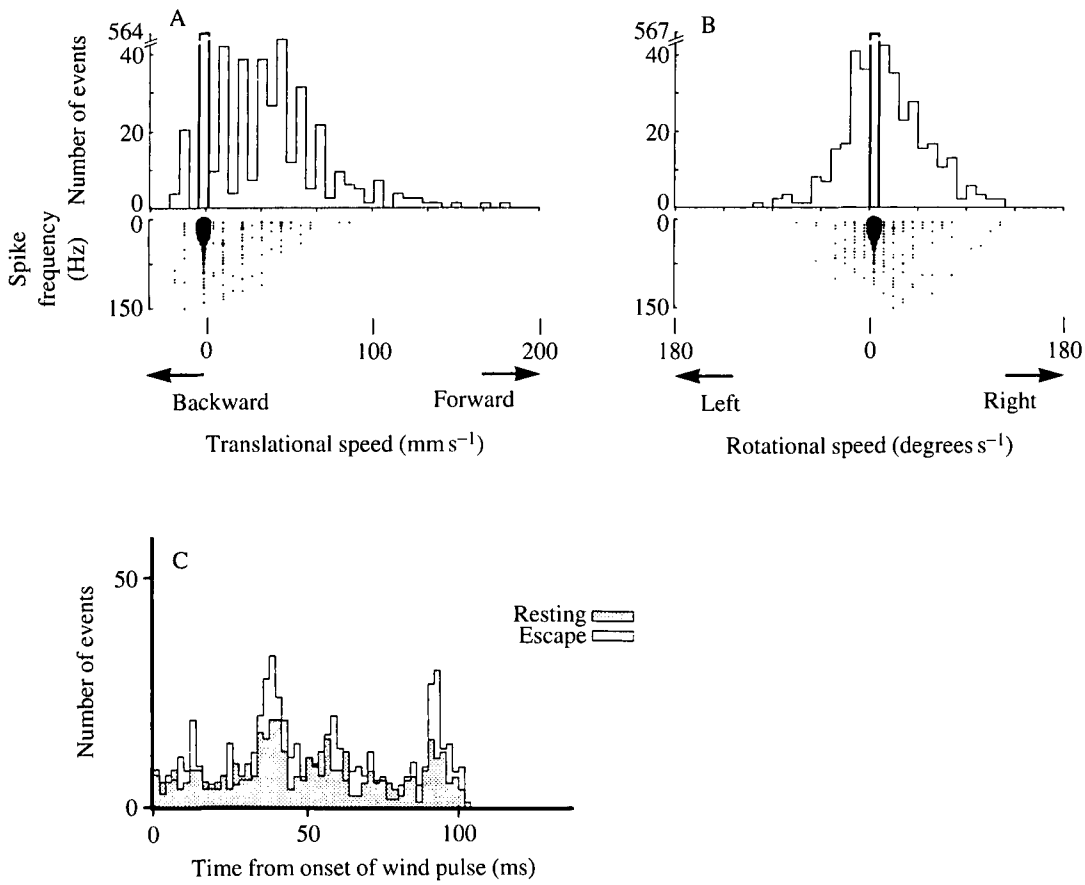

Fig. 8. Correlation between neuronal activity and walking behaviour. (A) Histogram of translational walking speed calculated from 172 s of spontaneous and wind-evoked locomotion and pauses (for further explanation, see Fig. 3). During about 60 % of the analysed period the animal stands still; the occurrence of high spike frequencies in this histogram class is caused by reactions to wind stimuli. Above a translational walking speed of about 70 mm s^{-1} spike discharge is blocked. (B) Histogram of angular velocity and spike frequency displayed as in A. (C) Comparison of sensory responsiveness to wind pulses (50 ms; 10 Hz; 0.5 m s^{-1}) during different behavioural conditions. The shaded bars show the neuronal response to wind stimulation in a resting animal (70 wind pulses) while the open bars (70 wind pulses with same parameters) represent the responsiveness during standing phases of wind-evoked behaviour.

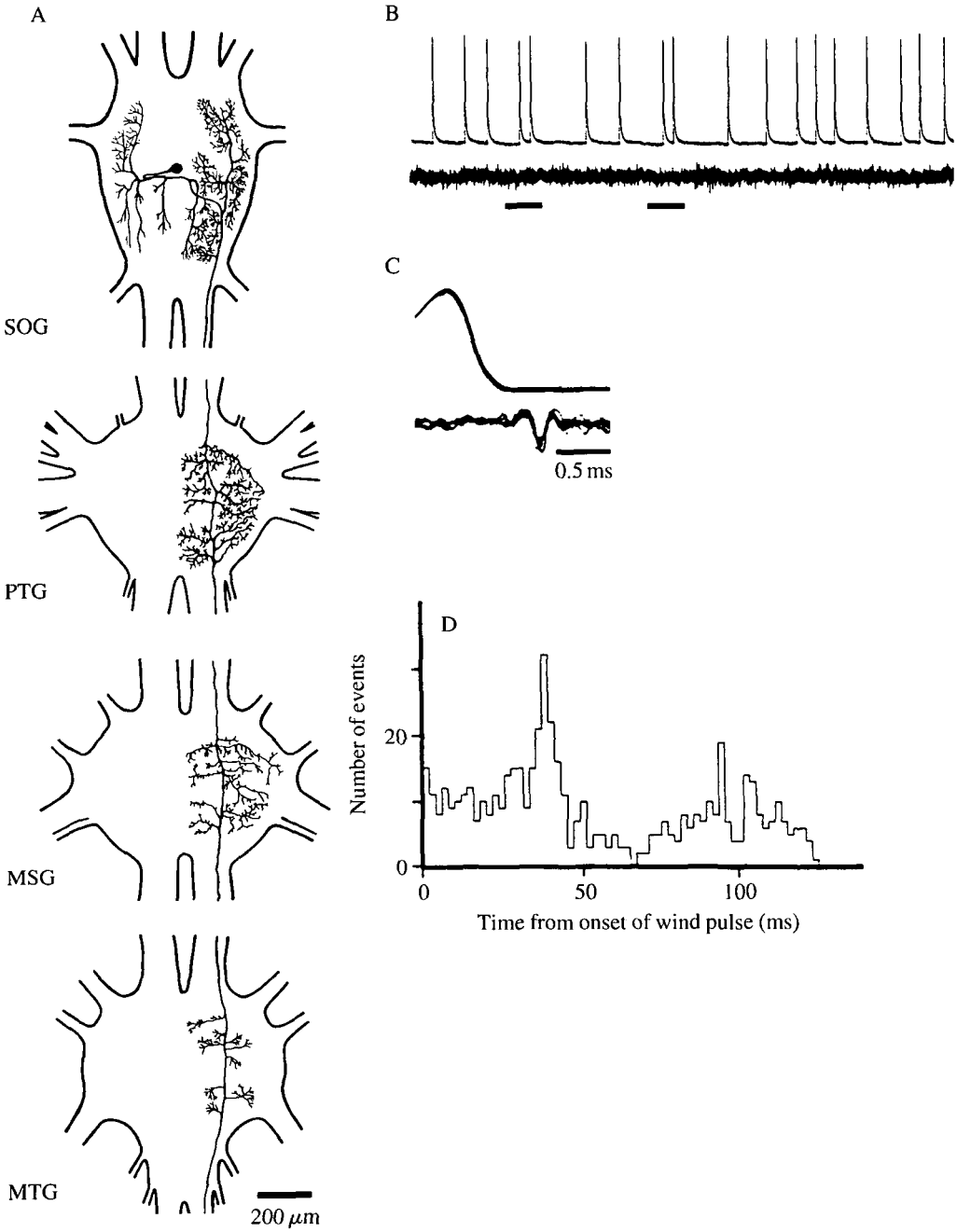

Fig. 9. For legend see p. 232.

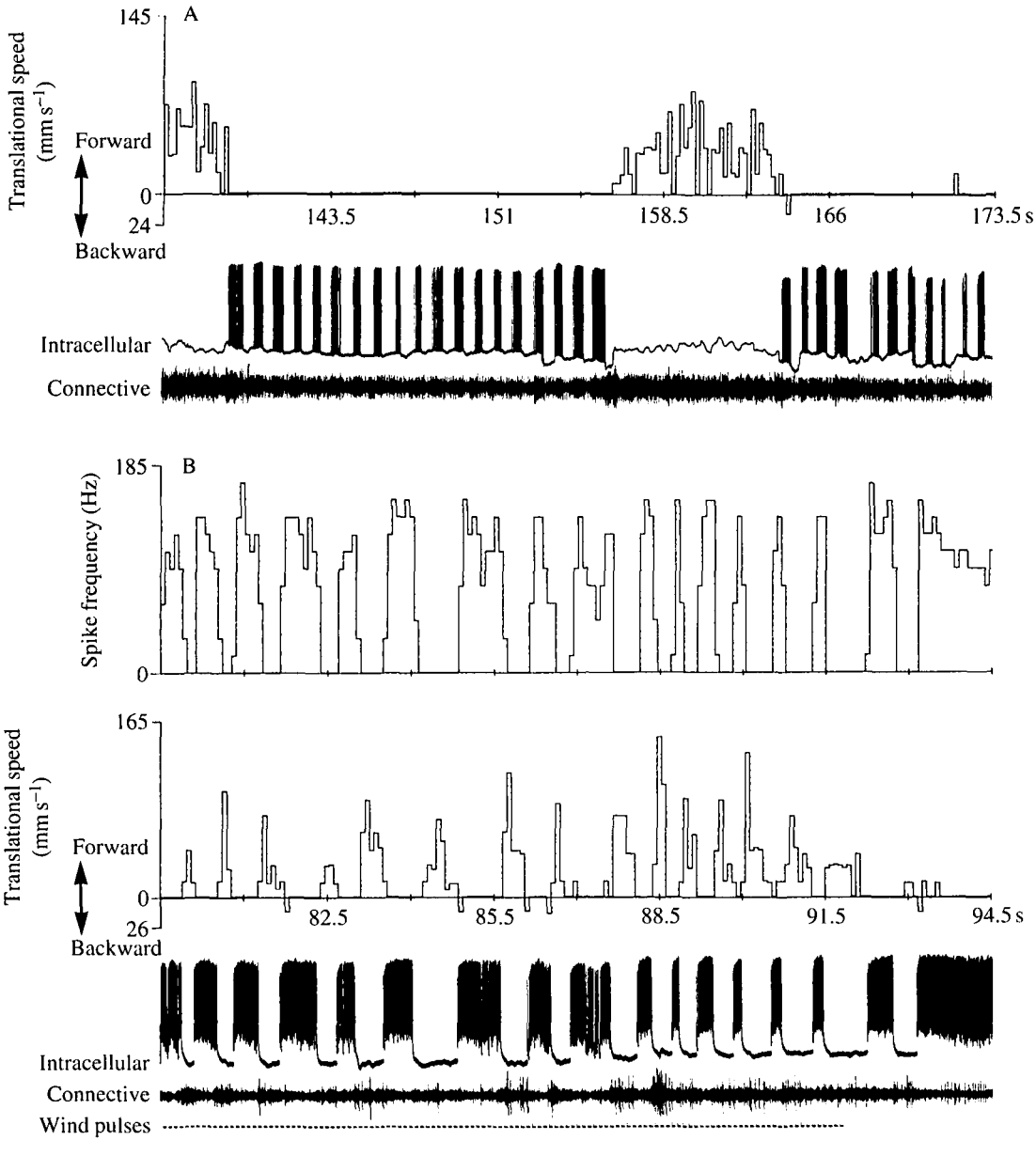

Fig. 10. For legend see p. 232.

multimodal input and reacts to sound stimuli and touching of the body surface or antennae. Its responses to wind stimulation are complex, having excitatory and inhibitory components (Fig. 9B,D). During walking, the spontaneous rhythm is tonically suppressed (Fig. 10A). At the end of a walking period, the rhythmic discharge pattern starts again, initially with an increased spike frequency (Fig. 10A,B).

Fig. 9. Morphology and physiology of an intersegmental interneurone with its soma in the suboesophageal ganglion. (A) *Camera lucida* reconstruction of the neurone in the suboesophageal, and pro-, meso- and metathoracic ganglia (top to bottom). (B) Response to wind stimulation presented during spike discharge phases. Intracellular recording from the axon within the PTG (top trace: spike amplitude, 70 mV) and recording of extracellular activity (middle trace) from the right neck connective (bottom trace: stimulus markers for two wind pulses; 50 ms; 0.5 m s^{-1}). (C) One-to-one correlation between the intracellular and extracellular spikes (bar, 0.5 ms; for identification of the extracellular correlate of the intracellular spike, the recording was replayed from the tape in the reverse direction). (D) The post-stimulus-time histogram shows the neuronal responses to 160 wind pulses directed to the right cercus (50 ms; 5 Hz; 0.5 m s^{-1}) given during rhythmically occurring phases of spike discharge.

Fig. 10. Intracellular recording from the interneurone shown in Fig. 9 during spontaneous and wind-evoked running. (A) Intracellularly recorded rhythmic spike discharge (spike amplitude, 70 mV) is interrupted during spontaneous walking episodes (top trace, translational speed; bin width, 180 ms; second trace, intracellular recording from the PTG; third trace, extracellular recording from the right neck connective). (B) Spike activity during wind-evoked behaviour (top trace, spike frequency; bin width, 80 ms; second trace, translational speed; third trace, intracellular recording from the PTG; fourth trace, extracellular recording from the right neck connective; bottom trace, stimulus marker; wind pulses directed to the right cercus; 50 ms; 10 Hz; 0.5 m s^{-1}).

During wind-evoked escape, SOG descending units of this type show – as do ascending neurones – phases of suppressed spike discharge coincident with fast running (Figs 10B, 11A,B). In contrast, spike bursts are present during standing phases. Interestingly, when escape behaviour has stopped after the termination of wind stimulation, a period of tonic spike activity is often observed until the rhythmic spike activity reappears (Fig. 10B).

Descending brain interneurones

Twenty-one interneurones descending from the brain have been characterized. Three types of descending brain neurones can be distinguished on the basis of their activity patterns during walking behaviour. The activity of brain neurones was correlated with the forward speed (N=6) or with the turning tendency (N=9) or showed no correlation with the existing walking behaviour (N=6).

Descending brain neurones with firing correlated to forward speed

Morphology. Six brain neurones whose firing correlated with forward speed have been recorded in the PTG. One example is shown in Fig. 12A. The axon (diameter, 7 μm) in the dorsal intermediate tract sends collaterals to mediolateral regions of the hemiganglion ipsilateral to the axon.

Physiology. No spontaneous spikes have been recorded from these neurones when animals were quiescent. The axonal spike conduction velocity in the posterior direction is 1.2 m s^{-1} (Fig. 12B). Wind and sound stimuli (16 kHz, 80 dB SPL) evoke weak and rapidly habituating responses. A tonic spike discharge

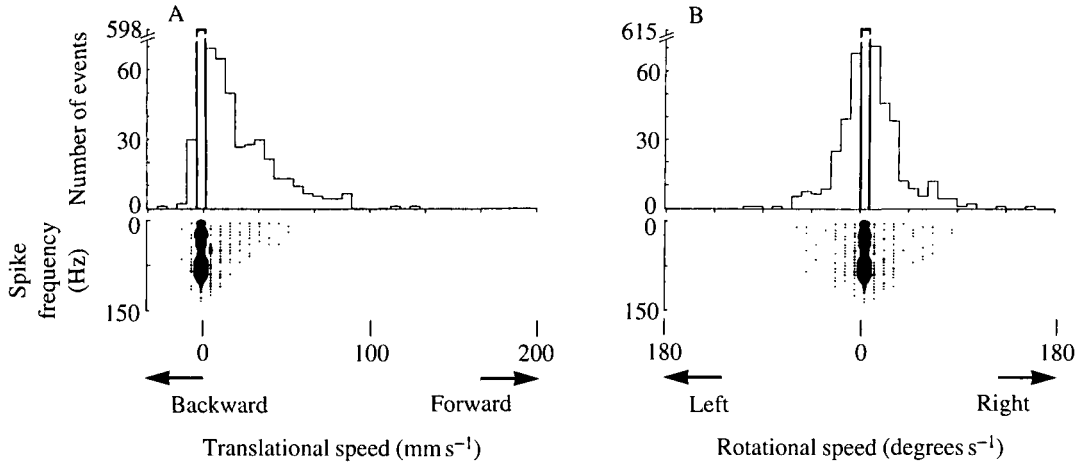

Fig. 11. Correlation between neuronal activity of the neurone shown in Fig. 9 and walking behaviour. (A) Histogram of translational walking speed calculated from 197 s of spontaneous and wind-evoked locomotion and pauses (bin width, 200 ms; for further explanation, see Fig. 3). During about 60 % of the analysed period the animal stands still (the zero bin of the histogram); the occurrence of high spike frequencies in this histogram class is caused by spontaneous rhythmic spike discharges (compare Fig. 10A). Above a translational walking speed of about 60 mm s^{-1} spike discharge is blocked. (B) Histogram of angular velocity and spike frequency displayed as in A.

begins 193±73 ms (N=15) prior to the start of each bout of walking (Fig. 12C). The neuronal activity during walking is positively correlated with forward speed (Fig. 12D). In contrast, no correlation is found between the spike frequency and the rotational speed of intended turns to either side (Fig. 12E). Neuronal discharges are in the range 20–30 Hz during spontaneous walking with a forward speed of 30–50 mm s^{-1}.

Descending brain neurones with firing correlated to intended turning

Morphology. Nine brain neurones whose firing correlated with intended turning have been recorded in the PTG. One example is shown in Fig. 13A. Its axon runs in the median dorsal tract and gives off several axonal collaterals, which project to the lateral margin of the ganglion in a medioventral position. A prominent axon collateral extends towards nerve 5.

Physiology. In the resting animal spike frequencies vary in the range 5–15 Hz (Fig. 13C). The spike conduction velocity in the posterior direction is 1.4 m s^{-1} (Fig. 13B). A significant increase in spike frequency is evoked by sound (16 kHz, 80 dB SPL) and wind stimuli. Sensory reactivity is weak and rapidly habituates.

During walking, the spike discharges are correlated with both the rotational speed and the direction of intended walking but are independent of the forward speed (Fig. 13D,E). Spike frequency increases prior to intended turns to the axon-ipsilateral side, whereas action potentials are suppressed during turns to the opposite side. There is a delay between changes in spike frequency and correlated

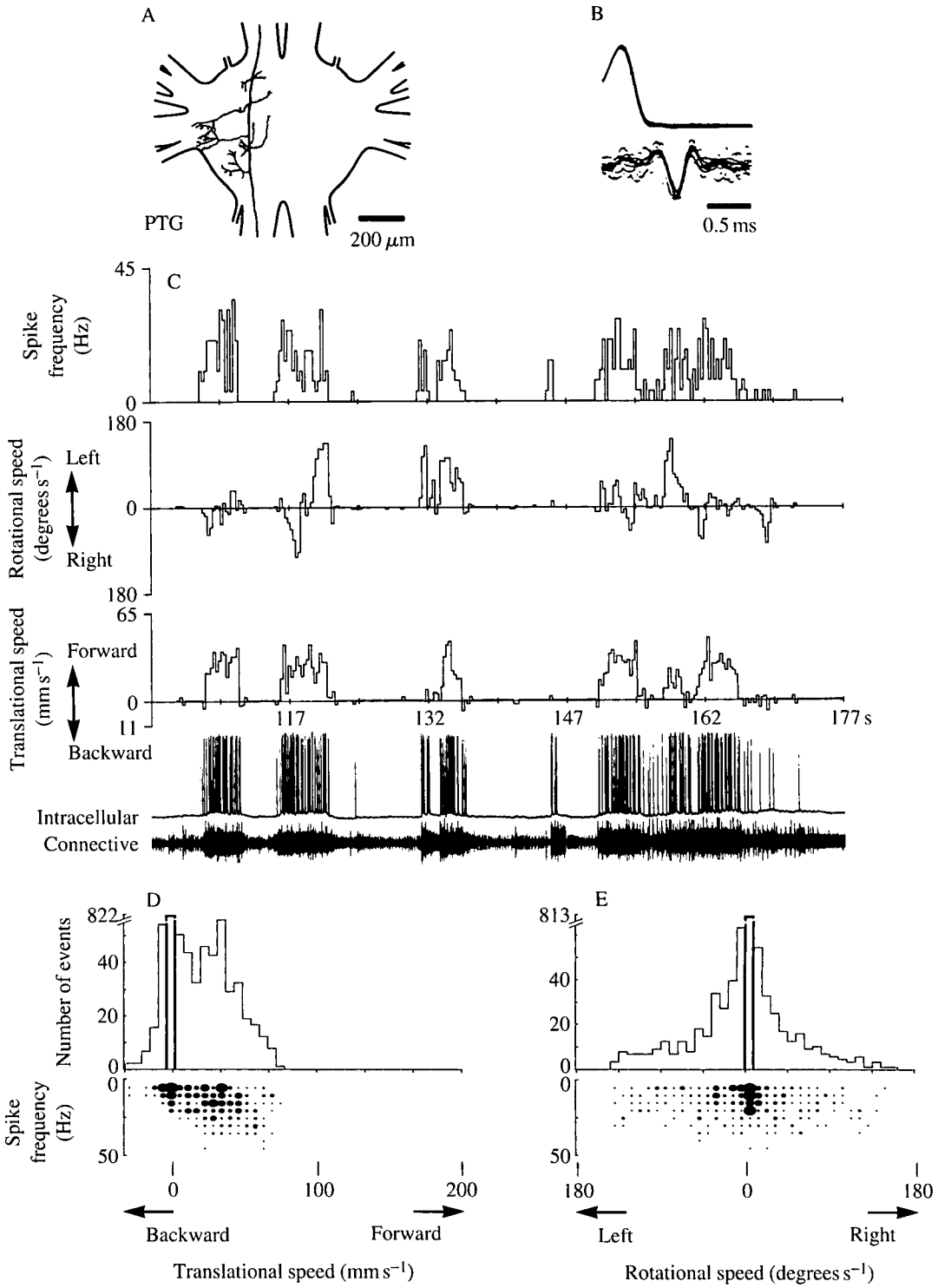

Fig. 12. For legend see p. 236.

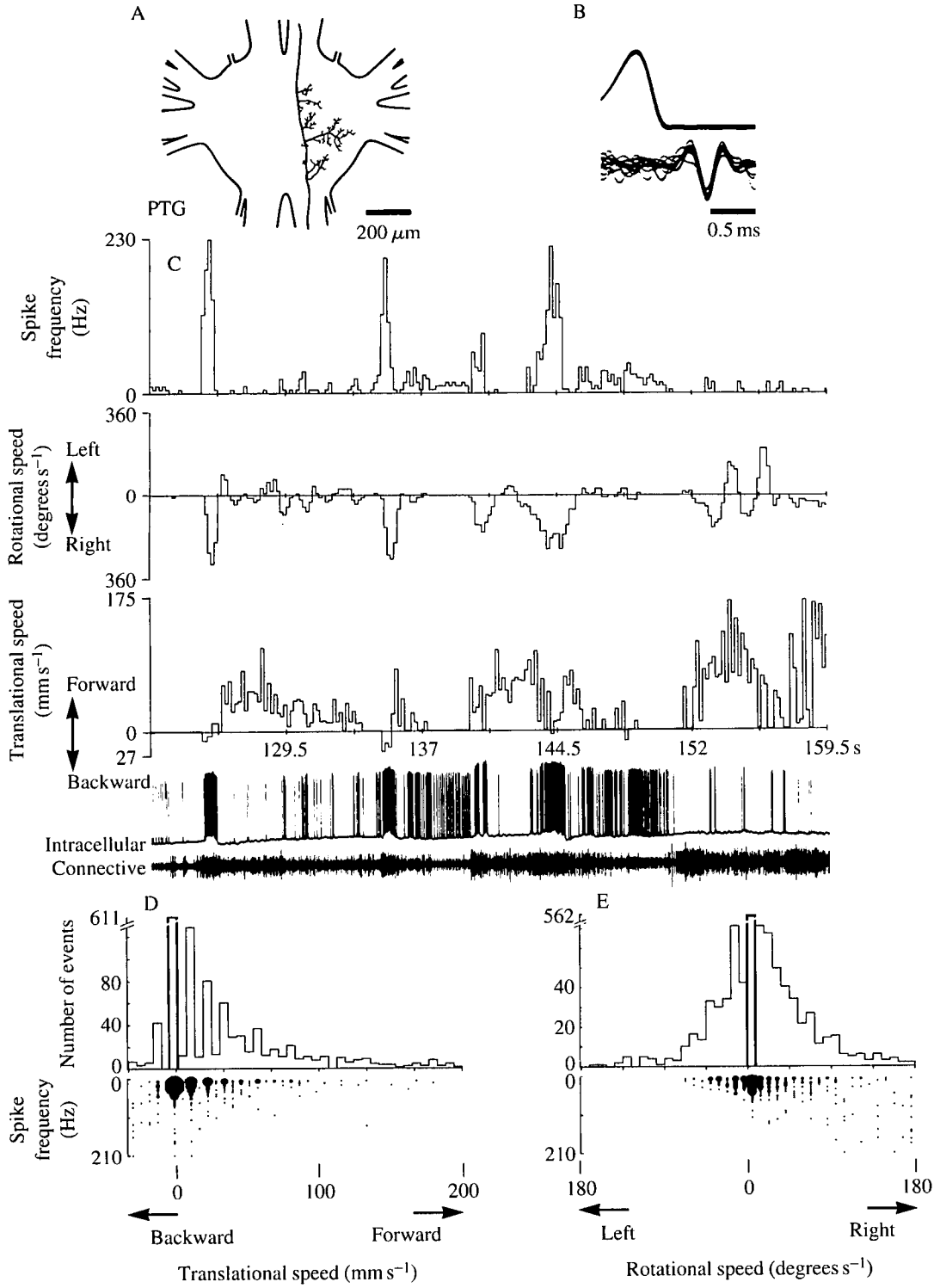

Fig. 13. For legend see p. 236.

Fig. 12. An intersegmental fibre whose firing was correlated with the forward walking speed. (A) *Camera lucida* reconstruction of the fibre running through the PTG. The axon was traced as far as the brain connective (not shown). (B) One-to-one correlation between the intracellular (top trace: spike amplitude, 70 mV) and extracellular spikes from the right connective (bar, 0.5 ms; see also caption to Fig. 9C). (C) Intracellular recording (spike amplitude, 70 mV) from the fibre shown in A during spontaneous walking (top trace, spike frequency; bin width, 280 ms; second trace, rotational speed; third trace, translational speed; fourth trace, intracellular recording from the PTG; bottom trace, extracellular recording from the left neck connective). (D) Histogram of translational walking speed calculated from 251 s of spontaneous locomotion and pauses (bin width, 200 ms; for further explanation, see Fig. 3). During about 60 % of the analysed period the animal stands still (the zero bin of the histogram); the occurrence of spikes in this histogram class is caused by neuronal activity preceding the start of walking behaviour (see text). Spike frequency increases as translational velocity increases. (E) Histogram of angular velocity and spike frequency displayed as in D.

Fig. 13. An intersegmental fibre whose firing was correlated with the turning speed and direction (for arrangement and further explanations, see Fig. 12). (A) *Camera lucida* reconstruction of the fibre morphology in the PTG. (B) One-to-one correlation between the intracellular (top trace: spike amplitude, 70 mV) and extracellular spikes from the right connective. (C) Intracellular recording from the fibre shown in A during spontaneous walking. (D) Histogram of translational walking speed calculated from 246 s of spontaneous locomotion and pauses (bin width, 200 ms; for further explanation, see Fig. 3). During about half of the analysed period the animal stands still (the zero bin of the histogram); the occurrence of spikes in this histogram class is mainly caused by background neuronal activity. Spike frequency is not correlated with increasing translational velocity. (E) Histogram of angular velocity and spike frequency displayed as in D. Although spike discharges are largely suppressed during intended turns to the left, spike frequency is increased with increasing angular velocities to the right (axon-ipsilateral) side.

changes in walking direction and speed of 151±65 ms (N=18). During escape behaviour, spiking was independent of the rhythmic changes in translational speed. Spike bursts correlated with the rotational speed occur exclusively during intended turns to the right (axon-ipsilateral) side. Particularly high spike frequencies are observed prior to intended turns to the axon-ipsilateral side that are accompanied by an additional backward component. These movements would cause a free-ranging animal to turn on the spot with only a little forward movement.

Discussion

In both this paper and Gras and Hörner (1992) a neuroethological approach is described which allows for the first time simultaneous measurement of oriented wind-evoked walking in combination with intracellular recordings from identified cells in the CNS of an insect (for a detailed discussion of the methods used for behavioural recording, see Gras and Hörner, 1992). Since the walking repertoire

Table 1. *Physiological properties of different neurone types in the central nervous system during rest and walking**

	Sensory response during		Activity pattern during	
Neurone type	Resting	Walking	Resting	Walking
Local within the PTG†	Weak, multimodal; summating to threshold excitatory/ inhibitory	Modulated (?)	Inactive; irregular subthreshold volleys	Spiking coupled to the step rhythm and intended turning tendency
Ascending from the PTG or MSG	Strong, bimodal (wind sound) non-habituating, partially direction-sensitive; excitatory	Velocity-dependent spike suppression; total spike block during running; enhanced response during standing phases of escape	Single, spontaneous spikes	Velocity-dependent spike suppression; excitation during standing phases; reflects the timing of escape running/standing
Descending from the SOG	Weak, multimodal; excitatory and inhibitory	Velocity-dependent suppression of spiking; total spike block during escape running bouts	Rhythmic in the frequency of abdominal expiratory contractions	Velocity-dependent spike suppression; excitation during post-walking and post-running standing phases
Descending from the brain	Weak, multimodal; strongly habituating; excitatory	Modulated; mostly decreased responsiveness, but no total response failure	Silent in case of units firing in relation to forward walking speed; regular spike activity in turning-specific units	Tonic excitation related to either forward speed or turning speed to one side (spike suppression during turning to opposite side)

* For comparison with another prothoracic cell type (dorsal unpaired median neurones), which has been studied in walking crickets, see Table 3 in Gras *et al.* 1990.

† See Gras and Hörner (1992).

PTG, prothoracic ganglion; MSG, mesothoracic ganglion; SOG, suboesophageal ganglion.

of crickets prepared for intracellular recordings differed only little from that of undissected tethered animals, the neuronal activity patterns recorded here during spontaneous or escape behaviour can be regarded as reflecting the information flow occurring in intact animals. Specific neuronal activity patterns can be described for different cell types in the thoracic ganglia, the SOG and the brain (Table 1).

Ascending interneurones

All recorded wind-sensitive neurones ascending from the PTG or MSG show similar velocity-dependent suppression of spike activity during walking. Sensory responsiveness persists at a reduced level during slow walking, but it is completely blocked during wind-evoked running bouts despite continuous wind-pulse stimulation and the unaltered position of the animal with respect to the stimulus (open-loop conditions).

Several modulatory effects have been described in the orthopteran cercal system, including synaptic and nonsynaptic, peripheral as well as central, mechanisms. Stimulation of the chordotonal organs at the base of the cerci (Bernard, 1987) inhibits spiking in cockroach giant fibres. Presynaptic inhibition plays a role in modulating the activity of neurones of the cercal system of cockroaches (Hue and Callec, 1983; Blagburn and Satelle, 1987), locusts (Boyan, 1988) and crickets (Levine and Murphey, 1980).

A central influence on the responsiveness of cercal afferent neurones during flight in cockroaches has also been reported (Libersat and Camhi, 1988). This decrease in sensory responsiveness has been attributed to the influence of central descending neurones on motor neurones that elicit movements of the cerci (Libersat *et al.* 1987). Cercal displacements have been shown partially to block the afferent information flow in the cercal nerve (Libersat *et al.* 1987). In crickets (Murphey and Palka, 1974; Schildberger *et al.* 1988) and cockroaches (Daley and Delcomyn, 1980*a*,*b*), both central and peripheral modulation of neuronal activity have been demonstrated during walking. It remains to be shown, however, whether movements of the cerci occur during walking in crickets and, if so, to what extent such movements contribute to the described modulatory effects on sensory responsiveness.

In contrast to the spike suppression seen in ascending neurones during walking, an increase in discharge frequency occurs after walking ends. This is most pronounced in the standing phases of wind-evoked behaviour. This increased activity cannot be attributed to the action of peripheral sense organs due to external stimulation since the animal is standing still. It seems more likely, therefore, that the observed increase in spiking represents a phase of rebound activity due to the release from spike suppression operative during the preceding walking phase.

The tonic character of activity changes in wind-sensitive thoracic neurones points to effects originating mainly centrally, since peripheral sensory cells usually show rhythmic spiking during rhythmic behaviour (Wendler, 1974; Hustert, 1985).

The observation that response modulations occur 20–40 ms prior to the start of walking and, thus, before peripheral sense organs receive any reafferent input, also suggests the influence of central neurones. One may speculate that the activity level in ascending thoracic interneurones is controlled by descending brain neurones, because the latter uniformly show tonic excitation during walking, which occurs well before the described effects are observed in ascending cells. However, influences from the periphery cannot be excluded.

Because recordings of subthreshold processes were beyond the scope of this study, it is not possible to determine at what level the observed modulatory effects are realized in the CNS. The observation that different cell types show identical effects at the same time points to an efferent control mechanism.

Cockroach thoracic interneurones with morphological characteristics similar to those of the cricket neurones presented here have been described by Ritzmann and Pollack (1988, 1990) and Ritzmann *et al.* (1991). These neurones receive inputs from giant fibres and excite leg motor neurones in different ganglia. Comparable actions of similar cricket cells seem likely, since their axon collaterals, which may be regarded as putative output sites (Pearson *et al.* 1985; Römer and Marquart, 1984), overlap with the dendrites of leg motor neurones (Hustert *et al.* 1981; Tyrer and Gregory, 1982). The uniform activity pattern of different ascending cells during walking suggests that there is a concerted action on thoracic motor centres. This influence is likely to be excitatory, since none of the large axon profiles in the LDT contains GABA (Spörhase-Eichmann *et al.* 1989), a transmitter known for its inhibitory postsynaptic actions (Watson and Burrows, 1987). Therefore, as has been proposed for the cockroach (Ritzmann and Pollack, 1988; Ritzmann *et al.* 1991), this group of ascending cells might belong to a parallel feedforward pathway coordinating motor neurone pools in different ganglia. However, owing to spike suppression during walking, these cricket neurones do not appear to control the behaviour directly, but they may predispose the motor centres for a walking command.

Spike suppression during behaviour has been demonstrated in many sensory systems (Murphey and Palka, 1974; Daley and Delcomyn 1980*a*,*b*; Heitler, 1983; Schildberger and Hörner, 1988; Wolf and von Helversen, 1986) and it has been suggested that it reduces saturation, especially in sensory systems involved in the control of escape behaviour (Bryan and Krasne, 1977). In the cricket, this mechanism might help to protect the responsiveness of ascending interneurones from habituation and to allow the temporal summation typically observed in this cell group. It has been shown in behavioural experiments that high wind pulse frequencies lead to a shortening of standing phases, and thus reduce the latency of wind-evoked running (Gras and Hörner, 1992). So, summation of sensory input may indeed be important for the release of escape behaviour in crickets. The reduction in sensory responsiveness observed in walking crickets might protect the animal from reafferent input from the cercal sense organs caused by the animals' own movements.

The modulation of sensory responsiveness according to the walking speed

allows continuous adaptation of the sensory threshold to the existing behaviour. The inevitable loss of continuous sensory information transfer in the group of ascending neurones studied here is probably of minor importance since the behaviour is reflex-like and would not require continous sensory control (Gras and Hörner, 1992).

Descending interneurones from the SOG

The SOG neurones identified in this study belong to one cell type. The observed switch from spontaneous bursting activity at the frequency of ventilatory pumping to the rhythm of escape running suggests that they participate in coordinating different rhythms in the CNS. An influence of the centrally generated ventilatory rhythm on activity patterns of various leg and wing motor neurones has been described in crickets and locusts (Bentley, 1969; Burrows, 1975*a*,*b*). It has been suggested that coupling between ventilatory pumping and flight activity produces an increased stiffness of the abdomen, which is required for rudder-like steering movements during flight (Ramirez and Pearson, 1989; Robert, 1989; Baader, 1990). A similar coordination of walking and ventilation mediated by the SOG neurones described here might establish the correct position of the abdomen, which has to be lifted from its resting position prior to and during locomotion.

The morphological and physiological features of the type of SOG neurone described here suggest that it is homologous to an identified cell type in the ventilatory system of *Gryllus campestris* that is active in phase with expiration (Otto and Janiszewski, 1989). Single-cell current injections showed that this interneurone has a direct influence on the ventilatory rhythm (Otto and Janiszewski, 1989). It has been shown that comparable SOG neurones not only control the rhythm of ventilation but are also involved in the initiation of behaviour by disinhibitory effects (Hedwig, 1986; Ramirez, 1988; Baader, 1990; Lins *et al.* 1991). The observation that walking occurs when the SOG neurones identified in the present study are silent is compatible with the hypothesis that these elements have an inhibitory influence on thoracic motor centres. The initiation of walking could thus be facilitated by disinhibition (i.e. suppressed spike activity during walking behaviour) mediated *via* the SOG descending units described here. In grasshoppers, SOG neurones comparable to those described in the cricket contain GABA (Lins *et al.* 1991).

Interneurones descending from the brain

The main difference between descending brain cells and all other neurones recorded in this study is that excitation in brain neurones does not simply reflect the timing of existing walking but it also contains information about the quality (i.e. speed or direction) of the intended walking (Table 1).

Descending brain units can be distinguished from each other by their activity: it is strictly related either to the forward speed or to intended turns. These findings point to a selective control of walking speed and walking course mediated by different sets of interneurones. Evaluation of long sequences of walking activity

and the spike discharge of descending brain neurones supports this view. Similar observations have been made in experiments concerned with the mechanism of flight steering: neurones with an influence on the direction of flight never changed the overall wingbeat frequency (i.e. flight speed; Reichert and Rowell, 1989; Thüring, 1986).

The capacity of descending brain neurones to control behaviour is also indicated by their responsiveness to high-frequency sound or/and wind pulses, which have been shown to influence oriented behaviour (negative phonotaxis: Nolen and Hoy, 1984; Brodfuehrer and Hoy, 1989; Robert, 1989; wind-evoked escape: Stabel *et al.* 1985; Gras and Hörner, 1992). Brain neurones recorded during walking all project to dorsomedial regions of the thoracic ganglia, where an influence on bifunctional flight and leg motor neurones could be exerted (Ramirez and Pearson, 1988). As demonstrated for other descending brain cells, only tonic activation patterns without any obvious correlation to the step rhythm were found. Therefore, as described in the flight system (Reichert *et al.* 1985) and probably also in the walking system, intercalated interneurones must connect descending cells to the motor neurones (Gras and Hörner, 1992). However, some direct connections from brain cells to motor neurones have been reported in orthopterans (Simmons, 1980; Tyrer, 1981; Rowell and Pearson, 1983).

Several morphologically different descending brain cells have been found which are active in a similar way during intended turns. All but one of these neurones have strictly ipsilateral projections and spontaneous spike discharges. Increased firing rates occur during turns to the side ipsilateral to the axon, whereas decreased spike activity (below the level of spontaneous activity) occurs when the animal turns in the opposite direction. It seems reasonable to assume, therefore, that the neural command for turns to one side implies an asymmetrical activity in the hemiganglia. Thus, walking seems to be controlled by a set of descending interneurones, each of which acts on a specific aspect of the existing behaviour, rather than by single command fibres. Similar conclusions have been drawn by Kien (1983, 1990) for locust walking.

Despite the limited number of recordings made from walking animals, there is evidence for specific discharge patterns in different thoracic and cephalic neurone types (Table 1). Based on these findings, walking behaviour seems to be controlled by parallel distributed pathways consisting of specialized neurone types located in different ganglia.

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