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The processing of directional vibratory signals in the ventral nerve cord of *Locusta migratoria*

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Summary. The ability of ventral cord neurons to code the direction of a vibration source was tested.

The vibration receptors in all six legs were stimulated simultaneously or successively (i.e. with a time delay between stimulation of several leg pairs) in order to simulate vibration signals coming from ahead or behind the animal.

Three groups of vibration sensitive neurons were investigated by extracellular recordings:

1. Bimodal vibro-acoustic ventral cord neurons ascending to the brain (VS-neurons). The response patterns of these neurons to vibrational stimulation does not significantly change, when the stimuli are presented simultaneously or successively. The effectiveness of the inputs from the several legs is remarkably different, however. Ipsilateral stimulation is more effective than a contralateral one; the influence of mid- and hindlegs is greater than that from the forelegs.

2. Vibratory ventral cord neurons ascending to the brain (V-neurons). If the different leg pairs are stimulated successively with vibration signals, some of these V-neurons show significant changes in their responses which depend on the direction and the time delay of the presented stimuli.

3. Vibratory interneurons restricted to the thoracic nerve cord. In these neurons (which connect the thoracic ganglia), the influence of the receptors of only one leg pair is dominant. Vibratory stimulation of other leg pairs does not alter the responses of these interneurons.

Abbreviations: fl forelegs; *ml* midlegs; *hl* hindlegs

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Introduction

The substrate is used by many arthropod species as an exclusive or additional medium for sound communication (Michelsen et al. 1982; Markl 1983; Kalmring 1983). The spatial localization of prey, predator or sexual partner by means of vibratory signals plays an important role in the animals' life. Behavioural experiments in backswimmers (Murphey 1973; Wiese 1974), scorpions (Brownell and Farley 1979) and spiders (Hergenröder and Barth 1983) have shown that the direction of a vibration source can be detected by means of the spatially distributed vibroreceptors in the different legs and the underlying neuronal network. The proposed models derived by behavioural tests in these three arthropod groups, have in common the fact that the basis of vibratory directionality detection is ipsi- and contralateral inhibition between sensory inputs at the level of the central nervous system. Such information processing may cause, in a single central neuron or in a group of them, a response pattern which changes with the direction of the vibratory stimuli. Such investigations have not yet been carried out in arthropods at the level of single neurons.

In the acridid and tettigoniid species investigated to date, the different vibratory receptors of the six legs and the acoustic receptors of the tympanal organs converge, at the level of the ventral nerve cord, on the same neurons ascending to the brain. They are bimodal vibratory-acoustic neurons (Čokl et al. 1977).

Grasshoppers and bush crickets produce substrate-borne sound when they stridulate; it is transmitted preferentially via the legs and the abdomen to the stems of the plants on which they sit or

to the ground. Bending waves and surface waves seem to be the most important signals for intraspecific communication (Michelsen et al. 1982; Markl 1983; Keuper and Kühne 1983). In woody plants, such vibratory waves can be detected by the receiver at distances up to 2 m from the emitter. Phonotactic behavioural experiments on *Tettigonia cantans* have shown that such vibratory signals are used to orientate to stridulating males within dense bushes. Females and males of *Tettigonia cantans* find the emitter more easily and more quickly when airborne sound and vibratory stimuli are presented simultaneously (Latimer and Schatral 1983).

One unsolved problem is how the grasshoppers are able to determine the direction of such vibration signals. One possibility is that the receptors of the different legs are stimulated at different times by the propagated vibratory signals. Excitatory and inhibitory interactions from the vibratory receptors of the different legs could then lead to the determination of the propagation direction of the substrate-borne sound signals. Determination of the direction of propagated signals by a gradient of intensity is another, or additional, possibility but this is a very difficult procedure because of the various kinds of signal interferences that occur in the substrate. A third possibility for grasshoppers living in bushes, may be the frequency modulation of the vibratory signal due to the different frequency dependent velocities of the bending waves.

As a first step in determining the mechanism of vibratory directionality processing at the thoracic ventral nerve cord level, we have investigated the response pattern of the different vibratory and vibratory/sound bifunctional interneurons stimulated by vibratory stimuli reaching the experimental animal from ahead or from behind. *Locusta migratoria* was chosen as the experimental animal because of its well-known receptor systems and the central neurons which process the 'sound' information detected by the tympanal organ and/or the vibrational receptor organs in all six legs (Kalmring 1975; Čokl et al. 1977; Kühne 1982a, b).

Materials and methods

Experiments were performed on a total of 83 male and female imagines of the migratory locust *Locusta migratoria*.

After removal of the wings and antennae the animals were waxed dorsal side down to a metal holder. The connectives between the pro- and mesothoracic ganglia were exposed ventrally. The legs, in different combinations, were fastened with wax to 10 cm long rods attached to the oscillating plates of two vibrators (Brüel & Kjaer Minishaker 4810). The two rods were positioned ahead and behind the animal about 1 cm above the animal and at an angle of 45° to the vertical plane. The position of the legs with respect to the body was as natural as possible.

The vibratory receptors of the different legs were stimulated by sinusoidal vibrations provided by the two minishakers driven by two separate sine-wave generators (Burchard AS II). The oscillations of the vibrated rods, i.e. the movement of the tarsi, were monitored by means of an accelerometer (Brüel & Kjaer 8307 coupled to a charge amplifier Brüel & Kjaer 2635). The measured accelerations of the stimuli showed neither onset distortions nor resonances and were linear within the frequency range used. The vibration stimuli were oscillations at frequencies between 50 and 1000 Hz of different acceleration peak values (0.02–4.0 m/s^2) and standard time parameters (20 or 100 ms duration, repetition rate 2/s). The parameters of the stimuli could be chosen independently, or both vibrators could be coupled in such a way that they produced stimuli of the same frequency, intensity and time characteristics and with or without one being delayed relative to the other.

For identification, the neurons were tested by a standard stimulation program of vibratory stimuli at various frequencies and intensities applied to each leg pair alone and then simultaneously to all leg pairs at the vibrators. Additionally, the reaction to airborne sound was tested in each case with white noise via a high frequency loudspeaker (sound intensity between 40 to 76 dB SPL, duration 20 and 100 ms, repetition rate 2/s).

In order to simulate the natural stimulation conditions of a vibratory wave travelling through the substrate from ahead or behind the animal we stimulated the different leg pairs with identical vibration pulses of 20 ms duration with certain time differences between the stimuli. The delays were between 1 and 20 ms. We chose the following combinations of separate stimulation of leg pairs with the two stimulators:

a) forelegs (Vibrator I) versus midlegs (Vibrator II);
b) forelegs (Vibrator I) versus mid- and hindlegs (Vibrator II), and
c) fore- and midlegs (Vibrator I) versus hindlegs (Vibrator II).

The responses of 120 vibratory central neurons were recorded extracellularly with glass micropipettes filled with 3 mol/l KCl or 3 mol/l $CoCl_2$ (tip resistances between 20 and 30 MΩ). The latter electrolyte permitted staining of the neurons by use of a combined recording and staining technique in combination with the silver intensification method (Rehbein et al. 1974; Bacon and Altman 1977). Action potentials were amplified (WPI VF-1, Tektronix AM 502), displayed on an oscilloscope (Tektronix 5112), photographed (Tönnies Recordine) on 30 mm film and stored on a cassette tape. Post-stimulus-time histograms were made from replayed responses to 20 successive identical stimuli using a computer program on a Z-80 microprocessor system.

Results

The vibrational directionality was tested in three groups of ventral cord vibratory neurons:

I. VS-neurons ascending to the supraesophageal ganglion: These are bimodal vibratory-auditory neurons, which respond to both vibration and airborne-sound stimuli with action potentials.

II. V-neurons ascending to the supraesophageal ganglion: These neurons respond preferentially to vibration stimuli, but also are always influenced by the tympanal acoustic receptors.

III. V-neurons restricted to the thoracic ventral nerve cord: These vibratory interneurons show responses to vibrational stimulation of, in most cases, only one leg pair.

I. VS-neurons: 24 neurons of this group were tested. 19 neurons could be clearly identified by their response characteristics into VS_2, VS_3 and VS_4 types (for classification see Kühne 1982b). Another 5 neurons of the group could not be classified and are described as a special group of VS-neurons.

The vibratory inputs from mid- and/or hindlegs are dominant in all the VS-neuron types; vibratory stimulation of these legs evokes stronger responses with shorter latencies (around 10 ms difference) compared with those obtained by foreleg stimulation. Broad-banded responses with high or low frequency dominance are typical.

a. VS_2-neurons (also known as G-neurons from airborne sound stimulation; Kalmring 1975) receive vibratory inputs from different vibratory receptors of all six legs with dominant input from the ipsilateral midleg. Additional stimulation of the other legs normally enhances the vibrational response (Čokl et al. 1977). Response latency to midleg stimulation is around 20 ms; the response to foreleg stimulation is weaker with latencies of 30–40 ms. The vibratory responses are broad-banded with low frequency dominance.

As expected by previous results, the simultaneous stimulation of fore- and midlegs enhances the responses compared with midleg stimulation alone (Fig. 1 A, dashed curve and white column). The response shows no significant differences if the forelegs are stimulated before or after the midlegs (delay range up to 10 ms).

b. VS_3-neurons (formerly described as C-neurons) respond tonically to airborne as well as to substrate borne stimuli (Kalmring and Kühne 1980). This neuronal type is represented by several neurons on each side of the ventral cord. In each case the vibratory inputs from the forelegs are weaker and have longer response latencies compared with the responses to mid- and combined mid-/hindleg stimulation. Broad-band vibratory neurons of this type preferentially respond to higher stimulus frequencies. The sensory input from the hindlegs is restricted to frequencies between 500 and 1000 Hz.

An example of midleg dominance is shown in the Fig. 1 A insets: midleg stimulation (ml) evokes 3 spikes per 20 ms stimulus with a latency of 20 ms. In contrast stimulation of the forelegs (fl) evokes only 1 spike per 20 ms stimulus with a response

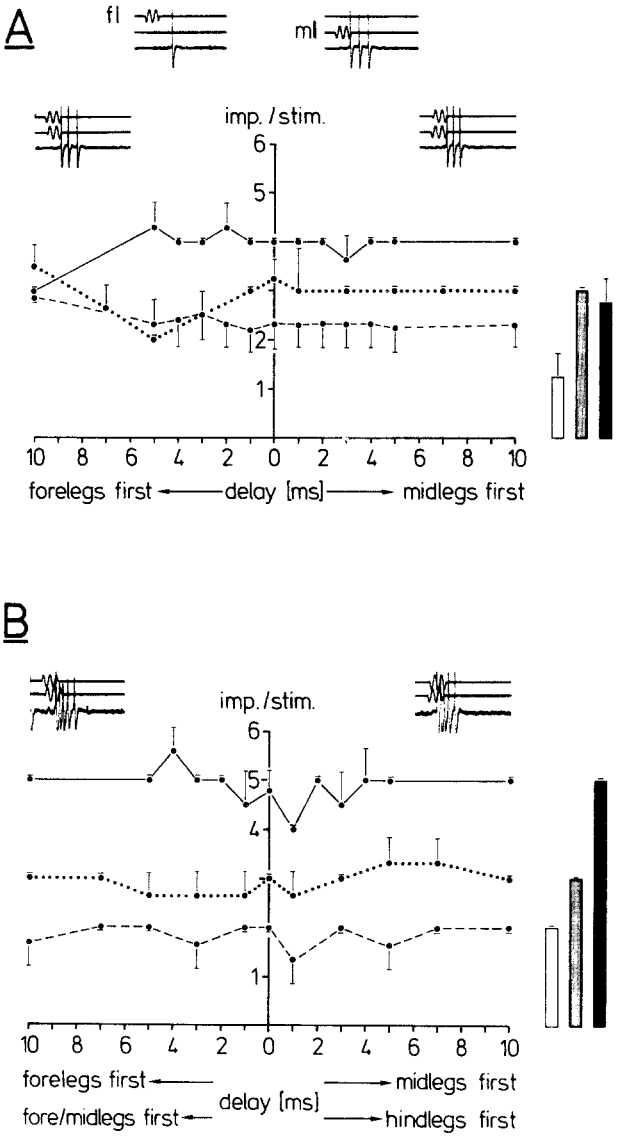

Fig. 1 A, B. Responses of different VS-neurons to vibration stimuli presented to two or three leg pairs. Reactions to simultaneous stimulation of two different leg pairs and stimulation with delays between them are shown in the diagrams. Indicated on the abscissa is the succession and time difference of stimulation of the several leg pairs, 0 ms delay means simultaneous stimulation. **A** Response characteristics of a VS_4 (●—●), VS_3 (●···●) and VS_2 (●---●) neuron to stimulation of forelegs versus midlegs. The columns indicate the neuron's responses to midleg stimulation alone (VS_4 black, VS_3 grey, VS_2 white). The recordings at the top show responses of VS_3-neuron to stimulation of forelegs alone (fl) and midlegs alone (ml); lower recordings of the VS_3-neuron are according to the 3 ms-delays in the dotted curve. Frequency 100 Hz, duration 20 ms, acceleration 3.8 m/s^2, repetition rate 2/s. **B** Response characteristics of two other VS-neurons. Neuron 1 (●—●) forelegs tested versus midlegs; black column; reaction to midleg stimulation alone. Insets: reactions of the neuron at 5 ms-delays. Frequency 100 Hz, duration 20 ms, acceleration 3.8 m/s^2. The reactions of neuron 2 to stimulation of fore- and midlegs versus hindlegs are shown at stimulation acceleration of 3.8 m/s^2 (●···●, grey column stimulation of hindlegs alone) and 0.38 m/s^2 (●---●, white column). Frequency 500 Hz, duration 20 ms

latency of 40 ms. Simultaneous stimulation of both fore- and midlegs gives again the response of 3 spikes per stimulus with an increased repetition rate of spikes but at same response latency (Fig. 1 A insets and dotted curve). When the forelegs are stimulated before the midlegs the response is significantly reduced in the delay range between 3 and 5 ms. In the opposite case (midlegs stimulated before forelegs) the response remains unchanged up to the 10 ms delay.

c. VS_4-neurons, formerly described as K-neurons, react to airborne or substrate-borne sound stimuli with on-burst responses when the stimulus duration is greater than 20 ms.

Vibratory input from midlegs dominates as in other VS-neurons; generally it is broad-banded with slight dominance of the higher frequencies. Simultaneous stimulation of the fore- and midlegs enhances the response compared with the response to midleg stimulation alone (Fig. 1 A solid curve and black column). Successive stimulation of both leg pairs exhibits no significant change in response pattern and strength except when the forelegs are stimulated before the midlegs with a time difference of more than 5 ms: the response is reduced under such stimulation conditions.

d. Some other VS-neurons that react well to vibrational stimulation show only weak responses to airborne sound stimuli. Their common feature is a high degree of spontaneous activity. The vibratory input from the midlegs dominates and produces a tonic response in the suprathreshold intensity and in the broad-band frequency range. The vibratory input from the hindlegs is restricted to higher frequencies. Successive stimulation of different leg pairs evokes no significant change in their responses compared with that obtained by simultaneous stimulation of all the legs (Fig. 1 B). A small reduction of responses was detected only when mid- and hindlegs were vibrated 1 ms before the forelegs (Fig. 1 B, both neurons). Simultaneous stimulation of all the legs evokes, in neuron 1, the same response as that to midleg stimulation alone and, in neuron 2, a response equal to that obtained by hindleg stimulation (Fig. 1 B, columns and response values at the time delay of 0 ms).

II. V-neurons ascending to the supraesophageal ganglion have been described as V_1, V_2, V_3... -neurons by Kühne (1982b). They can be divided into two groups, depending on the legs providing the dominant vibratory input. The representatives of the first group are mostly influenced by inputs from the forelegs and those of the second group give strongest responses to stimulation of the mid- and hindlegs. Altogether 28 different neurons of both groups were fully tested.

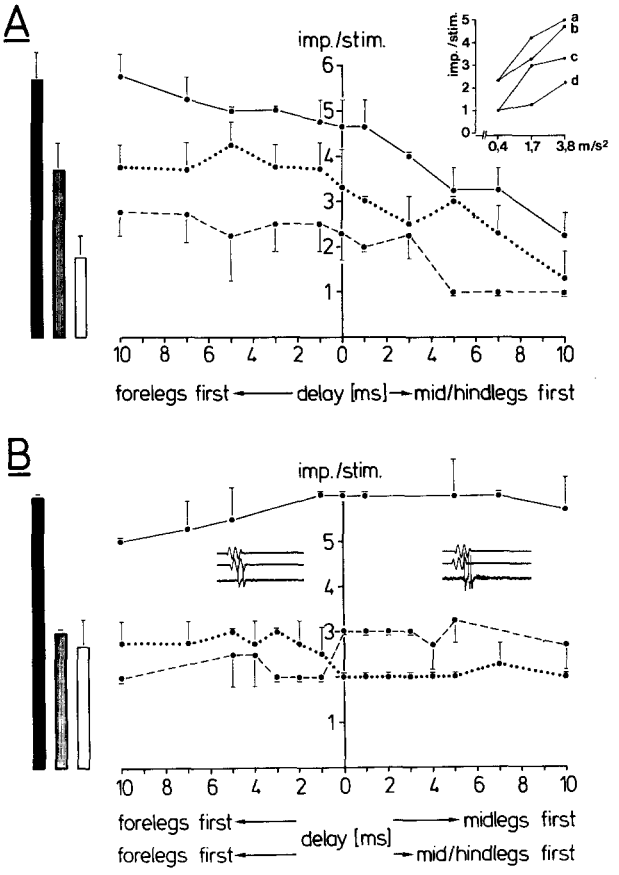

Fig. 2 A, B. Responses of different V-neurons to vibration stimuli presented to different leg pairs. Diagrams as in Fig. 1. **A** Response characteristics of one V-neuron with foreleg dominance to stimulation of forelegs versus mid- and hindlegs at accelerations of 3.8 m/s² (●——●, black column forelegs alone), 1.7 m/s² (●···●, grey column), 0.38 m/s² (●---●, white column). Inset: response-intensity characteristics of this neuron at different delays: *a* 5 ms forelegs first, *b* no delay, *c* 5 ms mid- and hindlegs first, *d* 10 ms mid- and hindlegs first. Frequency 100 Hz, duration 20 ms. **B** Response characteristics of three different V_3-neurons: neuron 1 (●——●, black column), stimulation of forelegs vs mid- and hindlegs; neuron 2 (●···●, grey column), stimulation of forelegs versus mid- and hindlegs; neuron 3 (●---●, white column), stimulation of forelegs versus midlegs. Insets: recordings of neuron 3 according to the 5 ms-delays. Frequency 100 Hz, duration 20 ms, acceleration 3.8 m/s²

a. V-neurons with clear foreleg dominance: the responses of most neurons of this group depend significantly on whether simultaneous or successive stimulation of different leg pairs is used. In most of the tested neurons an enhancement of the response was observed if the forelegs were stimulated before the rest of the leg pairs; a response reduction occurred if the mid- and/or hindlegs were vibrated before the forelegs.

In Fig. 2 A an example of a V-neuron is shown that exhibits a response pattern which is clearly

dependent on the succession (direction) and time difference of the two vibration stimuli presented to forelegs versus mid- and hindlegs. With each intensity – three different accelerations were tested – the response magnitude decreases as the interval between foreleg and mid-/hindleg stimulus decreases and also decreases as mid-/hindleg stimulation advances ahead of the foreleg stimulus (Fig. 2A, inset).

At least in the case of higher stimulus intensities (Fig. 2A, solid and dotted line compared with black and grey column) it appears that the underlying neuronal processing pattern is that of inhibition: the neurons responses to foreleg (columns) stimulation alone is reduced under stimulus conditions with decreasing mid-/hindleg delay, with simultaneous stimulation and with stimulation of the forelegs after the mid-/hindlegs.

The V_3-neurons are represented by at least three neurons on each side of the ventral cord. Each of them shows a different reaction to successive stimulation of different leg pairs.

In Fig. 2B examples of different V_3-neurons are shown. The neuron 1 with a strong response to vibratory stimuli shows no differences in its reaction to delayed fore- or mid- and hindleg stimulation in the delay range up to 10 ms (Fig. 2B, solid line). The other two V_3-neurons show a 'mirror' behaviour to successive stimulation of the legs. The response of the neuron 2 (Fig. 2B, dotted line) is stronger when the forelegs are vibrated before the mid- and hindlegs. In the reverse case of delayed stimulation, the responses to a delay 0 ms and of values up to 20 ms remain unchanged. The 'mirror-image' neuron 3 reacts with reduced responses if the forelegs are stimulated before the midlegs (Fig. 2B, dashed line). Again, in both cases, the responses in the preferred direction are of the same level as that for foreleg stimulation alone, whereas in the other case of stimulus succession, a reduction of response magnitude occurs.

The typical reactions of a V_3-neuron are shown in the Fig. 3. Airborne sound evokes only weak responses which habituate very quickly. The frequency response shows a broad-band characteristic with stronger responses in the lower frequency range. The dominance of the vibratory input of the forelegs is evident compared with that of the midlegs (Fig. 3A, fl and ml responses). Simultaneous stimulation of the fore- and midlegs leads to no clear enhancement of the response compared with the response to foreleg vibration alone (Fig. 3A, fl/ml responses). This V_3-neuron shows no difference in its responses if the leg pairs are vibrated simultaneously or one pair after another;

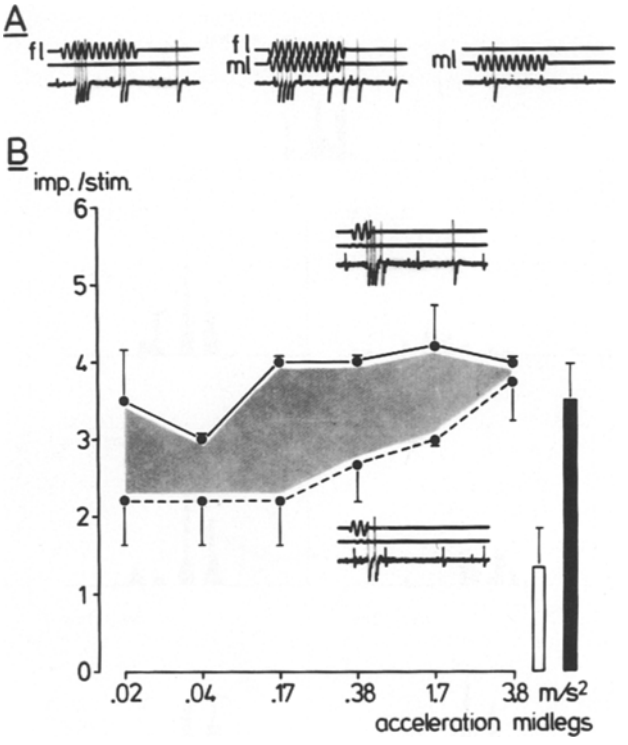

Fig. 3A, B. Reactions of V_3-neurons to vibration stimuli. **A** Responses to stimulation of forelegs alone (fl), fore- and midlegs simultaneously (*fl, ml*) and midlegs alone (*ml*). Frequency 100 Hz, duration 100 ms, acceleration 3.8 m/s². **B** Response characteristics to stimulation of fore- and midlegs with a delay of 5 ms: midlegs vibrated 5 ms before forelegs (●——●), forelegs stimulated 5 ms before midlegs (●---●). The acceleration of the stimulus applied to forelegs is kept constant (3.8 m/s²), the acceleration of the midleg stimulus is indicated on the abscissa. Insets: recordings taken at 0.38 m/s² midleg acceleration. Columns: responses to foreleg (black) and midleg (white) stimulation alone (3.8 m/s²). Frequency 100 Hz, duration 20 ms

however, a significant effect can be obtained by successive stimulation with a pair of stimuli of different intensity values. In Fig. 3B the responses evoked by a stimulus of 3.8 m/s² presented to forelegs alone (black column) and midlegs alone (white column) are shown; if both leg pairs are stimulated simultaneously no enhancement of the response compared with the foreleg response is visible. Successive stimulation of the two leg pairs in both directions with a delay of 5 ms between them shows no significant differences when both stimuli are of the same intensity (3.8 m/s²). However, when the intensity of foreleg stimulation is kept at a constant value (3.8 m/s²) and the intensity of the midleg stimulation is reduced in 10 dB steps, significant differences occur if the forelegs are stimulated first (dashed curve) compared with stimulation of the midlegs first (solid curve). This result could mean that grasshopper central vibratory

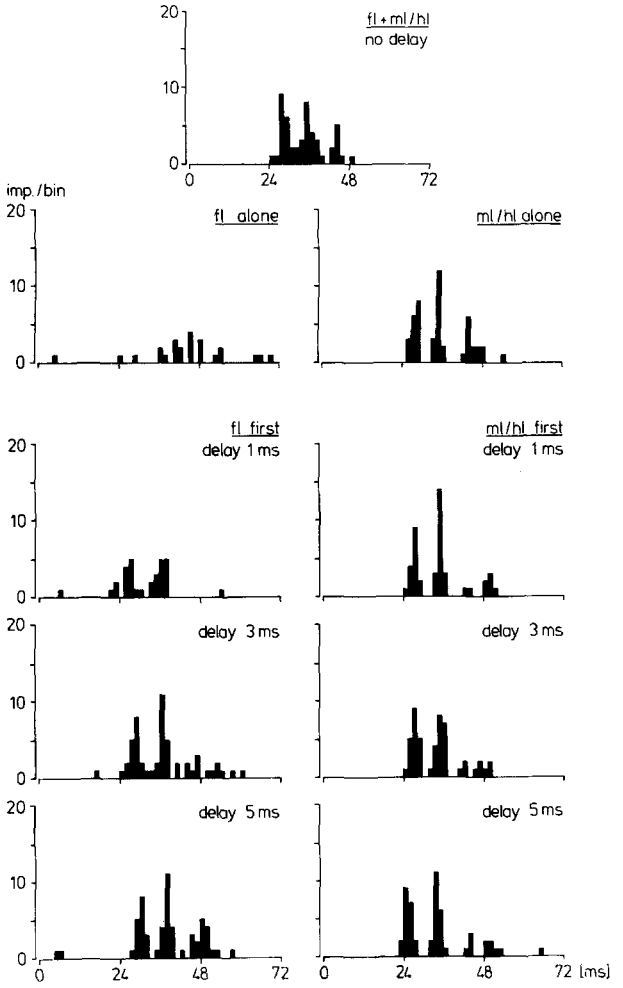

Fig. 4. Reactions of a V_2-neuron to stimulation of forelegs versus mid- and hindlegs shown as post-stimulus-time histograms (bin width 2 ms, responses of 20 successive identical stimulations are added). Frequency 500 Hz, duration 20 ms, acceleration 3.8 m/s^2

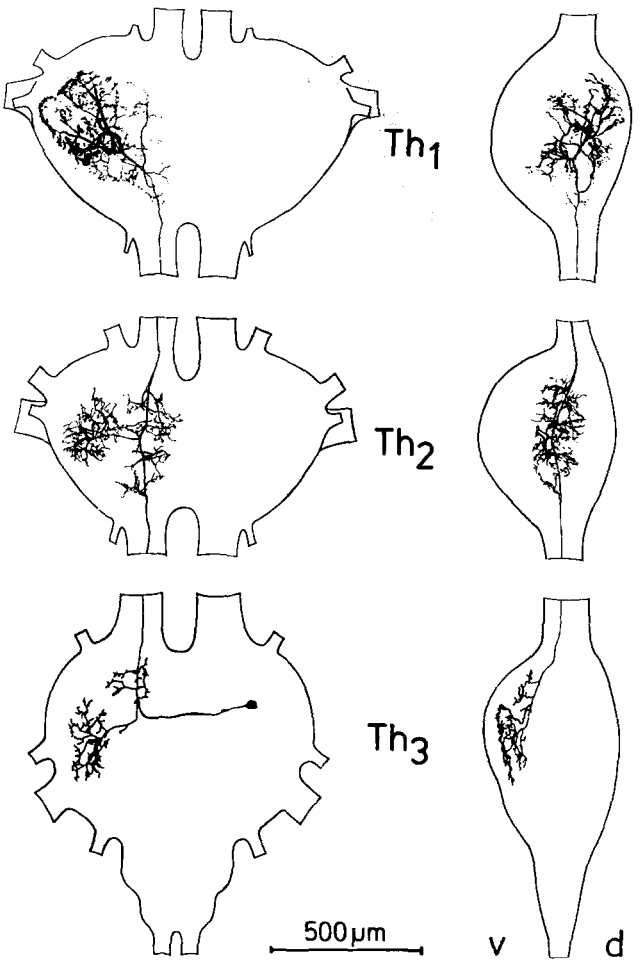

Fig. 5. Morphology of a V-neuron restricted to the thoracic ventral nerve cord. Dorsal (left) and lateral view (right) of pro- (Th_1), meso- (Th_2) and metathoracic ganglion (Th_3). Dorsal (*d*) and ventral side (*v*) as indicated

neurons are also able to detect intensity differences or vibratory gradients in combination with time delays of the vibratory signals reaching the different leg pairs at different times.

b. V-neurons with mid- or mid- and hindleg dominance: this group is formed mostly of V_1 and V_2-neurons. One example of their response pattern is shown in Fig. 4. PST-histograms show a strong reaction to mid- and hindleg stimulation compared with a weak response to foreleg stimulation. If all six legs are vibrated simultaneously the response of the neuron is not altered significantly compared with that of combined mid-/hindleg stimulation. The response pattern also remains practically unchanged during successive stimulation when mid- and hindlegs are stimulated before the forelegs. A clear difference occurs when the forelegs are vibrated before the remaining legs with a time difference of 1 ms. A weaker, less-synchronised response occurs.

III. V-neurons restricted to the thoracic ventral nerve cord show suprathreshold responses only to vibratory stimulation of a certain leg pair. 26 neurons of the group were tested. No clear influence from other legs could be observed either by simultaneous or successive vibrational stimulation. These neurons seem to perform a function of locally connecting the vibratory inputs from a certain leg or leg pair with other higher order interneurons ascending to the brain, or they transmit the information to motor neuropils. Figure 5 shows the shape and branching pattern of such a V-neuron with foreleg dominance.

Discussion

Arthropods have different types of vibratory receptors preferentially located on the legs. Orthopterans possess the most sensitive vibration receptors known in insects: the subgenual organs (Autrum 1941; Autrum und Schneider 1948; Schnorbus 1971). In addition, campaniform sensilla respond to low frequency vibrations. Both vibration receptor types are found in all six legs. By having many different inputs for the vibrational stimuli (more than 100 campaniform sensilla and about 25 subgenual receptors per leg) and the use of different channels for vibrational information could enable the animals to perform a precise analysis of substrate borne signals.

The localization of a vibration source (a stridulating partner or vibrational signals of a prey) is not easy because of changes in the frequency spectrum, time structure, and intensity of the stimulus. This happens to vibration signals much more than to airborne-sound signals because of the different physical properties of the different substrates (Michelsen et al. 1982; Markl 1983). For a long time it was thought that the localization of a vibrational source was almost impossible for small insects because of the high propagation velocities of most of the vibrational wave forms (Schwartzkopff 1974). However, recent biophysical measurements of signal propagation in branches of plants or on a substrate interface have demonstrated that there are also vibrational waves with relatively small propagation velocities, e.g. bending waves in plants or Raleigh surface waves on the ground (Brownell and Farley 1979; Michelsen et al. 1982).

Bending waves seem to be the most important waveforms propagated in plants as a result of the vibrations induced by insects. Their propagation velocity (ca. 15–150 m/s) depends on the properties of the substrate as well as on the frequency components of the signal. Both wave forms have high attenuation factors of 20–50 dB/m in plants; they are even greater in the ground (Bell 1980; Markl 1983).

In grasshoppers of the size of *Locusta* as well as in tettigoniids, the distances between the points on the substrate where the tarsi are positioned are large enough to create a biologically reasonable delay when the vibratory signal travels from one leg position to another. At a distance of 5 cm, which corresponds with the distance between fore- and hindlegs in *Locusta migratoria,* these velocities would create a time delay between 0.4 and 4 ms. Such a time difference could be processed in the central nervous system as demonstrated for scorpions (Brownell and Farley 1979). In addition an intensity gradient will occur even over these short distances. Depending on the damping factors, the remarkable attenuations of the vibratory signal will be coded by the different vibration-sensitive receptors.

At least the frequency-dependent group propagation velocities of bending waves travelling in stems may be of importance for directionality processing: high frequency components of the vibratory signals will appear earlier than low frequency components. Since grasshoppers have receptors for different frequency ranges (subgenual organs and campaniform sensilla) this kind of signal propagation could be used for distance measurement. A similar possibility was shown for scorpions by Brownell and Farley (1979). This seems to be a common principle in the animal kingdom for determination of the distance to a vibration source. This phenomenon was also recently described for fishes excited by surface waves at the water-air interface (Tittel et al. 1984).

The neuronal analysis carried out in this work revealed direction-dependent response patterns in some of the central vibratory ventral cord neurons. Clear differences in the reactions of some neurons ascending to the brain have been shown and these depend on the stimulus succession and time delays.

The results shown in Figs. 2 and 4 indicate that directionality processing occurs at the ventral cord level by integrating the inputs from the vibratory receptors from several legs or leg pairs. As described for other animals (Brownell and Farley 1979; Hergenröder and Barth 1983; Murphey 1973; Wiese 1974) it seems that an inhibitory neuronal network between the different sensory inputs underlies the directional response. In most cases a stimulus simulating a vibratory signal coming from ahead gives stronger responses than a stimulus coming from behind. But, as shown in the V_3-neurons of Fig. 2B, there occurs a mirror-image behaviour in a neuron which codes the posterior position of a stimulus better than an anterior position.

In these examples the temporal pattern of leg stimulation is the dominant cue for vibrational directionality. The detection of the direction of a travelling wave by intensity gradients, however, also takes place in the locust CNS. The directionality coding of some V_3-neurons is improved if, in addition to the time delayed stimulation, a signal attenuation is simulated. So, the perception of signal amplitudes and its neuronal comparison also leads to directionality dependent response patterns in ascending neurons.

VS-neurons normally do not react with changed responses to vibratory stimuli of different leg pairs with delays in the ms-range. The response patterns in these neurons are established by differently weighted inputs from the vibratory receptors of the six legs. Normally, the ipsilateral receptors of the mid- and hindlegs dominate over the inputs from forelegs and from the contralateral legs. This could mean, as demonstrated in the spider (Hergenröder and Barth 1983), that vibratory stimulation of one or some ipsilateral legs alone could enable the animal to determine the direction to the vibration source.

All the vibratory neurons ascending to the brain are bimodal neurons, with inputs from the tympanal organs responding to the airborne sound signals. Normally both stridulation and substrate-conducted vibration will be used for orientation to a sound source.

The results of these investigations demonstrate that many of the vibratory neurons ascending to the brain respond with high sensitivity to simulations of propagating vibration waves. This means that their responses are dependent to a great extent on temporal differences and/or intensity differences of the vibratory signals reaching the different legs.

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