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**Effects of Vibration Input on Auditory Responses
in the Brain of *Mecopoda elongata*
(Tettigoniidae)**

By

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(With 2 Text-figures)

Introduction

It is well established that in the central nervous system of orthopteroid insects, mutual interaction between auditory neurons play an important role in encoding auditory informations. One of the good examples that mutual interaction can produce some dynamic function is the auditory T-fibers in the ventral nerve cords of Tettigoniidae, which show the strong directional sensitivity to sounds, since the tympanic input excites the ipsilateral and inhibits the contralateral T-fiber (Suga and Katsuki, 1961; McKay, 1969; Rheinlaender et al., 1972). In locusts, the beta neurons are known to have similar strong directionality which may partly be due to a mutual inhibition between the two beta-systems (Rowell and McKay, 1969).

Main sound receptor of locusts is the tympanic organ, but the central auditory neurons may receive some additional informations. Yanagisawa et al. (1967) demonstrated that some other end organs were possible to play a part in the frequency analysis. They recorded the response of two central units (I and II), and the threshold curve of unit I became broader at the low frequency end of the scale when the non-tympanic nerves were cut, indicating the existence of inhibitory interaction mechanism of auditory inputs from different end organs.

In the preceding paper (1980), we detected that responses to substratum vibrations can be recorded at the site extremely close to the acoustic centers in the brain, which are discovered in locusts by Adam (1969) and in tettigoniids by Reinlaender and Kalmring (1973). This anatomical proximity appears to suggest the existence of close interrelations between auditory and vibratory informations. Therefore, in the present study, we investigated whether responses of auditory neurons in the brain are interfered by vibratory input from legs or not.

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Material and Methods

Both sexes of adult *Mecopoda elongata* (Tettigoniidae) were used. The way of making the preparations and the recording apparatus were the same as described in the preceding paper (Kumai and Hisada, 1980). Auditory responses were recorded at the acoustic center in the brain by tungsten microelectrodes (10–30 M Ω).

Sound stimuli used were pure sinusoidal tones. Rise and fall times of the burst were adjusted by an envelope-shaping circuit. The low frequency speaker (woofer) was used to produce sounds in the range of 0.05–5 kHz and the high frequency speaker (tweeter), 5–20 kHz. Both speakers were placed 30 cm distant from the front of the preparations. Sound pressure levels were measured by the half inch microphone (Bruel and Kjaer, no. 2615) and the measuring amplifier (no. 2608).

For vibratory stimuli, square pulses with 5 msec durations, whose intensity and rate of repetition could be varied, were supplied through moving coils to the legs (two fore-legs and two mid-legs). The timing relation and the selection of legs stimulated were controlled by the control circuit, and presented together with a sound burst.

All experiments were carried out in an anechoic dark room. The temperature in the room was 22–28°C.

Results

(1) Inhibitory effect of vibration on auditory response.

Many auditory units were found at the acoustic centers in the supraesophageal ganglion. Among them, responses of units that had sensitivity to relatively high frequency sounds (of higher than about 1 kHz) were never affected by the presence of vibrations to any legs of the four, however strong they were.

In contrast, there was distinct interference of vibratory stimuli to the response of the units that responded well to low frequency sounds. The auditory responses of the units having the maximum sensitivity around 300 Hz, which were frequently picked up at the acoustic centers, were clearly inhibited by vibrating the leg(s). Fig. 1 shows a general feature of the inhibitory effect of vibrations on the auditory responses (in this case, sound stimuli used were 300 Hz 60 dB (trace-A and -B) and 290 Hz, 68 dB (trace-C)). The inhibitory effect was caused by vibrating not only the ipsilateral fore-leg but also the other three legs, and ordinarily, single square vibration was enough to suppress the auditory responses. In the record of trace-C, which was the different unit from the trace-A and -B, the repetition rate of vibration presented to the ipsilateral mid-leg was increased gradually from 8 to 100/sec. The auditory responses were completely suppressed by the vibration of about 30/sec (indicated by a bar under the record of trace-C).

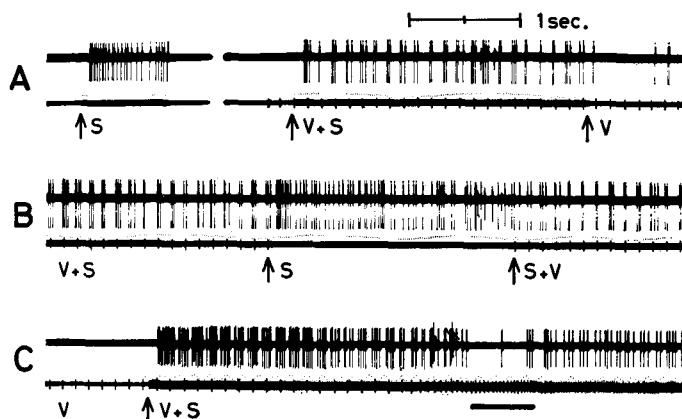


Fig. 1 Responses from auditory units having sensitivity to low frequency sounds and its inhibition by square pulse vibration. A-B; Responses to sounds of 300 Hz, 60 dB (S) and inhibition by the vibrations presented to the ipsilateral fore-leg with repetition rate of 8/sec (V). C; Responses to sounds of 290 Hz, 68 dB and inhibition by the vibrations presented to the ipsilateral mid-leg with a repetition rate being gradually increased from 8/sec to 100/sec (the repetition rate of vibration at the bar under the record is about 25–35/sec). The sign S+V or V-S means that the sound burst and vibratory stimuli are presented simultaneously but in the indicated sequence. Arrows indicate the start of stimulation. A and B was a same unit but C.

(2) Inhibition as a function of the timing relation between single vibration and sound burst.

In another experiment, single vibratory stimuli of square pulse were supplied to each of the four legs (but one leg at a time) synchronized with repetitive sound bursts but with various timing relations. The record of A in Fig. 2 is an example of the response to sound (290 Hz, 68 dB), where the auditory response was inhibited by preceding single vibratory stimulus given to the ipsilateral mid-leg. When vibrations were given at various timings with the sound burst, shortening of the interval between the vibration and the sound burst resulted in a decrease of the impulse number (the sign + means that a single vibration precedes a sound burst and the sign - means the reversed relation). Judged from the number of impulses initiated, the vibratory inputs from each of the four legs have inhibitory effect in a greater (in case of the ipsilateral mid-leg) or less degree (in case of the contralateral fore-leg) (Fig. 2, C). The intensity of vibration was carefully chosen, but selective inhibition by the stimulation of certain leg(s) was not observed. In the case of stimulating the ipsilateral mid-leg, the inhibitory effect started at more than 110 msec before the auditory stimulus and gradually became greater with shortening the interval between the vibration and the sound burst. In proportion to increase of the inhibitory effect, an increase of a latency was also

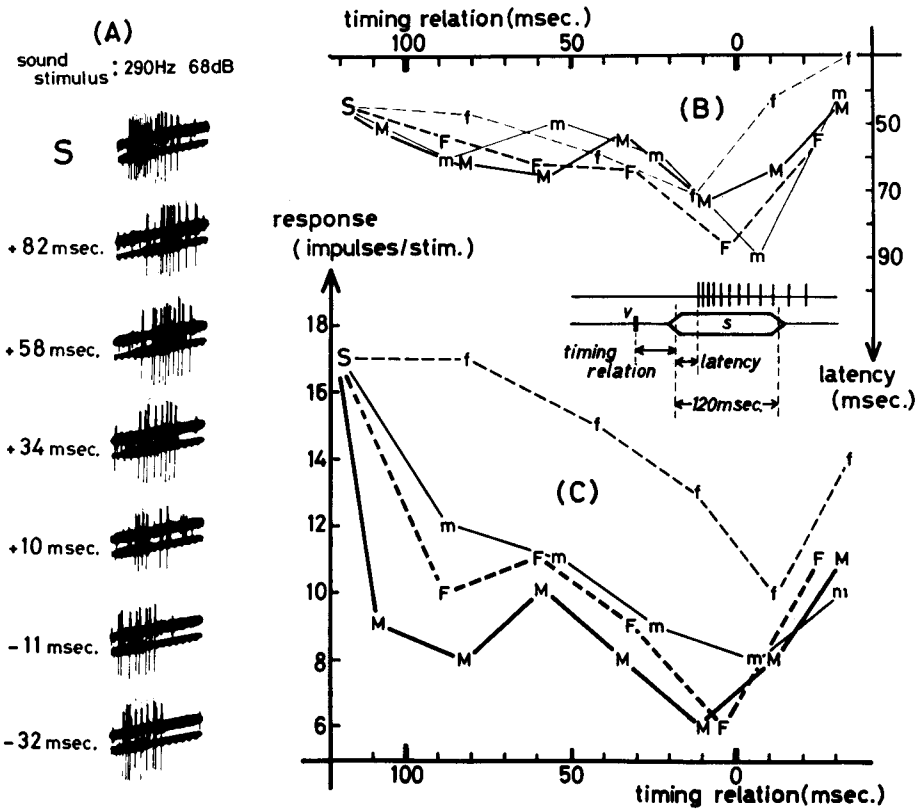


Fig. 2 Inhibitory effects of vibration presented to the ipsilateral mid-leg on the response to low frequency sound (290 Hz, 68 dB) (A), and effects of vibratory stimuli at various timing relation presented to each of four legs on the latency (B) and on the response magnitude (C). The left half of the graphs from zero on abscissa indicates that a vibration precedes a sound burst. In the graph (B) and (C), the line F-F shows the results of vibrating the ipsilateral fore-leg; f-f, contralateral fore-leg; M-M, ipsilateral mid-leg; m-m, contralateral mid-leg, respectively, and the mark S means a sound stimulation only. Further explanations, see text.

observed. The latency of the unit for auditory stimulus only was about 45 msec, and the value increased more than two times when the interval between the vibration and sound burst became null.

Discussion

In the study of hearing mechanism in the central nervous system of Orthoptera, many investigators have reported that it is generally composed of neurons having sensitivity to fairly high frequency sounds. For example, in *Decticus verrucivorus*,

Rheinlaender and Kalmring (1973) found nineteen types of second-order neurons on each side of the ventral nerve cord and eight types of third-order neurons in the supraesophageal ganglion. Most of them showed the sensitivity to sounds ranging 3–40 kHz. Similar frequency range was reported in the auditory system of *Locusta migratoria* by Kalmring et al. (1972).

However, the results of the present investigation showed existence of another type of auditory neurons, which respond to low frequency sounds, optimum frequency being around 300 Hz. Hair sensillae on the body surface may be receptors of such low frequency sounds. In orthopteroid insect, long hair sensillae on anal cerci of grasshopper (Haskell, 1956), cercal sensillae of cricket (Pumphrey and Rawdon-Smith, 1936b) and hair sensillae on the thorax and abdomen (of *Locusta migratoria*, Pumphrey and Rawdon-Smith, 1936a; of grasshopper, Haskell, 1956) have been known as the receptors of air-borne sounds. In the present experiments, as the ventral nerve cords were sectioned at the connectives between metathoracic and 1st abdominal ganglion, hair sensillae on the thorax only are the most likely candidate.

Signals of the vibration must be derived from subgenual organs situated in the tibia of each leg, considering from (1) the auditory response was inhibited by stimulating both fore- and mid-legs and (2) the stimulation to the mid-legs was more effective than to the fore-legs (Dambach, 1972).

The fact that vibratory stimuli to the legs never interfered the units which responded to high frequency sounds, but inhibited the responses of low sound frequency units may mean that the insects can hear only high frequency sound when they are in locomotion. This kind of mechanism which enables the animal to discriminate the external from the self generated signals would be quite important in the behavioral context.

Summary

1. Effects of square pulse vibrations presented to the legs of *Mecopoda elongata* (Tettigoniidae) on the auditory neurons at the acoustic centers in the brain were investigated using tungsten micro-electrodes.

2. Responses of auditory neurons sensitive to relatively high frequency sounds (of higher than about 1 kHz) were never affected by the vibrations, whereas those of neurons sensitive to low frequency sounds, which had maximum sensitivity around 300 Hz, were clearly inhibited by vibrating the legs.

3. The stimulation to the mid-legs caused the inhibition more effectively than the fore-legs, indicating the subgenual organs act as the receptors of vibration.

4. The receptor organ for the response to low frequency sounds around 300 Hz was not certain, but hair sensillae on the thorax are suspected.

5. The inhibition of low frequency auditory response by the vibratory input indicates that the insects may hear only high frequency sound during their locomotion.

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