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Author(s)	KUMAI, Toshifumi; HISADA, Mituhiko
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Central Interactions among Vibration Sensitive Neurons in the Brain of *Mecopoda elongata* (Tettigoniidae)

By

Toshifumi Kumai* and Mituhiko Hisada

Zoological Institute, Hokkaido University

(With 4 Text-figures and 1 Table)

Introduction

The first investigation of the subgenual organ of tettigoniid insects using electrophysiological techniques by Autrum (1941, 1942) showed that the organ responds to substratum vibration, and also to air-borne sounds of frequencies below 1000 Hz. Insects possessing the subgenual organ are much more sensitive to substratum vibrations than those without it (Autrum and Schneider, 1948). Among the former group, Orthoptera has the highest sensitivity to the vibrations.

The mode of the action potential of the subgenual organ was studied. In cockroach, Howse (1964) indicated that the sense cells of this organ did not respond to "steady state" condition but to alteration of the steady state.

Dambach (1972, a b) was able to record the responses of vibratory neurons from the neck connectives of freely moving crickets. He reported that some fibers in the neck connectives of crickets may be even more sensitive and selective to vibrations than the leg nerve and that they responded to both ipsilateral and contralateral inputs, and that the vibratory stimulation of the mid-legs caused the largest central response. This suggests that there should be a central integration of the vibratory information producing the enhanced sensitivity.

However, this integrative function of the brain has not yet been studied. In the present paper, we report that there are complicated interactions among vibratory inputs in the central nervous system of tettigoniids.

Material and Methods

1. Preparation.

Both sexes of adult *Mecopoda elongata* (Tettigoniidae) were used. First, the

* Present address: Department of Oral Physiology, Matsumoto Dental College, 1780 Hirooka, Goobara, Shiojiri, 399-07, Japan.

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two hind-legs had been removed to avoid jumping during experiments, and each antenna was halved. Small area of exoskeleton of the frontal head around the ocellus and a pair of large trachea which lie just below it had been removed carefully to expose the supraesophageal ganglion. In all preparations, the ventral nerve cords were severed at the connectives between metathoracic and first abdominal ganglion to eliminate any influence from the caudal parts and to diminish the periodical movements caused by the respiration. The mouth parts were glued up with a cyanoacrylate adhesive.

After these pre-arrangements, the methonotum of the insects was tightly fixed upon a plastic holder with the glue. The tarsi of remaining four legs (two fore-legs and two mid-legs) were set on the top of four wooden rods, each of which glued to the moving coil in such a way that the four legs maintained a natural posture. The platform on which the experimental insect and the four moving coils were held was isolated from the steel substratum by a plasticin and a layer of glass fiber to avoid interference by unexpected vibrations other than the experimental stimuli.

All experiments were carried out in a sound-proof dark room. The temperature was about 22–28°C.

2. Stimulation.

For vibratory stimulation, continuous vibrations consisted of square pulses of 5 msec duration and of various intensity and rate of repetition were applied to the legs through a driving circuit and the moving coils. What leg or legs were vibrated were controlled by four switches, each of which was exclusive for the each leg. When a pair of legs were vibrated, the same vibrations (repetition rate, duration of the continuous vibration and intensity) were applied. If necessary, another artificial vibrations were applied by tapping the steel substratum with a glass rod, at the top of which a little crystal earphone was attached to monitor the vibrations.

3. Recording.

Units responding the vibratory stimuli were recorded at the paired lateral border region between protocerebrum and deutocerebrum in the supraesophageal ganglion (vibratory centers), which is very close to the acoustic centers in *Locusta* (Adam, 1969) or in *Decticus* (Rheinlaender and Kalmring, 1973), but appeared to be further lateral.

Tungsten micro-electrodes coated with poly-styrene (10–30 M Ω) were used for recording the neural responses. The responses were led into one channel of a dual beam oscilloscope (Nihonkoden, type VC-7) through a high-input impedance pre-amplifier, and another channel was used to monitor the vibratory stimuli.

Results

1. Interactions between vibratory inputs from different legs.

Many units sensitive to vibrations were found at the vibratory centers in the

supraesophageal ganglion. Common features observed in their responses were; (1) the threshold intensity for the vibration presented to the legs was very low, (2) the following up rate of the response to the repetitive vibrations of single square pulse was about 20-50/sec and (3) complicated interactions between the inputs from different legs existed.

To investigate the interactions, vibratory stimuli were presented to each of

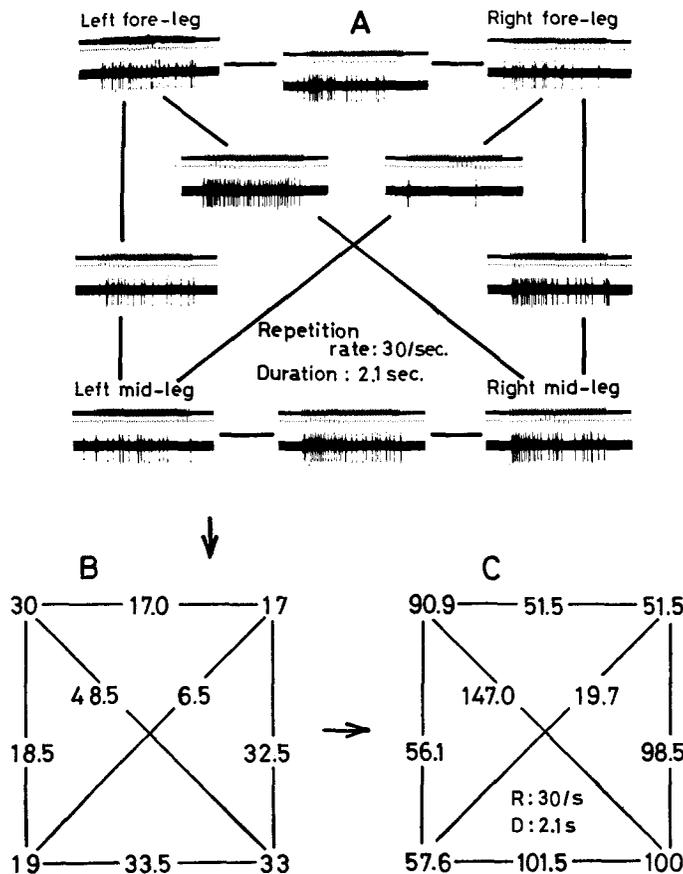


Fig. 1 Diagrammatic representation of responses of a single unit to vibrations applied to each individual leg and various pairs of the legs. A shows the actual record of the responses, where left is the ipsilateral side. Response for each leg is shown at the corners, and response for paired stimulation of the legs shown in between. B shows impulse counts. C represents the normalized values, where the value of 100 represents the largest response among the four legs. D, duration of continuous square pulse vibration; R, repetition rate of square pulse. Further explanation, see text.

the four legs individually and in various pairs of the legs. Fig. 1A is an example of the responses of a single unit in left half of the ganglion to vibrations. The records spanning two legs represent responses to vibrations presented to the two legs simultaneously. The impulse number elicited by the vibration to each leg was counted, and the mean of impulse number in two trials was taken in the case of vibrating the pairs of legs (Fig. 1, B). In Fig. 1C, the numbers were shown as relative values with one of the response (the largest one among the four legs) expressed arbitrarily as 100. This diagram illustrates quantitatively that the main input of this unit is from the contralateral mid-leg. Excitatory interaction exists between this input and inputs from ipsilateral fore- and contralateral mid-legs. From contralateral fore- and ipsilateral mid-legs inhibitory interactions exist.

Fig. 2 shows the other vibratory units, where left side of each diagram represents an ipsilateral side. In each diagram, a dotted line means that responses of connected two legs interact inhibitory, being of the value below the spontaneous level that is indicated under an alphabet in parenthesis, and a heavy line means the excitatory interaction, being of the value above 110. As Dambach (1972b) described, majority of them responded more or less to both ipsilateral and contralateral inputs, and the leg having the highest sensitivity was the ipsilateral or

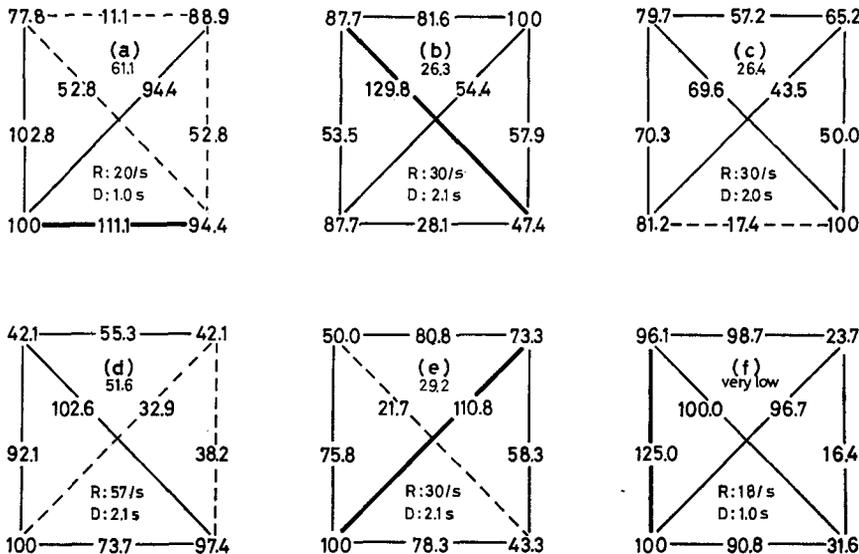


Fig. 2 Response diagrams for six units other than that shown in Fig. 1. A value under an alphabet in each diagram represents the relative level of spontaneous discharge. Dotted lines and heavy lines in the diagrams mean inhibitory and excitatory interactions, respectively. In all diagrams, left is the ipsilateral side. Further explanation, see text.

contralateral mid-leg in all but the unit-b. The lowest value was obtained when two legs having the lower sensitivities among the four legs were simultaneously vibrated (unit -a, -b, -e and -f in Fig. 2 and the unit shown in Fig. 1), and the highest value was seen when two legs having the higher sensitivities among the four were simultaneously vibrated (unit -a, -e and -f in Fig. 2 and the unit shown in Fig. 1).

Then a question that these complicated interactions would not be caused by the neural interactions but by some mechanical coupling arises, but the existence of the unit-f, in which the ipsilateral fore- and mid-leg are apparently main inputs and the contralateral legs has no influence to the ipsilateral ones definitely eliminates the mechanical coupling as the possible cause.

2. Response of the other units to substratum vibrations.

Another type of vibratory units was found. They were very sensitive to vibrations such as that produced by footsteps of a person walking around the experimental set-up or by tapping the substratum. (They were so sensitive that the shock absorber placed under the preparations were not effective enough to absorb the vibrations.) However, the square pulse vibrations presented to a leg or legs not only failed to produce any response but also had an inhibitory effect on the response.



Fig. 3 Responses of a unit which responds to vibration of the substratum (repetitive tapping: conditioning stimuli), and inhibited by the test stimuli (continuous square pulse vibrations) presented to the ipsilateral mid-leg. x- and o-marks above the record indicate affected and unaffected responses, respectively.

Table 1. Comparison of inhibitory effects of test stimuli on responses to the substratum vibration among the four legs.

Leg vibrated by test stimuli	Number of samples	Number of impulses (mean \pm SD)	Ratio of Xi to Xc (Xi/Xc)
Ipsilateral fore-leg	20	$X_i=10.5\pm 2.7$	0.72
Control	22	$X_c=14.5\pm 2.0$	
Ipsilateral mid-leg	27	$X_i=7.1\pm 1.9$	0.52
Control	31	$X_c=13.7\pm 2.9$	
Contralateral fore-leg	34	$X_i=10.4\pm 2.2$	0.78
Control	32	$X_c=13.3\pm 3.6$	
Contralateral mid-leg	26	$X_i=8.1\pm 2.9$	0.59
Control	25	$X_c=13.8\pm 2.1$	

The inhibitory effects of the continuous square pulse vibrations (repetition rate, 30/sec; duration, 2.2 sec) presented to each of the four legs (test stimulus) on the responses to repetitive tapping of the steel substratum with low rate (about 2/sec) and suitable intensity (conditioning stimulus) were examined. The record in Fig. 3 is an example of the inhibitory effect of vibrations presented to the ipsilateral mid-leg. The impulse number generated per single conditioning stimulus was fairly steady throughout the experiment, even though the stimulation was done manually with a glass stick. The inhibited responses (x-mark above the record) were compared with the unaffected responses (o-mark above the record). Table 1 shows the results, where the mean values of impulse number generated under the test stimuli (X_i) are clearly lower than the values for the conditioning stimuli only (X_c). To clarify the degree of the inhibitory effect, the ratio of X_i to X_c ($R=X_i/X_c$) was calculated. The obtained ratios indicate that the stimulation to the mid-legs has more inhibitory effect than that to the fore-legs.

Discussion

Dambach (1972b) reported that vibration sensitive neurons in the neck connectives of crickets respond to both ipsilateral and contralateral inputs, and stimulation of the mid-legs causes the largest central response. Similar results were obtained in the present investigation, that is, majority of the units in the vibratory centers responded more or less to vibration of any of the four legs, and the units whose responses had the maximum sensitivity to vibrations of the ipsilateral mid-leg were more in number.

The experiment of simultaneous vibration of various pairs of legs revealed that there are further complicated interactions between inputs from two different legs. Beside summation between excitatory inputs, in most central vibratory neurons, input from a leg or legs, although itself elicits a considerable central response, have inhibitory effects on the response to the vibration of the other legs. Summation between the inhibitory effects was also observed, especially when two legs having the lower sensitivities among the four legs were simultaneously vibrated. It seems to be difficult to clarify the meanings of these interactions in regards of the behaviour of this species. However, the existence of excitatory and inhibitory interactions between different legs may suggest the possibility of a directional sensitivity to vibration sources like the auditory T-fibers in the ventral nerve cords of *Gampsocleis* (Tettigoniidae) (Suga and Katsuki, 1961). In the T-fiber, the activity of the tympanal nerves varies only little with the direction of sound, but a considerable central sharpening of the location is obtained, since the tympanic input excites the ipsilateral and inhibits the contralateral T-fiber. Similar mechanism may exist in the vibration-sensitive central units.

The sense organ responsible for the responses described above would be the subgenual organ situated in the tibia of the legs, if one consider that (1) the following up rate of the response to square pulse vibrations was up to about 30–50/sec

and similar to that been reported in cockroach by Howse (1964) and (2) the responses were more or less bilateral and the ipsilateral mid-leg showed the highest sensitivity in most units. However, the possibility that inputs of some units of them might be derived from hair sensillae on the tarsal or trochanter segment of the legs, which are also known to be able to respond to substratum vibrations (Runion and Usherwood, 1968; Spencer, 1974) appears not to be denied completely.

Responses of vibration sensitive units as shown in Fig. 3 indicate the existence of another vibration sensitive system. Two possibilities are thought for producing the response of this neuron. One is that the neuron can elicit the response only when some legs are vibrated in due order, which means a directional sensitivity to the vibration source, and the other is that it responds to only specific wave form such as that produced by the locomotion of certain predatory animals of the insect. Quantitative analysis about the directionality was not done, but the change of responsiveness seemed not to be significant when the position of tapping the substratum was changed. The neurons of this type, therefore, would respond preferentially to vibrations containing specific wave form.

The inhibition may mean that the responses to certain specific vibrations are interrupted by locomotion of this insect. Although the inhibitory input appears to be mediated by the subgenual organs, the receptor organs responsible for the response to the specific vibration are not certain.

To clarify the neuronal connection in more detail, further experiment such as a direct electrical stimulation of identified fibers, or stimulations of legs with more complicated temporal patterns and various wave forms is needed.

Summary

1. Responses of single vibratory neurons to vibrations of legs of *Mecopoda elongata* (Tettigoniidae) were recorded. In the brain, the vibratory centers are located at the lateral border region between protocerebrum and deutocerebrum of both sides.

2. Majority of the vibration sensitive units responded to vibration applied to any of the four legs (two fore-legs and two mid-legs), but with different responsiveness. The inputs appeared to be derived from the subgenual organs. Majority of units have the highest sensitivity to vibrations to the mid-legs, others have the highest sensitivity for the fore-legs.

3. Simultaneous vibration of pairs of the legs revealed that the leg having the lowest sensitivity tended to have inhibitory influence, and the leg having the highest sensitivity was excitatory influence upon the responses for the other legs. This suggests the possibility of a directional sensitivity to vibration sources.

4. Existence of vibration sensitive system other than the subgenual organs was also suggested. Neurons of this type respond to specific wave form. Stimulation of the subgenual organs inhibited this response.

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