MECHANICAL AND ELECTRICAL EVENTS IN THE MAIN SOUND MUSCLE OF CICADA

TSUTOMU WAKABAYASHI*
Physiol. Institute, Tokyo University, Tokyo

AND

SUSUMU HAGIWARA†
Physiol. Institute, Tokyo Med.-Dent. University, Tokyo

A pair of large muscles called the main sound muscle of the male cicada is an appropriate material for the study of insect muscle physiology. The mechanical as well as the electrical activity of the sound muscle were investigated either during sound production or in silence.

A pair of large muscular columns (main sound muscles) joining together to form a V in the resonance cavity is shown in fig. 1. It can be readily seen when the caudal part of the wall of the cavity is removed at the third abdominal segment. Each column arises from the median line of the inner surface of the body wall, and ends with a truncated stump. A fine tendinous thread arising from the stump centre combines the muscle end with the centre of a small chitin membrane (the drum membrane), which is the vibration disc of the sound organ. After removal of the caudal wall, a slight touch on the body wall, the coxa, or the trochanter of the insect with a piece of paper or a tip of a small feather, was sufficient in most cases to make the insect shrill by reflex. We did not succeed in making the insect keep shrilling in such a long period as in its voluntary shrilling.

The species of the cicada employed were Graptopsaltria nigrofuscata, Oncotypana maculaticollis, Tanna japonensis and Meimuna opalifera.

FIG. 1. Main sound muscles of G. nigrofuscata.
M: Main sound muscles.
D: Drum membrane.

METHOD

The electrical changes were led off with a pair of silver or silver chloride wire electrodes which were attached to or inserted into the sound muscle, am-

Received for publication May 2, 1953.
* 若林 篤, † 截原重

249
plified by an ordinary R.C. coupled 3 stage amplifier, and recorded with an
electromagnetic or a cathode-ray oscillograph.

The mechanical changes were recorded on the same oscillograph paper by
the aid of a small mirror (1.0 to 0.5 mm.) attached to the muscle surface or
to the drum membrane.

All of the experiments were carried out during the hot reason (26°–31° C.)
from July to September, 1944–1947.

RESULTS OBTAINED

1) Electrical responses of the muscle when the insect is excited to shrill

Typical recordings of the electrical discharges of muscle are shown in fig.
2, A and B. Series of regular discharges are separated into several groups by
a silent period. The group is usually composed of 5 to 10 discharges, in some
cases over 100 discharges. The uniformity of the regular discharges can possibly
be due to the single fibre innervation of the whole muscle.

Although the height of each discharge was usually quite uniform, in some
cases the first impulse in a group was higher to some extent than the following
ones as indicated in fig. 2, B, and moreover the longer the preceding silent
interval the higher the following discharge. So it can possibly be said that the
muscle cannot set up a full-sized response during the highly frequent repeti-
tions of discharges in the case of spontaneous shrilling because of incomplete
recovery from the preceding refractory state.

FIG. 2 (left). A: Electrical discharges of the sound muscle when the insect was excited.
B: First discharge is higher than the followings. C: Trains of twitches of the sound muscle
when the insect was excited. D: Simultaneous recording of electrical (E) and mechanical
(M) responses. Time markers in all the record are 100 per sec.

FIG. 3 (right). Frequency of discharges (ordinate) and temperature (I : 31° C., II : 29° C.,
III : 26.5° C.), N (abscissae) is the number of the discharge in one series.
The frequency of potential in a group was fairly constant about 100 per second. The potential of discharge was of the order of milli-volt.

The frequency was high at high temperature (fig. 3). Q 10 was found to be 2.8 or so. The above mentioned results in the case of Graptopsaltria were applicable to some of the other species.

2) Mechanical responses of the muscle when the insect is excited to shrill

As fig. 2, C and D show, each rapid twitch corresponds to each discharge, when the insect was excited to shrill by reflex. Each twitch in a group was interrupted by a brief resting phase.

Tension developed in the muscle was also recorded by deflection of the mirror stuck on the drum membrane when the insect was shrilling or when the muscle was stimulated through the electrodes attached to its surface. The results were similarly brief responses. The duration of a single twitch was always about 10 msec. or less.

3) Electrical and mechanical variations when the insect is silent

Another kind of potential wave of small amplitude and different form was observed, and at the same time a scarcely detectable mechanical variation was recorded in the silent muscle into which the electrodes were inserted. Fig. 4, A shows both the small waves and the ordinary shrill discharges in the same condition of recording. The discharges were recorded clearly by higher amplification, in fig. 5. The magnitude of the wave was at most about one-eighths to one-tenths of that of the shrill discharge. The amplitude of the mechanical changes was also much smaller than that of the shrill reaction. The frequency of the waves varies to a considerable extent. Sometimes it was only 30-40 times per second, which is far less than that of the discharge of shrilling.

---

**FIG. 4 (left).** A: Shrill discharges and small waves in silence were recorded in a paper. B: Small irregular waves recorded in silence. C: Small waves disappeared by narcotics.

**FIG. 5 (right).** Several cases of small waves recorded with higher amplification.
The form and height of this small waves usually varied even in the same record, but somewhat regular and occasionally simple waves were recorded as in fig. 5, A. It is probably due to only a few units acting with slightly different frequency and phase. In this case the application of some narcotics to the muscle, for example, ether or alcohol, made the waves disappear within a few seconds. So it is clear that the phenomenon is not due to the noise of the amplifying circuit. This wave remained unaltered even after dissection of the nerve attached to the muscle. Moreover similar discharges could be recorded in the dissected strip of the muscle. It is apparent from this that the wave is of muscular origin.

In the course of the observation the intensity as well as the frequency of the wave was gradually reduced until they could not be recorded. The wave which was irregular at the beginning became relatively regular. This is probably due to the reduction of the number of acting units (fig. 6). In this stadium, the mechanical responses could not be detected in most cases, while the electrical waves were still observed.

This may be due to the reason that the sensitivity of our equipment was insufficient to record such a weak mechanical response. We detected the wave in the muscle in situ placing a tip of the electrode firmly on the muscle, and noticed that the wave disappeared after a while, but reappeared spontaneously in the same condition. Moreover we experienced that pushing a thin glass capillary into the muscle the waves of which had just disappeared caused them to appear again. In this way the waves usually reappeared in a few seconds after this stimulation and they were at first small in magnitude and soon grew to full size. From these facts it may be concluded that the waves described above must be ascribed to the so-called injury discharges due to the contact or the insertion of the electrode to the muscle.

Even in the spontaneous reappearance described above, it could not be denied that it was a kind of injury discharge in nature (2).

DISCUSSION

Heidermanns (1937) (3) expressed an opinion that the wing muscle of *Aschna coerula* is called into action as an incomplete tetanus in natural flying, because
the contraction rate of the isolated wing muscle is too slow to account for the beating frequency of the wing. However, it is clearly shown above that the natural activity of the sound muscle of the cicada was a series of extremely brief, discrete twitches. There can be several types of muscles in the insect muscle. As to the extremely fast rate of contraction in the sound muscle, it must not be overlooked that the size of the muscle is sufficiently small enough to shorten itself instantaneously and that the temperature of the environment in our case is high enough for fast muscle activity. Dotterweich (4) reported that in case of a certain moth a rapid vibration of the wings is necessary to increase the temperature of the wing muscle itself, that is to say, the warming up or the preparation for flying. Afterwards Krough and Zeuthen (5) recorded small electrical changes during preparation for flight. Small electrical and mechanical changes in the sound muscle of the silent cicada may, however, be considered different from the above mentioned changes.

Our results show that the small electrical waves detected in the silent muscle is most probably caused by the damage of the muscle. These waves may probably be due to the excitation of individual muscle fibres or of smaller local part of the muscle fibre. Whether or not the excitation is caused through the terminal nerve fiber is still beyond this discussion.

SUMMARY

In the responses of the sound muscle of the shrilling cicada (i) a train of action potentials and (ii) a train of rapid twitches are observed synchronously. Its frequency is about 100 per second. Not only the electrical but the mechanical small changes can often be observed during the silent period of the insect. These are probably due to the damage of the muscle caused by the leading electrodes. Related reports of several authors are discussed.

ACKNOWLEDGEMENT

We should like to express our thanks to Prof. M. Kume, Higher Normal School for Women, Tokyo, for his kind suggestions of this experimental material. We desire to acknowledge our indebtedness to the late emeritus Prof. K. Hashida, Tokyo University and ex-Prof. S. Sakamoto, Tokyo University, for their encouragement and criticism throughout this investigation.

REFERENCES

5. KROGH, A. AND ZEUTHEN, F. *J. exp. Biol.* 18: 1, 1940.