Electrical Characteristics of Insect Mechanoreceptors

M. L. WOLBARSHT

From the Naval Medical Research Institute, Bethesda

ABSTRACT External direct coupled recordings from the neurons of the mechanosensory hairs of insects show nerve impulses and graded slow potentials in response to deformation of the hair. These slow potentials or receptor potentials are negative going, vary directly with the magnitude of the stimulus, and show no overshoot when returning to baseline. The impulses have an initial positive phase which varies in size directly with the amplitude of the receptor potential. The receptor potential is related to the generator potential for the impulse in that it must attain some critical level before impulses are produced, and the frequency of impulses varies directly with amplitude of the receptor potential. The receptor potential does not return to the baseline after each impulse. In some receptors static deformation of the hair will maintain the receptor potential. It appears likely that both the receptor potential and the variation in size of the impulses are caused by a change in conductance of the cell membrane at the receptor site, and that the receptor potential originates at a site which is not invaded by the propagated impulses.

INTRODUCTION

When a vertebrate mechanoreceptor, the Pacinian corpuscle for example, is stimulated, the electrical response can be separated into two components: a receptor potential and a propagated nerve impulse (Gray (1959)). The receptor potential is a graded response; its amplitude is a smooth function of the stimulus strength. The receptor potential always begins earlier than the nerve impulse and its amplitude must reach some critical level before the nerve impulse is initiated. When repetitive discharge takes place the frequency is directly related to the amplitude of the receptor potential. Presumably, the receptor potential is a graded depolarization of one part of the neuron and acts as a local current sink to cause depolarization of some part of the neuronal membrane which can, when sufficiently depolarized, initiate propa-

The opinions or assertions contained herein are the private ones of the author and are not to be construed as official or reflecting the views of the Navy Department.

Received for publication, March 4, 1960.

gated impulses.[1] The site of origin for the impulses may be quite remote from the site of origin for the receptor potential.

There are many types of insect mechanoreceptors, but a common one consists of a bipolar neuron with the cell body just under the cuticle. The proximal fiber joins a common nerve trunk and proceeds into the central nervous system of the insect. The short distal process of the neuron goes up to the cuticle and terminates near the base of a hollow hair-like projection of the cuticle. Fig. 1 shows the anatomy of this receptor in schematic form. The distal fiber here is shown ending in a disc which is closely applied to the cuticle. In some mechanoreceptors the distal process does not end in a disc but enters the lumen of the hair for some way before it ends (Hsü, 1938). Deformation of the hair causes stimulation of the neuron so it is likely from the geometry that the termination of the distal process is the site of origin of any receptor potential.

There may be more than one neuron terminating at a single hair. In most cases these extra neurons subserve some function other than that of mechanoreception. The chemosensory hairs on the labellum of the blowfly are of this type—they have three neurons. Two of these neurons respond only to chemical stimulation and the third to mechanical stimulation (Wolbarsht and Dethier (1958)). In this case the mechanoreceptor distal process terminates in a doughnut shape. The distal processes of the two chemosensory neurons pass through the hole in this doughnut-like termination of the mechanoreceptor to enter the lumen of the hair (Grabowski and Dethier (1954)).

Nerve impulses can also be recorded from the distal process through an electrode in contact with the hair in respose to a mechanical stimulation of the hair (Wolbarsht and Dethier (1958)). Graded slow potential changes can also be recorded in response to mechanical stimulation (Wolbarsht and Gray (1959)). The impulses recorded from the distal process are the same as the ones seen in the proximal nerve fiber by Pumphrey (1936).

Recordings from the mechanoreceptors indicate that there are two functional types: the velocity-sensitive and the pressure-sensitive. The velocity-sensitive mechanoreceptors give impulses only while the stimulus is changing. They may fire repetitively at a very high rate during stimulation; the receptors on the fly wing respond at a rate of 600 or more impulses per second. The pressure-sensitive receptors show a repetitive discharge during a static deformation in addition to responding during a changing stimulus. This type is not found as frequently as the velocity-sensitive type (Wolbarsht and Dethier (1958)).

[1] The term "receptor potential" is applied to those non-propagated potentials recorded near a receptor. It may refer to an intra- or extracellular potential and may be hyper- or depolarizing in nature. The term "generator potential" is reserved for those potentials existing intracellularly at the site of impulse initiation.

Two mechanoreceptors that have been studied in detail are the Pacinian corpuscle and the lobster stretch receptor. In the Pacinian corpuscle the receptor potential originates at the most distal portion of the neuron, and the nerve impulse is initiated slightly proximal to this and is propagated proxi-

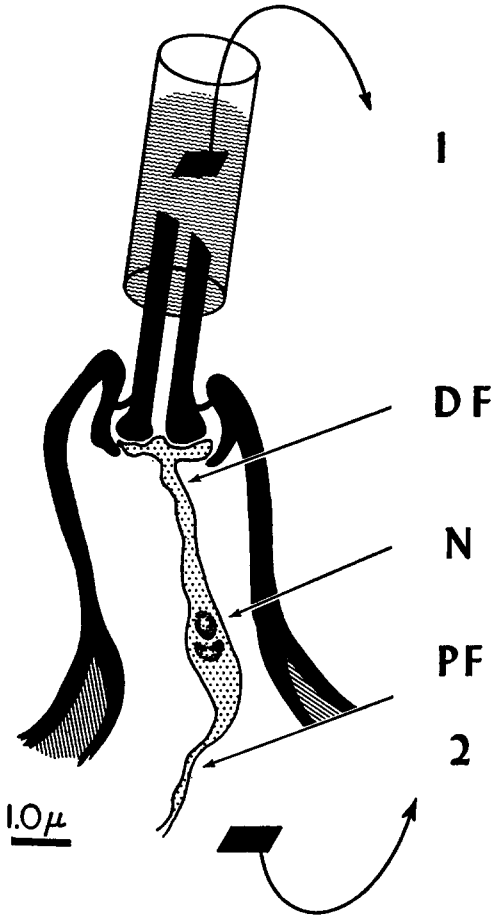

FIGURE 1. Schematic representation of hair type mechanoreceptor of an insect showing electrode placement. *PF*, proximal fiber, *N*, mechanosensory neuron, *DF*, distal fiber, 1, recording electrode, 2, indifferent electrode. The tip of the hair has been cut to allow the fluid in electrode 1 to make contact with the fluid-filled interior of the hair.

mally only. The nerve impulse does not invade the site of origin of the receptor potential (Lowenstein (1959)). In the lobster stretch receptor, however, the conducted action potential does appear to invade the dendritic processes where the receptor potential is located even though it originates in the axon near the cell body (Edwards and Ottoson (1958)). These receptors were used as models in interpreting the data obtained from the insect mechanoreceptors.

The work presented in this paper indicates that the graded slow potential recorded from the distal process is a receptor potential in that it occurs prior to any impulses, varies smoothly, and must attain some critical level before any impulses are initiated. The amplitude of the slow potential also varies directly with the frequency of discharge of impulses. It seems likely that the insect mechanoreceptor is similar to the Pacinian corpuscle in that the site of origin of the receptor potential is not invaded by the nerve impulse. It is also possible that the graded slow potential seen in the insect mechanoreceptor is caused by a change in permeability of the cell membrane at the receptor site. This change in permeability of the cell membrane may also explain the increase in the size of the nerve impulses with increased frequency of discharge which has been described previously (Wolbarsht and Dethier (1958)).

METHODS

The experiments described below were performed on the following insects:

Blowfly *Phormia regina* Meigen
Fleshfly *Sarcophaga sp?*
Grasshopper *Melanoplus femur rubrum*
Cockroach *Periplaneta americana*
Potato beetle *Leptinotarsa decemlineata* Say

Any hairs on these insects that appeared to be innervated were tested for electrical responses to mechanical stimulation.

The recording technique was the same as that described previously (Wolbarsht and Dethier (1958); Wolbarsht (1958)). The recording electrode was a 1 to 50 μ glass capillary filled with distilled water or 0.01 M NaCl. This pipette was placed over the cut tip of a mechanosensory hair. The liquid in the capillary was in contact with a large silver-chloride–coated silver surface connected to the input grid of the preamplifier. The indifferent electrode was similar to the recording electrode except that it was always filled with 0.01 M NaCl. This electrode was inserted into the excised portion of the body bearing the mechanoreceptor. In the wing, for example, the pipette was inserted into the marginal vein. The recording situation is shown diagrammatically in Fig. 1. The preamplifier was modified to allow current pulses of known direction and amplitude to be inserted into the electrode circuit to measure any changes in resistance. The output of the preamplifier was led into a D.C. oscilloscope for visual observation and photography.

The mechanical stimulus was administered by manually moving the micromanipulator that held the recording electrode. No attempt was made to more than roughly quantify the amplitude of this stimulus. The force exerted by the electrode on the hair was as far as possible perpendicular to the long axis of the hair. The hair could be held motionless at any desired degree of deformation by this apparatus.

RESULTS

I. *General Characteristics of the Receptor Potentials and Nerve Impulses*

The mechanoreceptors on all insects tested have similar electrical responses. However, the initial resting potential seen when electrical contact is made with the fluid interior of the hair is quite variable and may be either positive or negative although similar types of hairs have similar resting levels. The chemosensory hairs of the labellum of *Phormia* have been examined in detail concerning this point (Wolbarsht (1958)). The initial resting potential is quite steady until a mechanical stimulus is applied.

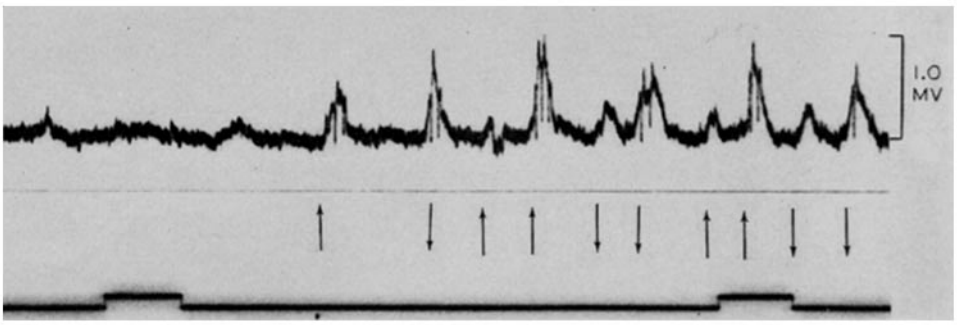

FIGURE 2. Response of *Sarcophaga* wing chemosensory hair to repetitive mechanical stimulation. Each arrow indicates the onset of a rapid one directional displacement, and the direction of the displacement with reference to the preceding stimulus. Positive potential at recording electrode is down. Time marks recur at 0.2 second intervals.

When the hair is deformed, thereby stimulating the mechanosensory neuron, a graded potential change or receptor potential is seen. This potential is always an increase in negativity at the recording electrode which varies smoothly as the stimulus is increased or decreased. The receptor potentials were of two extreme types: one lasting only during the motion of the hair and the other lasting for the duration of the deformation of the hair. The first type is shown in Fig. 2. It has a rapid rise time and an equally rapid return to the baseline, even though the hair is still bent. The return motion of the hair to the unstrained position produces another receptor potential. Some of the mechanoreceptors of this type have a receptor potential which persists for a second or two after the motion has ceased and during a continued static deformation as shown in Fig. 3. The second type of receptor potential, shown in Fig. 4, was maintained as long as the stimulus persisted and appeared to be proportional to the static deformation of the hair. Only a decrease in potential was seen while the hair was being returned to the un-

stimulated position from any other position. This type adapted slowly. In some preparations adaptation was not complete even after 20 minutes.

The impulse activity occurs only after some threshold receptor potential is reached as is described in detail below (section II). It has been shown

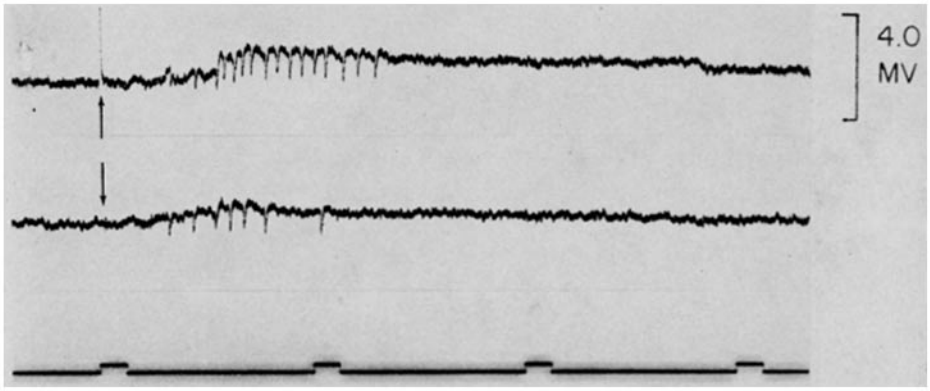

FIGURE 3. Response of long chemosensory hair on labellum of *Phormia* to slowly increasing mechanical stimulation. Onset of stimulation is indicated by arrow in each record. The stimulus continues until the end of the record. Positive potential at recording electrode is down. Time marks recur at 0.2 second intervals.

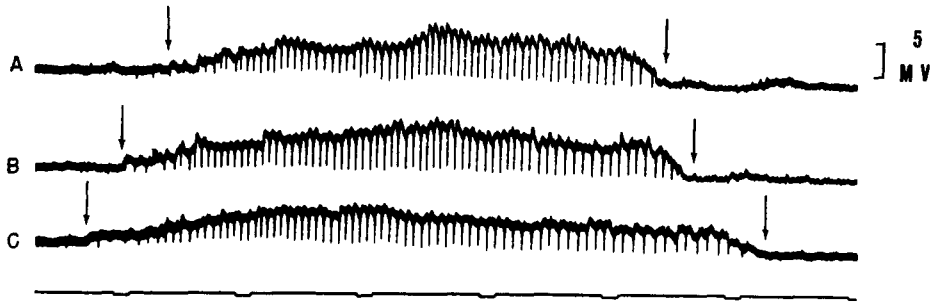

FIGURE 4. Response of mechanosensory hair on outer clasper of male *Phormia* to mechanical stimuli. *A*, *B*, *C* are successive records taken from the same hair but the stimuli were not the same. Arrows indicate onset and cessation of deformation. The deformation of the hair was approximately proportional to the amplitude of the response for each record. Time marks recur at 0.2 second intervals. Positive at the recording electrode is down.

previously that the nerve impulses recorded with the electrode in contact with the distal fiber are the same ones that can be recorded from the proximal neuron after it has joined a nerve bundle (Wolbarsht and Dethier (1958)). The impulses recorded from the distal fiber always have an initial positive phase in contrast to the negative going receptor potential. The impulses are usually, but not always, monophasic. The positive phase of the impulse

may be larger or smaller than the magnitude of the receptor potential. The impulse, therefore, is not just a return of the receptor potential to zero. After the impulse has gone the receptor potential is at the same level that it was before the impulse appeared. There is no residual hyperpolarization or depolarization following the spike. It is likely that the impulse is just riding on the slow potential—that the record shows only the algebraic sum and there is no interaction of the two beyond this.

The frequency of the impulses is directly related to the size of the receptor potential (see section III below). The variation in the size of the nerve impulse with frequency of discharge has been reported before (Wolbarsht and Dethier (1958)). The impulse size seems also to vary directly with amplitude of the receptor potential. This correlation is treated in detail in section IV below.

Measurements of the resistance of the electrode circuit were taken at 0.1 second intervals during the stimulation of those receptors which adapted slowly. The resistance in the unstimulated state was from 80 to 500 megohms, 400 megohms being the most usual. No changes were detected during stimulation; however, changes smaller than 5 per cent of the initial value could have been masked by the noise level.

II. *Threshold Phenomena Connected with the Receptor Potential*

In all the receptors studied there appears to be some minimum receptor potential below which no impulses occur. Threshold measurements can be made easily on those neurons which adapt rapidly to static deformations, as here the unstimulated level of baseline is easily determined. Figs. 5 and 6 show the level at which the first impulse in a volley occurred as the receptor potential was increased gradually from zero. These plots show a defined clustering of thresholds about a particular value of the receptor potential which value is, of course, different from preparation to preparation.

In the mechanoreceptors which adapt slowly, it is difficult to make accurate measurements of the size of the receptor potential at the threshold for an impulse as the baseline cannot always be determined with sufficient accuracy to get meaningful measurements of the impulse threshold. This indeterminancy of the baseline is due to the small residual receptor potential which does not adapt out. It is quite difficult to be certain that any particular hair of this type was in a really stimulus-free state as the hair may always be distorted slightly by the recording electrode. However, for all mechanoreceptors some position of the hair can always be found in which no impulses are recorded. In this position small mechanical stimuli applied very slowly always produce a finite receptor potential before an impulse occurs.

III. *Relation between Receptor Potential and Impulse Frequency*

When repetitive spike discharge takes place in a neuron the frequency is determined by two factors: the refractory period of the impulse-initiating mechanism, and the size of the generator potential (Bernhard *et al.* (1942)). As the generator potential increases, the neuron discharges earlier in the

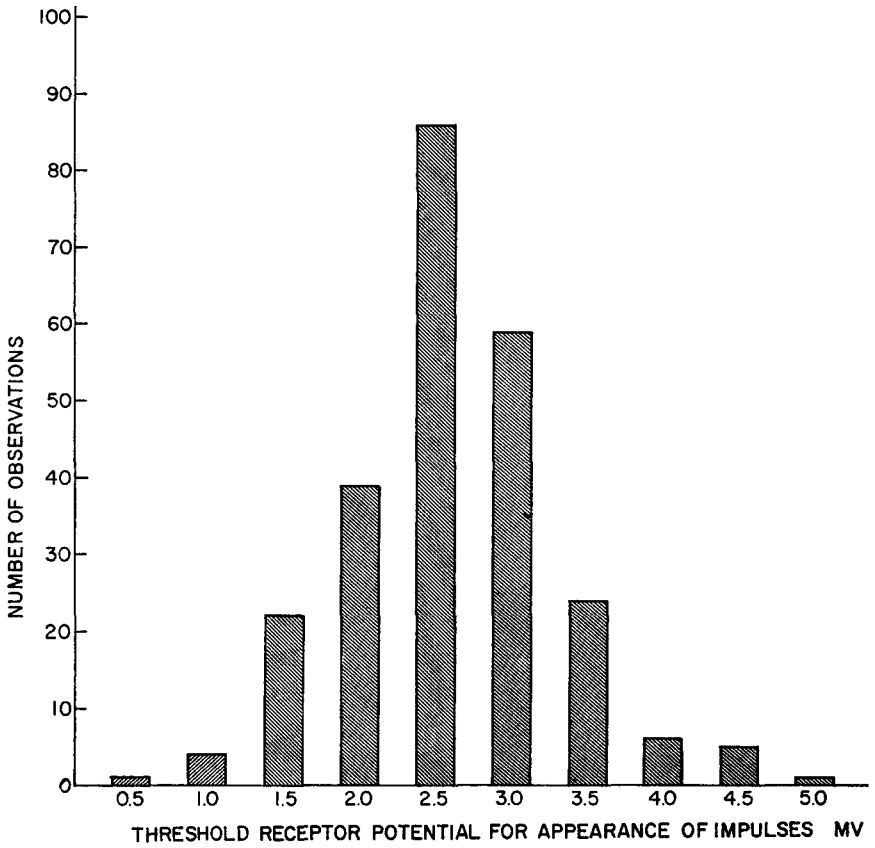

FIGURE 5. The threshold receptor potential of a mechanoreceptor on the grasshopper claw which is accompanied by an impulse is plotted for a series of test stimuli. In the largest number of trials the threshold was 2.5 mv. with the spread as shown.

relatively refractory period following the previous impulse. The frequency of discharge increases until the interval between the impulses is equal to the absolute refractory period of the neuron. Further increase of the generator potential will cause no increase in impulse frequency. Up to this point, however, the frequency of discharge is a monotonic function of the generator potential. That is, the impulse frequency varies directly with the amplitude of the receptor potential.

In all the insect mechanoreceptors that we have studied, the relation

between the receptor potential and the impulse frequency is monotonic. This relation is most obvious in those receptors which adapt slowly. Fig. 4 shows the response from a mechanoreceptor on the clasper of a male *Phormia* which adapts to a steady deformation quite slowly. Fig. 7 is the response from a receptor on the anal plate of a female *Phormia* which also has a slow rate of adaptation. In Fig. 8 the frequency of the impulses is plotted against the size of the receptor potential for this type of receptor. The indication that at 0 mv. receptor potential the impulse frequency will also be 0/sec. is not signifi-

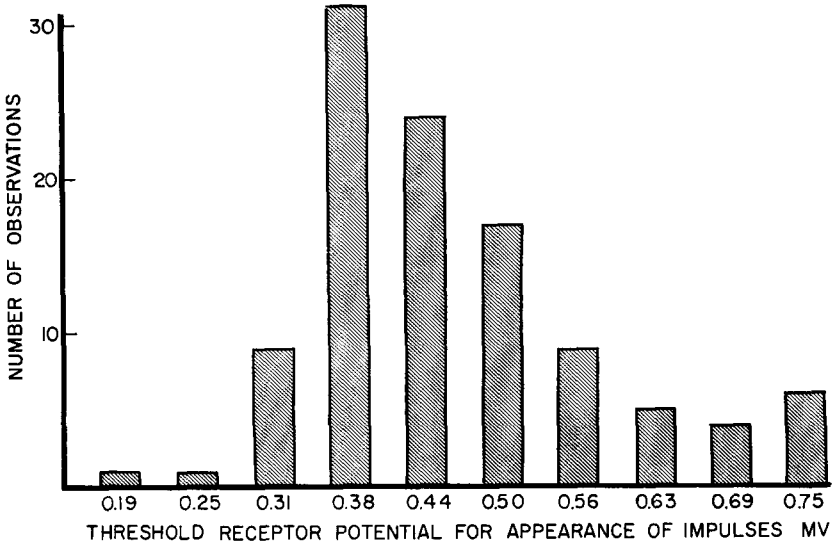

FIGURE 6. The threshold receptor potential of the mechanosensory neuron of a chemosensory hair on the wing of *Sarcophaga* which is accompanied by an impulse is plotted for a series of mechanical stimuli. In the largest number of trials the threshold was 0.38 mv. with the spread as shown.

cant, however, due to the difficulties of finding a non-stimulated or resting level. This difficulty has been mentioned above in section II.

The plots from other receptors show the same monotonic relation between the size of the receptor potential and the impulse frequency. At high values of the receptor potential the impulse frequency appears to reach a limiting value and little or no change is seen when the receptor potential is increased still more.

IV. *Relation between Receptor Potential and the Size of the Impulses*

The most striking feature of the recordings made from the mechanoreceptors is the change in size of the impulse as the receptor potential changes. In some receptors the impulse seems to reach the same absolute potential

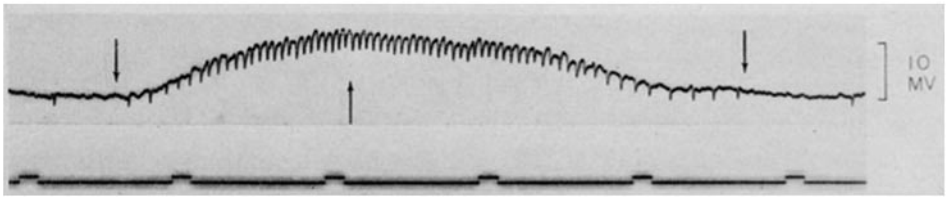

FIGURE 7. Response of mechanosensory hair on the anal plate of a female *Phormia* to changing mechanical stimulation. The left-hand arrow indicates the approximate beginning of the deformation; the middle arrow, the maximum; and the right-hand arrow the return to the undeformed position. Time marks recur at 0.2 second intervals. Positive at the recording electrode is down.

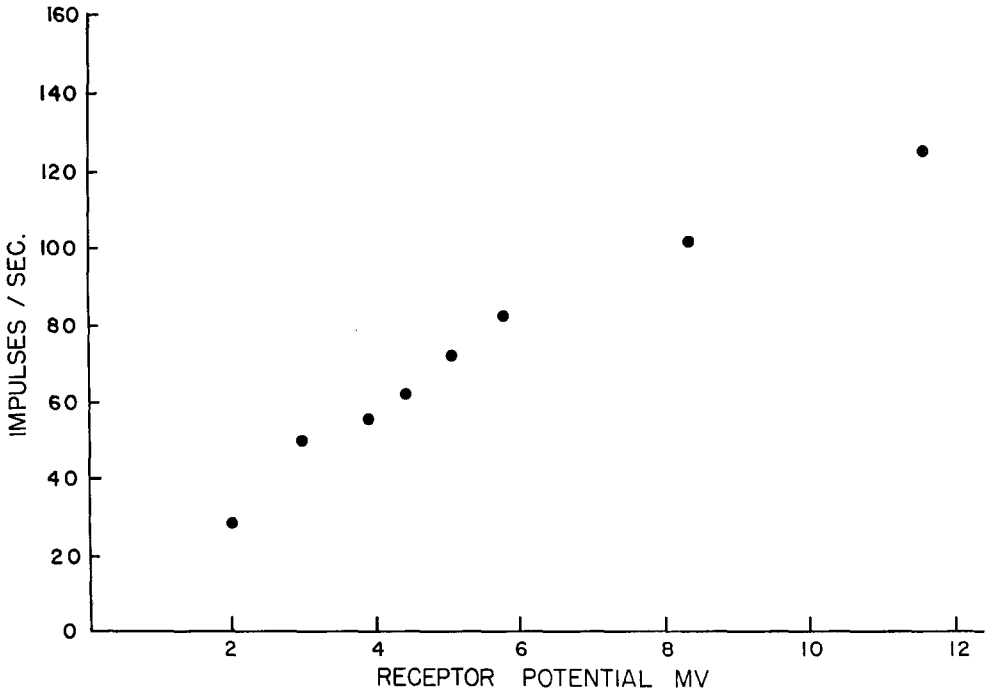

FIGURE 8. Receptor potential amplitude plotted against frequency of impulses for a mechanosensory hair on the anal plate of a female *Phormia* whose typical response is shown in Fig. 7. Each point is the average for 2 seconds.

regardless of where it begins, as is shown in Fig. 4. The relation between the receptor potential and the impulse size for these records is plotted in Fig. 9. In other receptors the impulse does not rise to the same absolute level, but the impulse size does vary directly with the generator potential. Fig. 10 shows this relation for the receptors on the grasshopper antenna whose typical response is shown in Fig. 11.

This change in spike size occurs not only in the neurons of singly innervated

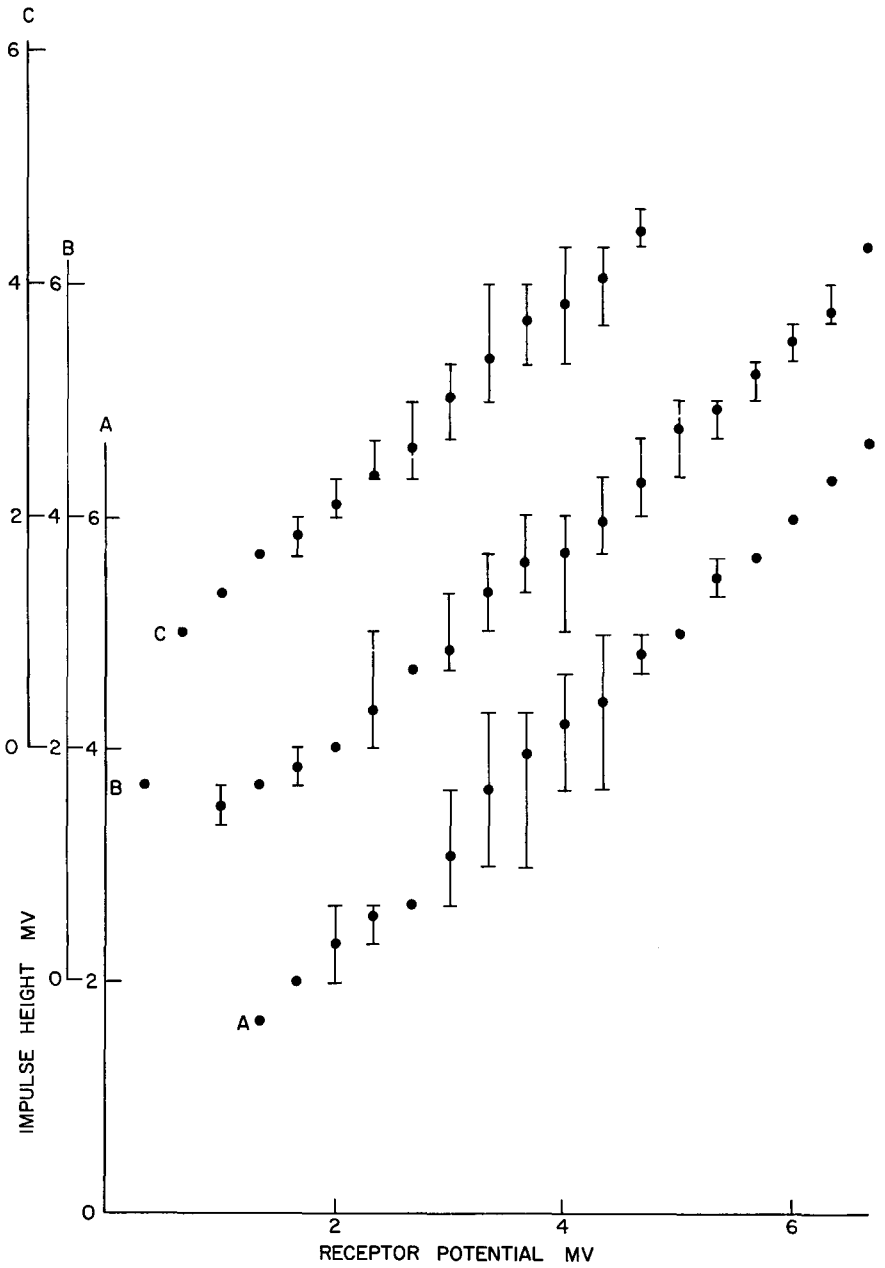

FIGURE 9. Impulse size plotted against receptor potential for a mechanosensory hair on the outer clasper of a male *Phormia*. These plots were made from the records shown in Fig. 4, where *A*, *B*, *C* refer to the individual records. The points are average values, the bars denote extreme values.

hairs but also in the mechanosensory neurons of multiple innervated hairs. The chemosensory hairs of most Diptera have three neurons—only one of which is a mechanoreceptor. Fig. 12 shows that these mechanosensory neurons exhibit the same relation between the impulse size and the receptor potential.

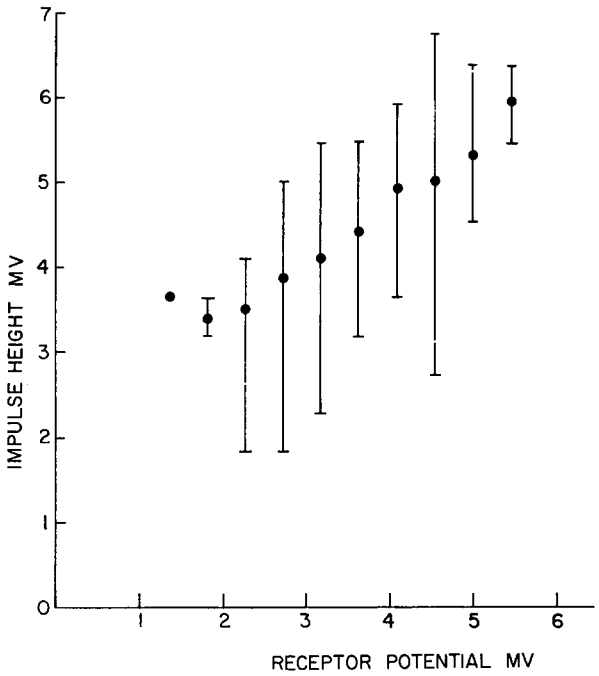

FIGURE 10. Impulse size plotted against receptor potential for a mechanosensory hair on the second antennal joint of *Melanoplus*. All points, except lowest receptor potential, are averages of at least twenty impulses. Lowest value is a single impulse. Bars denote extreme values. The typical response of this receptor is shown in Fig. 11.

DISCUSSION

The receptor potential in the insect mechanoreceptor is related to impulse initiation in most of the ways that a generator potential is. There is a critical level of threshold voltage that the receptor potential must attain before any impulses appear. An increase in the size of the receptor potential is accompanied by an increased frequency of impulses. However, when the impulses are initially positive, which is characteristic of an intracellular recording, we would expect to see the generator potential also positive going, that is, depolarizing in nature. In our recording situation in the mechanoreceptor the impulses are positive but the receptor potential is negative. Also, the variation in size of the impulse as the receptor potential changes is not found in an intracellular recording.

The most probable explanation of the receptor potential in the insect

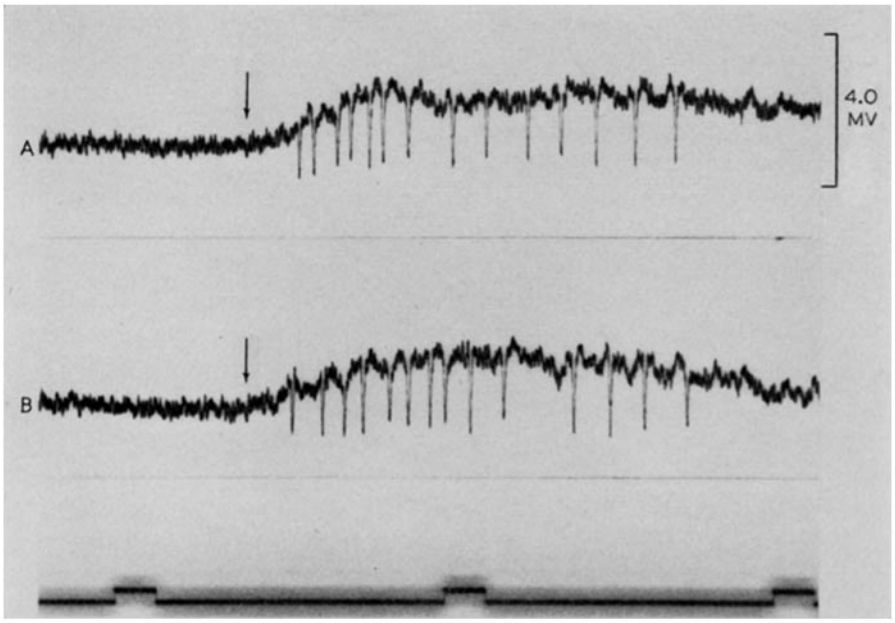

FIGURE 11. Response of mechanosensory hair on the second antennal joint of *Melanoplus* to increasing mechanical stimulation. Approximate onset of stimulation is indicated by arrows. The stimulus continues until the end of the record. Time marks recur at 0.2 second intervals. Positive at the recording electrode is down. *A* and *B* are responses to successive stimuli of approximately the same size.

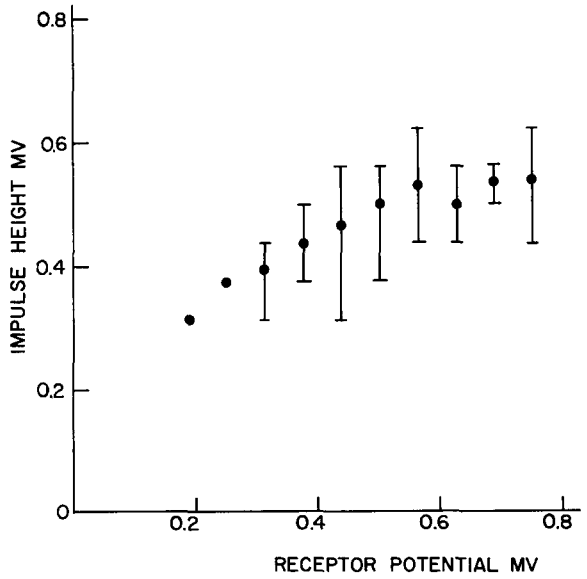

FIGURE 12. Impulse size plotted against receptor potential for a chemosensory hair on the wing of *Sarcophaga*. All points, except the two lowest receptor potentials, are averages of at least twenty impulses. Lowest two values are single impulses. Bars denote extreme values. The typical response of this receptor is shown in Fig. 2.

mechanoreceptor is the one suggested by Gray and Sato (1953) for the Pacinian corpuscle receptor potential. There is a change of membrane permeability due to the stimulation and charge is transferred across the membrane by ions moving down their electrochemical gradients. The change in membrane permeability may be due to mechanical distortion of part of the neuron membrane. The insect mechanoreceptor is probably similar to the Pacinian corpuscle in that there is a specialized portion of the membrane across which the receptor potential is developed.

An examination of both the histology of the mechanoreceptor and the recording conditions suggests the following explanation for the various phenomena described above:

The recording conditions are analogous to those encountered in a motoneuron when a micropipette is pressed tightly up against the soma membrane but has not penetrated it, yet positive going impulses are recorded (Freygang and Frank (1959)). If the resistance of the membrane under the electrode is less than the resistance of the leakage pathway between the electrode tip and the membrane then this electrode will record spikes generated at the axon hillock as positive. This, of course, is the case when the impulse does not invade the soma. The size of the impulse will depend upon the ratio of the resistances of the portion of the membrane under the electrode and the leakage pathway. Fig. 13 shows an equivalent circuit of this situation. R_m is the resistance of the membrane under the recording electrode and R_{leakage} is the resistance of the leakage pathway around the pipette tip. Since E_{spike}, the impulse potential, is thought to originate at the axon hillock, it is separated from the soma by the intracellular resistance R_2 and the extracellular resistance R_3. Since R_1, R_2, R_3, and R_4 are negligible with respect to R_m and R_{leakage}, the recorded size of the impulse is determined by the ratio of R_m to R_{leakage}. Any changes in R_m due to residual depolarization or hyperpolarization of the cell would change the impulse size although Freygang and Frank (1959) do not report any changes in impulse size, possibly because the percentage change in R_m under these conditions was very small.

The resting potential recorded between the electrodes in the model shown in Fig. 13 is E_1–E_2 where E_1 is the polarization of that portion of the membrane under the electrode tip. E_2 is the average polarization of that cell body. Any depolarization of the membrane under the electrode caused by a change in the membrane permeability would be represented by a decrease in E_1 and would be seen as an increased negativity whose time course and amplitude follow the change in membrane permeability.

In recording from the insect mechanoreceptor the electrode is not, in fact, pressed tightly up against the cell membrane as in the case of the motoneuron just described. The recording electrode is, however, in contact with the fluid

center of the hair. The hair is covered with a hydrophobic wax so that the only electrical contact is through the fluid in the central cavity of the hair. The lumen of the hair is almost completely occluded by the distal process of the receptor. The membrane covering this lumen represents part of the receptor site if not all of it. Although the studies with the light microscope by Hsü (1938), Grabowski and Dethier (1954), and Schneider and Kaissling (1957) do no more than hint at the space between the distal process of the

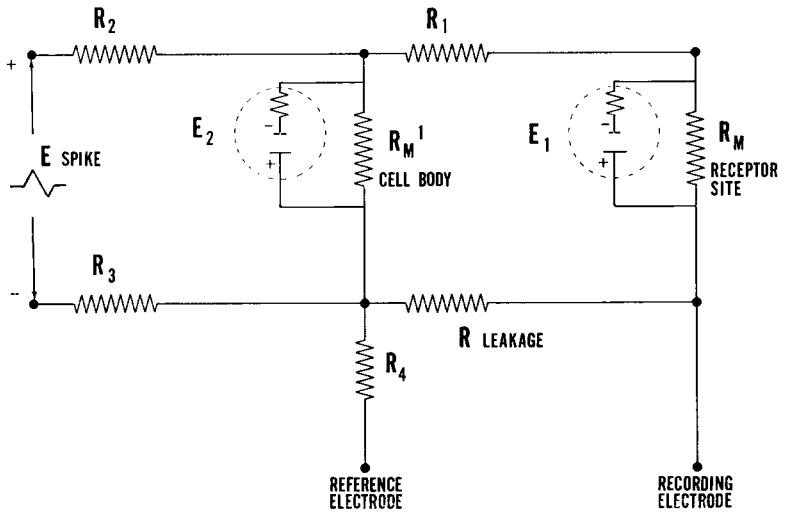

FIGURE 13. Electrical model of recording situation in which the recording electrode sees the external potential of a portion of the neuron which is isolated from the rest of the neuron by a high external resistance. In the case of the motoneuron R_{leakage} is made high by the pressure of the micropipette on the cell membrane. In the insect mechanoreceptor R_{leakage} is naturally high because of the anatomy. R_1 and R_2 are intracellular resistances, R_3, R_4, and R_{leakage} are extracellular resistances. R_m^1 is the average resistance of the cell membrane, while R_m is the membrane resistance at the receptor site. See text for explanation and typical values of components.

mechanoreceptor and the base of the hair, recent electron micrographs by Dethier and Larson (unpublished) show that the membrane is so close to the hair walls as to anatomically seal it off from the rest of the animal. This seal provides naturally the high leakage resistance pathway obtained by the pressure of the electrode against the cell membrane in the case of the motoneuron. The fluid-filled hair is thus an extension of the electrode and the recording situation may be represented by the equivalent circuit shown in Fig. 13.

The counterparts in the insect mechanoreceptor of the components shown in Fig. 13 are as follows:—

The receptor site is R_m, and the polarization across it E_1. The resistance of

the cell body is R_m^1 and the average polarization of it is E_2. The resistance of intracellular fluid is R_1 and the resistances of the intra- and extracellular fluids from cell body to that portion of the axon where the impulse is initiated are R_2 and R_3 respectively. R_1, R_2, and R_3 are probably quite small in relation to the other resistances in the circuit. If R_2 and R_3 are small, as we have just assumed, then the polarization of the site of initiation of the impulse can be represented by E_2. Variations in E_2 would be the generator potential responsible for impulse initiation. The leakage pathway between the distal process and the base of the hair is R_{leakage}. The resistance from the cell body to the reference electrode is R_4. R_4 may be large due to the presence of the basement membrane or some other structure between the cell and the reference electrode, as discussed by Wolbarsht (1958).

The potential recorded between the electrodes can be represented by the following expression:

$$(E_2 - E_1)\frac{R_{\text{leakage}}}{R_1 + R_{\text{leakage}}} + E_{\text{spike}}\frac{R_m^1 R_{\text{leakage}}}{R_m^1 R_m + R_m^1 R_{\text{leakage}} + R_{\text{leakage}}}$$

In the unstimulated state $E_1 = E_2$. We assume that a mechanical stimulus will increase the conductivity of the membrane at the receptor site, which change would be represented by a decrease in R_m. A decrease in R_m will decrease E_1 causing a negative potential to be seen between the electrodes.

It is evident in this model that the receptor potential seen at the recording electrode is only partially caused by the variation of E_1. It is really the difference between E_1 and E_2. Any decrease in E_2 would properly be termed the generator potential for it is this that would be responsible for the generation of impulses. E_2 will decrease as R_m decreases, but the electrode will only record the difference between E_1 and E_2 no matter how much E_2 has changed.

Any impulses that occur will be positive going with their amplitude changing as R_m varies.

One would expect in this situation that both the impulse and the receptor potential would change by the same percentage when R_m is changed, but this may not be the case if there is any appreciable external shunting action of E_{spike} caused by changes in R_m^1.

In the case of those receptors on the fly claspers we can estimate values for the various circuit components as follows:—

E_1, E_2 are about 60 mv.

R_1, R_2, R_3 are very small (about 10K each)

In the unstimulated state we know that the resistance as measured between the two electrodes is about 5×10^8 ohms. This resistance is equal to:

$$\frac{R_{\text{leakage}}(R_m + R_m^1)}{R_{\text{leakage}} + R_m + R_m^1} + R_4$$

The area of the receptor membrane represented by R_m does not appear to be more than 1 μ^2. If we assume the membrane at R_m has a specific resistance similar to that of a cat motoneuron, which is about 4000 ohm centimeters, then $R_m = 4 \times 10^{11}$ ohms. R_m^1 is around $1/100$ of that value. If we neglect R_4 then R_{leakage} is about 5×10^8 ohms. To cause a receptor potential of 10 mv., R_m would decrease to 3.0×10^9 ohms with R_m^1 unchanged. The resistance measured between the two electrodes then has changed less than 5 per cent which cannot be accurately detected due to instabilities of this order of magnitude in the baseline. If the value of R_4 is not negligible then changes in R_m would be even more difficult to detect.

This model of the mechanoreceptor appears to account for all the data available at the present time. We can say the following things about the receptor based on this model:

1. The mechanical stimulus effects a change in the membrane resistance at the receptor site.

2. The receptor potential seen in our recording conditions is the difference between the potential across the membrane at the receptor site and the general polarization of the cell.

3. The impulse is generated proximally to the receptor site and does not invade it.

4. The changes in the impulse size are due to the changes in the membrane resistance of the receptor site.

5. There is a high resistance between the fluid-filled center of the hair and the general body fluid. The value of this resistance is effectively determined by the close anatomical conjunction of the receptor membrane and the lumen of the hair cavity.

Further experimentation will, no doubt, suggest modifications of this model and lead us to a clearer understanding of the nature of the receptor site membrane.

The author is indebted to Dr. V. G. Dethier, Professor J. A. B. Gray, Dr. D. Goldman, Dr. F. Julian, Dr. E. F. MacNichol, Jr., Mr. B. Sandok, and Dr. H. G. Wagner for many helpful suggestions and discussions.

REFERENCES

BERNHARD, C. G., GRANIT, R., and SKOGLAND, C. R., 1942, The breakdown of accommodation-nerve as model sense-organ, *J. Neurophysiol.*, **5**, 55.

DETHIER, V. G., and LARSON, J. R., private communication.

EDWARDS, C., and OTTOSON, D., 1958, The site of impulse initiation in a nerve cell of a crustacean stretch receptor, *J. Physiol.*, **143**, 138.

FREYGANG, W. H., JR., and FRANK, K., 1959, Extracellular potentials from single spinal motoneurons, *J. Gen. Physiol.*, **42**, 749.

GRABOWSKI, E. T., and DETHIER, V. G., 1954, The structure of the tarsal chemoreceptors of the blowfly, *Phormia regina* Meigen, *J. Morphol.*, **94**, 1.

GRAY, J. A. B., 1959, Initiation of impulses at receptors, *in* Handbook of Physiology, Section I: Neurophysiology, (J. Field, H. W. Magoun, and V. E. Hall, editors), Washington, American Physiological Society, **1**, 123.

GRAY, J. A. B., and SATO, M., 1953, Properties of the receptor potential in Pacinian corpuscles, *J. Physiol.*, **122**, 610.

Hsü, F., 1938, Étude cytologique et comparée sur les sensilla des insects, *La Cellule*, **47**, 5.

LOWENSTEIN, W., 1959, The generation of electric activity in a nerve ending, *Ann. New York Acad. Sc.*, **81**, 367.

PUMPHREY, R. J., 1936, Slow adaptation of a tactile receptor in the leg of the common cockroach, *J. Physiol.*, **87**, 6P.

SCHNEIDER, D., and KAISSLING, K. E., 1957, Der Bau der Antenne des Seidenspinners *Bombyx mori*. I. II. Sensillen, cuticulare Bildungen und innerer Bau, *Zool. Jahrb.*, (*Anat.*), **76**, 223.

WOLBARSHT, M. L., 1958, Electrical activity in the chemoreceptors of the blowfly. II. Responses to electrical stimulation, *J. Gen. Physiol.*, **42**, 413.

WOLBARSHT, M. L., and DETHIER, V. G., 1958, Electrical activity in the chemoreceptors of the blowfly. I. Responses to chemical and mechanical stimulation, *J. Gen. Physiol.*, **42**, 393.

WOLBARSHT, M. L., and GRAY, J. A. B., 1959, Receptor potentials in the mechanoreceptors of insects, *Anat. Rec.*, **134**, 655.