

ELECTRICAL VARIATIONS DUE TO MECHANICAL TRANSMISSION OF STIMULI

BY W. J. V. OSTERHOUT AND S. E. HILL

(From the Laboratories of The Rockefeller Institute for Medical Research)

(Accepted for publication, January 7, 1931)

The electrical changes hitherto described for *Nitella* are (1) reversible responses, or propagated negative variations, and (2) irreversible ones or death waves. Responses of a different sort are often produced by bending, pinching, or cutting.¹ Although as reversible as propagated negative variations they resemble death waves in traveling rapidly and in passing a killed spot. As they are locally produced by a mechanical stimulus which travels down the cell they will be called mechanical variations to distinguish them from propagated negative variations (in which it is not the stimulus but the resulting excitation that moves along the cell).

These various responses are illustrated in the figures. Fig. 1 *a* shows a death wave² (a photographic record is shown in Fig. 2). This is the result of a drastic mechanical disturbance. A less vigorous

¹ In cutting, bending, or pinching care was taken to avoid communicating a charge. By means of a glass rod the cells were bent over the edge of the paraffin block on which they rested, or pinched between the glass rod and the paraffin block, and were touched only with materials insulated from the body of the operator and at the same potential as the cell.

Cells were bent at various angles up to 90° and as a rule were released at once whereupon they resumed their normal state and seemed to suffer no injury (save in the case of certain exceptional material, possibly belonging to a different species). In most cases the cell could be bent repeatedly at the same spot, giving a response each time.

The experiments were made on *Nitella flexilis*, the average temperature being about 21°C. The technique has been previously described (Osterhout, W. J. V., and Harris, E. S., *J. Gen. Physiol.*, 1928-29, 12, 167, 355; Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1930-31, 14, 385). The method of measuring and recording potentials is essentially electrostatic.

² Cf. Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1930-31, 14, 385.

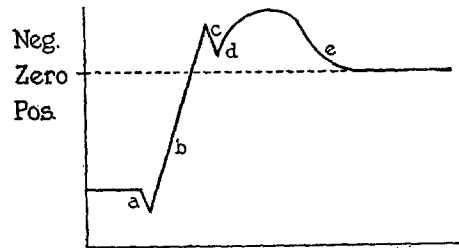


FIG. 1 *a*. Diagram to show successive movements of the death wave, the duration of *a*, *b*, and *c* being exaggerated. (The curve does not always go above zero and sometimes has but one crest, as in Fig. 7.) Cf. Figs. 2 and 7.

(The death wave can pass a killed spot and the rate of transmission is very high.)

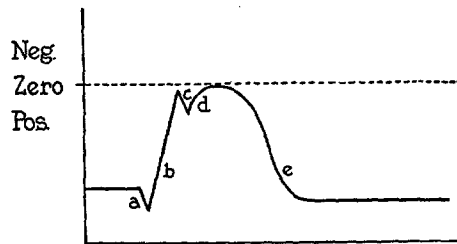


FIG. 1 *b*. Diagram to show the successive movements in the mechanical variation, the duration of *a*, *b*, and *c* being exaggerated. (The curve sometimes has but one crest.) Cf. Figs. 2 and 5.

(The mechanical variation can pass a killed spot and the rate of transmission is very high.)

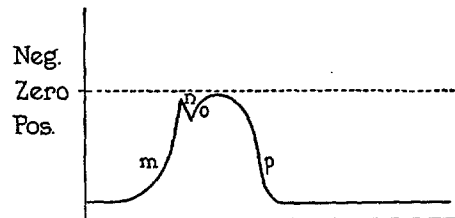


FIG. 1 *c*. Diagram to show the successive movements in a propagated negative variation. (The curve sometimes has but one crest.) Cf. Figs. 4 and 9.

(The propagated negative variation cannot pass a killed spot and the rate of transmission is very low.)

one produces a mechanical variation (Fig. 1 *b*), whose curve begins like that in Fig. 1 *a*, but is reversible and returns to the level from which

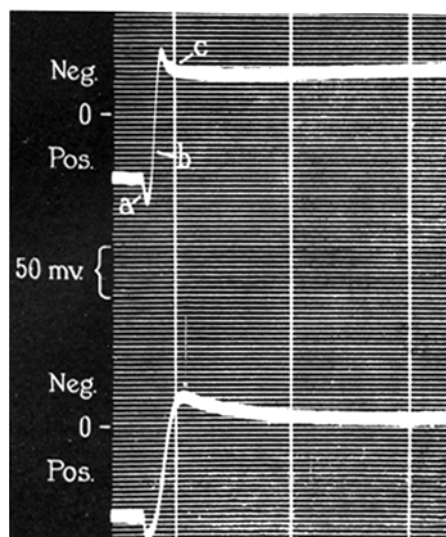


FIG. 2. Fast photographic record of an experiment arranged as in Fig. 3: the upper curve records the p.d. of *A* with reference to *C*, the lower curve that of *B* with reference to *C*. Cutting at *Q* produced the movements *a*, *b*, and *c* followed by others not shown on the record but indicated in Fig. 1 *a*.

The intervals between vertical lines represent 0.1 second.

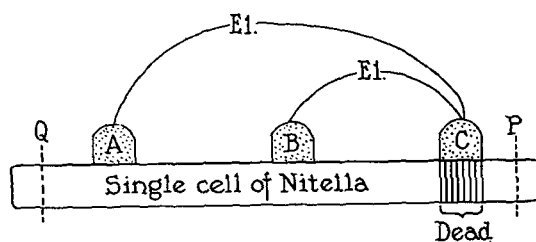


FIG. 3. Diagram to show the arrangement of an experiment. The spot *C* was killed by chloroform before the stimulus was applied: 0.001 M KCl was applied at all contacts.

it started without going above zero. The curve of the propagated negative variation (Fig. 1 *c*) commences with an upward instead of a

downward movement, and this starts upward less abruptly than in the other cases (cf. Fig. 4).

Passage beyond a killed spot is illustrated by Fig. 5 which may be interpreted as follows: Cutting³ at *X* (Fig. 6) resulted in a vigorous mechanical disturbance which traveled down the cell to *A*, and caused the irreversible change (death wave) shown by the upper curve (which does not return to the level from which it started). The disturbance passed the killed spot (*C*) but its intensity fell off as it progressed, and on reaching *B* it produced only the reversible response (mechanical variation) shown by the lower curve.

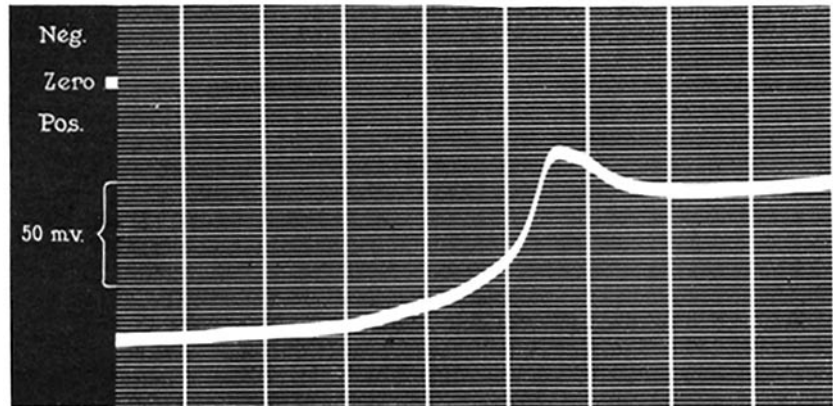


FIG. 4. Fast photographic record of an experiment arranged as in Fig. 3 with contacts *A* and *C* only. No mechanical stimulation but only a propagated negative variation (originating at *Q*), showing the gentle upward slope of the first movement *m*. Cf. Fig. 1 *c*.

The interval between the vertical lines is 0.2 second.

Such falling off is characteristic of mechanical disturbances: for example, even when the death wave does not pass a dead spot there is a loss of intensity as it travels.³ This is shown in Fig. 7 (the loss is often very much greater). Both the amplitude and the speed of the

³ Osterhout, W. J. V., and Harris, E. S., *J. Gen. Physiol.*, 1928-29, **12**, 167, 355; Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1930-31, **14**, 385.

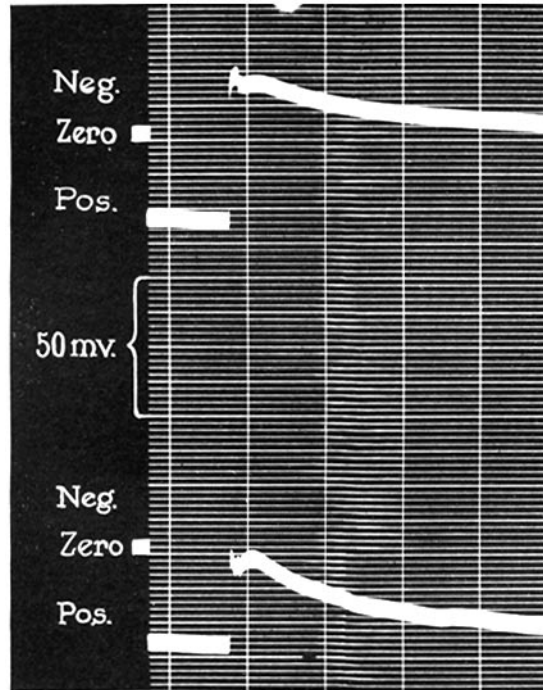


FIG. 5. Photographic record of an experiment arranged as in Fig. 6. The upper curve records the p.d. of *A* with reference to *C*, the lower curve that of *B* with reference to *C*. When the cell was cut at *X* (Fig. 6) a mechanical disturbance traveled to *A* producing an irreversible response (upper curve), continued past the dead spot (*C*), and produced a reversible response at *B* (lower curve).

The interval between the vertical lines is 5 seconds.

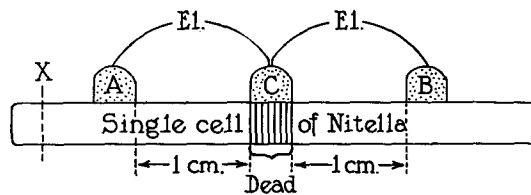


FIG. 6. Diagram to show the arrangement of an experiment. The spot *C* was killed by chloroform before the cell was stimulated; 0.001 M KCl was applied at all contacts.

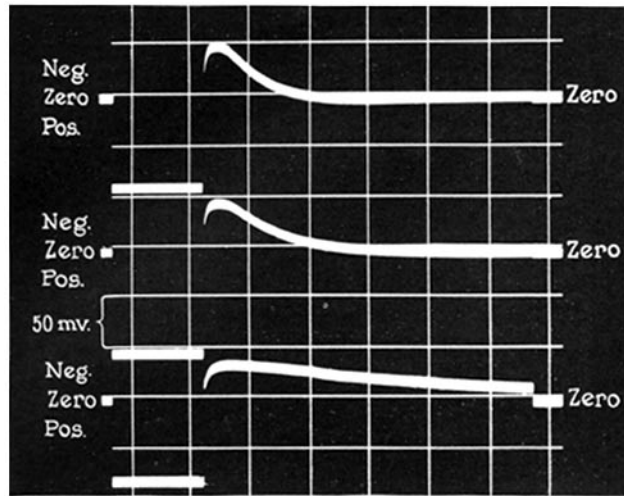


FIG. 7. Photographic record of an experiment arranged as in Fig. 8. The uppermost curve shows the P.D. of *A* with respect to *C*, the middle curve that of *B* with respect to *C*, and the lowest curve that of *D* with respect to *C*. When the cell was cut at *X* a death wave traveled down the cell, losing intensity as it progressed, as shown by the lessened amplitude and speed of the movements constituting the response.

The interval between the vertical lines is 5 seconds.

In this case the curve has but one crest but more commonly it has two as in Fig. 1a.

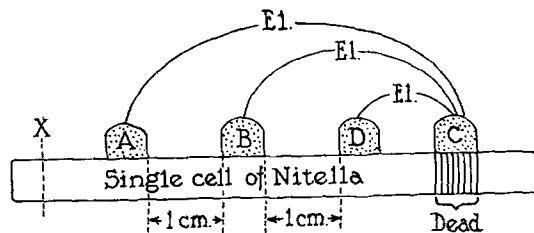


FIG. 8. Diagram to show the arrangement of an experiment. The spot *C* was killed by chloroform before the cell was stimulated: 0.001 M KCl was applied at all contacts.

movements (but not the speed of transmission⁴) fall off⁵ as the stimulus moves along the cell.

On superficial examination the curve of a mechanical variation (lower curve in Fig. 5 and both curves in Fig. 10) might be confused with that of a propagated negative variation such as is shown⁶ in Fig. 9, but there are evident differences. In the first place, the upward movement in Figs. 5 and 10 is much more abrupt (the record is

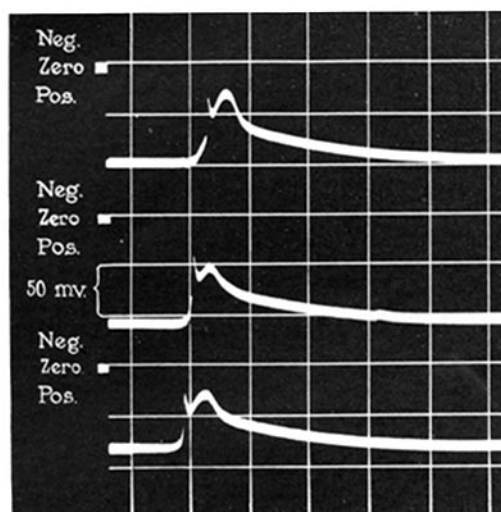


Fig. 9. Photographic record of an experiment arranged as in Fig. 8. The uppermost curve records the p.d. of *A* with reference to *C*, the middle curve that of *B* with reference to *C*, and the lowest curve that of *D* with reference to *C*. A propagated negative variation started by chemical stimulation at *C* (Fig. 8) appeared at *D* (lowest curve), then at *B* (middle curve), and a little later at *A* (uppermost curve).

The interval between the vertical lines is 5 seconds.

⁴ The speed of transmission is estimated from the first movement *a* observed on fast records.

⁵ The amplitude of the response also falls off as a mechanical disturbance travels in a rubber tube, as elsewhere explained.² This amplitude likewise diminishes as the force of the blow decreases.

⁶ In this case the curves do not go to zero. This will be discussed in later papers.

too slow⁷ to show the first downward movement *a*). In the second place the time of transmission differs; in Figs. 5 and 10 the first upward movement *b* appears to be simultaneous in the upper and lower

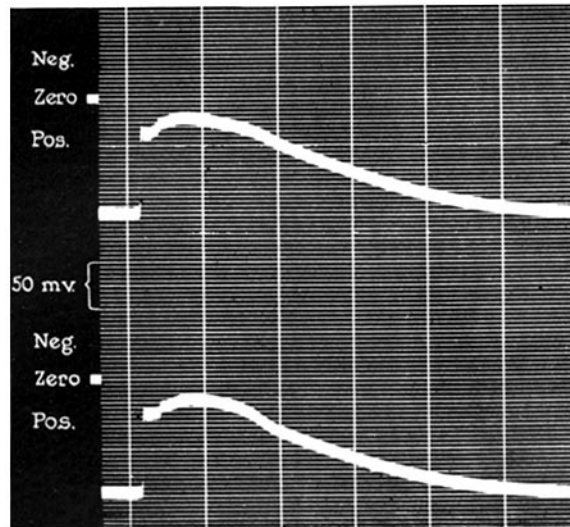


FIG. 10. Photographic record of an experiment arranged as in Fig. 3. The upper curve records the p.d. of *A* with reference to *C* and the lower curve that of *B* with reference to *C*. When the cell was pinched at *P* (Fig. 3) a mechanical disturbance traveled along the cell producing mechanical variations at *B* (lower curve) and at *A* (upper curve). The responses appear to be simultaneous in this record.

The interval between the vertical lines is 5 seconds.

curves (and presumably this applies also to the downward movement *a*), but in Fig. 9 the first upward movement⁷ occurs later at *A* (uppermost curve) than at *B* (middle curve). The difference in time between the first upward movement⁸ at *A* and *B* is about 1 second (and

⁷ Figs. 1 *a*, 1 *b*, and 1 *c* are based on faster records in which the photographic paper moved at least 12.5 cm. per second.

⁸ This need not always be the case. For the corresponding relations in movements *c* and *d* see Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1930-31, 14, 385.

this is also true for *B* and *D*). Since the distance between *A* and *B*⁹ (and between *B* and *D*) is 1 cm. the rate of transmission is about 1 cm. per second.¹⁰

The transmission time is characteristic. Mechanical variations as seen⁶ in Fig. 10 have the appearance of being simultaneous at both

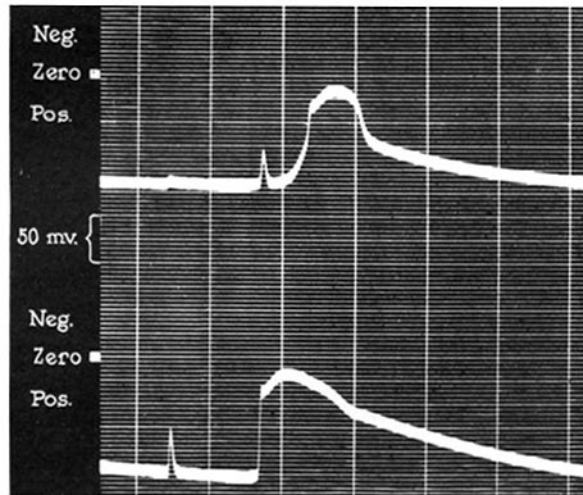


FIG. 11. Photographic record of an experiment arranged as in Fig. 3. The upper curve records the p.d. of *A* with reference to *C* and the lower curve that of *B* with reference to *C*. When the cell was pinched at *P* a mechanical disturbance traveled rapidly to *B*, producing an incomplete mechanical variation (lower curve), and then to *A*, producing a still smaller response (upper curve). A second pinch produced a complete mechanical variation at *B* and an incomplete one at *A*, but a little later a propagated negative variation arrived at *A* (it is characterized by a gradual upward movement and a slow rate of transmission).

The interval between the vertical lines is 5 seconds.

contacts: the figure indicates that the mechanical disturbance, produced by pinching at *P* (Fig. 3), traveled rapidly along the cell, pro-

⁹ *I.e.*, the distance from the right edge of contact *A* to the left edge of contact *B*. Cf. footnote 2.

¹⁰ In this case the propagated negative variation originated by chemical stimulation at *C* as elsewhere explained (Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1929-30, 13, 459).

ducing the same response at *B* (lower curve) and at *A* (upper curve). The mechanical disturbance probably travels at the rate of sound in water, as elsewhere explained,² in which case the responses at *A* and *B* would appear to be simultaneous on our records.

When the intensity of the mechanical disturbance falls off so that it can no longer produce a complete mechanical variation (*i.e.*, one whose curve goes to zero), it often produces a less extensive change, which may be called an incomplete mechanical variation. Such changes are shown⁶ in Fig. 11 resulting from a bend at *P* (Fig. 3) which produced a small response at *B* (lower curve) and a still smaller one at *A* (upper curve). A few seconds later the cell was more vigorously bent at *P* and we see at *B* a complete mechanical variation (going practically to zero) and simultaneously an incomplete one at *A*. Soon afterwards *A* made still another response whose gradual upward movement and slow rate of transmission are characteristic of a propagated negative variation. The interval between the first visible movement¹¹ at *B* and the slow upward movement at *A* after the second pinch is about 1 second and as the distance is 2 cm. we may regard the rate of transmission as about 2 cm. per second (the speed of a propagated negative variation¹²).

It would seem that a mechanical disturbance strong enough to produce a complete local variation at *B* fell off so much that when it reached *A* it caused only a small response and presumably nothing more would have happened at *A* had not the local variation at *B* passed over into a propagated negative variation which then traveled on to *A*. A change of this sort is to be expected if a mechanical disturbance can greatly reduce the p.d. across the protoplasm at any point and travel no further, for a flow of current will presumably start from the next point¹³ having a sufficient p.d. and so produce a propagated negative variation.

¹¹ *I.e.*, between the start of the upward movement at *A* and that at *B*: this can be determined with sufficient accuracy for our present purpose which is merely to find the approximate rate of transmission.

¹² Cf. Blinks, L. R., Harris, E. S., and Osterhout, W. J. V., *Proc. Soc. Exp. Biol. and Med.*, 1928-29, **26**, 836.

¹³ Cf. Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1929-30, **13**, 459, 547. Osterhout, W. J. V., *Electrical phenomena in the living cell*, in Harvey Lectures, 1929-30, The Williams and Wilkins Co., Baltimore, 1931, 169.

In some cases the change from a mechanical to a propagated variation may occur so early that we see little or nothing at the second contact save the propagated negative variation. This is most often observed when the bending or pinching is so gentle that the cell can be repeatedly stimulated in the same spot without seeming to suffer any permanent injury.¹⁴ As an illustration we may turn⁶ to Fig. 12. Bending at *Q* (Fig. 3) produced a mechanical variation at *A* (as

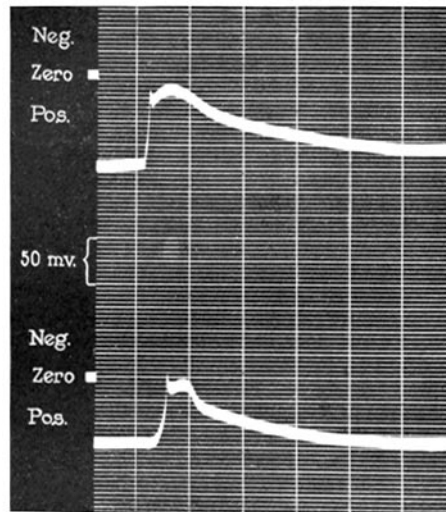


FIG. 12. Photographic record of an experiment arranged as in Fig. 3. The upper curve shows the P.D. of *A* with reference to *C* and the lower curve the P.D. of *B* with reference to *C*. When the cell was bent at *Q* a mechanical disturbance traveled to *A* producing a mechanical variation (upper curve) but the intensity of the disturbance fell off so that it changed over to a propagated negative variation, as shown by the gentle upward slope at *B* (lower curve) and slow rate of transmission.

The interval between the vertical lines is 5 seconds.

shown by the abrupt upward movement on the upper curve). But before it reached *B* it passed over into a propagated negative variation (as shown by the gentle upward slope of the first movement on the lower curve): this appeared at *B* about a second after the first move-

¹⁴ A very vigorous bend or pinch may produce irreversible changes (death waves).

ment at *A*, and as the distance between *A* and *B* is 1 cm. the rate of transmission is about 1 cm. per second (*i.e.*, that of a propagated negative variation).

It seems justifiable to conclude that a mechanical disturbance may produce a death wave which, as it travels, may lose intensity so that it can set up only a mechanical variation and later only an incomplete one which may finally pass over into a propagated negative variation.

It is of interest to note that in the spring and fall cells are often found which cannot be stimulated either electrically or chemically to give propagated negative variations but repeated bending or pinching at the same spot (at intervals of 20 seconds or more) may produce each time a mechanical variation (which on superficial examination might pass for a propagated negative variation).

How does a mechanical disturbance produce an electrical response? Aside from streaming potential¹⁵ a rupture of the non-aqueous surface film might lessen or abolish the P.D. across the protoplasm: possibly the mechanical disturbance may cause ions to move into the protoplasm and thus lower the P.D. without rupturing the film.¹⁶ As such changes could not arise in a homogeneous medium they furnish evidence in favor of the idea that the aqueous protoplasm is covered by non-aqueous films.

It would be interesting to know how general such phenomena are in the field of mechanical stimulation, which includes such diverse features as the senses of touch and hearing, the mechanical stimulation of motile organs in plants,¹⁷ and thigmotropism; geotropism seems to be in the same category as it depends on deformation of the protoplasm.¹⁸

The all or none law does not apply to incomplete mechanical variations, for the response varies with the strength of the stimulus. Although this is sufficiently evident from a qualitative standpoint it

¹⁵ The effects of streaming potential (which have been considered in a previous paper²) seem to be relatively transitory.

¹⁶ Osterhout, W. J. V., Electrical phenomena in the living cell, in Harvey Lectures, 1929-30, The Williams and Wilkins Co., Baltimore, 1931, 169. Osterhout, W. J. V., and Hill, S. E., *J. Gen. Physiol.*, 1929-30, **13**, 547. Blinks, L. R., *J. Gen. Physiol.*, 1929-30, **13**, 361, 495.

¹⁷ Cf. Stern, K., *Elektrophysiologie der Pflanzen*, Julius Springer, Berlin, 1924.

¹⁸ This might occur either with or without otoliths, starch grains, etc.

cannot be investigated quantitatively until we have a satisfactory method of regulating the strength of the stimulus.¹⁹

There is an interesting point touching the form of the curves. Gasser and Erlanger²⁰ have shown that in the case of nerve the double crest indicates different rates of conduction in different fibres. Evidently the double crest in our curves cannot be explained by assuming different rates of conduction in different parts of the protoplasm. For if this were the case we should have a wider separation of the crests as the conducting path lengthened but this is certainly not the rule and occasionally we find records like Fig. 9 which shows that the contact nearest to the point of stimulation (lowest curve) has a greater separation of crests than the others. Furthermore we find (Figs. 5, 10, 11, and 12) a double crest where no conduction of the stimulus is supposed to occur but each variation is due to a mechanical stimulus acting at the point where the response occurs.

We desire to add that we began our investigation by repeating preliminary experiments made by Mr. E. S. Harris²¹ (in collaboration with the senior author).

SUMMARY

Mechanical stimulation of *Nitella* often produces responses resembling propagated negative variations but traveling faster and going past a killed spot. They appear to result from a mechanical disturbance traveling along the cell and stimulating each spot it touches (*i.e.* the stimulus itself travels). They are called mechanical variations to distinguish them from propagated negative variations.

A mechanical disturbance may cause an irreversible change (death wave), but in traveling along the cell it may lose intensity and then produce only a reversible response (mechanical variation) which may eventually change to a propagated negative variation.

The all or none law does not apply to incomplete mechanical variations, for the response varies with the strength of the stimulus.

¹⁹ It is easy to strike the cell a measured blow, but since the effect depends on the physical characteristics of the cell (*e.g.*, diameter, flexibility of wall, turgidity, etc.) a given series of blows can be compared only qualitatively from cell to cell.

²⁰ Gasser, H. S., and Erlanger, J., *Am. J. Physiol.*, 1927, **80**, 522.

²¹ Blinks, L. R., Harris, E. S., and Osterhout, W. I. V., *Proc. Soc. Exp. Biol. and Med.*, 1928-29, **26**, 836.