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Receptor Potentials and Action Potentials in *Drosera* Tentacles

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Summary. Voltage fluctuations identified as receptor potentials can be detected with electrodes applied to the mucilage surrounding the head of a tentacle of *Drosera intermedia* if the head is stimulated by contact with a live insect, by the touch of a clean, inert object, or by application of salt solutions. Associated with a low receptor potential are action potentials, which occur at a frequency dependent on the magnitude of the receptor potential. These action potentials can be detected with electrodes applied to any region of the stalk of the tentacle. Inflection of the lower stalk follows the occurrence of action potentials. Inflection is minute for isolated action potentials but large and rapid when several occur within a brief interval.

The apparent amplitude of action potentials recorded from the stalk is independent of receptor potential amplitude, but that of action potentials recorded from the mucilage commonly decreases as the receptor potential deviates from the baseline and increases as it returns. It is suggested that variation of apparent amplitude of the action potentials may result from postulated variation in the resistance of receptor membranes.

Introduction

When an insect lights on the mucilage-laden tentacles of a vigorous *Drosera* leaf, its feet become caught and in its thrashing efforts to escape it is apt to bump into still more tentacles and to become well coated with sticky slime. If the insect becomes immobilized in the middle of the leaf, within an hour or so the outer tentacles will fold in around it. If the insect is trapped on the edge of the leaf, the stimulated outer tentacles begin to bend inward relatively rapidly, carrying the insect to the center. Again, within 1–2 h the remainder of the outer tentacles will surround the insect.

The immediate movements are nastic, while the delayed slow movements are considered to be tropistic in most species (Behre, 1929); the former are brought about by direct stimulation of the responding tentacles and the latter are evoked indirectly by stimulation of nearby tentacles (Darwin, 1875). It is with the rapid bending that the present study deals.

The curious insect-trapping behavior of *Drosera* attracted the attentions of a great many early biologists, whose work is culminated by the comprehensive and painstaking study of Charles Darwin (1875). Darwin showed that the tentacles are sensitive to both chemical and mechanical stimulation. He assayed the effectiveness of a variety of both ill-defined and well-defined chemical substances ranging from oil of cloves to "poison from the fang of a living adder" and from antimony tartrate to ammonium phosphate. The latter produced bending when tentacles were immersed in solutions as dilute as 3.5 μM, and many ammonium salts were active at somewhat higher concentrations. Sodium salts were less effective but were demonstrated to cause bending when applied in concentrations of about 20 meq Na^+/l. In contrast, potassium salts brought about no bending and a 30 min pre-immersion of a leaf in KCl was stated to inhibit response to subsequently applied ammonium carbonate for 5 h. Drops of rain failed to cause tentacles to bend, but small solid objects such as grains of sand, when placed on the head of a tentacle, brought about bending. Rubbing with a hair or a fine glass rod was a particularly effective means of causing inflection.

By localized application of raw meat and other stimulatory substances as well as by localized rubbing, Darwin (1875) established that reception is strictly confined to the heads of the tentacles. However, bending occurs primarily in the basal region of the stalks. The separation of stimulus and response in space and time led Darwin to propose that in the case of nastic movement an impulse passes from the sensory head of the tentacle to the motor region of the stalk, and in the case of indirectly stimulated tropistic movement the same impulse additionally travels through the leaf blade to the motor region of neighboring tentacles. Darwin compared the postulated impulse with that of an animal nerve, but believed that differences were greater than similarities. He suggested that transmission might occur by spreading changes in the physical state of the protoplasm (aggregation).

Even before Darwin published his findings on *Drosera*, Burdon-Sanderson (1873) established that in the closely related carnivorous plant *Dionaea* an action current links stimulation of mechano-receptive trigger hairs to motor response of the trap lobes. Darwin had encouraged Burdon-Sanderson to work with *Dionaea* (F. Darwin, 1903, letters 716 and 726), and supplied him with his first experimental plants (Burdon-Sanderson, 1873; F. Darwin, 1903, letter 716). Burdon-Sanderson telegraphed his first findings to Darwin, who promptly responded that he "really ought to try *Drosera*" (F. Darwin, 1903, letter 717). Although Burdon-Sanderson apparently never extended his studies to *Drosera*, Charles Darwin's son Francis took up the suggestion, but only went so far as to demonstrate that electric shocks could trigger movement in *Drosera* tentacles as well as in *Dionaea* traps (Darwin, 1875, footnote, page 37). He seems never to have reported measurement of action currents or potentials in *Drosera*. Darwin did not mention an earlier failure of Nitschke (1860) to stimulate tentacle movement by shocking with an induction coil, but Pfeffer (1906), unaware of the younger Darwin's success, analyzed Nitschke's failure as due to both improper magnitude and application of shocks.

In 1907, the first graphs purported to represent action currents in *Drosera* tentacles were presented by Bose; these particular records, though lacking in detail, appear credible, but accompanying pictures showing "action currents" from such an unlikely source as India rubber and similar "response by resistivity" of tungsten powder make the interpretation difficult. Then Umrath in 1929 (see also 1937, 1959) reported action potentials in *Drosera*; most of his evidence deals with voltage variations recorded from the surface of leaves which were stimulated by cutting the blade or pulling off tentacles. Umrath (1937) obtained similar data with a number of unrelated species, so the significance of such damage potentials for the

normal carnivorous behavior of *Drosera* is questionable. Of considerably more physiological interest is Umrath's report (1929) that irregularly spaced action potentials of erratically variable height and with rise times of from 1 to 10 s may be recorded on the leaf near the base of the tentacle when the head is stimulated by a living or dead mosquito larva. Making electrical contact with the plant by inserting a thin, gold-plated sewing needle and using an iron wire for a reference electrode, he was able to observe action potentials only near the stimulated tentacle, and not at other sites on the leaf. Assuming implicitly that transmission is slower than reception and the generation of action potentials, he calculated that action potentials travel 0.3 mm s^{-1}. This is about the same as the minimum propagation rate which may be calculated from Darwin's report (1875) that the lag separating stimulation of the head and bending of the basal region of a 2 or 3 mm tentacle may be as brief as 10 s.

Umrath's two published records are, however, difficult to interpret. The great irregularity in size and spacing of what one might presume to be action potentials raises the question whether action potentials of constant size pass along multiple tracks down the stalk, whether action potentials of variable height and brief refractory period pass along a single track, or whether the records (which exhibit considerable drift) are badly confused by polarization of electrodes or by electrical interference. Umrath (1929, 1959) suggested that because he could not detect action potentials from any portion of the leaf blade excepting cells at the base of the tentacle, conduction must be decremental. He believed that multiple stimuli could somehow reinforce each other and result in propagation of an action potential across the leaf from one tentacle to the next. However, the possibility that conduction occurs without decrement within the tentacle but cannot spread into the cells beyond must also be considered; the damage potentials which Umrath observed in the leaf are not necessarily closely related to action potentials or propagated in the same way, so that it cannot be assumed without further evidence that cells in the leaf blade are capable of coordinating behavior by propagating action potentials.

The purpose of the present paper is to demonstrate that action potentials, triggered by receptor potentials, do mediate the rapid bending response of the outer tentacles of *Drosera*, and to extend understanding of the behavior and role of both types of signal.

Materials and Methods

a) Plants. The figures of this paper illustrate experiments with *Drosera intermedia* Hayne, but similar action potentials and receptor potentials were also observed in *D. rotundifolia* L. Voucher specimens, S. Williams No. 6 (MO 1959591) and S. Williams No. 7 (MO 1959590), respectively, are filed in the Herbarium of the Missouri Botanical Garden. Plants were collected from the bog on the eastern edge of Mud Lake near Michigan Biological Station. They were grown in their sphagnum substratum in terraria covered with clear, thin, perforated plastic sheets. These terraria were placed in a Sherer Model CEL 257 HL growth chamber (Sherer-Gillett, Marshall, Mich.) with a 14-h day at 24°C and a 10-h night at 19°C. The plants received about 100 μW mm^{-2} illumination from a bank of 10 Sylvania F48T12-VHO-GRO-WS Gro-lux tubes (Sylvania Electric Products, Mountain View, Cal.) and 10 60-W incandescent lamps. Sensitivity of the tentacles was low early in the morning and rose during the day; experiments were usually performed late in the day.

It was necessary to maintain the plants at high humidity at all times in order to prevent mucilage from drying on the surface of the tentacles. Thus, immediately

before each experiment a plant and the associated spagnum in which it was rooted was carefully removed to the bottom of a Petri dish containing deionized water and covered with an inverted beaker for transport to the laboratory. For experimental manipulations the plant in the Petri dish was placed on the stage of a Wild stereomicroscope (Wild Heerbrugg, Heerbrugg, Switzerland) in a chamber fitted with a hose through which cool water vapor flowed at an adjustable rate. It was determined with a thermistor that the temperature of the secretion drop on a moderately illuminated tentacle head was close to that of the ambient air of the chamber; all experiments were carried out between 21 and 28° C. Under these conditions, plants secreted actively for many hours.

b) Cytology. In order to provide a firmer basis for both method and theory, a preliminary study of the cytology of tentacles was carried out (Williams, 1971).

c) Recording Methods. All recordings were made from intact plants by means of Ag; AgCl electrodes. Each recording electrode was connected to the plant by means of a salt bridge consisting of a strand of fine cotton thread protruding from the tip of a pipette filled with 1% Difco Bacto-Agar (Difco Labs., Detroit, Mich.) and 0.1 M NaCl or KCl. (0.01 M KCl was used for the experiments of Results section 1a.) It is important that the solution-soaked strands, less than 0.5 mm in diameter, remained moist within the humidity chamber. A similar salt bridge connected the Ag; AgCl reference electrode with the sphagnum-filled water in which the roots of the plant were immersed. The recording electrodes were connected to unity gain, negative capacitance, electrometer-amplifiers (Pico-metric Model 181, Instrumentation Lab., Inc., Watertown, Mass.). In order to eliminate interference, amplfier outputs were usually passed through one of two types of low-pass filters. The first of these, Type LLP-15 FR6RXIIFAI from United Transformer Corp. (U.T.C.), New York, N. Y., with pass band 0–15 Hz and rise time (10–90%) 32 ms, reduced voltage amplitude in the pass band by a factor of 0.47. The second was a simple low-pass RC filter made of 5 cascaded stages, with rise time 100 ms, pass band 0 to 2.8 Hz, and essentially no voltage reduction in the pass band. (The U.T.C. filters responded to a sharp pulsatile input—specifically, the electrical stimulus—by giving a brief oscillatory output. This output, seen at the beginning of many action potentials in the figures of this and the following paper, is called the filter artifact. This artifact will vary with the nature of the input to the filter which in turn is controlled by the nature of the stimulatory pulse and by the passive electrical properties of the tissue, such as its impedance. It will be noticed in some figures that a positive-going portion of the filter artifact may overshoot the baseline in one part of a recording but not in other parts. However, because no consistent patterns of overshoot behavior were discerned when the recordings made through the U.T.C. filter were compared, no judgements about tissue impedance should be based on the properties of the filter artifact.) The filtered signals were recorded on a Mark 220 Recorder from the Brush Instrument Div. of Gould, Inc., Cleveland, Ohio. If further amplification was required a two-channel preamplifier with a gain of 100 and a 50-μs rise time was also used. Frequently one of the amplifier outputs was led off ahead of the low pass filter into a Model 159 Recorder from Hitachi Perkin-Elmer, South Pasadena, Cal.

When preparing recordings for photography, space was saved by cutting apart the chart from the Brush recorder and carefully splicing the traces closer together. Although the event marking channel was set to produce a time mark once each second, this trace was frequently replaced with one showing marks every 5 s in order to assure readability after photographic reduction. If a recording was filtered through the U.T.C. filter, voltages were corrected for attenuation. Upward pen deflection indicates a positive voltage change.

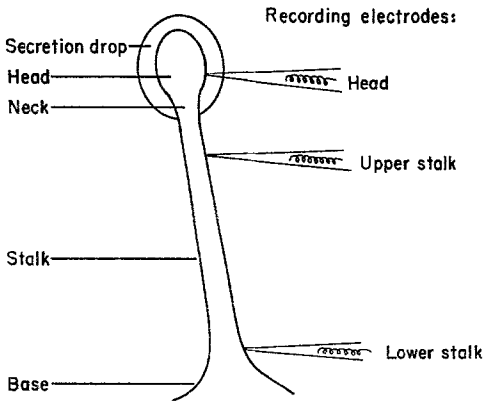

Fig. 1. Morphology of a tentacle and typical recording sites. The tentacle chosen for illustration was located at the inner edge of the outer zone. Tentacles were always studied on the intact plant, and the reference electrode was always inserted in the solution surrounding the roots

d) Electrode Placement. The leaf of *D. intermedia* consists of an inner zone containing fairly symmetric tentacles which typically range in length from 1 to 1.5 mm, and an outer zone with slightly dorsiventral tentacles about 2–4 mm long. Recordings were made from the heads of tentacles in both zones, as well as from the petiole and from the leaf blade near to and distant from the bases of stimulated tentacles. The outer tentacles, in which electrical activity of interest was more pronounced, were explored more thoroughly; typical salt bridge placements are illustrated in Fig. 1.

Early experiments involving electrical activity of the stalk were begun as soon as a salt wick was satisfactorily in position, but in later experiments, a series of widely separated 80-ms shocks of intensity great enough to trigger action potentials was administered until the elicited action potentials were negative-going and of large, regular size. The rationale for this procedure is provided elsewhere (Results, section 3, Williams and Pickard, 1972).

e) Stimulation. The insects used for natural stimulation were *Drosophila melanogaster*, wild type, Oregon strain. Mechanical stimuli were administered by rubbing tentacles with a cotton thread wetted with deionized water. The effect of chemical substances was tested by applying 5–20-μl drops of aqueous solution from a 21-gauge hypodermic needle onto the mucilage surrounding the tentacle heads. A convenient way of generating action potentials was to place a 0.1 M NaCl or KCl salt wick directly against the surface of the tentacle head, thus combining mechanical and chemical stimulation with the recording operation. Duration of electrical shocks was 80 ms.

f) Na^+, K^+, and NH_4^+ Available from the Surface of Fruit Flies. 100 fruit flies (*D. melanogaster*, wild type, Oregon strain) were chilled to 6° and shaken very gently for about 5 min in a vial containing 10 ml of chilled deionized water. The vial was then enclosed in a larger, warmer container into which the flies escaped. The process was twice repeated with fresh chilled water, and the aliquots were combined. Na^+ and K^+ content were measured on flame photometer Model 143, Instrumentation Lab., Inc., Watertown, Mass., and NH_4^+ was assessed by the method of Weatherburn (1967).

Results and Interpretations

1. Stimulation

a) Stimulation of Action Potentials by an Insect. When a fruit fly was impaled on an insect pin and positioned so that his feet stroked the head of a tentacle on the margin of a leaf, action potentials could be detected at any point along the tentacle stalk. Fig. 2 shows a representative train of such action potentials, recorded through a salt bridge contacting the lower part of the stalk. Several moments after the occurrence of action potentials, the tentacle began to bend toward the center of the leaf. Apparently, the "impulse" which Darwin suggested must transmit the bending stimulus from the head to the stalk of a directly stimulated tentacle may be identified with a train of action potentials.

b) Mechanical Stimulation. In order to measure the effect of mechanical stimulation, it was first necessary to establish good electrical contact between electrode and tentacle head by means of a salt bridge which did not itself give rise to voltage variations. For this purpose, a 0.01 M KCl salt bridge was touched to the mucilage of a tentacle on the margin of the leaf without contacting the surface of the head itself. During this procedure, a small negative voltage transient could often be observed at the head (but not on the stalk). Within 0.5–3 min, the potential at the head (a liquid junction potential between mucilage and salt bridge?) achieved a fairly stable value. When an adequately stable baseline had been established, a cotton thread wetted with deionized water was pushed through the mucilage until it made contact with the surface of the head. As illustrated in Fig. 3, the surface voltage measured at the head typically began to drop at the moment of contact. This drop, which was never detected on the stalk except in a very much attenuated form, would seem to be a receptor potential. Whenever the receptor potential attained a certain threshold, action potentials were detected through both the head and the stalk electrodes. These recurred until the receptor potential dropped below the threshold. Since the area of the probe and the force exerted were not measured, the precise relation of receptor potential magnitude to stimulus strength was not worked out; however, qualitatively it seemed that a light tap produced a small, brief receptor potential, whereas steady pressure produced a higher and longer receptor potential and vigorous stroking yielded a still more negative receptor potential of considerable duration. The receptor potential sometimes declined before the probe was removed from the surface and sometimes afterward, but always disappeared within 4 or 5 min after withdrawal. After a receptor potential disappeared, restimulation resulted in reappearance of a receptor potential, which again gave

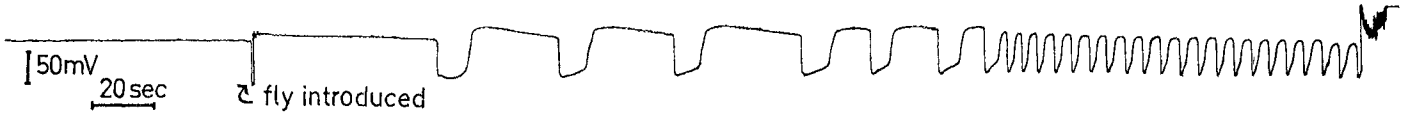

Fig. 2. Action potentials measured from the stalk as a result of placing a live fly on the head of a tentacle. For a discussion of the change in amplitude apparent beginning with the 8th action potential, see Results, section 1a, of the following paper. The slight negative drift beginning 263 s after the fly was introduced is believed to correspond to the severe attenuation of the saline drop connecting stationary salt wick and bending stalk. Ultimately, the tentacle bent enough to break the circuit; this occurrence is indicated by the replacement of the signal by noise at the end of the recording. The change in duration of the action potentials with firing frequency is normal behavior, and is analyzed in Results, section 1b, of the following paper

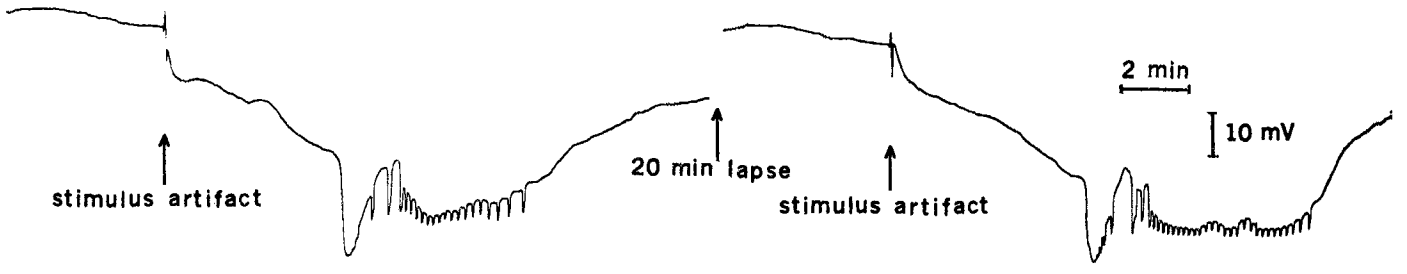

Fig. 3. Two consecutive receptor potentials and associated action potentials stimulated with a thread soaked in deionized water and recorded through a 0.01 M KCl salt bridge placed in the mucilage. Note the rapid drop of the receptor potential. It was not unusual for a receptor potential to drop erratically, as illustrated here, although drops could be fairly regular. The small action potentials riding piggyback on the first, exceptionally large, action potentials in each of the two trains were a common occurrence. However, the exceptionally large and long-lasting action potentials may have occurred simultaneously with a brief negative peaking of the receptor potential; because it is impossible in such cases to sort out the contributions of the receptor potentials and action potentials to the net voltage fluctuation, analysis of action potential shape is better carried out with recordings from the stalk (see Fig. 6)

rise to action potentials if the threshold voltage was exceeded. (See second stimulation, Fig. 3).

In order to stimulate effectively, objects must touch the surface of the head or (in air of low humidity) pull at it indirectly through stiff drying mucilage. Objects applied to any other part of the tentacle or to the leaf itself failed to alter the resting potential of the head and did not give rise to action potentials.

Mechanical stimuli eliciting two to four action potentials almost always resulted in inflection of the tentacle, but continuing stimulation during or after bending nevertheless gave rise to additional action potentials.

Thus, mechanical stimuli similar to those which an insect delivers to the tentacle head during capture result in the appearance of a receptor potential which, upon exceeding a threshold value, in turn induces action potentials. As will be more clearly demonstrated in the following paper (Williams and Pickard, 1972), these action potentials are propagated basally to the motile region of the stalk, which bends after a sufficient number of action potentials have passed within a reasonable interval of time.

c) Chemical Stimulation. Although it is likely that the triggering of rapid inflection by insects is largely if not entirely mechanical, Darwin observed that solutions of many substances, if applied to the mucilage of outer tentacles, cause their stalks to inflect fairly rapidly. Thus, it is of interest to learn how simple chemical agents influence the receptor. It was checked in preliminary experiments that certain salts may cause inflection, whereas sugars do not. In somewhat more refined experiments, several substances were screened for effectiveness in eliciting a change in potential between the reference electrode and an electrode recording from fluid surrounding the head. For each of these experiments, it was necessary to select a tentacle on a relatively insensitive plant in order to avoid the triggering of action potentials with consequent bending of the stalk away from the electrode. After recording the baseline voltage, the recorder was turned off for 5 s while the head was syringed with a gentle stream of deionized water; at the end of the rinse, a large drop of water clung to the head. The median voltage during the next 144 s was taken as an index of the change of potential. Continuing with this procedure, various substances were assayed; 0.2 M sucrose and 0.1 M NaCl were tested as reference solutions at frequent intervals throughout the experiment. Fig. 4 presents average values for the largest single experiment conducted. It is clear that water tends to cause a rise in the potential; the magnitude of the rise would of course be expected to depend on the extent of hydration of the mucilage at the start of the experiment. A sucrose solution, like water, causes an erratic but definite

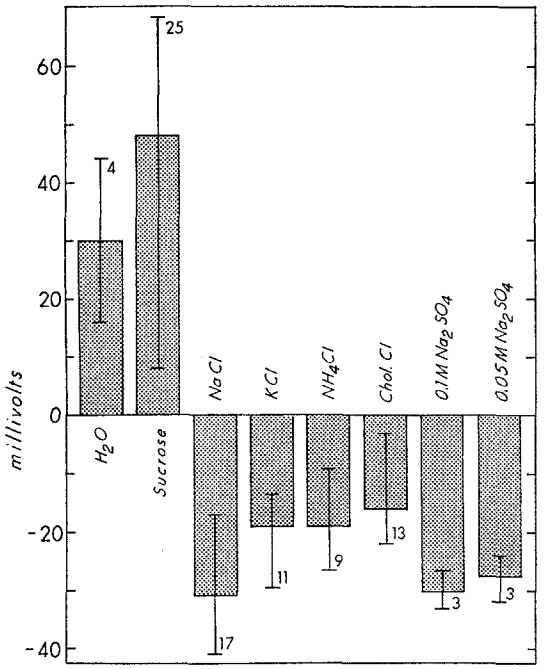

Fig. 4. Potential between ground and perfusion drop surrounding head. The reference voltage is that recorded from the original mucilage. All solutions were 0.1 M except sucrose (0.2 M) and the Na_2SO_4 solution marked 0.05 M. These data are taken from the most extensive of a group of experiments; the number of samples and the extreme values are indicated in addition to the averages

rise. In other experiments, the effects of sucrose and glucose were found indistinguishable. On the other hand, all of the salts tested lowered the potential. The considerable differences in the average potential hint that Na^+ might be more effective than K^+, HN_4^+, and the choline ion, but because of the large range in individual values, the relatively small total number of measurements, and the complexities of interpreting extracellular recordings, it is improper to make such detailed comparisons.

A control experiment was also performed, using a 6-cm wet cotton thread in place of the plant. Voltage differences recorded while sequentially rinsing the end of the thread with water, 0.2 M sucrose, 0.1 M NaCl and 0.1 M KCl were usually negligible and maximally as great as 0.5 mV. Thus, the control experiment suggests that the 30–80 mV differences in response of the tentacle to switching between drops of sugar solution and drops of saline might be of biological origin. That the results do not depend primarily on osmotic properties of the salt solution is indicated by the opposing influence of sucrose solutions. Changes in the Donnan potential due to binding of ions to cell walls cannot, of course, be ruled out. The magnitudes of the liquid junction potentials have not been assessed; presumably these were relatively greater when water or sugar solutions were placed on the head than when the physiologically reasonable concentrations of salts were tested. (Net junction potentials were small, of course, in the control experiment.) In spite of the crudeness

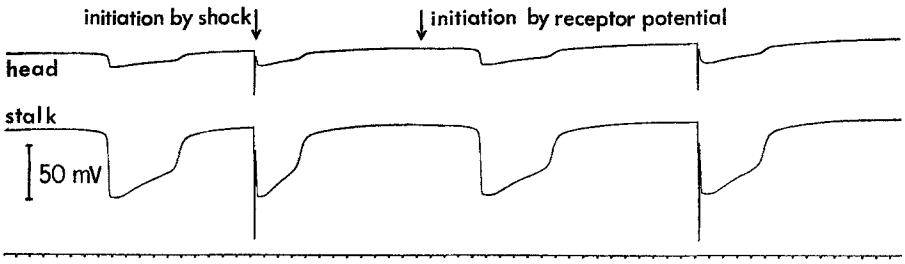

Fig. 5. Action potentials elicited alternately by a receptor potential induced with a 0.1 M NaCl wick and by 80 ms, −100mV shocks (note shock artifacts). Although the initial 10% of the drop of the action potentials initiated by the receptor potential occupies over 4 s, the drop of the shock-induced action potentials is accomplished abruptly. The upper recording is from the head electrode and the lower is from the stalk electrode, through which the shocks were administered. The ticked line records 1-s intervals

of the data, that the changes are at least in part due to changes in the receptor potential is strongly suggested by the tendency for action potentials to occur (even in relatively insensitive plants) when large negative changes of potential were induced, and by their disappearance when the voltage rose.

Because common salts were effective in inducing action potentials, washings from fruit flies were examined for Na^+, K^+, and NH_4^+ content. As expected, these ions were present in such low amounts (2, 1, and < 50 neq per fly, respectively) that they are unlikely to play a significant role in the stimulation of action potentials by insects described in section 1a.

d) Electrical Stimulation. Although the plant is not apt to be stimulated by an electric shock in its native bog, such an artificial stimulus is of interest in the laboratory because in some excitable tissues it can be used to trigger an action potential at a precisely specified moment. Therefore, recording was carried out while electric shocks of 80 ms duration and variable amplitude and polarity were delivered to the tentacle head and stalk. Action potentials could indeed be elicited. The minimal shock required to trigger an action potential varied with the history of stimulation of a tentacle; under optimal conditions a −20 mV shock was enough to trigger an action potential no matter where on the tentacle the electrode was placed. Fig. 5 shows action potentials elicited alternately by a receptor potential induced by touching the head with a 0.1 M NaCl wick and by −100 mV shocks delivered through an electrode placed on the lower stalk. The lower trace, recorded through the shocking electrode, shows that shock-induced action potentials had much the same form as regular ones except that the early, slowly falling phase is eliminated and the attainment of a half-maximal voltage change requires less than 0.1 s instead of roughly 4.5 s. The apparent differences in duration of action potentials are to be attributed to the intervals between successive action potentials rather than to differences between electri-

cally-induced and regular action potentials; the duration may be predicted approximately by a relation to be described in the following paper.

The upper trace of Fig. 5 shows electrical variations on the head during the occurrence of the action potentials shown for the stalk in the lower trace. All action potentials are as usual readily detected on the head but appear smaller than when recorded from the stalk. The receptor potential dropped about 5.3 min earlier and is essentially steady in this section of the recording; it appears to be unaltered by the −100 mV shocks, which have been attenuated to about −40 mV in the head. In general, no alteration was observed for single shocks of either polarity as long as their magnitude remained below 1 V. (However, the receptor potential often did show a sudden negative shift when shocks of 5–10 V of either polarity were delivered directly to the head, and 100 mV shocks delivered at frequencies greater than 2 s^{-1} often resulted in a negative shift of the receptor potential.) Data such as those of Fig. 5 suggest that shocks of sufficient magnitude bypass the ordinary receptor mechanism and induce action potentials anywhere along the conductive path of the tentacle. This idea is reinforced by the finding that shocks delivered to decapitated tentacles also gave rise to action potentials.

e) Tentacle Sensitivity as a Function of Position on the Leaf. All the tentacles of *D. intermedia* respond in a qualitatively similar way to stimulation with a salt wick, but there is considerable variation in the sensitivity of tentacles in different positions to more or less equivalent stimuli. The large, outermost tentacles are the most sensitive, giving receptor potentials of great amplitude and duration which result in long trains of action potentials. The neighboring tentacles on the inner side are only slightly less sensitive. Sensitivity falls off noticeably, however, in the next ring of tentacles, and drops dramatically for tentacles of the inner portion of the leaf. In central tentacles, a fairly strong stimulus is apt to elicit only a transient rise of the receptor potential; extremely strong stimulation is required to raise the receptor potential high enough to elicit two or three action potentials.

Stalks which have propagated three or four action potentials within a short while will usually bend regardless of their position on the leaf. Of course, the short, centrally located tentacles bend through a much smaller angle than do the long, reflexed tentacles near or at the leaf margin.

2. Relation of Action Potentials to Receptor Potentials

a) Dependence of the Interval between Action Potentials on the Amplitude of the Receptor Potentials. The upper of the paired traces of Fig. 6A shows a representative receptor potential stimulated with and recorded

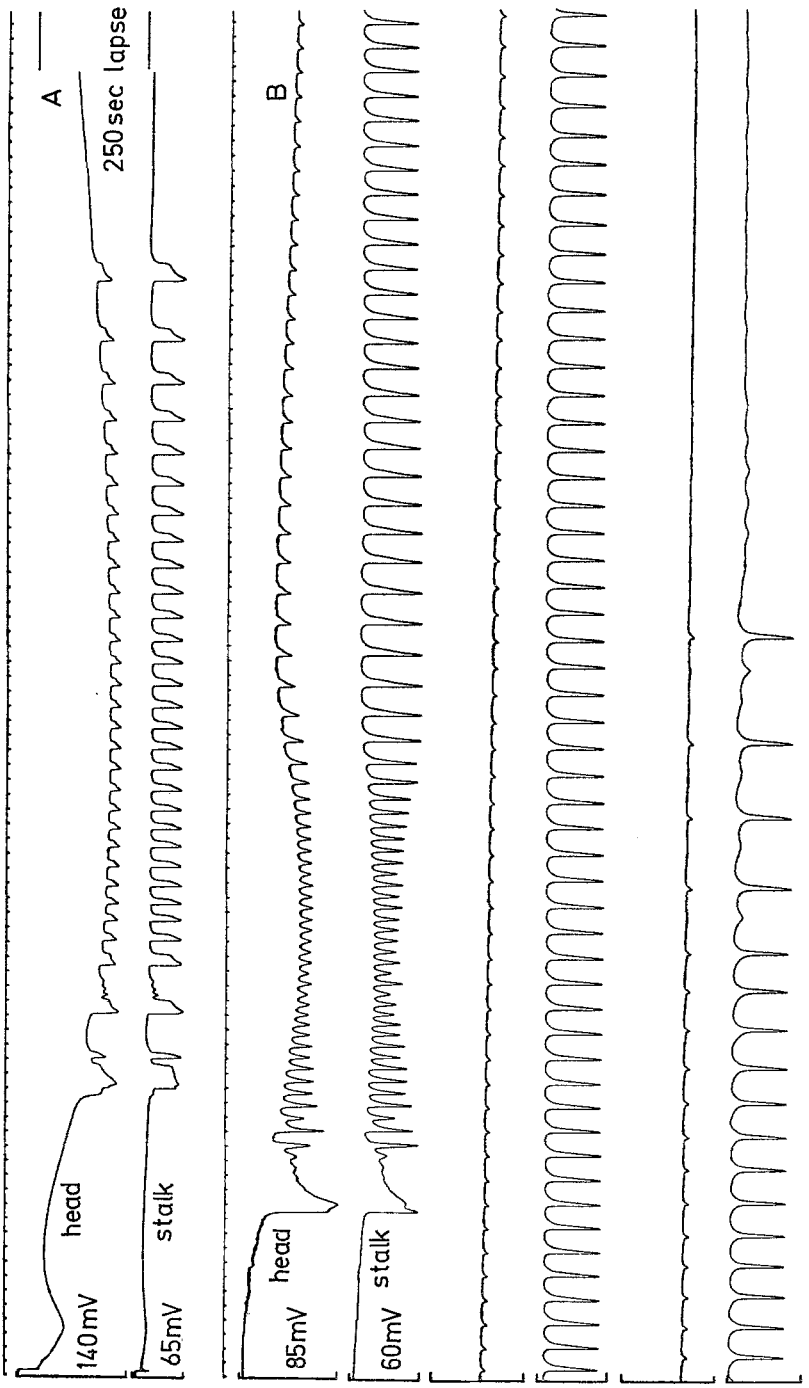

Fig. 6 A and B. Photographs of simultaneous recordings from head (upper trace of each pair) and lower stalk (lower trace of each pair). Ticks indicate 5-s intervals. Initiation of action potentials in A ceased because the receptor potential rose, initiation in B ceased because of fatigue. Because of the narrow channel width of the recorder, the pen recording voltage at the head was moved just off scale prior to stimulation: the voltage drop illustrated for the head is thus a minimal value and the zero does not necessarily represent the precise level of the resting potential

through a 0.1 M KCl wick placed on a tentacle head. The action potentials associated with the receptor potential occurred at intervals which decreased as the receptor potential gained amplitude and increased as it returned toward the resting potential. The lower trace of Fig. 6A shows a concomitant record of action potentials on the stalk; although there is doubtless a small lag due to the finite speed of propagation (following paper, section 2), the temporal features of the trains of action potentials measured from the head and the stalk are essentially the same. Fig. 7A is a graphical representation of the data of Fig. 6A, with the peak-to-peak intervals associated with the phase of increasing negativity marked by open circles and intervals associated with the return phase marked by dots. In this as in all experiments the first action potentials elicited did not behave as regularly as did subsequent ones (note open circles marked by numerals). However, thereafter the action potentials were quite regularly related to the receptor potential amplitude, though in hysteretic rather than reversible fashion.

At least two factors might in general contribute to the irregularity of action potential behavior during the rapid drop of the receptor potential. First, the rate of drop might have a direct influence on the firing of an action potential. Second, firing of an action potential during the negative after-potential of another action potential might be facilitated by rapidity of the receptor potential drop.

Fig. 7B illustrates the similar relationship which obtained in the experiment of Fig. 6B. In this plot, a dramatic change of slope is associated with the period of receptor potential "peaking". Presumably the portion of the graph which is level at a value of about 3 s indicates limitation of interval by refractory period. The 3 or 4 s minimum interval observed in experiments such as that of Fig. 6B and 7B is compatible with measurements of the refractory period (following paper, Results section 1). The increase in the interval between action potentials which occurs at essentially constant receptor potential amplitude late in the sequence indicates fatigue, which will be discussed in the following paper.

In striking parallelism to animal sensory systems, then, the magnitude of receptor response in *Drosera* tentacles is encoded as the frequency at which neuroid conductive cells relay action potentials to distant sites.

b) The Dependence on Receptor Potential Amplitude of the Amplitude of Action Potentials Recorded from the Mucilage. The recording of Fig. 6A is typical in showing that in the absence of fatigue (cf. Results, section 3c, following paper) action potentials recorded on a stalk are generally of uniform height. Early and late portions of the stalk recording of Fig. 6B similarly show uniformity, but action potentials on the stalk do become smaller when the receptor potential drops rapidly to a large negative value. In contrast, as also shown in Fig. 6A and B, records of action potentials obtained through a salt bridge placed in the mucilage

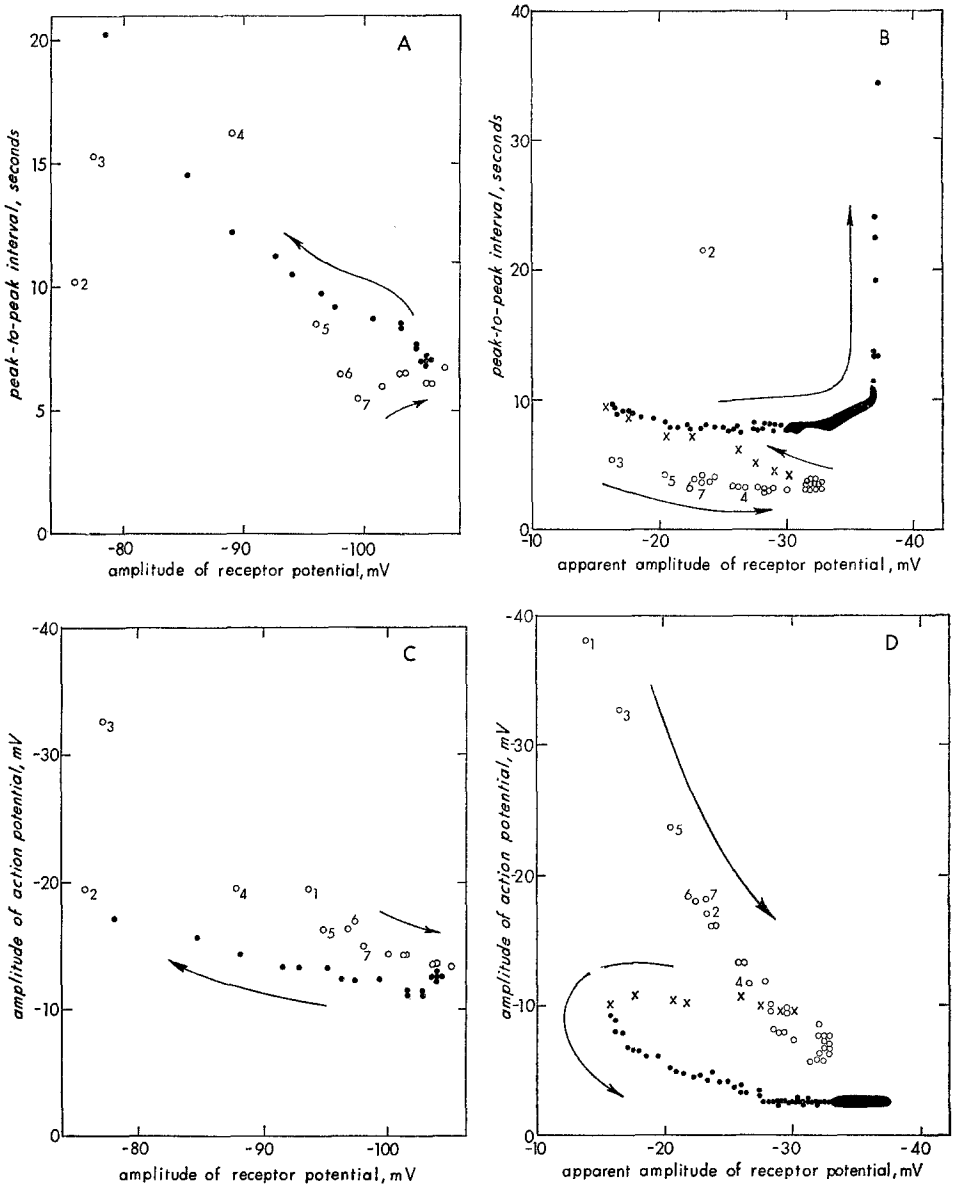

Fig. 7. A and B Peak-to-peak interval of action potentials from Fig. 6A and B, respectively, plotted against the receptor potential amplitude. C and D Amplitude of action potentials recorded from the head of Fig. 6A and B, respectively, plotted against apparent receptor potential amplitude. The apparent receptor potential amplitude in C and D may be greater than the true receptor potential amplitude from the 2nd to the 5th minute of the experiment because in Fig. 6B the action potentials did not return to the baseline in the stalk recording during this period,

of the head show marked variation in amplitude as the receptor potential drops and returns, tending to remain constant when the receptor potential is very negative. In Fig. 7C and D, the recorded amplitudes of the action potentials of the upper traces of Fig. 6A and B, respectively, are plotted as a function of receptor potential magnitude, with action potentials occurring during the phase of increasing negativity represented by open circles and those during the return phase by dots. The curves for the two phases are similar but are not superimposed.

Examination of Fig. 6A and B suggests that two different processes are controlling the amplitude of action potentials measured from the mucilage around the head. First, when the magnitude of the receptor potential is relatively small, action potential amplitude on the stalk is essentially constant, and it might be guessed that action potential amplitude measured on the head is, like that on the stalk, unrelated to firing interval. Second, when the magnitude of the receptor potential is very large, action potential amplitude measured on the stalk varies with interval, and it seems probable that a dependence on interval may come into play for the head recording as well. The second situation is plausible in terms of refractory properties of the excitable membranes of the cells producing the action potentials, as will become more apparent in the following paper (Results, section 1). The first situation deserves further scrutiny, however: since examination of Fig. 6A and B and comparison of Fig. 7A, B, C, and D show that both the apparent amplitude and the separation of action potentials recorded on the head vary in a similar way with the magnitude of the receptor potential, it may be asked whether the amplitude of these action potentials might normally depend on their separation rather than on the receptor potential *per se*.

A partial answer can be provided by delivering periodic electric shocks to tentacle heads undergoing shifts of the receptor potential due to concurrent stimulation with a wick. Fig. 8 shows a portion of one such experiment in which the variation in receptor potential amplitude was never greater than −25 mV and in which the frequency of the shocks, one per 2.67 s, was carefully selected to avoid stimulation during the relative refractory period (see Results, section 1, of the following

and similar behavior would be expected to occur on the head (see Results, section 1, following paper). Action potentials which occurred during the fall of the receptor potentials are represented as open circles and are numbered during the first part of the fall where their behavior is more irregular. They are represented as closed circles during the receptor potential recovery in A and C and as X's during the partial recovery of B and D. Action potentials during the second fall of B and D are closed circles. The large blackened area in B represents a cluster of 68 points, and the blackened area in D represents 37 points

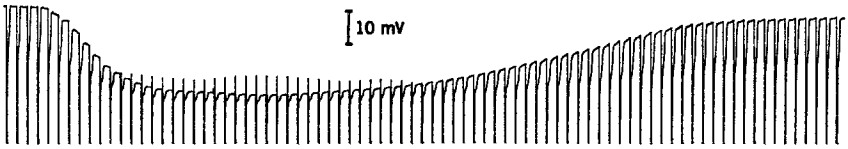

Fig. 8. Photograph of a recording through an electrode in the mucilage surrounding the tentacle head. 80 ms, −200 mV shocks were administered every 2.67 s (note abruptly falling shock artifacts) while the receptor potential dropped due to rubbing of the head by the wick of the recording electrode. The U.T.C. filter was employed; hence the oscillatory filter artifacts

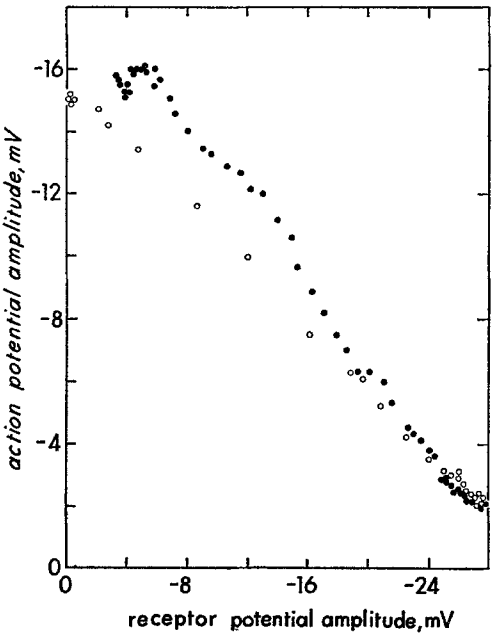

Fig. 9. Amplitude of action potentials shown in Fig. 8, plotted as a function of receptor potential amplitude

paper). Because the shocking frequency in this experiment was higher than the natural firing rate for the action potentials, they were initiated periodically by the shocks but not between them. Action potential amplitude obtained in this manner as an isolated variable depends inversely on the absolute magnitude of the receptor potential, as was of course found during more natural triggering (compare Fig. 8 with Fig. 6A and B, and Fig. 9 with Fig. 7A).

Similar results were obtained in experiments with lower shocking frequencies, although when the receptor potential amplitude was maximal, naturally elicited action potentials were interspersed with shock-induced action potentials. Further, no variation of amplitude of action potentials was seen if shocking interval was varied while the receptor potential was steady. Therefore, when relative refractoriness is excluded from consideration, the amplitude of an action potential measured on the head does not depend on the interval separating it from the preceding action potential.

To account for the apparent discrepancy between the typical all-or none behavior of action potentials recorded on the stalk and those of variable amplitude recorded on the head, it may be argued that the primary step in reception is an increase in the permeability of receptor membranes. Extracellularly recorded receptor potentials were always negative-going, as would be expected if they are an expression of depolarization of the receptor membranes of cells which are normally internally negative with respect to the surrounding medium. With the qualifications to be discussed in the Results, section 3, of the following paper, action potentials externally recorded from the stalk were also negative-going, as would be expected if they too are expressions of membrane depolarization of internally negative cells. Further, action potentials recorded from the mucilage of the head were most typically negative. However, these latter may well be compound signals consisting of a positive-going and a negative-going component, and, because the mucilage wets several cells of the upper stalk, must always contain a negative-going component from the stalk. The membranes giving rise to receptor potentials must be situated in the head, for there and only there do we see receptor potentials. Ultimately, action potentials travel down the stalk, and might perhaps be generated either in the neck or inner layer of the head. Thus, the head might serve as a current source, so that the signal conveyed across the receptor membranes to the electrode might well be positive-going. Such a positive-going signal would become larger if the conductance of the receptor membrane were to increase. This would result in diminution of the amplitude of composite negative-going recorded action potentials or, if the conductance of the receptor membrane were to be very high, in a reversal of sign. Viewed simply, then, this model predicts that very strong stimulation of the tentacle could result in a transition to positive-going action potentials when a large receptor potential nears its peak, and a return to negative-going potentials when it diminishes.

In order to test this prediction, standard 0.1 M NaCl stimulating and recording wicks were dipped in 1.0 M NaCl and tentacles were then stimulated with them. Representative results are shown in Fig. 10A and B. As expected, positive-going signals were found (note the first two action potentials of Fig. 10A); these typically had an elaborate shape,

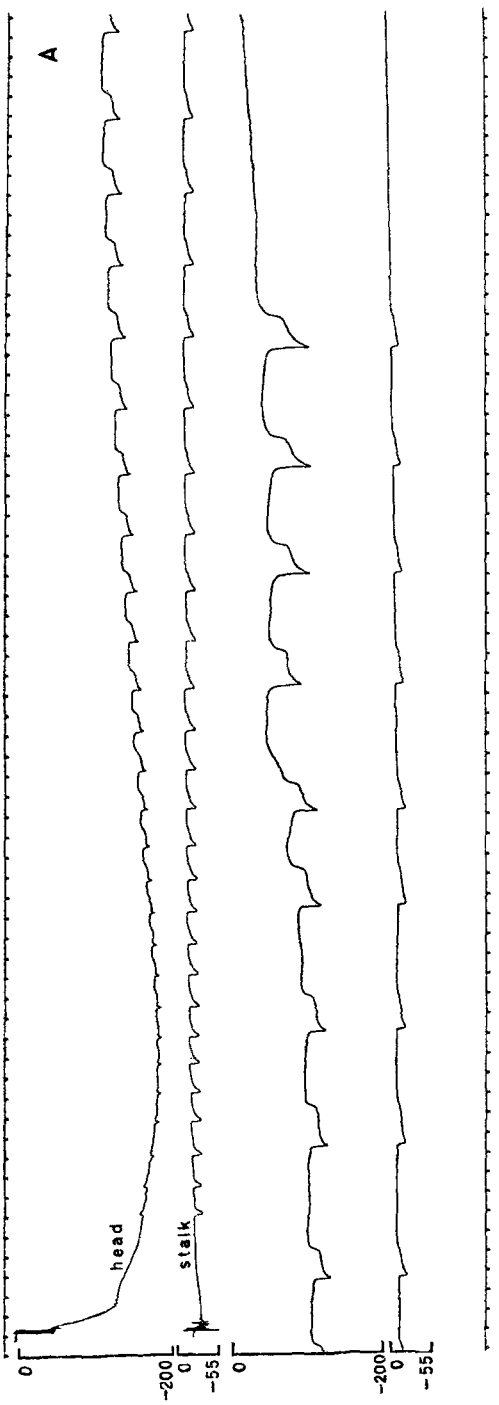

Fig. 10. A and B Inversion of action potentials recorded on the head. Additionally, the lower of the paired traces of A illustrates the constant sign and essentially constant amplitude of action potentials recorded simultaneously from the stalk. Since the pen recording voltage from the head was moved just off scale prior to stimulation, the zero does not necessarily represent the exact level of the resting potential. Most of the initial drop of the head voltage of B was obscured by noise resulting from electrode adjustments and is not included in the photograph

suggesting a complex origin (Fig. 10B). However, contrary to expectation the inverted signals were always found on the rapidly falling portion of the receptor potential rather than at its peak.

The successful prediction of inversion lends support to the hypothesis of changing receptor membrane permeability; yet the failure to predict the timing of the occurrence suggests a weakness of the hypothesis. Therefore, a more searching test was designed. If the normally observed action potentials are indeed composite signals resulting from positive components recorded through the membranes of the head and negative components recorded from the neck or stalk cells, action potentials recorded from heads with very small amounts of mucilage should appear positive-going. Moreover, the height of positive-going action potentials should be greatest when the receptor potential is most negative and should decline when the receptor potential returns toward the baseline. Accordingly, leaves were permitted to sit in dry air until the drop of mucilage had shrunk so small that it barely touched the cells of the stalk, and recording was then carried out in the standard manner. Fig. 11 illustrates such an experiment fulfilling both aspects of the prediction: action potentials are positive, and are largest near the "peak" of the receptor potential. The irregular shape of the action potentials indicates that even in this case there may be a negative component combined with the positive component; however, it is relatively small. Thus, most of the data seem consistent with the hypothesis that the receptor potential is generated by a shift in the permeability of the receptor membranes. The occurrence of inversion during rapid, large drops of the receptor potential might indicate that the rate of depolarization as well as the amount of depolarization determines the net flow of current past a salt bridge recording from the mucilage.

The above model is similar to models developed for several animal systems; in particular see Wolbarsht (1960) or the review by Mellon (1968).

3. Inflection

It was observed that a single shock-elicited action potential rarely caused a tentacle to inflect, but that the tentacle bent if a second action potential was induced within a minute. Initiation of bending lagged the shock by about 8–10 s, approximately the duration of an action potential. If the second action potential was elicited about 1.5–2 min after the first, movement could not be detected. A somewhat longer series of action potentials occurring at 1.5 or 2 min intervals could nevertheless lead to inflection. Rate and extent of movement varied greatly from tentacle to tentacle. Sometimes, two closely spaced action potentials would cause the tentacle to bend so that within 30 s to a few minutes it touched the

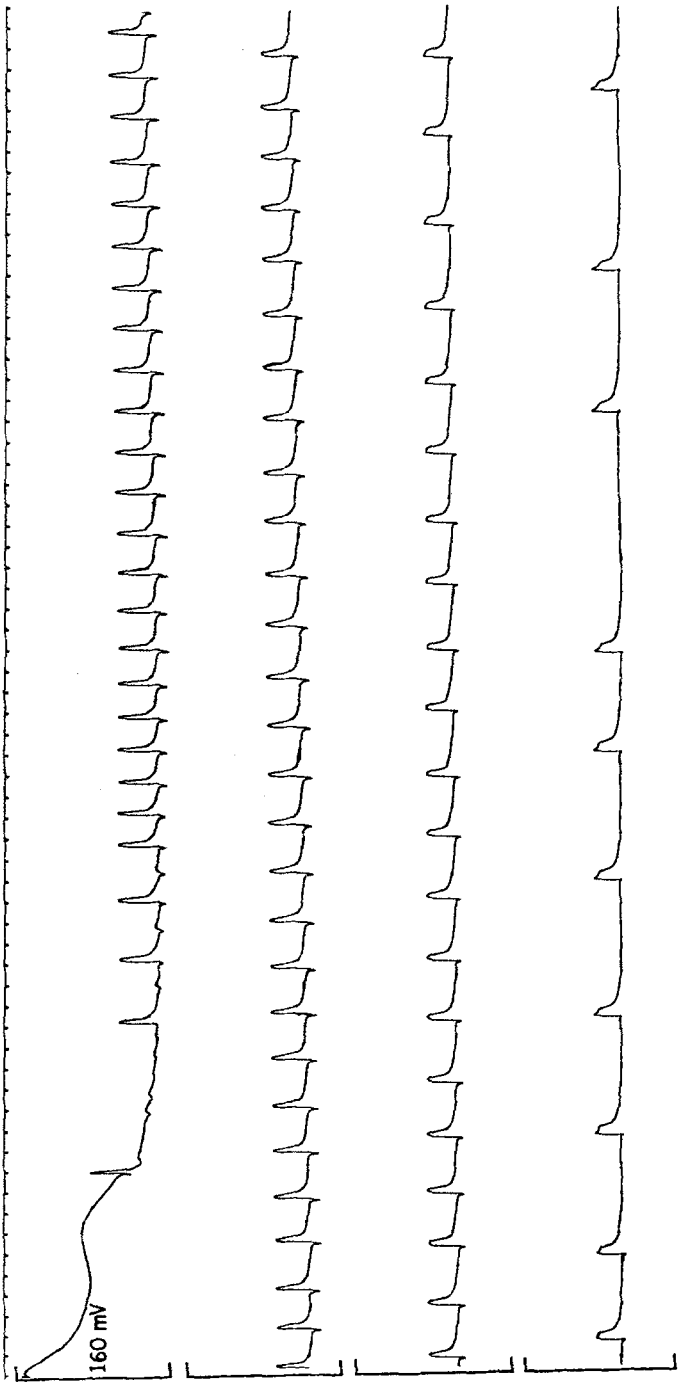

Fig. 11. Photograph of a recording from a head maintained at low humidity until the mucilage was nearly dry. The initial drop of the receptor potential occurred off the chart; the zero is thus arbitrary

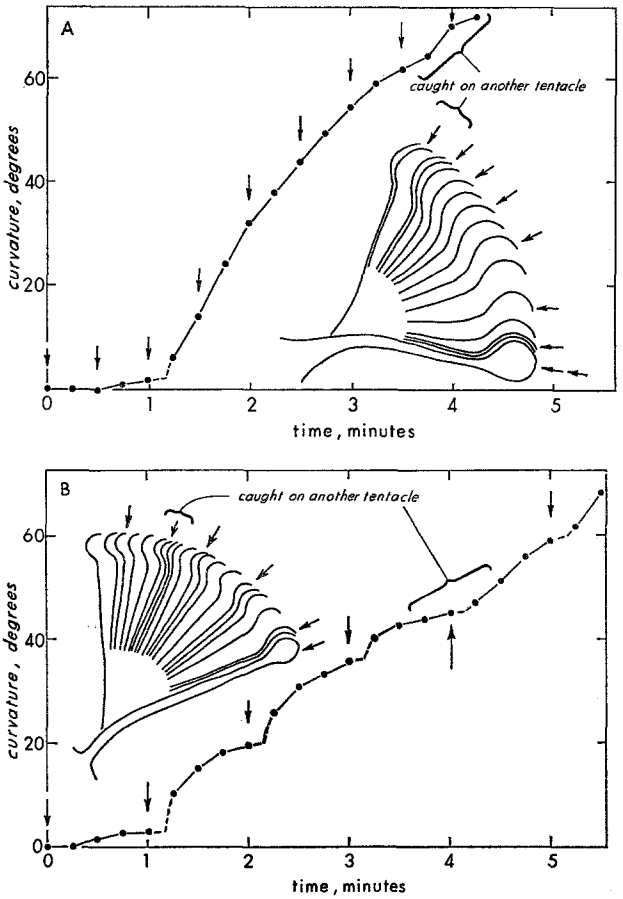

Fig. 12 A and B. Plots of tentacles bending while shocks were administered at intervals of 30 s (A) or 60 s (B). Broken lines are interpolations based on the visual observation that motor responses lag shocks by perhaps 8–10 s; with the particular photographic equipment used it was not possible to take pictures often enough to record such lags. Insets are superimposed tracings from which the measurements were made

surface of the leaf blade, but usually the bending slowed when only a small angle had been attained and further action potentials had to be elicited in order to cause a large inflection.

In order to confirm some of these qualitative observations, tentacles were photographed through a microscope at 15-s intervals as action potentials were induced at intervals of either 30 or 60 s. The photographic images were projected onto a sheet of paper and traced; each picture was superimposed, using for reference several stationary markers. Two

representative sets of tracings are reproduced as insets of Fig. 12A and B. As was always observed, the greater part of the bending took place in a small zone in the lower region of the stalk (cf. Darwin, 1875; Hooker, 1916). The angles made by the upper region of the stalk with a reference line were measured from the tracings and plotted in Fig. 12A and B as a function of time. Shocks are indicated along the time axis with arrows; it was confirmed that each shock elicited an action potential. In neither of the illustrated experiments did much bending occur until after the second shock, but in Fig. 12B the tentacle did respond to the first action potential with a very slight curvature (almost 3° within 1 min). In several of the replicate experiments, similarly small responses to the first shock were measured: apparently the visual impression that curvature rarely occurs in the absence of a second shock is not strictly accurate. Following the second, third, and fourth shocks of the 60-s series of Fig. 12B, bending occurred rapidly, but the rate decreased within a minute of each shock. In the 30-s series chosen for illustration in Fig. 12A, bending progressed fairly smoothly. Evidently, the movements resulting from individual action potentials tended to grade into each other when the shocks were closely spaced. (As ultimately happened during most such experiments, the tentacles illustrated in Fig. 12A and B each collided with another tentacle, after which time their further movement was physically restrained.)

In sum, the bending response of a *Drosera* tentacle depends both on the number of action potentials which travel down the stalk and on the intervals between them.

Discussion

a) Direct and Indirect Stimulation. Darwin, in his 1875 publication, stressed that stimulation of an inner tentacle causes a delayed movement of surrounding tentacles, whereas stimulation of an outer tentacle causes movement of that tentacle alone. The latter movement, though sometimes slow, may be both immediate and rapid. Darwin proposed that following stimulation of either inner or outer tentacles an "impulse" moves rapidly down the tentacle stalk, stopping at the base of the stalk of an outer tentacle but spreading slowly into the lamina and up the stalks of neighboring tentacles in the case of stimulated inner tentacles.

In the present study, it has been confirmed that mechanical or chemical stimulation of a single outer tentacle causes inflection of its own stalk but not inflection of its neighbors, although the neighbors are capable of responding when indirectly stimulated by placing a dead insect in the center of the leaf. The impulse which moves down the stalk of a directly stimulated outer tentacle has been identified with a train of action potentials, which have not been detected to travel beyond the

tentacle base. It has also been shown that vigorous mechanical stimulation of a central tentacle may give rise to a few action potentials in its own stalk, and that these are followed by weak bending.

However, in a companion study, Van Sambeek and Pickard (unpubl. data) have found that a chemical agent mediates the delayed bending of neighboring tentacles which occurs when an inner tentacle is provided with an insect. It is not known whether the agent works its influence directly or by triggering action potentials at the bases of the tentacles, but though the latter possibility could account for nastic responses it is unlikely to account for tropistic ones, since the transmission of action potentials along the stalk seems to be symmetric. There is of course much evidence that indirectly stimulated movements are tropistic (Darwin, 1875; Behre, 1929).

b) Fast and Slow Movements in the Droseraceae. Although there is typically a marked difference in the time required for the direct and indirect responses of *Drosera*, this temporal distinction has not previously been stressed. Under natural conditions, the distinction is a conspicuous one: the outer tentacles touched by an insect quickly carry it to the center of the leaf, and the enclosure of the insect by the remainder of the tentacles follows gradually. As described in detail by Darwin (1875) and Ashida (1934, 1935), there are also rapid and slow phases in the movement of the lobes of a leaf of *Dionaea* or *Aldrovanda*, carnivores of the same family as *Drosera*. When insects or other small animals touch the trigger hairs on the adaxial surface of the leaf, the lobes shut rapidly. If no insect is caught in the cage thus formed, within a number of hours the lobes will swing open again. On the other hand, if an insect has been trapped the surfaces of the lobe, originally concave inward, tend to become concave outward, ultimately squeezing the insect so tightly that the outlines of its body can often be seen in relief on the lobe surface. The first, rapid phase can be brought about by touching the sensory hairs with a very clean object, and has not been shown to be triggered by chemicals in low concentration. While the second, slower, tightening phase may be induced by continued mechanical stimulation of the trigger hairs, the leaf is very sensitive to certain chemical substances, which bring about tightening in the absence of mechanical stimulation. Thus the lobes snap closed when an insect disturbs the hairs mechanically, and facilitate ultimate digestion of the insect by squeezing closer together in response at first to the efforts of the insect to escape and later to chemical substances released (through excretion or deterioration) by the insect.

Functionally, the directly induced movements of *Drosera* tentacles are analogous to the rapid phase of trap closure in *Dionaea* and *Aldrovanda*, and the indirectly induced movements are analogous to the slow

phase. In nature, the rapid movements are evoked in all three plants primarily by mechanical stimulation, while the slow phases appear to be elicited primarily by low concentrations of certain chemicals.

Structurally, an analogy is harder to draw. In *D. intermedia*, the capacity to carry out the rapid, directly induced movements in response to mechanical stimulation is graded from outer to inner tentacles, whereas the capacity to slowly evoke bending by neighboring tentacles in response to chemical stimulation seems restricted to the inner tentacles. The distribution of these two capacities varies greatly from species to species (Behre, 1929). In general, however, whether the two capacities are located in the same or different tentacles, they are at least located in tentacles. Furthermore, although stimulation of central tentacles may cause the lamina of the leaf to fold around the insect, both directly and indirectly provoked responses can occur in the tentacles themselves.

In contrast, *Dionaea* has separate emergences for detecting the presence of live, moving insects and the chemical products of dead prey. Movement is of course sensed by the trigger hairs, while chemoreception and digestion are combined in small sessile glands abundantly distributed over the upper surface of the leaf (Darwin, 1875). Thus, in *Dionaea* both fast and slow movements occur in the leaf blade, but are controlled by two types of emergences, whereas in *Drosera* both fast and slow movements occur in a single type of emergence within which are also located the fast and slow control mechanisms. Additionally, the emergence controls a slow reaction in the lamina.

In its responses to mechanical, electrical, and chemical stimulation, *Aldrovanda* (Czaja, 1924; Ashida, 1934, 1935) seems to resemble *Dionaea* in considerable detail. If Ashida's belief that chemoreception and mechanoreception both occur in the sensitive hairs is true, this would constitute a significant difference between *Aldrovanda* and *Dionaea* but a similarity between it and *Drosera*. However, Ashida does not remark on the presence of the small glands which Darwin guessed to serve both chemoreceptive and digestive functions, and his experiments did not discriminate between stimulation of the small glands or the sensitive hairs.

c) The Receptor Potential and the Generation of Action Potentials. Although the mechanically sensitive cells in both *Drosera* and *Dionaea* appear to be activated by deforming the cell membrane, the time-courses of receptor potentials in the two plants are rather dissimilar. In the case of *Dionaea* (Benolken and Jacobson, 1970), the receptor potential rises rapidly when a sensory hair is deformed, and if threshold is exceeded, typically elicits a single action potential. The receptor potential then begins a decline requiring only a few seconds, regardless of whether the hair is maintained in the bent position or released. In general, in order

for a second action potential to be elicited, a second receptor potential must occur. In contrast, a long train of action potentials may be fired by a single depolarization event in the head of *Drosera* tentacles, the number in the train being controlled by the receptor potential duration and intensity. Although the natural mode of stimulation for *Drosera* is continued rubbing or friction, prolonged length of stimulation cannot alone account for the conspicuously longer duration of the receptor potential, since it was found (Results, section 1 b) that it sometimes lasts several minutes after a mechanical probe is removed from the head and surrounding mucilage.

d) The Site of Action Potential Generation. On the basis of the complex forms and properties of action potentials recorded extracellularly from the head of *Drosera* (Results, section 2 b), it was argued that the separation of the external electrode from the membranes giving rise to the receptor potential was smaller than the separation of the electrode and the site where action potentials originated. This argument makes it likely that one layer of cells in the head is responsible for receptor potentials, while action potentials are generated in another layer of cells basipetal to the receptor cells (for cytology see Williams, 1971). If intracellular recording confirms this reasoning, the situation might perhaps stand in contrast to that in *Dionaea*, for which data of Benolken and Jacobson (1970) suggest that the graded receptor response and the action potential might both occur within a single sensory cell.

d') Elicitation of Movement in Drosera and Dionaea. Almost a century ago, Burdon-Sanderson and Page (1876) attached a recording stylus to a lobe of a trap of *Dionaea* and showed that at room temperature the trap responds to each but the first in a series of deflections of the trigger hairs. The beginning of each response lags the stimulus by 1 to a few seconds (see also Burdon-Sanderson, 1911). If the stimuli are delivered at intervals smaller than 2 min, the responses grade into each other and a relatively continuous motion can be observed. Since Burdon-Sanderson and Page also demonstrated that each deflection of the trigger hair results in the spreading of one action potential of about 1 s duration across the leaf, it is clear that the rapid movements of the *Dionaea* leaf and of the *Drosera* tentacle are alike in that 1) the motor tissue responds to individual action potentials, and 2) its response to any given action potential depends on the number of action potentials which preceded it and on the intervals between them.

Brown, unaware of the extent of the elegant experiments of Burdon-Sanderson and Page, independently demonstrated in 1916 that the number of times the trigger hair of *Dionaea* must be touched in order to cause trap closure depends on the intervals separating the stimuli and that the trap closes gradually during prolonged stimulation at low

frequency. Brown also showed that the number and timing of stimuli required for rapid closure varies conspicuously with temperature.

The means by which the first action potential facilitates the response of the motor tissue to the action potential which follows it is as little understood today as a century ago. However, similar behavior occurs in animal systems; a particularly striking example is found in the coelenterates (e.g. Bullock and Horridge, 1965; Josephson, 1966).

e) Fast Influences of Chemicals on the Receptor Potential. Of the large number of chemical substances tested by Darwin (1875) for ability to cause movement of *Drosera* tentacles, only some salts and sugars have been checked in the present study for ability to cause rapid response. As a control, Darwin's finding that drops of water do not cause rapid inflection was confirmed. Additionally, it was observed that water could actually raise the potential recorded from the fluid surrounding the head; this may well account for Darwin's finding that drops of water reduce the sensitivity of the head to mechanical stimulation. The action of 0.2 M sucrose and glucose solutions was similar to that of water, as expected on the basis of Darwin's finding that sucrose never induces inflection. While definitive experiments require recording from inside rather than outside the receptor cells, it might be suggested on the basis of the limited extracellular data available that the main effect of water and sucrose solutions is to dilute the mucilage, which may well be a solution of fairly high ionic content[1].

NaCl, KCl, NH_4Cl, choline chloride, and Na_2SO_4 each lower the potential recorded from the fluid surrounding the head. It may be postulated that this lowering represents a depolarization of the receptor membranes, since firing of action potentials is associated with it[2]. However, because of the problems of interpreting extracellular measurements, a quantitative assessment of the relative contributions of the various ions to the postulated depolarization would be unrealistic. Because of the similarity of the effects of the tested salts, and because of the relatively high concentrations necessary to elicit action potentials, it may be guessed that the effect of salt might well result primarily from direct contributions of the ions to transmembrane potentials rather than to reaction at specific chemoreceptor sites.

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1 An incomplete but useful analysis of mucilage is provided by Whitaker (1949); data for inorganic cations are unfortunately lacking, but a 0.1 osmole/l approximation for ion concentration can be obtained by comparing osmotic concentration (0.107 osmoles/l) with reducing sugar concentration (1.4 mg/ml) for typically hydrated mucilage.

2 For *D. rotundifolia*, Darwin reported K^+ ineffective or inhibitory; this discrepancy might of course be due to a difference between *rotundifolia* and *intermedia* but may well require a more elaborate explanation.

Effects of perfusing sensory hairs of *Dionaea* with a series of salt solutions have been reported in detail by Jacobson (1968), and Ashida (1935) has studied the influence of salt solutions on rapid closure of *Aldrovanda* traps. While there seem to be some similarities in the rapid responses of *Drosera*, *Dionaea*, and *Aldrovanda* to salt solutions, it is premature to make detailed comparisons.

f) The Utility of Drosera as an Experimental Organism. It may be hoped that electrophysiologists have much to learn by comparing the highly specialized cells of advanced nervous systems with more primitive neuroid systems such as those of *Drosera* and *Dionaea* (and presumably, of *Aldrovanda*) or such as those of the hydrozoans and possibly the sponges. The Droseraceous systems may indeed turn out to have distinct experimental advantages over animal systems in that the number of cells in the system is limited, every cell in the system is large enough to permit intracellular recording, and every cell is close to the surface of the active organ. In common with other neuroid systems, receptor potentials and action potentials of *Drosera* have time-courses described in seconds rather than in milliseconds: electrical fine structure could be resolved without the use of elaborate electronic instrumentation. Finally, *Drosera* is easy to obtain, is readily propagated, and requires little space.

g) The Botanical Significance of Neuroid Activity in the Droseraceae. The receptor potentials and action potentials of *Drosera* and *Dionaea* are conspicuously similar to those with which the nervous systems of animals operate. Although plant action potentials have been viewed in the past as isolated evolutionary freaks, it may be questioned whether the elaborate animal-like system of *Drosera* is likely to have arisen unless the capability to generate receptor and action potentials is widespread in plant cells.

A little reflection suggests that, indeed, receptor potentials and action potentials may well be found in every species of green plant. Regarding receptor potentials, which might be difficult to detect in many situations, little is known. The "negativation" of the stigma which Sinyukhin and Britikov (1967a, b) describe following pollination might turn out to be another example of a receptor potential in plants, but might result from secondary changes. It seems worthwhile to search for receptor potentials on a broad scale. Regarding action potentials, evidence is mounting that in eukaryotic cells variations in membrane potential may partially control all cilia and flagella (Dryl and Grębecki, 1966). Excepting the angiosperms and higher gymnosperms, at least one stage in the life cycles of green plants involves flagellated cells. In the angiosperms, it appears that action potentials may participate in pollination responses (Sinyukhin and Britikov, 1967a, b). Fluctuations which resemble action potentials occur in response to mechanical stimula-

tion of the plumular hook of the pea seedling (Pickard, 1971). It is likely that many more plant responses of a very general nature will be found to be mediated by action potentials when proper searches are undertaken.

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