ELECTROMYOGRAPHIC STUDIES OF THE GASTRO-INTESTINAL TRACT

I. THE CORRELATION BETWEEN MECHANICAL MOVEMENT AND CHANGES IN ELECTRICAL POTENTIAL DURING RHYTHMIC CONTRACTION OF THE INTESTINE

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Action currents from the intact musculature of the intestine do not follow the simple forms described in the textbooks as characteristic for skeletal muscle. When recorded they show themselves usually as irregular curves of varying form. Often the records of the electric potential will show a wave-like form which will be more or less regular for a time and in phase with the mechanical contractions of the muscle, but suddenly their appearance will change; the wave form will become irregular, and it will be hard to trace a relationship between the electrical and the mechanical waves.

Recourse to the literature will hardly help clarify matters. Many records of researches on the action potentials of striated and cardiac muscle have been published, and one can find a didactic description of the behavior of electric potentials in any work on the electrocardiogram. The action currents from smooth muscle, on the other hand, have received little attention. From the published work in this field, one obtains the general impression that in interpreting the electrograms one may apply to smooth muscle the same principles that are involved in the electobiology of skeletal muscle and nerve. When we first undertook this investigation it was with the idea of employing these principles to interpret observed changes of potential in relation to the mechanical movements. Our original plan was merely to continue with an improved technic the studies initiated by Alvarez and Mahoney. We had not proceeded far, however, before it became evident that the relationship between contraction and electric change obtaining in this domain required careful scrutiny, for it presented a number of features not to be expected on the basis of the usually accepted notions regarding action currents in muscle. This fundamental aspect of

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the problem was therefore made the first objective of our investigations. We believe we have made significant progress in that direction, and this report presents the results which we have obtained thus far.

APPARATUS AND EXPERIMENTAL TECHNIQUE. In order to register simultaneously mechanical contraction and variation in potential we adapted a form of enterograph used by Alvarez so that it should act also as a pair of receiving electrodes. It is pictured to scale in figure 1. The small clip, or serrefine, requires special description. It is made from steel piano wire, 0.018 inch in diameter, bent into the shape shown in the insert of figure 1. Unlike some observers, we have found it impossible to obtain satisfactory results with a polarizable metal electrode, and it was necessary to render the steel serrefine nonpolarizable. This was accomplished by first plating it with silver, and then chloridizing the silver electrolytically. Before use, each pair of electrodes was tested for its nonpolarizable quality.

For most of the investigations reported here, rabbits were used. The animals were anesthetized with urethane or iso-amyl-ethyl barbiturate (amytal) and pithed following the technic described by Alvarez. A median line abdominal incision was made and the intestines were freely exposed.

Action currents may be recorded from the intestines with the animal in the air, or in a warm bath of salt solution but both these arrangements have practical objections. In the air, the animal must be kept warm artificially and the intestine tends to dry, thereby changing the circuit resistance while a record is being taken. In the bath of salt solution the surrounding fluid tends to short-circuit the electrodes and thus to diminish sensitivity. Such a bath tends also to conduct to the electrodes extraneous currents developed here and there in the body. For these reasons an arrangement was made to permit the animal to rest in a warm bath of water, while the intestines floated in inert mineral oil.

It was soon found that any metal coming in contact with the solution of salt would produce electric currents and we therefore had recourse to a

3 For any who may wish to duplicate this part of the apparatus there are a few practical precautions which must be taken: 1. The steel wire serrefine must be scrupulously clean of fatty covering, and therefore before silver plating it should be boiled in concentrated alkali. For convenience in handling the serrefine during the plating process a short piece of the same type of wire is soldered to the loop. This serves also to lead in the current. 2. Pure silver must be used as the anode in the silver plating process, and for the plating bath, a solution is made up as follows: AgCN, 36 grams per liter, KCN, 52 grams per liter, 1 drop CS₂. 3. The tendency is to silverplate too slowly which gives a rough surface; we use a current density of 10 to 15 milliamperes for each electrode, and plate for three to four hours. 4. In the chloridizing process, the electrode is the anode. A N/2 NaCl or HCl solution is used for the bath, and a low current density, about 1 to 2 milliamperes for each electrode, is applied for about half an hour. 5. In chloridizing, the juncture of the serrefine and the lead-in wire must not be allowed to get into the solution lest the joint forms an electric cell with resultant disintegration.
wooden tank water proofed with wax and varnish. The thermostat and heating elements were all enclosed in glass. The tank was filled to a convenient height with physiologic sodium chloride solution kept at 37°C, and the opened animal was placed into it, its head resting on a canvas support out of the water. A wooden frame about 30 cm. square was then inserted in the tank, and the intestines were allowed to float up into it. The electrodes were now attached to the moistened intestine, and then a quantity of mineral oil sufficient to provide a layer 2 cm. in depth, was poured into the frame to surround the intestines. The tissue to be examined was now in an electrically non-conducting medium. The remainder of the body was in a congenial environment which was electrically conducting, a point important for certain of the experiments to be described later. In this state the animal could be maintained for an entire day’s observation. At the end of the experiment, the oil was recovered by siphoning.

The changes of electrical potential were recorded by means of a Cambridge string galvanometer, the shadow of the string being photographed on moving bromide paper 12 inches in width. The movement of the intestine was recorded simultaneously on the same paper, by attaching the freely-
swinging electrode with a fine thread to an aluminum lever suspended in the lighted area in front of the camera slit.

Results of Experiments. If a pair of nonpolarizable electrodes are attached to the rabbit's intestine and a simultaneous electrical and mechanical record is made, the results will in general appear as an irregular electric disturbance, with a mechanical record that seems in many instances to have little relation to it. In figure 2 is presented a sample of various records, selected at random from our series. The forms shown are diverse, and still other examples could be multiplied indefinitely. It must be remembered that the intestine commonly shows various types of activity such as pendular movements, tonus waves, and peristaltic rushes,

and the rhythmic contractions have different rates in different parts of the intestine. It was reasonable to assume that the varying and irregular form of the electric record, so commonly obtained, was due to the fact that many muscular elements contract with imperfect synchronism and thus contribute many changes of potential to the record. If this were true, we could expect to simplify the record obtained by including smaller amounts of muscular tissue. For this reason we took a very small bite of the serosa with the serrefine-electrode, and attached the electrodes in close approximation to each other, that is, about 1 or 2 cm. apart. These conditions

The electrodes were always attached in a standard way. The one which is free to move back and forth was attached caudally to the fixed one, and the galvanometer was so wired to the electrodes that an upward deflection in the record indicates that the oral electrode has become relatively negative to the caudal one. In the mechanical record an upward deflection corresponds to contraction, and a downward to relaxation.
were adhered to in all the experiments to be described except when otherwise stated.

Doubtless the seeming anarchy of the variations of potential as usually seen is only apparent. If we could analyze completely the multifarious

![Fig. 3](image1)

![Fig. 4](image2)

**Fig. 3.** a. An example of a characteristic electric wave, with accompanying mechanical record. The upper is the electric, the lower the mechanical record. b. An example of an inverted wave (see text), obtained with bipolar attachment; below it is the simultaneous mechanical record. c. A bipolar record from an isolated segment of a dog's intestine, for comparison (Puestow).

**Fig. 4.** a. A unipolar record from the oral electrode. b. A unipolar record from the caudal electrode. c. A bipolar record from the same electrodes made in the standard way. The bipolar record is the algebraic difference of the oral and caudal unipolar records. d. A characteristic wave enlarged to show rapid oscillation during the contraction phase. e. To show the presence of a positive variation during the course of rhythmic contraction. The line at the right, $x$, is the level of zero potential relative to the bath. A deflection below the line indicates a positive change in potential.
activities of the intestine, the record of electric potentials would probably also be clarified. To simplify the analysis somewhat we are reporting only on records obtained from intestine which was executing regular rhythmic contractions. Under these circumstances more regular records are obtained, but they are still far from uniform. In many cases the records are complicated because the electrodes pick up currents that arise in movements of respiration. In what follows we shall describe in some detail a particular form of wave, which we have been able to analyze more successfully than any other. In doing so we do not wish to convey the impression that we have made a complete analysis of the electromyographic record. Much more work must yet be done before this can be effected. The type of electrogram which we here describe appears about once in every ten records taken at random along the intestine, and when seen in its characteristic form it has a definite relationship to the mechanical record.

Both the electric and mechanical records show clearly-defined wave forms, which have the same rate (fig. 3a). The beginning of the wave of contraction, however, does not coincide in time exactly with the beginning of the corresponding electrical wave, but occurs somewhat later. The interval varies in our records and it is most easily accounted for as lag due to the inertia of the mechanical system of recorders. If we align the beginnings of two corresponding waves, a simple relationship over their whole course is apparent. The contraction phase of the mechanical record corresponds exactly to the first half of the electric wave, and the relaxation phase exactly to the second half. These relations are shown more clearly in figure 5, which outlines what we believe to be the correlation of the electric and mechanical phases of rhythmic contraction. The electric wave is seen to consist of two parts. The first half of the wave is a deflection in the upward direction, the second half in the downward direction. The second half is a mirror image of the first. The first part corresponds in time to contraction, the second to relaxation; in other words, the observed electric changes during relaxation are the same as those during contraction, but they occur in the reverse order.

Our accumulated records are illustrative of another striking feature. There are a large number in which the same form of wave appears in the same time relation to the mechanical record, but the entire wave is inverted, that is, the initial deflection in its varying amplitude is in the downward or positive direction (fig. 3b). The record is such as one would expect to obtain by reversing the leads to the galvanometer. It is to be remembered that for all these records, not only those that give the upright type of wave but also those that give the inverted type, the fixed and the movable electrodes bear the same relationship to the oral-caudal direction of the intestine, and that the galvanometer string always deflects upward when the oral attachment is becoming negative relative to the caudal.
Why, then, does the oral attachment sometimes become relatively negative, and sometimes relatively positive to the caudal?

For a while, the explanation was sought in some condition of the intestine, or in the part of the intestine from which the record was obtained. But the question was resolved very simply when a different type of experiment was performed. Instead of connecting the galvanometer to both electrodes that are attached to the intestine, we attached only one; the other was connected with a neutral or standard nonpolarizable electrode, immersed in the bath in a corner of the tank at a distance from the body of the animal. The galvanometer was connected in such a way that an upward deflection indicated that the electrode on the intestine was negative relative to the inactive standard electrode.

When unipolar records were thus taken, the initial deflection was always directed upward, that is, in the negative direction. It is at once clear how

Fig. 5. Diagrammatic illustration of the relationship of the phases of the electric wave to those of the mechanical contraction, when the beginnings of both waves are made to coincide.

an inversion of the wave occurred in the bipolar records. At each electrode the typical wave of the upright type was produced. Since the electrodes were reasonably close, the mechanical contraction was generally in the same phase at both points, and the electric waves were generally identical except for amplitude. If it happened that the wave at the caudal electrode had the larger amplitude the bipolar record would be reversed, for the galvanometer registers the difference in potential between the leads, and it is to be recalled that under the arrangements of the experiments, it was the caudal electrode of the bipolar records that replaced the standard of the unipolar.

That this is the explanation of the appearance of the inverted form of the wave is easily demonstrated experimentally. In figure 4 a, b, and c are shown, first, two unipolar records, one from the oral, the other from the caudal electrode; both are typical wave forms in the normal direction, al-
though that from the oral electrode is not so sharply defined on account of disturbances due to respiratory movements. When the electrodes are attached to these same points for a bipolar record in the regular way, the algebraic difference of these is obtained, and since the caudal wave is of greater amplitude it predominates and the resultant wave is in the reversed direction.

Up to this point we have considered the characteristic electric wave, obtained during rhythmic contraction, in its general outline. We shall now take up several details:

1. The part of the typical wave corresponding to contraction, that is, the first half of the wave, is further divisible descriptively into two elements, quite sharply defined (fig. 5). The first of these is a rapid upward deflection occupying about one-fifth of the entire contraction period, and ending abruptly. This is followed by a deflection, indicating a stationary, or slowly rising negative potential occupying the rest, that is, the last four-fifths of the contraction period. The latter is completed by a short rapid rise just before the beginning of relaxation. The relaxation phase, being the mirror-image of that corresponding to contraction, consists of two similar parts occurring in reverse order. It is to be presumed that the two component parts of each half wave of electric potential so strikingly different in appearance, represent different processes in the physiology of muscular activity. These findings raise the question of what may constitute these physiologic differences.

2. The contraction phase of the electric record contains one detailed character not present in that of relaxation. Just after the sharp rise at the beginning of contraction, there is a rapid oscillation of the string at the rate of about 10 per second. It can be seen clearly in the enlarged figure 4 d and can be made out in the waves of figure 3. These oscillations are not always observed, but are seen so frequently that we are inclined to believe that if they are absent, it is because of a lack of sufficient sensitivity in the recording devices. We have seen the same sort of rapid oscillation of the string, regularly, during tetanic contraction of the intestine, when studying peristaltic rushes. Perhaps, during rhythmic contractions, too, they represent a tetanic-like state of the muscle as a part of the contraction process.

3. The next feature to be considered is not evident in all records. In fact, it was not observed until late in our investigations, and only after special consideration did we decide that it forms a definitive part of the potential wave. We refer to the appearance, at times, of a sharp positive deflection just when one wave ends, and the next begins. This is shown in figure 4 e, in which the level of zero potential relative to the standard electrode of the bath is shown by the line at the right. When the shadow of the string is below this line, the intestine at the point of attachment of the
electrode is at a positive potential, when above, at a negative potential relative to the standard electrode. It is to be observed that at the end of a wave there is a rapid deflection of the string below the zero line (positive) and an equally rapid return merging into the next wave. The sharp downward deflection referred to is, then, due to a relatively positive potential of the intestine.

Considering the conditions of the experiment, the foregoing observation is surprising. According to the almost universally stated theories, action currents in muscle originate in a wave of negativity that accompanies excitation. According to this conception, a positive deflection in the action curve can be produced only when a bipolar record is made, and in that case the positive deflection is due to an active negativity in the distal electrode. But we were working with a unipolar arrangement. It is difficult to frame any hypothesis by which the standard electrode in the bath could be affected negatively by the contraction of the intestinal muscle far removed from it. But, more important still, it is well nigh impossible that it should be so affected, in such precise relationship to the phases of the wave of potential from the muscle, for these phases do not coincide in time for waves from different parts of the intestine. A negative pulse at the standard electrode, coordinated to the phases of one wave, would necessarily be out of phase with another. We seem, therefore, to be driven to the conclusion that the origin of the downward throw of the string referred to, is produced by a positive potential at the site of the active intestine. For such a phenomenon there is no place in the negativity hypothesis usually advanced to explain action currents from muscle and nerve. Similar observations have been made for striated muscle by Craib.

4. Another point is noteworthy because of its contrast with what is seen in the usual action-current tracings. We have shown that the wave of potential during relaxation is quite as marked in its definitive character as that during contraction. Such is not the case for action currents from striated muscle or nerve ordinarily. For instance, the entire P-Q-R-S-T wave of the electrocardiogram is completed during systole; no changes in electric potential occur during diastole. The same is essentially true for skeletal muscle; the electric changes observed during relaxation are merely due to the passing off of the previously established negative potential. This is not the case in our observations; there was a definite character to the potential wave during relaxation (the same indeed as during contraction), it has a point-to-point correspondence with the mechanical record of relaxation, and its duration in time is exactly the same. In view of the fact that it is so unusual to observe action-current changes during relaxation of muscle, we hesitate to advance this observation as contradictory of the general finding.

It is conceivable that what we have observed in these experiments is
not strictly comparable with the ordinary action currents. Also it may be
that the lengthening of the muscle is not always due entirely to relaxa-
tion, but is due partly at least to a pull resulting from contraction of the
muscle in neighboring segments of the intestine. It is hard to see how such
stretching could produce the particular form of wave observed, but the
possibility should be kept in mind. It would not be surprising, however,
to find indications of active potential changes accompanying relaxation
in smooth muscle because this tissue is always in a state of tonus between
complete relaxation and complete contraction. Since relaxation as well
as contraction can be produced by stimulation of the appropriate nerve it
may be looked on perhaps as an active process at least under some circum-
stances.

The wave of electric potential, which we have described for rhythmic
contractions of the rabbit’s intestine, does not appear to be limited to that
animal. We have found evidence of its presence in some experiments on
the dog and cat which we hope to report later. Puestow, working with
segments of the dog’s intestine transplanted to the abdominal wall ob-
tained action currents which we would interpret as corresponding to the
inverted type of wave in a “bipolar record” obtained in the rabbit. For
comparison an example from Puestow’s records is included in figure 3 c.
Electrograms obtained by Castleton also of isolated dog’s intestine, which
he has kindly permitted us to examine, corroborate this impression.

SUMMARY

Simultaneous electric and mechanical records from the intact intestine
of the anesthetized rabbit were made. Bipolar and unipolar records were
studied. The unipolar is fundamental; the bipolar represents the algebraic
difference between the unipolar potential changes at the two electrodes.
During rhythmic contraction of the intestine, a characteristic type of wave
of electric potential can be observed which has a definite relation to the
mechanical contraction. The electric wave has a symmetric form; the first
half occurs during contraction and the second half during relaxation. As a
part of the contraction phase there are often a number of small rapid oscil-
lations similar to those observed during tetanus. Unipolar records show
that a positive variation sometimes occurs during the course of the contrac-
tion process.

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