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inhibition of voluntary muscular contractions, but failed to do so even with very strong currents. Eulenberg (*Deutsch. Archiv f. klin. Med.*, iii., 1867) obtained, on the nerves of men, changes in irritability closely resembling those obtained by Pflüger on the nerves of frogs. Erb (*Deutsch. Archiv f. klin Med.*, iii., 1867) at first found a decrease of irritability near the cathode and an increase near the anode. Later, however, his attention having been called by Helmholtz to the way in which the current spreads, he repeated his experiments and decided that the nerves of men behave like those of animals (Ziemssen's "Patholog. u Therapie," iii., S. 90, 1882). Samt, Bruecker, Runge, and Ziemssen also studied this question but failed to obtain uniform results.

De Watteville (Thèse inaug., 1883) reached the conclusion that human nerves react like those of frogs to the battery current; and Waller and de Watteville (Philos. Trans. Royal Soc., London, 1882) obtained definite proof that the irritability of the human nerve is decreased in anelectrotonus and increased in catelectrotonus. Waller ("Lect. on Physiol.," first series, on Animal Electricity, p. 81, London, 1897) describes the following experiment: A large flat electrode is placed on the back of the neck and the knob of a small electrode over the ulnar nerve at the back of the elbow. The electrode is pressed carefully upon the nerve, and then tapped at regular intervals with a light mallet, just hard enough to give distinct twitches of the fingers. If while these light blows are being given the current is sent into the nerve, the electrode being made a cathode, the effect of the taps is seen to be more pronounced; if the current is then reversed, and the electrode is made an anode, the taps are seen to be without effect.

Excitation Effects of the Voltaic Current.—Not only does the voltaic current produce alterations within the nerve which greatly modify its irritability and conductivity during the flow and after the withdrawal of the current, but it causes excitation effects at the instant that the current begins and at the instant that it ceases to flow through the nerve. These excitation effects are intimately related to the electrotonic changes produced by the current, and, to be understood, must be considered in this connection.

The amount of excitation depends on two sets of conditions: those conditions of nutrition, etc., which determine the excitability, the molecular stability, of the nerve as a whole; and those conditions which determine the extent and character of the electrotonic changes which occur at the two poles. This latter set of conditions are, viz., the strength and density—*i.e.*, the intensity of the current; the rate of change of intensity; the duration of the current; and the length of nerve subjected to its influence.

It has been frequently pointed out that a rise of irritability is closely associated with increased molecular instability. If the change be sufficiently sudden there may be molecular disintegrations which result in the liberation of energy and the development of an excitation process. At the instant the current is sent into a nerve, there is a sudden rise of irritability at the cathode, from the normal to something above the normal, and a fall at the anode, from the normal to something below the normal. When the current is opened the reverse is true: a sudden rise of irritability at the anode, from below the normal to a level above the normal, and a fall of irritability at the cathode, from a point above the normal to a level below the normal. The sudden rise of irritability and sudden increase of molecular instability occurring at the cathode when the current is closed, and at the anode when it is opened, cause an excitation process to develop at the cathode on the closing and at the anode on the opening of the current.

Pflüger* stated his "law of polar excitation" as follows ("Untersuchungen," S. 456): "A given stretch of a nerve is irritated by the development of catelectrotonus and the disappearance of anelectrotonus, but not through the disappearance of catelectrotonus or the development of anelectrotonus."

The cathode closing effect is the stronger and is the only one seen when the current is weak; as the current is strengthened the anode opening excitation also develops, so that by medium currents both closing and opening effects are seen. By strong currents, these excitation effects are rendered still stronger; but a new condition begins to show itself, viz., the effect of the current on the conductivity. The conductivity of the nerve suddenly lessens at the region of the anode at the instant the current is closed, and at the cathode at the instant the current is broken, and if the current be strong the decrease of conductivity acts as a block for excitation processes developed higher up.

The results of the excitation of the nerve of the frog, by making and breaking battery currents of different strengths and different directions, have been formulated by Pflüger ("Electrotonus," S. 454) as follows:

PFLÜGER'S LAW OF CONTRACTION.

Current.	ASCENDING.		DESCENDING.	
	Closing.	Opening.	Closing.	Opening.
Weak	Contraction.	Quiet	Contraction.	Quiet.
Medium	Contraction.	Contraction.	Contraction.	Contraction.
Strong	Quiet	Contraction.	Contraction.	Quiet.

The same law is found to hold good for afferent nerves, the reflex response being taken as the index, only in this case the organ to be excited being at the central end of the nerve, the effects of descending and ascending currents are reversed.

That the closing excitation is developed at the cathode and the opening at the anode may be proved by subjecting special regions of the nerve to agents which will alter the irritability. Gotch and Macdonald (*Journ. of Physiol.*, xx., p. 257, 1896) found that if the irritability of the nerve be raised at one pole by the cooling of that part of the nerve, and lowered at the other by warming the part, one obtains with suitable strengths of current an excitation only from the pole that is on the cooled region, a closing if this is the cathode, an opening if this is the anode. Similar results are got if the irritability of the nerve is locally raised by the application of NaCl and locally lowered by the application of ammonia.

Effect of Rate of Change.—DuBois-Reymond formulated his "law of excitation" as follows: "It is not the absolute value of the current at each instant to which the motor nerve replies by a contraction of its muscle, but the alteration of this value from one moment to another; and, indeed, the excitation to movement which results from this change is the greater the more rapidly it occurs by equal amounts, or the greater it is in a given time." Although this rule is not without exceptions, the general statement holds good that excitation effects fail in case catelectrotonic changes develop and anelectrotonic changes pass off gradually; the suddenness with which the equilibrium of the nervous molecules is altered appears to play an important part in producing what we call the nerve impulse. For this reason the rate at which the change of intensity of the existing current occurs has a marked influence on the result, and within certain limits (varying with the special type of nerve) the more rapid the changes the greater the exciting effect.

Effect of Duration of Current.—The catelectrotonic and anelectrotonic states do not develop with equal rapidity, the former developing very rapidly and the latter somewhat more slowly. For this reason, weak currents of short duration excite only on the closure, at the cathode. This is true of brief voltaic currents, breaking induction currents and condenser discharges. Anodic excitations with induced currents are to be obtained only when very intense currents are used.

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* The statement is not infrequently made that Chauveau (Jour. de Physiol., ii., pp. 490-511; *ibid.*, pp. 553-576, 1859) discovered the "Law of Polar Excitation." Those who are interested in this subject are referred to the article by Pflüger, Pflüger's Archiv, xxxi., S. 119, 1883.

Effect of Length of Nerve.—That excitation fails when the electrodes are applied to the opposite sides of the nerve is due not to the resistance, although this is increased, but to the fact that the antagonistic anelectrotonic and catelectrotonic effects neutralize each other. On the other hand, we find that the effect of irritation is the greater the longer the stretch of nerve between the electrodes, because the further they are apart the more complete the anelectrotonic and catelectrotonic changes.

The Opening and Closing Tetanus.—Ritter observed that if a strong ascending current flows through a nerve for a considerable time, on the opening of the circuit the muscle enters into vigorous continued contraction, which only gradually passes off. This phenomenon has received the name of Ritter's opening tetanus. The excitation develops at the anode, as is shown by the fact that it persists after the nerve is cut above the anode in the intrapolar region. The cause of the excitation is to be found in the anelectrotonic chemical changes which have been produced during the flow of the current, and which, because widespread, require considerable time for their disappearance. The tetanus ceases at once if the current is again closed, and the decrease of irritability which exists at the anode when the current is closed is again established. On the other hand, the tetanus becomes still stronger if the current be closed in the reverse direction, and the irritability in the region of the former anode is now still further increased by putting that region into a condition of catelectrotonus.

If the irritability of a nerve be increased by some agent, a salt or a mechanical influence, for example, but not enough for the state of heightened irritability to pass over into a condition of excitation, the closure of the current, by still further increasing the irritability at the cathode, will cause a closing tetanus.

These effects can be summed up as follows: If the irritability of a nerve be heightened by any influence of a kind to produce a condition of latent excitation, this state manifests itself by a continuous excitation starting at the cathode on the closure, and at the anode on the opening of the current. There are some nerves, especially the non-medullated of crayfish, which under normal conditions show prolonged closure effects in a very striking manner, and Biedermann ("Elektrophysiologie," S. 596, 1895) argues that the medullated nerves of voluntary muscles, although normally excited only by the make and break of the current, may under altered conditions respond as well to the polar changes resulting from a prolonged flow of the current.

The Law of Contraction for Human Nerves.—The law of contraction which applies to human nerves under normal conditions differs considerably from the law of contraction established by Pflüger for the isolated nerves of frogs. The differences are, however, more apparent than real, and are readily reconciled if one takes into account the conditions under which the work is done. The so-called unipolar method is used for the excitation of human nerves (see page 769). By this method both opening and closing effects are to be obtained beneath the positive and beneath the negative electrode, because under each of these there are physiological anodes and cathodes where the current enters and leaves the nerve. This condition is illustrated in the following figure.

The current enters the nerve beneath the anode, and leaves it beneath the cathode as a comparatively dense stream; but where it leaves the nerve beneath the anode and enters it beneath the cathode, the stream is diffused. These differences in density play an important part in determining the reactions.

The current spreads widely as it passes from or to the electrodes through the nerve, so that to either side of the anode and cathode the current is flowing in both directions along the nerve: for this reason we cannot find the effects of direction of current such as show themselves on the isolated nerve.

Closing excitations developing at the physiological cathodes, when the nerve passes from the normal state to one of catelectrotonus, always tend to be stronger than opening excitations, developing at the physiological anodes, when the nerve passes out of the state of anelectrotonus. Of the two closing and two opening excitations, that which occurs where the density of the current is greater is the stronger.

If the effect of closing and opening excitations be tested at the positive and negative electrodes with gradually increasing strengths of current, under normal conditions the following order will be observed, viz.:

1. Cathode closing contraction (KCC), *i.e.*, the contraction which results from the development of catelectrotonus at the physiological cathode beneath the physical cathode.

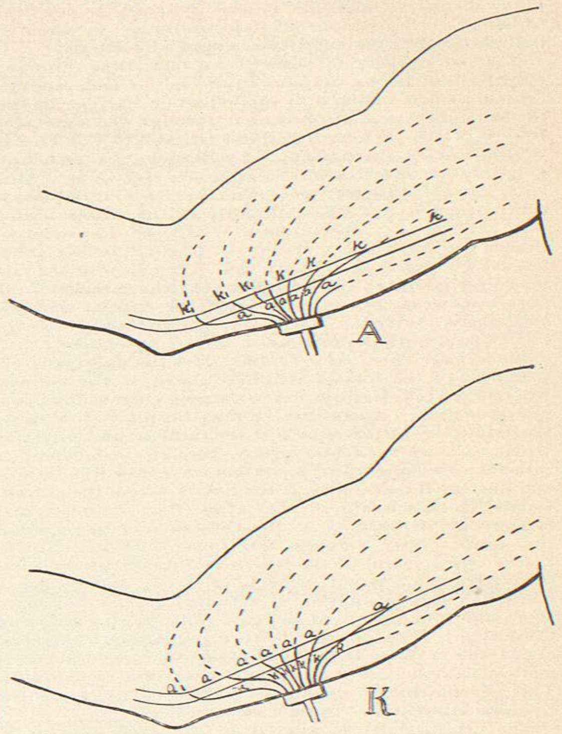

FIG. 1850.—Unipolar Excitation of Human Nerve. *A*, The positive electrode, the physical anode; *K*, the negative electrode, the physical cathode; *a*, *a*, *a*, physiological anodes; *k*, *k*, *k*, physiological cathodes.

2. Anode closing contraction (ACC), *i.e.*, the contraction which results from the development of catelectrotonus at the physiological cathode beneath the physical anode.

3. Anode opening contraction (AOC), *i.e.*, the contraction which results from the cessation of anelectrotonus at the physiological anode beneath the physical anode.

4. Cathode opening contraction (KOC), *i.e.*, the contraction which results from the cessation of anelectrotonus at the physiological anode beneath the physical cathode.

It is convenient to describe the results in three stages, corresponding to weak, medium, and strong currents.

First stage, only KCC is seen.

Second stage shows KCC (stronger), ACC and perhaps AOC, the latter being feeble, or more rarely AOC being stronger than ACC, these variations depending on differences in the density of the current due to relation of nerve to surrounding tissues.

Third stage gives all four contractions, the KCC being vigorous and prolonged, tending to take on the character of a continuous contraction (the closing tetanus), and the

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KOC being very feeble. By this third stage the coming of the AOC may be delayed. Waller (*Archives de Physiol. normal et Pathol.*, p. 383, 1882) finds this delay may be as much as 0.3 second, and attributes it to the loss of conductivity which occurs in the region of the physiological cathode for a short time after the opening of the current.

Effect of the Voltaic Current on the Irritability and Conductivity of Muscle.—If a constant battery current is allowed to flow through a muscle, it acts upon it as it does upon the nerve, and puts it into the peculiar condition called by DuBois-Reymond "electrotonus," in which its irritability and conductivity are markedly altered.

If a battery current is sent for a short time through a curarized sartorius muscle, from end to end, and the muscle is then irritated by an induction current having the same direction, applied to it through the same electrodes, it will be found that the irritability is increased by the flow of the current. Von Bezold ("Untersuchungen über die electrische Erregung der Nerven und Muskeln." S. 211, Leipzig, 1861), who was the first to observe this, supposed that the irritability of the whole muscle was increased. Biedermann ("Electro-Physiology," translation by Frances Welby, i., p. 291, London, 1898) has shown that this is not the case. The flow of the current first increases the irritability at the cathode if the current is weak, but decreases it if the current is strong and long-continued. The changes in irritability are not to be found in the intrapolar or extrapolar regions.

Biedermann (*loc. cit.*, p. 286) gives the following explanation of the loss of irritability seen at the cathode when the muscle is subjected to a strong current for a considerable time: An electric current during its flow raises the irritability of the muscle at the cathode, and produces latent excitation effects, which, though insufficient to cause the discharge of an excitation wave, result in fatigue and decreased irritability at the points where the current leaves the muscle fibres. The after-effect of the current is decreased irritability at the cathode and increased at the anode, these changes, too, being localized at the poles. On account of the loss of irritability produced at the cathode, a current sufficiently strong to produce a marked closing excitation, if withdrawn after flowing a short time and then sent in again, fails to give a closing excitation. If the current be then put through the muscle in the reverse direction, so that the former anode is made a cathode, a good closing contraction is obtained. This phenomenon is analogous to what is known as the "voltaic alternative" in the case of nerves.

The conductivity is altered in the same way as in nerves. Contrary to the view of von Bezold, it is not changed in the intrapolar region. Engelmann (Pflüger's *Archiv*, iii., 1870), studying the ureter of the rabbit, found that the conductivity is lessened at the anode by medium currents and is lost there by strong currents. Further, by strong, continued currents, the conductivity decreases at the cathode. Biedermann (*loc. cit.*, 296) associated this with the lessened irritability and regards it as an effect of the fatigue caused by the latent excitation. He did not find it less at the anode in the case of striated muscles, but as it is lessened at the anode in the case of the nerves and non-striated muscle, he thinks there must have been some experimental error.

Polar Excitation of Muscle by the Battery Current.—In the case of muscles as of nerves, the excitation process develops at the cathode on the closing and at the anode on the opening of the current.

Both Vulpian (*Gaz. méd. d. Paris*, p. 618, 1857; Compt. rend. (2), iv., 1857; *Journ. de Physiol.*, i., p. 569, 1858) and Schiff (Molesch. "Unters.," v., S. 187, 1858; "Beiträge z. Physiol.," ii., S. 13) observed that when a muscle is dying and can no longer transmit the excitation wave, it may show a localized contraction, an "idiomuscular welt," at the point of application of the cathode. They failed to recognize the significance of the phenomenon, and we are indebted to von Bezold for the proof that the "law of contraction" found by Pflüger and Chauveau for nerves holds good for muscles. He connected a myograph lever with the tibial end of a curarized sartorius muscle, and then recorded the latent period of the muscle when the upper part was held firmly by two electrodes placed at unequal distances from the tibial end. The latent period was longer by closing excitations when the cathode was farther away from, and shorter when it was nearer to, the recording part of the muscle.

Engelmann (Pflüger's *Archiv*, iii., S. 247, 1870) reported that the ureter of the rabbit exhibits in an admirable manner the polar effects of the current, a peristaltic contraction wave starting from the cathode on the closing and from the anode on the opening of the current. Hermann ("Handbuch der Physiol.," Bd. ii., Abth. 1, S. 93, 1879) states that if loops of wet thread be used as electrodes and placed on the curarized muscle, a welt-like contraction develops at the cathode on the closing, and at the anode on the opening, and draws the whole muscle toward the electrode in question. Engelmann (Pflüger's *Archiv*, xxvi., S. 97) and Biedermann ("Sitzungsbr. d. k. Akad. d. Wiss. z. Wien," Bd. lxxx., Abth. 3, S. 367) ascertained that if a part of a muscle be injured by being dipped into a hot salt solution, and electrodes be applied, the one to the injured the other to the normal part, the closing contraction is very feeble if the cathode be applied to the injured part, but vigorous if it be applied to the normal part. These and many other similar observations have fully established von Bezold's conclusions.

Not only does the muscle contract when the current is made or broken, but during the flow of the current a continuous slight contraction may be observed at the cathode. If a current be led through a muscle from end to end, one can see with a lens a swelling of the muscle at the point where the current leaves it. The difference between the two kinds of contraction is well brought out in the following experiment of Engelmann (Pflüger's *Archiv*, iii., S. 316): He clamped a curarized sartorius muscle in the middle, applying the clamp firmly enough to prevent the muscle from moving but not enough to interfere with its conductivity; he then placed the electrodes near the two ends, and connected the tibial end with a recording lever When the anode was on the writing end, a single twitch was seen on the opening of the current; when the cathode was on that end, the twitch caused by the closing of the current was followed by a prolonged contraction. The tendency of the muscle to give a prolonged localized contraction at the cathode during the flow of the current is increased by cold or any influence which slows muscular reactions.

In conclusion it may be said that the battery current can arouse two different kinds of contraction in the muscle; a sudden change in the intensity of the current at the instant it is closed or opened causing a simple twitch, and a continuous flow of the current causing a prolonged tetanic contraction. When the current is closed the excitation develops at the cathode, and when it is opened at the anode, and it is probable that in the case of the muscle as of the nerve the excitation processes are associated with the sudden passage of the tissue into a state of catelectrotonus and out of a state of anelectrotonus. In a like manner we can compare the continuous contraction which is developed in the muscle at the cathode when the flow of the current is prolonged, with the continued state of heightened irritability which exists in the nerve while it is subjected to the flow of the current. As Gotch (Schaefer's "Textbook of Physiology," ii., p. 436) says: "In the muscle, contraction is the sign of the cathodic state; in the nerve, increased excitability."

There is another interesting effect which may be mentioned in this connection, viz.: the inhibitory action of the anode during the flow, and of the cathode on the opening of the current. Biedermann ("Electro-Physiology," trans., i., p. 257, 1896) states that if the electrodes are applied to the ventricle of the heart, the muscle relaxes during systole at the point of application of the anode when the current is closed, and at the point of application of the cathode when it is opened. A stronger current is required for the cathodic than for the anodic effect.

The inhibitory influence of the anode can be well seen if a battery current is allowed to flow through a piece of smooth muscle when in tonic contraction (Biedermann, *loc. cit.*, p. 256). It is also observed on striated muscles, when put into a state of tonus by veratrine. The phenomenon is undoubtedly associated with the decrease of irritation which takes place at the anode on the closure and at the cathode on the opening of the current (Biedermann, *loc. cit.*, p. 265).

Electrotonic Currents.—If a constant current be sent through a special part of a nerve, and a galvanometer be connected with any portion of the nerve, either central or peripheral to the region subjected to the polarizing current, the instrument will indicate the presence of an electric current having the same direction as the battery current. The battery current by means of which these changes are produced is frequently spoken of as the polarizing current, and the electrodes connecting the battery with the nerve as the "polarizing electrodes." The electrodes which connect the nerve with the galvanometer, or electrometer, when the electrotonic currents are being studied, are referred to as the "leading-off electrodes."

The fact that the flow of a constant battery current through a part of a nerve can alter the electromotive state of the whole nerve was first observed by DuBois-Reymond ("Untersuchungen über thierische Electricität," Bd. ii., Abth. 1, S. 289, 1849), who called the electric currents which result from the change "electrotonic currents," those to be obtained from the side of the anode being termed "anelectrotonic," and from the side of the cathode "catelectrotonic" currents (see Fig. 1851).

I. The anelectrotonic current strengthens the effect of the demarcation current on the galvanometer.

II. The catelectrotonic current weakens the effect of the demarcation current on the galvanometer.

This can be taken as a proof that electrotonic currents are independent of the current of rest. Another proof is that they can be observed when, on account of the symmetrical arrangement of the leading-off electrodes, demarcation currents cannot be detected. With this arrangement a change in the electrical condition of the nerve is caused by the polarizing current, of such a type that all points of the nerve on the side of the cathode are more negative and all points on the side of the anode more positive than normally, the change being greater close to the electrodes, and shading off from these points in both directions along the nerve. This is true of the extrapolar regions at least, and probably is true of the intrapolar region also, though considerable uncertainty exists as to just what happens in this part. To state the change with reference to the direction of the polarizing current, a battery current flowing through a portion of a nerve alters the chemical condition of the whole nerve, all points of which become electrically active in the direction of the current, each point becoming galvanometrically negative in respect to other points in advance of it in the direction of the current.

If one would avoid confusion in studying this subject, he must always bear in mind the fact that a current is always to be considered as flowing in a circuit, from the positive to the negative sign, and consequently the flow in the part of the circuit containing the nerve must have the opposite direction to the flow in the part containing the galvanometer. A point which is positive with reference to the direction of flow through the galvanometer is negative with reference to the direction of flow through the nerve, and *vice versa*.

Electrotonic currents are not to be identified with currents of action, because they are to be seen when the battery current is flowing constantly through a motor nerve, and is too weak to cause a state of excitation, sufficient at least to produce a current of action and a contraction of the muscle. Further, as Hermann ("Handbuch d. Physiol.," Bd. ii., Abth. 1, S. 158, 1879) says, the fact that electrotonic currents increase with increase of strength of the polarizing current, and do not reach a maximum, is against the view that they are the result of a condition of excitation. Finally, the electrotonic effects are the stronger the nearer the part of the nerve examined to the region through which the battery current is flowing, which would not be true of currents of action.

To any one familiar with the tendency of electrical currents to spread through moist conductors, the first thought is, that electrotonic currents are due to the ordinary spread of the battery current beyond the electrode bringing it to the nerve. That this is not the immediate cause is proved by the fact that whatever interrupts the physiological conductivity of the nerve, as a ligature or strong acid applied between the polarizing electrodes and leading-off electrodes, although not lessening the physical power of the nerve to conduct electric currents, often wholly does away with the phenomenon. The same is true of anything which will lessen the physiological activities of the nerve. DuBois-Reymond failed to find electrotonic currents on dead nerves, moist threads, and muscles, which offer favorable conditions for the spread of electrical currents. Schiff ("Lehrbuch d. Muskel u. Nervenphysiologie," S. 69, Larr, 1858–59) and Valentine (*Zeitschrift. f. rat. Med.* (3), xi., S. 1, 1861) failed to find them on degenerated nerves, while Gruenhagen

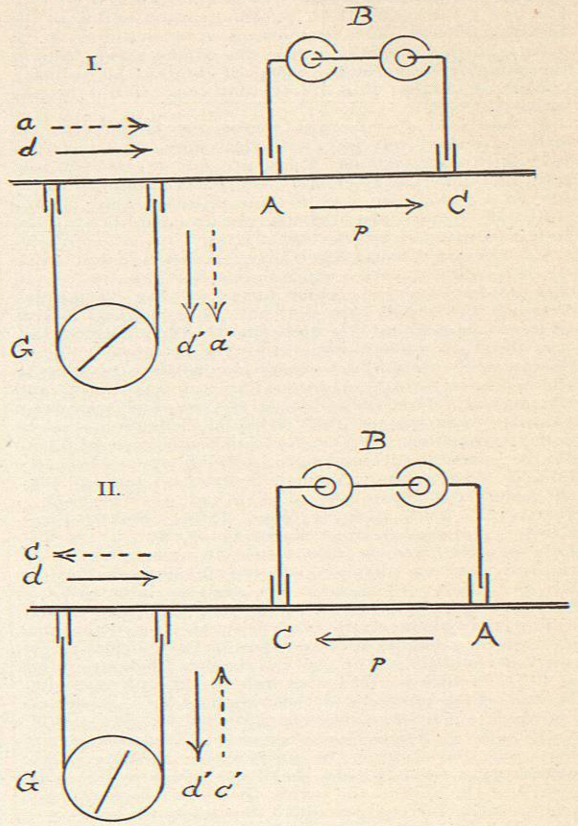

FIG. 1851.—Effect of Electrotonic Currents on the Demarcation Current. *B*, Battery; *A*, positive electrode, the anode; *C*, negative electrode, the cathode; *G*, galvanometer; arrow *p* shows the direction of the polarizing current; arrow *d* shows the direction of the demarcation current in the nerve; arrow *d′* shows the direction of this current in the galvanometer circuit; arrow *a* shows the direction of the anelectrotonic current in the nerve; arrow *a′* the direction of this current in the galvanometer circuit; arrow *c*, the direction of the catelectrotonic current in the nerve; arrow *c′*, the direction of this current in the galvanometer circuit.