(*Königsberger med. Jahrb.*, iv., S. 199, 1864) thinks that he observed them. Boruttau (Pflüger's *Archiv*, Bd. lviii., S. 29, 1894) observed electrotonic currents on the nerves of frogs ten or twelve days after their removal from the body, and long after they had lost the power to excite the muscles. As long as the ordinary structure of the nerve is retained, these currents can be detected; but they weaken the more the chemico-physical condition departs from the normal. Hermann ("Handbuch d. Physiol.," Bd. ii., Abth. 1, S. 158) draws attention to the fact that electrotonic currents have been found to be greater in frog's nerves, at the side of the anode than at the side of the cathode, though if due to the ordinary spread of current it is likely that they would be the same.

Probably, under certain conditions, feeble currents which are of purely physical origin may be detected in the extrapolar regions; these are not to be confused with physiological electrotonic currents, although these, too, as we shall see, are in their ultimate analysis the result of chemico-physical changes brought about in the living substance by the polarizing current. Waller ("Lectures on Animal Electricity," p. 104, London, 1897) discusses this question, and shows how by the use of anæsthetics, ether and chloroform, one can distinguish between the purely physical and physiological factors of the phenomenon He finds that the physiological factor, the true anelectrotonic and catelectrotonic effects, disappears as the physico-chemical conditions peculiar to the living state are suppressed by the anæsthetic, and the physical factor, the "physical electrotonus" of certain German monographs, the "residual deflection" as he calls it, remains. Physical electrotonus, according to Waller, means nothing more than current escape (see (Waller, "Lectures on Animal Electricity," note, p. 106). Biedermann ("Sitzungsbr. d. k. Akad. d. Wissensch.," Bd. xcvii., Abth. 3, S. 84, Wien, 1888; "Elektro-Physiology," translated by Frances C. Welby, ii., S. 294, London, 1898) was the first to use an anæsthetic to distinguish between physiological and physical electrotonic effects. His conclusions, as we shall see later, differed from those of Waller (see effect of anæsthetics, p. 775).

The effect of the temperature is another proof that true electrotonic currents are dependent on the normal physiological condition of the nerve. Raising the temperature to 40° C. (which would be favorable to the physical conduction of the current), or lowering it to 5° C., causes the extrapolar currents to disappear (Waller, *loc. cit.*, p. 107).

Strength of Electrotonic Currents.—Electrotonic currents are the stronger the greater the intensity of the polarizing current, within the limits which would cause injury of the nerve; the longer the stretch of nerve subjected to the current, provided the resistance be allowed for; the nearer the leading-off electrodes are placed to the polarizing electrodes; the more normal the condition of the nerve, and the greater the polarizability of the nerve. A maximum strength of electrotonic current has not been found. Anelectrotonic currents are stronger than catelectrotonic, and DuBois-Reymond (*Archiv f. Anat. u. Physiol.*, S. 441, 1867) obtained anelectrotonic currents twenty-two times the strength of the demarcation current, and requiring an electromotive force of 0.5 of a Daniel cell for their compensation.

Secondary Electrotonus.—The strength of the electrotonic current developed in a nerve may be enough to excite another nerve in contact with it. The current in the first nerve flows through the second, which completes the circuit for it; when the current enters or ceases to flow through the second nerve, on the make and break of the polarizing current in the first nerve, the second nerve is excited and a muscle connected with it will contract. For example, exciting the central stump of the peroneal may excite the fibres of the tibial, where they run by the side of the peroneal fibres in the sciatic, and may cause a contraction of the gastrocnemius. This "paradoxical contraction" of DuBois-Reymond ("Untersuch.," ii., 1, S. 528, 1849) is not to be confused with the "paradoxical contraction" of Hering (Hermann's "Handbuch," Bd. ii., Abthl. 1, S. 160, 1879), due to excitation of a second nerve by the current of action of the first. The electrotonic current from the first nerve can put the second into secondary electrotonus, as can be shown with a galvanometer; and Moleschott ("Untersuch.," Bd. x., S. 649, 1870) has seen even a tertiary electrotonus.

Rate of Development and Spread of Electrotonus in Nerves. — DuBois-Reymond ("Untersuch.," Bd. ii., S. 321, 391, 540, 1849) concluded that electrotonus begins to develop at the two poles at the instant the polarizing current is closed. Pflüger ("Untersuch. u. d. Physiol. d. Electrotonus," S. 442–444, 1859, Berlin) agrees with this; he writes: "DuBois-Reymond has shown that the growth of the electrotonic current finds sufficient time for its development even by the quickest induction currents. I can affirm the same for the rate at which, with strong currents, the change of irritability occurs after the closing of polarizing currents." Helmholtz ("Monatsberichte d. Berliner Akad.," S. 329, 1854), making use of DuBois-Reymond's "paradoxical contraction," *i.e.*, letting the electrotonic current of one nerve excite another nerve resting upon it, concluded that "the condition of electrotonus does not appear demonstrably later than the electrotonic current which excites it." Bernstein ("Naturwiss. Rundsch.," S. 9, 1887; "Untersuch. a. d. physiol. Inst. d. Univers. z. Haller," S. 75, 1888) ascertained, with the aid of his rheotome, that extrapolar electrotonus shows itself near the poles within 0.001 second after the battery current has been closed, and Hermann (Pflüger's *Archiv*, lxii., S. 1, 1888) concluded that the polarization changes causing these currents begin at the instant that the polarizing current enters the nerve.

The method of the rise and fall of the electrotonic change was first described by DuBois Reymond (*Archiv f. Anat. u. Physiol. u. wissensch. Med.*, S. 446, 1867), who found that anelectrotonic currents of nerves grow to their maximum somewhat less rapidly than catelectrotonic, and then gradually fall, while catelectrotonic currents reach their maximum almost immediately and then forthwith fall, the decline occurring even during the rise of the anelectrotonic currents.

It is generally conceded that electrotonus begins to develop at the poles at the instant the current is closed, and spreads thence along the nerve in the form of a wave; great differences of opinion exist, however, as to the rate at which it travels along the nerve. Pflüger ("Electrotonus," S. 442) decided that anelectrotonic alterations of excitability occur at the same instant as the anelectrotonic currents, and he considered that those two phenomena were merely different expressions of the change produced in the nerve by the polarizing current. This makes the rate of spread of the change of irritability of interest in this connection. Gruenhagen (Pflüger's *Archiv*, iv., S. 549, 1871; vi., S. 181, 1872) found that the changes in irritability associated with anelectrotonus and catelectrotonus are transmitted with equal rapidity, and appear in all parts of the nerve at the instant that the current is closed. Wundt ("Untersuch. z. Mechanik. d. Nerven u. Nervencentren," i., 1871) arrived at a different result, deciding that the alterations of irritability of the nerve of the frog do not develop in all parts of the nerve at the instant of the closure of the current, but spread over the nerve as a comparatively slow, wave-like process, comparable to the excitation wave, "the anodic wave of inhibition" travelling at the rate of 80–700 mm. per second, according to the strength of the current. Baranowsky and Garre (Pflüger's *Archiv*, xxi., S. 446, 1880) got rates which were entirely different from those of Wundt, and which were favorable to Gruenhagen's conclusions. They found that the decrease of excitability in the anodic extrapolar regions must spread at a rate of not less than 165 metres per second. Ascher (*Zeitsch. f. Biol.*, xxxii., S. 473, 1895), on the other hand, concluded the rate of propagation to be 30 metres per second.

Experiments on the rate of transmission of electrotonic currents both in the nerve and in "core-conductor models" of nerves, have given equally contradictory results. DuBois-Reymond (*Archiv f. Anat u. Physiol.*, S. 449, 1867; Ges. Abthl., S. 258), reviewing Helmholtz's experiment, cited above, decided that it showed that the changes in the nerve which underlie electrotonus are transmitted as rapidly as the excitation process. Tschirjew (*Archiv f. Anat. u. Physiol.*, S. 525, 1879) concluded that the rate was about the same, or perhaps slightly slower than the excitation process; and Bernstein (*Archiv f. Anat. u. Physiol.*, S. 197, 1886) found that the propagation of electrotonic changes is less rapid than that of the excitation wave, the catelectrotonic wave travelling at the rate of 9–10 mm. per second. Lately, Hermann and Weiss (Pflüger's *Archiv*, lxxi., S. 237, 1898) have expressed themselves in favor of Gruenhagen's view, that the electrotonic state develops in all parts of the extrapolar regions of nerves instantaneously.

Experiments on "core-conductor models" (see page 777) are of great interest in this connection, for the results obtainable with them imitate with wonderful accuracy the phenomena observed on nerves. Boruttau (Pflüger's *Archiv*, lviii., S. 1, 1894) finds on his core-conductor models of nerves what DuBois-Reymond found for nerves themselves, viz., that catelectrotonus develops faster and declines more rapidly than anelectrotonus. A study of the galvanic alterations in these models, under the influence of a polarizing current, shows the extrapolar electrotonic currents to be transmitted in the form of a wave, the rate varying with the composition of the model, the temperature, etc., and averaging about 100 metres per second. Hermann and Samway (Pflüger's *Archiv*, xxxv., S. 1, 1884) had found the rate to be at least 60 metres per second. Gotch and Burch (Schaefer's "Textbook of Physiol.," ii., p. 549, 1900), employing capillary electrometres and recording the movements of the mercury by photography, found the rate on models to be over 100 metres per second.

An explanation of the conflicting results which have been obtained by those who have studied this question may be found in the way in which electrotonic currents in nerves and core conductors develop and decline, and in the fact that they lessen in intensity as the distance from the poles increases. Hermann (Pflüger's *Archiv*, xvi., S. 423, 1880; Hermann and Weiss, Pflüger's *Archiv*, lxxi., S. 237, 1898) points out that a difference in the strength of the current at the different parts of the nerve might well result in a difference in the lag of the recording instrument. Both Biedermann ("Electro-Physiol.," ii., S. 280, 1895) and Gotch (Schaefer's "Textbook of Physiol.," ii., pp. 497 and 549, 1900) in their reviews of this subject agree that all the slower times which have been given are for this reason open to suspicion. On the whole the evidence is in favor of the view that the electrotonic changes spread to all parts of the nerve almost instantaneously.

Electrotonus in Non-Medullated Nerves.—It was for a long time generally believed that the electrical phenomena, at least, of electrotonus occurred only in medullated nerves and were absent from non-medullated nerves. This difference was attributed to the peculiar structure of the medullated nerve, an axis cylinder surrounded by a sheath of different chemical composition.

It has been shown by Biedermann ("Bericht. d. Wien. Acad. d. Wiss.," Bd. xciii., Abth. 3; Bd. cxvii., Abth. 3; Pflüger's *Archiv*, liv., S. 24; "Electrophysiology," ii., p. 281, 1895) that certain electrotonic effects may be observed on the non-medullated nerves of a mollusk, the Anodonta. If such a nerve be connected by its longitudinal surface and cross section with a galvanometer, it shows a strong demarcation current; if this be compensated, and a battery current be applied to a distant part of the nerve, there is at the instant of closure a swing of the galvanometer in a direction corresponding to a negative variation of the demarcation current, this being due to the action of the current resulting from excitation. If the polarizing current passes through a part of the nerve not far from the leading-off electrodes, the negative variation is followed by a positive variation when the polarizing current is ascending (flowing away from the leading-off electrodes), *i.e.*, when the anode is nearest to the leading-off electrodes. If the negative effect was large, the positive after-effect is delayed and increases more slowly during the passage of the current. Its maximum strength comes with a greater intensity of battery current than is required to produce the maximum of the initial negative variation. Of course these two influences antagonize each other, and produce more or less conflicting results, according to their relative strength. This anelectrotonic effect is greater the stronger the polarizing current, the nearer the leading-off electrode to the anode, and the greater the vitality of the nerve. When the polarizing current is descending, *i.e.*, when the cathode is nearest the leading-off electrodes, little or no increase in the effect of the current of action on the galvanometer is seen.

It would appear from these results of Biedermann that non-medullated, like medullated nerves show anelectrotonic galvanic effects, but that they fail to show catelectrotonic effects. von Uexhuell (*Zeit. f. Biol.*, x., S. 550) failed to find any marked electrotonic effects on the non-medullated nerves of cephalopods; but Boruttau (Pflüger's *Archiv*, lxvi., S. 285, 1897; *ibid.*, lxviii., S. 351, 1897; lxxxiv., S. 378, 1901) reports that these nerves show the same electrotonic changes as medullated, except that catelectrotonic effects are feeble, and the anelectrotonic condition may extend over into the cathodic area. Mendelsohn (*Bul. de la Soc. de Biol.*, 1900; Richet's Dictionnaire de Physiologie, v., p. 414, 1901) also, as a result of work on many different forms, asserts that in general the non-medullated nerves of lower animals present the same qualitative electrotonic manifestations as the medullated nerves of the higher animals. Quantitatively, however, there are great differences; catelectrotonic changes are always less pronounced than anelectrotonic changes in non-medullated nerves (in some forms, indeed, may be absent), and very much less marked than in medullated nerves. It is to be remembered that the medullated nerves of higher animals differ in regard to the strength of anelectrotonic and catelectrotonic effects. In frog's nerves anelectrotonus is usually stronger than catelectrotonus, while in mammalian nerves, according to Waller ("Lectures on Animal Electricity," p. 97, and p. 122, 1897), they are of equal importance. Boruttau finds (Pflüger's *Archiv*, lxxxiv., S. 380, 1901) that in mammalian nerves anelectrotonic effects are always somewhat more than catelectrotonic, though the difference is considerably less than in the case of the nerves of frogs.

Influences which Alter the Physiological Activity of the Nerve Alter the Electrotonic Currents.—The death of a nerve, however produced, does away with electrotonic currents, and conditions which merely modify the physiological activity of the nerve alter the intensity of these phenomena.

Effect of Anæsthetics.—Biedermann ("Elektrophysiologie," S. 696, Jena, 1895; Sitzungsbr. d. k. Akad. d. Wissensch., Bd. xcvii., Abth. 3, S. 84, Wien, 1888) observed that if a nerve were etherized, although the irritability and conductivity were lost, electrotonic effects were still to be observed. Normally, anelectrotonic effects are considerably in excess of catelectrotonic, but after etherization they are about the same. Biedermann attributed the electrotonic effects which remained after etherization to the electrolytic effects of the current, and concluded that they were purely physical phenomena, while those which were lost he considered to be the true physiological electrotonic changes. He regarded the physiological factor to be the result of a reaction of the nerve, dependent on increased assimilation in Hering's sense, and to correspond to greater functional activity.

Waller ("Lectures on Animal Electricity," p. 104, London, 1897) also made use of anæsthetics to distinguish between the physical and physiological elements of electrotonus, but arrived at different results. He found (Proc. Physiol. Soc., *Journ. of Physiol.*, vol. xix., 1896) that both the anodic and cathodic effects, and their diminution on excitation of the nerve, are influenced by all the agencies which alter the electrical response of the nerve. Ether, chloroform, and carbon-dioxide gas may abolish both anelectrotonic and catelectrotonic effects, the abolition being succeeded by secondary augmentation. This result is in favor of the view that the total electrotonic effect is physiological, if we except the minor effects of current escape which may occur when very strong polarizing currents are employed. A similar conclusion is reached by Boruttau (Pflüger's *Archiv*, lxxxiv., S. 381, 1901); Waller also found that electrotonic currents may be temporarily modified by narcotics in such a way that the catelectrotonic effect may be relatively strengthened and the anelectrotonic current weakened, so that the quotient $\frac{A}{K}$ may be less than one. This has been corroborated by Boruttau (Pflüger's *Archiv*, lxxxiv., S. 335, 1901).

Effect of Acids and Bases.—This question is of importance with reference to the electrolytic changes which the current produces in the nerve. Waller ("Lectures on Animal Electricity," p. 125, 1897) studied the effects of weak acid and alkaline baths, and carbon-dioxide gas and the fumes of ammonia, upon anelectrotonus and catelectrotonus. He found catelectrotonus to be increased by slight acidification and decreased by slight basification; anelectrotonus, on the other hand, is generally decreased by slight acidification and but little affected by slight basification. To state the effects in the order of their occurrence with respect to the strength of the acid, first there is increase of anelectrotonus; second, diminished anelectrotonus and increased catelectrotonus, this being the typical effect; third, diminished catelectrotonus, as the last effect. These effects come out clearly only when the strength of the acid is nicely graded, as otherwise the finer effects are lost. The relation of anelectrotonus to catelectrotonus under these influences can be expressed by the quotient $\frac{A}{K}$. Generally the early stages are lost, and by acidification both A and K are lessened; but A is lessened more than K, so the total effect is to lessen $\frac{A}{K}$ by acidification. The characteristic effect by basification is to increase $\frac{A}{K}$. The effect of tetanizing the nerve is, according to Waller, the same as the effect of carbon-dioxide gas upon the nerve, and he argues that the effect during tetanization is due to the production of carbon-dioxide gas by the active nerve tissue, a view which Boruttau is inclined to favor.

Effect of Temperature.—According to Biedermann ("Elektrophysiol.," S. 690, 1895), if the nerves of frogs are cooled, they appear to approach the state of non-medullated nerves in their electrotonic reactions, the ordinary difference between the strength of the anelectrotonic and catelectrotonic effects being accentuated, because the cold enhances the physiological anelectrotonic reaction. Waller, however, has seen both anelectrotonus and catelectrotonus disappear under the effect of temperatures of 40° C. and 0° C. If the exposure to the abnormal temperature was not too prolonged, electrotonic currents were again seen on the return of the temperature to 15° C. The effect of lowering the temperature to normal after heating to 40° C. was to cause the catelectrotonic currents to be greatly increased, so as to be even more than the anelectrotonic. This fact is attributed to the chemical disruption of the living matter under the influence of the heat, the effect being the same as that produced by acid and by tetanization of the nerve.

Effect of Excitation on Electrotonus and the Effect of Electrotonus on the Current of Action.—Bernstein (*Archiv f. Anat. u. Physiol. u. wissensch. Med.*, S. 614, 1866) was the first to study this question. He found that the current of action causes a negative variation of electrotonic currents, similar to that which it produces in demarcation currents. This change is known as the "electrotonic decrement" of Bernstein. The view was advanced that the excitation process lessened the susceptibility of the nerve to polarization. Hermann ("Handb.," Bd. ii., Abth. 1, S. 165, 1879) corroborated the fact but gave another explanation. His view, which has since been generally accepted, is that the electrotonic currents are peculiar threads of currents from the polarizing circuits, and that the apparent negative variation of the same is due to a change caused by the excitation process in its passage through the polarized nerve. He explains the facts on the assumption that the wave of negativity which accompanies the irritation-process gains intensity as it spreads toward more strongly anelectrotonic or more weakly catelectrotonic parts of the nerve, and loses intensity as it spreads toward more weakly anelectrotonic or more strongly catelectrotonic parts of the nerve (law of the polarization increment of irritation). According to this view, the irritation process would be at its maximum at the anode and at its minimum at the cathode, *i.e.*, the galvanometer would indicate a marked negativity in the region of the anode as compared with the cathode, which would mean that there would be in the intrapolar region a strong axial current of action of the same direction as the polarizing battery current, which would make it appear that this was strengthened. This is in fact observed in galvanometer experiments, and was explained by Gruenhagen as due to a lessening of the resistance during excitation. Hermann found, however, that this does not happen, and that the effect is, as has been stated, the result of an electro-motive force resulting from the excitation. The current of action, then, because of the same direction as the polarizing current, makes it appear that this is strengthened; on the other hand, because of the opposite direction to the polarization current, it makes it appear that the polarization is less.

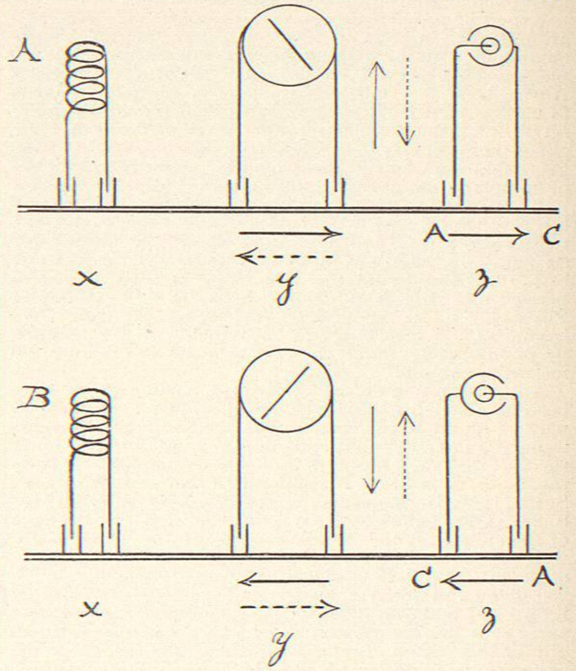

FIG. 1852.—*A*, Showing Lessening of Anelectrotonic Current. *B*, Showing Lessening of Catelectrotonic Current. *X*, Exciting circuit; *Y*, galvanometer circuit; *Z*, polarizing circuit; black arrow, direction of electrotonic currents; dotted arrow, direction of electromotive effect due to excitation.

In the extrapolar regions there is a decrease of the electrotonic currents, both on the side of the anode and on that of the cathode. If, for example, the galvanometer circuit is between the part excited and the part subjected to the polarizing current, the effect of the anodic electrotonic current on the galvanometer will be lessened when the excitation is given, because the part of the nerve near the anode will become more negative than more distant parts, and the effect of the cathodic electrotonic current on the galvanometer will be lessened because the part of the nerve near the cathode will become less negative than more distant parts.

Similar effects are observed when the galvanometer electrodes are connected, the one with the cut end and the other with the longitudinal surface, only in this case the presence of the demarcation current complicates the result. The current of action undergoes a marked alteration in its passage through the polarized region, the wave of negativity increasing as it approaches parts relatively more positive (as the region of the anode), or leaves parts relatively more negative (as the region of the cathode), and decreasing as it approaches more negative, and leaves more positive parts of the nerve. These effects are best observed with a capillary electrometer (Gotch and Burch, Proc. of Roy. Soc. London, vol lxiii., p. 300, 1898; Schaefer's "Textbook of Physiol.," vol. ii., p. 552, 1900). Boruttau (Pflüger's *Archiv*, lxxxiv., S. 334, 1901) says, if the part of the nerve connected with the electrometer is between the point irritated and the part of the nerve subjected to the battery current, when the anode is nearest, the second phase of the current of action is strengthened, and when the cathode is nearest it is weakened; while the first phase, if superposition be allowed for, is lessened in the first case, and generally increased in the second, although here, too, it may be lessened. Just the opposite happens when the region subjected to the battery current is between the part irritated and the portion connected with the electrometer. If with this arrangement the electrometer electrodes connect the longitudinal surface with a cross section, the single phase of the current of action is lessened if the anode is nearest, and strengthened if the cathode is nearest, as Bernstein found (1866) for the negative variation caused by excitation of the nerve with an interrupted current.

The After-Effects of Polarization, Secondary Electromotive Phenomena.—When a strong polarizing current is withdrawn from a nerve, two different phenomena present themselves. On account of the electrolytic effects produced in the nerve by the polarizing current, polarization currents of opposite directions to the battery current are present after its removal. On account of alterations in irritability of the tissue, excitation effects may not only occur at the instant of the removal, but they may continue for some time after. The effect of the condition of excitation is to make the former anode negative as compared with the rest of the nerve, from the standpoint of the galvanometer circuit, which means that within the nerve currents would flow away from this point. These internal currents of action would have the opposite direction to the polarization current, and in the anodic extrapolar region tend to nullify its action on the galvanometer. The result is that the anodic polarization changes are overpowered, and the cathodic extrapolar currents alone manifest themselves. This interpretation is in harmony with the results observed in muscle after the removal of the battery current.

Electrotonic Currents of Muscle upon Removal of the Battery Current.—Muscles if subjected to the flow of a battery current become polarized just as the nerves do, the electrotonic effects differing only in respect to intensity. DuBois-Reymond ("Untersuch.," Bd. ii., Abth. 1, S. 329, 1849) was the first to observe polarization currents in muscle and termed them "secondary currents." Valentin (Pflüger's *Archiv*, i., S. 512, 1868) reported that muscles might show extrapolar electrotonic currents, and Hermann ("Handbuch d. Physiol.," Bd. i., Abth. 1, S. 91–93; Bd. ii., Abth. 1, S. 168, 1879) confirmed this result. The effects are most marked in the immediate vicinity of the electrodes, and as in the case of nerve are strongest near the anode. DuBois-Reymond observed two opposite effects on removing the battery current, the one indicating a polarization current of the same, and the other of the opposite direction to the polarizing current. The former of these (which he called the positive polarization current) is a current of action, due to a condition of excitation developed at the region of the anode, which becomes suddenly relatively negative at the instant that the battery current is broken. That this current is the result of the opening excitation is shown by the following facts, viz.: it can be observed best by placing one electrode at the anode and the other at a short distance from this, the electrode at the anode becoming negative in relation to the other; it is best developed when the battery current is strong, of short duration and rapidly broken; the effect is only to be observed on fresh muscles. Later writers have generally employed the term "anodic after-effect" for this change.

The polarization currents which have the opposite direction to the battery current, the negative polarization currents of DuBois-Reymond, are purely physical phenomena, such as can be obtained in any electrolyte as the result of the flow of a battery current. These polarization currents are found throughout the intrapolar region, and, although weak, in the extrapolar. They last but a short time after the withdrawal of the battery current, and their amount varies with the strength and duration of the battery current. Although physical phenomena, they are intimately related to the physical and chemical structure of the protoplasm of the muscle, for they fail if it is altered by heat, etc. Nevertheless they are not the result of the physiological activities of the muscle, because they can be obtained when the muscle is too fatigued to respond to stimuli.

Theories of Electrotonic Currents.—Two principal theories as to the origin of electrotonic currents have been evolved. The first of these, known as the "molecular theory," was set forth by DuBois-Reymond ("Untersuchungen über thierische Electricität," ii., S. 289–389, 1849). According to this, the battery current altered the position of hypothetical electromotive molecules of the nerve, giving them a columnar arrangement. We need not dwell on this conception, as the theory and its various modifications (Bernstein, Pflüger's *Archiv*, vi., S. 335, 1872; Fleischl, "Sitzungsbr. d. Wiener Akad.," Abth. 3, lxxvii., 1878) have been displaced by the theory of electrolytic polarization. Hermann discusses the earlier literature of this subject in his "Handbuch der Physiologie," Bd. ii., Abth. 1, S. 171–196, 1879.

Peltier discovered the occurrence of polarization in animal tissues, and DuBois-Reymond ("Unters. ü. thier. Electric.," i., S. 376, 1848; ii., 2, S. 377, 1849) repeated his observations, and detected after the removal of a battery current from an isolated nerve an electromotive force of opposite direction. He termed the polarization effects produced by the flow of the current "secondary electromotive effects." DuBois-Reymond also ("Monatsbr. d. Akad. z. Berlin," S. 395, 1856; Ges. Abth. 1, S. 1) reported that the polarization occurs at the bounding surfaces of dissimilar electrolytes. Matteucci (Comptes rend., l., p. 412, 1860; lii., p. 231, 1861; lvi., p. 760, 1863; lxv., p. 151, 194, 884, 1867; lxvi., p. 580, 1868), influenced by the results of Peltier and DuBois-Reymond, studied these secondary electromotive effects, and found an explanation of electrotonic currents in the internal polarization of the nerve; he also thought to have proved the existence of electrolytic products within the nerve, viz., acids at the anode and alkalies at the cathode.

Hermann ("Untersuch. z. physiol. d. Muskeln u. Nerven," Heft 3, S. 71, Berlin 1868; Pflüger's *Archiv*, v., S. 233; *ibid.*, vi., S. 312) studied the polarization after-current of the nerve, and concluded that the polarization effects are not equally distributed through the nerve, but occur at the bounding surfaces of sheath and core; that polarization explains all the galvanic effects of electrotonus; and that Pflüger's anelectrotonus and catelectrotonus correspond with the regions of positive and negative polarization of the core of the nerve.

Core-Conductor Models.—It was in 1863 that Matteucci discovered that if a constant current flows through a portion of a platinum wire covered with a sheath saturated with a fluid, extrapolar currents can be led off which