

ON THE ORIGINS OF DORSAL ROOT POTENTIALS*

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Observations of potential changes occurring in dorsal roots during activity of the spinal cord date from the experiments of Gotch and Horsley, commenced in 1888 and fully described in their Croonian Lecture of 1891 (18). Recent attempts at analysis and interpretation of such potential changes may be said to begin with the work of Barron and Matthews (1), who described a simple fluctuation of long duration, provoked by afferent stimulation and having negative electrical sign at the more centrally located of two leads placed on the central segment of an isolated severed dorsal root: the so called dorsal root potential. So far as this single potential change is concerned the observations of Barron and Matthews are substantially correct. During the past decade essential experimental confirmation has come from the work of Bonnet and Bremer (2, 3), Bremer and Bonnet (5), Bremer, Bonnet, and Moldaver (6), Dun and Feng (11), Eccles and Malcolm (16), and during the course of the present investigation.

In contrast to the general agreement hitherto found at the level of observation, there has been widespread divergence of opinion concerning interpretation, due in part to the lack of an adequate theoretical background and in part to the lack of an adequate description of the sequence of potential changes that constitute the dorsal root potential. The present account of dorsal root potentials in the main is concerned with those parts of the sequence that have not received due attention; it adds little to what is already known about that part of the sequence represented by the negative deflection of Barron and Matthews.

Procedure

Bullfrog and cat preparations have been employed. In the former entire dorsal roots were isolated for stimulation and recording, but in the latter it was necessary to segregate individual rootlets to obtain well defined root-cord junctions. The roots or rootlets, severed distally, were raised into an insulating medium (paraffin) and fitted with electrodes as desired. Recording leads routinely were placed on dorsal roots one close to, but not touching, the spinal cord, the other at a distance toward the severed end. Throughout the present discussion these will be designated the proximal

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and distal leads respectively, and the sign of a potential change, as is customary in work with dorsal root potentials, will be expressed in reference to the proximal lead. When stimulating electrodes were applied to roots from which recordings were to be made they were placed near the severed end distal to the distal recording lead. Any root that was stimulated to carry an afferent volley will be designated the active root, others will be designated neighboring roots. Direct coupled amplification has been standard practice.

The Problem

Fig. 1 illustrates potential changes in bullfrog dorsal roots evoked by single dorsal root volleys and recorded, in A, from the active root and, in B, from a

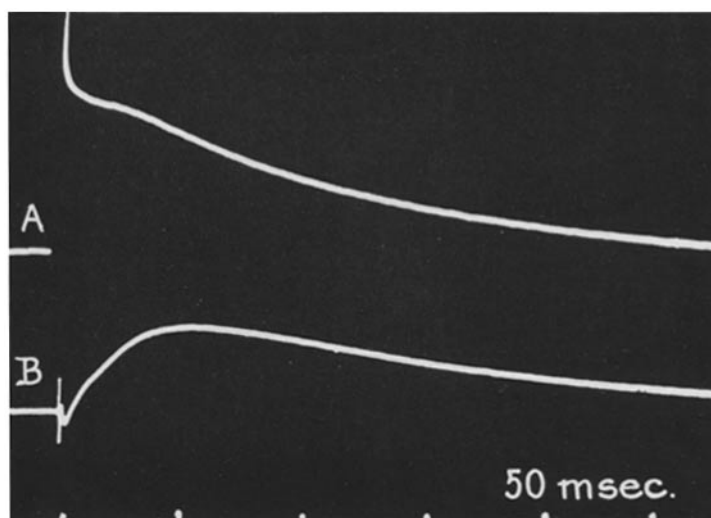


FIG. 1. Potential changes following single shock stimulation of a dorsal root and recorded by means of an electrode pair applied to the root stimulated (A) and to a neighboring root (B). Negativity at the root lead closer to the cord, in this and all other figures, is recorded upwards. Bullfrog preparation.

neighboring root of the same side. In record A, the tail of the large diphasic (positive-negative) spike potential of the traveling afferent volley may be seen, followed by a prolonged negative potential. In record B there is a sequence of potential changes culminating in a prolonged negative potential, that is the dorsal root potential of prior description. During the first 50 msec. following stimulation the relation between potential changes in the active and neighboring roots is not immediately apparent, but beyond that interval the changes in the two roots are comparable in size, duration, and electrical sign.

One must assume that the recording from an active root is of complex origin. Contributing to the over-all potential change will be: (a) potential gradients instituted in the dorsal root fibers by the stimulating current, a not insignifi-

cant factor considering the necessary proximity of electrodes placed four on a root, (b) after-potentials of the root fibers consequent upon conduction of a volley of impulses, a factor recognized by Woolsey and Larrabee (28), (c) gradients that might exist in the intramedullary segments of the stimulated fibers and which could propagate themselves back into the extramedullary segments, and (d) electrotonic potentials appearing in the root as the result of polarization of its intramedullary projection by the flow of current about active neurons.

Dorsal root potentials recorded in a neighboring root are less complex in origin than those of the active root, for the direct consequences of the flow of stimulating current and of impulse conduction cannot be contributing fac-

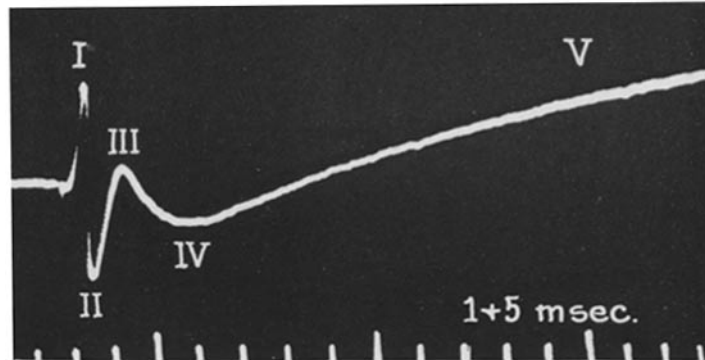


FIG. 2. Early course of dorsal root potential recorded, as in Fig. 1 B, from a root adjacent to that stimulated to show in greater detail the succession of deflections, D.R.I, II, III, IV and the beginning of D.R.V, which last is the dorsal root potential of prior description. Bullfrog preparation.

tors. A glance at record B of Fig. 1 reveals that there exist potential changes in a neighboring root additional to and anteceding the negative wave of the usual descriptions. Although these potential changes are to be found partially resolved in many of the previously published records of dorsal root potentials, they have been neglected except by Eccles and Malcolm (16) who regard them as artifacts introduced by contact between proximal recording lead and spinal cord. Such is not the case in the present recordings for which contact between lead and cord was scrupulously avoided. Furthermore the characteristic sequence is still recorded, but with the anticipated decrement, after the proximal lead is moved distally along the dorsal root.

Recorded by the use of higher oscillograph sweep speed, the early course of the dorsal root potential in a neighboring root may be seen in greater detail. Fig. 2, presenting such a recording, reveals that there are in all five deflections in the potential sequence. These deflections in order of temporal sequence are

to be designated D.R.I, D.R.II, D.R.III, D.R.IV, and D.R.V. Of these D.R.V is the negative wave of Barron and Matthews.

The dorsal root potential of a neighboring root is propagated electrotonically to the extramedullary segment of the contained primary afferent fibers from their intramedullary projections. The spinal cord constitutes a volume conductor within which the intramedullary projections of primary afferent fibers may be polarized by physical spread of current flow about active nervous elements. Such polarizations are the cause of electronic propagation into the extramedullary segment. Since the dorsal roots are raised into an insulating medium that extends to the cord junction, there is no significant *physical* spread of current from the cord into the extramedullary segment.

As a convenient simplification all the neurons within the cord are considered together as secondary neurons. This being done, one may state that polarization of the intramedullary segment must be due to either (*a*) the activity of primary afferent fibers or (*b*) secondary neurons. Now it is immediately obvious that D.R.I, II, and III together bear some relation to the triphasic intramedullary spike potential (17) of a primary afferent volley occupying the intramedullary segment of the stimulated dorsal root fibers. For this reason their origin may be ascribed with confidence to activity of primary afferent fibers. Secondary neurons clearly are responsible for D.R.V, as was first suggested by Bonnet and Bremer (2). Concerning the general properties of D.R.V the experimental description of Barron and Matthews is quite adequate. It remains then to clarify by experiment the origins and general properties of D.R.IV.

General Properties of D.R.IV

No *a priori* judgment may be made concerning the intramedullary activity responsible for the appearance, in a neighboring dorsal root, of the D.R.IV deflection. There exist three possible origins of that activity: (*a*) primary afferent fibers, (*b*) secondary neurons, and (*c*) both primary afferent fibers and secondary neurons. An advantageous means for study of D.R.IV is to compare its behavior in varied circumstances of stimulation, on the one hand with that of the D.R.I, II, III complex of primary afferent fiber origin, and on the other hand with that of D.R.V relating to secondary activity.

Antidromic Stimulation of Ventral Roots.—It is well known that a dorsal root potential of the type resembling D.R.V can be recorded, in the frog preparation, following antidromic stimulation of the motoneurons (1, 16). In Fig. 3 may be found records of dorsal root potentials evoked by stimulation with single shocks of an ipsilateral dorsal root (A and C), and of a ventral root (B and D), ipsilateral to, and of the same segment as, the dorsal root used for recording. Amplification was adjusted so that D.R.V and the antidromically evoked

potential that mimics it, would be of comparable recorded magnitude. At the left of Fig. 3 it can be seen that the two potential changes are reasonably comparable in general outline. In the early course of these potential changes, however, there are distinct differences seen to better advantage in C and D of Fig. 3, recorded with faster sweep speed. Present in record C, as the result of dorsal root stimulation is the characteristic sequence of deflections, D.R.I to V. By contrast the dorsal root potential consequent upon antidromic ventral root stimulation reveals between stimulus artifact and the onset of the prolonged negative deflection, some 12 msec. later, no change in the electrical state of the dorsal root. Thus the appearance in a dorsal root of a deflection re-

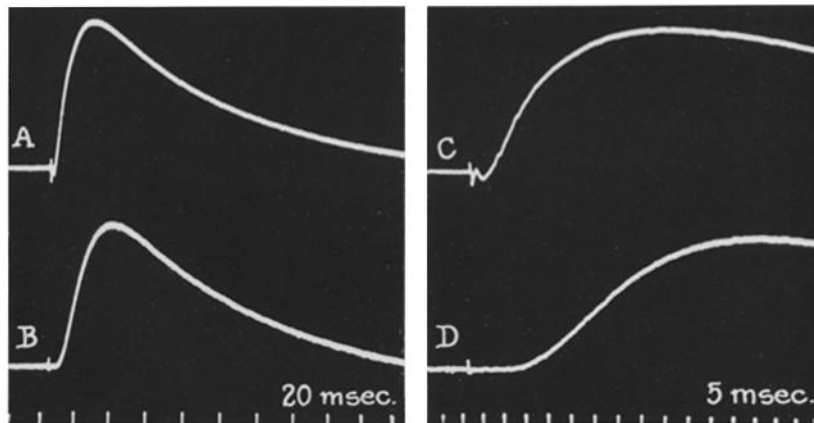


FIG. 3. Dorsal root potentials recorded, at two sweep speeds, following orthodromic stimulation of an adjacent dorsal root (A and C) and following antidromic stimulation of a ventral root (B and D). Bullfrog preparation.

sembling D.R.IV is not a necessary prelude to the appearance of a deflection resembling D.R.V. The observation demonstrates that activity in motoneuron somata, admittedly of a kind that results in a D.R.V-like wave, does not also polarize primary afferent fibers in the D.R.IV tempo, and suggests therefore that collaterals rather than somata may be responsible for D.R.IV.

Stimulation of Ipsilateral and Contralateral Dorsal Roots.—It is known from the observation of Barron and Matthews that the latency of D.R.V is longer when dorsal root potentials are recorded from a root contralateral to that stimulated than when recorded from an ipsilateral root. Fig. 4 illustrates a repetition of the observation to examine the antecedent potential deflections following ipsilateral (A) and contralateral (B) dorsal root stimulation. In each instance D.R.I, II, and III are present; so too is D.R.IV. As expected

the latency for D.R.V is widely different in the two recordings.¹ Despite this fact, virtually an identical temporal sequence exists between the D.R.I, II, III complex and D.R.IV, indicating the close association between these potential changes in circumstances that reveal a variable relation between D.R.IV and D.R.V.

Influence of Volley Size.—Fig. 5 presents a series of recorded dorsal root potentials arranged in order of increasing strength of stimulation. Record A of Fig. 5 was obtained by the use of a stimulus just over threshold strength; that

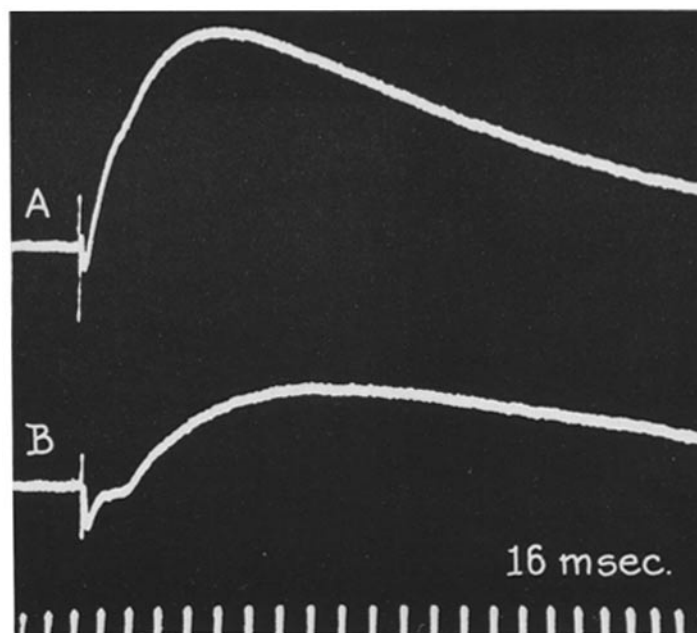


FIG. 4. Dorsal root potentials evoked by stimulation of an adjacent dorsal root (A) and of a contralateral dorsal root (B). Bullfrog preparation.

for record J was maximal. Dorsal root potentials evoked by contralateral dorsal root volleys were employed to avoid significant incursion of D.R.V upon D.R.IV with consequent distortion of the latter. Record A of Fig. 5 demonstrates that D.R.IV appears with D.R.I, II, III as threshold for dorsal root

¹It is not possible to define with precision the latency of D.R.V. In ipsilateral recording, as may be seen in subsequent experiments, D.R.V would appear to begin as early as the peak of D.R.IV. Indeed, by interrupting the course of D.R.IV, D.R.V may determine in part the location of its peak. As an aside, recordings such as Fig. 4 A and Fig. 1 B, showing obvious discontinuities on the rising phase of D.R.V suggest that the potential change is not as simple as sometimes supposed (*cf.* also reference 11).

stimulation is exceeded, and records B to J show that the first four deflections of dorsal root potential increase in parallel with increase in volley size. In contrast to this parallel behavior D.R.V appears only after the antecedent deflections are well developed.

Experiment has shown that the clear-cut separation between the first four deflections of the dorsal root potential and the fifth that is obtained by varying the strength of contralateral dorsal root volleys is not so easily reproduced when ipsilateral dorsal root volleys are substituted for contralateral volleys. The fact is not surprising in view of the ever-present difficulties involved in segregat-

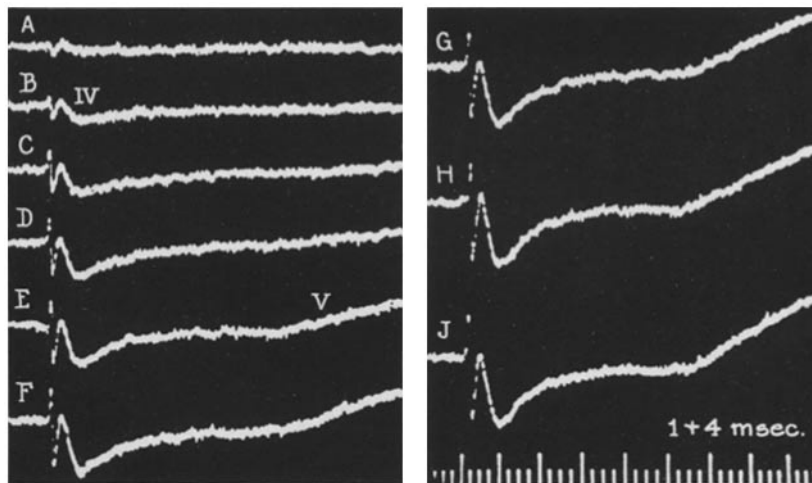


FIG. 5. Dorsal root potentials recorded, as in Fig. 4 B, from a root contralateral to that stimulated. Between each observation, A to J, stimulus strength was increased, that employed for A being just above dorsal root threshold, that for J being maximal. Sweep speed was such that only the onset of D.R.V appears in the recording. Bullfrog preparation.

ing one from another the various ipsilateral responses evoked by dorsal root stimulation (*cf.* reference 20, page 421).

When seen virtually free from interference, as in A, B, and C of Fig. 5, D.R.IV, in the bullfrog preparation, appears as a simple positive wave characterized by a rising phase of about 2 msec. duration and an approximately exponential decay to half-value in about 5 msec. It would seem a reasonable assumption that D.R.IV recorded from an ipsilateral root would exhibit a similar time course if, on recording, it were possible to divorce it from all interference from D.R.V. A number of experimental means have been tried, the most satisfactory being by the imposition of an asphyxial block. This is a simple procedure when studying the decapitate cat preparation, less so when employ-

ing the bullfrog preparation, due largely to the easy reversibility of the process in the former preparation.

Effect of Asphyxia on Dorsal Root Potentials.—In the experiment illustrated by Fig. 6, records of dorsal root potentials in a neighboring root were taken at regular intervals during a bout of asphyxia sufficiently prolonged to remove all trace of D.R.III, IV, and V. Representative records from the experiment have

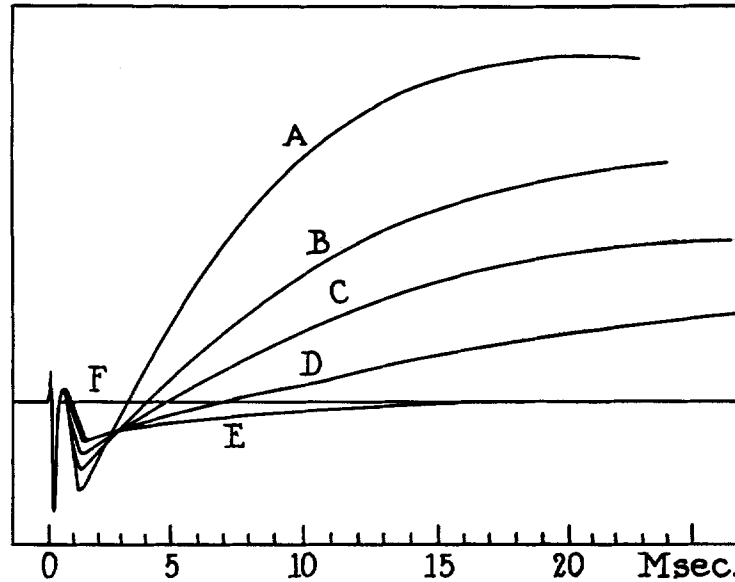


FIG. 6. Modification by asphyxia of dorsal root potentials recorded on a root adjacent to that stimulated. Cat preparation. A, normal dorsal root potential. E stage at which production of D.R.V is blocked (see also Fig. 7 B). F, stage at which only D.R.I and II appear. In the original records A to C, a small and progressively decreasing dorsal root reflex appeared; it has been omitted in reproduction. Details of the asphyxial block of dorsal root reflexes may be seen in Fig. 7.

been superimposed by tracing to illustrate successive stages of the asphyxial change, A being the normal dorsal root potential, E being the stage at which D.R. I to IV are still present but no trace of D.R.V remains, and F being the "final" stage in which only D.R.I and II are recorded. Thus of the five deflections D.R.I and II are the most resistant to asphyxia, D.R.III and IV are less so, and D.R.V is the most labile.

Fig. 7 contains actual records from another preparation of the normal dorsal root potential (A), and of the dorsal root potential at the stage of asphyxia in which D.R.V is removed. It is interesting in passing to note that the dorsal

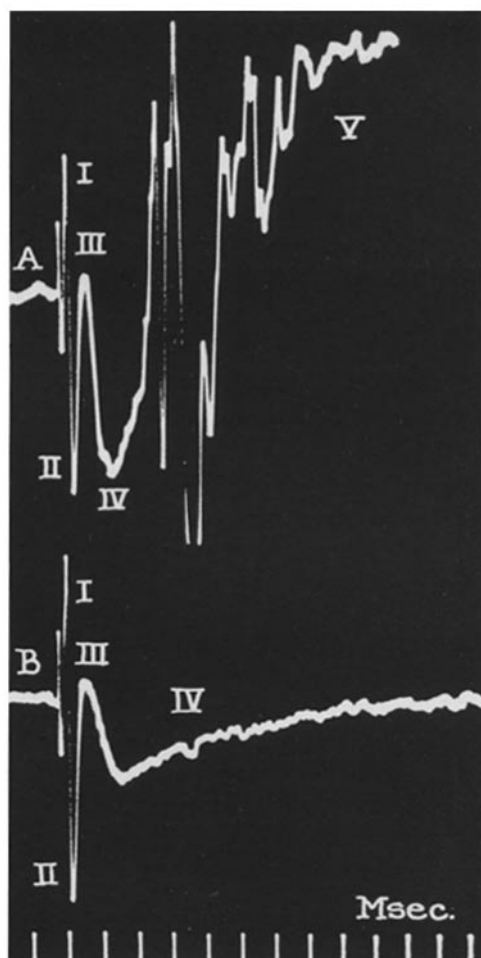


FIG. 7. Dorsal root potential recorded from a root adjacent to that stimulated. Cat preparation. A, normal, showing in this instance a large dorsal root reflex recorded in approximate diphasicity. The successive deflections of the dorsal root potential are identified by Roman numerals. B, to illustrate dorsal root potential as modified by asphyxia, the stage being comparable to that of Fig. 6 E. Deflections D.R.I, II, and III are not demonstrably altered from the normal. D.R.V and the dorsal root reflex have not been produced. D.R.IV is reduced and possibly slowed but on this latter point an unequivocal statement cannot be made. In this preparation, and in the stage of asphyxia represented in record B, it was seen that D.R.IV deflections evoked by simultaneous combination of two dorsal root volleys summed exactly. In accordance with the present analysis record B illustrates that part of the dorsal root potential referable to the activity of primary afferent fibers.

root reflex discharge, recorded diphasically on the rising phase of D.R.V in the normal condition, disappears along with D.R.V.

Seen cleared from D.R.V during the course of asphyxia, D.R.IV, in the cat, appears as a simple positive wave characterized by a rising phase of from 0.8 to 1.0 msec. in duration, and an approximately exponential decay to half-value in 3 msec., 2.6 to 3.5 being the observed variation in the series of experiments under consideration.

Summation and Occlusion of D.R.IV and D.R.V.—When two volleys of impulses enter the spinal cord through separate dorsal roots or rootlets, the dorsal root potentials being recorded in a third, and when the recorded dorsal root potentials evoked by the two volleys severally and together are compared, it is found that D.R.IV and D.R.V behave in a widely different manner. Results obtained from the bullfrog preparation and the cat preparation are qualitatively comparable.

If the two dorsal root volleys reach the spinal cord together over roots of opposite sides, the recorded D.R.IV deflection is equal, or very nearly equal, to the sum of the D.R.IV deflections resulting from the two volleys in isolation, whereas D.R.V suffers almost total occlusion. In Fig. 8 this finding is illustrated from an experiment with the bullfrog preparation. Represented by the broken lines (I) and (C) are the dorsal root potentials recorded, above with a fast sweep, below with a slow sweep of the oscillograph spot, following ipsilateral and contralateral dorsal root stimulation. The solid line (I + C) represents the dorsal root potential following combined stimulation.

If the two dorsal root volleys reach the cord both by roots ipsilateral to the root employed for recording, D.R.IV exhibits a degree of occlusion, greater in the cat preparation than in the bullfrog preparation, but at no time comparable to the subsequent occlusion of D.R.V. Fig. 9, constructed in the same fashion as Fig. 8, illustrates an experimental result in a bullfrog preparation. In the lower part of Fig. 9, it will be seen that the D.R.V deflection following simultaneous combination of two ipsilateral dorsal root volleys is little more than the greater of the two D.R.V deflections caused by the volleys in isolation, whereas there is only a slight failure of summation on the part of the D.R.IV deflections (upper part of Fig. 9).

In the normal cat preparation, when dorsal rootlets of the same side are stimulated in simultaneous combination and the dorsal root potential resulting is recorded from a third rootlet on the same side it is usual to find a degree of occlusion in D.R.IV potential. The deficit, as seen in the upper part of Fig. 10, is typically greater in the cat preparation than in the bullfrog preparation. If now the cat preparation be subjected to asphyxia until the stage is reached wherein D.R.V is abolished, but D.R.IV is still present, occlusion of D.R.IV disappears to be replaced by exact summation. This change in behavior is illustrated by Fig. 10, in which summation of D.R.IV in the normal state (above) and in the partially asphyxiated state (below) may be compared.

Conclusion as to the Origin of D.R.IV.—It seems quite clear that D.R.IV may have origin in more than one type of intramedullary activity. The fraction

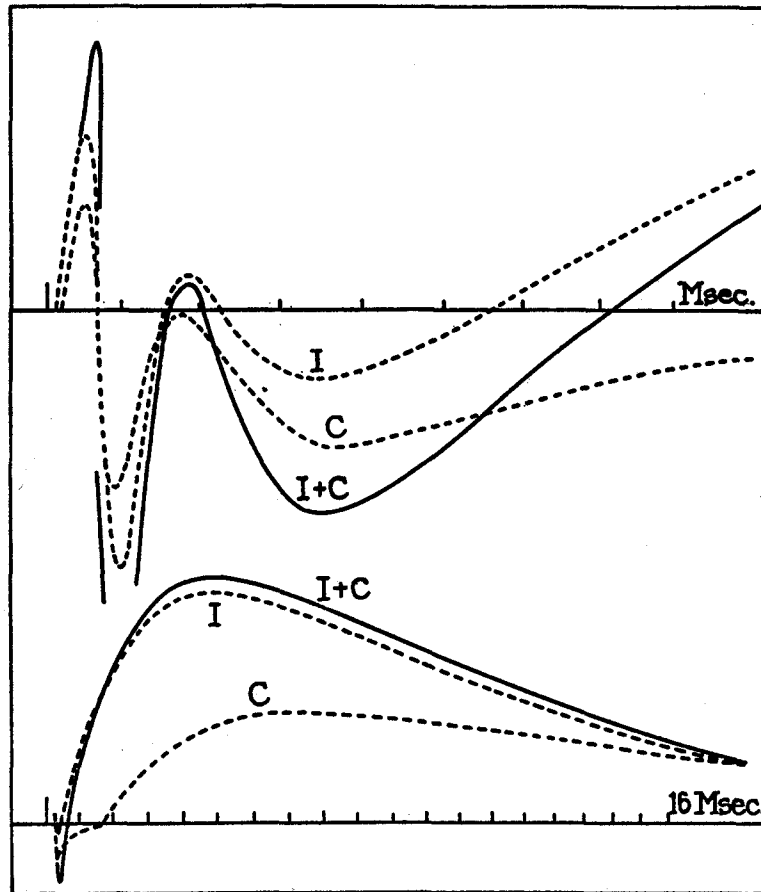


FIG. 8. Above, early course of dorsal root potentials elicited by stimulation of an ipsilateral adjacent dorsal root (I); by stimulation of a contralateral dorsal root (C); and by concurrent stimulation of both ipsilateral and contralateral roots (I + C) to illustrate exact summation of D.R.I, II, III, and IV. Below, full course of dorsal root potentials similarly evoked and similarly identified to illustrate almost complete occlusion of D.R.IV. Bullfrog preparation.

that appears in contralateral recording, or in ipsilateral recording when reactivity of the spinal cord is reduced by asphyxia is closely tied with events in primary afferent fibers. This non-occluding fraction of D.R.IV is most reasonably interpreted as being due to the activity of primary afferent fibers. However the evidence so far presented is compatible with the view that secondary

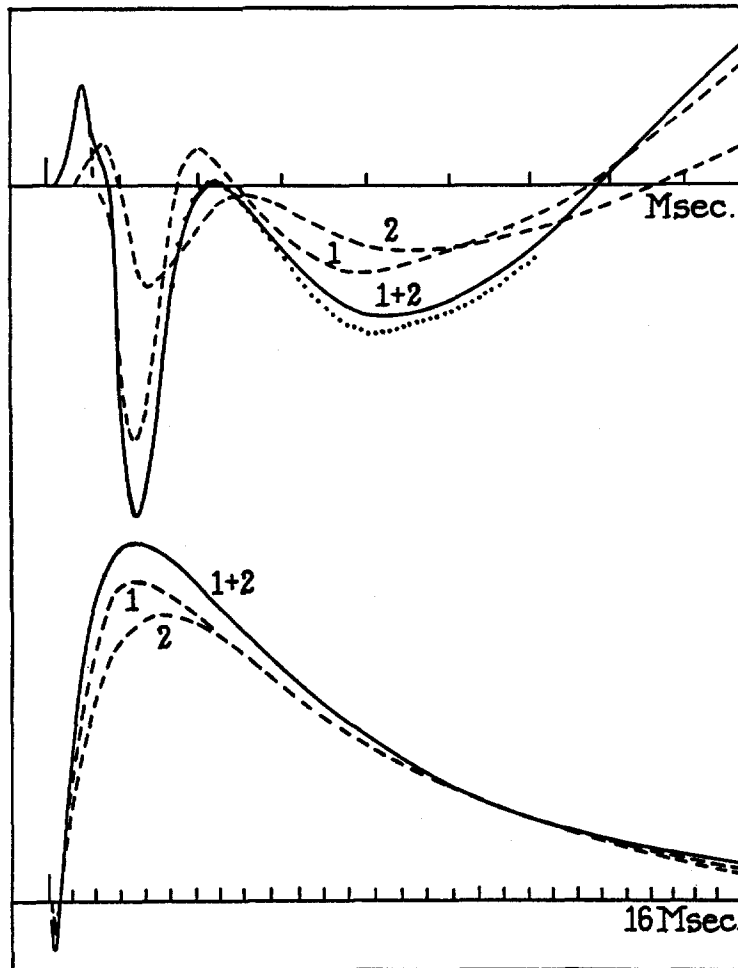


FIG. 9. Above, identified by broken lines, 1 and 2, is seen the early course of dorsal root potentials elicited by stimulation in isolation of two dorsal roots, the recording being from a third, all three roots pertaining to the same side. Identified by the solid line (1 + 2) is the dorsal root potential, similarly recorded, but evoked by concurrent stimulation. The dotted line, constructed by addition of 1 and 2 illustrates the slight occlusion of D.R.IV attending concurrent stimulation. Below, later course of the dorsal root potentials illustrating almost complete occlusion of D.R.V. Bullfrog preparation.

neurons are responsible for the non-occluding fraction of D.R.IV if one makes certain ancillary assumptions: that the responsible group of secondary neurons

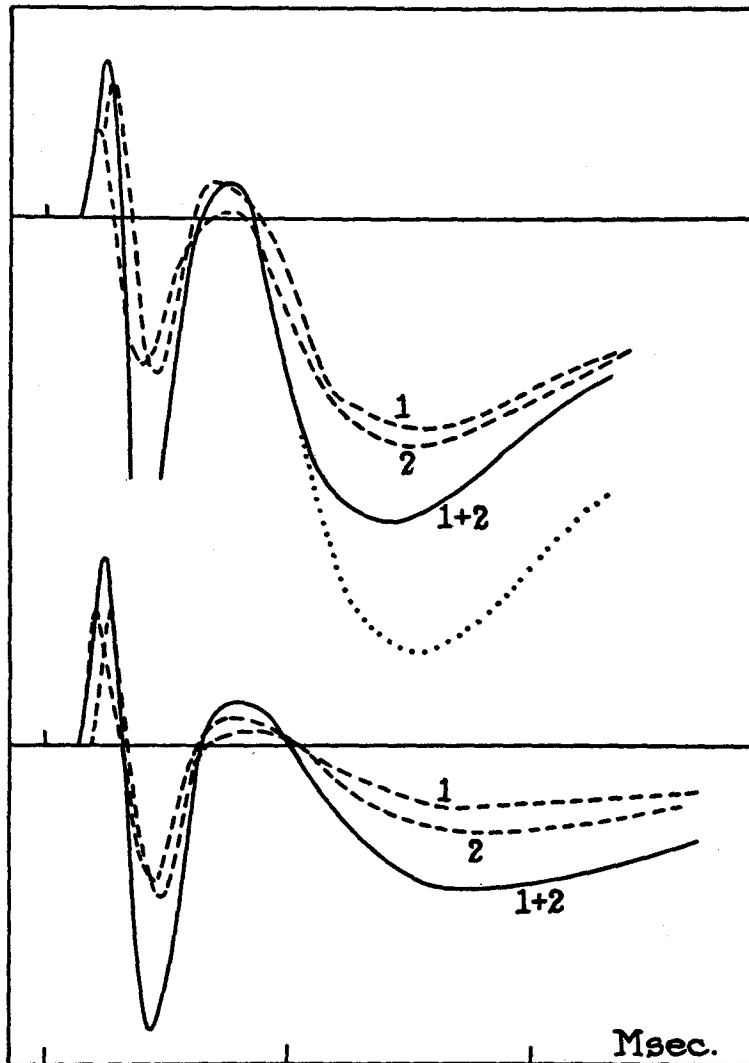


FIG. 10. Experiment similar to that illustrated in Fig. 9, but from a cat preparation. The broken, solid, and dotted lines have the same significance as that given in the legend of Fig. 9. Above, normal preparation, from which it is seen that D.R.IV is occluded to an extent typically greater than is found in experiment with the bullfrog preparation (but not to the same extent as is D.R.V in either preparation). It is significant that occlusion does not appear in the early course of D.R.IV either here or in Fig. 9. Below, as above, but in the partially asphyxiated state, sufficient for the removal of D.R.V. Note absence of occlusion.

would stand in "one-to-one" synaptic relation with primary afferent fibers, that the primary afferent fibers supplying those secondary afferent fibers do so without functional overlap, and that the activity of these secondary neurons does not lead to subsequent production of D.R.V potential. These assumptions being rather unlikely, it is concluded that the non-occluding fraction of D.R.IV results from polarization of primary afferent fibers by the activity of other primary afferent fibers. In the analysis of dorsal root potentials that follows certain consequences of the foregoing conclusion emerge. They may be put to test.

The remaining fraction of the D.R.IV potential, by the very fact that it exhibits occlusion, must be adjudged the result of activity in secondary neurons.²

Preliminary Considerations for an Analysis of Dorsal Root Potentials

An analysis of dorsal root potentials in a neighboring root must take into account a sequence of five deflections. The first three of these are *a priori* the result of activity in primary afferent fibers. The fourth apparently is due in part to the activity of primary afferent fibers, and in certain circumstances in part due to the action of secondary neurons. The last potential change of the sequence is, in its measurable extent, surely the activity of secondary neurons. It is profitable at this point to investigate dorsal root potentials in the light of what little is known of the neuronal architecture of the spinal cord and of recent advances in the general understanding of interaction between active and inactive fibers in nervous tissue (19, 24).

Considerations of an Anatomical Nature.—Primary afferent fibers on reaching the root-cord junction penetrate the dorsal columns with an approximately dorsoventral orientation and bifurcate in Y- or T-shaped fashion into longitudinally orientated fibers that ascend and descend the dorsal column. From the parent fibers and from their longitudinal projections, collaterals are directed into the gray substance. Of these collaterals some, derived from the parent fibers of greatest caliber, penetrate to the ventral horn. Others, in dense bundles, flow into the intermediate region. Still others curve on themselves to enter the dorsal horn by a ventral approach. In short the collaterals course through the gray substance in a variety of directions. Since each dorsal rootlet of a group contains a representative population of primary afferent fibers, it follows that the intramedullary projections of neighboring rootlets will lie in parallel array, not only in their longitudinal course within the dorsal column,

² The ingenious hypothesis of Barron and Matthews advanced to account for occlusion of D.R.V is relevant only to their assumption that D.R.V represents activity of primary afferent fibers. Once the assumption is seriously questioned, the older view that occlusion is a sign of response to convergent pathways (27) stands until proved incorrect.

but also in the gray substance, regardless of the direction taken therein by the individual collaterals. Now if of two neighboring rootlets one be stimulated and the other not, it further follows that, whatever their course in the cord, active and inactive fibers will lie in parallel. This is a fact of fundamental importance because it makes possible a treatment of dorsal root potentials in terms of relatively simple models of interaction between nerve fibers (24) without the necessity for intimate knowledge, which we do not now possess, of the exact spatial relationships between the many dendritic and axonal structures thrown into activity as a sequel to dorsal root stimulation.

Another important consequence of the parallel arrangement of primary afferent collaterals from neighboring roots concerns the polarization of them by the action of secondary neurons. Stimulation of a dorsal root, as is well known, leads to secondary activity as well as primary activity. Apart from the immediate consequences of impulse conduction by that dorsal root and its intramedullary projections, it follows from the fact of parallel orientation with intramedullary projections of a neighboring root that, whatever the orientation of the secondary neurons with respect to the primary projections, the net polarization of the latter by secondary activity, and so the resulting electrotonus in the two dorsal roots, will have similar duration and electrical sign, and approximately the same intensity.

A special case arises in consideration of dorsal root potentials led from contralateral roots. Primary afferent fibers from the two sides lie in parallel within the dorsal columns, but the collaterals diverge, each group to enter the gray substance of its side. The consequences of this fact emerge in subsequent discussion of ipsilateral and contralateral dorsal root potentials.

Considerations Relating to the Interaction of Neighboring Fibers in a Volume Conductor.—Since primary afferent fibers of a given rootlet may be considered as having similar properties, since they are activated synchronously by a single stimulus, and since the direction of their individual collaterals in the first approximation is inconsequential for the purpose of analyzing dorsal root potentials in a neighboring ipsilateral rootlet, they may be represented by a single fiber (A) of the shape illustrated by diagram A of Fig. 11. Likewise the primary afferent fibers of a neighboring rootlet may be represented by a similar fiber (N). Arrows in fiber A indicate, in diagram A of Fig. 11, the direction of impulse conduction from the extramedullary segment into the volume conductor (stippled) constituted by the spinal cord, thence in three directions, into the longitudinal fibers of the dorsal column and into the collaterals.

It is obvious that the electrical sign of electrotonic potentials in the extramedullary (E) segment of fiber N will depend finally upon the direction of current flow through the membrane of the intramedullary continuation of the parent fiber or I segment, and that this intramedullary continuation of the parent fiber lies in parallel with part of the intramedullary projection of fiber

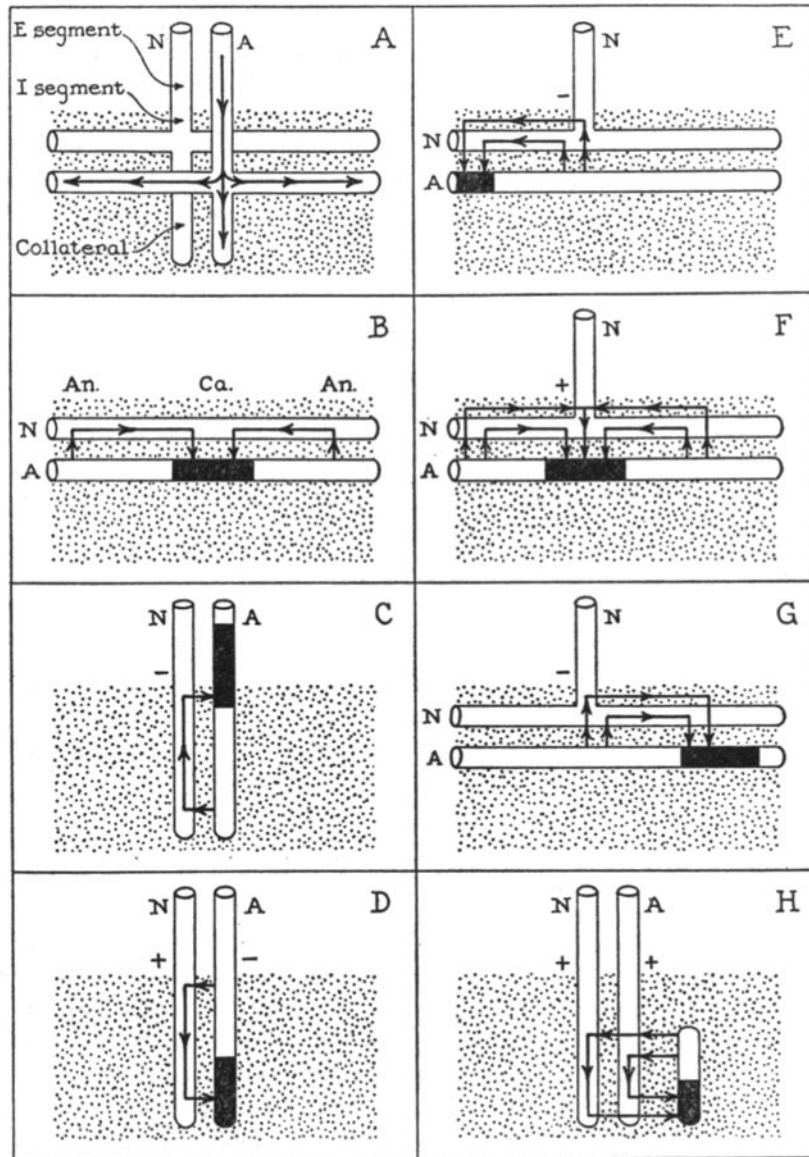


FIG. 11. Fundamental propositions relating to the analysis of dorsal root potentials. Fully described in text. In this figure and in Figs. 12, 14, and 17, fibers A and N represent active and neighboring fibers respectively; the shaded area represents the volume conductor; the black area of fiber A, in each instance, represents the impulse proper; while arrows indicate the external field about the active fibers. Plus and minus signs indicate the direction of electrotonus in the extramedullary (E) segment resulting from physical spread of current polarizing the intramedullary (I) segment.

A and at right angles to the remainder. It is convenient whenever possible to treat as separate problems the interactions resulting from impulse conduction in the parallel and 90° components of fiber A, synthesizing the two only as required by special considerations.

Fig. 11 presents in diagrammatic form the propositions necessary for a qualitative analysis of electrotonus in dorsal roots. Diagram B, recognizable as the fundamental proposition relative to the interaction of parallel neighboring fibers (19, 24), describes the changes that take place in resting longitudinal fibers as a volley of impulses travels along the dorsal column (26). Fiber N forms part of the external conductor of fiber A. Arrows indicate the three phases of membrane current in fiber A: outwards, inwards, outwards. In fiber N membrane current flows in a direction opposite to that in fiber A: inwards, outwards, inwards. The interaction is only detectable by measurement of threshold changes associated in fiber N with the anodal-cathodal-anodal succession of current flow through its membrane. It is important, because the principle is generally applicable, to note that an electrode placed near fibers A and N (*i.e.* on the dorsal column), and pitted against an electrode elsewhere on the preparation records the changes of membrane current in the active fiber A, not those in the neighboring fiber N.

Considered in connection with diagrams C and D of Fig. 11 are the interactions possible as the result of impulse conduction in fiber A from parent fiber to collaterals. Until the crest of the action reaches the root-cord junction current flow in the I segment of fiber N will be outgoing and the electrotonic potential in the E segment will be negative (diagram C). After the crest of the action passes the root-cord junction and until the collateral completes its recovery, current in the I segment will be ingoing and the resulting electrotonic potential of the E segment will be positive (diagram D). The situation described by diagrams C and D of Fig. 11, is none other than a special form of the situation at a fork in nerve (24, 13) and the proposed interaction therefore may be regarded as established in principle.

When an impulse travels in the longitudinal segment of fiber A the pattern of interaction between fiber A and fiber N is more complex, as may be appreciated by reference to diagrams E, F, and G of Fig. 11. To simplify the argument it is assumed for the present that the dorsal roots A and N are sufficiently far apart that interaction between the parent fibers is negligible. Further simplification by omitting the collateral of fiber N is possible since current flow there as the result of conduction in the longitudinal segment of fiber A is not of consequence to the I segment of fiber N. Illustrated by diagrams E, F, and G of Fig. 11 are three stages of interaction as the impulse in the longitudinal segment of fiber A approaches, resides at, and regresses from the level of dorsal root N. Current flow in the longitudinal segment of fiber N of course has the character defined by diagram B of Fig. 11, but the fact that the parent fiber of N enters the conducting medium has important additional consequences.

Briefly stated, membrane current will flow in the I segment of fiber N in a direction identical with that in the longitudinal segment A. Thus while the longitudinal segment of fiber N is polarized anodally by the outgoing current of A, the I segment is polarized cathodally, and the electrotonic potential of the E segment is negative (diagram E). Next in order, as the sink of current flow in the longitudinal segment of fiber A reaches the level of root N, the longitudinal segment of fiber N is cathodally polarized by the inward flowing current about A while the I segment is anodally polarized resulting in an electrotonus of the E segment (diagram F). Finally, as the impulse in A recedes (diagram G) the entire sequence reverses again causing a catelectrotonic potential to appear in the E segment of fiber N.

In contrast to diagrams B, C, and D of Fig. 11, which are based on theoretical propositions that have already received experimental verification, the predictions of diagrams E, F, and G, as they apply to the I segment, lack prior experimental verification in a system which, by its evident simplicity, permits unequivocal demonstration of their validity. The following section is devoted to experimental confirmation of these latter predictions.

Diagram H of Fig. 11 serves to illustrate the only generally acceptable proposition concerning polarization of primary afferent fibers by the action of secondary neurons. Deliberately to discourage overly facile identification, in diagram H of Fig. 11, of the external polarizing source with any supposed or real structure, it is represented as a simple dipole devoid of anatomical meaning. Diagram H is but one of an infinite number of diagrams that might be drawn to illustrate the fact that, as long as fiber A and fiber N lie in parallel array, the result of polarization by a secondary source must be qualitatively similar in the two fibers.

On the Interaction, in a Volume Conductor, between Parts of Nerve Fibers Lying at Right Angles to One Another.—The theoretical argument advanced in connection with diagrams E, F, and G of Fig. 11 is susceptible of experimental verification in a nerve model. Fig. 12 illustrates the experimental arrangement and the expectation that electrotonus in the insulated segment will pass through three successive stages: cathodal, anodal, and cathodal respectively. It will be noted that the nerve model in many details differs from the spinal cord. For instance the absence of secondary neurons and collaterals removes any possibility that structures other than the longitudinal tract of fiber A could contribute to, or subtract from, the result. Furthermore, in the nerve model fiber N is L-shaped rather than T-shaped, giving rise at the angle to interesting differences in the course of interactions as may be appreciated by comparing Fig. 12, B, C, and D with Fig. 11, E, F, and G, but the qualitative aspects of polarization in the I segment of the primary afferent fibers and in its analogue in the nerve experiment should be similar.

Fig. 13 illustrates the result of an experiment, utilizing a bullfrog sciatic

nerve preparation in the manner defined in diagram A of Fig. 12. An electrode (A) was placed in contact with the "active" nerve near the fork, and at some distance in the volume conductor another electrode (B) was located. Since electrode A is situated at a distance from the point of entry of impulses into the volume conductor, electrodes A-B should record, as a triphasic deflection, the

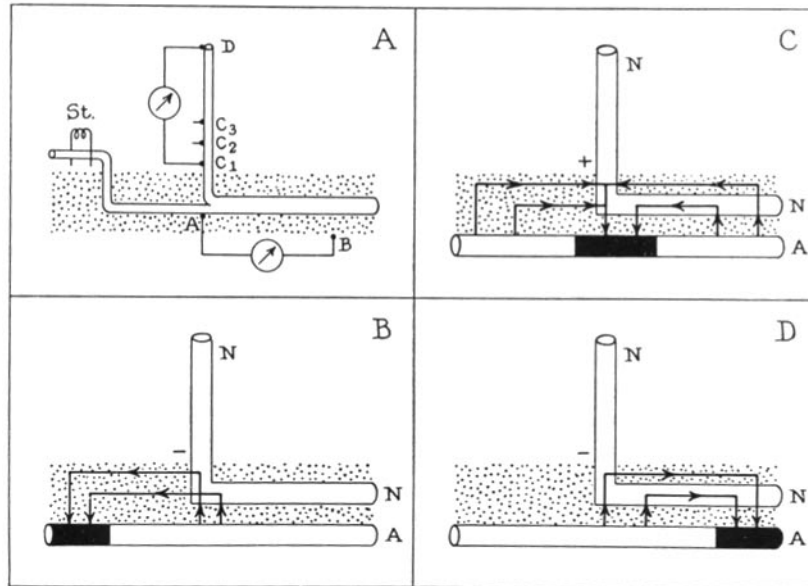


FIG. 12. In diagram A is illustrated the experimental arrangement for demonstration in nerve of interaction between fibers orientated at 90° to each other. Bullfrog sciatic nerve with its two principal subdivisions. St, location of stimulating electrodes. A-B, leading arrangement to record impulses in the active fibers. C-D, leading arrangement to record electrotonus in the inactive fibers, positions C_1 , C_2 , C_3 of electrode C serving to demonstrate the electrotonic decrement of potential changes in the inactive fibers. Diagrams, B, C, D, to illustrate the anticipated course of interaction as impulses in active fiber A approach, reside at, and depart from the region of 90° orientation.

passage of impulses evoked by stimulation through electrodes St. The "neighboring" branch of the sciatic nerve was drawn up into oil, in such a manner as to leave a short stretch near the fork within the volume conductor to form with the active branch a 90° angle. Electrodes C and D were placed on the insulated segment, the former held by a micromanipulator so that it could assume the successive positions C_1 , C_2 , C_3 . . . , in order to record electronic propagation into the insulated segment and demonstrate its decremental character.

Record A of Fig. 13, obtained by use of the leading electrodes A-B (Fig. 12),

contains the familiar triphasic deflection expressing changes in membrane current during the passage of a volley of impulses (23). The sequence, as antici-

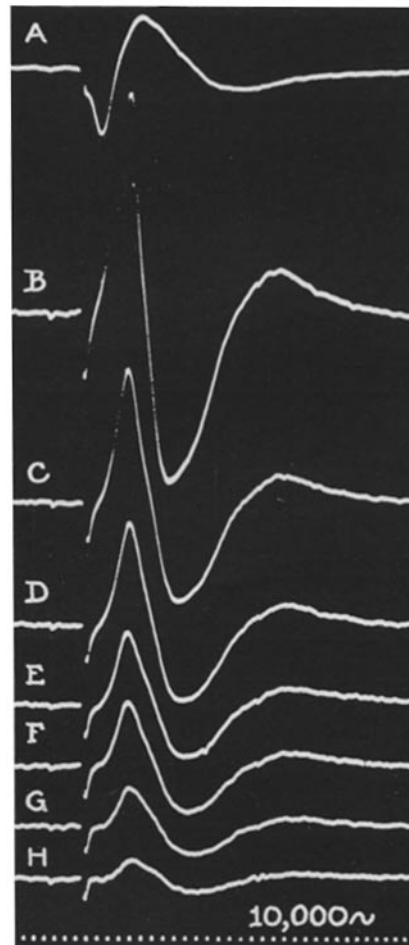


FIG. 13. Experimental findings relating to the recording arrangement of Fig. 12 A and in confirmation of the interactions proposed in Fig. 12, B, C, and D. Record A, obtained by means of electrodes A-B in Fig. 12 A. Records B to H, obtained by means of electrodes C-D in Fig. 12 A, the successive records being made with electrode C at locations C_1 , C_2 , C_3 ,

pated is positive-negative-positive. Illustrated in B to H of Fig. 13 are records obtained by the use of electrodes C-D, the successive observations recording the change as electrode C is moved, in millimeter steps from C_1 to C_2 to C_3 For observations B to H of Fig. 13 negativity at electrode C relative to elec-

trode D is recorded upwards. It is clear that the electrotonic currents in the insulated segment exhibit in succession an outward, an inward, and an outward direction. In accordance with expectation, test stimulation, in the neighborhood of C_1 , of the insulated segment reveals there a succession of enhancement, depression, and enhancement.

One need hardly emphasize the purely qualitative nature of the present analysis of interaction between fibers, undertaken for the sole purpose of verifying the physical possibility of the previously unsubstantiated propositions (Fig. 11, E, F, and G) necessary for analysis of dorsal root potentials.

Analysis and Interpretation of Dorsal Root Potentials

Analysis of D.R.I, II, III.—Since the first three deflections of the dorsal root potential bear a remarkable resemblance to the intramedullary spike potential that signals conduction of a volley within the dorsal columns, there can be little doubt that interaction of the type outlined in diagrams E, F, and G of Fig. 11, by accounting for the electrical sign of these deflections, contains the elements of a satisfactory interpretation of their origin. However, in order to simplify the initial presentation, in Fig. 11, E, F, and G, of the concept of interaction between fibers lying at right angles to one another, a limiting case was chosen, that in which the dorsoventral components of fibers A and N are too far apart for effective interaction. Fully to describe the origin of D.R.I, II, and III it is necessary to present the other limiting case, that in which the dorsoventral components of fibers A and N are so close together that the root-cord junction of fiber N is in effect at the point of entry into the volume conductor of impulses in fiber A. This limiting case, presented diagrammatically in Fig. 14, is particularly interesting, for, despite the fact that the intramedullary spike potential recorded at the root-cord junction of fiber N (and naturally of fiber A) is diphasic, negative-positive (*cf.* reference 23), D.R.I, II, and III are all present in the E segment of fiber N.

For construction of Fig. 14 it will be seen that no propositions have been employed other than those advanced in Fig. 11. When fibers A and N are immediately adjacent (diagram 14 A) it is the entering impulse in the parent fiber A that determines outward flow of current in the I segment, and the appearance of catelectrotonus in the E segment of fiber N. After the crest of the action enters the cord and until the beginning of recovery in the longitudinal segment of fiber A (diagram 14 B) three sources of current flow, S_1 , S_2 , and S_3 , exist in fiber A, all of which are capable of causing current to flow inward through the I segment of fiber N with resulting anelectrotonus in the E segment. Finally, as recovery of the longitudinal segment of fiber A progresses (diagram 14 C), current again will flow outwards in the I segment of fiber N producing catelectrotonus in the E segment.

It is obvious that, in most instances, the recorded D.R.I, II, and III deflections will represent current flows of complex origin intermediate between the

two limiting cases. No useful purpose would be served by carrying this analysis further, since an individual problem is raised by each experimental arrangement for the recording of dorsal root potentials.

Analysis of the Primary Fraction of D.R.IV.—Following a study of the properties of D.R.IV, it was concluded above that a considerable fraction of this deflection, the non-occluding or primary fraction, could most reasonably be attributed to the activity of primary afferent fibers. If this be true, it further

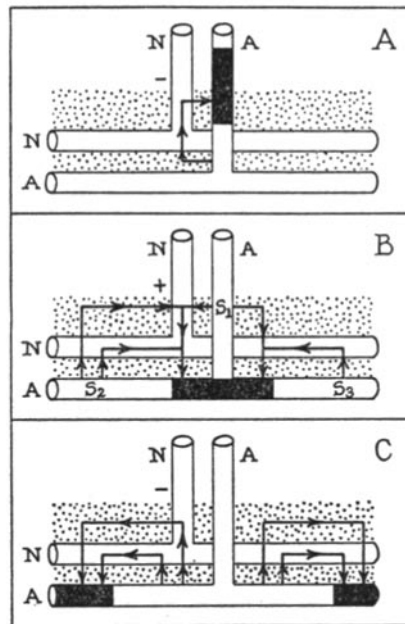


FIG. 14. Diagrams to illustrate one limiting case, the other being illustrated in Fig. 11, E, F, and G, for fiber interaction determining the production of the D.R.I, II, and III deflections of dorsal root potentials.

follows that the responsible activity must be centered in the collaterals, since it is unreasonable to attribute activity having the character of D.R.IV to simple conduction along tract fibers the known properties of which so closely resemble peripheral nerve.

Recourse to the fundamental propositions of Fig. 11, reveals that D.R.IV could only result from the current flows described in diagram D and diagram H. That fraction of D.R.IV that results from activity in primary afferent collaterals (the non-occluding or primary fraction) must arise in the manner of diagram 11 D, the occluding fraction must arise in the manner of diagram 11 H.

Considering the positive sign and prolonged duration of the primary fraction

of D.R.IV, it is possible to predict that this potential deflection represents a persistent negativity in the primary afferent collateral A, resembling rather the residual negativity at a nerve block described by Lorente de N6 (22) although in this instance the gradient must be relatively much more powerful. This prediction carries with it a consequence that may be put to experimental test. Since the parent fibers certainly have recovered during the period of D.R.IV, it would be expected that the supposed residual negativity of the active collaterals should be propagated backwards into the parent fibers and would appear in the active dorsal root as a negative deflection at the more proximal of two recording leads placed thereon.

Now it is known that the dorsal root potential of an active root is a complex event (*cf.* discussion in relation to Fig. 1 A). A negative potential difference of the sort postulated would be written upon the fiber potentials of the root itself and would be overlaid by the large negative potential difference paralleling D.R.V. The required procedure for its demonstration then rests upon the fact that D.R.IV during asphyxia is less labile than D.R.V, and more labile than the potentials relating to spike conduction (including in this instance the afterpotentials of the active dorsal root fibers in contact with the recording leads). Polarization potentials, the result of the stimulating current, should not change by virtue of intramedullary changes during asphyxia. With these propositions in mind, one may consider the observations recorded in Fig. 15, taken from the same experiment as was Fig. 6, but showing changes wrought by asphyxia in the active rather than in a neighboring root.

The records reproduced in Fig. 15 were made during the course of recovery from a period of asphyxia. Figure 15 A illustrates the course of dorsal root potential that was maintained constant over a period of some minutes, and thus is taken to be the contribution from extramedullary sources. Following re-establishment of respiration (and circulation³) the dorsal root potential changed first to the form illustrated in Fig. 15 B, and later recovered through the stages represented by records C to G. Fig. 15 clearly indicates that, in addition to the extramedullary components of the dorsal root potential in an active root, there are two gradients of negativity, exhibiting differing temporal course and differing susceptibility to asphyxia. The more resistant of these, as judged by earlier recovery after asphyxia, is represented by the difference in potential level between records A and B of Fig. 15. When plotted on an isopotential base line (dotted line in Fig. 15) the potential difference represented by (B-A) is seen to match closely, but with opposite electrical sign, the D.R.IV deflection recorded in similar conditions from a neighboring root (Fig. 6E).

Identification of the early negative potential difference in an active root with

³ In the course of the experiment from which Figs. 6, 15, and 18 were prepared in each instance the asphyxia was so severe that cardiac arrest resulted. Circulation was restored by massaging the chest.

the positive D.R.IV of a neighboring root is greatly facilitated by means of simultaneous recordings from the two roots in question. Fig. 16 presents an experiment in which asphyxial changes in the dorsal root potential of the active root (A to D above) and of a neighboring root (A to D below) were recorded simultaneously with the aid of a twin-beam oscillograph. In each instance A, B, C, and D illustrate successive changes in the dorsal root potentials from the onset of asphyxia (A) until only D.R.I and D.R.II remained in the dorsal root potential of the neighboring root (D). Records A, B, and C illustrate the

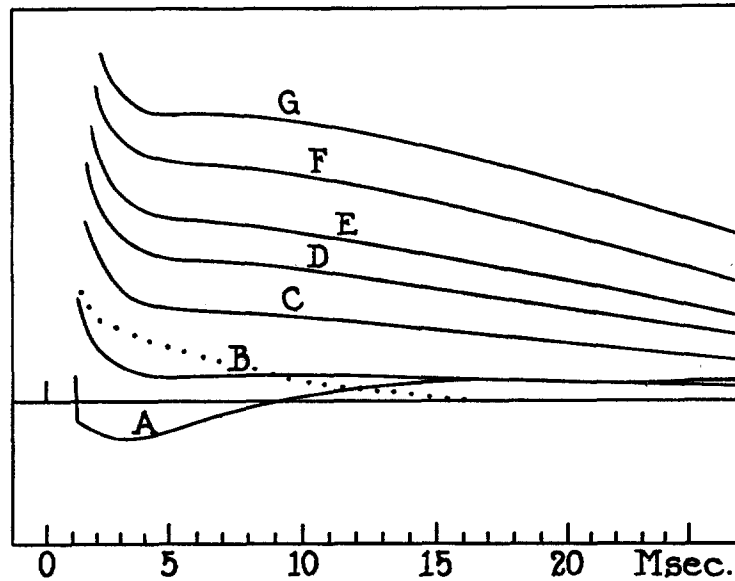


FIG. 15. Modification by asphyxia of dorsal root potentials recorded from a stimulated root. A, course of dorsal root potential after prolonged asphyxia. B, first stage of recovery. C to G, subsequent stages of recovery to normal. The dotted line plots on an isoelectric baseline the potential difference between records A and B

progressive loss of D.R.V and its homologue in the active root. The further change (D) in the active root, consisting of loss of the early negative potential, exactly parallels the loss of D.R.IV in the neighboring root. For this reason it is concluded that the two potential changes indeed are associated. This being so it is a necessary consequence of their electrical signs that the causal activity resides not in secondary neurons, but in the active primary afferent fibers.

Concerning Potentials in the Terminal Regions of Presynaptic Fibers.—The foregoing observations call for the existence, following the arrival of impulses at the primary afferent endings, of an enduring flow of current in the direction from parent fibers to terminal regions. In the absence of interfering secondary activ-

ity such a current flow would be recorded by a microelectrode appropriately situated in a nucleus of termination as a negative wave detectable for nearly 15 msec. and decaying over an approximately exponential course to half-value

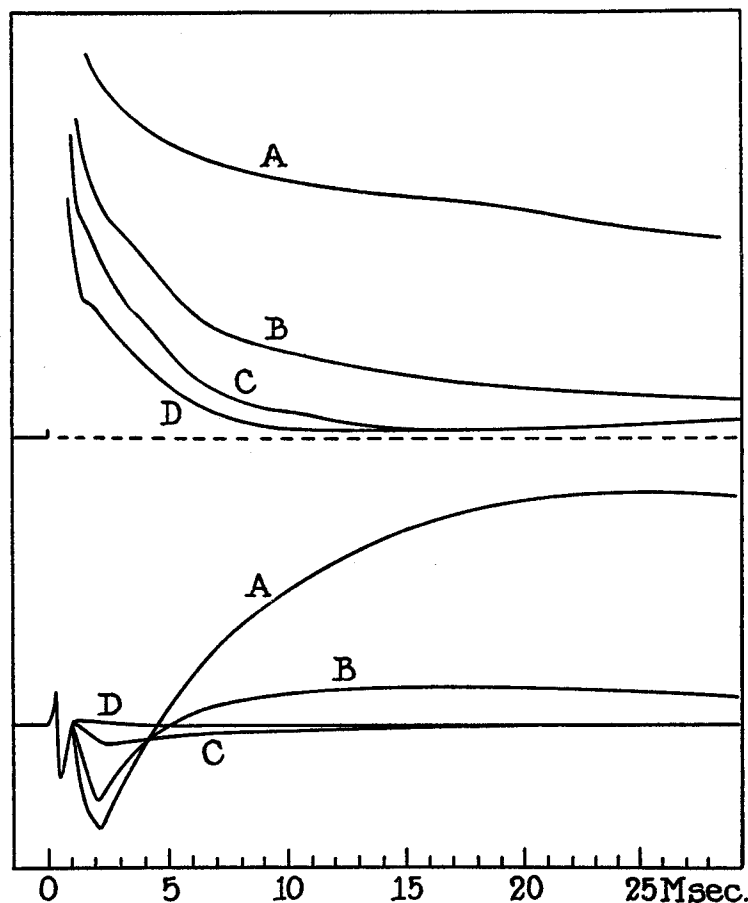


FIG. 16. Simultaneous recording of dorsal root potentials from the stimulated root (above) and a neighboring root (below) to show, in A, B, and C parallel progress in the two roots of asphyxial block of the D.R.V deflection and its homologue, but in particular to illustrate, by comparison of the potential level of C and D in each case, the parallel loss of early negativity in the active root and of D.R.IV in the neighboring root.

in slightly less than 3 msec. In experiments that fulfill the stated conditions, Brooks and Eccles (7) have recorded such a potential to which they have given the name "focal synaptic potential." It is their hypothesis that the sinks of

current flow giving rise to this recorded potential difference lie in the motoneuron somata, the sources at the motoneuron axons, whereas the present experiments demand that a similar if not identical potential difference must be recorded by virtue of sinks of current flow located in the presynaptic fibers at or close to the endings, the sources being located in the presynaptic fibers at some greater distance from the endings.

Potentials referable to activity in the terminal regions of presynaptic fibers have been recorded, but not free from interference by secondary activity, in the oculomotor nucleus by Lorente de N6 (22) and in the quadriceps nucleus of the spinal cord by Renshaw (25). While postulating that the " β deflection" of Renshaw is identical with their "focal synaptic potential" Brooks and Eccles (7) have disputed Renshaw's conclusion that his " β potential" is produced by the terminal portions of the presynaptic fibers. Considering the present evidence, however, it would seem that Renshaw's surmise undoubtedly was correct.

It should be emphasized that the recording by microelectrode within a motor nucleus of a potential change of the type under discussion does not yield of itself sufficient information by means of which to decide whether the recorded potential is referable to presynaptic or postsynaptic structures. Since the potential change in the nucleus is of negative sign it follows that the sinks of current flow are there. It likewise follows, in the monosynaptic system, that the sources must be either in the motoneurons, or in the primary afferent fibers. On the assumption that the motor axons supply current to the somata during the "synaptic potential," Brooks and Eccles (7) regard the existence of a ventral root "synaptic potential" as proof of the postsynaptic origin of the "focal synaptic potential." But the sources of current flow that determine the course of the ventral root synaptic potential outlast by two to three times the sinks that determine the "focal synaptic potential" (7). On the contrary the sources in primary afferent fibers that determine the appearance in an active dorsal root of the early negativity (Figs. 15 and 16) have a duration comparable to that of the sinks determining the "focal synaptic potential." In view of this last fact it seems unlikely that electrotonic slowing assumed to occur in the intramedullary course of the ventral root fibers (14) could account for the discrepancy between "focal synaptic potential" and ventral root "synaptic potential." In the circumstances the simplest conclusion must be that the two "synaptic potentials" are manifestations of different systems of current flow. One may assume a causal relationship while recognizing the obscurity of its nature.

It is important to recognize that the fraction of dorsal root potential of primary origin (as seen in Fig. 7 B) cannot reflect in precise detail all phases of the potential sequence in the terminal regions of the presynaptic fibers although in general they are not dissimilar except in electrical sign. To simplify the argument the reasons for this fact are presented diagrammatically in Fig. 17. From a study of diagrams A, B, and C of Fig. 17 it will be seen that from the time that

the crest of the action in fiber A reaches the volume conductor of the spinal cord (immediately after the condition represented by diagram A) until it reaches the presynaptic terminals (diagram C) the polarization of the I segment of fiber N, and consequently the dorsal root electrotonus, is caused by a flow of current different from that surrounding the collaterals (diagram B). Consequently it is only after the crest of the action reaches the presynaptic ter-

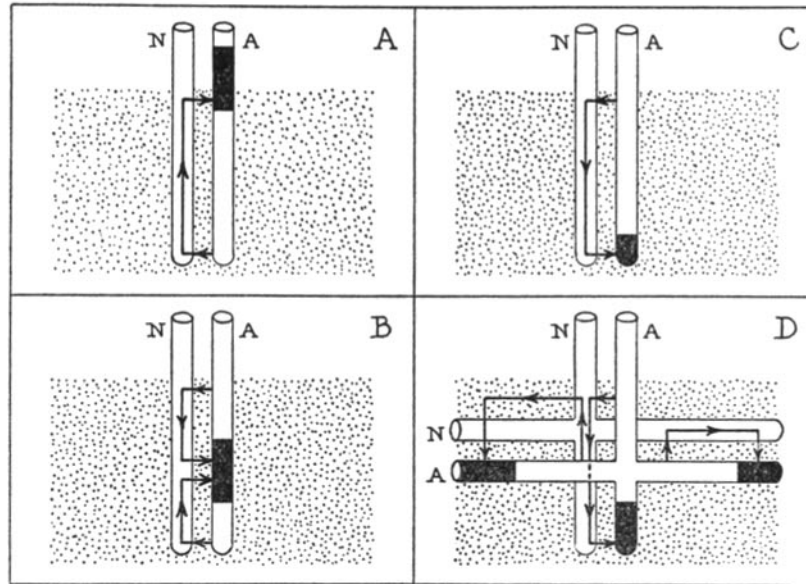


FIG. 17. Diagrams to illustrate the fact that D.R.IV and the potential changes of active primary afferent collaterals for part of their time course could be related to the same current flows, but that also for part of their time course they cannot be so related, the dorsal root electrotonus being determined by a current flow different from that surrounding the collaterals (diagram B). Diagram D illustrates the manner in which the I segment may be subjected to opposing current flows during the course of the D.R.III deflection.

minals (if, indeed, it does) that D.R.IV and an "ending potential" could be compared in detail.

Another factor that must contribute to differences of the sort under discussion may be mentioned in connection with diagram D of Fig. 17, for it provides in addition an understanding of the fact that D.R.III uniformly has not been of as great amplitude as one might reasonably have expected. Diagram 17 D shows how, once the primary impulse conducts beyond the parent fiber, and until recovery following the impulses that continue in the longitudinal segment of fiber A is complete, the I segment of fiber N is subjected simultaneously to

anodal and cathodal flows of current. In short D.R.III is written, not upon an isoelectric base line, but interrupts, so to speak, an otherwise more or less continuous anelectrotonus consisting of D.R.II and D.R.IV.

The Occluding or Secondary Fraction of D.R.IV.—Although there can be no reasonable doubt but that the occluding fraction of D.R.IV results from the activity of secondary neurons, there is no direct evidence bearing on the mode of its production. Indirect evidence, however, would seem to justify the view that the occluding fraction is produced by essentially the same type of activity on the part of the secondary neurons as that which in primary afferent fibers are responsible for the appearance of the non-occluding or primary fraction. The argument is as follows: Activity in primary afferent fibers, which is entirely axonal, produces a D.R.IV potential, but no D.R.V potential. Secondary activity, in which, among the internuncial pools, both axons and somata are equally involved, produces both a D.R.IV potential and a D.R.V potential. Secondary activity elicited by antidromic volleys, in which case the activity in the main must be referred to somata, produces no D.R.IV potential but (in the bullfrog) results in a dorsal root potential indistinguishable from D.R.V. Finally, given a parallel orientation of secondary axons and primary afferent fibers (as is found, for instance, between the axons of neurons of the intermediate nucleus and the "reflexomotor" collaterals) the essential anatomical requirement is satisfied, and activity of secondary collaterals becomes a sufficient explanation of the occluding fraction of D.R.IV.

It has not been possible in a satisfactory manner to distinguish among the components of the dorsal root potential in an active rootlet one that corresponds to the occluding fraction of D.R.IV in a neighboring rootlet.

Ipsilateral and Contralateral Dorsal Root Potentials.—Dorsal root potentials recorded in an adjacent ipsilateral root and in a contralateral root differ in two important respects: (a) The secondary fraction of D.R.IV is relatively large in ipsilateral recording, relatively small or absent in contralateral recording, and (b) a D.R.V deflection appears contralaterally only after considerable latency and at a time when ipsilateral D.R.V may have reached 60 to 70 per cent of peak amplitude. Both of these differences express the fact that secondary activity centered in the gray substance of one-half of the spinal cord does not in a significant degree polarize primary afferent fibers of the other side. There could be two reasons for the fact, both anatomical. It may be, at the distances involved, that the field generated by active secondary neurons is too weak to cause appreciable effect, or it may be that the orientation of the field is such that little or no net polarization of contralateral primary afferent fibers results. The two factors are not in any way mutually exclusive.

Since the primary afferent collaterals on the two sides of the cord diverge and course laterally to splay out into the gray substance, it is improbable that activity confined to the endings of one group could influence the other group any

more than could secondary neurons of the contralateral gray substance. The fact that a D.R.IV deflection is recorded contralaterally therefore can only be explained by the additional fact, demonstrated in Figs. 15 and 16, that the residual negativity of primary afferent collaterals propagates itself backward into the I segment (and hence presumably also into the longitudinal fibers) which parts of the primary neurons are suitably orientated in sufficient proximity (as shown by the appearance of D.R.I, II, and III in contralateral recording) to permit the necessary interaction to take place.

The appearance of a D.R.V deflection in contralateral recording apparently depends upon the spread, by decussation through commissural neurons, of activity from one to the other half of the spinal cord.

On the D.R.V Deflection.—It has already been stated that the present experiments add little to what is known of the D.R.V deflection. Since this prolonged negative wave appears in active and neighboring roots alike with the same electrical sign, it follows from the propositions considered in connection with Fig. 11 that secondary neurons are responsible for the polarization that produces this deflection. To this extent the present experiments are in agreement with the interpretations of Bonnet and Bremer (2, 3) and of Eccles and Malcolm (16). Furthermore, for reasons that have been discussed, it seems likely that the activity of somata rather than that of axons is the causal agent.

The observation at times has been made, initially by Barron and Matthews in their original description of "the dorsal root potential" (1), that the D.R.V deflection evoked by a dorsal root volley parallels in time course the positive intermediary potential (17) similarly evoked. It would seem that this is a significant fact, and, as a first approximation, it would further seem justified to assume as did Barron and Matthews, that the two phenomena are intimately related despite the obscurity that at present surrounds the relationship.

D.R.IV and Negative Cord Potential.—During the analysis of the D.R.I, II, III complex it was seen that these deflections bear a reasonably definable relation to the intramedullary spike potential of the cord potential. Likewise there exists a close similarity, but ill defined relationship between D.R.V and the positive intermediary potential. The similarity between D.R.IV and negative intermediary potential at first sight, however, is neither close nor well defined. Some observations on cord potentials during the course of asphyxia have interest in this connection. Illustrated in Fig. 18 are records, superimposed by tracing, of cord potentials recorded at various stages of asphyxia by means of electrodes placed one upon the dorsum of the cord, the other at a distance on non-nervous tissue. The records are from the same preparation as that from which Figs. 6 and 15 were obtained. Record A of Fig. 18 represents the normal cord potential, B to E, successive stages in the asphyxial effect. From these recordings it is quite clear that the negative intermediary potential is divisible into two fractions, one associated with and succeeded by positive intermediary

potential, the other not. The latter, seen in isolation in record E of Fig. 18, has properties similar to those of the primary fraction of D.R.IV and the early negativity in an active dorsal root, including virtually identical duration and regression: it would appear to share with them a common origin.

The problem raised by the electrical sign of the presumably primary fraction of the negative intermediary potential (Fig. 18 E) is different from that involved in the study of similar deflections in dorsal roots for the precise orientation of the individual collaterals within the volume conductor of the spinal cord

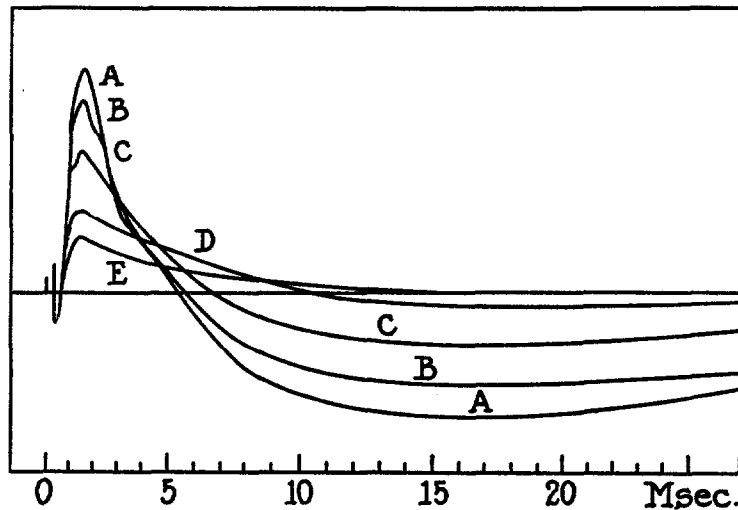


FIG. 18. Cord potentials recorded with one electrode on the cord dorsum, the other on non-neural tissue, to illustrate progressive stages, A to E, in the course of modification by asphyxia. The negative intermediary potential contains two components separable by asphyxia, one of which (E) in many ways is comparable with D.R.IV.

can no longer be neglected. In other words a unique solution is only possible following a study of the fields about active primary afferent fibers in the light of knowledge as to the precise orientation of the active fibers. The knowledge not being available the problem cannot as yet be solved.

The other fraction of negative intermediary potential is clearly the result of internuncial activity (17), possibly on the part of the interneurons responsible for the secondary fraction of D.R.IV. There is not much resemblance between these potentials, a fact that could mean among other things merely that the aspect of internuncial activity that dominates the intermediary potential does not possess the appropriate spatial orientation to result in a net polarization, one way or the other, of the I segment of primary afferent fibers. Since the action of secondary axons is the likely cause of the polarization producing the secondary fraction of D.R.IV, one might suppose that activity in inter-

nuncial somata predominates in the cord lead, and so accommodate the discrepancy.

On the Relative Susceptibility to Asphyxia of Various Parts of the Reflex Arc.—The present experiments utilizing asphyxia have provided an opportunity to study the relative sensitivity to asphyxia of the several structures encountered by impulses on their way through the spinal cord. To recapitulate the experimental observations, in each instance D.R.V and the occluding (secondary) fraction of D.R.IV disappear together, leaving for a short period the D.R.I, II, III deflections and non-occluding fraction of D.R.IV (Figs. 7 and 10). Next to fail with continuing asphyxia are the remainder of D.R.IV and D.R.III. A resistance to asphyxia comparable to that of peripheral nerve characterizes the D.R.I and D.R.II deflections. These observations can only mean that the ability of somata to generate impulses in response to presynaptic volleys is the first asphyxial failure, although to judge from the observations of Brooks and Eccles (8) the somata (of motoneurons) should still be able to respond to antidromic impulses. Subsequent and conjoint failure of D.R.III and the non-occluding fraction of D.R.IV indicates that the “weak point” of the primary afferent fibers is the region where parent fibers branch to form longitudinal fibers and collaterals, rather than the collaterals or terminals themselves.

An Analysis of Synaptic Excitatory Action

It has been shown (14, 20) that the facilitatory action of a near synchronous presynaptic volley in a monosynaptic reflex system can be detected for nearly 15 msec., the decay of facilitation being an approximately exponential regression to half-value in 2.8 msec. (20). At the time that the prolonged facilitation was documented reason was given (20) for supposing it to be the expression of a process additional rather than alternative to the brief excitatory action of earlier descriptions. Hence, and because of certain analogies with phenomena at a block in nerve (22), the prolonged facilitation was called *residual facilitation*. In other words it was concluded that presynaptic impulses exert upon postsynaptic neurons two actions: the initial (or detonator⁴) action and a

⁴ Attention must be brought to the fact that the term employed herein, and previously (20), is detonator *action*, not detonator *response*, since, to the extent that one term has been substituted for the other, the earlier paper (20) has been misquoted (15). By detonator action is implied, in accordance with Eccles' first use of the term (reference 12, page 6), a brief excitatory action exerted by presynaptic impulses. The term detonator response, again in accordance with original usage (reference 12, page 11), implies an action *sui generis* on the part of the postsynaptic neuron presumed to mediate between the excitatory action of presynaptic impulses and the generation of postsynaptic impulses. If, however, the term detonator action is to be construed in such a way (*cf.* reference 12, page 17) that it includes a detonator response, then present use (20, and above) has been in error.

residual action. Despite differences in detail, this conclusion in itself is nothing more than a reiteration of the views advanced by Bremer (4). From the foregoing experiments and consideration it is now concluded that the residual action of presynaptic impulses consists of a current flow about presynaptic collaterals during the period of residual negativity, and that such current flow about primary afferent collaterals is a sufficient agent to account for the phenomenon of residual facilitation in monosynaptic reflex pathways.

None of the experimental material upon which this paper is based bears on the nature of the event (initial excitatory action) by means of which the transmission of impulses is secured. As a matter of fact two important properties of the initial action, its brevity⁵ and sharp spatial decrement (22), preclude the possibility of electrotonic propagation into dorsal roots. However, there is still no reason to doubt the existence of an initial action to which the residual action is appended, and indeed the most recent experiments of Brooks and Eccles (10) have yielded facilitation curves that indicate a brief early phase preceding or superimposed upon the residual facilitation. Furthermore, the conditions that Brooks and Eccles have found necessary for demonstration of the initial facilitation are in full accord with the notion of sharp spatial decrement. Although Brooks and Eccles now accept the postulation of two phases of facilitation in monosynaptic reflex arcs, their interpretation as to origins is necessarily quite different from that here presented, being founded upon the fundamental assumption (7-10, 12-14) that current flow at the presynaptic endings has essentially the brief duration of axon spikes in peripheral myelinated fibers. As a consequence (and in consideration of "synaptic potentials") it was necessary further to assume that the more prolonged phenomenon, by whatever name it may be called, resides in the postsynaptic neurons. Now that the assumption concerning brevity of the presynaptic action is demonstrably untenable, the hypotheses of excitation (10, 13), inhibition (9), and of the origin of the dorsal root potential (16) predicated upon it appear unnecessarily complicated.

Although the major emphasis is now placed upon presynaptic events as agents for transmission and facilitation (not to speak of direct inhibition) it must not be supposed thereby that membrane changes do not occur also in postsynaptic neurons when acted upon by presynaptic impulses. However, in the presence of active presynaptic changes during orthodromic reflex activity, it seems highly unlikely that membrane changes of postsynaptic origin would be revealed by recording at the region of synapsis unless and until the postsynaptic neurons respond in turn with conducted impulses. In the absence of discharge, therefore, the demonstration of threshold change, as by the use of monosynaptic test

⁵ To avoid misunderstanding it is well to note that brevity is a factor only in the active root.

reflexes, provides the only clue to the existence of membrane changes at the regions the threshold of which is tested.

The foregoing argument is based upon certain considerations of interaction between nerve fibers. If of two closely proximate groups of nerve fibers in a common conducting medium one group is active in the sense of conducting a volley of impulses, the other not, then: (a) fluctuations of membrane current occur in both groups of fibers (24); (b) threshold changes associated with the fluctuations of membrane current in the inactive fibers may be detected by means of suitable experimental procedure (24); but (c) an electrode placed in close proximity to the two groups of fibers (in association with an electrode elsewhere) records the membrane changes of the active fibers to the effective exclusion, at least, of those in the inactive fibers, unless and until the inactive fibers, by one means or another, as in "ephaptic" phenomena, themselves become active.

SUMMARY

The "dorsal root potential" consists of five successive deflections designated for convenience, D.R.I, II, III, IV, and V. Of these, D.R.V alone constitutes the dorsal root potential of prior description. A study has been made of the general properties of those deflections not previously described.

Dorsal root potentials are electrotonic extensions into the extramedullary root segment, the result of electrical interactions within the cord comparable to those that have been studied in peripheral nerve. Although the anatomical and electrical conditions of interaction are infinitely more complex in the cord than in nerve, it is seen that the fact of parallel distribution of primary afferent fibers pertaining to neighboring dorsal roots provides a sufficient anatomical basis for qualitative analysis in the first approximation of dorsal root potentials.

An extension of the theory of interaction between neighboring nerve fibers has been made to include an especial case of interaction between fibers orientated at right angles to one another. The predictions have been tested in a nerve model and found correct. Given this elaboration, and the stated anatomical propositions, existing knowledge of interaction provides an adequate theoretical basis for an elementary understanding of dorsal root potentials.

The study of general properties and the analysis of dorsal root potentials have led to the formulation of certain conclusions that follow.

D.R.I, II, and III record the electrotonic spread of polarization resulting from the external field of impulses conducted in the intramedullary segment and longitudinal tracts of primary afferent fibers.

D.R.IV arises in part as the result of activity in primary afferent fibers, and in part as the result of activity in secondary neurons. In either case the mode of production is the same, and the responsible agent is residual negativity in

the active collaterals, or, more precisely, the external field of current flow about the collaterals during the period of residual negativity.

Current flow about active primary afferent collaterals during the period of residual negativity is the agent for residual facilitation of monosynaptic reflex pathways. Since the changes in reflex threshold follow the course of residual negativity there is no need to postulate especial properties for prolonging action at regions the threshold of which is measured by means of monosynaptic test reflexes.

D.R.V results from polarization of primary afferent fibers by current flow about secondary neurons. There is indication that somata rather than axons of secondary neurons generate the polarizing currents. Similarity between D.R.V and the positive intermediary potential further indicates that soma gradients established during the recovery cycle are responsible for D.R.V.

Little or no net polarization of primary afferent fibers results from activity confined to the contralateral gray substance, the dorsal root potentials in contralateral recording resulting from interaction in the dorsal column or in the ipsilateral gray substance following decussation of contralaterally evoked activity.

During the course of asphyxia the initial defect in reflex pathways is the failure of secondary neurons to respond to primary impulses. Subsequently block is established at the branching zone of primary afferent fibers.

A relation exists between the sequence of dorsal root potentials and the cord potential sequence, the major departure from exact correspondence occurring in the region of D.R.IV and the negative intermediary potential and being of a nature to suggest that different aspects of internuncial activity are emphasized by the two methods of leading.

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