THE COMPOUND ORIGIN OF POTENTIAL IN A STIMULATED DORSAL ROOT*

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For 100 to 200 msecs, after a dorsal root has been stimulated there exists along it a potential gradient of negative sign near the spinal cord (see Fig. 1). Except for the first 35 msecs, this gradient is identical in magnitude, duration, and sign with that in an adjacent unstimulated rootlet.

Lloyd and McIntyre in 1949 (9) were the first to demonstrate clearly that the potential of an active root differs from that of a neighboring root by virtue of additional early negativity. As a result of their studies they proposed that the electrotonus of a stimulated root is a resultant of two independent systems of current. It was suggested that one component, a prolonged negative potential, exists equally developed in stimulated and unstimulated rootlets even during the first 35 msecs. This is the dorsal root potential of classical description (1-4), DRV in their terminology (9). The additional negative potential appearing solely in the stimulated rootlet and written upon DRV was thought to have a separate origin.

In support of this formulation two experimental procedures have demonstrated the compound nature of stimulated root electrotonus and closely related events. Lloyd and McIntyre (9) showed that the electrotonus could be fractionated into at least two components which are susceptible to asphyxia in different degree. Rudin and Eisenman (14) by means of excitability studies demonstrated that dorsal column extensions of stimulated root axons also undergo membrane potential changes which can be differentiated into two components. One component, a depolarization of DRV form, has a limited spatial distribution along the cord. It was concluded in agreement with others that it arises from a generator located external to the tract either in collaterals of primary cells or in secondary cells and propagates out a stimulated rootlet with essentially unaltered form. The other component shows an extended spatial distribution and arises apparently within the dorsal columns as their negative after-potential. It also appears by electrotonic spread in the stimulated rootlet as suggested previously.

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(14) and discussed in the succeeding paper (16). In the present study a third, independent line of evidence based on an analysis of occlusion will be presented to show the dual nature and compound origin of electrotonus in a stimulated dorsal root.

The terminology of Lloyd and McIntyre will be retained, the potential deflections in a neighboring unstimulated rootlet being labelled consecutively, DRI, II, III, IV, and V corresponding to each change in sign. Only DRIV (positive) and DRV (negative) are labelled in Fig. 1. The post-spike electro-

![Diagram](image)

**Fig. 1.** Superposed tracings of potential deflections at same amplification and time base recorded from a dorsal root when it was stimulated maximally (DRα and β) and when the stimuli were applied to its neighbor (DRIV and V). Light sodium pentobarbital anesthesia. Freshly cut rootlet 40 mm. long. Distal recording electrode 31 mm. from cut end.

...tonic deflections in a stimulated rootlet will be divided into two components, labelled DRα and DRβ, consistent with purely formal definition. DRβ will refer to the potential component whose form, magnitude, and sign in a stimulated root are assumed to be identical with DRV in a neighboring root (9, 14).

DRα will be defined as the remaining potential in the stimulated root; i.e., as the difference between the post-spike potentials in stimulated and in neighboring rootlets. If the entire post-spike potential in an active (stimulated) rootlet

1 Actually, Lloyd and McIntyre also proposed that occluding DRIV appears in a stimulated root. We have nothing to contribute to this, and from the standpoint of our analysis, the question may be neglected since the magnitude of the potential is relatively small.
is labelled DRA and that in the neighboring rootlet is labelled DRN then the following simple relations will hold.

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\begin{align*}
DRA &= DR_\alpha + DR_\beta \\
DRN &= DRIV + DRV \\
DR_\alpha &= DRA - DRN \\
DR_\beta &= DRN
\end{align*}
\]

Lloyd and McIntyre, in addition to describing in detail all the root potentials, provided a comprehensive theory permitting an analytical approach to the study of root electrotonus. Most important, these authors concluded that DRα arises from activity in the primary afferent spinal neuron. Their major reason for this conclusion came from the results of a formal analysis of current interaction between active and neighboring adjacent fibers. This analysis, by placing the generator underlying DRα in the primary cell, satisfied their experimental findings that there exists in a neighboring rootlet a potential of opposite sign, of identical asphyxial sensitivity, and of possibly similar time course (i.e. DRIV).

In a search for additional evidence on the origin of DRα, methods are presented here for examining its degree of occlusion. The data demonstrate that DRα is unique among the multitude of post-spike potentials to be recorded from either dorsal roots or the cord dorsum in being the only one which appears to be completely non-occluding. Except for rather complex and unlikely assumptions this finding provides strong evidence that DRα has its ultimate origin within the primary neuron.

It is appropriate to present a brief summary of the general theory upon which the investigation in this and the succeeding paper (16) is founded. The analyses, since they are concerned with after-potentials, rely on Helmholtz's general theory of the behavior of electromotive double layers in a volume conductor especially in the form presented by Lorente de Nó to cover the special cases of fast and slow components of the action potential (10-12).

External currents and a potential field appear about a neuron whenever the value of membrane potential is not uniform throughout the cell. Conversely, any membrane potential change which occurs simultaneously over the whole neuron will do so without external potential sign. The fluctuations of membrane potential described as after-potentials take place almost simultaneously over the surface of a neuron of uniform properties, their voltage gradients in space amounting to only a few microvolts/centimeter. In consequence, after-potentials occurring in a cell with uniform membrane properties generate no significant external current or potential field. On the other hand, in an axon having contiguous segments with different after-potential sequences sharply localized differences in membrane potential will arise; and systems of currents will appear in the external conductor about the junction between the regions of dissimilar properties. Henceforth, we shall call any such current-generating system an "electromotive surface"; for a given external potential field defines one and only one equivalent electromotive surface.
The statements above hold whether the external conductor is relatively extensive, as in the spinal cord, or relatively limited, as in a root in an insulating medium. Such differences in the extent of the external conductor may reasonably be assumed to affect only the configuration of the potential field. If, in addition to knowing the membrane potential intrinsic to each segment at a given instant, one knows the shape of the external conductor about the junctional region, then the configuration and magnitude of the resulting extracellular current and potential field can be approximated. In the analysis, as undertaken here, of potential gradients along roots connected to volume only at one end, the circumstance of a thin, approximately linear, external conductor provides that all root RI drops can be recorded in one dimension and will be developed entirely by those currents which pass across the axon membranes in the root.

Electrotonic Potentials in an Active Dorsal Root

In undertaking an analysis of potentials in a stimulated dorsal root it is necessary first to review the potentials appearing there and then to consider the conceivable origins of potential gradients in such a structure.

Experimental Methods

The cats used for this study were anesthetized with sodium pentobarbital (27 mg./kilo) although a few critical experiments were performed in decapitate or decerebrate preparations not less than 1 hour after termination of ether anesthesia. Warm mineral oil, equilibrated with 5 per cent CO₂, 95 per cent O₂ (as suggested by Lloyd (7)) was layered over roots and cord to a depth of several centimeters and maintained within 0.5° of rectal temperature (37.5 ± 1°C.) by radiant heating. Throughout the experiment 5 per cent CO₂ and 95 per cent O₂ were continuously and vigorously bubbled through the mineral oil. Two adjacent dorsal root filaments (taken from L₄, or S₃) were then severed distally under the oil and raised into the insulating medium. On one were placed two recording leads, one close to but not touching the spinal cord, the other 8 to 12 mm. distally. Both rootlets were fitted with pairs of stimulating electrodes near their severed distal ends. Supramaximal stimuli were then delivered (1/second) separately to either one of the rootlets and the resulting potentials recorded. When the root being recorded from has been stimulated the electrotonus is designated as “active.” When the stimuli are applied to the neighboring root, the electrotonus is termed “neighboring.” In either case negativity at the electrode nearer the spinal cord was recorded upward on the oscilloscope. The characteristics of stimulating and recording circuits have been given elsewhere (14, 15).

RESULTS

Set forth in Fig. 2 with appropriate time bases and amplifications is an integrated survey of all the potentials appearing in a cut dorsal root carrying a maximal afferent volley (cf. Lloyd’s Fig. 6 (8)). In A, following the stimulus

2 Lorente de Nó has shown that loading sufficient to alter significantly the membrane potential is not likely to occur under these conditions (chapter I, p. 13 of reference 12).
Fig. 2. Potential deflections occurring in a maximally stimulated dorsal root recorded at successively increasing amplifications and time bases. Decapitate cat. Freshly cut dorsal root 39 mm. long. Distal recording electrode 29 mm. from cut end.

Artifact, the root spike potential is seen at low amplification recorded biphasically, positive-negative, in transit to the spinal cord. In B and C the vertical amplification has been increased by factors of 10 and 100 respectively. D and E provide the potential sequence at slower sweeps than C but at the same amplification. The spike is succeeded by about 35 msecs. of negativity not pres-
ent in a neighboring root (DRα). Subsequent to DRα the potential of an active root resembles closely that of a neighboring root and has been labelled DRβ.

As shown in Fig. 1 from another preparation the difference between active and neighboring rootlets (DRα) is best visualized by superposing the potentials recorded from a long, freshly cut dorsal root when it and a neighboring rootlet are stimulated maximally in succession.

On Possible Origins of DRα.—

Two conceivable origins of DRα lie external to the root itself: (A) polarizing currents delivered through the electrodes applied to the root; (B) electrotonus propagating out the root from intramedullary activity of either primary or secondary cell origin. Two cases must be distinguished under B. In the first case (B1) one may conceive of the root segment of the afferent neuron undergoing purely transient polarization in the absence of a resting DC gradient of membrane potential. In the second case (B2) one may conceive of the primary cell as having such a gradient in its resting membrane potential. Two imaginable origins of DRα lie within the root: one (C) due to artificial non-uniformities produced by injury currents at the cut end, and the other (D) the result of a natural gradient of properties intrinsic to the membrane recovery cycle of the root.

Evidence that stimulus polarization, case A, is negligible can be obtained by reversing the polarity of the stimulating circuit while maintaining an afferent spike potential of constant height. On numerous occasions the post-spike potentials were found to be unchanged when this was done as indicated by careful superposition of the photographic records. In addition, studies of the first derivative in space of the longitudinal potential distribution of DRα, measured at a time when DRβ is poorly developed (4.5 msecs.) show that the longitudinal current of DRα increases as the cord is approached and the distance from the stimulating electrodes increases (unpublished observations).

With respect to origin B2 there is adequate reason given in the literature for supposing that there could exist in the resting state steady membrane potential differences in various segments of the primary afferent neuron. Such differences might arise either as a consequence of intrinsic dissimilarities in membrane properties of various regions of the afferent cell (S) or extrinsically as a result of the steady influence of secondary cells. If, for example, there were sufficient depolarization of the afferent neuron centrally, the accompanying currents would act in every way like the distal injury currents and would provide a monophasic lead for root after-potentials at the root-cord junction. Whatever their sign, if the currents were intense enough, significant gradients at least in the value of the L fraction would exist in the immediate vicinity of conventionally placed root electrodes. Evidence is provided in Fig. 3 to show that there is no profound gradient of this kind. The external longitudinal DC
potential of a dorsal root cut 34 mm. from the root-cord junction has been plotted. The potential profile shows only an exponential decay of the distal demarcation potential with no sign of any comparable gradient projecting outward from the cord. It is concluded from 6 similar experiments that if DC electrotonic gradients emanating from the cord exist under ordinary experimental resting conditions, they are negligible for our purposes.

![Figure 3](image)

**Fig. 3.** Longitudinal potential gradient of a dorsal root freshly cut distally. Ordinate, potential difference between an exploring electrode and a reference electrode at the root-cord junction (negativity of the exploring electrode plotted upward in millivolts). Abscissa, distance in millimeters from anatomical root-cord junction. Sharp crush at 34 mm. Inset plots the same data on a logarithmic potential scale.

Two methods have been used as routine to exclude the possibility (C) that the recordings were contaminated by any fraction of root after-potential arising from the spread of injury effects from the cut end. The first consisted of monitoring for the absence of longitudinal current in the vicinity of the distal recording electrode. The monitoring technique is demonstrated in Fig. 2 of the succeeding paper (16) and consisted simply of measuring the potential difference between two “guard” electrodes, 2 mm. on either side of the distal recording electrode. The absence of transients following each volley demonstrated (as originally stated by Lloyd (8)) that with 30 mm. of intact root beyond the distal recording electrode such currents were absent. The second
method measured the spread of demarcation potential from the cut root end as already illustrated in Fig. 3. A detectable demarcation potential has not been observed more than 30 mm. from the cut end. Both of these methods permit appropriate placement of the distal recording electrode to obtain records free of after-potential resulting from the presence of injury currents.

The only other physiological origin of potential gradients to be considered, beyond that due to transients arising at the root-column junction or more centrally (B1), lies along the root itself (D). Direct bipolar recording of root after-potential in a root of uniform properties cannot be significant since calculation from experimental data (16) shows that the first derivative of its after-potential with respect to space amounts to no more than 20 microvolts/cm. at any time after the first few milliseconds. However, there is evidence that a dorsal root is not a uniform structure longitudinally (13, 17). Accordingly, this possibility for the generation of root potential must be admitted; and if the physiological change in membrane properties were such that the negative after-potential is larger nearer the cord, then central negativity would be recorded in an active dorsal root for this reason.

The foregoing analysis demonstrates that DRα can be ascribed neither to the effects of stimulating current nor to the recording of root after-potential from either artificial gradients of injury distally or physiological d.c. gradients centrally. Consequently the conclusion is reached by exclusion that DRα must arise either (1) from a naturally existing spatial gradient in the transient post-spike recovery process somewhere along the intramedullary or extramedullary portion of the primary afferent neuron or (2) from the transient polarizing action of secondary cells on primary cells. Evidence discussed in the introduction and to be presented in the next section by demonstrating a primary cell origin for DRα requires the first conclusion.

On the Nature of Occlusion in an Active Dorsal Root.—

The phenomenon of occlusion poses certain problems with which any theory of evoked potentials must contend. Heretofore occlusion has not been examined in active roots. But it is well known that DRIV, DRV, the negative intermediary dorsal cord potential, and the positive intermediary dorsal cord potential all show marked occlusion (6, 9). In addition, it will be shown here that DRβ occludes. However, no reasoning a priori necessitates that DRα occlude. In fact, it is unlikely that it would if it arises as a function of events intrinsic to the primary afferent neuron.

In this section we will show that active root electrotONUS can be analyzed into two parts which overlap in time. One part (DRβ) occludes strongly and has the form of the DRIV-V complex in a neighboring rootlet. The other part occludes not at all, to within the limits of detection, and has exactly the form and magnitude of the potential defined as DRα in this paper.
Occlusion in an active dorsal root has been studied by maximally stimulating first separately and then together two adjacent rootlets while recording the electrotonus either from both rootlets together or separately (see Fig. 4 B, inset). All potentials were recorded without manipulation of the rootlets on the electrodes after their initial placement. This was accomplished by laying each rootlet on two different but comparably arranged pairs of stimulating and recording electrodes. The recording electrodes could then be led from separately, in conventional manner, or shorted together externally for combined recording. Separate stimulators supplied maximal shocks to the two rootlets (hereafter labeled A and B) either simultaneously or individually. Care was taken to avoid any recording of root after-potential by monitoring for the absence of extracellular longitudinal current flow in the vicinity of the distal recording electrodes on each rootlet. The combined recording situation in the above experiment is unconventional. It was chosen to provide constant external resistance enabling one to manipulate the data as below (i.e., to add and subtract root extracellular currents). Maximal stimulation of each of the two rootlets was used to avoid possible heterogeneity of current-generating behavior in roots as a function of the distribution of root thresholds and other factors.

Results

Curves A and B of Fig. 4 A show the responses to stimulation of rootlets A and B separately while recording from both rootlets together. The dashed curve \((A + B)\) is their arithmetical sum. Curve \(AB\) is the response to their simultaneous stimulation (again combined recording). In Fig. 4 B, curve \(A + B - AB\) provides the arithmetical difference of curve \(A + B\) and curve \(AB\). It gives the form of the imaginary potential which failed to appear with combined stimulation under the expectation that the individual rootlet responses would sum linearly; i.e., were entirely non-occluding. This potential represents the hypothetical occluding component of the entire active root potential complex.

The form of the hypothetical occluding component is identical at all instances of time with the classical potentials (DRIV, DRV) developed in an unstimulated dorsal root. This may be demonstrated by comparison of curve \(A + B - AB\) with the arithmetical average of the electrotonus recorded conventionally from rootlet A alone (Fig. 4 C, curve C) and rootlet B alone (Fig. 4 C, curve D) while stimulating in turn their partners. In Fig. 4 D curve E is the average of curves C and D. In order to facilitate comparison (there being no significance for present purposes in absolute magnitude) the ordinates of the occluding component \((A + B - AB)\) have been multiplied by a factor of 1.275 to give the circles in 4 D. They superpose well on the curve representing the average neighboring root potential. In 10 experiments of this kind the scatter has been small and random.

It may therefore be stated that all of the potential in an active dorsal root which shows occlusion has the form of neighboring root potential only; i.e.,
the DRIV-V complex. By the same token it follows that DRα which does not have the form of neighboring root electrotonus can have no detectable occluding component. If such were present, the circles in Fig. 4 D would lie above the line during the first 35 msecs.

The converse analysis is also possible. Under the label $AB - \frac{A + B}{2}$ in Fig. 4 B is the average of curves A and B subtracted from curve AB as shown in 4 A. Curve $AB - \frac{A + B}{2}$ gives the form of the non-occluding potential;

![Image](https://example.com/image.png)

**Fig. 4.** Occlusion in a stimulated dorsal root. Heavy lines are tracings of recorded potential data. Description in text.

i.e., the real potential which did appear with combined as compared to individual rootlet stimulation. This curve resembles the difference in potential between active and neighboring roots as demonstrated in Fig. 1. It begins at a maximal value and declines thereafter. The prolonged tail, however, represents, as in neighboring roots (cf. Fig. 9 in reference 9), that portion of DRβ which is non-occluding. In order to determine the form of DRα alone one may subtract the small non-occluding DRβ component from the total non-occluding potential $(AB - \frac{A + B}{2})$. This may be accomplished by subtracting a potential of DRβ form (given by curve E) from curve $(AB - \frac{A + B}{2})$ after scaling
their heights to coincide at some time when it is certain that $\text{DR}_\beta$ is the sole remaining event in active fibers (e.g., after 50 msecs). This has been done and the remaining potential has been transposed with appropriate scale (i.e., after multiplying the ordinate by 1.275) to Fig. 4 D and labelled $\text{DR}_\alpha$. Treatment of the data in this manner has consistently shown that the duration of $\text{DR}_\alpha$ exceeds the value of 15 msecs, determined by Lloyd and McIntyre under conditions of asphyxia (9). 35 msecs would seem a more likely value from our data.

**DISCUSSION**

It is concluded that there exists in a stimulated dorsal rootlet a potential component which does not occlude and which has the form, magnitude, and sign of the potential defined as $\text{DR}_\alpha$. In addition, there exists in a stimulated rootlet a potential component which occludes strongly and has the form, magnitude, and sign of the potential defined as $\text{DR}_\beta$. The latter is identical with $\text{DR}_{IV}$ and $V$ in a neighboring rootlet. Thus the purely formal definitions given in the introduction to $\text{DR}_\alpha$ and $\text{DR}_\beta$ acquire physical significance.

Since the potential components in an active root are highly dissimilar their origins must be quite different. The fact that $\text{DR}_\alpha$ adds linearly as do the after-potentials of peripheral nerve constitutes strong evidence for a primary cell origin of this potential. This is particularly true in view of the fact that all other post-spike potentials recordable in the locality—$\text{DR}_{IV}$, $\text{DRV}$, $\text{DR}_\beta$, the negative dorsal cord potential, and the positive dorsal cord potential—occlude strongly. Thus, there is every indication that events arising in the vicinity of synapses are not proportional to input. Nor is synaptic transmission itself generally proportional to input since a variety of non-linearly distributed factors are usually at play. Considerations such as these virtually exclude the existence of simple proportional relation between primary cell input and secondary cell output. These observations, together with the results of the first portion of this paper, permit the conclusion that $\text{DR}_\alpha$ is generated specifically

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3 This procedure of equating the form of non-occluding $\text{DR}_\beta$ with the form of total neighboring root potential (curve E) is justified as follows. The form of $\text{DR}_\beta$ equals the form of $\text{DR}_N$. This has been established by considerations presented in the introduction and by the correspondence of the curves in Fig. 4 D. Further, the form of the non-occluding component of $\text{DR}_\beta$ equals the form of $\text{DR}_\beta$ (occluding plus non-occluding). This relation is apparent in Fig. 4 A once $\text{DR}_\alpha$ is complete. A similar relation holds for all instances in a neighboring root (i.e., non-occluding $\text{DR}_N$ equals $\text{DR}_N$). A demonstration of this statement may be found in Fig. 9 (reference 9) and has been confirmed in the cat. Indeed, by comparing late in Fig. 4 A with the comparable time in Fig. 9 (reference 9) it can be seen that the ratio of the magnitudes of occluding to non-occluding potential is similar in both active and neighboring roots. Therefore, since $\text{DR}_N$ equals $\text{DR}_\beta$ and the form of non-occluding $\text{DR}_\beta$ equals the form of $\text{DR}_\beta$ it follows that non-occluding $\text{DR}_\beta$ and $\text{DR}_N$ (curve E) have similar form.

4 Unpublished data of Lorente de Nó (personal communication).
by physiological changes in the transient recovery cycle of membrane potential somewhere along the primary afferent neuron as it alters its properties in progressing from the character of peripheral nerve to that of presynaptic collaterals. In the following paper (16) certain portions of the primary neuron will be examined for the purpose of identifying the locus of this change.

SUMMARY

The electrotonic potential appearing in a stimulated dorsal root is found to be the resultant of two independent systems of current of different origin.

One component, labelled DRα, is non-occluding.

The other component, labelled DRβ, occludes strongly and has the characteristics of the potential which appears in a neighboring unstimulated rootlet (DRIV-V).

Because DRα does not occlude, its origin is assigned to the primary afferent neuron. The result of a general examination of its origin leads to the additional conclusion that it must arise from a physiological spatial gradient in the post-spike recovery cycle of membrane potential along the afferent neuron.

The specific locus of this gradient within the primary neuron is the subject of the succeeding paper (16).

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