

POTENTIAL CHANGES OF THE SPINAL CORD
FOLLOWING DIFFERENT TYPES OF
AFFERENT EXCITATION

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The slow potentials that can be recorded from dorsal and ventral roots as a consequence of arrival of impulses at the cord have been studied by a number of authors. Barron & Matthews (1938) have shown that they propagate electrotonically along the roots, that the dorsal root potential (DRP) follows the arrival of impulses and spreads widely along the cord, following nervous pathways, and that the reflex discharge of the motoneurons follows and presumably is occasioned by a certain rise of the ventral root potential (VRP). They assume (p. 315) that the two components which are sometimes seen in the VRP of mammals are originated by the impulses reaching the motoneurons via a monosynaptic and a plurisynaptic path respectively.

Fessard & Matthews (1939) have recorded the DRP which follows the arrival at the cord of single impulses originating in skin receptors of frogs, but could not detect any appreciable DRP as a consequence of a single impulse arriving from muscular receptors, though some spinal negativity could be recorded from the dorsal roots following repetitive stimulation of purely muscular nerves. This finding implies that the reaction of spinal structures to impulses arriving from muscular or cutaneous nerves can have quite different features. The results obtained by Lloyd (1943), using electrical stimulation of purely muscular or cutaneous nerves in mammals, support this, showing that the features of the reflex arising from the excitation of the two different sources are clearly different, mainly on account of the fact that (in the cat) monosynaptic relays subserve the myotatic reflex, while impulses flowing along skin nerves reach the neurones via the interneurons (see also Renshaw, 1940). Eccles (1946) considers that muscular impulses stimulate the motoneurons through the interneurons as well as through a monosynaptic path, and interprets the effects of a certain degree of anaesthesia on the VRP of both cats and frogs as due to the selective block of the plurisynaptic path. Evidence of dual spinal reaction to

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mixed stimulation has also been obtained by Dun & Feng (1944) who have observed that the DRP of frogs after propagation along the cord is composed of two waves, the second and more conspicuous of which he considers to be due to the activity of the internuncial neurones.

The present research has been performed with the aim of studying the slow potentials of the spinal cord and their relationships with the propagated impulses, following selective excitation of muscular or cutaneous nerves and receptors.

METHOD

The experiments have been performed on frogs. The animals have been dissected under ether and have been allowed to recover before recording. The spinal cord was generally severed at the level of the 3rd roots, and the immobility of the animal was secured by cutting an adequate number of ventral roots. When sensory stimulation was used, a muscle or a small area of the skin or both were dissected free, maintaining their nervous connexions with the central nervous system, and severing all other nerve branches. Graded tension of the muscle or pressure of the skin were obtained from a moving coil device energized electrically, and so the sensory stimulus could be synchronized with the cathode-ray oscilloscope for photography. For the electrical stimulation, induction shocks were delivered to the peripherally cut sciatic trunk, or to one of its muscular or cutaneous branches in the thigh, or to a dorsal root. When electrical stimuli were delivered to a nerve trunk, the ventral roots were severed. Chlorided silver electrodes, none of which was earthed, have been used for leading off: as a rule the proximal one made contact with the cord, and the distal one was 2-8 mm. away, but controls have been made avoiding contact with the cord. In some experiments, the conventional method of leading off from a cut dorsal root was used, but in most cases the dorsal root used for recording was kept intact. In these cases, controls have been performed to identify the artifacts that may result from the use of this technique. Electrodes and roots have been lifted in air or oil. Direct current (d.c.) or condenser coupled (r.c.) amplifiers have been used. The half value time of the r.c. amplifier was about 0.6 sec. The input was balanced in both instances. The recording was performed with a double-beam cathode-ray oscilloscope; the photography on moving paper or with a Leica camera.

RESULTS

I. Sensory stimulation

(a) Dorsal root potential

(1) *Skin*. Following the touch of an adequate area of the skin, a train of afferent impulses and a slow negativity (of the central electrode with respect to the peripheral one) appear on the dorsal roots. The relationships between impulses and slow waves are best seen when the discharge is unitary (Fig. 1A), and the findings agree with those of Fessard & Matthews (1939). The brief discharge of impulses which follows a light touch of short duration evokes as a rule a DRP of much the same shape as the one following the arrival of a single impulse or of a synchronous volley of impulses (Fig. 1C); a prolonged touch evokes instead a prolonged negativity which lasts as long as the stimulus.

(2) *Muscle*. When a pluck is applied to a muscle of the thigh, leg or foot, the potential changes which arise in the dorsal roots are formally similar to those following cutaneous stimulation (Fig. 1D). Although it has not been possible to compare the shape of the DRP's following one single impulse from cutaneous and muscular receptors respectively, it has been found that the DRP evoked by

a limited number of unitary muscular impulses (Fig. 1 B) is generally of smaller size, but is well comparable in its general outline to the one arising in analogous conditions from skin impulses. Increase of the strength and duration of the stimulation increases and prolongs the 'muscular' DRP. Prolonged pull of a muscle evokes a sustained negative deflexion, as occurs with continued cutaneous stimulation.

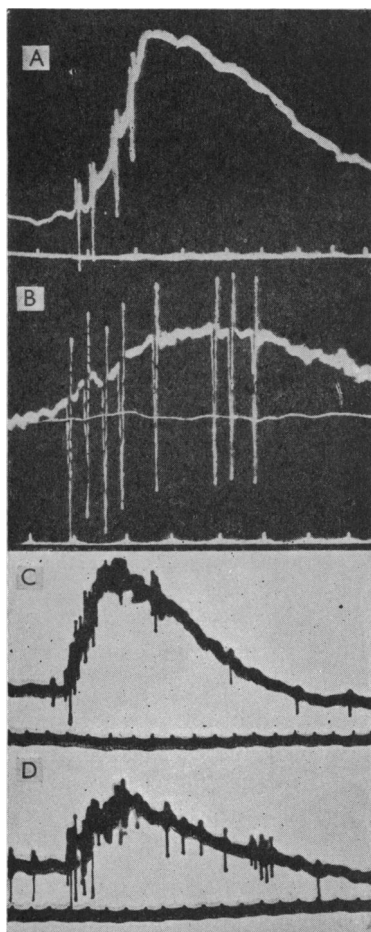


Fig. 1. Dorsal root potential evoked by unitary activity from skin (A) and from muscular receptors (B). Same following multi-fibre activity from skin (C) and muscular receptors (D). RC Amplifier. Electrodes on intact dorsal root, all other dorsal roots cut. Time 20 msec.

(3) *Spread along the cord.* Using a preparation containing two intact adjacent roots, some properties of the propagation of the DRP along the spinal cord can be easily studied: after having checked that the sensory stimulus evokes

approximately the same effect in both roots, records are taken with the electrodes on one of them. This root is then severed peripherally, and the recording is continued, taking care not to alter the position of the electrodes and to keep constant the sensory stimulus. In these conditions the DRP from cutaneous stimulation becomes apparently bigger on the cut root, presumably because of the increase of the interelectrode resistance, while muscular stretch which evokes an obvious DRP in the root through which the impulses enter the cord induces a DRP of smaller size (Fig. 2), and in some cases no potential can be detected on the adjacent cut dorsal root. It thus appears that the DRP's arising from cutaneous and muscular stimulation respectively differ in their propagation along the spinal cord.

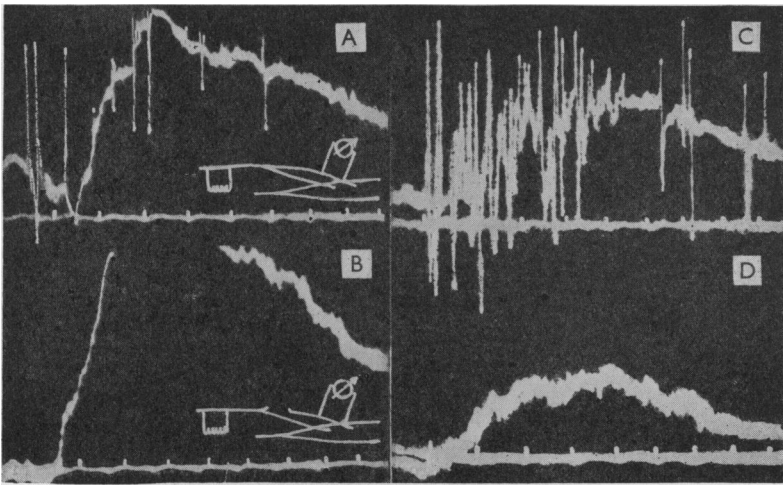


Fig. 2. Dorsal root potentials evoked by equal sensory stimuli in an intact (A and C) and in a cut root adjacent to the root of entry (B and D). A and B cutaneous, C and D muscular sensory stimulation. Time 20 msec. Insets: arrangement of the electrodes (for details see text).

(b) Ventral root potential

(1) *General features.* In recent work (Bonnet & Bremer, 1948) there is a close parallel between VRP and DRP. But in the present work this has only been found to occur under limited conditions. Often the VRP and DRP may be quite unlike, as is also true in the mammal (Barron & Matthews, 1938). Moreover, the spike-like waves on the VRP, which in the past have been taken as the signs only of propagated impulses, have often been found to be non-propagating. This is illustrated in Fig. 3, and emphasizes the need for caution in interpreting records taken from electrodes close to the cord. Sometimes decrementally propagated sharp waves and efferent impulses are both present on the slow component of the VRP, but it has been generally observed that

when the nonpropagated sharp waves are most developed, very little or no reflex discharge is seen. This unexpected finding has not been considered here in relation to its possible physiological significance, but only as an undesired complicating factor; and until future work has clarified the nature of the non-propagated sharp waves, discussion of them will be omitted.

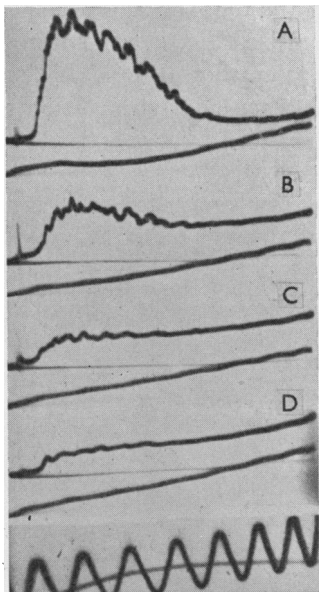


Fig. 3. Ventral root potential evoked by sensory stimulation. No propagated efferent discharge. Electrodes on cut ventral root, interelectrode distance 2 mm. A: proximal electrode in contact with the cord; B: 2 mm. away; C: 4 mm. away; D: 6 mm. away. Time: 20 msec.

(2) *Skin*. The shape of the VRP, with its slow and fast components, may display a great variability in different conditions, as Barron & Matthews (1938) have already emphasized. When sensory stimulation of the skin is used, its height and duration vary with the intensity and duration of the stimulus. As a rule, a suddenly applied stimulus of medium strength and short duration evokes a smoothly rising and decaying negativity with superimposed spikes (Fig. 8 A). The negative deflexion may last for a long time if the stimulation is maintained, as happens for the DRP. The sharp waves only appear when the slow negativity exceeds a certain minimal level, and may quite often be present also on its descending slope.

(3) *Muscle*. The VRP following the arrival of muscular afferent impulses is strikingly different from the one consequent upon the arrival of skin impulses. The slow wave is generally so small that, using the amplification which is

optimal for recording the 'cutaneous' VRP, only a hardly appreciable negative deflexion can be observed (Fig. 4 D). The physiological significance of this inconspicuous wave is shown, however, by the eventual presence on or near its highest point of spike potentials. These are less numerous than those following stimulation of the skin. The relative proportion of propagated and non-propagated components has not yet been studied. No effect has been observed on the ventral roots when the muscular impulses reach the cord via an ipsilateral dorsal root not corresponding to the ventral root used for recording, whereas cutaneous impulses entering by other roots produce an effect. Prolonged muscular excitation induces sustained negativity, but this is also much lower than the one following continued stimulation of the skin.

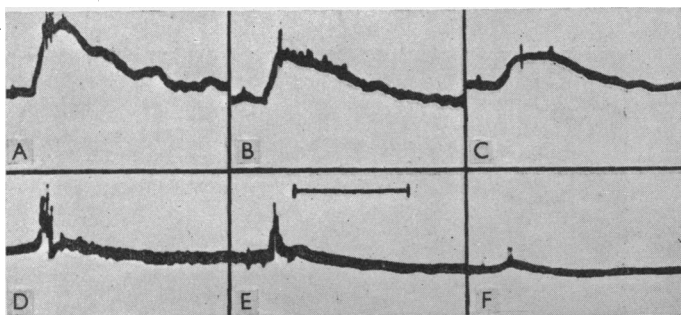


Fig. 4. Ventral root potential recorded from cut X ventral root following brief sensory stimulation of decreasing intensity, A-C: of skin, and D-F: of muscular stretch receptors. Time 250 msec.

II. *Electrical stimulation*

Sensory stimulation gives the most reliable selection of impulses of pure cutaneous or muscular origin, but selective excitation of various nerve trunks or twigs has also been performed, with the aim of obtaining slow potentials of the simplest form on the arrival of a synchronous spike. The differential stimulation of muscular or cutaneous fibres has been attempted by using terminal twigs of the sciatic to different muscles or skin areas, or by applying graded stimuli to mixed nerve trunks. None of these methods has been found completely reliable for obtaining (in frogs) selective excitation of fibres of different origin, and perhaps only very weak stimuli delivered to more or less pure muscular nerve twigs could consistently evoke selective excitation of muscular fibres. Owing to the small average size of the English frog, there is, in fact, the possibility that the stimulating current may spread and reach other fibres of high excitability contained in the main trunk. It seemed therefore that an analysis of the effects of the electrical excitation of purely muscular or cutaneous nerve fibres could more conveniently be carried out in mammals, and the only analysis attempted here was based on the study of series of DRP's and

VRP's resulting from stimuli of smoothly increasing strength, delivered to various nervous branches of the sciatic. It has never been assumed *a priori* that the excitation was limited to particular types of afferent fibres.

(a) *Dorsal root potential after sciatic stimulation.* Lloyd & McIntyre (1949) have pointed out some of the factors which can complicate the picture of the DRP when it is led off from an intact dorsal root. Despite all precautions, some complications could not be avoided in the present experiments: the potential changes recorded from an intact dorsal root when electrical stimulation of medium strength was applied to the sciatic consisted in a monophasic sharp wave apparently revealing negativity of the central electrode, followed by the conventional, smooth dorsal root potential. This latter slow wave can start from the end on the zero line, or, when stronger stimuli are used, from any

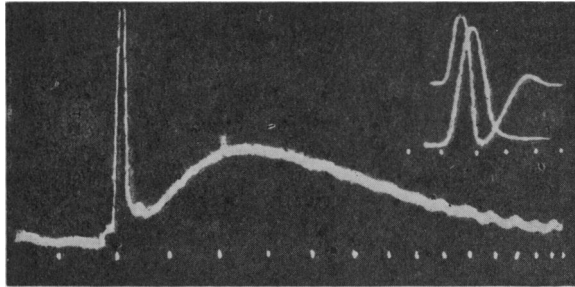


Fig. 5. Dorsal root potential evoked by electrical stimulation of the sciatic, and recorded from an intact dorsal root. Time 20 msec. Inset: superimposed records of afferent spike led off from electrodes on the intact dorsal root, near (monophasic spike) and at some distance (diphasic spike) from the cord. Time 3.3 msec.

point of the descending slope of the initial sharp wave. Above a certain degree of strength of the stimulus, a small sharp wave is very often seen at the junctional point of the two major waves, or soon after (Fig. 5). It has been possible to ascertain that the first sharp wave is due to a deformation of the incoming spike. The second smaller wave may represent the outcoming discharge along the recurrent fibres contained in the dorsal roots, as it was never observed when the neighbouring dorsal roots were severed. With reference to the problem of the selective stimulation it may be noted that on increasing the stimulus smoothly from a minimal value, no characteristic changes of the DRP are observed that can safely be attributed to excitation of different types of fibres.

(b) *Ventral root potential after sciatic stimulation.* The VRP evoked by stimulation of the sciatic nerve may have quite different shapes in different preparations and experimental conditions, as Barron & Matthews (1938, p. 294, fig. 14) have already noted. Stimuli of medium strength evoke in some cases

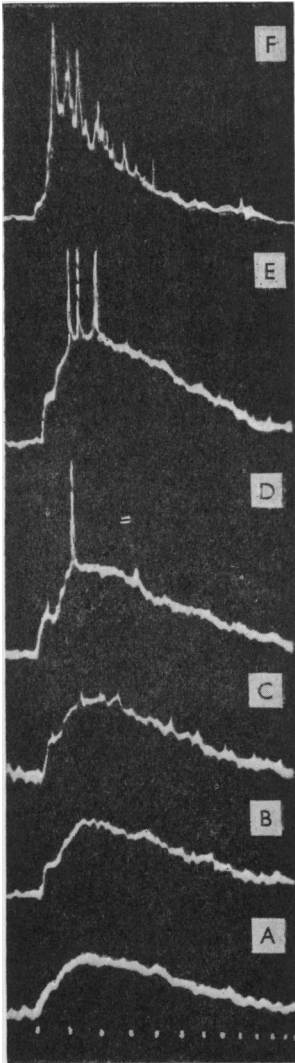


Fig. 6.

Fig. 6. Ventral root potentials recorded from IX ventral root following stimulation of the sciatic of increasing strength (from below). Two components of the slow wave are apparent in the lower records. Gain reduced between E and F. Time 20 msec.

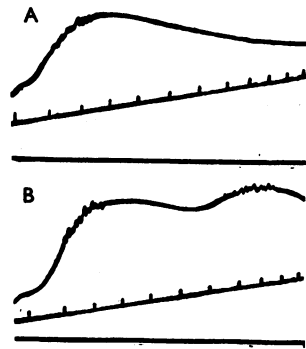


Fig. 7.

Fig. 7. Ventral root potential. A: following one shock to the sciatic, delivered after a period of quiescence; B: following another equal shock, 1 sec. later. Note change in form of potentials. Time 20 msec.

a VRP in which two components are evident, while in other cases the overlapping of sharp waves (among which are possibly efferent discharges) makes the shape of the VRP highly irregular. The double or triple wave which Barron & Matthews (1938) often found in mammals has never been observed in the present experiments on frogs, but monophasic or complex sharp waves sometimes preceded the slow potential when the proximal electrode made contact with the cord. These waves have been considered as unrelated to the VRP and have been disregarded in this study.

Weak electrical stimulation of the sciatic or of a dorsal root resulted in many cases in a very small VRP, possibly overlapped by sharp waves, much like that following muscular sensory stimulation (Fig. 9 F). The earliest change induced by increase of the stimulus consisted generally in the building up of a further and apparently different hump: this hump increases with the increase of the stimulus, and may eventually become fused with the earlier wave. Above a certain degree of depolarization, irregular sharp waves and efferent discharges can appear (Figs. 6 and 9). When the conditions of excitability are good, the efferent reflex activity following the arrival of a synchronous spike can last for many seconds. In some cases this delayed activity appears to be 'self-sustained', and actually, instead of decreasing progressively with time, it may build up in bursts of intense efferent activity, which is also superimposed on a late slow negative wave (Fig. 7).

(c) *Stimulation of pure branches.* Similar results are obtained both in dorsal and ventral roots following stimulation of muscular or cutaneous branches of the sciatic, but it is doubtful whether these stimuli really evoke selective excitation of fibres of different origin in the present experimental conditions (see above).

III. Relationships between DRP and VRP

Though the study of the relationships between DRP and VRP was not the primary object of this research, some of the features which have emerged will be briefly mentioned here.

When electrical stimulation is applied to a mixed nerve, the general course of the VRP may follow closely that of the corresponding DRP, provided that a suitable strength of stimulus and adjustment of gain of the two channels are chosen (Fig. 9 C). Also when cutaneous sensory stimulation of medium strength is employed, no sharp discrepancies between the courses of the corresponding slow waves are observed (Fig. 8 A). The similarity of the two curves, however, is not a general feature: a weak electrical or sensory stimulus can evoke the appearance of a well-developed DRP, but no apparent deflexion on the ventral roots record, and, when the strength of the electrical stimulus to a nerve or dorsal root is such that only a simple and small VRP results, its highest point and the first sharp waves or spikes appear much earlier than the summit of the corresponding DRP (Fig. 9 F). Also when strong electrical stimuli evoke

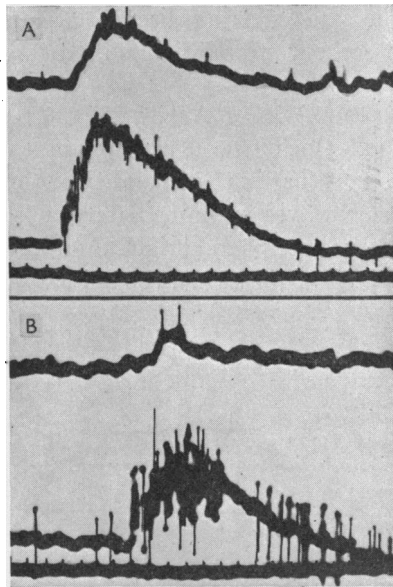


Fig. 8. Corresponding ventral (above) and dorsal (below) root potentials evoked by sensory stimulation of skin (A) and of muscular receptors (B). Time 20 msec.

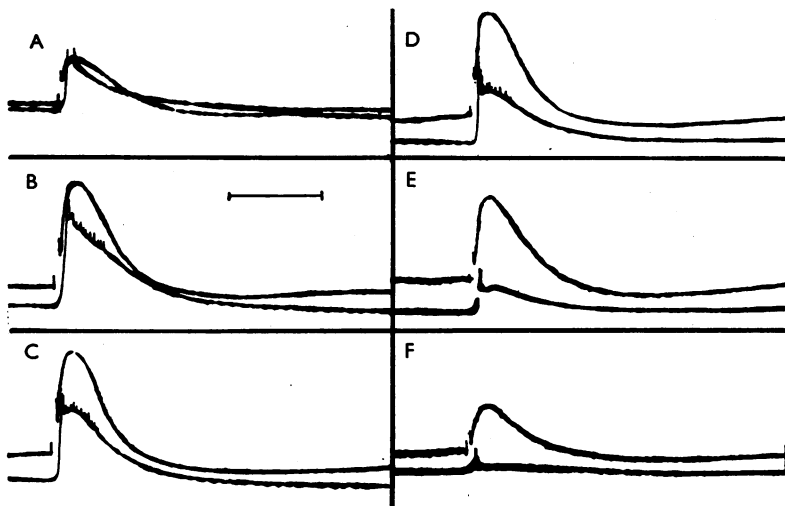


Fig. 9. Simultaneously recorded dorsal and ventral root potentials evoked by electrical stimulation of decreasing strength. Gain increased between A and B. Time 200 msec.

irregular non-propagated sharp waves on the VRP, no corresponding change results in the DRP. The same striking discrepancies of form are even more obvious when muscular sensory stimulation is used (Fig. 8 B).

IV. Relationships between slow waves and impulses

(a) *Dorsal root potential.* One of the advantages of leading off the DRP from an intact root lies in the fact that in these conditions the relationships between incoming impulses and slow waves are immediately apparent. The arrival of one or more impulses of whatever peripheral origin, is followed in normal conditions by the appearance of a DRP. Only when the animal is in deep anaesthesia or

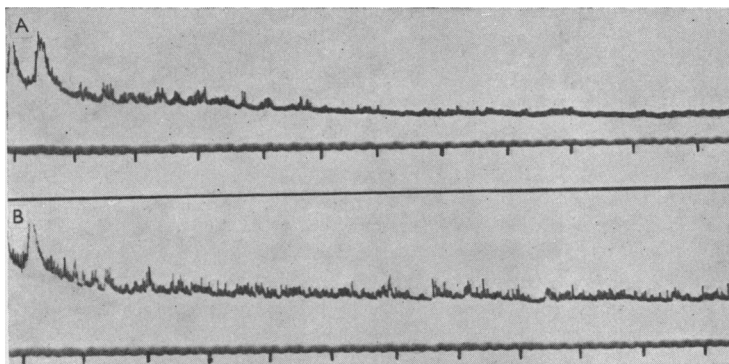


Fig. 10. Decaying slopes of ventral root potentials evoked by repetitive stimulation of the sciatic, d.c. amplifier. The last two of a series of 5 (A) and 17 (B) equal stimuli (frequency 18/sec.) are visible at the left of the records. Slower rate of decay and more intense and prolonged discharge after longer repetition. Time 100 msec.

when there was reason to believe that the root used for leading off had suffered some damage (Barron & Matthews, 1938; Fessard & Matthews, 1939) do impinging impulses fail to give rise to the slow wave.

The use of d.c. amplification shows that impulses may be present on the decaying slope of the DRP only when the slow wave was evoked by an irregular train of impulses (sensory stimulation): however, electrical stimulation of constant strength or unitary sensory excitation evoked a prolonged negativity which was regularly maintained for the whole duration of the train of impulses.

(b) *Ventral root potential.* Electrical signs of efferent activity can start from a very low level of central negativity of the VRP, especially when the reflex is evoked by selective excitation of muscular fibres, and they not only appear on the rising slope or highest point of the VRP, but can quite often be present in its decaying phase (Fig. 10). It should be noted, however, that the discharges evoked in the ventral roots with the present technique of stimulation and recording have always been very irregular and never displayed the signs of unitary activity. After repetitive afferent stimulation, the rate of decay from

the central negativity of the ventral roots is slower when the repetition is longer sustained, and also the spike potentials superimposed on this slowly decaying terminal slope are more numerous and longer sustained after longer stimulation (Fig. 10). Depending on the conditions of the reflex excitability of the preparation, a strong train of impulses may be followed only by the slow component of the VRP, or, in other cases, a few afferent impulses may evoke intense and prolonged activity in the ventral roots. A synchronous afferent volley evoked in the afferent path by electrical stimulation was never observed to induce a synchronous discharge in the ventral roots, but the resulting activity was always a more or less long-lasting irregular train of asynchronous impulses, if the intensity of the stimulation was sufficiently high.

DISCUSSION

In order to compare the shape of the DRP's evoked by cutaneous and muscular stimulation respectively, it would be desirable to obtain in both cases slow waves of the simplest form. The unitary DRP evoked by sensory muscular stimulation could not be recorded in this research (the slow adaptability of the muscular receptors renders it difficult to evoke a single afferent impulse), but the slow potentials following a brief asynchronous discharge or short unitary activity from cutaneous and muscular receptors, did not reveal an obvious qualitative difference in the general shape and time course.

The observation that the DRP following muscular excitation has much less tendency to spread along the cord provides however a consistent functional distinction.

The gradually increasing electrical stimulation of peripheral nerves also failed to show qualitative changes in the DRP that could be referred to excitation of different types of fibres. In particular, when leading from the same dorsal root by which the impulses enter the cord, the double wave which Dun & Feng (1944) have observed in a root far apart from the root of entry of the impulses, has never been noted. This finding can be explained by assuming that the presence of the afferent spike (deformed as above-mentioned by the conditions of recording) obscures the first wave described by Dun & Feng (1944); or, alternatively, it suggests that the two components of the DRP only become evident after propagation of the slow wave along the cord. The latter interpretation seems to be more consistent with the finding that no evident duality of the DRP is apparent when the potential wave is led off from a cut dorsal root adjacent to the root of entry of the impulses.

In contrast with the stability of the shape of the DRP's evoked by different types of stimulation, the VRP showed a great variability of shape both for different types of sensory stimulation and following electrical stimulation of increasing strength. As already stated, the lowest electrical stimulus capable of evoking a VRP, quite often only gives rise to a very small deflexion with

steep-ascending and slowly-decaying slope (see Eccles, 1946, fig. 5). It is suggested here that this simple VRP is a consequence of the selective excitation of muscular afferent fibres, and thus identical in nature (not necessarily in shape) with that evoked by sensory muscular excitation. On the other hand, the better known VRP which follows an electrical stimulus of medium strength to a mixed nerve is considered here to be the result of fusion of two more elementary slow waves that can be distinguished when weaker stimuli are used (Fig. 9 C-E).

The observation that the level of negativity from which the first signs of efferent activity start is lower when the afferent impulses arrive through muscular than when they arrive through cutaneous fibres can be compared with Eccles' (1946) finding that the early reflex discharge which follows excitation of the monosynaptic path of mammals, actually arise from a very low slow potential.

An attempt to interpret the present results on the basis of the findings which have been established in mammals, however, is made difficult by the fact that the temporal course of the slow potentials, and apparently also some fundamental features of the reflex, are widely different in mammals and amphibia respectively. In mammals, the reflex wave attributed to activation of the monosynaptic path is a synchronous volley which follows the stimulus by about 1 msec. (see, however, the different results and interpretations of Barron & Matthews, 1938). In frogs, instead, when the adjustment of the stimulus is such that efferent discharges only appear on the points of maximal negativity of the two waves which constitute the VRP following mixed stimulation, it can be observed that the early efferent waves have a delay of 10–20 msec., and the following ones of 25–50 msec. from the stimulus. When the strength of the stimulus is increased, the delay of both reflex discharges can be considerably reduced, but in no cases have minimal latencies of much less than 5 msec. been measured. Moreover, a synchronous early discharge has rarely been seen, but a long and asynchronous train of efferent impulses followed the synchronous incoming volley when the conditions of excitability were good. The divergence of shape of corresponding DRP's and VRP's which has been observed in many conditions, like the observation that the VRP only appears when the DRP exceeds a certain minimal value, suggests that the two slow waves do not originate in the same structures, and that the VRP is a response evoked by the stimulating action of the DRP (or, possibly, of the incoming spike). The idea that corresponding DRP and VRP may be different recordings of the same process (see Fessard & Posternak, 1950, p. 389) receives no support from the present work. The shape of the two corresponding slow waves is most different following afferent muscular excitation: if the connexions between muscular afferent fibres and motoneurons is monosynaptic in the frog, this observation would then be in agreement with Barron & Matthews's (1938) original view

that the terminals of the afferent fibres are the locus of origin of the DRP, which is primarily an index of changes in the dorsal horns of the spinal cord (Dun, 1939). When the relationships between slow waves and impulses are considered, the finding that the DRP evoked by unitary activity of sufficient strength maintains a steady level of negativity for the whole duration of the train of afferent impulses assumes importance. For it shows that the occurrence of impulses in the descending slope of a composite DRP does not necessarily mean that the late impulses fail to give rise to a slow negativity except on account of the development of occlusion.

As already mentioned, efferent impulses may be present also in the decaying slope of a composite VRP, but it cannot be stated here whether this is a feature of the elementary relationships between unitary VRP and efferent impulses, or whether it is a consequence of the compounding of many VRP's arising more or less asynchronously in different motoneurones. A unitary reflex discharge has never been recorded in this research, and it is probably experimentally impossible to evoke a unitary VRP.

The use of d.c. amplification shows that intensity and duration of the reflex after-discharge which follows repetitive stimulation run parallel with the duration of the slow negativity itself, which, like the reflex, is longer after more prolonged repetition of the stimuli. The facilitation which is sometimes observed when the stimuli are repeated at low frequency (1/sec.) can be explained on the basis of the finding that the decaying slope of the VRP can at times last longer than 1 sec., and that summation of the slow negativities is present up to a certain ceiling. It seems, therefore, that a certain degree of depolarization of the motoneurones is the main factor conditioning the discharge of impulses. Barron & Matthews's (1938) finding that some motoneurones have very slow accommodation to constant currents is in good agreement with this view.

A tentative interpretation of the differences between the VRP's following muscular and cutaneous excitation can be based on the assumption that the terminals of the muscular afferent fibres have greater convergence on few motoneurones than that of the fibres originating in the skin. In these conditions, the excitation of the former path could evoke a high and eventually supraliminal depolarization of but few neurones, while that of the latter would evoke a possibly lower depolarization of a larger pool of neurones, and it might be easily conceived that the total depolarization, as recorded from a ventral root, might be higher in the second case. The greater spread of the DRP of cutaneous origin along the cord could also be explained on the basis of this assumption. However, as this interpretation requires a number of assumptions, it should be considered no more than a provisional working hypothesis.

SUMMARY

1. The slow potentials of the spinal cord following different types of sensory and electrical stimulation have been recorded from dorsal and ventral roots of frogs.

2. The dorsal root potentials evoked by sensory stimulation of cutaneous or muscular receptors respectively are formally similar (Fig. 1), but the dorsal root potential evoked by muscular excitation is more localized in the cord (Fig. 2).

3. The ventral root potentials evoked by brief cutaneous and muscular sensory stimulation respectively are widely different: the former is a smoothly rising and decaying wave, while the latter consists in a much smaller wave with sharply rising phase and slow decay (Fig. 4).

4. Electrical stimulation of increasing strength applied to a peripheral nerve or dorsal root evokes dorsal root potentials of increasing voltage and of similar temporal course. The shape of the ventral root potentials, instead, changes as a consequence of the increase of the strength of the stimulus: at first only a small sharply rising wave appears, then a wave composed of two different humps, and finally a smooth wave in which the two elementary curves are probably fused together (Figs. 6 and 9).

5. Corresponding dorsal and ventral root potentials have widely different shapes in many experimental conditions (Figs. 8 B and 9). Stimuli that give rise to a well-developed dorsal root potential may still be insufficient to evoke a ventral root potential.

6. It is suggested that a different morphological organization of the terminal branches of muscular and cutaneous fibres may account for the different formal and functional properties of the slow spinal waves and of the reflex evoked by activation of these two afferent paths.

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REFERENCES

- Barron, D. H. & Matthews, B. H. C. (1938). *J. Physiol.* **92**, 276.
 Bonnet, V. & Bremer, F. (1948). *J. Physiol., Paris*, **40**, 117 A.
 Dun, F. T. (1939). *J. Physiol.* **95**, 41 P.
 Dun, F. T. & Feng, T. P. (1944). *J. Neurophysiol.* **7**, 327.
 Eccles, J. C. (1946). *J. Neurophysiol.* **9**, 87.
 Fessard, A. & Matthews, B. H. C. (1939). *J. Physiol.* **95**, 39 P.
 Fessard, A. & Posternak, J. (1950). *J. Physiol., Paris*, **42**, 319.
 Lloyd, D. P. C. (1943). *J. Neurophysiol.* **6**, 111.
 Lloyd, D. P. C. & McIntyre, A. K. (1949). *J. gen. Physiol.* **32**, 409.
 Renshaw B. (1940). *J. Neurophysiol.* **3**, 373.