J. Physiol. (1941) 100, 283–298 612.832

THE LATENCY AND CONDUCTION OF POTENTIALS IN THE SPINAL CORD OF THE FROG

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(*Received* 11 *June* 1941)

THE electrical activity in the spinal cord has been observed mainly in two different ways. Gasser & Graham [1933] have used leads placed longitudinally on the dorsal surface of the spinal cord in the cat cephalad to the root stimulated, and recorded the electrical changes in response to stimulation of a dorsal root. The changes consist of a negative spike followed by a longer and slower negative complex which is usually succeeded by a prolonged positive wave. Of these the spike has been attributed to afferent fibres and the succeeding components to internuncial neurones. It is because of this that the latter group of potential changes are denoted by them as intermediary potentials. The same method of observation was adopted later by Hughes & Gasser [1934*a*, *b*] and Hughes, McCouch & Stewart [1937]. A second method of studying the electrical activities in the spinal cord is to observe the electrotonus they produce in the roots. This method was used by Umrath [1934], Umrath & Umrath [1934], Barron & Matthews [1936*a*, *b*; 1938*a*] and Eccles & Pritchard [1937]. The electrical changes recorded with two electrodes on the root consist of a prolonged negativity of the electrode near the cord. The characteristics of this slow negativity correspond in most respects to those of the positive wave in the records obtained by Gasser & Graham from the dorsum of the spinal cord. Barron & Matthews, however, express the opinion that this slow negativity arises at the terminations of the dorsal root fibres themselves, and not in the internuncial neurones.

The origin of these slow potential changes inside the cord is a problem of importance, for such changes are the only direct signs of physiological processes taking place inside the cord. Unless we know definitely where

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these potential changes originate and which of the many physiological processes inside the cord they represent, we cannot hope to make use of them successfully as a means of studying the spinal cord activities.

The present experiments were undertaken to determine the origin of the potential changes recorded in the dorsal roots by observation of the latency of the dorsal root potentials, and the manner of their conduction in the spinal cord.

Method

In all experiments *Rana esculenta* were used. The spinal cord was exposed from the dorsal aspect under ether anaesthesia, decerebration was effected by pithing the brain or by section of the brain stem. Care was taken to maintain the circulation of the cord in good condition. The roots prepared for recording the potentials were severed immediately central to the spinal ganglion. The sciatic nerve with the 10th dorsal root and the brachial nerve with the 3rd dorsal root were sometimes dissected free for stimulation and recording. Subcutaneous injections of curare just sufficient to stop limb movements were given. Except at the moment when the records were being taken, oxygenated Ringer was kept continuously dropping on the surface of the cord throughout the experiment.

For the investigation of conduction of the dorsal root potentials in the spinal cord, various spinal cord lesions were produced. The operations were usually made with a razor blade or a pair of sharp scissors at the region of the posterior enlargement between the 9th and the 10th dorsal roots. The preparation was then given at least 3 hours to recover before the commencement of the test. A stretch of cord of about 7 or 8 mm. long containing the lesion was removed after the observations, and a drop of Indian ink was dropped on the surface of the lesion. Then it was prepared with osmic acid and cut into serial sections. The extent of the lesion was examined under the microscope.

The potentials were ordinarily recorded with a balanced input three-stage condenser coupled amplifier and a Matthews' oscillograph. The records obtained were, however, frequently checked with a direct coupled amplifier. For electrical stimulation a coreless coil was used. Silver silver-chloride Ringer electrodes were used with worsted leads to the nerve for recording. Silver silver-chloride electrodes were put directly in contact with the nerve for stimulation.

The speed of the recording camera was 184 mm. per sec. With a microscope it was possible to measure records accurately to 0·05 mm. Time intervals were thus measured to about 0·3 msec.

PART I

The latency of the dorsal root potentials

If a volley of sensory impulses is sent into the cord through the 3rd or 10th dorsal root, the electrical changes inside the cord can be detected in practically all other roots on the ipselateral side as well as in the stimulated root itself. On the contralateral side potential changes have been recorded in all the thicker lumbar dorsal roots. The amplitude is much smaller than that in the corresponding ipselateral roots. There are also potential changes in the thinner thoracic dorsal roots on the contralateral side, but they have not been investigated. A sharp beginning of the potential changes is necessary for an accurate measurement of latency, and observation was confined to the potential changes in the ipselateral roots.

The amplitude of the dorsal root potential is apparently determined by at least three different factors: (1) the size of the root in which it is recorded, (2) that of the root stimulated, and (3) the distance between these two roots. Generally speaking the amplitude of the dorsal root potential increases with the size of the roots but decreases with the distance between them. There may be another factor in the structural relationship between two roots, but this has not been investigated thoroughly.

The latency of dorsal root potentials in roots cephalad to the root stimulated

Fig. 1 shows the potential changes recorded from three different dorsal roots on the right side of the spinal cord when the ipselateral 10th dorsal root was stimulated. A shows the potential changes in the 9th dorsal root, which is nearest to the root stimulated. B shows the potential changes in the 6th dorsal root. C shows the potential changes in the 4th dorsal root, which is the most distant root in the three. One sees that the 4th dorsal root potential has the longest latency and the 9th dorsal root potential the shortest. The magnitude of the 4th dorsal root potential was smaller than that of the 6th, this was again smaller than that of the 9th. In order to compare the latency the smaller dorsal root potentials were, however, subjected to larger amplifications. So that their recorded size is approximately the same.

Besides the increase of latency it is also of interest to see that the shape of the dorsal root potentials changes gradually as the root in which it is recorded is situated farther and farther away from the root

stimulated. The 4th dorsal root potential reaches its maximum more slowly than the 9th one.

Table 1 shows the latency of dorsal root potentials in roots on one side of the spinal cord when the ipselateral 10th dorsal root was stimulated.

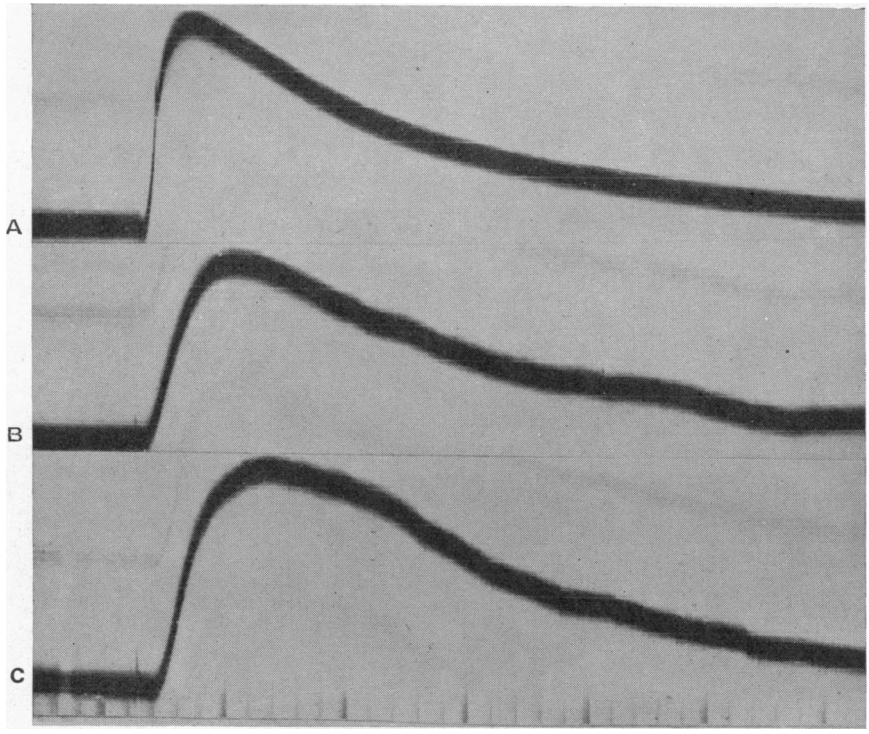

Fig. 1. Showing the increase of latency with the distance between the root stimulated and the root in which it is recorded. A sensory volley of impulses was sent into the cord through the 10th dorsal root. A, the potential changes in the 9th dorsal root, which is 2·2 mm. from the 10th root. B, the potential changes in the 6th dorsal root, which is 8·7 mm. from the 10th dorsal root. C, the potential changes in the 4th dorsal root, which is 13·5 mm. from the 10th dorsal root. Recording electrodes 1 and 7 mm., stimulating electrodes 4 and 4·5 cm., from the cord. 15·0° C. (Time, 0·1 and 0·02 sec.) Direct coupled amplifier.

It contains the results obtained from eight different preparations. For each preparation the distance between the 10th root and the root in which the potential was recorded is given under column D. Under column L are the latencies of different dorsal root potentials. The value of each latency is an average of at least five readings, although they are

TABLE 1*

Root no.	Frog no. 60 L 16·8° C. D mm.	L msec.	Frog no. 60 R 16·8° C. D mm.	L msec.	Frog no. 61 L 15·7° C. D mm.	L msec.	Frog no. 61 R 15·7° C. D mm.	L msec.	Frog no. 62 L 15·8° C. D mm.	L msec.	Frog no. 62 R 16·0° C. D mm.	L msec.	Frog no. 63 L 16·8° C. D mm.	L msec.	Frog no. 63 R 16·8° C. D mm.	L msec.
4	—	—	—	—	—	—	—	—	—	—	—	—	13·1	13·8	13·5	—
5	9·2	12·3	9·5	13·8	9·5	12·7	9·7	14·0	8·4	15·7	8·4	11·1	11·1	13·4	11·2	13·5
6	8·1	11·0	8·2	—	8·2	12·5	8·7	12·9	7·2	13·0	7·2	11·0	9·9	11·5	9·5	11·6
7	6·6	9·7	6·4	11·2	6·5	12·4	7·0	10·1	5·6	9·4	5·6	9·7	8·1	9·8	8·2	9·4
8	4·0	8·6	—	—	3·7	10·2	3·8	8·6	3·4	8·6	3·4	7·4	4·9	8·6	4·2	8·6
9	1·8	7·3	2·1	7·6	1·9	8·9	1·3	7·2	1·8	6·9	1·4	6·3	2·5	7·0	2·0	6·4

TABLE 2*

Root no.	Frog no. 71 15·8° C. D mm.	L msec.	Frog no. 72 13·0° C. D mm.	L msec.	Frog no. 73 15·5° C. D mm.	L msec.	Frog no. 75 15·0° C. D mm.	L msec.	Frog no. 92 20·0° C. D mm.	L msec.	Frog no. 93 18·0° C. D mm.	L msec.	Frog no. 94 16·0° C. D mm.	L msec.	Frog no. 95 16·5° C. D mm.	L msec.
4	1·5	7·8	1·2	6·5	1·2	7·2	1·6	5·4	1·8	6·9	1·5	5·6	1·7	6·0	1·4	5·2
5	—	—	4·0	8·0	3·6	8·5	4·2	6·6	4·2	8·0	—	—	3·6	7·1	3·7	6·3
6	5·0	10·7	5·6	9·8	4·6	9·6	5·8	7·7	5·0	8·5	5·0	7·5	4·4	8·2	4·9	6·9
7	6·0	11·4	7·1	11·3	6·4	11·5	7·3	9·8	6·7	9·7	6·5	8·8	6·0	10·0	6·6	8·2
8	9·8	13·3	11·0	12·3	9·6	13·2	10·5	10·9	10·0	11·3	9·5	10·1	8·1	—	9·4	9·4
9	12·0	14·3	13·0	14·3	12·0	14·2	12·4	12·6	12·5	12·0	12·0	11·3	9·5	11·3	11·2	10·7
10	14·0	15·3	—	—	14·5	15·3	15·0	13·0	14·5	12·8	14·0	—	11·2	12·5	12·5	11·9

* The latencies given in Tables 1 and 2 include the time for the conduction of impulses in the afferent nerve fibres. This is, however, a constant for each preparation.

remarkably constant for each dorsal root potential. From this table we see that the latency of the dorsal root potentials increases with the distance between the root in which it is recorded and the root stimulated.

The latency of dorsal root potentials in roots caudal to the root stimulated

The slow dorsal root potential can be recorded in roots caudal to the root stimulated as well as in those cephalad to it. Thus when the 3rd dorsal root is stimulated, the slow potential changes can be detected in the 10th ipselateral dorsal root. Table 2 shows the results obtained from another eight preparations. A sensory volley of impulses was sent into the cord through the 3rd dorsal root by stimulating the brachial nerve. The arrangement of this table is the same as that of Table 1. Here again the larger the distance between the recording root and the root stimulated, the longer the latency of the dorsal root potential.

The latency of the dorsal root potential in the root stimulated

In a previous short note [1939] the author has published a figure of the potential changes in a dorsal root when the same root was stimulated. In that figure the second phase of the diphasic spike, which indicates the

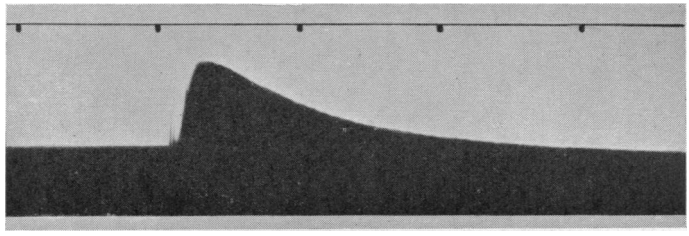

Fig. 2. The potential changes in a 10th dorsal root, when the root itself was stimulated. Recording electrodes 1 and 12 mm., stimulating electrodes 4 and 4·8 cm., from the cord. 16·0° C. (Time, 0·1 sec.)

arrival of the impulses at the electrode near to the cord, overlaps with the beginning of the dorsal root potential. So it was impossible to measure the latency of the potential changes in the root stimulated. At the end of the above experiments more attempts were made to record the dorsal root potentials in the root stimulated, and records were obtained in which the diphasic spike does not overlap with the beginning of the dorsal root potential (Fig. 2). The latency of the dorsal root potential in such records is about 4·4 msec. at room temperature

(15·5–17·8° C.). This agrees with the latencies of unitary dorsal root potentials in the frog which have been measured by Fessard & Matthews [1939].

The direction of conduction and the latency of the dorsal root potential

In a fourth group of frogs the 3rd and the 10th dorsal roots on one and the same side of the spinal cord were used alternatively as root for examination and stimulation. The leading electrodes were kept in each case approximately 1 and 10 mm. from the cord, and the stimulating

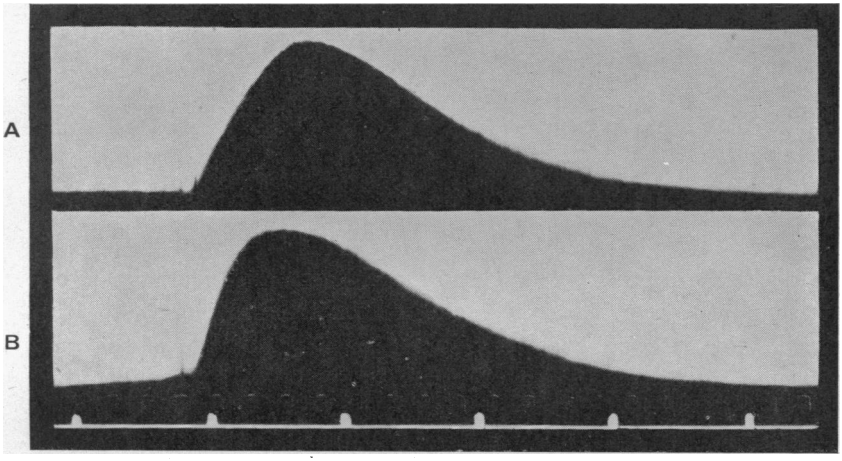

Fig. 3. A, 3rd dorsal root potential when the 10th dorsal root was stimulated. B, 10th dorsal root potential when the 3rd dorsal root was stimulated. Recording electrodes 1 and 10 mm., stimulating electrodes 10 and 15 mm., from the cord. 16·8° C. (Time, 0·1 sec.)

electrodes 10 and 15 mm. from it. Thus the distance between the stimulating and recording electrodes was the same in both cases. The latency of the dorsal root potential is the same for conduction in either direction.

Fig. 3 A shows the potential changes in the 3rd dorsal root when the 10th dorsal root was stimulated. Fig. 3 B shows the 10th dorsal root potential of the same preparation when the 3rd dorsal root was stimulated. Besides the equality of the latency of these two potentials, it is interesting to notice the difference in their shape. The rising phase of the 3rd dorsal root potential is definitely slower than that of the 10th root. This difference is typical for all the records obtained in this section of experi-

ments. A small spike is often seen at the beginning of the slow dorsal root potential in the 3rd dorsal root. This spike never occurs in the 10th one.

The intensity of stimulation and the latency of the dorsal root potential

In the course of experiments reported in the first two sections above, it has also been found that the variation of the intensity of stimulus from threshold to just supramaximal caused in none of the dorsal roots any unmistakable change of the latency of their potential. A stronger stimulation gives rise only to a negativity of larger amplitude. Thus there does not appear to be any evidence of a synaptic delay varying with the size of the afferent volley preceding the start of the dorsal root potential, such as was found by Eccles & Sherrington [1931] to occur in the flexor reflex, and it accords with the hypothesis that the potentials originate presynaptically.

The latency of the dorsal root potential to the second of two centripetal volleys

Eccles & Sherrington have also found that if two centripetal volleys are sent into the spinal cord in the cat one following another within a certain time interval, the latent period of the discharge of the motor-neurones to the second volley is smaller than to the first. The largest decrease of latency occurs when the second volley is applied approximately 10 msec. after the first. Experiments to see whether this applied to the dorsal root potentials were made and it was found that the latency of the dorsal root potential to the second of two centripetal volleys is always the same as to the first centripetal volley, no matter what is the interval between these two stimuli (Fig. 4).

Strychninization, asphyxia and the latency of the dorsal root potential

If the spinal cord is subjected to an oxygen-lack environment by substituting nitrogen for air, the dorsal root potential diminishes gradually. Re-admission of oxygen at the moment when the dorsal root potential entirely vanishes can bring it back again to its normal size. Through all these stages, however, there is no unmistakable change in the time relationship of the different phases of the dorsal root potential. Nor is there any change in the latency.

By dropping 1/10,000 strychnine solution on the surface of the spinal cord, the animal can be brought into a convulsant condition in about

30 min. Although the excitability of the spinal cord becomes under these conditions enormously enhanced and the dorsal root potential prolonged. There is no shortening of its latency.

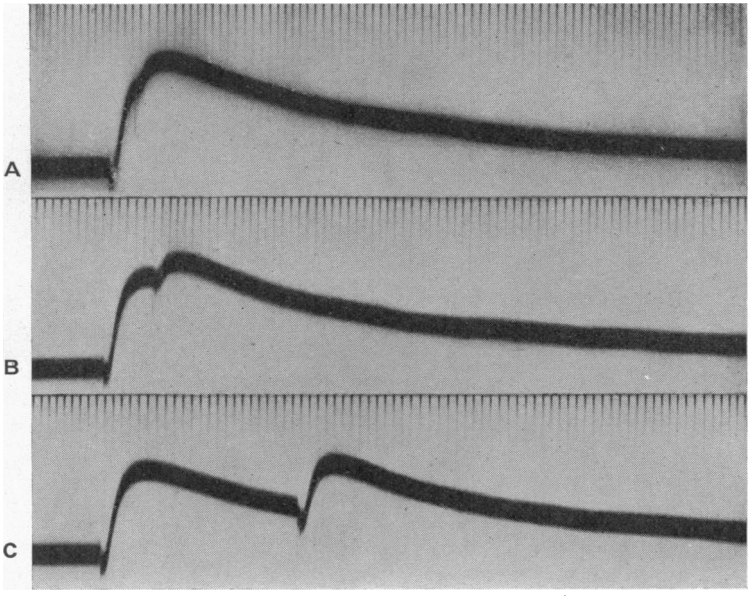

Fig. 4. Potential changes in the 8th dorsal root when two sensory volleys of impulses were sent into the cord through the 10th dorsal root with various intervals between them. Recording electrodes 1 and 10 mm., stimulating electrodes 4 and 5 cm., from the cord. 15·0° C. (Time, 0·01 sec.) Direct coupled amplifier.

Discussion

The latency of the dorsal root potential includes the time for conduction of impulses in nerve fibres before and after their entrance into the cord and the time for the development of the slow negativity either pre- or post-synaptically. The increase of this latency when the roots in which the potential is recorded are situated farther away from the root stimulated, may be due either entirely to the increased distance for conduction or to additional synaptic delays as well. Fessard & Matthews [1939] have by recording the unitary dorsal root potentials found that the latency is about 5 msec. This agrees with the present measurement of the latency of the potential changes in a whole dorsal root when the root itself was stimulated. In Tables 1 and 2 the latency of the dorsal root potentials in the root immediately next to the root stimulated is

about 7 msec. This figure includes also the time for the conduction of the nerve impulses in the peripheral part of the nerve, which is approximately 1·5–2 msec.

Fessard & Matthews are of the opinion that the slow dorsal root potential originates pre-synaptically. However, if the dorsal root potential arises in the internuncial neurones, then this latency of *ca.* 5 msec. would be regarded as the synaptic delay. If it arises pre-synaptically we suppose that excitation of the secondary neurones takes place during the rising phase of the dorsal root potential (Dun, 1939; Barron & Matthews, 1938*c*).

The results in Tables 1 and 2 show that the latency of the dorsal root potential in a root most distant from the root stimulated is only about 5–7 msec. longer than that in the root nearest to it. This suggests strongly that the increase of the latency of the dorsal root potential with the distance between the root examined and the root stimulated is due entirely to the increased time for conduction and not to synaptic delays, because the increase of latency in the adjacent roots is too small to be regarded as due to an additional synaptic delay. If we postulate no additional synaptic delay in the latency of the dorsal root potentials given in Tables 1 and 2 we can calculate the rate of conduction in the spinal cord. It amounts approximately to 1–2 m./sec. and is reasonably uniform for the roots examined (see Tables 3 and 4).

TABLE 3

	Frog no.								
Root no.	60 L m./sec.	60 R m./sec.	61 L m./sec.	61 R m./sec.	62 L m./sec.	62 R m./sec.	63 L m./sec.	63 R m./sec.	Average m./sec.
4	—	—	—	—	—	—	1·6	—	?
5	1·5	1·2	2·0	1·2	0·8	1·4	1·4	1·3	1·4
6	1·7	—	1·8	1·3	0·9	1·2	1·6	1·5	1·4
7	2·0	1·2	1·3	1·9	1·5	1·2	2·0	2·1	1·7
8	1·7	—	1·4	1·7	1·0	1·7	1·5	1·0	1·4

TABLE 4

	Frog no.								
Root no.	71 m./sec.	72 m./sec.	73 m./sec.	75 m./sec.	92 m./sec.	93 m./sec.	94 m./sec.	95 m./sec.	Average m./sec.
5	—	1·8	1·8	2·2	2·2	—	1·7	2·1	1·9
6	1·2	1·3	1·4	1·8	2·0	1·8	1·2	2·1	1·6
7	1·3	1·2	1·2	1·3	1·7	1·6	1·1	1·7	1·4
8	1·5	1·7	1·4	1·6	1·9	1·8	—	1·9	1·7
9	1·6	1·5	1·5	1·5	2·1	1·8	1·5	1·8	1·7
10	1·7	—	1·6	1·8	2·2	—	1·5	1·7	1·7

Eccles & Sherrington found in the cat that if two stimuli are applied within a certain time interval, the reflex response evoked by the second centripetal volley has a smaller latent period than that by the first.

They have found also that the latent period of the flexor reflex decreases if the strength of a submaximal stimulus becomes stronger. They explained these results as being entirely due to a shortening of the synaptic delay. If the slow dorsal root potential were to arise in the internuncial neurones, then we should expect under similar conditions a shortening of the latent period of the dorsal root potentials. The results of the present experiments show that the latency of the dorsal root potential cannot be reduced either by increasing the stimulus strength or by a previous sensory volley applied at any time interval. They favoured the view that the dorsal root potentials arise at the terminations of the primary dorsal root fibres themselves and not at the internuncial neurones.

The dorsal root potential at a distant root may result from the arrival of impulses which are conducted slowly in the cord. A slow conduction in the grey matter, however, might occur, but this is dismissed on the evidence given below.

According to the theory of Barron & Matthews [1938*a*], the active depolarization of one nerve termination may cause the passive depolarization of another termination. The spread of the dorsal root potential inside the cord might, therefore, be carried out by the process of induction from termination to termination. In this case there might be a slowly conducted process travelling in the grey matter of the spinal cord comparable to that seen in the grey matter of the cortex [Adrian, 1936]. The results of the present experiments show that the rate of conduction of the dorsal root potentials in the spinal cord is about 1–2 m./sec. It is known that the intracordal parts of the primary dorsal root fibres have many collaterals and become thinner and thinner as they go farther up or down the spinal cord, and thus the conduction rate of the sensory impulses in them might be reduced to 1–2 m./sec. By alternative stimulation and examination of the 3rd and the 10th dorsal roots we have seen that the rate of conduction in both directions is the same; suggesting that no synaptic conduction is involved. The difference in the shape of these two potentials is however considerable. This may be due to different local conditions prevailing in the neighbourhood of the entrance of the two different roots, but it is equally possible that the two dorsal root potentials are the result of sensory impulses which are conducted in the spinal cord in different groups of primary dorsal root fibres. In the latter case the difference in the shape of the potentials would result from differences in the degree of dispersion of the sensory impulses.

Part II

The conduction of the dorsal root potentials

If the dorsal root potentials were conducted by some process of induction from termination to termination, then the grey matter would be the conducting part of the spinal cord. If, on the other hand, the production of the dorsal root potentials in the distant roots depended mainly on conduction of sensory impulses in the primary dorsal root fibres, then the dorsal column would be the conducting tissue. In the following series of experiments the effect of various spinal cord lesions on the production of the dorsal root potentials in the distant roots has been investigated, and it has been found that the dorsal column is the main structure in the spinal cord responsible for the conduction of those processes which produce the dorsal root potentials.

Dorsal and ventral hemisection

If a dorsal hemisection is produced at the level between the 9th and the 10th segments, all the dorsal root potentials in the roots beyond the lesion are eliminated. The stimulation of the 10th dorsal root causes only a negativity in the root itself. A stimulation of the 9th dorsal root or any dorsal root cephalad to it gives rise to potential changes in all the roots except the 10th one. If a dorsal hemisection of the spinal cord is produced just below the 3rd dorsal root, the stimulation of it is followed by no potential changes in any of the lower caudal dorsal roots. The hemisection of the dorsal half of the spinal cord blocks the spread of the dorsal root potentials in both directions. A ventral hemisection, on the other hand, at the corresponding levels of the spinal cord has no detectable influence on the production of the potential changes in roots beyond this lesion, even when it extends far above the level of the central canal occupying nearly four-fifths of the cross-section of the whole spinal cord (Fig. 5).

The relation between the dorsal and ventral root potentials

After seeing that the dorsal hemisection alone stops the production of the dorsal root potentials in the distant dorsal roots, the question arises whether the ventral hemisection has any effect on the production of ventral root potentials in the ventral roots beyond it. It has been found that the presence of the ventral root potentials depends largely on the presence of the dorsal root potentials in the same level of the spinal cord. If a dorsal hemisection is produced at the level between the 9th and the 10th segments of the spinal cord, the stimulation of the

10th dorsal root fails not only to produce the potential changes in the 9th dorsal root but in the 9th ventral root as well. If a ventral instead of a dorsal hemisection is produced at the same level, the 9th ventral root potential can be recorded without any apparent diminution in amplitude, when the 10th dorsal root is stimulated.

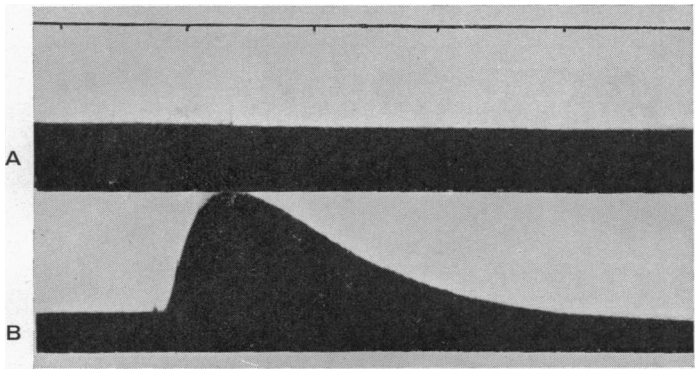

Fig. 5. A, frog C 12. After *dorsal* hemisection at the level between the 9th and 10th segments, no potential changes can be detected in the 8th dorsal root when the ipselateral 10th dorsal root is stimulated. B, frog C 14. After *ventral* hemisection at the same level the 8th dorsal root shows potential changes as before when the 10th dorsal root is stimulated. Recording electrodes 0·8 and 15 mm., stimulating electrodes 4 and 5 cm., from the cord. 15·0° C. (Time, 0·08 sec.)

Lateral and bilateral hemisection

In a number of preparations hemisection was produced on one side of the spinal cord at the level between the 9th and the 10th segments. The lesion extended in each case just beyond the middle line of the spinal cord. The stimulation of the 10th dorsal root on the side of the lesion caused in the ipselateral 8th and 9th dorsal roots no potential changes whatever. On the contralateral side potential changes can be recorded in the 10th, 9th and 8th dorsal roots as in the normal preparation, but no potential changes can be detected in root more distant than that. The ipselateral 8th and 9th dorsal roots gave potentials when the contralateral 10th dorsal root was stimulated. The amplitude of these potential changes was only slightly reduced in comparison with that recorded just before the operation.

The effect of two hemisections one on each side of the spinal cord 2 mm. apart is similar to that of a dorsal hemisection. The stimulation of one root on one side of the bilateral hemisections can cause no potential changes in roots on the other side of the lesions.

The dorsal column and the potential changes in the distant roots

After it seemed fairly clear that it is the sensory impulses conducted in the dorsal column which give rise to the potential changes in the distant roots, attempts were made to isolate the dorsal column at the level between the 9th and the 10th segments. This was done by first making a ventral hemisection and then destroying the remaining grey matter with a needle. This method proved to be quite easy and efficient, if carried out under a microscope. Several preparations which showed large 8th dorsal root potentials when the 10th dorsal root was stimulated, proved later to have nothing but the dorsal column intact at the level of the lesion.

Discussion

Our results suggest that the dorsal root potential at any level is evoked by impulses that travel slowly in the spinal cord. The potential changes on the contralateral side might be evoked by impulses travelling in collaterals of the primary dorsal root fibres which cross over to the other side of the spinal cord through the dorsal commissure [Gaupp, 1899]. Slow conduction of activity from neurone to neurone observed by Adrian [1936] in the cortex of mammals does not seem to be responsible for the slow conduction we observed in the frog spinal cord because it occurs when only the dorsal columns are intact. Many fibres of the dorsal columns of the frog, e.g. those going to the medulla, conduct rapidly (18–25 m./sec., Matthews' personal communication). These fibres cannot be responsible for the conduction of the impulses which evoke the dorsal root potentials. There are many very fine fibres in the dorsal column of the frog, and it appears likely that these carry the impulses that evoke the dorsal root potentials in distant parts of the cord. Measurements of latency of dorsal root potentials evoked by stimulation of the sciatic nerve and those by stimulation of a root show, however, that the peripheral parts of the fibres responsible for evoking the dorsal root potential conduct rapidly and belong to the A group of Gasser and Erlanger.

Eccles & Sherrington [1931] defined the 'synaptic delay' as 'the time necessary to build up C.E.S. to threshold value' or 'the interval between the incidence of the first impulse on a motor neurone and the setting up of a reflex discharge'. The length of the synaptic delay is determined by the dispersion of the impulses arriving at the motor neurone and by the C.E.S. already present there. It varies with the stimulus strength as well as the interval between the conditioning and the testing sensory volleys. These variations have not been found in the latency of the dorsal root potentials.

If we suppose that the beginning of the slow potential change indicates the beginning of C.E.S. and arises pre-synaptically, the above-mentioned difficulties do not arise. And the reflex latencies (*ca.* 20 msec.) observed by Bremer & Kleyntjens [1937] and Kleyntjens [1937] agree with the hypothesis that reflex excitation of secondary neurones occurs during the rising phase of the dorsal root potential, as in the case of re-excitation of dorsal root fibres when the spinal cord has been cooled [Barron & Matthews, 1938*b*; Dun, 1939].

The potential changes observed indicate physico-chemical changes occurring in the cord. The hypothesis that excitation occurs on the rising phase of the dorsal root potential is not incompatible with transmission being mediated by some specific ion such as that of acetylcholine. Presumably, however, both the electrical change and constitution of the ion are significant and, as the two are inseparable, discussion of which is responsible for excitation is perhaps not at present of great profit.

Summary

1. When a volley of sensory impulses is sent into the spinal cord, potential changes can be detected in practically every dorsal root on the ipselateral side and also in some roots on the contralateral side.

2. The latency of the dorsal root potential in the root stimulated is *ca.* 4·4 msec.

3. The latency of the other dorsal root potentials increases with the distance between the root in which it is recorded and the root stimulated.

4. This increase of latency is thought to be due to increased distance of conduction and not to synaptic delays.

5. Variation in the intensity of stimulation does not change the latency of the dorsal root potential. Nor is it influenced by a previous sensory volley, no matter what is the interval between these two stimuli.

6. Asphyxia diminishes the dorsal root potential but does not lengthen its latency. Strychninization increases the dorsal root potential but does not shorten its latency.

7. If the 3rd and the 10th dorsal roots on the same side are used alternatively as recording and stimulating roots, the latency of these two potentials is the same, but the difference in their shape is considerable.

8. The production of the dorsal root potentials in the roots other than that stimulated depends on the intactness of the dorsal column, which conducts the sensory impulses to them. The dorsal root potentials on the contralateral side are thought to be evoked by impulses travelling in the collaterals which form the dorsal commissure.

9. The rate of conduction of impulses responsible for the production of the dorsal root potentials is of the order 1–2 m./sec. in the cordal part of the fibres.

10. The view that the dorsal root potentials arise presynaptically is strengthened by the above results.

11. The beginning of the slow dorsal root potential is supposed to indicate the beginning of C.E.S. and the excitation of secondary neurones is supposed to occur during the rising phase of the dorsal root potential. This hypothesis is shown to be in agreement with the measurements of the reflex latencies by Bremer & Kleyntjens and Kleyntjens.

12. The above hypothesis is not incompatible with transmission being mediated by some specific ion, e.g. that of acetylcholine.

I wish to thank Dr B. H. C. Matthews for his advice and help. I also wish to acknowledge gratefully the facilities afforded by Prof. E. D. Adrian in allowing me to work in his laboratory.

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