J. Physiol. (1955) 127, 252–264

THE DELAY AND BLOCKAGE OF SENSORY IMPULSES IN THE DORSAL ROOT GANGLION*

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(*Received* 28 *June* 1954)

Early in 1876 Wundt reported a delay of sensory impulses in their passage through the dorsal root ganglion, but this was denied by Exner in 1877. In 1889, Gad & Joseph reported the delay again, but it was denied by Moore & Reynolds (1898). After the appearance of cathode-ray oscilloscope, that enabled Erlanger, Bishop & Gasser (1926) to measure exactly very small time intervals, the delay of sensory impulses in their passage through the ganglion was again described. But in 1938 the existence of this phenomenon was denied, this time by one of its original observers (Erlanger & Blair, 1938).

The aim of the present series of experiments is to try to clarify these controversial issues and to determine whether the dorsal root ganglion modified in any way the passage of sensory impulses. Besides suffering a delay under normal conditions, the sensory impulses are found to be blocked in their passage through the dorsal root ganglion during the early relatively refractory period of the afferent fibres.

METHOD

In most of the experiments the 9th or 10th dorsal root ganglion of the frog (*Hyla aurea, Rana catesbiana* and *R. pipiens*) was used. These ganglia were dissected intact and in continuity with the roots and the trunk. The roots were severed adjacent to the spinal cord. The trunk was either cut prior to its entry into the sciatic plexus, or followed into one or several of the branches of the plexus, e.g. (1) posterior femoral cutaneous nerve, (2) lateral crural cutaneous nerve, (3) tibial nerve, and (4) peroneal nerve (see Ecker, 1881). The fibres of the posterior femoral cutaneous nerve have been found to go mainly to the 10th dorsal root, while those of the lateral crural cutaneous nerve go mainly to the 9th. The preparations were always scrupulously cleaned to remove connective tissue and blood clots. Every effort was made to avoid injury of the preparation.

In some experiments requiring a small number of nerve fibres the 11th dorsal root ganglion was used. This ganglion is very small, lying on the lateral surface of the columella. As a considerable segment of its nerve trunk is buried in the coccygeal muscle and as its roots are thin and penetrate

* Part of the work was carried out in the Department of Physiology, University of Otago Medical School, Dunedin, New Zealand, and has been reported as short communications (*J. cell. comp. Physiol.* **38**, 131–135, 1951).

into the columella to reach the spinal cord, the dissection is much more difficult. It was after long practice that intact preparations were obtained.

The preparations were soaked, as a rule, in Boyle & Conway's (1941) fluid saturated with 97% O_2 and 3% CO_2, before observations were begun and during the intervals between observations. Platinum electrodes fixed on a mobile carrier were used for mounting the preparation, thus enabling the preparation to be lifted from the fluid into paraffin oil for observation without any change of the position of the electrodes. The detecting electrode was controlled by a micromanipulator and could be easily and accurately set or re-set at any point along the preparation. The potential changes were recorded with push-pull direct-coupled amplifiers and cathode-ray oscilloscope.

RESULTS

The delay of sensory impulses in the dorsal root ganglion

The delay of sensory impulses passing through the dorsal root ganglion was deduced by Erlanger *et al.* (1926) from indirect calculations. Assuming that the fastest sensory impulses travel at the same rate as motor impulses, they compared the arrival times of the two kinds of impulses from the same point on the nerve trunk to recording electrodes on the two roots set at equal distances from the dorsal root ganglion. The delay of sensory impulses in the ganglion was obtained by subtracting the conduction time of the motor impulses from that of the sensory ones.

Their assumption was later disputed by Erlanger & Blair (1938), who measured the rate of conduction of sensory impulses directly by recording and plotting their times of arrival at many points along the preparation.

In the present experiments the latter method was used. Thus in Fig. 1A there are five records of a single volley of sensory impulses initiated by stimulating a 9th dorsal root. *R*, *G* and *N* indicate whether the detecting electrode was on the root, ganglion or nerve trunk. The numbers give the distances (in mm) between the electrode and the centre of the ganglion. For example, *R*3·81 means that the detecting electrode was on the root 3·81 mm from the centre of the ganglion. The distance between the successive recording points was made constant (2·54 mm), enabling the records to be placed evenly in a vertical column and giving a semi-graphical representation with the time base as abscissa and the conduction distance as ordinate. The inclination of the two dotted lines indicates the velocity of the volley of impulses along the nerve trunk and the dorsal root respectively. The gap between the two dotted lines on curve *N*1·27 shows the delay of the fastest impulse in the volley in passing through the ganglion (0·09 msec).

Erlanger & Blair (1938) were unable to demonstrate the delay in many preparations, and did not think the delay a sufficiently constant phenomenon to be of physiological significance. However, as they reported, some of the ganglia they used were injured, and others had been kept overnight in a refrigerator.

The delay of sensory impulses in the ganglion was always evident, provided

the preparations were dissected with great care and only those used that were not injured in any way. Moreover, the delay no longer appeared following deliberate traumatization of the ganglion. The storage of the preparation in a refrigerator has in itself no detrimental effect, if optimum temperature

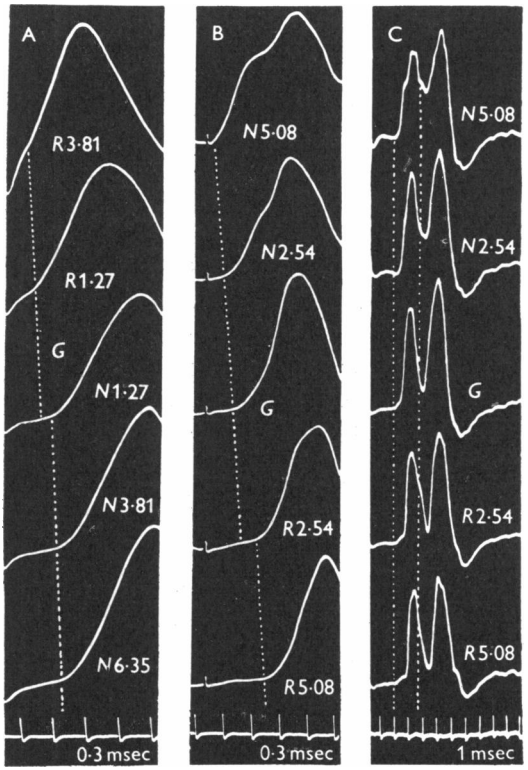

Fig. 1. Delay of sensory impulses in dorsal root ganglion. Numbers indicate distance (mm) of recording electrode from ganglion centre, and letters whether the electrode was on root (*R*), nerve trunk (*N*) or ganglion (*G*). Note equal steps between recording positions (2·54 mm). A, dorsal root stimulated; B, lateral crural cutaneous nerve stimulated; C, same as B, slower sweep. *Hyla aurea*.

(about 5° C) was used. But the composition of the fluid bathing the preparation was of great importance. While a preparation could be kept in good condition even for days in Boyle & Conway's (1941) solution, it degenerated overnight in common Ringer's fluid. The delay of the sensory impulses often became very small or undetectable.

From the velocity of the impulses, the delay in Fig. 1A can be easily identified as that occurring in alpha fibres (Gasser & Erlanger, 1927). To investigate the delay in beta and gamma fibres, the lateral cutaneous nerve

or posterior femoral cutaneous nerve was stimulated. As can be seen in Fig. 1 B, the beta impulses were also delayed (0·16 msec) in passing through the ganglion. Fig. 1 C is the same as Fig. 1 B, but a much slower sweep was used to show both the beta and gamma impulses. The two vertical dotted lines indicate the portion that is shown in Fig. 1 B.

To measure the delay in gamma fibres, the beta fibres were made either non-conductive by applying pressure at a point midway between the stimulating and recording electrodes or refractory by applying first a conditioning shock. The average delays of the three groups of impulses, as calculated each from ten selected records (*Rana pipiens* and *Hyla aurea*), are 0·093 msec for alpha impulses (varying from 0·07 to 0·11 msec), 0·15 msec for beta impulses (varying from 0·12 to 0·17 msec), and 0·23 msec for gamma impulses (varying from 0·16 to 0·25 msec).

Since the delay occurred regularly in undamaged preparations and showed a close correlation with types of nerve fibres, it appears to be a genuine physiological phenomenon.

The change in shape of refractory curves plotted by measuring the height of sensory volleys before and after their passage through the dorsal root ganglion

In discussing the cause of the delay, Erlanger *et al.* (1926) rejected the possibility that the impulses were making a detour up and back through the process of the ganglion cells. Further, they said: 'The only normal basis for a delay that occurs to us is some hindrance to the passage of the potential wave through the point where the centripetal (with respect to the spinal ganglion) joins the centrifugal branch, and evidence is lacking for or against such a view.' To see if any evidence could be obtained with regard to the nature of the hindrance, refractory curves of sensory and motor impulses were recorded at various points before and after their passage through the ganglion.

In Fig. 2, the refractory curves A, B and C were obtained when the dorsal root was stimulated. A was recorded at a point on the dorsal root just proximal to the ganglion, and B on the nerve trunk at a point just distal to it. C was recorded at a point further distal to B. The refractory curves D, E and F were obtained when the ventral root was stimulated. D was recorded at a point proximal, and E, F at points distal to the ganglion. Each refractory curve is constructed by superimposing many single sweeps, with each single sweep representing a different time interval between the conditioning and testing stimuli (Dun, 1954).

In the column of refractory curves for sensory fibres, there is a sudden change in shape between curves A and B. In A the sensory fibres are shown to recover as fast as the motor fibres (cf. curves D, E and F). But in B and C, when the sensory impulses were recorded after their passage through the dorsal root ganglion, the fibres seemed to recover much more slowly. The

refractory curves of the motor nerve fibres (D, E, F) show no other change than what is expected from the increasing distance of conduction.

Similar records were obtained first by Amberson & Downing (1929) and later by von Brücke, Early & Forbes (1941). The latter authors clearly recognized the passage of sensory impulses through the dorsal root ganglion as a necessary condition for the change of refractory curve, without, however, identifying the mechanism underlying this change.

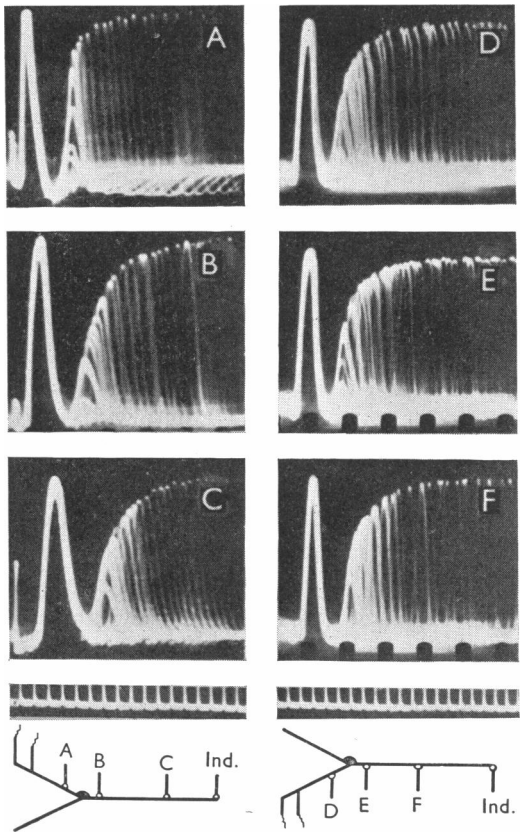

Fig. 2. Change of refractory curve of sensory impulses after passing through dorsal root ganglion. Arrangement of stimulating and recording electrodes for corresponding curves shown below each column. Note sudden change in shape between refractory curves A and B. *Hyla aurea.*

The cause of the delay of sensory impulses and the change of refractory curves

From the all-or-nothing law of the normal conducted impulse the corollary can be derived, that the energy represented by each impulse is of a limited quantity (Lucas, 1917). Part of the energy is used to excite the next segment.

When an impulse is conducted to a point such as the T-shaped branching of the sensory nerve fibres in the dorsal root ganglion, the excitatory current produced by it has to be divided between the unipolar process of the sensory cell and its other branch. Although the presence of a large safety factor (Hodgkin, 1937; Tasaki, 1939) ensures that the sensory impulses can be conducted through the dorsal root ganglion, the simultaneous initiation of impulses in the unipolar process and its other branch may require a longer time. The delay of normal sensory impulses in the dorsal root ganglion may be a natural consequence of the strength-duration relationship of the stimulating current, here the current produced by an impulse in the pre-bifurcation segment.

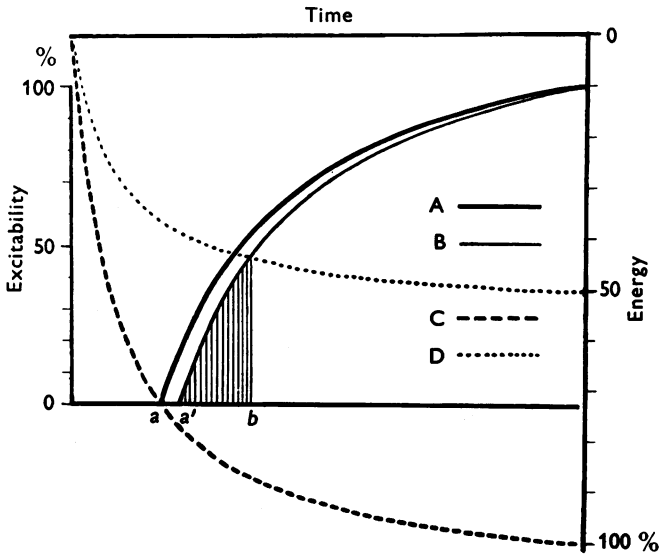

Fig. 3. Diagram showing blockage of early 'refractory' impulse at bifurcation point of a nerve fibre. Ordinates: left upright (excitability) for curves A and B, right reversed (energy) for curves C and D. Abscissae: time after arrival of conditioning impulse at bifurcation point. With conduction distance under consideration reduced to minimal and with no delay at bifurcation point, recovery of excitability in both pre- and post-bifurcation segments would be represented by curve A. As conditioning impulse is delayed at bifurcation point, the curve of excitability in post-bifurcation segment is shifted from A to B. C, total amount of energy recovered in pre-bifurcation segment. D = ½C, amount of energy available to excite each branch. *a–b*, interval of blockage. *a'–b*, interval during which the branches should be able to conduct impulse if stimulated adequately. *a* and *a'*, assumed beginning of relatively refractory period in pre- and post-bifurcation segments respectively.

Fig. 3 illustrates the situation during the refractory state of the nerve fibre. In this figure there are two sets of curves, one reversed and one upright. The abscissae of both represent one and the same time interval. At point O the pre-bifurcation segment of a nerve fibre is assumed to become absolutely

refractory after conducting an impulse. As the exact mechanism by which a nerve fibre recovers from its refractory state is still unknown, the whole process is here regarded simply as a recovery of lost energy and is represented by curve C. It is assumed to begin with the absolutely refractory period. During this period, the recovered energy enables the nerve to produce only a subthreshold or local response on strong stimulation.

With the beginning of the relatively refractory period, which is arbitrarily chosen as being at point *a*, propagated impulses first appear. It is only from now on that the nerve can be said to have a measurable threshold (Rosenblueth & Luco, 1950), the reciprocal of which (i.e. excitability) is represented by curve A. The safety factor of an impulse at any moment during the relatively refractory period is represented by the ratio between the distances as measured perpendicularly from the corresponding point on the upper time scale to curves C and A respectively.

The recovery of excitability of the post-bifurcation segment is represented by curve B. Its time course is assumed to be the same as in the pre-bifurcation segment but starting a little later, due to the delay of the conditioning impulse. From point *a'* onward this segment will be able to produce a propagated impulse, if it is stimulated adequately. However, as the stimulating current produced by an early 'refractory' impulse in the pre-bifurcation segment is small and has to be halved, no impulse can be set up in it until the time when curve D ($\frac{1}{2}$ energy) crosses curve B; only then will the available stimulating current be equal to what is required. Thus the analysis shows that there should be a small time interval during which early 'refractory' impulses could not pass through the ganglion. Moreover, it shows that the first 'refractory' impulse conducted in the post-bifurcation segment should be larger than the one first conducted to the bifurcation point, because at the time when impulses can be conducted through the ganglion the post-bifurcation segment would have entered a later stage of recovery.

Blair & Erlanger (1933) have shown that the thinner the fibre, the longer its refractory period. If the interval of blockage is also longer in thinner fibres, then the change in shape of the refractory curves can be easily explained.

In Fig. 4I there are twelve imaginary recovery curves of single nerve fibres. From bottom to top, the first four are supposed to belong to alpha fibres, and the second and last four to beta and gamma fibres respectively. The continuous curves represent the recovery of excitability of the pre-bifurcation segment, the dotted curves that of the post-bifurcation ones, and the shaded areas the interval of blockage. As slower impulses lag behind faster ones in the conditioning volley, the refractory curves of the thinner fibres are shown to begin later. The algebraic sums of these curves are shown in Fig. 4II. Curves A and C in this figure are comparable to curves A and B in Fig. 2.

In constructing Fig. 4, the increased scattering of 'refractory' impulses

within one volley has not been taken into consideration. As an impulse conducts more slowly in a relatively refractory fibre than in a normal one, and as the thicker fibres recover faster than the thinner fibres, a volley of impulses in a relatively refractory nerve is expected to become more scattered during conduction. This will retard the recovery of the refractory curves as shown in Fig. 2, where only the height of the potential waves was measured. Neglecting this factor must have necessitated the assumption of blockage intervals in the thinner fibres longer than they really are.

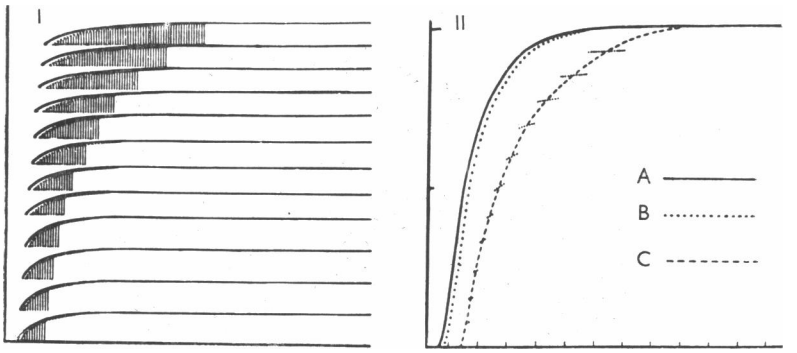

Fig. 4. Diagram showing how blockage of early 'refractory' impulse causes change in shape of refractory curve of a bundle of nerve fibres. I, assumed recovery curves of twelve sensory fibres. For each fibre two curves (continuous and dotted lines) are drawn corresponding to curves A and B in Fig. 3. Impulses in the conditioning volley assumed to be slightly scattered. Origin of abscissa represents time of arrival of the fastest impulse. II, sums of corresponding individual curves in I, showing refractory curves obtainable in a whole nerve branch under different hypothetical conditions. A, fibre branching has no effect on impulse conduction. B, impulses are only delayed at points of branching. C, early 'refractory' impulses are blocked.

The blockage of early 'refractory' sensory impulses in the dorsal root ganglion

Whether the above analysis is tenable depends on the actual demonstration of the existence of such a small time interval during which early 'refractory' sensory impulses are conducted to the ganglion but no further. Fig. 5 shows the result of one such test. To minimize the distortion caused by positive after-potential of the conditioning volley when large amplification was used, the 11th root ganglion was chosen for its smaller number of nerve fibres. A, B, C, D and E show simultaneous records of sensory impulses before (broken line with time marker indicating 0·1 msec) and after (continuous line) their passage through the dorsal root ganglion. Two stimuli were applied during each sweep, and the two amplifiers were adjusted so that the two curves recorded cover approximately equal areas. In A and B, the second stimulus fell within the absolutely refractory period of the nerve and failed to set up

any impulse. See the superimposed records in the right column. In C the interval between the two stimuli was slightly increased and two small potential waves were set up by the second stimulus and were conducted to the ganglion but not beyond it (see BC). From C to D the interval between the two stimuli was further increased, and there was an increase in the size of the 'refractory' volley conducted to the ganglion. But the blockage remained complete (CD). It was not until E that two small potential waves began to be conducted through the ganglion (DE). The total interval of blockage from C to E was 0·2 msec.

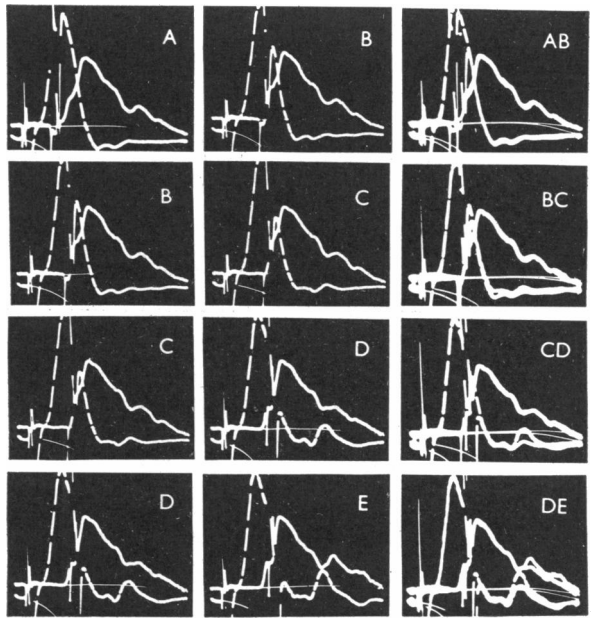

Fig. 5. Blockage of early 'refractory' impulses in a dorsal root ganglion. A–E, response to double supra-maximal shocks on dorsal root at increasing intervals, recorded proximally (trace with 0·1 msec time marks) and distally (continuous line) to the ganglion. AB–DE, superimpositions of pairs of records A–E. Blockage of impulses shown during latter half of records BC and CD. DE shows partial blockage. *Rana catesbiana.*

In this experiment the interval between the two stimuli was varied in very fine steps (about 0·01 msec). C and E represent two very critical intervals. The slightest decrease of these intervals caused the disappearance of the small potential waves at the respective leads. In one record at interval E, only the second small wave disappeared and the first showed no decrease of magnitude. If these facts are enough evidence that the two small potential waves represent two single impulses, then it is very likely that the two fibres first excited by the second stimulus were also the fibres that first conducted 'refractory'

impulses through the ganglion. Comparing the magnitude of the small waves in BC and DE, it seems that the second prediction in the above analysis has also been confirmed, because the two small waves in DE are larger than those in BC.

In carrying out these experiments care was taken to make sure that the fast conducting fibres were not injured at any point between the two points of recording. This was done by first applying a just-threshold stimulus to see if the impulses set up by it were conducted to both detecting leads.

The distance of conduction for impulses to reach the ganglion and the change of refractory curves

It is known that the impulse set up in a relatively refractory nerve fibre is subnormal in size and conducts slowly. Both its size and velocity increase during propagation, while the fibre recovers gradually (Forbes, Ray & Griffith, 1923; Gasser & Erlanger, 1925). If the delay and blockage of impulses represent one and the same mechanism, and if the blockage occurs only because the early 'refractory' impulses are too small, then the change of refractory curve must vary with the position of the stimulating electrodes. If a 'refractory' impulse is given enough time to grow before reaching the ganglion, the blockage should be replaced by delay. In other words the refractory curve C in Fig. 4II is expected then to take the shape of curve B, which is very similar to the normal refractory curve A.

In Fig. 6C are superimposed three pairs of refractory curves traced from simultaneous records made with a two-gun cathode-ray oscilloscope. The originals of the first two pairs of records are shown in Fig. 6A and B. The insert in Fig. 6C shows the arrangement of the stimulating and recording electrodes, and serves also as a key for identifying the individual refractory curves. I*a* means, for example, that the curve was obtained with the stimulating electrodes at I and the recording lead at *a*. In constructing this figure, the tracings of each of two simultaneous records were first superimposed with the time of arrival of the conditioning volley (indicated by short dotted vertical bars at the left end of the base-line) as zero point. Then the three pairs of tracings were again superimposed with the beginning of the *a*-curves as a common reference point. The differences in amplification were corrected before superimposition.

From this figure it is seen that the refractory curves recorded at *a* are not very much affected by the position of the stimulating electrodes. The slight but systematic changes of these curves can easily be explained as due to different degrees of scattering of impulses within each volley. The curves recorded at *b*, on the contrary, vary greatly with the position of the stimulating electrodes. The further away the stimulating electrodes from the ganglion, the more similar the refractory curves to those recorded at *a*. With the stimulating

electrodes at position I, the refractory curve recorded at *b* shows an apparent absolutely refractory period 0·22 msec longer than that recorded at *a*. This difference is in reality due to blockage of the early 'refractory' impulses in alpha fibres as has been demonstrated in Fig. 5. When the stimulating

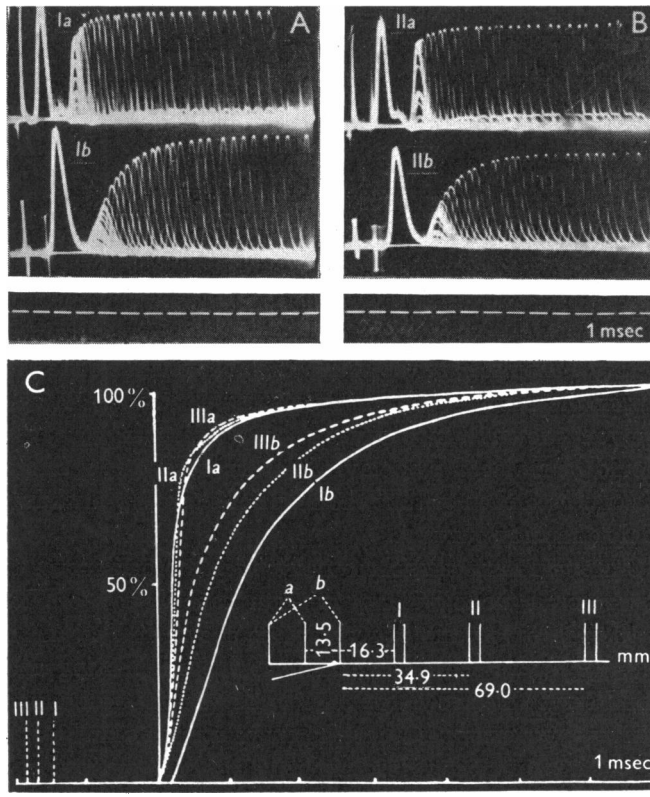

Fig. 6. Position of stimulating electrodes as an important condition for the change of refractory curves. A and B, original records of two of three pairs of refractory curves shown in C. Each pair was recorded simultaneously from pre- and post-ganglionic positions. Tracings from original records were superimposed in C after correction for differences in amplification. Individual curves are identified by respective position of stimulating (I–III) and recording (*a*–*b*) electrodes, see insert in C *Rana catesbiana*.

electrodes were moved to position II, these impulses began to pass through the ganglion, but those in thinner fibres must have still been blocked. This is evidenced by the further increase in the rate of recovery of curve III*b*. Had the distance between the ganglion and the point of stimulation been able to be increased without limit, the refractory curves recorded at *a* and *b* might have become eventually indistinguishable from one another.

DISCUSSION

The prolonged controversy over the delay of sensory impulses in the dorsal root ganglion originates apparently from two technical difficulties. (1) The amount of delay is too small to be measured with ease and confidence. (2) The presence of the phenomenon depends on a condition of the preparation that cannot be ascertained by merely observing whether it can still conduct impulses. The works of Bethe (1897) and of Steinach (1899) provided here a helpful warning. They stated that the absence of the ganglion cells did not impair the conduction of sensory impulses. The question then arises, may not their presence or physiological integrity be a necessary condition for the occurrence of the delay? By careful treatment of the ganglion and by correlating the delays with different types of fibres the above two difficulties have been overcome, and the delay has been proved a genuine phenomenon.

The change of refractory curve, or the blockage of early 'refractory' impulses in the dorsal root ganglion, disproves experimentally the hypothesis that the delay was due to a detour of impulses up and back through the central process of the ganglion cells. No impulse has ever been known to be blocked by simple increase of conduction distance. Such an assumption would be contradictory to the basic concept of nervous conduction, namely the concept of local energy. The only plausible explanation for the delay and the blockage of impulses is the simultaneous excitation of the two fibre branches. The site of the delay and blockage is naturally at the bifurcation point.

However, the presence of the cell body in the very neighbourhood of the bifurcation point may have diverted through its large surface area a considerable portion of the stimulating current generated by the impulse in the pre-bifurcation segment, and thus prolonged both the delay and the interval of blockage (Dun, to be published).

Besides describing the change of refractory curve in frog preparations, von Brücke *et al.* (1941) reported also negative results in their few experiments on cats. They did not specify the exact positions of their stimulating and recording electrodes. Had they stimulated the sciatic nerve at a point far away from the dorsal root ganglion and recorded from the roots, the discrepancy would then be expected. As has been shown in the present experiments, the passage of sensory impulses through the dorsal root ganglion is only one necessary condition for the occurrence of the change, the other being that the stimulating electrodes must be near enough to the ganglion.

SUMMARY

1. Sensory impulses are delayed in their passage through the dorsal root ganglion.

2. The delay occurs whether the impulse is conducted centrifugally or centripetally.

3. The slower the impulse, the longer the delay.

4. The refractory curve recorded with the ganglion lying between the stimulating and recording electrodes changes in shape, owing to blockage of early 'refractory' impulses in the ganglion.

5. The site of delay and blockage is at the bifurcation point of the sensory fibres in the dorsal root ganglion.

6. The cause of delay and blockage is simultaneous excitation of two fibre-branches by one single impulse in the pre-bifurcation segment.

I wish to express my gratitude to Prof. T. C. Ruch for his kindness and helpfulness which rendered my sojourn in his laboratory a very happy experience. I wish also to thank my good friends Prof. A. K. McIntyre and Dr D. M. Easton for reading my manuscript and giving valuable suggestions for improvement.

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