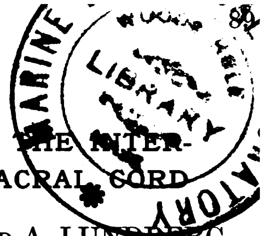
J. Physiol. (1960), **154**, *pp.* 89–114
With 12 *text-figures*
Printed in Great Britain



TYPES OF NEURONE IN AND AROUND THE INTERMEDIATE NUCLEUS OF THE LUMBOSACRAL CORD

BY J. C. ECCLES, ROSAMOND M. ECCLES AND A. LUNDBERG
From the Department of Physiology, Australian National University, Canberra, A.C.T., Australia

(*Received* 4 *May* 1960)

Certain types of neurone of the spinal cord have been specially investigated, and as a consequence there are sharply defined categories of cell: alpha and gamma motoneurones, Renshaw cells, cells of origin of the dorsal spinocerebellar tract, and of the ventral spinocerebellar tract. This paper is devoted to an attempt to define additional types of neurone, particularly types of interneurone. This definition of cell type has been based on the synaptic connexions impinging on them and on the destination and functions of their axons. These two criteria will be employed in the classification attempted here for cells located exclusively in and around the intermediate nucleus at L6, L7 and S1 segmental levels. The designation 'interneurone' will be restricted to neurones whose axons were confined within the lumbosacral cord. It is particularly important to restrict the criterion of synaptic connexions to monosynaptic connexions either from primary afferent fibres or from other identifiable fibres which can be directly stimulated. When interneurones are interpolated on the afferent pathway to the cell under investigation, criteria of specificity no longer obtain, because the serial arrangement of only one or two interneurones causes a very wide spatial and temporal dispersal of the various afferent inputs. For example, Group III afferent fibres from muscles or high-threshold afferent fibres from skin can activate many neurones of the types which are defined here by the criteria of their monosynaptic connexions.

The present classification follows on from a preliminary attempt (Eccles, Fatt, Landgren & Winsbury, 1954; Eccles, Fatt & Landgren, 1956), in which interneurones in the intermediate nucleus were distinguished according to their monosynaptic activation by Group Ia or Group Ib afferent impulses from muscle. Brief reference was also made to a third category of neurone monosynaptically activated by cutaneous afferent impulses. Since that time there has been a very comprehensive attempt at interneuronal classification by Kolmodin (1957), which was based on the receptor pathways activating interneurones. Unfortunately,

activation by adequate stimulation precludes accurate latency measurements, which are essential in defining monosynaptic connexions; hence Kolmodin's classification is complicated to an unknown degree by activation through polysynaptic channels. In addition, no attempt was made to discriminate between the different stretch receptors of muscles, e.g. between annulospiral endings, Golgi tendon organs and secondary endings in muscle spindles. It is, therefore, not possible to attempt any synthesis between Kolmodin's classification and the partial classification attempted here. All the types defined by Kolmodin (1957) were also widely dispersed throughout the grey matter.

Altogether almost 100 neurones have been arranged in three main types; but with about thirty others this has not been possible, either because the data were inadequate or because they belonged to types not yet defined. Finally, the most common type of interneurone has eluded our classification; such interneurones occur ubiquitously throughout the grey matter, and are activated to fire repetitively by high-threshold afferent fibres in both muscle and cutaneous nerves.

There is now a considerable literature on the electrophysiological properties of interneurones as studied by intracellular recording (Woodbury & Patton, 1952; Frank & Fuortes, 1955, 1956*a*; Suda, Koizumi & Brooks, 1958; Haapanen, Kolmodin & Skoglund, 1958; Kolmodin & Skoglund, 1958; Hunt & Kuno, 1959*a*, *b*; Wall, 1959; Kostyuk, 1959). It will emerge that, so far as the interneurones themselves are concerned, the *A* and *B* types defined here are not distinguishable by their electrophysiological properties. On the other hand, the cells of origin of the ipsilateral cutaneous tract (*CT* type) resembled motoneurones in many respects; the spike showed a similar initial segment–soma dendritic (IS–SD) composition and was followed by a long after-hyperpolarization (100 msec). These tract cells were also much more tolerant of intracellular electrodes than were interneurones.

METHODS

The experiments were performed at the same time as the investigations reported in three previous papers (Eccles, Eccles & Lundberg, 1957*a*, *b*, *c*), and the methods of experiment were identical with those described there. The micro-electrodes were filled with 3 M-KCl and usually had a resistance of 5–10 MΩ. A wide range of nerves were mounted for stimulation and could be tested in quick succession in the way previously described. Special precautions were taken in freeing the nerves so that their blood supply was preserved; and they were mounted on electrodes with an interpolar distance of about 1·5 cm so that the stimulating current would be uniformly applied to the nerve fibres, and there would be a negligible influence of the killed and at the region of application of the cathode. The nerve volleys evoked by the stimuli were always monitored by a surface-recording electrode applied to the spinal cord at the point of entry of L7 dorsal root, and recorded against the large indifferent earth electrode, which was applied to the back muscles. No potential scales are given, in the figures, for these records, which were employed to reveal the I a, I b composition

of the ingoing volley and also to time the entry of the Ia and Ib volleys into the spinal cord. Throughout this paper the entry has been assumed to occur at the first reversal point of the triphasic surface records of the Ia and Ib afferent volleys. In most experiments the spinal cord was severed at the lower thoracic level and the ventrolateral columns on each side were prepared and mounted on stimulating electrodes (Laporte, Lundberg & Oscarsson, 1956*a*). In the remaining experiments the cord was severed at the upper lumbar level and no stimulation of the tracts was attempted.

Usually separation of the Ia and Ib afferent volleys could be detected only with biceps-semitendinosus and quadriceps afferent volleys (cf. Bradley & Eccles, 1953; Eccles *et al.* 1957*a*). However, investigations on the disynaptic Ib action on motoneurones have shown that with other nerves from limb muscles (gastrocnemius-soleus, plantaris, flexor digitorum longus, etc.), the Ib threshold was lower, relative to Ia, than with the nerves from thigh muscles (Eccles *et al.* 1957*a*, *c*). This difference in threshold has also been used to some extent in the present investigation. When in a particular experiment it was observed that one group of interneurones was excited by low-threshold Group I afferents and another group by high-threshold Group I afferents, it was assumed that these afferents were Ia and Ib, respectively. By recording from motoneurones in the same experiments it was often possible to verify this assumption when Ia synaptic actions from the particular nerves were evoked exclusively at low strength and Ib action exclusively at higher Group I strength. Ib actions were seldom observed with a stimulus below 1·2 times threshold for Group I fibres, and as tested by the monosynaptic excitatory post-synaptic potential (EPSP) maximum Ia volleys were usually generated by stimuli only 1·25–1·35 times threshold (cf. Eccles *et al.* 1957*a*, *c*).

The micro-electrode was always inserted from the dorsum of the cord medial to the line of root entry, the direction and depth of the tracks being in general similar to those plotted by Eccles *et al.* (1954). When the recording was intracellular, records were usually taken on withdrawal of the electrode from the cell in order to determine the field potential. These records have not been reproduced, since the external fields were negligible relative to the large intracellular potentials. Many of the spike potentials in the figures have been retouched.

RESULTS

Monosynaptic action by Group Ia fibres of muscle (type A)

Altogether there have been 27 interneurones monosynaptically activated by Group Ia fibres of one or more muscle nerves. They have been located in the zone of synaptic activation by Group Ia volleys from muscle, as indicated by the focal synaptic potential (Eccles *et al.* 1954, Figs. 2, 4), which approximately coincided with the intermediate nucleus of Cajal (1909). The most superficial was at 1·95 mm and the deepest at 3·3 mm from the dorsum of the cord; i.e. they were all dorsal to the motoneuronal nuclei. None of the fourteen cells so tested was antidromically activated from the spinal funiculi of either side, though many were synaptically activated by descending volleys (Fig. 1M). On account of their similarity in other respects, monosynaptic Ia activation and location, it was assumed also that the fourteen untested cells did not have their axons in the ascending tracts of the cord. As a rule type *A* interneurones were rapidly killed by a penetrating micro-electrode, so most have been studied by extracellular recording. Nevertheless, five have been extensively investi-

gated intracellularly. Their membrane potentials ranged from −50 to −70 mV.

The potentials of Fig. 1 A–F were evoked by graded stimulation of the biceps-semitendinosus nerve at strengths from just above threshold for Group Ia (A) to supramaximal for Ib (F). There was a very high level of background synaptic noise, which is characteristic of most types of interneurone. Superimposed thereon were excitatory post-synaptic potentials

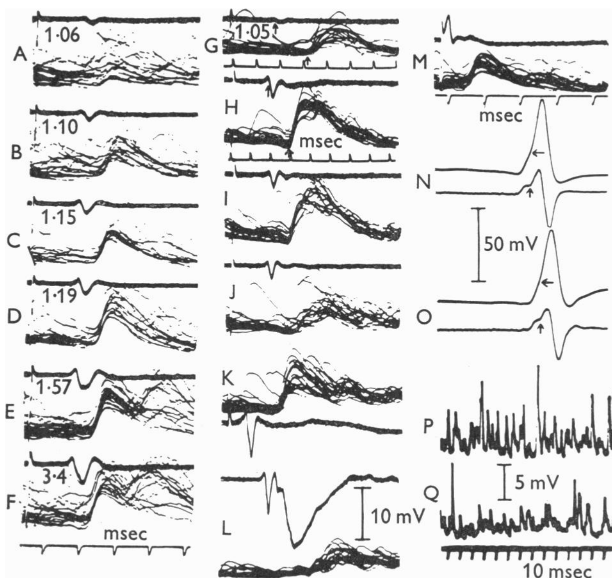


Fig. 1. Intracellular recording from a type *A* interneurone in the intermediate nucleus at a depth of 2·4 mm from the cord dorsum and in the middle of L 7 segment. The membrane potential was about −60 mV throughout. The high background of synaptic noise (P) was diminished (Q) after injection of pentobarbital sodium 5 mg/kg. A–F, superimposed traces of EPSPs evoked by stimuli of progressively increasing strength applied to biceps-semitendinosus nerve, the numbers giving strengths relative to the threshold stimulus. The potential produced by the afferent volley in the L 7 dorsal root (surface recording) is shown above the corresponding intracellular record. Upward deflexions in both signal increasing positivity relative to the indifferent earth electrode. G and H, similar recording of potentials evoked by a very weak (1·05T) and a maximum Group I stimulus to gastrocnemius nerve, Ga; I–K, similar recording for maximum Group I volleys for plantaris, Pl; flexor digitorum longus, FDL; quadriceps, Qu, nerves. L and N similarly recorded, but for volleys evoked by stimuli of several times threshold strength in superficial peroneal (SP) and the ipsilateral ventrolateral funiculus (IF). N and O are spikes arising from EPSPs set up by Pl and Ga volleys (cf. I, H) when the recording conditions had improved so that the larger EPSPs generated spikes at the arrows. Lower traces in N and O are the electrically differentiated records, showing abrupt transition from EPSP to spike at the arrows. Various time and potential scales are shown at appropriate places, A–F having the same time scale, as also H–M. Note that G was faster than H. Same potential scale for A–M.

even with the smallest Group I a volley (seen best at the lower margin of the superimposed traces). The latent period was about 0·35 msec from the time of arrival of the afferent volley at the spinal cord. When there was a I b afferent volley in addition, there was often a later EPSP (E, F) with a latency of about 1·25 msec, measured from the time of arrival of the I b volley. This indicates the interpolation of an interneurone on the I b pathway (cf. Eccles *et al.* 1957*c*).

Potentials generated by afferent volleys from other muscle nerves, and by a descending volley in the ventrolateral funiculus of that side, are shown in Fig. 1 G–M. By graded stimulation it was shown that the lowest threshold afferent fibres of both the gastrocnemius and plantaris nerves were effective in generating the earliest EPSPs of Fig. 1 H and I, respectively. For example, the stimulus to gastrocnemius nerve was at a strength only 5 % above threshold in G. Since the central latency of the EPSP in H and I was 0·6–0·7 msec longer than for the BST response, it is likely that an interneurone was interposed on these I a excitatory pathways.

The time course of the monosynaptic EPSP's generated by the I a afferent volleys is better illustrated in Fig. 2 A–D, where the background of synaptic noise was much lower. Just as with motoneurones, increasing the size of the afferent volley increased the EPSP without greatly altering its time course. The only variant consisted of the superposition of a small partial spike response on the largest EPSP (D). The critical level at which an EPSP generated the spike is shown in G and H, though a partial spike response was superimposed on the EPSP in F. The latent period for the EPSP was 0·6 msec with the just threshold condition obtaining in E and F.

The potentials following the spike are well shown when two traces are superposed, as in Fig. 2 K, but they are also seen by comparing E and F with G and H. The spike rapidly declined to a brief after-hyperpolarization, just as observed with motoneurones having low membrane potentials (Coombs, Eccles & Fatt, 1955); but there was, in addition, a much more prolonged after-hyperpolarization, which, in K, was still large 15 msec after the end of the spike. This long after-hyperpolarization has been seen with other type *A* cells, but has not been investigated at slow sweep speeds to see if it is comparable in duration with the after-hyperpolarization of alpha motoneurones (Eccles, Eccles & Lundberg, 1958). It was certainly more than 50 msec in duration for the interneurone of Fig. 1.

The spikes of Fig. 2 differed from those of motoneurones in that there was no sign of a separation into IS and SD components even with electrical differentiation of very fast sweeps (I, J). The initial slowly rising phase of the EPSP changed smoothly to the steep rise of the spike without any trace of an inflexion, as may be seen also with the spike arising (at the arrow) from the steep EPSP in the undifferentiated records of Fig. 1 N, O.

In view of the depolarized condition of cells penetrated by the micro-electrodes, the threshold depolarization for initiation of a spike by the EPSP was high, just as with the soma-dendritic membrane of moto-neurones (Araki & Otani, 1955; Fuortes, Frank & Becker, 1957; Coombs,

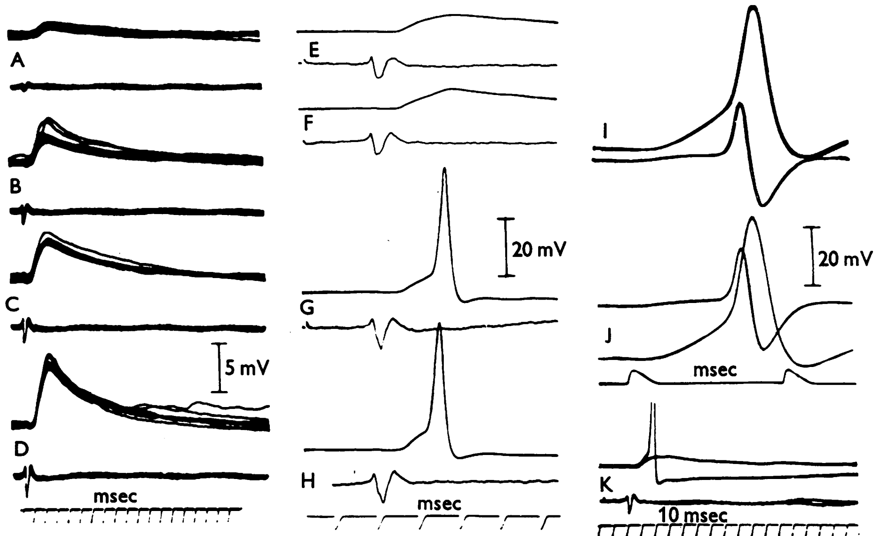


Fig. 2. Intracellular recording from a type *A* interneurone in the L7 segmental level at a depth of 2·0 mm from the cord dorsum. Membrane potential, about −70 mV throughout. A–D are superimposed traces of EPSPs (above) and dorsal root action potentials (below) evoked by progressively increasing stimuli, applied to the combined FDL–Pl nerves. E–H are single traces at faster sweep and lower amplification, the evoking stimuli being about same strength as in C for E and F, and in D for G and H. Lower trace of I and upper of J are electrically differentiated records of the EPSP and superimposed spike evoked by a volley from the posterior tibial nerve, which supplies flexor digitorum brevis and the various toe muscles, there being two superimposed traces in I. K shows, at slow sweep speed, a record of potentials evoked in response to a stimulus of same strength as in C, but at lower amplification. The EPSP was just at threshold, evoking a spike in one of the two traces. Potential and time scales are given at appropriate places, one of the potential scales obtaining for A–D and the other for E–K, as shown. Note very fast sweep for I and J.

Curtis & Eccles, 1957*b*), being about 15 mV in Fig. 1N, O, and 13 mV in Fig. 2I, J. This absence of an IS–SD separation has previously been reported for interneurones (Haapanen *et al.* 1958; Hunt & Kuno, 1959*a*), so it appears that many interneurones lack the zone of low-threshold membrane which occurs in the initial segment of motoneurones.

The interneurone of Fig. 2 was excited through polysynaptic pathways by cutaneous afferent fibres. As is indicated by the EPSPs of Fig. 3, single volleys in cutaneous nerves produced a prolonged irregular bombardment,

particularly when set up by strong stimuli (D, H). These EPSPs generated spike potentials (Fig. 3J, K) if they attained the threshold level of depolarization (about 8 mV). The interneurone of Fig. 1 was also excited by a polysynaptic cutaneous path (L).

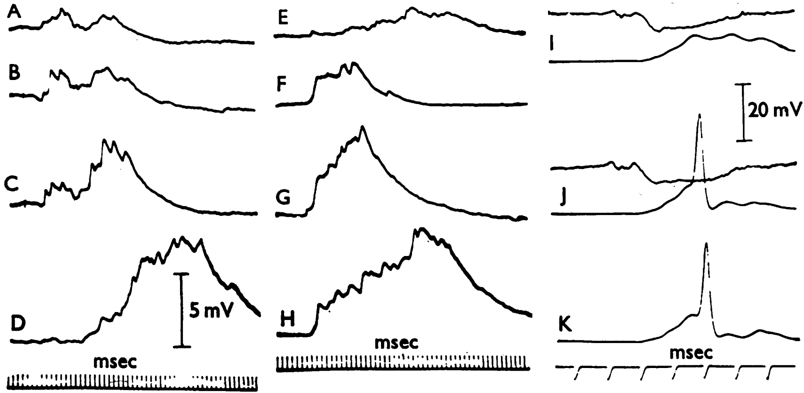


Fig. 3. Intracellular recording from same interneurone as in Fig. 2, A–D and E–H showing prolonged irregular EPSPs produced by stimuli of progressively increasing strength to two cutaneous nerves: sural, A–D, and superficial peroneal, E–H. I–K show records, at lower amplification and faster time base, of potentials evoked by a superficial peroneal volley, the EPSPs evoking a spike in J, K. Upper traces in I and J are potentials led from the L7 dorsal root at its cord entry. Upward deflexion always signals increasing positivity relative to earth. Potential and time scales are given at appropriate places.

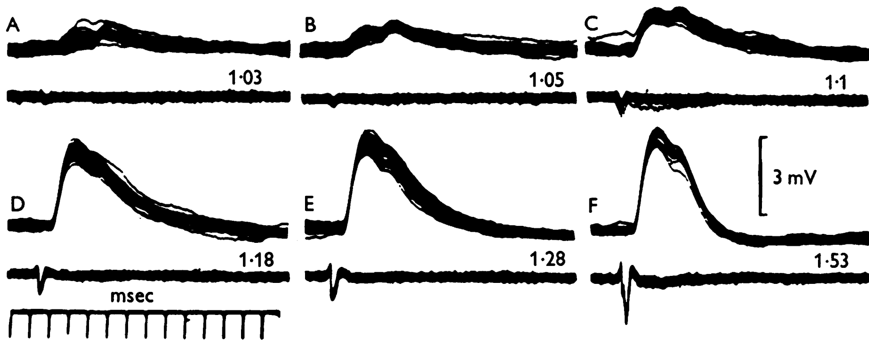


Fig. 4. Intracellular recording from a flexor digitorum longus motoneurone (upper trace) on stimulation of the FDL nerve at the indicated strengths relative to threshold. The lower traces are from the L7 dorsal root entry zone, negativity being signalled downwards, and show that the Group I volley displayed the separation in Ia and Ib components.

It was unexpected to find (see Fig. 1G–I) that Group Ia impulses generated an EPSP after such a long latent period that it was necessary to postulate an interpolated interneurone. It is relevant to report here

that there is some evidence of Ia excitatory action occasionally reaching ipsilateral motoneurones by a polysynaptic pathway. In the experiments of Fig. 4 the nerve to flexor digitorum longus displayed separation in Ia and Ib components (D–F). A single volley from this nerve evoked in a flexor digitorum longus motoneurone a double EPSP which is best seen in records A–C, Fig. 4. The central latent periods were 0·6 and 2·6 msec which would be monosynaptic and probably trisynaptic respectively. High-threshold Group Ib fibres evoked the usual IPSP in F. The late EPSP component was evoked in A at a strength 1·03 times threshold for the nerve, and this was also the threshold strength for the fibres with monosynaptic connexions to the motoneurone. Hence it is difficult to escape the conclusion that the polysynaptic EPSP in Fig. 4 was evoked by impulses in Ia afferents.

None of this series of 27 interneurones has exhibited monosynaptic activation by Ib as well as by Ia impulses of the same or another nerve. Thus there was no overlap between type *A* and type *B* interneurones. However, type *A* interneurones were sometimes disynaptically activated by Ib impulses, as illustrated in Fig. 1A–F.

Extracellular records of type *A* interneurones have been shown previously (Eccles *et al.* 1956, Figs. 2, 4, 5). Since only spike potentials can be recognized, the information on synaptic activation was limited, though specification by monosynaptic Group Ia activation was essential before the interneurone could be classed as type *A*. It is conceivable that some of the interneurones that could not then be classified were subliminally activated by Group Ia volleys.

Many of the type *A* interneurones were very restricted in their synaptic activation, as illustrated in Fig. 5, where the cell was effectively activated by very low-threshold Group Ia volleys from biceps-semitendinosus (A), but by no other afferent volley from muscle or skin. Tests by the double-volley technique (F–I, cf. Fig. 2, Eccles *et al.* 1956) showed that maximum Group Ib volleys (H, I) did not excite a discharge from this cell. However, the cell was synaptically excited from the ventrolateral funiculus with a latency of 2 msec after the arrival of the descending volley, which would suggest a pathway through one or two interneurones. The power of the monosynaptic activation from biceps-semitendinosus was shown by the responses to repetitive stimulation, the cell following perfectly all tested frequencies, even as high as 480/sec (L).

In contrast, some type *A* cells discharged impulses in response to a wide range of high-threshold afferent fibres, as has already been reported (Eccles *et al.* 1956, Fig. 5). A very wide field of action is shown in Fig. 6 for an interneurone which was activated monosynaptically only by Group Ia fibres from biceps-semitendinosus. This activation was powerful; fast

records gave a central latency of only 0·5 msec for the spike (cf. first spike of G), and there was very good following of a stimulus frequency of 680/sec (I). The response to strong stimulation of the muscle and cutaneous nerves was a repetitive discharge beginning after a long latency for all but flexor longus digitorum (D), and this exceptional discharge was probably spontaneous (cf. H), for it was not seen with weaker stimulation of this

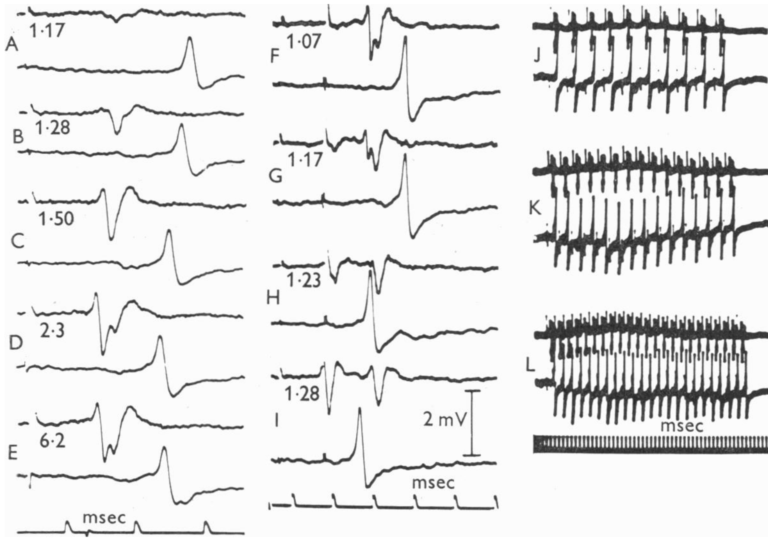


Fig. 5. Extracellular recording from a type *A* interneurone in the intermediate nucleus at a depth of 2·5 mm from the cord dorsum. In A–E the stimuli to BST nerve were at the indicated strengths relative to threshold, the upper trace being recorded as usual from the L 7 dorsal root, upward deflexion signalling positivity. In F–I a second stimulus was given at a fixed interval of 1·1 msec after the first and at a strength (2·5T) supramaximal for Group I, while the first stimuli were at the strengths indicated on each trace. In J–L the BST nerve was stimulated at a strength of 6·2T and at frequencies of 230, 345 and 480/sec, respectively. Same potential scale obtains throughout for the micro-electrode records (upward deflexions signalling negativity), and the time scales belong to the appropriate columns. No other afferent nerve nor descending tract fibres had any action on this interneurone.

nerve. These late bursts of discharges were evoked by Group III afferent volleys, which are very powerful in activating interneuronal pathways, so giving prolonged reflex discharges (Lloyd, 1943; Eccles & Lundberg, 1959*b*).

Type *A* cells have usually received monosynaptic Ia innervation from only one muscle nerve. Exceptionally there was double innervation, even from such widely divergent muscle groups as quadriceps and the anterior tibial muscles.

Monosynaptic activation by Group Ib fibres of muscle (type B)

Type *B* interneurones have been specified by two criteria, monosynaptic activation by Group Ib impulses from muscles and absence of antidromic invasion from the ventrolateral funiculi on either side of the spinal cord. This second criterion distinguishes between interneurones and tract cells, but it has been applied with only 21 of the total of the 30 interneurones classified as belonging to type *B*. In addition to these 30 there

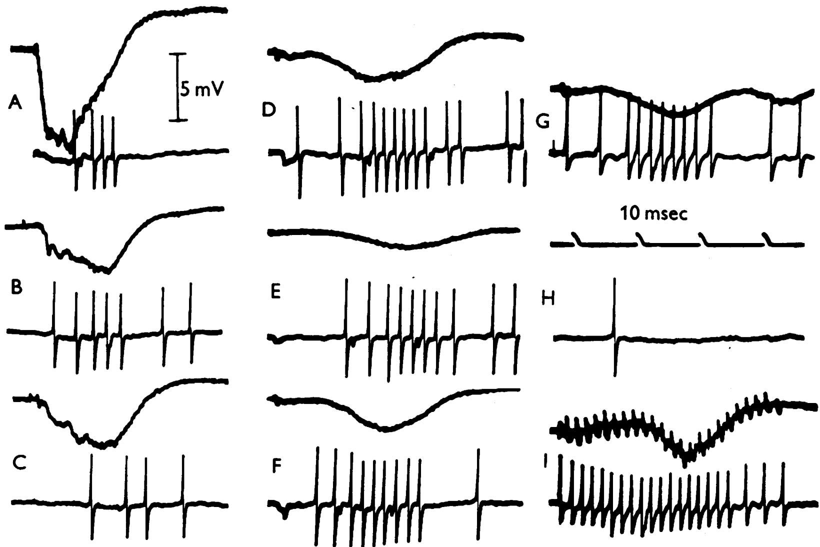


Fig. 6. Lower traces were extracellular recordings from a type *A* interneurone activated monosynaptically only by the Ia fibres of BST, the spike discharge having the brief central latency of 0·55 msec. Upper traces were recorded as usual from the L7 dorsal root entry. A–G are responses evoked by single stimuli at a strength sufficient to excite Group III fibres of muscle nerves and the corresponding fibres of cutaneous nerves: A, SP; B, sural; C, saphenous; D, FDL; E, Pl; F, gastrocnemius; G, biceps-semitendinosus; H shows one of the occasional responses occurring spontaneously; and in I the BST nerve was stimulated at 680/sec, by stimuli supramaximal for Group I.

were four interneurones which were not sufficiently investigated to determine whether their monosynaptic activation was through Ia or Ib fibres, or through both. Apart from this small indeterminate group, type *A* and *B* cells appeared to be sharply distinguishable, none being monosynaptically activated by both Ia and Ib impulses from muscle. Type *B* cells were located at depths ranging from 1·5 to 3·5 mm below the dorsum of the spinal cord, all but two lying between 1·9 and 3·2 mm, which is within the area of extensive Ib synaptic action as revealed by the large extracellular synaptic potentials produced by Ib volleys (Eccles *et al.* 1954).

A rigorous distinction between Ia and Ib afferent volleys was possible when the respective spikes were distinguishable in records led from the appropriate dorsal root, as in the upper records of Fig. 7A–F. Discrimination between the actions of the Ia and Ib volleys was effected by

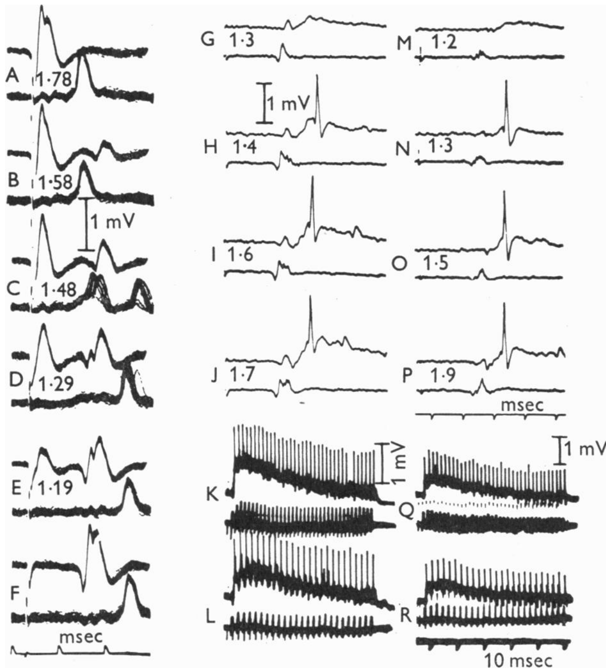


Fig. 7. A–F: Extracellular records of a type *B* interneurone (depth of 3·5 mm) activated from BST nerve, and with double stimulation as in Fig. 5F–I. Second stimulus was at a constant strength, supramaximal for Group I, and at 0·93 msec interval. First stimuli were at the indicated strengths relative to threshold. In both the upper dorsal root record and the lower micro-electrode record, upward deflexions signal negativity, but potential scale is only for micro-electrode traces. All records were made by superposition of about forty faint traces. G–R: Extracellular records of a type *B* interneurone at a depth of 2·4 mm in another experiment. It was activated both by gastrocnemius (G–L) and plantaris (M–R) afferent volleys. The upper trace was always from the micro-electrode (same potential scale throughout except for Q and R), the lower from the lower L7 dorsal root entry. The strengths of the single stimuli are given relative to the threshold of that nerve. The repetitive stimuli were well above maximal for Group I and were at 670/sec (K, Q) and 460/sec (L, R).

varying the strength of the stimulus applied to the biceps-semitendinosus nerve at 1·15 msec before a second testing stimulus, which was at a constant strength supramaximal for Group I (F). As is shown in A, the testing stimulus was unable to excite any Group I fibres that had been excited by the first stimulus. In B the first stimulus (1·58T) was submaximal for Ib.

C shows a transitional state where the first stimulus (1·48T) excited only about one third of Group Ib, as indicated by the large Ib spike set up by the second stimulus; yet it still evoked the interneuronal spike on every test, though with a longer and more variable latency than in A and B; but now the Group Ib volley set up by the second stimulus was also effective, so that the interneurone usually discharged twice at an interval of about 1 msec. The next weakest initial stimulus (1·29T), in D, excited very few Group Ib fibres and never evoked a discharge of the interneurone, though it was almost maximal for Group Ia, as revealed by the small Group Ia spike set up by the second stimulus. E shows a further stage of the series (first stimulus 1·19T) where the second stimulus excited about half of Group Ia and probably all of the Ib fibres. In contrast to C, and even D, it was now just as effective in exciting the interneurone as the maximal Group Ia–Ib volleys in A and F. It may be concluded that the interneurone was very effectively excited by Group Ib impulses, and that there was no evidence for a Ia excitatory action. The incomplete separation between Ia and Ib prevented such analyses from being decisive (cf. Laporte & Bessou, 1957; Eccles *et al.* 1957*a*), and it is desirable to have tests by adequate stimulation of receptor organs (cf. Lundberg & Winsbury, 1960*a*, *b*).

The series of Fig. 7G–R shows extracellular records of another interneurone classified as type *B* by graded stimulation of nerves to gastrocnemius (G–J) and plantaris (M–P) muscles. The gastrocnemius afferent volley showed a separation into Ia and Ib spikes (G–J). In G, where the Ib volley was small or absent, the interneurone was not excited despite the almost maximal size of the Ia volley. Figure 7M–P shows that the interneurone was also excited by the higher threshold component of the Group I plantaris volley, which presumably was also a Ib action (cf. Eccles *et al.* 1957*a*). The generation of impulses in the interneurone was accomplished in the short central delay of 0·7–0·8 msec for both plantaris and gastrocnemius afferent volleys. An intense excitatory action of both afferents was further shown by the responses to repetitive stimulation, there being virtually a perfect following of frequencies as high as 670/sec (Fig. 7K, L, Q, R). This type *B* cell was also excited by superficial peroneal volleys after a long central delay, but by no other muscle afferents.

There was a much more extensive receptive field for the type *B* cell of Fig. 8, though the frequency tests showed that, except for the plantaris afferent volley (D, E), it was a field of low intensity (I, J, N, O). The plantaris volley also showed its effectiveness in the very short central latency (0·6 msec in C) and relatively small size of the Group I volley (A) which evoked a discharge from the interneurone. By contrast, the gastrocnemius Group I volley had to be almost maximal (F) and the minimum

central latency was 0·9 msec (H). It was of interest that, although the Group I volley from flexor digitorum longus had to be almost maximal in order to be effective (K–M), it evoked a double discharge even at threshold, the central latencies for the two discharges being about 1·0 and 2·0 msec with a maximal Group I volley. Three criteria established that the

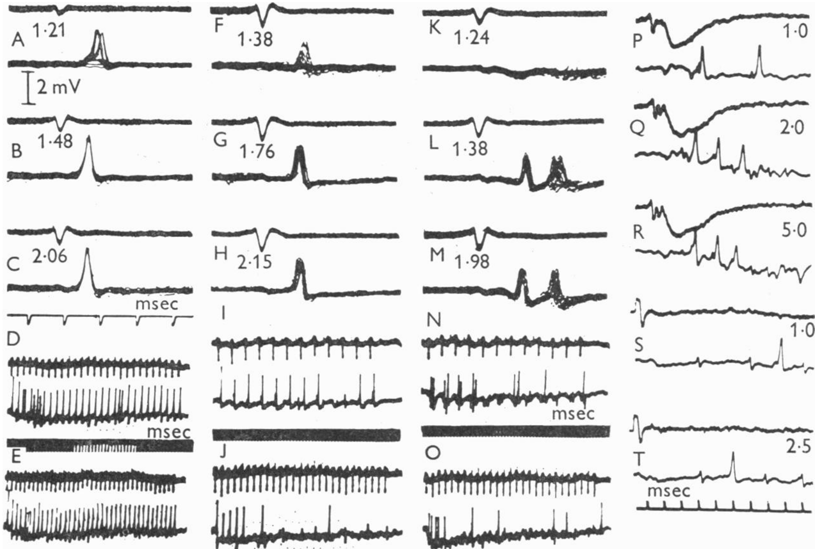


Fig. 8. Extracellular records from a type *B* interneurone in the intermediate nucleus at a depth of 2·1 mm from the cord dorsum. Upper traces are potentials led from the L 7 dorsal root entry, positivity upwards. Same potential scale for all micro-electrode records, upward deflexions signalling negativity. A–E, F–J and K–O are series with stimuli at the strengths indicated applied to plantaris, gastrocnemius and flexor digitorum longus nerves, respectively. In A–C, F–H and K–M the records are formed by the superposition of about forty faint traces. The stimulus frequencies in D, E are 480 and 690/sec, while in I, J and N, O they are 220 and 480/sec, respectively. In P–R single stimuli were applied to the superficial peroneal nerve at the strengths indicated relative to that of P, and similarly in S and T to the quadriceps nerve. Note different time scales in appropriate places.

Group I b and not the I a impulses from plantaris were effective in exciting the interneurone. The very short central latency of the discharge evoked by a plantaris volley (C) and particularly the very high frequency of repetitive discharge (690/sec followed perfectly in E) showed that a maximal Group I plantaris volley excited the interneurone very powerfully. The tests (A–C) could indicate that the interneurone was weakly excited by I a impulses, the volley evoked at a strength of 1·21 T being just sufficient to evoke a discharge (A); but this interpretation is inconsistent with the powerful excitation by high-threshold Group I afferents revealed by the other tests. Thus excitation by lowest threshold Group I b fibres may be presumed in

Fig. 8A, particularly as a stimulus of strength 1·21T has been found to evoke a disynaptic Ib inhibitory action in motoneurones (Eccles *et al.* 1957*c*, Figs. 3, 4). On this interpretation the interneurone would be excited monosynaptically by Ib not only from gastrocnemius (F–H) and flexor digitorum longus (K–M), but also from plantaris (A–C). In addition,

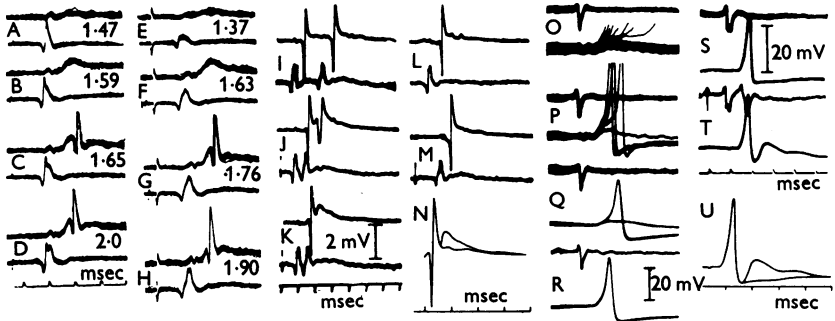


Fig. 9. A–M are extracellular records of a type *B* interneurone in the intermediate nucleus at 2·2 mm below cord dorsum. Upper traces are micro-electrode records (note potential scale), while lower records are from L7 dorsal root entry, upward deflexions for both records signalling negativity. In A–H records are formed by superposition of about forty faint traces. A–D and E–H are evoked by single stimuli to the gastrocnemius and plantaris nerve respectively at the indicated strengths relative to threshold. In I–K the gastrocnemius stimulus was applied at short intervals before the plantaris stimulus, both stimuli being supramaximal for Group I, and L, M show the respective single responses. Superposition of responses L and K (in N) reveals the time course of the EPSP set up by the plantaris nerve when refractoriness prevented generation of a spike. Actually the tracings of N are the means of two closely similar records. The same interneurone was later penetrated by the micro-electrode, the membrane potential having the low value of −38 mV. O–R show intracellular responses evoked by gastrocnemius afferent volleys set up by a stimulus of 1·59T strength (cf. B), with many superimposed in O, 4 in P, 2 in Q and 1 in R. Note that Q and R are at lower amplification than O, P, S, T. S, T and U are intracellular records corresponding to the extracellular series L, K, N, respectively. Upward deflexions in intracellular records signal positivity.

it was excited at longer latency by a wide range of cutaneous afferents in the superficial peroneal nerve (P–R) and very slightly by high-threshold quadriceps afferents (S, T). Several type *B* interneurones were synaptically excited by descending volleys in the ipsilateral funiculus.

Intracellular records were made from only three of the total of 30 type *B* interneurones. The cell illustrated in Fig. 9 was shown to be type *B* by the threshold tests with gastrocnemius (A–D) and plantaris-flexor digitorum longus volleys (E–H), and was later penetrated by the micro-electrode. A just-threshold gastrocnemius volley then gave the responses (O, P), showing the spike arising from an EPSP at a rather low threshold level

(about 6 mV), which may be attributed to the depolarized state of the cell, the membrane potential being only −38 mV. The spike showed no sign of IS–SD composition and initially had a duration of 0·5 msec (P), but later it lengthened to 0·8 msec (Q, R), there being a large after-hyperpolarization, which seemed to be comparable with that given by type *A* interneurones (Fig. 2K). The large size of the EPSP produced by a maximal Ib volley is shown in T, where a plantaris volley 0·8 msec after a gastrocnemius volley generated only an EPSP, which is revealed by comparison with the control records (S) and in the superimposed tracings (U). During the earlier extracellular series a similar test had been made (K, L, M), showing the time course of the extracellular EPSP in the superimposed tracings (N). At longer volley intervals (I, J) the plantaris volley also evoked a spike in the interneurone, the interval between two successive discharges being as brief as 0·7 msec when the volley interval was 0·5 msec (J). The refractory period of the interneurone was thus very brief and the potency of the synaptic stimulation very high.

Monosynaptic action by impulses from cutaneous nerves (*type C*)

The interneurones of type *C* are specially concerned in the relaying of impulses from cutaneous nerves, and are monosynaptically excited by impulses from one or another cutaneous nerve. One subgroup has been characterized in addition by being invaded antidromically by impulses descending the ventrolateral funiculus on the same side, i.e. they were tract cells relaying cutaneous impulses up the ipsilateral side. At least 14 of the total of 33 type *C* cells were in this subgroup, which may be called *CT*, and 6 type *C* cells did not have a tract axon, being therefore primarily cutaneous interneurones, and forming a subgroup that may be called *CN*. The remaining 13 type *C* cells were not tested for antidromic invasion from the ventrolateral funiculi. The *CT* cells were remarkable in being much more tolerant of intracellular electrodes than interneurones, and extensive intracellular investigations were possible with four of them.

The cell illustrated in Fig. 10 had a membrane potential of −60 mV throughout a long investigation, and A–D show the responses evoked by progressively increasing stimuli to the superficial peroneal nerve. In A the spike is seen to arise from an EPSP, but with B–D the EPSP was so steep that there was barely any inflexion between it and the initial spike. In C the high spike frequency was associated with depression of size and this effect was even greater with the second and third spikes of D, where the initial frequency was about 1000/sec. The spike potential generated by antidromic invasion from the ipsilateral tract (E) clearly exhibited an IS–SD composition, particularly in the differentiated record. The total

duration of the spike was about 0·9 msec, and it was followed by the brief after-hyperpolarization characteristic of depolarized neurones. Slower records (F, G) revealed a much larger and longer after-hyperpolarization, which was over 100 msec in duration (H), and comparable with that occurring in motoneurones (Eccles *et al.* 1958). Similar after-hyperpolarizations were given by other *CT* cells. Finally, in I–L there was a

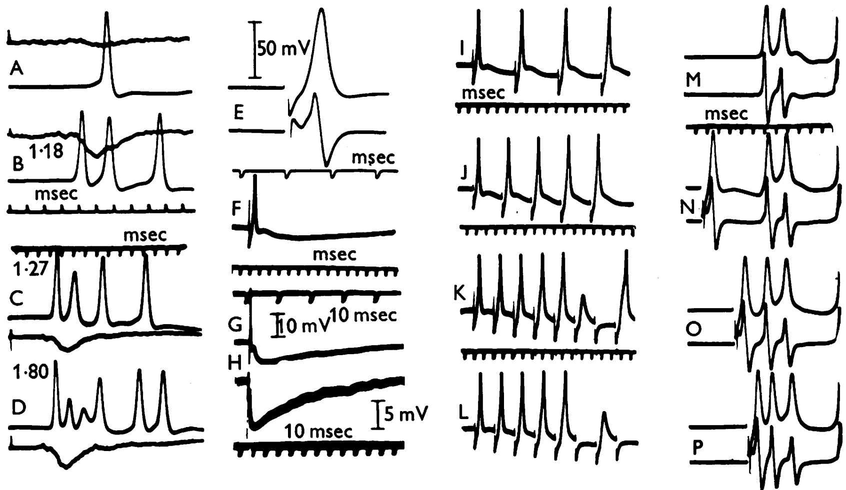


Fig. 10. Intracellular records from a type *CT* cell at a depth of 1·5 mm from the cord dorsum, the membrane potential being −60 mV. A–D are responses evoked by a stimulus to superficial peroneal nerve at the indicated strengths relative to the stimulus for A. Note change in time scale between B and C. There is a record from L 7 dorsal root entry (lower trace) as well as the intracellular record. Upward deflexions of both traces signal positivity. E–H are antidromically evoked potentials in response to a stimulus to the ventrolateral funiculus of the same side, E being an electrically differentiated record. Note changes in the potential and time scales. I–L show responses to antidromic tetani at respectively 230, 340, 490, 490/sec. M shows response to a superficial peroneal volley set up by a stimulus 1·2 times the strength for response, A. In N–P it was preceded at progressively shorter intervals by an antidromic spike response. No other nerves were effective in exciting this cell. Same potential scale for all records except G and H. Note time scales in appropriate places.

repetitive antidromic invasion of the cell, even for 5 impulses at 490/sec; thereafter blockage occurred, much as with motoneurones, for in K and L there were either IS spikes, or no detectable spike. Presumably this was due to an axonal block, just as occurs with motoneurones (Brock, Coombs & Eccles, 1953). The brief refractoriness of *CT* cells is further illustrated by the effect of a preceding antidromic volley on a synaptically evoked response (N–P), the control being shown in M. In P the synaptic stimulation generated a spike at 1·2 msec after the onset of the antidromic spike.

Somewhat similar observations have been made by Wall (1959) on repetitively discharging cells.

Further details of the spike responses of *CT* cells are illustrated in Fig. 11. With the antidromic spike in A, B, there was a separation into IS and SD components equivalent to that occurring in motoneurones (Araki & Otani, 1955; Fatt, 1957; Fuortes *et al.* 1957; Coombs, Curtis & Eccles, 1957*a*). This IS–SD separation also occurred with spikes generated by synaptic excitatory action. With a very small superficial peroneal volley

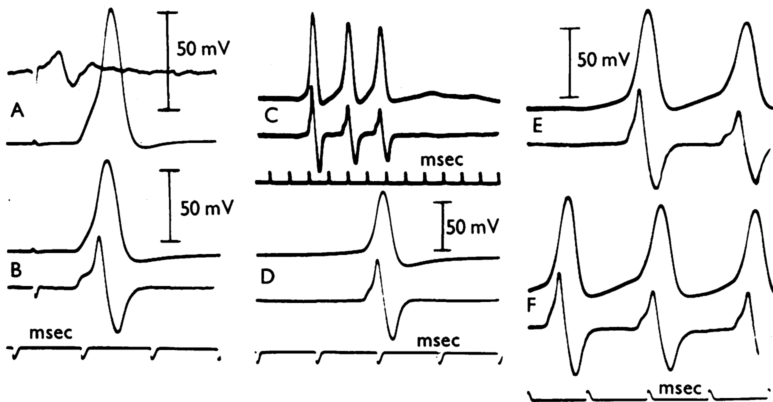


Fig. 11. Intracellular records from a type *CT* cell as in Fig. 10, but in a different experiment. Depth below dorsum of cord was 1·8 mm; membrane potential was not recorded. A gives antidromic spike response to a descending volley in the ventrolateral columns of the same side, the upper trace showing the field generated by the volley. In B the lower trace shows the electrically differentiated record of the antidromic spike. C–F are responses evoked by a superficial peroneal volley together with the electrically differentiated records. D shows response to a volley which just evoked a single spike. D–F have fast time bases and the initial rising phase of the EPSP was not fully recorded in F. Superficial peroneal was the only nerve evoking any response of this cell. Note potential and time scales related to appropriate records, C being at same amplification as E and F.

a single spike was produced by a slowly rising EPSP (D), there being a clear IS–SD composition in the differentiated record, as may also be seen in the repetitive spike discharges evoked by larger afferent volleys (C, E, F). Thus, cells of type *CT* give spike responses and after-hyperpolarizations resembling those of motoneurones; but they differ in that they can discharge at a much higher frequency.

It was remarkable that all the *CT* cells which were fully categorized (13) were activated monosynaptically by the superficial peroneal nerve, and none by the other cutaneous nerve (sural), which was always tested. These *CT* cells were, however, often activated by high-threshold muscle afferents, giving a repetitive response after a long latent period.

Figure 12 illustrates the responses of a cell belonging to the other subgroup (type *CN*). Such cells were often synaptically activated by descending impulses in the ventrolateral funiculus of the same side, as shown by the various sizes of EPSPs evoked by graded volleys (A–C). In G and H the EPSP evoked a spike after a rather long rising phase, and differentiation (I) showed that it also had an IS–SD composition. Finally, in D–F are spike responses evoked by progressively increasing volleys in

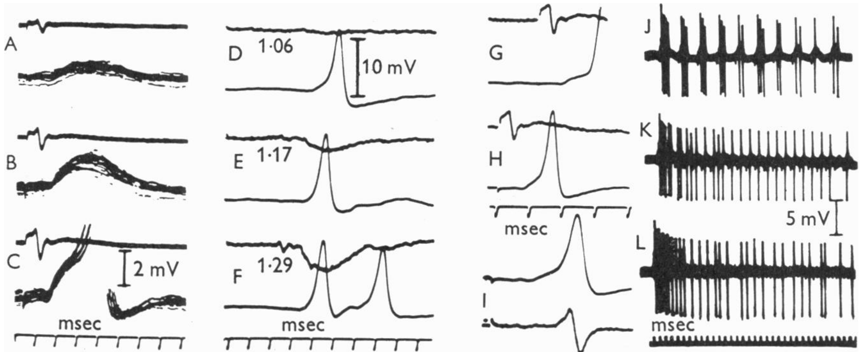


Fig. 12. Intracellular records of a *CN* type interneurone at a depth of 2·0 mm and with a membrane potential of −40 mV. A–C show records evoked by stimuli to the ventrolateral funiculi of the same side and of progressively increasing strength, each record formed by superposition of about 40 faint traces. D–F show responses to a single superficial peroneal volley at the indicated strengths relative to threshold. Upper traces in A–F are records from the L7 dorsal root entry. G–I show single responses to a descending volley evoked by a stimulus of the same strength as in C, the EPSP being just at threshold for evoking a spike. In G, H there is also a surface record (above) from the spinal cord dorsum, while in I there is an electrically differentiated record of the spike potential (below). Same time scales for all but record I (shown above it); one potential scale for A–C and another for D–I. J–L show responses of another C type cell to repetitive stimulation of the superficial peroneal nerve at frequencies of 22, 67 and 150/sec. In the absence of test by a descending cord volley, it was not known if it was a tract cell (*CT*) or an interneurone (*CN*).

the superficial peroneal nerve. In D the spike clearly arose from an EPSP, much as in G and H. This cell had highly specific synaptic connexions, being activated from no other cutaneous or muscle nerves. Several *CN* cells were activated by high-threshold muscle afferents, however, showing a repetitive response after a long latency.

Type *C* cells in general had much less ability to follow high-frequency stimulation of their monosynaptic path than those of types *A* or *B*. For example, in Fig. 12J–L the type *C* cell responded repetitively at high frequency to a single afferent volley in superficial peroneal nerve (cf. Fig. 10B–D). At a frequency of 31/sec (J) the cell usually responded twice to each afferent volley, and after an initial response at higher fre-

quency it followed 67/sec almost perfectly (K). It failed quickly at 150/sec (L), however, and it also failed to follow 100/sec after the first twelve volleys, showing intermittent following thereafter.

DISCUSSION

In many respects these investigations on the responses of individual interneurones agree with previous investigations in which intracellular recording was used. With the exception of the special cutaneous tract cells (type *CT*) the membrane potential has been much less well sustained than with motoneurones (cf. Haapanen *et al.* 1958; Hunt & Kuno, 1959*a*; Kostyuk, 1959), though it has often been in the range −40 to −60 mV.

There is also general agreement that activated excitatory synapses produce brief depolarizations, the excitatory post-synaptic potentials (EPSPs) closely resembling the EPSPs of motoneurones (Frank & Fuortes, 1956*a*; Eccles *et al.* 1956; Kolmodin & Skoglund, 1958; Haapanen *et al.* 1958; Hunt & Kuno, 1959*a*). Sometimes these EPSPs had a rapid rise and a slower, approximately exponential, decay, as in Figs. 1C; 2A–D; 9O, corresponding to Hunt & Kuno's (1959*a*) description, and also resembling monosynaptic EPSPs of motoneurones. For example, the EPSPs of Fig. 2A–D closely resemble motoneuronal EPSPs even in respect of the half-time of decay, which was about 4 msec. The EPSPs often had a more complex form, however, which is clearly the result of temporal dispersion in the synaptic bombardment (cf. Haapanen *et al.* 1958; Hunt & Kuno, 1959*a*). This was particularly evident when the synaptic bombardment tended to be synchronized into two phases, as in Fig. 1E, F. An extreme temporal dispersion of the synaptic bombardment produced by a single afferent volley is well illustrated in Fig. 3, and can be assumed to be responsible for the prolonged spike discharges of Figs. 6A–G, 10B–D and 11C, E, F. Evidently this synaptic bombardment occurred after transmission through polysynaptic pathways of varying degrees of complexity. The wealth of pathways converging on interneurones is well illustrated by the synaptic noise (cf. Brock, Coombs & Eccles, 1952) produced by continuous random bombardment (cf. Figs. 1A–M, P, Q; Kolmodin & Skoglund, 1958; Haapanen *et al.* 1958).

An analysis of simple EPSPs such as those of Figs. 1C, 2A–D, 9O, P is not possible, because no measurement of the electric time constant of the membrane has been made. Hunt & Kuno (1959*a*) attempted to determine this constant from the strength–duration curves for interneurones, so deriving times with a mean value of only 0·46 msec. With motoneurones, however, this method has given values very much briefer than those derived from the time course of potential changes produced by the application of a rectangular pulse (Frank & Fuortes, 1956*b*; Coombs, Curtis &

Eccles, 1959). Prolonged EPSPs such as those of Fig. 3 would arise by summation of the temporally dispersed unitary EPSPs.

In the present intracellular investigations the spike potential always arose from an EPSP, so it can be presumed that the micro-electrode was inserted into the soma of the neurone and not into the axon, as was sometimes the case with previous investigations (Frank & Fuortes, 1955; Haapanen *et al.* 1958; Hunt & Kuno, 1959*a*). With interneurones of types *A* and *B*, the spike was simple and brief (0·4–0·8 msec), without any trace of the double (IS–SD) composition characteristic of motoneurones (cf. Figs. 1N, O; 2G–J; 9P–T); and this agrees with Haapanen *et al.* (1958) and Hunt & Kuno (1959*a*). On the other hand, types *CT* and *CN* showed a prominent IS–SD configuration (Figs. 10, 11, 12), which clearly indicated a low-threshold area for spike initiation comparable with that of motoneurones (Araki & Otani, 1955; Fatt, 1957; Fuortes *et al.* 1957; Coombs *et al.* 1957*a*; Kostyuk, 1959), and correspondingly the spike complex had a longer duration, about 1 msec. Usually the sizes of spikes were low as a result of cell injury, but overshoot, as in Fig. 10, has been observed by other investigators.

There was a very wide range in the threshold depolarization for initiating a spike discharge. As would be expected, the threshold was high in types *A* and *B*, where there was no specialized low-threshold area. For example in Figs. 1, 2 and 3, it ranged between 8 and 15 mV, while for type *C* cells in Figs. 10–12 the range was 4–8 mV. The range for types *A* and *B* is higher than that (2·5–10·9 mV) reported by Hunt & Kuno (1959*a*). The intensity of excitatory synaptic action appears to be higher with cells of types *A*, *B* and *C* than with motoneurones. Not only is the synaptic depolarization very large as a rule, but it produces high-frequency discharges, as in Figs. 6, 8R, 10, 11; and discharges of the *A* and *B* type cells, can be driven in phase with afferent volleys of very high frequency (Figs. 5, 6, 7, 8). Figure 10P also illustrates the capacity of the EPSP to generate an impulse at only 1·2 msec after the initiation of an antidromic spike.

There is general agreement that the spike declines on to a brief phase of hyperpolarization, such as generally occurs when the membrane potential is low. However, longer after-hyperpolarizations were not found by previous investigators (Haapanen *et al.* 1958; Hunt & Kuno, 1959*a*; Kostyuk, 1959), and were certainly less prominent than with motoneurones (cf. Kolmodin & Skoglund, 1958). *CT* cells by contrast had an after-hyperpolarization as well developed as motoneurones (Fig. 10G, H). With types *A* and *B* there was also evidence of a long after-hyperpolarization (Figs. 2K, 9Q).

A considerable proportion of *A* and *B* cells can follow quite high

frequencies in afferent volleys, up to 700/sec being followed for as many as 30 responses (Figs. 5, 6, 7, 8). The same cell may vary greatly in its responses to repetitive volleys from different afferents, which is satisfactorily accounted for by the relative excitatory potencies of the different volleys (cf. Figs. 7, 8). No distinction can be made between the frequency responses of type *A* and *B* cells. Such high-frequency following of interneurones has not been reported by other investigators (cf. Frank & Fuortes, 1956*a*; Haapanen *et al.* 1958). Possibly their investigations were largely restricted to the interneurones activated only through polysynaptic paths, which we have not classified. Many of these give high-frequency responses (up to 1000/sec) to single volleys, but follow repetitive afferent volleys very poorly (e.g. Fig. 12J–L). In some cases the mixed afferent volleys had an inhibitory action which cumulatively depressed the responses to the later volleys (cf. Hunt & Kuno, 1959*b*). At least four factors are probably concerned in the high frequency with which type *A* and *B* cells can follow repetitive synaptic bombardment: the high level of monosynaptic excitatory action; the brevity of the spike and consequently of the refractory period (cf. Fig. 9J); the relatively low level of the after-hyperpolarization; and, finally, the high-frequency potentiation of EPSPs (cf. Curtis & Eccles, 1960) may be as well developed with interneurones as it is with many cells of origin of the ventral spinocerebellar tract (Eccles, Hubbard & Oscarsson, unpublished observations).

The primary afferent fibres from which a cell draws its monosynaptic activation have been a relatively unambiguous guide to the definition of cell type, so that there are numerous specimens belonging uniquely to one or other of the three main types *A*, *B* or *C*. There have been four interneurones, however, which could not be classified as *A* or *B*. For the present it may be assumed that this ambiguity was due to inadequate investigation and to unfavourable threshold discrimination between the Ia and Ib afferent fibres of the muscle nerves. It can be expected that the much more selective conditions provided by adequate stimulation will allow the complete separation into types *A* and *B*, just as with the cells of origin of the dorsal spinocerebellar tract (Lundberg & Winsbury, 1960*a*, *b*). If further investigation confirms this prediction, there would be further support for the general proposition that the primary afferent fibres belonging to Groups Ia and Ib do not establish synaptic connexions on the same nerve cell. There are already several well established instances of this principle of exclusion. Ia fibres alone make direct synaptic connexions with motoneurones (Bradley & Eccles, 1953; Eccles *et al.* 1957*a*) and with the interneurones (a subgroup of type *A*) concerned in direct inhibitory action (Eccles *et al.* 1956; Eccles *et al.* 1957*a*). Furthermore, the cells of origin of the dorsal spinocerebellar tract activated by Ia and Ib fibres now

appear to be distinct (Lundberg & Winsbury, 1960*b*). Finally, the Ib afferent fibres are alone concerned in activation of the cells of origin of the ventral spinocerebellar tract (Oscarsson, 1956, 1957). It would seem likely that in the development of all these specific central connexions of Ia and Ib afferent fibres there is some chemical specificity in the respective growing fibre tips or growth cones. This postulate would be of particular significance in accounting for the specific afferent connexions made on the *A* and *B* cells interspersed in the intermediate nucleus.

The destination and functional action of the axons of the nerve cells give a basis for further classification. This criterion is well established for such spinal nerve cells as motoneurones, and the cells of origin of the dorsal and ventral spinocerebellar tracts. It has been applied above in subdividing type *C* cells into *CT* and *CN* subtypes, but it also can be applied to cells of types *A* and *B*.

It is now necessary to postulate that Ia afferent fibres exert not only a monosynaptic, but also a disynaptic or polysynaptic excitatory action on some interneurones (Fig. 1G, H) and motoneurones (Fig. 4A–F). Both general considerations and specific investigations have led to the hypothesis that nerve cells are either excitatory or inhibitory in action (Eccles, 1957). Hence it would be predicted that type *A* cells could be subdivided into two sub-types according as they are excitatory or inhibitory in function, i.e. sub-types *AE* and *AI*, respectively. Possibly the *AI* cells are those with the very restricted receptive field, in conformity with their special function as interneurones of the very specific direct inhibitory path (cf. Fig. 5), whereas type *AE* might include the cells with wider receptive fields (Figs. 1, 2, 6). Further investigation is desirable in order to see if the cells of type *A* can be subdivided in this way in relation to their receptive fields.

Since the disynaptic inhibitory action of Group Ia impulses is much more in evidence than di- or polysynaptic excitatory actions, it would be expected that type *AI* would be more numerous than type *AE*. Impulses passing down the descending tracts of the spinal cord profoundly depress the interneuronal pathways from primary afferent fibres to motoneurones, with the sole exception of the 'direct' inhibitory path (Eccles & Lundberg, 1959*a*; Holmqvist & Lundberg, 1959). It would therefore be expected that such descending inhibitory action would distinguish other interneurones from *AI* cells.

Similar considerations apply to type *B* cells, for Ib afferent impulses have a powerful disynaptic inhibitory action on motoneurones and also have powerful disynaptic or polysynaptic excitatory actions (Laporte & Lloyd, 1952; Eccles *et al.* 1957*c*). Hence it may be postulated that there are many cells in each of the subtypes *BI* and *BE*.

The type *CT* cells have the properties which would be expected for the cells of origin of the cutaneous component of Fleschig's fasciculus (Morin, 1955; Laporte *et al.* 1956*a*, *b*; Catalano & Lamarche, 1957) which makes synaptic connexion with the lateral cervical nucleus (Rexed & Ström, 1952). Recording from the fibres of this tract (Laporte *et al.* 1956*a*, *b*) shows that the cells are activated monosynaptically by the lowest threshold cutaneous fibres, the synaptic delay being less than 1 msec, while larger cutaneous volleys cause the repetitive discharge of several impulses with a frequency as high as 1000/sec, exactly as in Figs. 10 and 11. The fast conduction velocity of the axons of this tract, 100 m/sec (Laporte *et al.* 1956*a*; Oscarsson, 1958), indicates that it arises from large cells, which agrees with the tolerance of intracellular electrodes shown by *CT* cells. This cutaneous tract would include the dorsal spino-olivary tract described by Grundfest & Carter (1954); but there are minor discrepancies, the conduction velocity (maximum at 75 m/sec) being considerably lower (di Biagio & Grundfest, 1955). Possibly some systematic error was responsible for this discrepancy, because this conduction velocity was linked with a localization of the tract cells to the L 5 segmental level, whereas the *CT* cells were actually at the L 7 level in our experiments.

The *CT* cells have been located at depths of 1·6–2·0 mm from the cord dorsum, except for one at 2·5 mm, being thus more superficial than the intermediate nucleus. There was a corresponding location (maximum at 1·7 mm depth) for the synaptic field potential evoked by low-threshold cutaneous volleys (Coombs *et al.* 1956). Presumably the *CT* cells are the large neurones reported by many investigators in the deeper part of the dorsal horn, the 4th and 5th layers of Rexed (1952, 1954). Lenhossék (1893) and Cajal (1909) both give illustrations showing the axons of some of these neurones passing into the lateral columns. The *CN* cells have been scattered more widely, their depths ranging from 1·2 to 2·7 mm in our few samples. The depth of the *A* and *B* type cells would place them in the 6th layer of Rexed (1952). Certainly they are far too widely dispersed for location in the very slender nucleus intermedio-medialis. On the other hand Cajal (1909, Fig. 115) has depicted a very dense plexus of collaterals of primary afferent fibres in the precise region where *A* and *B* type cells are found. Clearly further work is needed to correlate cytoarchitectonics with synaptic connexions and electrophysiological investigations.

In addition to the 90 neurones of the *A*, *B* and *C* types, about 30 other interneurones were investigated, but could not be classified. Four were monosynaptically activated by Group I fibres from muscle nerves, but the data were inadequate for separating them into *A* and *B* types. The remaining unclassified neurones were not monosynaptically activated from any of the muscle or cutaneous nerves prepared for stimulation. No doubt

many would have been identified as belonging to one or other type if they had been tested by all muscle and cutaneous nerves of the hind limb. It should also be pointed out that we have not defined any neurones by the criterion of monosynaptic activation by Group II afferent fibres from muscle. Nevertheless, it would seem likely that some interneurones have no monosynaptic activation from primary afferent fibres. Another type of interneurone, recently found in the dorsal horn (Eccles & Krnjević, 1959), is characterized by very large (up to 40 mV) and prolonged (200 msec) EPSPs without any detectable spike potential.

SUMMARY

1. Micro-electrode techniques have been employed in studying types of neurones which are located in a restricted zone in and around the intermediate nucleus of the spinal cord from lower L6 to upper S1 levels.

2. The receptive fields from which these neurones exclusively draw their monosynaptic innervation have been the basis of their subdivision into three main types, about 30 of each type having been investigated: Ia afferent volleys and type *A*; Ib afferent volleys and type *B*; cutaneous afferent volleys and type *C*. Many neurones could not be so classsified; some because the data were inadequate, but many because they had no monosynaptic activation.

3. The axons of some type *C* cells ascend the cord in the ventrolateral funiculus of the same side, i.e. they are cutaneous-tract cells. The axons of type *A* and *B* cells and the remaining type *C* cells do not ascend the cord. The cells would be interneurones taking part in spinal reflexes or mediating actions to ascending pathways.

4. Intracellular recording showed that synaptic excitatory action evoked discharge by a depolarizing action (the EPSP) which was often large.

5. Besides their monosynaptic excitation many cells of all types have polysynaptic innervation from muscle and cutaneous nerves, which may give high-frequency discharge up to 1000/sec, particularly from *C* type cells.

6. The spike potentials of type *C* cells have a double composition resembling the IS–SD spike of motoneurones. With cells of types *A* and *B* the spike was simple, so it is presumed that they have no low-threshold area for initiating spikes.

7. Type *C* cells have a large and prolonged after-hyperpolarization, and so possibly do *A* and *B* cells; nevertheless, on account of the powerful monosynaptic action, *A* and *B* type cells can follow high frequencies of afferent volleys, even up to 700/sec.

8. There is a brief discussion of problems which arise in attempting to account for the development of specific central connexions by primary afferent fibres.

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