Pathological plantar response

Part I Flexor and extensor components in early and late reflex parts

LENNART GRIMBY

From the Department of Neurology, Karolinska Institutet, Stockholm, Sweden

In previous investigations (Kugelberg, Eklund, and Grimby, 1960; Grimby, 1963a, b) the spinal part of the human plantar reflex in normal and pathological cases was studied by means of electromyographic techniques. Special attention was paid to the reflex patterns obtained during simultaneous recordings from the short hallux flexor and extensor, since the strength of the electrical response in the flexor proved to be a sensitive index of the tendency to plantar flexion, and the response in the extensor to the tendency to dorsiflexion of the hallux.

In normal subjects flexor activity is strongly predominant in the reflex pattern, and it was assumed that the suprasegmental control system could discriminate among the available types of reaction, selecting that best serving a protective function. In pathological cases extensor activity may be predominant. In some cases the reflex pattern obtained on stimulation of the plantar surface of the foot may consist of an early part predominantly extensor, and a late part predominantly flexor in type. In other cases it may consist of an early part predominantly flexor and a late part predominantly extensor in type. It was assumed that both these components are transmitted in such a way that one may be affected by the pathological process independently of the other.

The purpose of the present investigation was to study why in pathological cases the extensor activity in the plantar response, *viz.*, the deviation from normal, may sometimes be limited to the early, and sometimes to the late, part of the reflex pattern.

MATERIAL AND METHODS

The investigation is based on a study of 120 patients with lesions of the central nervous system of types indicating pathological changes of the plantar reflexes. They were selected so as to illustrate adequately the problems under study.

The technique employed was essentially the same as that used in previous investigations (Grimby, 1963a). Thus, a spot on the plantar surface of the foot was exposed to painful repetitive electrical shocks over a period of

10 msec. and the reflex responses evoked were recorded simultaneously in the short hallux flexor and extensor. Confirmation of the electrode placing was obtained from voluntary contractions where possible, and from reflexly evoked contractions or from nerve stimulation in cases of total paralysis. Care was taken to attain very sensitive recording conditions, and contractions too weak to result in discernible toe movements were often recorded. Equally good responses from both the flexor and the extensor muscles were a prerequisite. No conclusions were drawn from experiments in which only a few units were activated in one of the muscles. All remarkable results were confirmed by repeated experiments.

RESULTS

In practically all pathological cases examined, the reflex pattern consisted of both flexor and extensor activity and all kinds of transitional forms were observed, from cases in which the responses obtained were predominantly flexor in type, to cases in which extensor activity was equally dominant. There was no absolute correlation between the degree or site of the nervous lesion and the amount of extensor activity in the reflex pattern. Thus, strongly dominant flexor activity might occur in cases of complete cord transection, while cases with only slight cerebral disorders might show reflex patterns dominated throughout by extensor activity.

In about half of the cases studied the relation between the strength of the extensor and flexor activities was the same in the early and the late parts of the reflex pattern. In the other half this relation varied, consistently or only occasionally, with the reflex latencies, to such an extent that the reflex pattern seemed to be composed of two antagonistic components. The change from one component to the other occurred at latencies from 150 up to several hundred msec., varying with their relative strength.

The following account of the observations made will deal mainly with the reflex patterns composed of two antagonistic components. These types of pattern were observed in 48 patients, but for clarity

of presentation, three cases have been selected for more complete description, since in these cases the relative variations observed in the two reflex components, on changes in the experimental situation, were large enough to be particularly illustrative and, at the same time, of such a type as to be fully representative also of the other cases. Reflex patterns in which extensor activity was predominant in the early, and flexor activity in the late part of the reflex will be termed 'extensor-flexor' patterns, while patterns with early flexor and late extensor dominance will be termed 'flexor-extensor' patterns.

EXTENSOR-FLEXOR PATTERNS Case 1 (Fig. 1) was a 26-year-old man with spasticity of uncertain origin in one leg. Clinical stimulation (slow stroking along the sole by a blunt needle) invariably gave a flexor plantar response on the healthy side, while on the spastic side alternating flexor and extensor reflexes resulted. Voluntary movement of the toes was apparently not affected. Voluntary responses to stimulation of the dorsal side of the foot (from which no reflex activity could be evoked) had a minimum latency of 200 msec.

On the healthy side electrical stimulation evoked pure flexor patterns and pure plantar flexion of the hallux, independently of the stimulus strength. On the spastic side weak stimuli gave rise to extensor-flexor patterns (Fig. 1 A) and to reflex movements consisting of an initial dorsiflexion and a secondary plantar flexion of the great toe. The initial extensor activity invariably had a latency of about 100 msec., and its strength and duration remained constant as long as the stimulus strength was kept unchanged. The latency of the part dominated by flexor activity ranged between 150 and 250 msec. Its strength and duration varied with the patient's attention and expectancy, the response being strong and long-lasting on anticipation of a painful stimulus but weak and brief on anticipation of a weak one. The

FIG. 1. Cerebral lesion without paralysis (case 1). A, strong stimulation; B, weak stimulation. Recordings from flexor hallucis brevis (top) and from extensor hallucis brevis (lower tracings). Time 10 msec. Further description and comments in text.

short-latency extensor activity increased in strength and duration as the stimulus intensity was raised, while the late flexor activity tended to decline. On strong stimuli the entire reflex pattern was predominantly extensor (Fig. 1 B) and no late plantar flexion of the hallux could be observed; a few flexor units were, however, activated in the initial part of the pattern, which agrees with previous observations that on sufficiently strong stimulation there is a certain amount of antagonistic activity in addition to the predominant activity (Grimby, 1963a).

Hagbarth and Finer (1963) have shown that the human nociceptive withdrawal reaction involves a late component, probably of cerebral origin, which is apparent particularly if the stimulus is not interrupted by the movement produced by the initial spinal reflex. In order to study the correlation between this cerebral reaction and the late flexor activity the following experiment was performed with the aid of case 1.

The recording electrodes were mounted on a piece of wood which was attached to the patient's heel and hallux. The electrodes were so arranged that they were withdrawn from the sole on plantar flexion of the hallux but not on movements at the ankle joint or in the leg. A stimulus of long duration was applied. Because of the duration of the shock artefact it was not possible to study the electromyographic recording in the short hallux flexor, but the latency of the effective plantar flexion of the toe could be measured since the shock artefact changed in appearance when the stimulating electrodes were detached from the skin. The latency at which the stimulation was interrupted was found to correspond to that recorded for the late flexor activity in Figure 1 A. The same result was also obtained when applying the same high stimulus intensity which gave the long-lasting extensor response in Figure 1 B. The plantar flexion of the hallux was automatic insofar as the patient could not suppress it and need not consciously think of doing so, to escape the stimulus.

Extensor-flexor patterns were obtained in eight cases. The latency of the early extensor activity was brief and its strength and duration fully dependent on the stimulus strength, although the same strength and duration as in case 1 was only exceptionally attained in the other patients, on application of the available stimulus intensities. The late flexor activity had a latency around or just below that of the fastest voluntary response. Its strength could always be influenced by psychic factors such as the patient's attention or expectancy and its relative role in the pattern was invariably reduced as the stimulus strength was increased. In some patients the late flexor activity was entirely dependent on cerebral factors and was absent with brief and strong

stimulation, as in case 1; in other patients it was less dependent on cerebral factors and remained even with very strong stimuli. In half of the cases the plantar responses obtained on clinical stimulation were exclusively flexor, in the others alternating flexor and extensor.

Extensor-flexor patterns were observed only in patients in whom voluntary power of the toes was well preserved.

FLEXOR-EXTENSOR PATTERNS Case 2 (Fig. 2) was a 46-year-old man with total hemiplegia (voluntary influence of the reflex pattern was thus excluded), and partial hemianaesthesia caused by a minor bleeding in the internal capsule due to hypertension. At the examination, 24 hours after the onset of the lesion, clinical stimulation gave a flexor-plantar response on the healthy side and alternating flexor and extensor activity on that paralysed.

On electrical stimulation a pure flexor pattern appeared on the healthy side, independently of the stimulus strength. On the paralysed side strong stimuli gave a pure flexor pattern of short latency (Fig. 2 A), medium-strong stimuli a typical flexor-extensor pattern (Fig. 2 B), and weak stimuli a pattern with a predominant extensor activity of long latency (Fig. 2 C). In a series of 10 medium-strong stimuli applied at some minutes' intervals the latency, strength, and duration of the flexor activity were constant while the extensor responses

showed wide variations. Sometimes an extremely long-lasting and intense extensor activity set in while the flexor responses were still present; sometimes the extensor activity did not start until a second after the flexor responses had subsided and was then brief and weak. While the shortest latency observed for the flexor activity was 60 msec., the extensor responses had a minimum latency of 200 msec. and were, besides, built up gradually.

Flexor-extensor patterns in response to single stimuli were obtained in 15 cases. The short-latency flexor activity was always directly correlated with the stimulus strength; sometimes it was quite similar to that in case 2, sometimes its maximum duration was much shorter. The late extensor activity was always less dependent on the stimulus strength than on other factors. It might be extremely varying in all respects, as in case 2, or invariably have a fairly short latency (150-350 msec.) and high intensity, or else invariably have a latency of several seconds and low strength. An extensor plantar response could be evoked on clinical stimulation in all patients examined but a flexor response could only in exceptional cases be obtained.

Case 3 (Fig. 3) was a 58-year-old man who for three months had had a total hemiplegia (voluntary influence on the reflex pattern was thus excluded) and hemianaesthesia due to occlusion of the internal carotid and the middle cerebral arteries. Clinical stimulation gave a plantar response of flexor type

FIG. 2. Case of internal capsule bleeding with total hemiparesis (case 2). A, strong stimulation; B, medium-strong stimulation; C, weak stimulation. Recordings from flexor hallucis brevis (top) and extensor hallucis brevis (lower tracings). Time 20 msec. Further description and comments in text.

FIG. 3. Case of cerebral thrombosis with total hemiparesis (case 3). A, the first, and B, the last, reflex obtained in a series of supraliminal stimulations at a frequency of about 2/sec. C and D, same in a series of threshold stimulations. E and F, same in a series of subliminal stimulations. Recordings from flexor hallucis brevis (top) and extensor hallucis brevis (lower tracings). Time 10 msec. Further description and comments in text.

on the healthy and of extensor type on the paralysed side.

Electrical stimulation gave a pure flexor pattern on the healthy side, independently of the strength and frequency of the stimulus. On the paralysed side, single stimulation gave pure flexor activity, which increased in strength and duration as the stimulus intensity was raised. After some repeated supraliminal stimuli (Fig. 3 A) at a frequency of 1 to 3 per sec., the strength and duration of the flexor responses increased (Fig. 3 B) in the same manner as if the stimulus strength had been raised. With a repeated threshold stimulus (Fig. 3 C), there was hardly any change in the flexor responses but after some repeated stimuli, they were followed by an extensor activity of a latency of 300 to 500 msec. (Fig. 3 D). After some repeated subliminal stimuli, on the other hand, a pure extensor activity set in which increased in strength and diminished in latency as the number of stimuli and the frequency were increased (Fig. 3 F). At a frequency of less than 1 per sec., no extensor responses were obtained. At 1-3 stimuli per sec., a weak extensor activity was observed which could be correlated to a particular stimulus in the series; the latency was found to range between 500 and 150 msec. At frequencies of 5 to 10

per sec., a strong extensor activity resulted which was continuous so that no latency values were measurable.

In 25 patients a single stimulus invariably gave flexor activity, but on repeated electrical or mechanical (pinprick) stimulation extensor responses were also obtained. On strong repeated stimulation predominant flexor activity always resulted (as in Fig. 3 B). Its latency was invariably less than 800 msec. On very weak repeated stimulation extensor activity was always dominant (as in Fig. 3 F). In some cases it set in so suddenly and at such low stimulating frequencies that the initiating stimulus in the series could readily be identified, but as a rule these responses were built up too slowly and at too high stimulus frequencies to permit such identification. When measurable, the latency was never below 150 msec. The critical intermediary stimulus strength giving rise both to early flexor and late extensor activity (as in Fig. 3 D) could in some cases readily be found, but in most cases it could be traced only with difficulty.

In cases giving flexor-extensor patterns on single stimuli, the extensor activity could be considerably increased in strength and reduced in latency on a repeated weak stimulation. In cases where single

shocks gave both flexor and extensor activity of short latency, pure extensor activity could be evoked by means of repeated weak stimuli.

There is such a close similarity between cases 2 and 3 (cf. Fig. 2 A, B, and C with Fig. 3 B, D, and F) that it is justifiable to regard the flexor-extensor patterns obtained on single stimulation and those resulting only on repeated stimulation as being fundamentally equivalent. Flexor-extensor patterns were common in cases of slight paralysis, independently of the site of the lesion, and in cases of total paralysis caused by hemispheric lesions (12 out of 17 cases) but were only rarely observed in total paralysis due to spinal cord lesions (two out of 24 cases).

In the patients with severe cerebral lesions, the interval between onset of the injury and the examination was a matter of days or months, but only seldom of years. In the serious spinal lesions, on the other hand, the interval between onset and examination might be months or even years but was rarely as short as a matter of days. Flexor-extensor patterns were observed in cases with a history of only some hours, as well as in cases with a history of several years, but they were more common in acute than in chronic cases. Some patients with stationary lesions were followed up from acute to subchronic stages; in two of these cases the extensor activity successively increased in relation to the flexor activity, and in one case a flexor-extensor pattern changed into a pure extensor pattern.

The different incidence of the flexor-extensor pattern observed in spinal and cerebral cases respectively may in part be explained by the fact that the spinal cases were, as a rule, examined at later stages of their injuries than were the cerebral cases. There was, however, a marked difference also between spinal and cerebral lesions of some months' standing (flexor-extensor patterns in none out of seven, and in five out of nine cases respectively) and the site of the lesion *per se* must thus also play a part (cf. Discussion).

Fifteen cases with functionally complete spinal cord transection were examined. Although slight differences might be observed between the early and late components of the reflex patterns, both components were always dominated by one and the same type of activity. In two cases a flexor activity of very short latency was obtained, the strength and duration of which increased with the stimulus strength; this flexor activity was thus compatible with the early flexor activity in flexor-extensor patterns. Even on repeated stimulation, however, no extensor activity could be elicited in these cases. In three cases an extensor activity of long and varying latency was observed, which could be built up by repeated weak

stimuli, thus being compatible with the late extensor activity in the flexor-extensor patterns. No early flexor activity could, however, be evoked in these cases even by very strong stimuli.

DISCUSSION

The investigation has shown that a brief stimulus applied to the plantar surface of the foot may give rise to a reflex response consisting of early activity of constant short latency and of a strength and duration directly correlated with the stimulus strength, and of an antagonistic late activity of varying and fairly long latency, which is not directly related to the stimulus strength. The discussion below will exclusively deal with such responses.

The features of the short-latency activity are the same whether it is flexor or extensor in type. The latency of the initial discharge is so short that it must be a spinal reflex with short central delay, transmitted through rapidly conducting afferent A fibres (cf. Grimby, 1963a). The rest of the activity is a direct repetition of the initial discharge, and the duration is directly correlated to the stimulus strength, whether the cerebrospinal connexions are intact or completely severed. Throughout its activity the short-latency reflex must be presumed to be spinal. Its later parts may perhaps be sustained by slower afferent A fibres, which are known to play a significant role for the after-discharges in spinal reflexes (Tureen, 1941; Wilson and Talbot, 1964). No regular involvement of C fibres is possible, since the activity has disappeared when the C fibre responses begin to set in, except on very strong stimulation.

The long-latency flexor activity may in some cases bear a close similarity to the cerebral component of the withdrawal reaction described by Hagbarth and Finer (1963); it is, however, not always equally dependent on cerebral factors. On the basis of the present evidence it cannot be decided whether the late flexor activity is a purely cerebral defence reaction, or a highly organized spinal reflex under cerebral control; perhaps it may be sometimes the one, sometimes the other type.

The long-latency extensor activity increases in strength on repeated stimulation and is thus favoured by long-lasting central excitatory states. Its latency varies within wide limits, and thus the delay must be to a large extent central. The extensor activity in the flexor-extensor pattern seems to be identical with the late part of the pure extensor pattern which is common in cases of complete spinal cord transection, and therefore it must be presumed that it is conducted through purely spinal pathways.

The latency of the late extensor activity is generally so short that the reflex must be transmitted through A fibres, although its strength tends to increase gradually and its late parts are closely similar to the tonic C fibre response described by Kugelberg (1948) as being a component of the Babinski sign. The underlying excitatory state can be built up most readily by a series of weak electrical or mechanical stimuli. It is well known that a characteristic feature of the C reflex is a substantial increase of the discharge by summation of afferent volleys (Koll, Haase, Schütz, and Mühlberg, 1961), and that even very weak natural stimuli tend to give rise to repetitive C fibre activity (Zotterman, 1939). Afferent C fibres may thus be presumed to be involved in the late extensor activity, even though it is of too short latency to be a pure C fibre response.

The long-latency extensor activity is absent in healthy subjects and is inhibited by the short-latency activity in pathological cases. On administration of D.O.P.A. to spinal cats, Andén, Jukes, Lundberg, and Vyklický (1964) observed a reflex with long central delay which under normal experimental conditions was masked by inhibition from the short-latency reflex paths. The similarities between the two late activities are so striking that they may be assumed to be analogous phenomena.

Since extensor-flexor patterns were observed only in cases in which voluntary movement of the toes was well preserved, the cortex must be essential for this type of pattern.

Flexor-extensor patterns are common in all cases of cerebral lesions and in slight spinal injuries but rare in cases of grave spinal injuries. In cases of functionally complete spinal cord transection pure flexor patterns might occur but never flexor-extensor patterns, since whenever extensor activity was observed it was present both in the early and the late parts of the reflex pattern. The number of patients studied is, however, not very large, and it cannot be ruled out that a flexor-extensor pattern may occur also in patients with isolated spinal cords. It is evident however that this response is much more likely to occur when the cerebrospinal connexions are preserved. A large number of cases with verified complete cord transection have previously been extensively studied, although only by clinical routine methods (Head and Riddoch, 1917; Riddoch, 1917; Kuhn, 1947; Kuhn, 1950; Pollock, Boshes, Finkelman, Chor, and Brown, 1951; Marshall, 1954). The only reference made in those investigations to the significance of the duration and strength of the stimulus is that a brief and strong stimulus favours the elicitation of an extensor plantar response. If the series had included cases with flexor-extensor patterns, such a stimulus should,

instead, have increased the chance of obtaining a flexor plantar response.

Even severe lesions at levels above the brain-stem do not reduce the possibilities of obtaining a flexor-extensor pattern. The supraspinal influence which prevents the pathological extensor tendency from having any effect on the initial part of the flexor-extensor pattern is thus likely to derive from the brain-stem. This concept is supported by theoretical (Sherrington, 1910; Holmquist and Lundberg, 1961) as well as clinical observations (Walshe, 1914) showing that the brain-stem has an inhibitory effect on spinal 'flexor' reflexes, the term being used in its physiological sense, one of the flexor reflexes being the short hallux extensor reflex.

In cases of extensor-flexor patterns, clinical stimulation always results in flexor activity, and only sometimes in an extensor plantar response. At clinical examinations of cases of flexor-extensor patterns the resulting plantar responses are always extensor, seldom flexor in type. It is thus, above all, the late activity that gives rise to the clinical reflex. Even though extensor activity can be evoked in the normal subject, besides the dominant flexor activity in the early part of the plantar response, provided that very strong stimuli are applied (cf. Grimby, 1963a), it can be presumed that a regular dominant extensor activity is of pathological significance, whether it occurs in the early or in the late part of the pattern. Thus, the technique described above may perhaps be of some use in the clinical examination as a complement to the routine clinical tests.

This investigation has shown that an injury of the reflex mechanism may give rise to an early and to a late extensor activity in the plantar pattern, and that the properties of both these extensor activities differ in several respects. Further research is necessary before it can be decided whether they constitute two different pathological reflexes or whether they are to be considered as the beginning and end, respectively, of one and the same pathological reflex; maybe in the end the problem will prove to be a matter of nomenclature.

SUMMARY

In 120 patients with lesions of the central nervous system suggesting pathological changes of the plantar reflex, painful repetitive electric shocks were delivered over a period of 10 msec. to a spot on the plantar surface of the sole, and the reflex patterns obtained by simultaneous electromyographic recording in the short hallux flexor and extensor were studied.

In normal subjects flexor activity is strongly predominant in the reflex pattern, whereas there is a

tendency to dominant extensor activity when the reflex mechanism is injured. In the present study, attention has been focused on cases with different incidences of the pathological extensor activity in the early and late parts of the reflex pattern.

1 In some pathological cases the reflex pattern consists of an early part of predominant extensor activity and a late part of predominant flexor activity. The part with extensor dominance is of such a short latency that it must be a purely spinal reflex; its strength is fully dependent on the stimulus strength. The latency of the part with flexor dominance corresponds to that of the fastest voluntary reactions; its strength is sometimes fully dependent on cerebral factors.

2 In some pathological cases the reflex pattern consists of an early part of predominant flexor activity and a late part of predominant extensor activity. The latency of the part with flexor dominance is so short that it must be a purely spinal reflex; its strength is fully dependent on the stimulus strength. The latency and strength of the part with extensor dominance show wide variations; sometimes it is fully dependent on long-lasting spinal excitatory states which can be built up by, for example, weak repetitive stimuli.

3 Reflex patterns consisting of two antagonistic components were observed only in cases in which the cerebrospinal connexions were preserved.

4 The plantar responses studied in the clinical routine examinations are, on the whole, equivalent to the late part of the reflex pattern.

REFERENCES

- Andén, N. E., Jukes, M. G. M., Lundberg, A., and Vyklický, L. (1964). A new spinal flexor reflex. *Nature (Lond.)*, **202**, 1344-1345.
- Grimby, L. (1963a). Normal plantar response: Integration of flexor and extensor reflex components. *J. Neurol. Neurosurg. Psychiat.*, **26**, 39-50.
- Grimby, L. (1963b). Pathological plantar response: disturbances of the normal integration of flexor and extensor reflex components. *Ibid.*, **26**, 314-321.
- Hagbarth, K. E., and Finer, B. L. (1963). The plasticity of human withdrawal reflexes to noxious skin stimuli in lower limbs. In *Brain Mechanisms*, edited by G. Moruzzi, A. Fessard, and H. H. Jasper, pp. 65-78. Elsevier, Amsterdam.
- Head, H., and Riddoch, G. (1917). The automatic bladder, excessive sweating and some other reflex conditions, in gross injuries of the spinal cord. *Brain*, **40**, 188-263.
- Holmquist, B., and Lundberg, A. (1961). Differential supraspinal control of synaptic actions evoked by volleys in the flexion reflex afferents in alpha motoneurons. *Acta physiol. scand.*, **54**, suppl. 186, 1-51.
- Koll, W., Haase, J., Schütz, R. M., and Mühlberg, B. (1961). Reflexentladungen der tiefs spinalen Katze durch afferente Impulse aus hochschwelligen nociceptiven A-Fasern (post d-Fasern) und aus nociceptiven C-Fasern cutaner Nerven. *Pflügers Arch. ges. Physiol.*, **272**, 270-289.
- Kugelberg, E. (1948). Demonstration of A and C fibre components in the Babinski plantar response and the pathological flexion reflex. *Brain*, **71**, 304-319.
- , Eklund, K., and Grimby, L. (1960). An electromyographic study of the nociceptive reflexes of the lower limb. Mechanism of the plantar responses. *Ibid.*, **83**, 394-410.
- Kuhn, W. G. (1947). The care and rehabilitation of patients with injuries of the spinal cord and cauda equina. *J. Neurosurg.*, **4**, 40-51.
- Kuhn, R. A. (1950). Functional capacity of the isolated human spinal cord. *Brain*, **73**, 1-51.
- Marshall, J. (1954). Observations on reflex changes in the lower limbs in spastic paraplegia in man. *Ibid.*, **77**, 290-304.
- Pollock, L. J., Boshes, B., Finkelman, I., Chor, H., and Brown, M. (1951). Spasticity, pseudospontaneous spasms, and other reflex activities late after injury to the spinal cord. *Arch. Neurol. Psychiat. (Chic.)*, **66**, 537-560.
- Riddoch, G. (1917). The reflex functions of the completely divided spinal cord in man, compared with those associated with less severe lesions. *Brain*, **40**, 264-402.
- Sherrington, C. S. (1910). Flexion-reflex of the limb, crossed extension-reflex, and reflex stepping and standing. *J. Physiol. (Lond.)*, **40**, 28-121.
- Tureen, L. L. (1941). Form of the reflex response in relation to the pattern of afferent stimulation. *Proc. Soc. exp. Biol. (N.Y.)*, **46**, 543-544.
- Walshe, F. M. R. (1914). The physiological significance of the reflex phenomena in spastic paralysis of the lower limbs. *Brain*, **37**, 269-336.
- Wilson, V. J., and Talbot, W. H. (1964). Pattern of discharge of flexor motoneurons. *J. Neurophysiol.*, **27**, 451-463.
- Zotterman, Y. (1939). Touch, pain and tickling: An electrophysiological investigation on cutaneous sensory nerves. *J. Physiol. (Lond.)*, **95**, 1-28.