Acta physiol. scand. 1959. *46*. 165—173.

From the Nobel Institute for Neurophysiology, Karolinska Institutet,
Stockholm 60, Sweden.

The Discharge to Maintained Stretch of Spindles in Slow and Fast Muscles of Rabbit.

By

RAGNAR GRANIT and SABURO HOMMA.[1]

Received 19 December 1958.

Abstract.

GRANIT, R. and S. HOMMA. The discharge to maintained stretch of spindles in slow and fast muscles of rabbit. *Acta physiol. scand.* 1959. *46*. 165—173. — Systematic measurements of the maintained discharge to stretch at time 4—5 sec from onset have been carried out with 69 muscle spindles in ankle extensors and flexors of anaesthetized rabbits. Three main types of spindles can be separated on the basis of rate of discharge, slow, medium and fast spindles. The number of fast spindles is greater in fast muscle. Slow and medium spindles only are found in slow muscle.

It was noted by GRANIT, SKOGLUND and THESLEFF (1953) when testing muscle spindles with succinylcholine that spindles in tibialis anterior tended to put up higher average discharge rates than those in gastrocnemius or soleus (cat). Recently, when one of us (GRANIT 1958) studied the response of soleus spindles to maintained stretch in the decerebrate cat, frequency of discharge was plotted against extension of the muscle in mm at time 4—5 sec after onset of pull. There were considerable variations but the average rate of increase for 20 soleus spindles was as low as 3.5 impulses/mm, though the frequencies at zero extension, owing to gamma bias, averaged as much as 26 imp/sec. A limited number (7) of gastrocnemius spindles had been tested in the course of the same experiments. Their slopes averaged out at 6.5 imp/mm. These observations led to the surmise that spindles in slow and fast muscles might differ with respect to their frequency of discharge in maintained stretch.

When for other reasons some experiments were undertaken on rabbits the impression was obtained that in them the range of variation of the slope of the spindles' frequency-extension curves varied much more than in cats. It was then decided to study the response to maintained stretch in slow and fast muslces of this animal. The ankle muscles were used because of the relatively long dorsal roots in which their afferents are represented. In order to compare rabbits and cats measurements of spindle discharge were made at the same time as in the previous work, 4—5 sec after onset of stretch.

Methods.

The animals were given a dose of 5.0 ml/kg of a mixture of 10 % urethane and 1 % chloralose, one hind leg denervated except for the muscles to be used, laminectomy performed, and the leg fixed at the three joints. Muscle temperature was controlled by a thermocouple. Functionally isolated spindles were identified in thin dorsal root filaments. Conduction time was nearly always taken in order to determine conduction velocity from the nerve electrode at the knee to the dorsal root filament (average conduction distance 15 cm). A minority of the spindles had latent periods between 2 and 4 msec and thus conduction velocities below 75 m/sec, which generally are assumed to be myotube endings (MERTON 1953, HUNT 1954) but most of them had conduction times between 1.2 and 1.5 msec and therefore belonged to the rapidly conducting nuclear bag endings (100—125 m/sec). It was not possible to distinguish slowly conducting spindle afferents from the rapidly conducting ones by features other than conduction velocity.

The muscles used were soleus (S), gastrocnemius (G), plantaris (P) extensor digitorum longus (EDL) and tibialis anterior (TA). Abbreviations within brackets refer to the graph of Fig. 8. The two flexors, TA and EDL, were used with denervated ankle extensors and *vice versa*. All muscles were carefully isolated. Soleus in the rabbit is firmly fixed to the lateral gastrocnemius in the lower part of its belly, but for these experiments was dissected free.

---

[1] Present address: Laboratory of Physiology, Chiba University, Chiba, Japan.

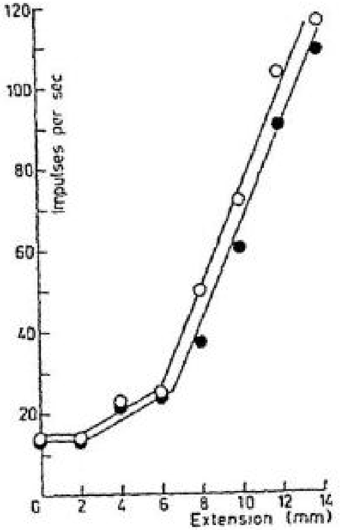


Fig. 1. Maintained discharge of gastrocnemius spindle.

Conduction velocity 100 m/sec.

Open circles, before, *filled circles*, after de-efferentation.

The myograph stand was fixed to a sliding device provided with a catch so that any extension in mm could be reproduced at will. Zero length was determined by the initial length necessary to make the myograph barely record a deflection. This would be a deflection of the order of 20 g.

The preparation just described usually had intact motor innervation of its spindles. This made it sensitive to painful stimuli or twist of the ear but, in between, the spindles discharged with the regular frequency characteristic of absence of, or very low gamma bias. In one animal the spinal cord was destroyed and, occasionally, in others, ventral roots were cut without noticeable influence on the discharge of spindles to stretch. If the basic rhythm of discharge was irregular, suggesting variations in gamma bias, more anaesthesia was given in small doses until the discharge became steady.

However, it is of interest to study the behaviour of a spindle before and after ventral root section in a specific case such as that of Fig. 1. Clearly its response to stretch has not changed after de-efferentation more than one is entitled to expect in comparing two series of stretches repeated at an interval of half an hour. In this time the injury discharge from the cut ventral roots should be gone.

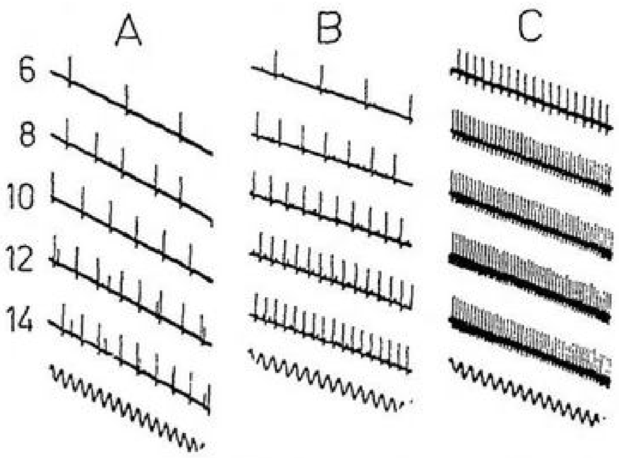


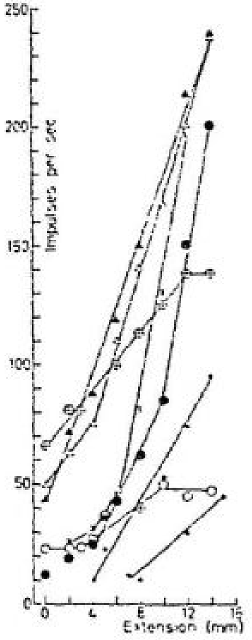
Fig. 2. Samples of maintained discharge of three spindles, A, B and C. Extension on the left in mm.

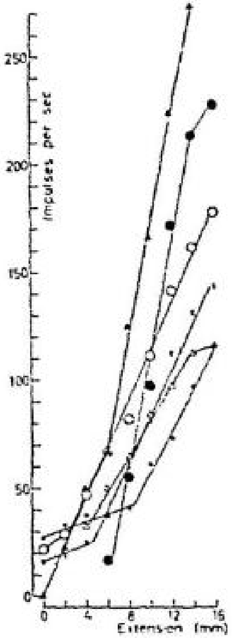
A: From medial gastrocnemius. Conduction velocity 115 m/sec.
B: From undivided gastrocnemius. Conduction velocity 100 m/sec.
C: From tibialis anterior. Conduction velocity 79 m/sec.
Time, 100 cps.

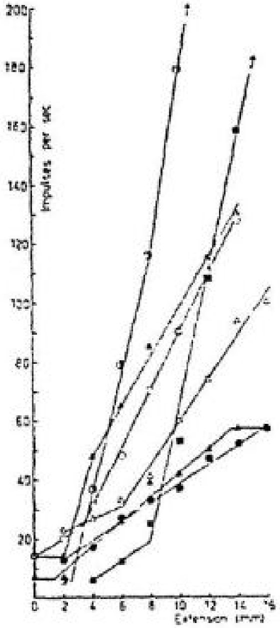
Results.

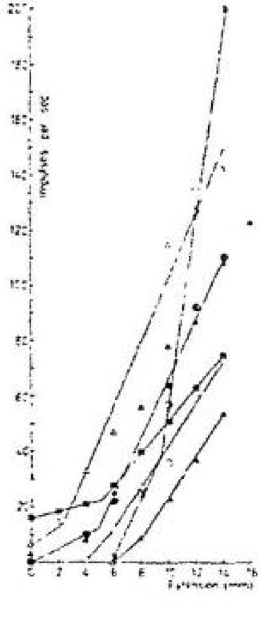
With respect to the frequency of discharge at comparable extensions, rabbit spindles may be subdivided into three main types, examples of which in Fig. 2 are shown under A, B and C respectively. The numerals 6 to 14 indicate muscle extension in mm. Rates of discharge are thus slow, medium or fast. Muscle spindles in ankle extensors of cats have been studied for several years in this laboratory, though — with the exception of soleus spindles (GRANIT 1958) — less systematically in relation to extension than in the present work. The general experience of one of us (R. G.) has been that very fast spindles do not occur in cat ankle muscles. However, flexors have but rarely been used for such purposes. Very high frequencies of discharge can, of course, be produced in cats by sufficient gamma bias.

Samples will now be given in Figs. 3—7 of discharge frequencies plotted against extension in mm for spindles in different muscles. Fig. 3 from tibialis anterior (TA) has been chosen to illustrate variations in a single experiment in which 8 spindles were isolated. Clearly this muscle contained spindles of different type but four of them belonged to type C with very fast frequencies of discharge and a slope above 12 imp/mm. The total number of TA spindles









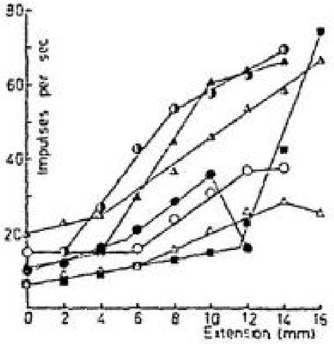


Fig. 3—7. Plots of frequency of discharge of muscle spindles against extension in mm.
Fig. 3. All spindles from the same animal's tibialis anterior.
Fig. 4. Spindles from extensor digitorum longus.
Fig. 5. Spindles from gastrocnemius.
Fig. 6. Spindles from plantaris.
Fig. 7. Spindles from soleus.

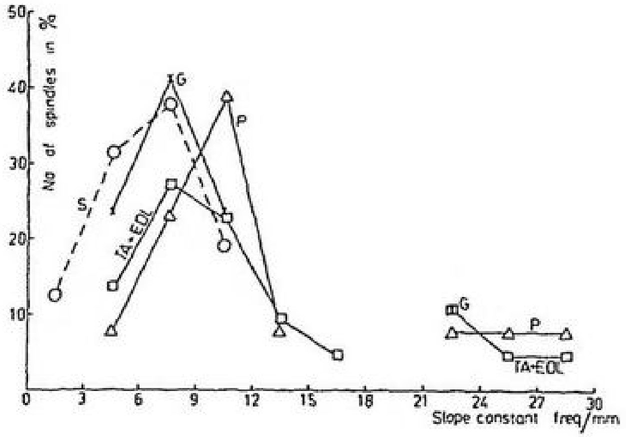


Fig. 8. Number of spindles in per cent of total in the muscles soleus (S), gastrocnemius (G), plantaris (P) and extensor digitorum longus (EDL) + tibialis anterior (TA) plotted against slope constants grouped as marked on the abscissa. Thus spindles with slope constants between end values of any group have been referred to midpoint of group. Slope constants slightly above 30 have been regarded as being 30. Number of spindles is for

$S = 16, G = 17, P = 13, TA + EDL = 23.$

was 16, from five animals. The maximum slope, measured, as always, from the upper, linear, portion of the curves, reached the incredibly high value of just over 30 imp/mm, the average being 13 spikes/mm. A graph will be given below in Fig. 8 for all experiments, a total of 69 spindles in different muscles.

Fig. 4 refers to the other flexor (EDL). Only 7 spindles in three animals were studied, the aim merely being to find out if there were spindles of type C also in this muscle. The average was 15 spikes/mm, the highest individual value 25. The flexors TA and EDL have been treated together in Fig. 8.

Fig. 5 shows samples from the gastrocnemius (G). The total was 17 spindles from 11 animals. Only two of them had slope constants above 12 spikes/mm and these are the two illustrated in Fig. 5, another one just reached 12 spikes/mm. The average was 9.8 imp/mm and so this muscle typically had B spindles. However, it also contains types A and C.

Fig. 6 illustrates samples from the extensor, plantaris (P). The total was 13 spindles only three of which had slopes below 8 spikes/mm (5.7, 7.5 and 7.5 respectively). There were four very fast spindles (slopes 12, 24, 26, 30). The average was 13.

Finally, Fig. 7 samples the extensor soleus (S). The total was 16 spindles in 9 animals. None of them had slope constants above 12 spikes/mm though one reached that value. The average was 6.0. Characteristically soleus has A and B spindles.

It is, of course, entirely arbitrary to divide spindles into groups with slope constants from 1 to 8 spikes/mm, 8 to 12 and beyond 12 spikes/mm and call them spindles of type A, B and C, or slow, medium and fast spindles respectively. A look at the graph of Fig. 8 suggests that the fastest spindles perhaps should be separated as a special group of their own because there is a gap between them and the others. This naturally raises the question of whether the fastest spindles might not in some way be abnormal. There are two very characteristic signs of abnormality in spindles: (1) they stop firing suddenly or start to discharge intermittently and many spindles will do this very early under excessive pull, (2) they become phasic and refuse to respond to maintained stretch, a fact that should make the experimenter suspect low blood pressure. Our fastest spindles by either of these criteria were not abnormal. On the contrary, they discharged at these high rates for many seconds beyond the 5 sec needed for the test, even at extensions as high as 12—14 mm. In order not to cause damage one hesitates to extend experiments at great extensions far beyond the time necessary for measurement. One more reason for regarding the fastest spindles as normal is their distribution in the graph of Fig. 8. There is no obvious explanation of why abnormal spindles would be so rare in the slow muscles and so common in the fast ones.

In rabbits contraction times in soleus tend to be between 55 and 60 msec, in gastrocnemius around 27, in plantaris around 20, in EDL around 17—19 and in tibialis anterior which is more variable, from 12—16 msec.

Discussion.

It has been shown by Gordon and Holbourn (1949) that contraction time in muscle twitch varies from fibre to fibre. Many muscles are mixed and in them the slow components tend to lie deeper than the fast ones (Denny-Brown 1929, Gordon and Holbourn 1949, review of earlier literature, Needham 1926). An example is tibialis anterior in the cat which is a fast muscle

(Denny-Brown 1929). Gordon and Phillips (1953) dissected out a deep, slow component which in the total twitch merely appeared as an insignificant tail after the fast events. In rabbits such a tail is often seen in the fast EDL. In embryological life intrafusal muscles grow out of extrafusal ones (*e. g.* Cuajunco 1927) and so, in the same muscle, may well have different mechanical properties depending upon site. The overall contraction time in twitch merely serves as a general guide. It will, of course, favour the fast components, partly because the slow ones are submerged in the fast twitch but also because slow muscle requires tetani to build up its response.

Now, this research was prompted by the notion that slow extrafusal systems may have correspondingly slow intrafusal ones and that the fast extrafusal fibres in fast muscles might give rise to spindle fibres with similar characteristics. Considering all the facts mentioned above there is nothing in our results that could not be explained by this hypothesis.

On the other hand, there is a very large anatomical literature on spindles from this and the previous century which demonstrates that intrafusal fibres have different lengths (see *e. g.* Sherrington 1894). One may distinguish short and long ones. It is not known how these are distributed in muscles. It is possible that the length of the intrafusal fibre may determine the amount of strain to which the sense organ will be subjected in stretch, provided that the spindle inserts on tendon or aponeurosis as it commonly does. Some spindles, however, insert on perimysium or endomysium at both polar regions. In the absence of precise histological data hypotheses based on intrafusal fibre length and site of insertion are useless. So also are theories based on nuclear bags of different properties. The simple mechanical hypothesis outlined above differs from mere speculation in that it has proved its value. It suggests that excessive pull on soleus should occasionally raise high frequencies of discharge in a spindle. We have seen this happen twice, one case being illustrated in Fig. 7. More often than not, however, soleus spindles stop increasing in frequency at great extensions.

As stated above, the frequency spectrum of spindles from the corresponding muscles in the cat does not extend to the high frequencies seen in the rabbit. What slope constants we possess for soleus and gastrocnemius in the cat also average out at lower values than in the rabbit. Why this should be so we do not know