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Phasic Stretch and 'Spindle Constant' in Slow and Fast Rabbit Muscle.

By

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Abstract.

GRANIT, R. and S. HOMMA. Phasic stretch and 'spindle constant' in slow and fast rabbit muscle. *Acta physiol. scand.* 1959. *46*. 174—184. — The aim of this paper is to find a mathematical expression for the inherent properties of muscle spindles as indicators of phasic changes. Rate of change of muscle extension and rate of change of interval between two successive spindle discharges have been measured and plotted, one against the other. Their ratio has been found constant at different rates of stretch. This is the spindle constant, defined in the paper.

It is well known from the work of MATTHEWS (1933) that the muscle spindle responds to rate of stretch as well as to maintained pull of the muscle. In the afferent terminals of individual muscle spindles in the frog KATZ (1950) recorded equivalent dynamic and static changes of 'generator potential'. It is hardly necessary to quote further papers in support of what is common knowledge,

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namely that fast stretch of limited amplitude may raise higher discharge frequencies than slow pull extending the muscle to considerably greater length.

The discharge frequency in maintained stretch varies a great deal from spindle to spindle but the relation between frequency and extension is linear (Eldred, Granit and Merton 1953, Granit 1958). We have recently (Granit and Homma 1959) found this rule well obeyed with rabbit muscle spindles and have also shown that there is a general relation between contraction time of a muscle and the slope of the frequency/extension-curve of its spindles. The slope tends to be small in slow muscle and steep in fast muscle. Nothing is known, however. of the phasic properties of different types of spindles in relation to rate of extension. This paper attempts to fill this gap in our knowledge.

The biological background of this work is partly an interest in receptor properties as such but mainly a desire to understand principles of rapid control in the particular situation when a brief contraction of one muscle stretches its antagonist at the same joint, and the muscles concerned — as often is the case — have different contraction times.

With this in mind we have developed a technique of stretching, the principle of which is that one ipsi- and one contralateral ankle muscle are jointed to the opposite ends of a horizontal lever pivoting around its midpoint. With this arrangement, when one muscle is made to contract by a tetanus to its nerve, pull will be exerted on the contralateral fellow muscle at the opposite end of the lever. Thus rates of stretch of a physiological order of magnitude can be conveniently obtained and it is possible to measure rate of extension together with the discharge frequency of an indicator spindle from the extended muscle. It is necessary in such work to use soleus for graded contractions because fast muscles such as the ankle flexors accelerate the spindle too rapidly for accurate measurements of frequency.

Methods.

Rabbits were anaesthetized by an intravenous injection of a mixture of 1 % chloralose and 10 % urethane (5 ml/kg). Ether was given during the operation but not during the experiments. This is the preparation already described in the previous paper (Granit and Homma 1959), with the difference only that the animals always were de-efferented from L5 to the end of the sacral roots. Spindle afferents were isolated in the dorsal roots, as described. Muscles were isolated and the leg denervated as described in the previous paper.

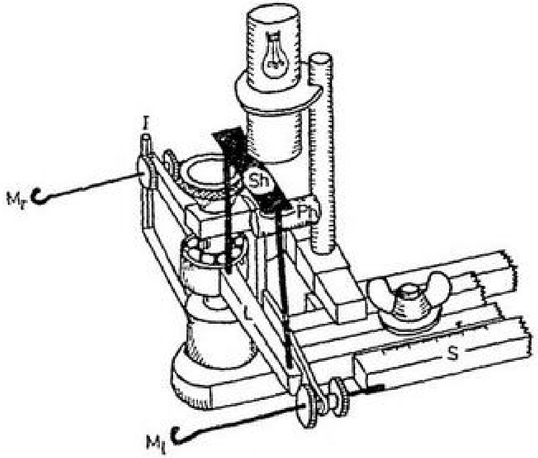

Fig. 1. Diagram of apparatus, as described in text.

The essential new feature of the experiment is the apparatus shown in Fig. 1. *L* is the horizontal lever mentioned in the introduction. It moves on ball bearings. Right and left ankle extensors (M_r and M_l) are attached to it by threaded hooks. By altering the length of these hooks, the correct initial alignment of the lever, as shown by the indicator *I*, is achieved. Light illuminates a photocell (*Ph*) whose exposed end faces a shutter (*Sh*) attached to the left lever arm. By this arrangement, the output of the photocell is directly proportional to movement of the lever arm, and hence, to change in muscle length. The strain gauge on the same arm records tension. The stand holding the midpoint of the lever can be shifted along the scale (*S*), so as to set initial length. The amplified outputs of photocell and strain gauge are led to one double beam cathode ray tube to give records of extension and tension respectively (see figures).

The impulses discharged by the indicator spindle are led to a pair of amplifiers in parallel. The output of one is displayed as a conventional record of spikes; the other amplifier drives an interval recorder, used in several papers from this laboratory and designed by Dr. Bernhard Frankenhaeuser. The output of the interval recorder is shown on the other beam of the same tube. In a typical interval record (Fig. 3 b) the height of each vertical stroke is directly proportional to the interval between two successive impulses and hence, inversely proportional to frequency. Joining the peaks of a series of these strokes gives the curve of change of impulse intervals. Direct recording of spindle discharge is merely a running control of the interval recorder, because the latter is sensitive to spike amplitude and may fail if this diminishes while a measurement is in progress.

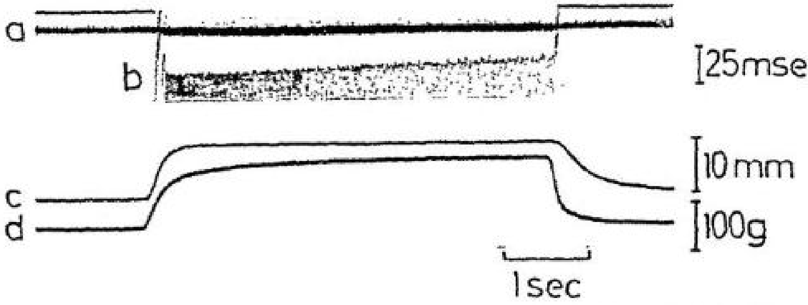

Fig. 2. Soleus stretched by contraction of contralateral soleus (tetanization of tibial nerve).

a: Spindle discharge from dorsal rootlet of L7.
b: Spindle discharge is led to interval recorder; the vertical height of each stroke is proportional to interval between two successive spikes. Calibration of 25 msec interval.
c: Extension curve recorded by photocell. Calibration of 10 mm.
d: Tension curve. Calibration of 100 g.

In the actual experiments muscle M_r was the right soleus which is tetanized from its muscle nerve. The lever then pulls on the left muscle M_l which in our experiments has been soleus, plantaris or, occasionally, tibialis anterior. In this way different smooth rates of exponential stretch can be obtained by varying the frequency of the supramaximal tetanic stimulus.

Results.

In Fig. 2 the two lower curves (*c* and *d*) show extension and tension respectively, in one de-efferented soleus when the other is tetanized for 5 sec. The upper records illustrate spindle discharge in the opposite soleus directly (*a*) and by the interval recorder (*b*). Tension (which in all records is the thicker line) as well as directly recorded discharge frequency (*a*) merely serve as general controls. All measurements to be presented below deal with mm extension (*c*) and interval (*b*) in msec which is easier to measure than its inverse value, the discharge frequency. It has also turned out that interval lends itself more readily to quantitative treatment than frequency. In Fig. 2 adaptation is well shown by the slowly rising contour of the peaks of the interval record. This figure is shown to illustrate the full course of the events at slow film speed.

For measurements the film has been run at higher speed, as

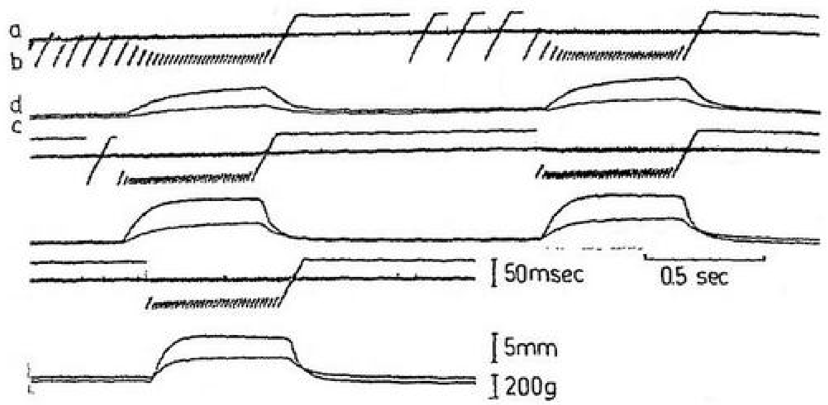

Fig. 3. As Fig. 2, but five experiments at increasing rates of extension from 1 to 5. Extension 3.4 mm. Note calibrations of interval recorder, strain gauge and lever excursion measuring extension.

in Fig. 3. We shall be concerned solely with the time from zero to maximum extension or minimum interval, respectively. Fig. 3 shows successive records of stretch of soleus at different rates of extension. Otherwise it is similar to Fig. 2. These records will now be analyzed in detail.

Extension: Let E_t be the extension at any early time t from zero onwards, and E_f the final semistationary state of extension which, from the point of view of the present problem, may be regarded as a stationary maximum.

Measured points on the five curves of Fig. 3 are plotted in Fig. 4 a on semilogarithmic paper. It is seen that log $(E_t - E_f)$ plots as a straight line against t, but only during the first 200 msec. However, this is the time during which discharge intervals rapidly shorten to reach a final minimum and, so, is the time in which we are interested. The lines drawn are described by the simple exponential equation

$$E_t = E_f\,(1 - e^{-t/\beta}), \tag{1}$$

in which β is the slope constant given by the numerals opposite each line of Fig. 4 a. It will be called the extension constant and its dimensions are time. For the present purpose equation 1 is a good enough approximation to our data.

The extension constant β decreases from 400 at slow rates of pull to 55 with fast extension.

Discharge intervals: Let I_f be the final minimum interval (in

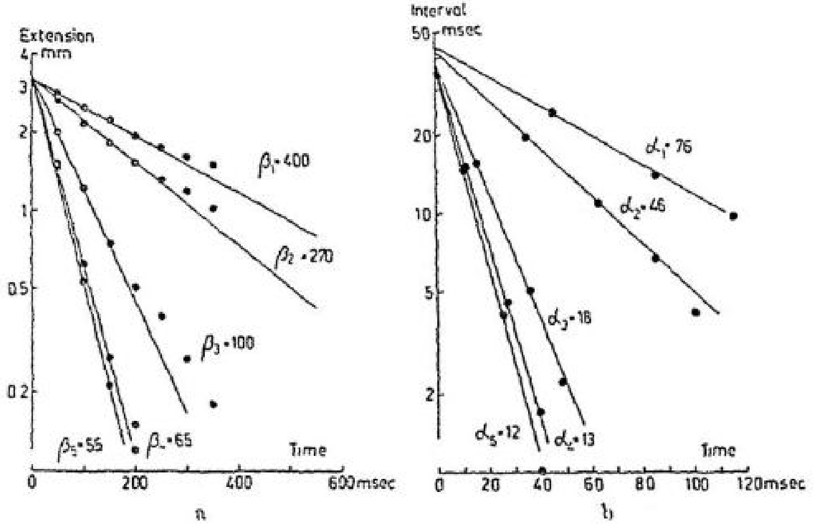

Fig. 4. Analysis of Fig. 3. Logarithmic ordinates. From above downwards the five curves refer to the experiments 1—5 of Fig. 3.

a: Relation between time and extension, latter defined as $E_f - E_t$. $\beta_1, \beta_2 \ldots \ldots \beta_5$ are the extension constants calculated from equation 1 (see text).
b: Relation between time and interval, defined as $I_t - I_f$. Curves drawn according to equation 2. $\alpha_1, \alpha \ldots \ldots \alpha_5$ are the interval constants (see text).

each of the five experiments of Fig. 3), I_t the interval at any early time t, and I_i the initial interval. These were found to be related by the equation

$$I_t = I_f + I_i e^{-t/\alpha}. \tag{2}$$

The points measured in the experiment are plotted in Fig. 4 b. There is a good fit when log $(I_t - I_f)$ is plotted against t. The slope of each line is an interval constant α, expressed in msec. It is seen that the values of α, just as those of β, decrease with faster pull.

With these data available it is possible to relate rate of extension to rate of change of interval. Fig. 5 shows the interval constant α plotted against the extension constant β. Clearly their ratio is constant and for this particular spindle β/α is 5.0. This ratio serves to characterize the sensory organ in phasic stretch and will be called the *spindle constant*.

Significance of spindle constant. Having shown how the spindle constant is obtained the next step is to demonstrate the biological value of this concept. The first comparison concerns slow and

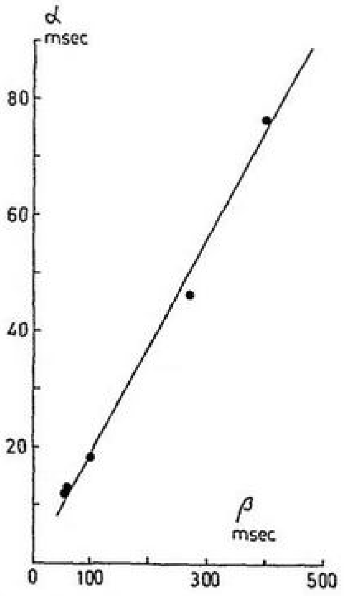

Fig. 5. Demonstration of constant ratio between interval constants α and extension constants β of Fig. 4. The spindle constant is defined as the ratio β/α which in the present case is 5.0.

fast muscle. In the rabbit (Granit and Homma 1959) soleus is slow, plantaris has a large fast component but also a small, slow one, tibialis anterior is fast and does not seem to possess the well-defined slow component that Gordon and Phillips (1953) found in the cat's tibialis. However, it is likely that most ankle muscles contain fibres of different contraction times. The dominant type will dominate the myographic record. A number of spindle constants measured in the manner demonstrated are shown in

Table 1.

Soleus	Plantaris	Tibialis anterior
7.1	5.0	2.7
5.2	3.2	2.1
5.2	3.1	—
5.0	2.7	—
5.0	2.1	—

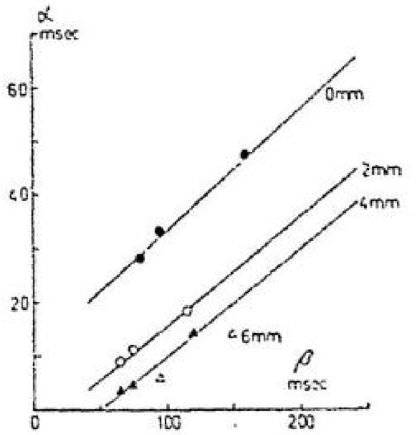

Fig. 6. Plot of α against β as in Fig. 5 but from another experiment with soleus at the initial lengths marked in the figures.

Thus, in the rabbit, the spindle constants are large in slow muscle and small in fast muscle. Values for tibialis anterior were difficult to obtain for reasons stated above. The spindle constants thus serve to differentiate spindle types in slow and fast muscle from the point of view of their phasic responses. In the case of tonic (steady) stretch, when spindle frequency is plotted against extension, a linear graph is obtained whose slope for a spindle in slow muscle is less than one in fast muscle, demonstrating a similar differentiation in spindle responses (Granit and Homma 1959).

Very generally, large spindle constants mean that fast rates of extension do not play the same role for the discharge of the sense organ as they do when the spindle constant is small. In the latter cases a little change in rate of extension greatly influences discharge rate. Slow muscles containing spindles with large spindle constants, when pulled upon at different rates by their antagonists, therefore will not signal variations in rate of stretch as efficiently as fast muscles in which the spindle constants are small.

The question next arises as to whether different levels of tonic gamma activity might influence the spindle constants. To a first approximation gamma activity is likely to cause a steady contraction of the muscular poles of the spindle and so be equivalent to an 'internal' variation in length of the nuclear bag. This effect can be imitated by starting stretch at different initial lengths.

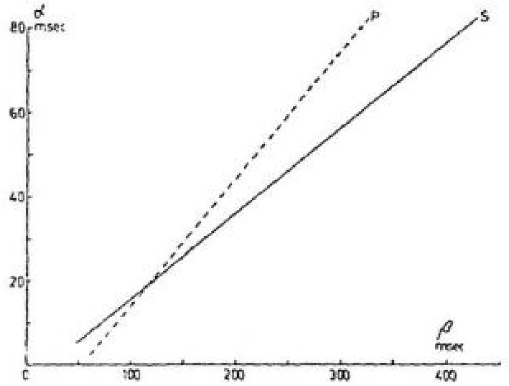

Fig. 7. Plot of α against β as in Fig. 5 in experiment in which one soleus spindle (*S*) and one plantaris spindle (*P*) were analyzed in succession, both muscles being at the same initial length.

Fig. 6 is an experiment with a soleus muscle at 0, 2, 4 and 6 mm initial length. It is seen that the three curves for 0, 2 and 4 mm are parallel when α is plotted against β, as in Fig. 5. (Only two values could be obtained at 6 mm owing to the technical difficulties mentioned, when frequencies of discharge are high.) Thus the spindle constant as such does not depend upon the extent to which the nuclear bag is biased by internal stretch caused by tonic gamma activity contracting the muscular poles. It is an inherent property of the sensory organ. Granit and Homma (1959) came to the same conclusion with regard to the variations of the slope constants in static stretch, mentioned above.

Inspection of Fig. 6 shows that the interval constant α diminishes under stretch (or gamma activity causing intrafusal stretch). This means that good gamma bias or an equivalent amount of extension makes the spindle more sensitive to fast phasic changes, as experimentally found by Granit and Henatsch (1956).

Fig. 5 has shown that, for a given spindle, the rate at which the interval changes is proportional to the rate at which extension changes. If, in one and the same experiment, one plantaris- and one soleus-spindle are selected and the same initial length is used for both muscles, it is possible to visualize directly an important implication of the concept here introduced by the 'spindle constant'.

S in Fig. 7 is the soleus spindle which had a constant of 5.0, P is the plantaris spindle with a constant of 3.1. The two curves in α—β diagram cross at a rate of extension around 120 msec. Assume the situation in the animal's body when these two synergist muscles are extended by contractions of the flexor antagonists. At the crossing point $\beta = 120$ the two spindles will give the same information α. At any other rate of extension than $\beta = 120$ they will differentiate rates of extension by differential behaviour. When rate of stretch grows slower (β increases), α continues to be reasonably small for the tonic soleus spindle but undergoes a considerable increase for the phasic plantaris spindle. This means that the soleus spindle, owing to its large spindle constant, senses slow phasic changes better than the plantaris spindle. Again, when rate of stretch increases to the left of the crossing point (β decreases); the faster plantaris spindle, owing to its small spindle constant, becomes the relatively better instrument of the two, because α grows small for it and changes very little for the soleus spindle.

In this experiment the crossing point was actually measured by the two curves of Fig. 7. This finding suggests that intrafusal contraction in a set of spindles may, by altering spindle length, displace their α—β curves along the α-axis (without altering their slopes) and thereby shift the crossing point in an appropriate direction — yet another example of what incredibly fine instruments for control the muscle possesses in its spindles. Intrafusal contractions are monitored both by reflexes and by supraspinal events (see summary, GRANIT 1955). Hitherto we have mostly considered tonic aspects of intrafusal activity. Considerations based on the spindle constant seem to offer a valuable line of approach to an understanding of integrations based on phasic differentiation.

Discussion.

Time is hardly ripe for a discussion of applications of the concept introduced here because no experimental work exists which compares rates of extension in a group of co-operating muscles. One does not know how the reflex effects emerge in terms of tonic and phasic motoneurones and muscles, still less is

it possible, on the sensory side, to go beyond the general statements made above that the new findings show the existence of grid of β/α curves which will shift their relative position and points of intersection under the influence of stretch and/or intrafusal control. Information from the muscle is bound to vary accordingly.

Summary.

1. Exponential stretch of tonic and phasic muscles in rabbits has been carried out by a special device (Fig. 1). Rate of change of extension of muscle (β) and rate of change of interval (α) between individual discharges of an indicator spindle has been measured.

2. It is shown that for any one spindle β/α is a constant, large in tonic muscle and small in phasic muscle. This is defined as the spindle constant.

3. The spindle constant is independent of initial muscle length.

4. Considerations based on plots of spindle constants show that spindles in fast muscles respond better to fast rates of extension, spindles in slow muscles better to slow rates of extension.

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