

J. Physiol. (1958) 143, 387-402

## NEUROMUSCULAR INTERACTION IN POSTURAL TONE OF THE CAT'S ISOMETRIC SOLEUS MUSCLE

BY RAGNAR GRANIT

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

(Received 24 February 1958)

To Liddell & Sherrington's (1924) classical work on the stretch reflex Denny-Brown (1929) added a fundamental contribution when he found red muscle to have a lower threshold for stretch for the postural or maintained component than pale muscle. He also showed that postural reflexes were run at very slow frequencies of motor discharge (5-25/sec), the motor units preserving an approximately even rate of firing at different extensions of the muscle. The increase of the stretch reflex with greater pull he attributed to recruitment of fresh motoneurones. On the muscular side this work was a vindication of Ranvier's (1874) view that 'les pâles, avec leur contraction brusque, seraient de muscles d'action par excellence; les rouges, avec leur contraction plus lente et plus persistante, seraient plutôt équilibrateurs ou régulateurs'. In the same paper Ranvier described their different mechanical properties. For recent histological work, see Krüger (1952).

Much new information in this field (summarized, Granit, 1955, 1957; Hammond, Merton & Sutton, 1956) calls for some attention to be devoted to the neuromuscular integration. An attempt will be made below to put the recent results from work on the  $\gamma$ -spindle system, the small tonic  $\alpha$  motoneurones, and inhibition brought about by the Golgi recurrent collaterals into their proper places in the functional or physiological totality serving to maintain tone. Muscular force must also be considered.

To Sherrington's (1909) acute observations we owe the distinction between elastic and plastic tone. From Blix (1895) onwards (cf. Evans & Hill, 1914; Buchthal, 1942; Hill, 1950*a*; Wilkie, 1956) a wealth of information exists which goes to demonstrate that an isolated contracting stretched muscle of the striate type could only produce elastic tone. The nervous system or an unknown factor has to be invoked to make striate muscle plastic, which means that it would have to approximate towards the same tension independently

of length. This state Sherrington actually described with isotonic recording, a situation in which the  $\gamma$ -spindle system must be set to a mode of action different from its behaviour in isometric recording. The two cases will be treated separately. Isometric conditions alone are discussed in the present work.

It has been found convenient to analyse these problems in terms of a concept such as loop gain, a derivative which is the amount of myotatic reflex tension (output) produced per unit extension (input) in grams per millimetre.

#### METHODS

Cats were decerebrated pre- or intercollicularly by suction. Sometimes Thiogenal (Merck, Darmstadt; sodium salt of 5-(2-methylthioethyl)-5-(L-methylbutyl)-2-thiobarbituric acid) was used for the first stage of the operation, later ether alone. Further surgical measures were: laminectomy, denervation of the left leg usually leaving intact only the supply to the ankle extensors, in some cases also to the freed tibialis anterior; fixation at hip, knee and foot of this leg; slings of silk occasionally placed around the ventral roots L6-S1 for easy de-efferentation; in the cases when the spinal cord was exposed, the ventral roots below S1 had mostly been divided. In some cases no laminectomy was performed. A detailed description of the technique is given in Eldred, Granit & Merton (1953), who measured input frequencies and in some experiments also tension as a function of extension without separating its active from its passive component. Temperature control has since been added, based on thermocouples in the rectum, under the skin of ankle extensors and in the paraffin oil covering the spinal cord.

Indicator muscular afferents in functional isolation from small filaments were nearly always used, mostly also electromyographic control of total output. In some cases tonic efferent units were isolated in the ventral roots. All indicator fibres were soleus spindle afferents and soleus tonic efferents isolated by the criterion that they responded to pull on this muscle more easily than to pull on the gastrocnemius. An exception is Fig. 1 (records 1 and 2) and one curve in Fig. 4, in which the undivided gastrocnemius-soleus was used. For electromyography steel pins, insulated except over some millimetres at the tip, were thrust into the soleus. Sometimes unipolar recording against earth was used.

The muscle was attached by light metal hooks and rods to the strain-gauge myograph. Zero tension at resting length could be adjusted to within 10 g. The muscle was extended by hand and set to the desired length by observing a pointer magnifying the movement about three times. Measurements were restricted to the time between the 4th and 5th second after onset of stretch. At this time elastic and contractile forces as well as neural governors have reached a semistationary state of equilibrium.

*Principles of measurement.* This paper is concerned with active postural tension, so that passive tension due to extension as such must be deducted from the total after suppression of the stretch reflex by inhibition. This was achieved by electrical or mechanical stimulation of the severed hamstring nerve (Liddell & Sherrington, 1924; Denny-Brown, 1929); occasionally the soleus reflex was inhibited by pull on the antagonist tibialis anterior (Cooper & Creed, 1927; Granit, 1952). Against large extensions inhibition may not be complete and occasionally nerve stimulation may produce mixed effects. Passive tension has therefore been regularly measured after denervation or (sometimes) after administration of Flaxedil (May and Baker, gallamine triethiodide). Figs. 1, 8 and 9 illustrate inhibitions during a stretch reflex.

*Discussion of errors.* Great accuracy can never be expected in measurements of active reflex tension. Reflex behaviour may vary and the curve for passive tension (examples of which are shown in Figs. 5 and 6) at great extensions differs from its active counterpart at equivalent lengths by the different amount of series elastic contributions to the total (see, for example, Hill, 1950*a, b*;

Wilkie, 1956). This error may occasionally account for a kink in the curves (cf. Fig. 4). With weak stretch reflexes it is a good precaution to tap the gastrocnemius tendon after long extensions, because this causes a jerk in soleus (Denny-Brown, 1929) and makes it taut before the next stretch.

Another uncertainty enters into the assessment of zero extension on the basis of zero tension. This is probably best understood by considering a specific case in which the stretch reflex is strong so that the muscle is already shortened by contraction in the resting state. An instance is the preparation used for the uppermost curve of Fig. 4. Since zero extension, there as always, is adjusted (within 10 g) on the basis of zero tension, pull on the muscle will actually start from a negative value of extension. At the same time intrafusal spindle fibres are likely to be too slack relative to the contracted extrafusal ones and so feel the full effect of stretch at an extension greater than the one needed for a preparation in which intra- and extrafusal fibres at zero tension are at the same extension. Again, with low  $\gamma$  bias, the muscle will have to be stretched a great deal before the spindles begin to discharge properly.

## RESULTS

### *Input and output frequencies*

Fig. 1 represents samples of discharge frequencies of indicator spindles and individual tonic efferent fibres. With regard to output frequencies Denny-Brown's (1929) findings were confirmed. The discharge in the isolated tonic ventral root fibre did not vary very much in frequency at different extensions of the muscle. In confirmation of Denny-Brown, recruitment was also found; fibres of higher threshold than the one isolated turned up at greater extensions unless considerable care had been given to the dissection of the filament. In Fig. 1 the records 1 and 2 belong to the same experiment and the efferent discharge frequency of the big unit was constant for all extensions. In record 3 the fibre discharges at a frequency of 6/sec at all extensions and in the figures its frequency is shown for 10 mm extension (see also Fig. 7). However, very little attention was given to this aspect of the problem as there seemed no reason to doubt Denny-Brown's (1929) conclusion that variation of output frequency per neurone is modest or absent, remarkable though this finding was in the light of what was known at the time of the properties of stretch receptors (Adrian & Zotterman, 1926). In all, six motoneurons were isolated in the same number of animals and their frequency of discharge was found not to vary significantly for extensions of the order necessary for stretch reflexes.

Fig. 1 also shows that during inhibition of active tone the frequency of the indicator spindle may be increased (cf. Granit, Pascoe & Steg, 1957). The reasons for this may be purely mechanical. There is also a body of evidence (Hunt, 1951; Eldred *et al.* 1953; Buller & Dornhorst, 1955; discussed by Granit, 1955) demonstrating autogenetic inhibitory effects on the  $\gamma$  motoneurons coming from tension-sensitive muscle receptors whose discharge frequency will diminish when tension decreases. For the present work, however, it is only necessary to know the average input frequencies of the spindles at different extensions and not what happens to them when the stretch reflex is gone. The average values from twenty soleus spindles are presented in Fig. 2.

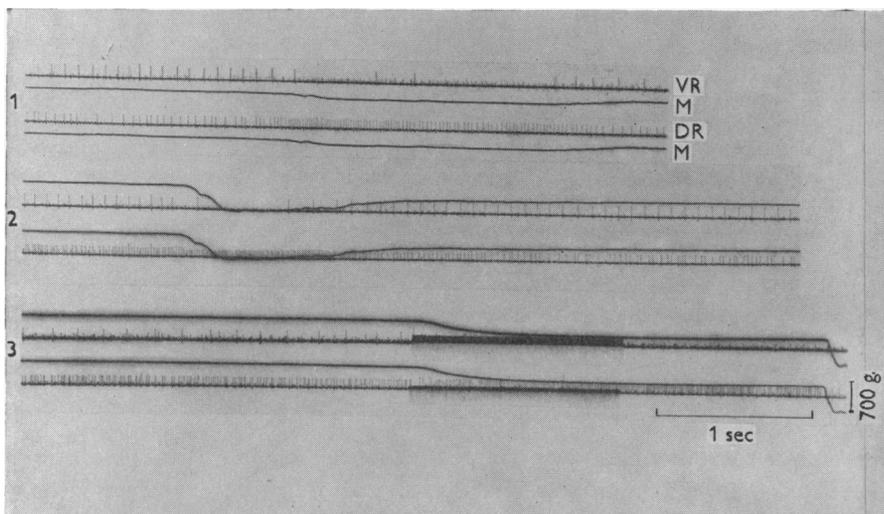


Fig. 1. Samples illustrating inhibition of stretched ankle extensors. The records are from two experiments (1-2 and 3) in each of which the upper pair shows discharge in a tonic ventral root fibre (VR) and myogram (M), the lower, discharge of the indicator spindle in a dorsal root fibre, (DR) and myogram (M). 1, slight initial reflex tension in the undivided gastrocnemius inhibited by squeezing cut end of hamstring nerve; 2, same during 7 mm extension, inhibition 530 g. 3, another animal, stretch reflex in soleus at 10 mm extension; inhibition 470 g by hamstring tetanus. Note the low ventral root frequencies of discharge, 13/sec in 1 and 2, 6/sec in 3, despite choice of experiments with very large stretch reflexes; also the increase of firing frequency from indicator spindle during inhibition and its highly irregular rhythms during reflex activity. On the right, calibration of myograph in this and all similar figures. Exceptionally, in records 1 and 2, the undivided soleus-gastrocnemius was used.

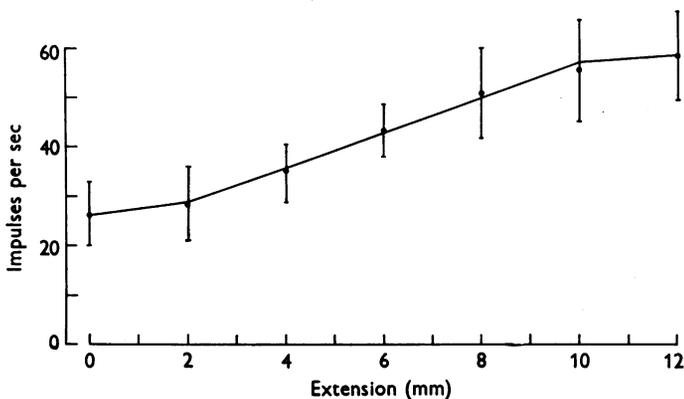


Fig. 2. Average discharge frequencies of 20 soleus spindles as a function of extension. The vertical lines are drawn on the basis of mean variations. The slope of the linear portion is 3.5 impulses/mm.

The final state of balance reached by the various spindle governors has led to the simple outcome that, on an average, discharge frequency increases linearly with extension, the slope being 3.5 impulses/mm (cf. Eldred *et al.* 1953, for individual curves). Beyond 10 mm the flattening of the curve is likely to be due to autogenetic  $\gamma$  inhibition (Hunt, 1951; Eldred *et al.* 1953). Setting of the zero is difficult (see above, Discussion of errors) and hence no accuracy can be expected between zero and 2 mm before the metal links joining muscle and myograph have been pulled taut.

#### *Myotatic loop gain and muscle*

Whilst passive tension (Figs. 5, 6) tends to be approximately proportional to log. extension, myotatic or active tension at its best behaves as in Fig. 3. The rule is that reflex tension is proportional to extension, as has also been found independently by Matthews (1958). The proportionality constant in grams per mm is a measure of myotatic loop gain. It is given in the legends of the figures and also, in the text, briefly referred to as the gain constant. One might say that the reflex increases 'stiffness' in such a way as to make the muscle the better conform to Hooke's law for elastic bodies. In the different reflexes of Fig. 3 the myotatic gain constant has varied from 19 to 102 g/mm extension. If total tension is plotted instead of the reflex fraction alone, passive tension may dominate the picture. The curves then tend to become logarithmic, as in a paper by Koella, Nakao, Evans & Wada (1956) in which the total tension of small reflexes was plotted.

Fig. 4 shows that the slope of the curves sometimes changes. Curve 1 can alternatively be made linear, but the points of curve 2 lie on two straight lines (P. B. C. Matthews, personal communication). Several possible explanations are available (cf. Discussion of errors), factors such as zero errors, onset of full effect of series elasticity at a certain tension or a late start of recruitment of fresh motoneurons. Curves 3 and 4 compare the same stretch reflex early and late in the experiment. The loss of gain over some hours is, no doubt, chiefly due to exposure of the spinal cord and isolation of a filament for dorsal root units. Matthews (1958, and personal communication), who has paid special attention to constancy of conditions and therefore generally left the spinal cord unexposed, finds greater stability of the reflex.

It is generally taken for granted that the greater stretch reflex at greater extensions follows from recruitment of fresh neurones and this undoubtedly is true of the spasticity of many rigid cats and of spasticity in man. There have been ample opportunities in the present work of confirming this finding (first made by Denny-Brown, 1929; and also confirmed by Matthews, 1958). But all tonic activity need not be run in this fashion. A complex organization may have several degrees of freedom. To be able to proceed with this problem it was necessary in the first instance to find out how soleus responds to constant

electrical stimuli to its nerve at different frequencies. The conditions differed from those used above merely by nerve section interrupting the connexion with the spinal cord. Fig. 5 shows an experiment with a 'muscle-nerve preparation' of this kind.

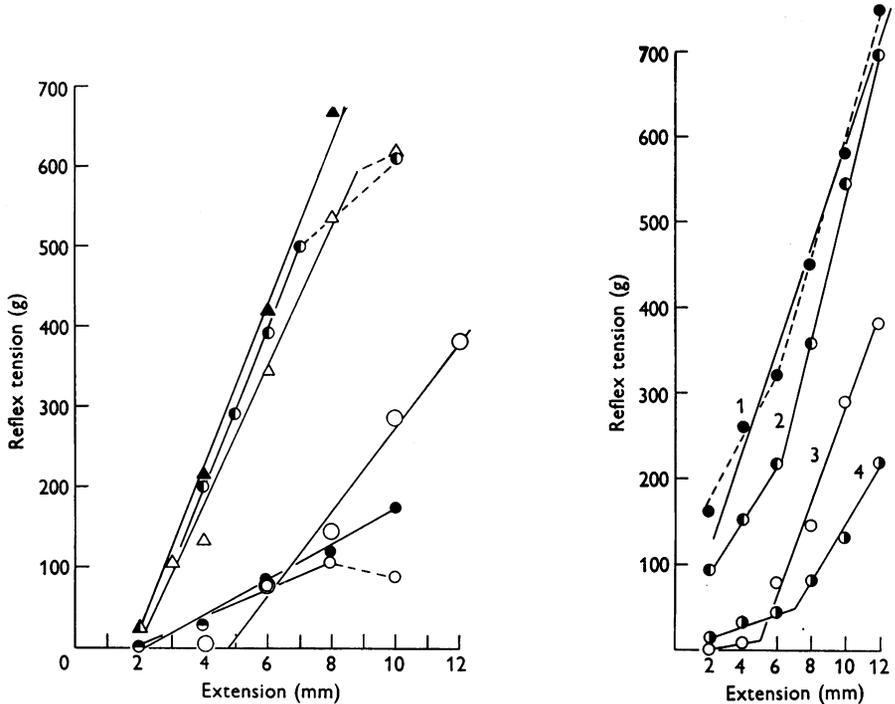


Fig. 3

Fig. 4

Fig. 3. Reflex gain constants. Plot of reflex contraction in stretch (g tension) against extension of muscle (mm). Muscle initially at zero extension. Uppermost curve refers to soleus and gastrocnemius together, the rest to soleus alone. The gain constants from above downwards are 102, 102, 88, 54, 22 and 19 g/mm and have been derived from the straight lines drawn through the data.

Fig. 4. Soleus. Same as Fig. 3. 1, drawn as one straight line with gain constant 59 g/mm as an alternative to a curve with a kink (broken line); 2, upper portion with gain constant 82 g/mm; 3 and 4 are plots of early and late stretches in the same experiment; reduction of gain from 54 to 33 g/mm some hours later assumed to be due to exposure of spinal cord.

In imitation of the reflex output a slow rate of 14 shocks/sec was used. In the analysis (right) of Fig. 5 tension again is proportional to extension, demonstrating that theoretically myotatic loop gain could also be constant without recruitment of fresh neurones, merely on the basis of a constant efferent output. In this particular case 8 mm is the range of definition of the rule.

Fig. 6 *A* and *B* is an analysis carried out at various frequencies and strengths of stimulation with one muscle, though not the only experiment of its kind.

These experiments agreed in proving that low stimulus strengths and frequencies often made the curves approach the logarithmic relationship characteristic of passive tension, as a function of extension. Such curves may also be drawn with two linear components. Thus, when the output is constant and recruitment excluded, the rule that tension is proportional to extension is obtained with the same fidelity and the same deficiencies at small extensions as in reflex action. The validity of this rule, therefore, does not necessarily demonstrate that the stretch reflex recruits fresh neurones when muscle length is increased. Active contraction in response to a constant stimulus (constant output) also increases in direct proportion to extension.

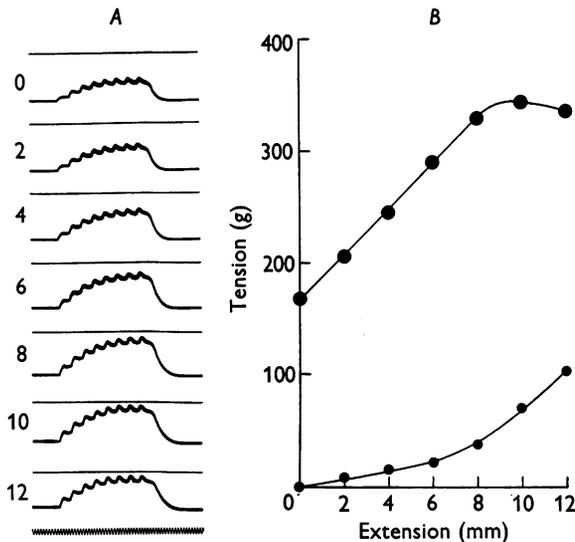


Fig. 5. Nerve-muscle preparation. *A*: soleus stimulated at rate 14/sec at the extensions shown alongside curves. *B*: experiment *A* analysed in a plot of active (above) and passive (below) tension in grams against mm extension. Time marker, 0.02 sec.

#### *Recruitment or constant output*

If the electromyogram fails to show signs of recruitment—as it occasionally does—it is always possible to argue that it has been selective and has failed to record from distant muscle fibres. It is not possible to disprove this argument even though it seems unlikely. The increase in spike activity with extension is so clear in most cases (cf. Denny-Brown, 1929; Matthews, 1958) that it should be obvious whenever present. Constant output can be expected, not only with weak stretch reflexes but also with strong ones acting with much synchrony of individual neurones or else mobilizing most of the small tonic motoneurones even at zero extension.

Consider, for instance, the case, illustrated in Fig. 7, of one of the muscles

used for Fig. 3 with gain constant 22 g/mm. The records refer to zero, 2, 4 and 8 mm extension. It is seen that the electromyographic output varies from stretch to stretch as, indeed, often happens with decerebrate animals, but actually the maintained rate of discharge of the motoneurone was slightly faster at 2 than at 8 mm and again slower at 4 mm. It bore no necessary relation to extension, and there is recruitment of fresh units only during the onset of pull in response to the initial avalanche of afferent input. This initial recruitment shows that fundamentally the electrodes could detect other units. These, however, were not maintained.

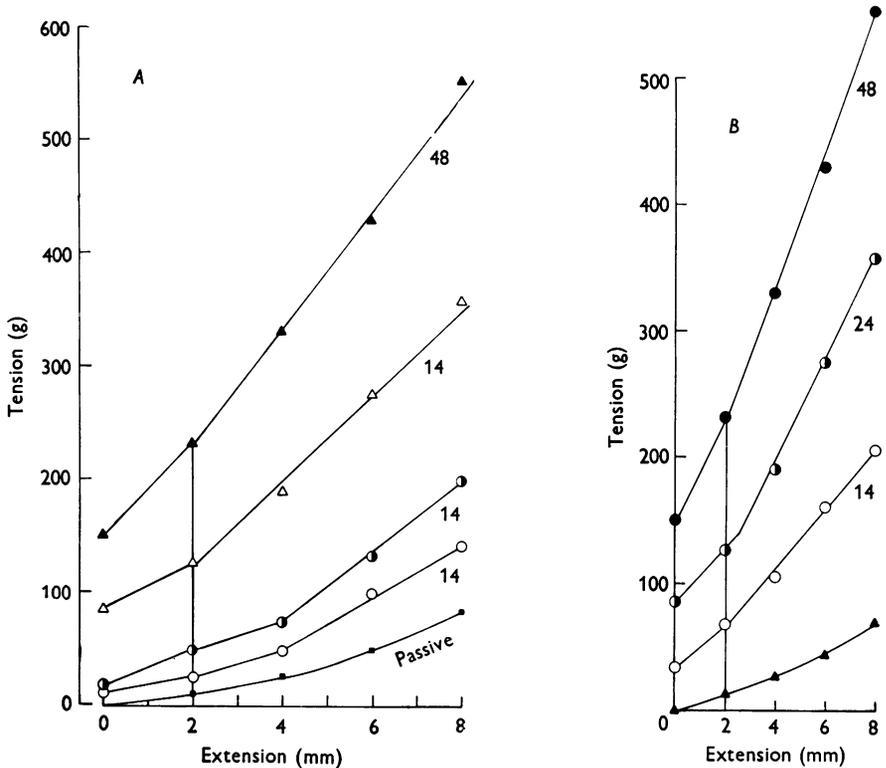


Fig. 6. Soleus tension-length diagrams. Tetani as in Fig. 5 to soleus nerve. *A*: lowermost curve illustrates passive tension to stretch, the rest active tension to stimulation at the frequencies on the right against the curves; stimulus strength varied, as shown by tension of responses at zero extension; uppermost curve nearly maximum. The line at 2 mm length put in for comparison with stretch. *B*: same to show effect of stimulus frequency alone.

Fig. 8 shows records of a highly synchronized response to stretch. The inhibition by hamstring stimulation (see legend) demonstrates that the reflex was large. The electromyograms do not suggest any recruitment whatever, except perhaps at 12 mm extension, so that this reflex well may have been run

on the basis of a steady output at all lengths. Its gain constant was 85 g/mm, valid over 8 mm from 4 to 12 mm extension. It is not necessary to illustrate recruitment since this is well known from previous work quoted above.

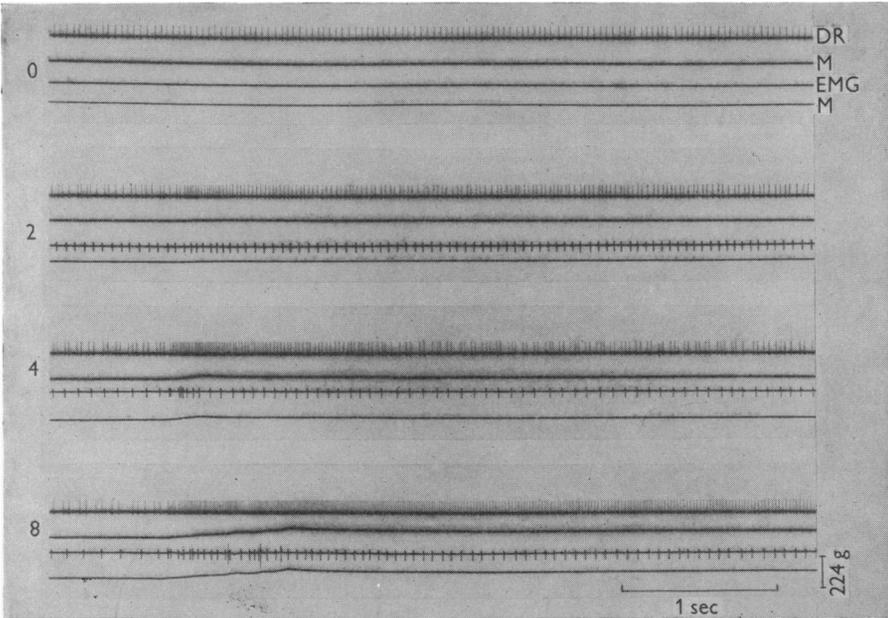


Fig. 7. Soleus stretch reflexes with moderate gain of 22 g/mm at the extensions marked on the left. Each set of records illustrates indicator spindle (DR), myogram (M), electromyogram (EMG) and myogram (M). Note irregularities in spindle firing.

#### *Significance of spindle control*

Even though soleus is slow and—one would surmise—builds up a considerable increase in the duration of active state (Hill, 1949) during tetanic stimulation (cf. for frog muscle Ritchie & Wilkie, 1955), most muscle units within it are forced to oscillate between contraction and relaxation. Its fusion frequency is 33/sec and up to 5–6/sec the individual twitches do not sum (Cooper & Eccles, 1930). The reflex output, as we have seen, is 5–25/sec.

Eldred *et al.* (1953), who noted the variations in both spindle frequency and myogram during stretch, held the spindle variations to be largely due to variations in central outflow of  $\gamma$  impulses which, indeed, is variable (Granit & Kaada, 1952; von Euler & Söderberg, 1956, 1957). Halliday & Redfearn (1956) and Hammond *et al.* (1956) have studied in man the oscillations in a voluntary task (references to work on man in their papers) and come to the conclusion that the rhythm with a peak frequency around 9/sec is an 'oscillation in the muscle servo'. This view is supported by Lippold, Redfearn & Vučo (1957).

From what has been pointed out above, it seems clear that the stability of the output frequency per neurone forces the muscle to oscillate. Records 1-3 of a stretch reflex at high sensitivity in Fig. 9 show such reflex oscillations. Inhibition by pull on the tendon of tibialis anterior (record 3) smooths out the oscillations and removes active tension.

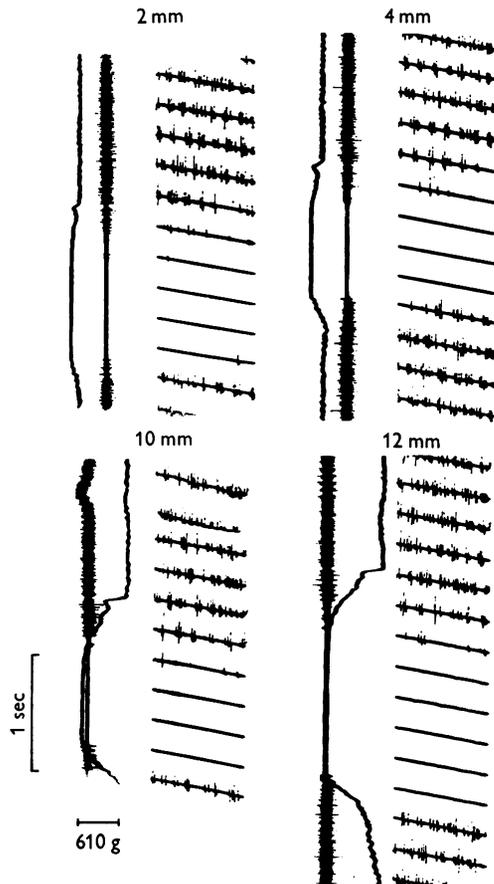


Fig. 8. Soleus stretch reflexes with gain constant 85 g/mm at 2, 4, 10 and 12 mm extensions, as marked above records, each of which shows myogram and electromyogram vertically and sample sweeps of the latter horizontally. Inhibition by electrical stimulation of hamstring nerve silences electrical activity completely. Note, by comparing with myograph calibration, the large stretch reflexes.

Finally, it is necessary to realize that soleus runs to the same tendon as the two gastrocnemii and the plantaris and that in sensitive preparations it is easily shown that there is synergy of a very interesting kind. This is illustrated in Fig. 10, in which both soleus (upper myogram) and gastrocnemius (lower myogram) are connected to myographs, the electromyogram being taken from

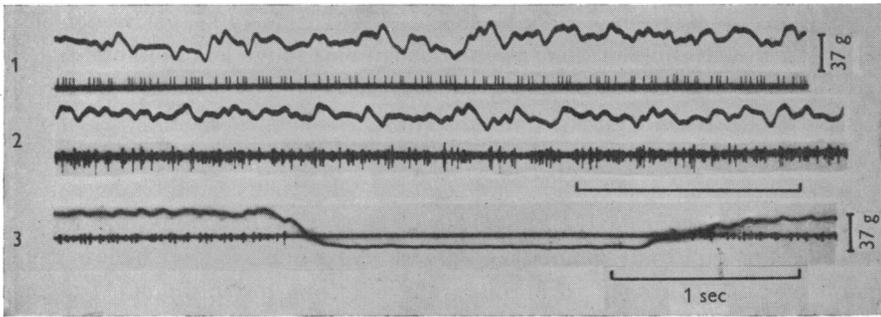


Fig. 9. 1 and 2, large soleus stretch reflex at 6 mm extension; continuous record, spindle discharge in 1 having been exchanged for electromyogram in 2. 3, soleus stretch reflex (at 6 mm extension) and electromyogram. Inhibition in the middle of the record by pulling slowly on the tibialis anterior tendon. Stretch reflex recovers when tibialis anterior released. Time marker, 1 sec.

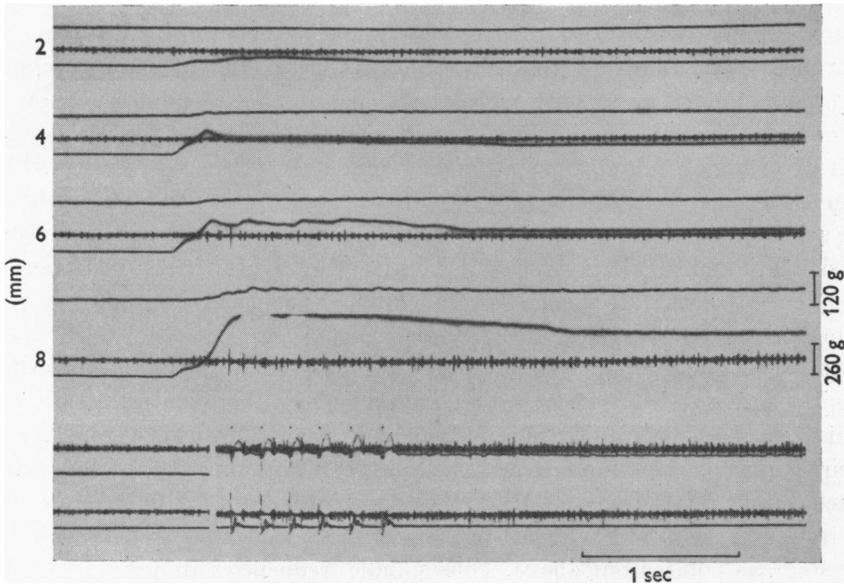


Fig. 10. Simultaneous records of soleus and gastrocnemius. Upper myogram (calibration 120 g) in each set of records refers to soleus at 4-8 mm constant extension and an average tonic stretch reflex of 40 g. Lower myogram refers to variable stretch of gastrocnemius to the extensions marked on the left in mm. EMG in soleus. There are small synergist stretch reflexes in soleus of 6, 12 and 38 g when gastrocnemius is extended by 4, 6 and 8 mm, respectively. Lowermost set of records illustrates in the same experiment the six last tendon taps on gastrocnemius of a series of twelve and the well maintained tension of around 100 g in soleus as against 18 g in gastrocnemius.

the soleus. Pull on the gastrocnemius (2–8 mm) elicits a small stretch reflex in soleus kept at around 4–8 mm constant extension (40 g active tension). There is also a stretch reflex in the gastrocnemius, though less well maintained, as is shown by the myogram, and small, considering the size of the muscle. Finally the gastrocnemius tendon is tapped 12 times (the last 6 taps shown) and soleus builds up a long-lasting postural reflex of 100 g while gastrocnemius only produces 18 g slow tension that soon vanishes. Thus rapid changes in the synergists are transformed by the soleus into a slow supporting postural reflex. Further, it is important to note that interrupted stimulation in the lowermost record of Fig. 10 proved to be more efficient than a continuous stream of gastrocnemius spindle impulses in the upper ones.

#### DISCUSSION

Whilst it would be wrong to maintain that the  $\gamma$  system only deals with postural tone, this is the aspect from which it has been considered in the present work. The state of decerebrate spasticity is an exaggeration of posture—as Sherrington always emphasized—but it illustrates several characteristic features of the mechanism. There is first the tonic  $\gamma$  drive operating a tonic afferent input, which in its turn operates slowly discharging tonic  $\alpha$  motoneurones destined for slow tonic muscle fibres. These, no doubt, are associated with both spindles and motor end-plates, which further research will show to differ from the corresponding organs in phasic muscle. There is thus a systemic unit of biological adaptations strongly reminiscent of the one described by Bremer, Bonnet & Moldaver (1942) in frogs. Muscular contraction, which is the ultimate net result of all these regulated operations, by the rule that reflex tension is proportional to extension reflects mechanical properties of slow muscle at different lengths. It should be recalled once more that the results refer to isometric reflexes and maintained elastic tone.

The synthetic view arrived at is best summarized by beginning from the proprioceptive end. The  $\gamma$  excitation, without which there is very little sensitivity to stretch, sets up tension in the spindles and thus, as it were, elevates their frequency/extension curve at the lower end far above that of the denervated spindle (cf. Eldred *et al.* 1953; Matthews & Rushworth, 1957). However, excitation is kept in check by tension-sensitive inhibitory reflexes on the  $\gamma$  system, as pointed out above. Thus spindle frequencies are prevented from reaching excessive values, at least at greater extensions. In the present paper interest has been centred on the net result of all these mechanisms, which is seen to be that in a tonic muscle the average static spindle frequency is a linear function of extension (Fig. 2). Results with individual spindle afferents by Eldred *et al.* (1953) suggested this rule.

On the output side a special set of motoneurones are mobilized, the small tonic  $\alpha$  motoneurones of Granit, Henatsch & Steg (1956). These have interest-

ing special properties. There are (i) the long after-hyperpolarization (Eccles, Eccles & Lundberg, 1957 *a, b*), and (ii) the fact that they always, when tested, have been found to be subject to recurrent inhibition (Granit, Pascoe & Steg, 1957; cf. also Holmgren & Merton, 1954). Both these influences will be counter-balanced by a sufficient depolarizing inflow from the spindles. But (iii) a third important property antagonizes depolarization, namely the strongly cumulative character of recurrent inhibition brought about through the Golgi collaterals (Granit, Pascoe & Steg, 1957). This process is so effective that, in the absence of  $\gamma$  bias, the tonic  $\alpha$  motoneurons under experimental conditions may be completely silenced. Sometimes when oscillations in stretch are vaguely described as being caused by instability in the muscle servo, the real state of affairs, on the contrary, is that the control of the output from the tonic  $\alpha$  motoneurons is super-stabilized by cumulative recurrent inhibition, and, indeed, at such low rates that the muscle is forced to oscillate (cf. Fig. 9).

The heavy stabilization of output frequency makes number of neurones (recruitment) a relatively more important variable and also raises the question of whether oscillations are a by-product or usefully employed in the maintenance of the stretch reflex for other purposes than to improve blood supply. Fig. 10 showed that maintained stretch of gastrocnemius was far less efficient in setting up a good soleus stretch reflex than were repeated tendon taps. Quite generally one finds that maintained discharge of the small tonic  $\alpha$  cells is much better upheld by spindle bursts interrupted by pauses than by a steady discharge (Granit, 1956; Granit, Pascoe & Steg, 1957; Granit, Phillips, Skoglund & Steg, 1957).

The spindle discharge may be described as tonic in stretch but its phasic oscillations are important and can cause higher discharge frequencies. Slack spindles do not follow phasic changes well, as was proved by Granit & Henatsch (1956). Thus, also on this view, it can be understood why  $\gamma$  activity is necessary for good stretch reflexes (Eldred *et al.* 1953; Henatsch & Ingvar, 1956; Matthews & Rushworth, 1957; Matthews, 1958). Recurrent, cumulative inhibition will, in a so-called ' $\gamma$  cat' (which is the Sherrington type of animal), be unopposed if  $\gamma$  bias runs down. The threshold for maintained stretch reflexes should be regarded as a state of balance between spindle input and recurrent inhibition on the output side.

Matthews (1958) has recently applied to this problem the technique of selective removal of  $\gamma$  activity by cocainization. First he established that myotatic loop gain, in agreement with the present results, was constant. When he then proceeded to cocaine the nerve, in order to produce a successive diminution of  $\gamma$  control, he obtained a series of curves shifted to the right in a diagram of the type shown above in Fig. 3. In other words, the threshold of the stretch reflex became increasingly higher. At any rate, therefore, the  $\gamma$  system sets the threshold of the spindles.

When in the present work constant loop gain was found, it was originally believed that such a simple rule indicated that one mechanism alone had been engaged, namely recruitment on a linear basis (Fig. 2) which would mobilize fresh neurones linearly. The experiments with contractions imitating constant output made it necessary to examine the electromyograms closely in order to exclude the possibility that constant loop gain simply followed from constant output. Some of the results (Figs. 7, 8) then suggested that this alternative must also be taken seriously.

It is difficult to know which alternative, constant or recruiting output, is more common in *normal* tone. The decerebrate animal, as stated, represents pathologically exaggerated tone. Both principles must be regarded as available mechanisms of motor control and be considered in future studies. In man some authors (see, for example, Ralston & Libet, 1953) seem to think that electromyographic activity is absent, whilst others, e.g. Joseph, Nightingale & Williams (1955, with references), see it clearly. It may well be that in man the tonic muscle fibres are sometimes difficult to detect, particularly if the output is small and constant. If so, the system serves as a regulated mechanism rather than as a 'follow-up' length servo. The latter term, to make any sense, would seem to require an increased output to increased stretch, i.e. recruitment.

Whichever way the organism chooses to act, it simply makes use of a system that goes off automatically as soon as the spindles are activated, and no sooner does the electroencephalogram or the experimental animal show signs of arousal than the spindles actually are activated (von Euler & Söderberg, 1956, 1957). Thus reflex standing becomes possible on the basis of tension being proportional to extension. The automatism of the loop places it at the mercy of the  $\gamma$  system. If the latter is over-excited, or somehow released, spasticity will follow.

#### SUMMARY

1. Isometric stretch reflexes have been elicited in the soleus of decerebrate cats in order to study the relation between extension of the muscle, average input frequency of muscle spindles, the output of the small tonic  $\alpha$  motoneurones, and active (reflex) tension.
2. In confirmation of Denny-Brown (1929) the discharge frequency of individual motoneurones was found to be steady and relatively independent of extension.
3. Within a considerable range average frequency of discharge of the nuclear bag spindle afferents was found to be directly proportional to extension. The proportionality constant was 3.5 impulses/mm.
4. Similarly, reflex tension was found to be proportional to extension. The proportionality constant (= myotatic loop gain) varied a great deal with state of rigidity from animal to animal (20–100 g/mm).

5. After interruption of all connexions with the spinal cord a constant tetanic stimulus to the muscle nerve also produces tension in proportion to extension over the range of extensions used in the analysis of the stretch reflex.

6. It is concluded that constant loop gain in stretch reflexes may be due to the way soleus responds to a constant reflex output and not only to recruitment. Evidence for this view is presented.

7. Alternatively, when there is recruitment of fresh motoneurons in response to increased extension, the reflex also exhibits constant loop gain. This is ascribed to the linear increase of average input frequency with extension, which is assumed to mobilize fresh motoneurons linearly.

8. Large oscillatory variations of muscle tension are seen with good stretch reflexes, the reason being that the small tonic motoneurons discharge at slow rates considerably below what is required for fusion of tetani. The mechanisms checking an increase in output frequency are discussed.

9. Quickly repeated tendon taps given to gastrocnemius raise maintained postural tone in soleus, but hardly any maintained tone in the phasic gastrocnemius itself. A steady pull on gastrocnemius influences soleus to a considerably less extent.

The author is indebted to the Swedish Medical Research Council for support of this work. Dr Lawrence Stark (Yale University) took part in some of the initial experiments. For a valuable discussion of the results the author wishes to thank Dr P. B. C. Matthews (Physiological Laboratory, University of Oxford).

## REFERENCES

- ADRIAN, E. D. & ZOTTERMAN, Y. (1926). The impulses produced by sensory nerve-endings. Part 2. The response of a single end-organ. *J. Physiol.* **61**, 151-171.
- BLIX, M. (1895). Die Länge und die Spannung des Muskels. IV Abhandlung. *Skand. Arch. Physiol.* **5**, 173-206.
- BREMER, F., BONNET, V. & MOLDAVER, J. (1942). Contributions à l'étude de la physiologie générale des centres nerveux. I. La sommation centrale. *Arch. int. Physiol.* **52**, 1-56.
- BUCHTHAL, F. (1942). The mechanical properties of the single striated muscle fibre at rest and during contraction and their structural interpretation. *K. danske vidensk. Selsk.* **17**, no. 2.
- BULLER, A. J. & DORNHORST, A. C. (1955). Autogenetic inhibitory impulses from human muscle. *J. Physiol.* **128**, 20 P.
- COOPER, S. & CREED, R. S. (1927). Reflex effects of active muscular contraction. *J. Physiol.* **62**, 273-279.
- COOPER, S. & ECCLES, J. C. (1930). The isometric responses of mammalian muscle. *J. Physiol.* **69**, 377-385.
- DENNY-BROWN, D. (1929). Nature of postural reflexes. *Proc. Roy. Soc. B*, **104**, 252-301.
- ECCLES, J. C., ECCLES, R. M. & LUNDBERG, A. (1957*a*). Durations of after-hyperpolarization of motoneurons supplying fast and slow muscles. *Nature, Lond.*, **179**, 866-868.
- ECCLES, J. C., ECCLES, R. M. & LUNDBERG, A. (1957*b*). The convergence of monosynaptic excitatory afferents on to many different species of alpha motoneurons. *J. Physiol.* **137**, 22-50.
- ELDRED, E., GRANIT, R. & MERTON, P. A. (1953). Supraspinal control of the muscle spindles and its significance. *J. Physiol.* **122**, 498-523.
- EVANS, C. L. & HILL, A. V. (1914). The relation of length to tension development and heat production on contraction in muscle. *J. Physiol.* **49**, 10-16.
- GRANIT, R. (1952). Reflexes to stretch and contraction of antagonists around ankle joint. *J. Neurophysiol.* **15**, 269-279.

- GRANIT, R. (1955). *Receptors and Sensory Perception*. New Haven: Yale University Press.
- GRANIT, R. (1956). Reflex rebound by post-tetanic potentiation. Temporal summation-spasticity. *J. Physiol.* **131**, 32-51.
- GRANIT, R. (1957). Systems for control of movement. (With discussion by J. C. Eccles, R. S. Schwab, G. von Schaltenbrand and H. J. Hufschmidt.) *I Congrès int. Sci. Neurol., Bruxelles*, **1**, 63-99. Acta med. belg. Getand: Snoeck-Ducaju Fils.
- GRANIT, R. & HENATSCH, H.-D. (1956). Gamma control of dynamic properties of muscle spindles. *J. Neurophysiol.* **19**, 356-366.
- GRANIT, R., HENATSCH, H.-D. & STEG, G. (1956). Tonic and phasic ventral horn cells differentiated by post-tetanic potentiation in cat extensors. *Acta physiol. scand.* **37**, 114-126.
- GRANIT, R. & KAADA, B. R. (1952). Influence of stimulation of central nervous structures on muscle spindles in cat. *Acta physiol. scand.* **27**, 130-160.
- GRANIT, R., PASCOE, J. E. & STEG, G. (1957). The behaviour of tonic  $\alpha$  and  $\gamma$  motoneurons during stimulation of recurrent collaterals. *J. Physiol.* **138**, 381-400.
- GRANIT, R., PHILLIPS, C. G., SKOGLUND, S. & STEG, G. (1957). Differentiation of tonic from phasic alpha ventral horn cells by stretch, pinna and crossed extensor reflexes. *J. Neurophysiol.* **20**, 470-481.
- HALLIDAY, A. M. & REDFEARN, J. W. T. (1956). An analysis of the frequencies of finger tremor in healthy subjects. *J. Physiol.* **134**, 600-611.
- HAMMOND, P. H., MERTON, P. A. & SUTTON, G. G. (1956). Nervous gradation of muscular contraction. *Brit. med. Bull.* **12**, 214-218.
- HENATSCH, H.-D. & INGVAR, D. H. (1956). Chlorpromazin und Spastizität. *Arch. Psychiat. Nervenkr.* **195**, 77-93.
- HILL, A. V. (1949). The abrupt transition from rest to activity in muscle. *Proc. Roy. Soc. B*, **136**, 309-420.
- HILL, A. V. (1950a). Mechanics of the contractile element of muscle. *Nature, Lond.*, **166**, 415.
- HILL, A. V. (1950b). The series elastic component of muscle. *Proc. Roy. Soc. B*, **137**, 273-280.
- HOLMGREN, B. & MERTON, P. A. (1954). Local feedback control of motoneurons. *J. Physiol.* **123**, 47P.
- HUNT, C. C. (1951). The reflex activity of mammalian small-nerve fibres. *J. Physiol.* **115**, 456-469.
- JOSEPH, J., NIGHTINGALE, A. & WILLIAMS, P. L. (1955). A detailed study of the electric potentials recorded over some postural muscles while relaxed and standing. *J. Physiol.* **127**, 617-625.
- KOELLA, W. P., NAKAO, H., EVANS, R. L. & WADA, J. (1956). Interaction of vestibular and proprioceptive reflexes in the decerebrate cat. *Amer. J. Physiol.* **185**, 607-613.
- KRÜGER, P. (1952). *Tetanus und Tonus der quergestreiften Skelettmuskeln der Wirbeltiere und des Menschen*. Leipzig: Akad. Verlag Geist und Portig.
- LIDDELL, E. G. T. & SHERRINGTON, C. S. (1924). Reflexes in response to stretch (Myotatic reflexes). *Proc. Roy. Soc. B*, **96**, 212-242.
- LIPPOLD, O. C. J., REDFEARN, J. W. T. & VUČO, J. (1957). The rhythmical activity of groups of motor units in the voluntary contraction of muscle. *J. Physiol.* **137**, 473-487.
- MATTHEWS, P. B. C. (1958). The effect of the activity of the  $\gamma$  motoneurons on the relation between tension and extension in the stretch reflex. *J. Physiol.* **140**, 54-55P.
- MATTHEWS, P. B. C. & RUSHWORTH, G. (1957). The selective effect of procaine on the stretch reflex and tendon jerk of soleus muscle when applied to its nerve. *J. Physiol.* **135**, 245-262.
- RALSTON, H. J. & LIBET, B. (1953). The question of tonus in skeletal muscle. *Amer. J. Physical Med.* **23**, 85-92.
- RANVIER, L. (1874). De quelques faits relatifs à l'histologie et à la physiologie des muscles striés. *Arch. Physiol. norm. path.* **6**, 1-15.
- RITCHIE, J. M. & WILKIE, D. R. (1955). The effect of previous stimulation on the active state of muscle. *J. Physiol.* **130**, 488-496.
- SHERRINGTON, C. S. (1909). On plastic tonus and proprioceptive reflexes. *Quart. J. exp. Physiol.* **2**, 109-156.
- VON EULER, C. & SÖDERBERG, U. (1956). The relation between gamma motor activity and the electroencephalogram. *Experientia*, **12**, 278.
- VON EULER, C. & SÖDERBERG, U. (1957). The influence of hypothalamic thermoceptive structures on the electroencephalogram and gamma motor activity. *Electroenceph. clin. Neurophysiol.* **9**, 391-408.
- WILKIE, D. R. (1956). The mechanical properties of muscle. *Brit. med. Bull.* **12**, 177-182.