GAMMA CONTROL OF DYNAMIC PROPERTIES
OF MUSCLE SPINDLES

RAGNAR GRANIT AND H. D. HENATSCH

Nobel Institute for Neurophysiology, Karolinska Institutet, Stockholm 60, Sweden

(Received for publication October 31, 1955)

So far the gamma control of the muscle spindles, of which a full review has been given by one of us (6) has been established in terms of only the slow components of the spindle discharge, a process gradually rising and falling in the recruiting fashion suitable for supporting slow or tonic reflexes and static performance. But the spindles, like most other sense organs, also respond to rate of stimulation. In agreement with our present notions about generator potentials as intermediaries in the production of the sensory discharge, Katz (10) found that spindle firing was begun by a dynamic potential, recordable in the sensory terminals as a rapid depolarization which afterwards quickly subsided to a semistationary level. Similarly, at cessation of stretch, there occurred a dynamic change in the opposite direction, a transient hyperpolarization during which the spindle ending was silent. His work was done on frogs but there is no reason to suspect that mammalian spindles would behave differently.

This being so, the question arises of whether the gamma innervation also is capable of controlling the dynamic properties of the spindles. If our present notions about the gamma fibres as instruments for contraction of the intrafusal fibres are true, we can make a number of predictions about the mode of reaction of the dynamic component in the spindle response, which at least are likely to be true for the nuclear bag (or primary) endings. First, being placed in the nuclear bag between the two striated or myotube portions of the organ, these endings will be stretched by intrafusal contraction and so should be able to follow faster rates than in the slack state—much as a tense string can follow faster rates than a slack one. If this inference is correct, increased gamma activity, even when slowly adjusted by the organism to the new level, will make the spindles respond in fast action more rapidly than before. Second, interference between the opposite dynamic on- and off-responses is likely to lead to specific resonance phenomena at certain frequencies.

The simplest way of approaching this problem would be to use vibratory stimuli and measure the frequency which spindles are capable of following when the amount of gamma activity is varied. For this purpose pentobarbitone cats and some lightly urethanized rabbits have been used because in

1 Fellow of the Rockefeller Foundation. Present address: Physiological Institute, University of Göttingen, Göttingen, Germany.
such preparations it is easy to activate the gamma fibres selectively, provided that the anaesthesia has not been carried too far.

**METHODS**

Spindle afferents were isolated in the S1 and L7 dorsal roots in animals with one hindleg denervated except for the medial and lateral nerves to the ankle extensors, gastrocnemius and soleus. These were well separated and each was attached to the strain gauge myograph, the hindlegs fixed at three points. Most spindles were located in the gastrocnemius, some in the soleus. Since the technique involved stimulating with the blunt point of a vibrator, it was generally found convenient to apply vibration to the gastrocnemius rather than to the deeper lying soleus. Superficially located spindles are extremely sensitive to touch and it is generally possible to locate the site of maximum sensitivity with considerable precision. By touching the skin with the tip of a pencil one finds intense firing at the appropriate spot and can then proceed to apply the vibrator to it. It is also possible to apply vibration to the tendon directly, as was done in some experiments, but this means that it is impossible to study spindle activity in slack muscles. Also, in view of the pennate structure of the gastrocnemius, extension (or tension) will bear a complex relation to length of the intrafusal fibre so that for mass movement through the tendon the parallel-fibred soleus seems better. The oscillation of the vibrator was recorded on one of the four cathode-ray beams available.

The vibratory movement was produced by a Goodman vibrator driven electronically. The movement was transferred to the skin by means of a plastic shaft, shaped and dimensioned like a small pencil with a rounded tip. The amplitude of the vibration was not constant throughout the frequency range. It was therefore calibrated by photographing its shadow in a beam of light. The excursion was found to decrease from a maximum of 2.8 mm. around 80–100 c./sec. to 0.65 mm. at 200 c./sec., 0.25 mm. at 300 c./sec. and 0.13 mm. at 400 c./sec. These figures refer to free movement and are thus maximal. The same general type of curve was obtained when the vibrator was tested against a rubber plug. A pressure of 50 g., a reasonable experimental value, reduced the amplitude by 38 per cent. However, the actual oscillatory movement of the nuclear bag itself will always remain unknown.

In order to activate the gamma system the tegmental portion of the brain stem was stimulated (8) with concentric needle electrodes directed by the Horsley-Clarke instrument. Technique and apparatus was as described by Granit and Kaada (8). In the present experiments the spindle afferents in the root were identified by their reflex behaviour and by the latent period to a shock at knee level. With one exception the latencies proved to fall between 1.2 and 1.5 msec., thus demonstrating that the endings belonged to the nuclear bag type which have large afferents and high conduction velocity (9).

**RESULTS**

1. **General observations.** When the spot on the skin had been found at which the vibrator made a spindle respond to the least amount of pressure, the instrument was clamped by a holder in a stand and its height properly adjusted above the muscle, stretched horizontally below it. Several factors such as location of spindle (if superficial or deep), amplitude and pressure of vibrator, tension of muscle, sensitivity of spindle, etc., combined into a pattern of variation in which it makes little sense to elucidate details and limits of variability. The experimenter tried to adjust for optimum result. Thus a few spindles, even in the de-efferented state, followed up to nearly 400 c./sec. Conditions were then in every respect optimal. Others barely ran up to 100 c./sec. The highest values recorded in these experiments have been between 440 and 460 c./sec. but then, as stated, the amplitude of the vibrator diminishes towards the highest frequencies. Some attempts at evaluation of
this factor will be found in the third section below. Generally vibration through the tendon gave lower limiting frequencies than direct stimulation by vibratory pressure but there have been exceptions (see Figs. 4, 5).

Figure 1 shows the effect of amplitude of vibration. With sensitive spindles it is usually possible to demonstrate that, as the amplitude increases, double discharges appear, provided the frequency is not too high. In this case the effect lasted up to frequencies as high as 100 c./sec. but then tension was considerable, 786 g. At slow frequencies one sometimes saw up to three successive spikes corresponding to each oscillation of the vibrator. Similar observations on the mecanoreceptors in the cochlea have recently been reported by Tasaki (12) who recorded from primary fibres of the eighth nerve. In Tasaki's case the spikes arose on the negative phase of the microphonic potential (cf. for saccular microphonics, 13); in Fig. 1 they are seen to arise in a constant position relative to the swing of the oscillator. The mechanism of impulse generation is likely to be similar in all mechanoreceptors.

The insensitive spindles require a great deal of pressure to respond at all. One is shown as A in Fig. 2, tested at 75 c./sec. The myogram (on the left) shows that the spindle picked up the frequency of the oscillator when the muscle had been stretched to give 286 g.

2. Effect of gamma control. As in all papers on the gamma system from this laboratory, so also in this case the pinna reflex served as an easy check on the reactivity of the gamma system. In Fig. 2, B1, stimulation of the tegmental reticular formation was used. The two first sweeps show failure of the spindle to follow the vibrator at 160 c./sec. Between sweeps 2 and 4 the brain stem was stimulated, as shown by the shock artefacts on sweep 3. Afterwards, for some time, the spindle easily responded to the rhythm of the oscillation. The slow after-effect is characteristic of reticular spindle activation. Later on in B2 it was proved that the spindle followed a rate of 110 c./sec., if stimulated for some time at this rate. The animal was then de-efferented in order wholly to remove spindle excitation by gamma impulses. After de-efferentation it is often necessary to wait for 20–30 min. in order to allow time for subsidence of the long after-effects of injury discharges which will keep intrafusal fibres contracted. Record B3 shows that in the de-efferented state this spindle for only a brief moment (the first sweep) could follow a rate of 66 c./sec.
Fig. 2. A—Pentobarbitone cat. Vibration at constant amplitude and frequency of 75 c./sec. of high-threshold spindle in lat. gastroc. muscle. Tension of muscle recorded vertically against baseline. Muscle slowly stretched (sweep intervals of 1.8 sec.) starting from 175 g. At 286 g, spindle picks up vibration frequency. B—Urethane rabbit. Spindle ending in gastroc. muscle. 1: Muscle at 242 g. tension. Vibration at constant amplitude and frequency 160 c./sec. Reticular tegmentum stimulated between sweeps 2 and 4, shock artifacts being marked by dots. 2: Same spindle at zero muscle tension and frequency 110 c./sec. of constant amplitude. Some seconds after application of vibration spindle picks up frequency of vibrator. 3: Same spindle but now de-efferented. Same muscle tension and amplitude of vibrator. For a brief moment spindle follows 66 c./sec. (first sweep) but then fails to respond.
The experiment of Fig. 3 illustrates the behaviour of a more sensitive spindle which at zero tension (on the left) had the high limiting frequency of 200–205 c./sec. at which occasional failures occurred. Adding tegmental stimulation at zero tension (middle) the spindle followed perfectly up to 400 c/sec. In trying to find the amount of external tension that would make it do the same, we arrived at 88 g. (right) and tried to force it up to 440 c/sec. which, as the record shows, was near the limit. Sometimes it followed the vibrator, sometimes it just failed to do so. Gamma firing is, of course, permanently variable and therefore, in an animal with definite gamma bias, the limiting frequency also varies. Sometimes these variations are of a considerable order of magnitude and—unless controlled—may lead to the premature conclusion that spindles have specific resonance frequencies.

Fig. 3. Pentobarbitone cat. Superficial spindle ending in lat. gastroc. muscle. At zero tension (left) spindle follows 200–205 c./sec. with occasional failures. After repetitive stimulation of tegmental reticulum (middle) it follows up to 400 c./sec. In these two records frequency is slowly increased downwards. At 88 g. tension (right) limiting frequency is just below 440 c./sec. Sweep interval 1.8 sec. Vibrator at constant amplitude throughout.

It is characteristic of gamma control that, by maintaining a higher spontaneous discharge, it counteracts the apparent adaptation of the spindle without influencing adaptation as such (4). After de-efferentation one often found the spindle to follow high rates of stimulation for a brief while but to be unable to maintain its vibratory response the way excited spindles did (Fig. 2, B3), a change likely to be due to adaptation. Another typical phenomenon is that only the most sensitive spindles seem to be able to respond well at zero tension without gamma bias. And then, if they are highly sensitive (often synonymous with superficial site), very little pressure of the vibrator suffices to keep them stimulated. Zero tension is thus in these cases to some extent fictitious. Figure 4 illustrates a characteristic result. The animal was decerebrated and so had good gamma bias (curve marked "Intact γ").
Twisting of pinna added but little (maximally 25 c./sec.) to the limiting frequency, plotted as function of gram tension. After de-efferentation it became apparent that there had been a large tonic gamma contribution to the state of tension in the spindle (Fig. 4, After de-eff.). Now the spindle completely failed to respond at zero tension. This is common. On the whole, gamma control is relatively more significant at low tensions. The curve joining the crosses shows the limiting frequencies obtained by putting the vibrator on the tendon, thus at a considerable distance from the spindle.

Very commonly the first effect of a twist given to the pinna is inhibition of the gamma impulses, afterwards followed by excitation. As an example might be mentioned a sensitive spindle that responded to particularly small excursions of the vibrator. Aided by tegmental stimulation, its limiting frequency at zero tension rose to 235 c./sec. Pinching of the loin made it follow for a brief while a vibratory rate of 280 c./sec. Tension was then increased to 175 g. A rate of 310 c./sec. was applied and the spindle failed to follow it. A superimposed pinna reflex gave strong inhibition followed by an excitatory phase during which the limiting frequency actually rose to 310. Long-lasting intense pinching of the skin added a little more gamma bias so that the spindle just failed to follow vibration at 360 c./sec. In this way, in active animals
the limiting frequency of the spindles could be shifted up and down by various measures known to influence gamma control.

3. Amplitude of vibration. It is not possible to deduce from the amplitude of the vibratory movement of the stimulating cone how big excursions occur in the wall of the nuclear bag. Nevertheless, it is of some interest to see what figures are obtained when the results are corrected for free amplitude (as distinct from amplitude under load), determined by photography. Free amplitude indicates maximal values probably approached only at the skin in cases when very little pressure has been needed. Even then the actual excursions of the wall of the nuclear bag will remain unknown. Figure 5, for a de-efferented soleus spindle, is a plot of these amplitudes against following frequency on the abscissa. De-efferentation was used to make the results independent of variations in nuclear bag tensions due to uncontrollable gamma influences. The values on the right (large circles) refer to application of vibrator on tendon, a mode of stimulation which in this particular case proved to be exceptionally efficient. For the values on the left, four different tensions were used as an empirical check on our view that large variations of pressure, and thus probably of mechanical properties of the tissue, would not influence the general shape of the curve. It is seen that up to about 150 c./sec. the relative amplitudes necessary for spindle following increased and then rapidly fell towards 200 c./sec. to reach an asymptotic minimum around

![Graph](image)

**Fig. 5.** Pentobarbitone cat. De-efferented soleus spindle. Relative amplitude of vibration plotted against limiting frequency for different tensions of muscle: crosses, zero tension; small circles, 88 g.; triangles, 175 g.; squares, 315 g. tension. Large circles: vibration now applied through tendon. Tension 140 g. and pressure of vibrator through tendon particularly effective.
Fig. 6. Pentobarbitone cat. Gastrocnemius spindle. Relative amplitude of vibration at the tensions marked against the readings plotted as function of limiting frequency. Open circles, natural gamma bias; filled circles, after stimulation of gamma system in tegmental reticular substance; squares, after de-efferentation. This spindle did not originally respond at zero tension unless specially biased by gamma stimulation. Amplitude needed for any given limiting frequency was more dependent upon variations in bias than upon tension.

300 c./sec. This general type of curve was independent of muscle tension and therefore is likely to be determined by the physiological properties of the spindles. Highly sensitive spindles would merely differ by requiring less energy at zero and low tensions. Curves of this type (Fig. 5) indicate specific resonance in the end organs.

Figure 6 plots amplitudes against limiting frequency for another spindle at the tensions (in g.) shown against the readings. Its purpose is to show the extreme efficiency of high gamma bias. The filled circles refer to tegmental stimulation, i.e., specially excited gamma fibres, the open ones to natural, variable bias, the squares to the same spindle in the de-efferented state. The exceptionally low frequency at 436 g. tension suggests a temporary inhibition of gamma activity leading to post-excitatory depression (10, 11). When biased from the tegmentum the spindle followed the same and higher frequencies in a manner almost independent of external muscle tension. Under natural bias (the amount of which is unknown) it needed far more amplitude to follow 100 c./sec. at 175 g. Under what must have been optimal gamma control it followed 380 c./sec. at zero tension with very low amplitude. Successful activation of the gamma system therefore decreases the amplitude necessary for spindle following to the low values characteristic for high frequencies at high tensions in the de-efferented state. With strong gamma bias muscle tension produced by stretch is of little importance. The decisive factor will be intrafusal tension.
Considering that free amplitude around 400 c./sec. is only 0.13 mm. at the skin, an incredibly small excursion of the wall of the nuclear bag must have actuated the dynamic component of the generator potential of the spindle in Fig. 6. One is reminded of the extreme mechanical sensitivity of the Pacini bodies (cf. 5), the cochlear organ (see e.g., 1), and other mechano-receptors.

**DISCUSSION**

Vibratory responses of single spindles cannot be compared with those from the afferent nerve or the whole dorsal root. Just as in other mechano-receptors (2, 12) alternation and composite rhythms occur also with spindles (3) giving rise to vibratory volleys of massed impulses at higher rates than those of the individual receptors. Echlin and Fessard, in cats, noted limiting frequencies as high as 530 c./sec. with massed effects, whereas individual receptors followed up to only 240 c./sec. In their case a tuning fork was used. However, they had only a couple of individual (receptors) fibres and did not know whether they were Golgi tendon organs or spindles. Relative energies of the excursions were unknown. Echlin and Fessard also discussed the question of specific resonance and made the pertinent remark that the rate of firing of the end organ at the particular state of tension used would provide a basic frequency which would adapt itself to vibratory frequencies at corresponding rates. It is certainly true that this factor is of importance. Thus, for instance, if spindles fire at a high rate, it can easily be shown that they often fail to respond at vibratory frequencies which are significantly below this value or, if they do so, require to be stimulated at higher amplitudes of vibration than would have been the case if the spontaneous or induced frequency (by fixed stretch) had been lower.

Another question, however, is whether spindles possess real resonance. A final solution of this problem would require microelectrode records from the spindle terminals in the manner of Katz (10). What do our results, as presented in Figs. 5 and 6, suggest? The high amplitudes which are required for de-efferentated spindles at rates of vibration around 100 c./sec. and which do not correlate with any specific firing frequency in the resting state, do make it probable that at such rates the inhibitory positive dynamic swing at “off” on the upstroke of oscillation counteracts stimulation so as to necessitate greater amplitudes of vibration. In this respect it acts as “accommodation” in nerve. At very low frequencies the positive “off” may be fast enough to have spent its force by the time the next vibration sets in. On the other hand, Fig. 6 also showed that at constant external tension the energy required for a given limiting frequency depended on the amount of gamma bias, decreasing after tegmental stimulation to a small fraction of its original value. It is unknown how the dynamic properties of the spindle are altered by intrafusal tension.

The main problem of this paper has been to investigate gamma activation in order to test the prediction that selective stretch of the intrafusal muscular apparatus by gamma stimulation would make the nuclear bag respond
better to vibration than it can do in the slack state. The evidence for this conclusion, now based on well-known modes of gamma activation as well as on de-efferentation in order wholly to remove the gamma influence, seems definite. Apart from the confirmation of present concepts entailed in this result, it is of interest for our understanding of how the relatively slow mechanism of spindle control could mediate the information necessary for rapid fine adjustment of muscular performance. It is well known from the work on the retina that the dynamic components at "on" and "off" are the most striking events in the visual message; indeed, in frogs, for instance, little is seen in between. It is safe enough to conclude that in vision dynamic events play a leading role in perception. Similarly, in muscular end organs, the dynamic responses to change of length constitute a potential source of information which adds to the sensitivity and usefulness of the mechanism and hence must be presumed to be significant. By properly setting its gamma control the organism, according to its needs, can avail itself of the full range of dynamic sensitivity of the spindles, different for slow and fast acts, different again for coarse and delicate movements and also largely independent of muscle tension.

The adjustment of gamma control from the brain stem has at its disposal a fast path in addition to slow ones (7). The latency of the fast path from brain stem to ventral root efferent is of the order of 7–10 msec. and thus compares favourably with pyramidal pathways. The slow route serves as a general "volume control" in tonic action.

**Summary**

The muscle spindle responds to rate of stretch by dynamic components of its generator potential (10). This fact raised the question of whether or not the fast or dynamic phases of the spindle response could be shown to be under gamma control.

By using single fibre preparations in cats and stimulating the spindles by vibratory movement over the skin or, sometimes, through the tendon of the muscle, it was found that the spindle, activated by gamma impulses, responded to considerably faster rates of vibration than in the slack state (de-efferentation, inhibition of the gamma discharge) and required less energy (amplitude of oscillation) to do so.

Lack of gamma activation could be compensated for by increased stretch of the muscle to which the isolated spindle belonged.

Figures are given for relative amplitudes of vibration in relation to muscular tension, gamma activation and maximum following frequencies of spindles.

It is concluded that, although gamma control as such may often be too slow to accompany fast movements, its strong indirect influence on the dynamic component of the spindle response nevertheless suffices to make the biased sense organ a very much faster and thus more efficient mechanism than the unbiased one.
ACKNOWLEDGMENT

A grant from the Swedish Medical Research Council towards the expenses of this work is gratefully acknowledged.

REFERENCES


