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FAST SUPRASPINAL CONTROL OF MAMMALIAN MUSCLE SPINDLES: EXTRA- AND INTRAFUSAL CO-ACTIVATION

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Histologists (Cilimbaris, 1910; Garven, 1925, Barker, 1948; Cooper & Daniel, 1956) have described motor fibres entering the polar regions of mammalian muscle spindles which appear to be larger in diameter than γ motor fibres (Leksell, 1945). In fact, a fibre which is thin just before forming an intrafusal motor ending may not necessarily be of small diameter throughout its length, since Eccles & Sherrington (1930) have demonstrated that larger motor fibres in muscle nerves give off smaller branches as they approach the muscle. Cooper & Daniel (1956) have expressed surprise that the problem of large-fibre motor innervation of mammalian spindles has been neglected in physiological work. This may be understood, in view of the complications which arise when a precise definition of the problem is attempted.

The motor fibres concerned are liable to stimulate intrafusal muscle at the very moment when extrafusal contraction begins. Consider now the situation of the spindles as they lie in parallel with the extrafusal muscle bundles. Proximally spindles are inserted on the endomysium or perimysium of extrafusal fibres. Distally, many spindles taper out into special tendinous slips inserted on aponeuroses or tendons, but those within the belly of the muscle usually stop short, to be inserted again on extrafusal endo- or perimysium (Sherrington, 1894; Huber & de Witt, 1897; Hinsey, 1927; Barker, 1948). In a twitch, therefore, one or both points of insertion will move with the extrafusal muscle as it shortens. Hence the effectiveness of the α fibre spindle innervation in terms of sensory discharge will depend upon the relative velocities of shortening of spindle fibres receiving such innervation and the extrafusal fibres to which they are attached, as well as upon the relative conduction velocities of intra- and extrafusal motor axons within the α group. No data of this kind are available. As a further complication, it may be that the large fibres seen entering mammalian spindles are branches of ordinary α fibres destined for extrafusal elements (Cooper & Daniel, 1956).

In a study of unit spindle afferents in dorsal root filaments, Hunt & Kuffler (1951) described an early discharge occurring when muscle contractions were set up by stimuli to motor nerves or ventral roots, but concluded that this was the result of tension changes in extrafusal muscle rather than a specific motor innervation of the spindles themselves. We have repeated their experiments with additions of our own in the following paper (Granit, Pompeiano & Waltman, 1959), but at the moment we propose something of a short-cut through the complications outlined above. We shall describe the effect of stimulating some regions of the brain stem which project to the spinal cord and raise the simple question of whether, under such circumstances, spindles discharge early enough to be activated by α fibres. This is a short-cut because it presents a physiological problem which is, in the first instance, independent of the peripheral mechanism by which such activation takes place. If spindles are co-activated in small contractions set up by, say, pyramidal stimulation, then this co-activation is likely to be a physiological mechanism in its own right, independently of whether it is the result of mechanical or nervous integration within the muscle.

METHODS

The technique of the present study has been used in previous publications from this laboratory (Granit & Kaada, 1952; Eldred, Granit & Merton, 1953; Granit, 1958). Spindle afferents arising in ankle muscles were functionally isolated from dorsal roots of twenty-four cats which had been given 20 mg chloralose and 10 mg pentobarbitone per kilogram, or else were decerebrated under ether. The former animals sometimes received additional small doses of pentobarbitone as the experiment progressed. In several animals records were also taken from filaments of ipsilateral ventral roots L7 and S1. The hind limb was denervated except for the branches of the tibial nerve to gastrocnemius, plantaris and soleus when these ankle extensors were used, or the appropriate branches of the peroneal nerve when the physiological ankle flexors, tibialis anterior and extensor digitorum longus, were used. Stimulating electrodes were placed on the tibial or peroneal nerve at knee level so that spindle afferents could be identified by their pause in a motor twitch as well as by their response to stretch and pinna twist (the γ reflex of Granit, Job & Kaada, 1952), and so that afferent conduction times from knee to dorsal root could be measured. The limb was rigidly fixed at hip, knee and ankle, and the appropriate muscle was connected to an isometric strain-gauge myograph or else left unhooked. The term 'slack muscle' refers to the latter condition, while zero extension is that length which just produces a deflexion on the myograph of 10 g. For supraspinal stimulation, a stainless steel needle, 0·5 mm in diameter and insulated to the tip, was placed in the brain by stereotaxic methods, and square pulses were applied between it and a large electrode on the divided temporal muscle. At the end of an experiment, electrolytic lesions were made at each stimulus site and then identified in serial paraffin sections stained alternately by Nissl's and Weil's methods.

RESULTS

Time of γ loop. Knowledge of this time is a necessary preliminary to the present work. From records published by Kuffler, Hunt & Quilliam (1951) and Hunt (1951) on stimulation of γ fibres in ventral roots, loop times of the order of 12–15 msec can be derived, counting from ventral to dorsal root.

Granit & Holmgren (1955(observed latencies varying from 10 to 20 msec, but at the time the possibility of large-fibre motor innervation of spindles was not considered. Accurate estimates cannot always be obtained since many spindles are not properly driven by stimulation of ventral root or nerve; instead, the afferent discharge slowly waxes and wanes and the latent period, if at all discernible, may be anywhere between 15 and 30 msec.

In order to exclude the effects of extrafusal contraction when measuring the latency of the γ loop, use was made of the drug Flaxedil (gallamine triethiodide; May and Baker Ltd.), which in mammals fully paralyses α motor end-

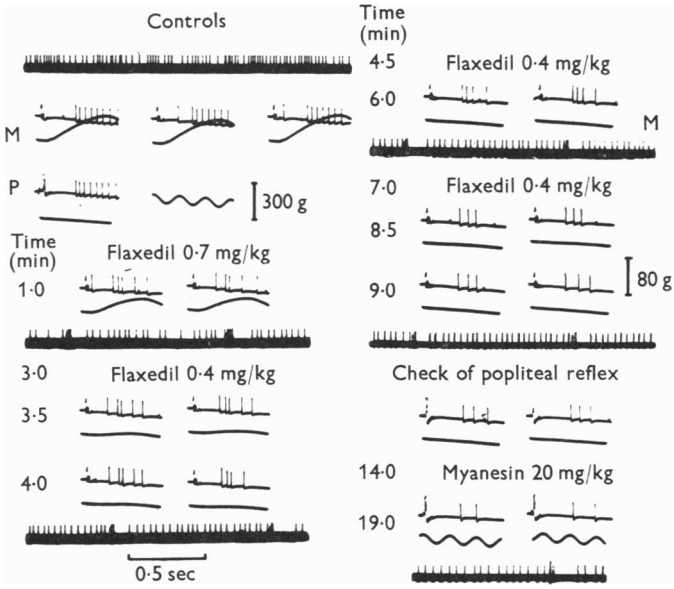

Fig. 1. Effect of Flaxedil on discharge of spindle afferent from extensor digitorum longus. Simultaneous records at slow speed sometimes added to sweeps run with time 100 c/s, as marked (left, middle). Slow speed, as marked below (left) for 0·5 sec. M, myogram. Stimulating muscle nerve at knee level with 0·5 V, 0·5 msec pulses except in P which shows flexor reflex excitation of popliteal nerve, checked later in the experiment. Flaxedil injected in doses and at times indicated, followed by tests of effect from nerve. Experiment ends with injection of Myanesin. Note change of sensitivity of myograph from 300 g to 80 g calibration made at time 9·0 min.

plates long before the γ system is silenced (Granit, Homma & Matthews, 1959). Figure 1 shows records obtained from a flexor spindle afferent which had strong γ control, as judged by the precision with which it was driven by nerve shocks as well as by a flexor reflex. Uppermost are controls at both slow and fast speed with three motor twitches to illustrate the regularity of the spindle's response. P is a reflex evoked by a stimulus to the central end of the cut ipsilateral popliteal nerve; this excites the spindle without causing a detectable

contraction at the given myograph sensitivity. Now the loop time for the earliest spike, about 15 msec, might include some delay as a result of extrafusal shortening making the spindle slack. To remove the contraction, Flaxedil was administered in small doses, while myograph sensitivity was augmented. There was a minimum latency of 10 msec, lengthening to 12 msec as more Flaxedil was given. The effect of the drug is also seen in the diminution and regularization of the resting discharge, but the direct response to nerve stimuli as well as the popliteal γ reflex remained to the very end, when extrafusal contraction was gone and γ bias considerably reduced. That some γ bias may have been left is suggested but not proved by the last test with Myanesin (3-ortho-toloxy-1,2-propanediol; British Drug Houses, Ltd.), which removes supraspinal γ control (Granit & Holmgren, 1955). The further decrease in discharge frequency may also have been due to some reduction in blood pressure consequent on the injection.

This experiment represents an ideal case of good driving. The minimum loop time, from nerve at knee level to dorsal root, was 10 msec. To obtain the loop time from ventral root to dorsal root, it is necessary to add the conduction time from ventral root to nerve at knee level, a distance of 15 cm. The average γ conduction velocity is 30 m/sec (Kuffler *et al.* 1951), which means the addition of 5 msec, giving a total time of 15 msec. This agrees well with the values of earlier studies quoted above and will be taken as the average γ loop time from ventral to dorsal root. It of course includes the time consumed by the γ fibre activation of intrafusal muscle and the subsequent excitation of the spindle afferent, apparently a rather slow process since only 2 msec of the total loop time can be attributed to afferent conduction from spindle to dorsal root. Boyd's (1959) observation of slow intrafusal contraction in isolated cat tenuissimus muscle is pertinent in this regard.

Supraspinal stimulation. Several descending pathways may be stimulated from the brain stem in order to excite motoneurones innervating hind-limb muscles. Of them the pyramidal tract is the best known from both anatomical and physiological studies. Although this tract in the cat contains chiefly small and hence slowly conducting fibres, there are larger fibres in it which descend to the lumbar and sacral spinal segments (for a summary, see Lassek, 1954). These fibres connect with motoneurones indirectly, via interneurones which lie in the zona intermedia at the base of the ventral horn (Szentagothai-Schimert, 1941).

Lloyd (1941) has shown that when the contralateral medullary pyramid is stimulated, descending impulses arrive in these internuncial pools with a latency of 4·5 msec, and after a further delay of as long as 7·5 msec, the motoneurones of the same segment are facilitated. However, Lloyd could reduce the internuncial delay to 1 msec by repetitive stimulation, so that the latency of the motoneurone facilitation became at the minimum 5·5 msec. In the present

experiments the contralateral pyramid was stimulated at the level of the medullary olivary complex or of the facial nerve, and it was found that single rectangular shocks of 2–3·5 msec duration, given once a second, were optimal for exciting the ankle muscles and their spindles. The latencies of muscle contraction or spindle response, measured from the onset of the shock in all cases, as in the work of Granit & Holmgren (1955), were not significantly reduced when tetani of briefer shocks were used instead. In a few experiments, where ventral root filaments were monitored, each pyramidal stimulus evoked a motoneurone discharge, often repetitive, which began with an average latency of 6 msec, although latencies as short as 4·5 msec were occasionally seen. This suggests that a prolonged single shock was equivalent in effect to a brief train of shorter stimuli (cf. Brookhart, 1952).

From the above it follows that if the average γ loop time is 15 msec and if γ motoneurones fire 6 msec after a pyramidal shock, then pyramidal stimulation may drive a spindle afferent over the γ loop with an average latency of 21 msec. Therefore, if a faster peripheral loop is to be demonstrated, latencies consistently below this figure must be found.

Figure 2 illustrates a typical experiment on pyramidal stimulation. The muscle, gastrocnemius, was studied in the slack condition and at extensions of 4 and 10 mm. In each case of A, four control sweeps and four with stimulation are shown. The contractions obtained, as in other cases of pyramidal stimulation of extensors, were quite small. It may be seen that the earliest spindle response appears early in contraction. In B histograms have been constructed for the latencies measured from a total of 68 sweep records, and the earliest significant values lie between 12 and 14 msec. These are obviously too short to be explained by the average time of the γ loop, In fact, if the stimulus had been given to the ventral root instead, these latencies would be short for that loop. When the muscle was extended to 4 and 10 mm, these same short latencies were obtained and, in addition, a later discharge appeared at 20 msec or more. Such a response may have been mediated over the γ loop.

To reduce the labour of measuring latencies from large numbers of single sweep records, photographic superposition, at a sweep repetition rate of 1/sec, was used in many experiments. Figure 3 is an example of such a case. The stimulus site was again the contralateral medullary pyramid (C) but this time the spindle was in a flexor, tibialis anterior, which responded to each shock with a sizeable contraction. It was, in fact, always easier to evoke contractions in the flexors when the pyramidal tract was stimulated. In the uppermost row are shown records formed by the superposition of 30 consecutive traces of resting discharge, at each of three muscle lengths. The spikes are randomly distributed. In the next row each superimposed sweep begins with a shock to the pyramid. Consistent driving was obtained at latencies of

13–16 msec, again too early for the average γ loop. Below follow single sweep records which emphasize the most characteristic feature of our findings, namely that the discharge begins at the foot of the contraction. In B the events are shown at slower speed and at lower myograph sensitivity; after the early discharge, the spindle is silent during contraction.

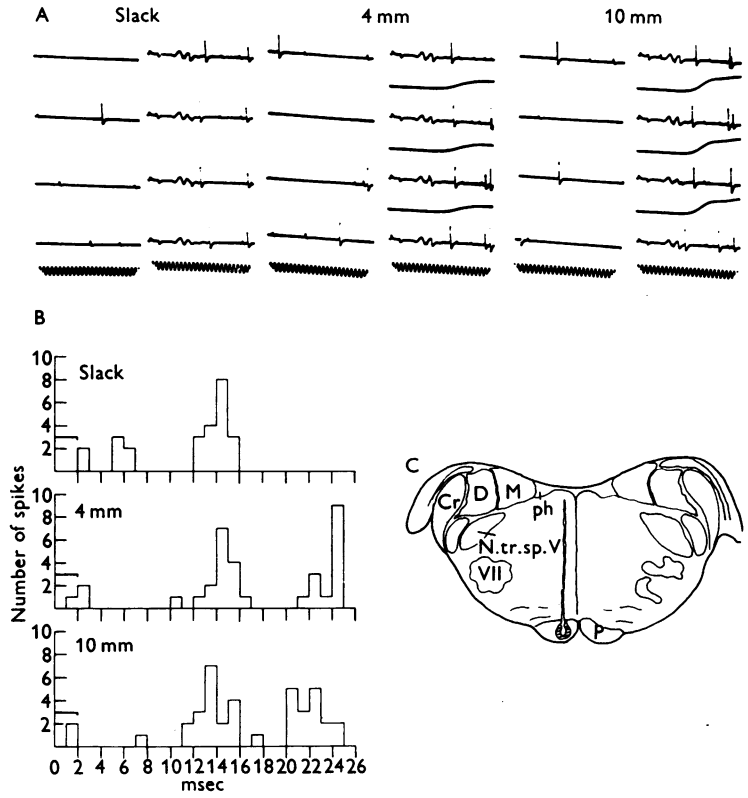

Fig. 2. Response of gastrocnemius spindle afferent to pyramidal stimulation. Decerebrate cat. A, resting and driven (note stimulus artifact) responses at three muscle extensions, slack, 4 and 10 mm respectively. Stimulus strength 10 V, duration 2·2 msec. Myograph sensitivity 80 g for vertical line on the right in all figures; time 1000 c/s. B, frequency distribution of latencies of driven spikes, measured from onset of stimulus artifact (note horizontal bar for stimulus duration); class interval 1 msec. C, camera lucida drawing of transverse section of medulla (Weil stain) showing electrode track and electrolytic lesion at stimulus site. Abbreviations in this and subsequent figures: Cr, corpus restiforme; D, descending vestibular nucleus; Dt, nucleus dentatus; F, nucleus fastigii; I, nucleus interpositus; L, lateral vestibular (Deiters's) nucleus; M, medial vestibular nucleus; N.tr.sp.V, nucleus tractus spinalis nervi V; P, pyramid; ph, nucleus praepositus hypoglossi; VII, motor nucleus of n. VII.

Although the latencies obtained with pyramidal stimulation were brief enough to argue against the γ loop, other sites were also tested for early spindle driving. Thus Fig. 4 illustrates an experiment in which the stimulus site was

Deiters's (lateral vestibular) nucleus of the ipsilateral side, the origin of the vestibulospinal tract.

Thulin (1953) stimulated Deiters's nucleus in the cat, using 5 msec pulses, and recorded the discharge in ventral roots L7 and S1; although latencies were not discussed, values of 4–5 msec from the *end* of the shock artifact may be estimated from his Fig. 2. In another study (Gernandt,

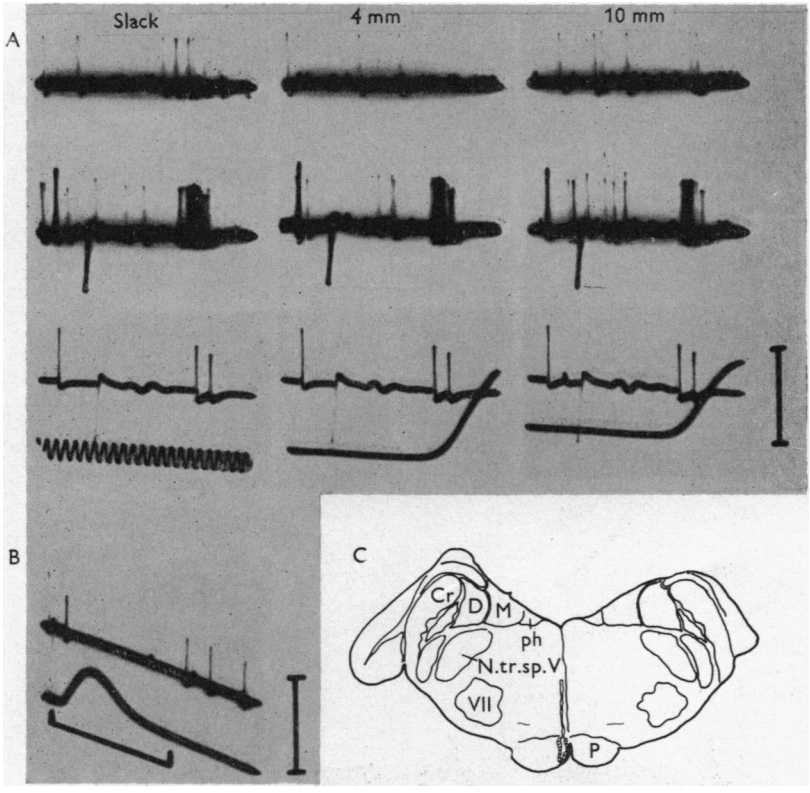

Fig. 3. Response of tibialis anterior spindle afferent to pyramidal stimulation. Decerebrate cat. A, upper and middle rows show resting and driven responses (30 superimposed sweeps each) at three muscle extensions, slack, 4 and 10 mm respectively. Lower row shows sample single sweeps with simultaneous myogram, calibration of myograph 80 g. Stimulus strength 20 V, duration 3·4 msec. Time 1000 c/s. B, single sweep record at slower speed (time 100 msec) and reduced myograph sensitivity 840 g. Note spindle pause after early discharge. Stimulus as in A. C, electrolytic lesion at stimulus site in contralateral pyramid.

Katsuki & Livingston, 1957) stimulation of the vestibular nerve with 0·5–1·0 msec shocks evoked a response in lumbosacral ventral roots with a minimum delay of 4–5 msec. Although these two reports are not quite in agreement with respect to latency, it does appear that in the cat the vestibulospinal tract, since it makes monosynaptic connexions with motoneurones (Schimert, 1938), may activate the motor horn somewhat sooner than the pyramidal tract. Recent anatomical observations (Pompeiano & Brodal, 1957) indicate that the spinal projection of Deiters's nucleus

is somatotopically organized, and that the dorsocaudal portion which was stimulated in this experiment (position 2 in C) projects to the lumbosacral cord and consequently to hind-limb muscles.

Only extensor muscles were studied during stimulation of Deiters's nucleus; in the experiment of Fig. 4 soleus was used and large contractions were obtained, as is seen in B. The uppermost records, formed by the superposition of

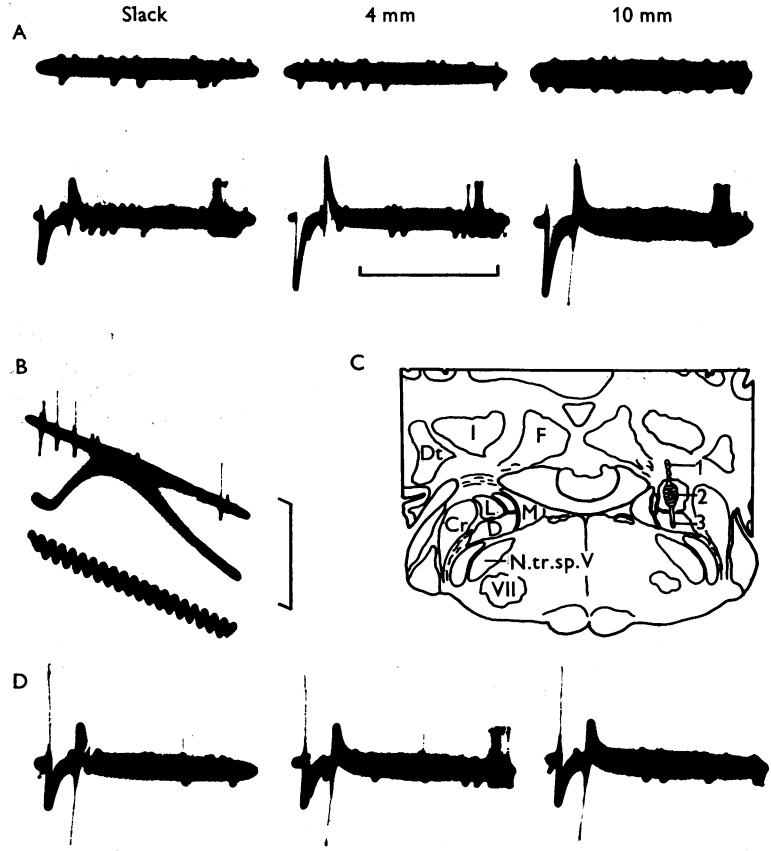

Fig. 4. Response of soleus spindle afferent to stimulation of Deiters's nucleus. Chloralose-nembutal cat. A, resting and driven responses (30 superimposed sweeps each) at three muscle extensions, slack, 4 and 10 mm respectively. Stimulus strength 5 V, duration 2·1 msec. Time 10 msec. B, single sweep record of driven response with myogram (calibration 300 g) at slower speed. Muscle at 4 mm, stimulus as in A, time 100 c/s. C, stimulus site, marked 2, in the hind-limb region of the ispilateral Deiters's nucleus. D, from left to right, responses obtained by stimulating at sites marked 1, 2 and 3 respectively, in C; muscle at 4 mm, stimulus 3·2 V, 2·1 msec, time as in A.

30 consecutive traces each, are controls showing the discharge at each of three muscle lengths; the lower records demonstrate the effects of stimulation. A response was consistently obtained with a latency as short as 13 msec. B illus-

trates a contraction at slower sweep speed and two spikes coming at its foot. Figure 4 also demonstrates that the actual site of stimulation was quite well localized to the tip of the electrode, for in D it is clearly seen that positions 2 mm dorsal or ventral to that labelled '2' in C gave hardly any afferent response to threshold stimuli.

In other experiments, the medullary and pontine reticular formation (particularly the nuclei reticularis ventralis, gigantocellularis and pontocaudalis), the mesencephalic reticular formation, and the medial longitudinal bundle were stimulated, both ipsi- and contralaterally, yielding afferent responses with shortest latencies of 13, 14 and 11 msec, respectively. Spindle afferents from flexor and extensor muscles were studied. The reticular formation does not send fibres to the lumbosacral segments of the cord (Torvik & Brodal, 1957) but probably activates hind-limb motoneurones via proprio-

TABLE 1. Summary of earliest latencies of spindle responses to supraspinal stimulation: 60 observations on 45 spindles

Stimulus site	Earliest latency (msec)
Pyramid	12, 13, 13, 13, 14, 15, 16, 16, 16, 16, 16, 17, 17, 18, 18, 19, 20, 20, 21, 22, 23, 25. No response from 4 spindles
Medullary and pontine reticular formation	13, 15, 15, 15, 16, 16, 16, 17
Mesencephalic reticular formation	14, 15, 15, 17, 18, 19, 21, 25, 29, 30. No response from 4 spindles
Deiters's nucleus	13, 14, 15, 15, 15, 16, 19, 27. No response from 1 spindle
Medial longitudinal bundle	11, 14, 16

spinal neurones, as suggested by Lloyd (1941). The medial longitudinal bundle was stimulated in its medial portion, which is said to contain descending fibres (see Nathan & Smith, 1955, for a review).

All observations on supraspinal stimulation have been summarized in Table 1. The total number exceeds the number of spindles because more than one stimulus site was often used in the study of a single spindle.

As a rule, spindles were driven with brief latencies from these selected sites only when measurable contractions were evoked, and the latency of the driven response in such a case was then found to bear a rather close relationship to the onset of the contraction. This was rather evident from the examination of sweep records but is more clearly shown by Fig. 5, which gives the distribution of time intervals between onset of contraction (zero time) and initiation of spindle response for a group of 31 observations on 20 spindle afferents. A high myograph sensitivity (80 g/cm film) permitted the measurement of time of onset of contraction to within ± 1 msec, while the time of initiation of the spindle response was obtained in the following way. The afferent conduction time from knee electrodes to dorsal root (an average distance of 15 cm) was

measured in each case and the afferent fibre conduction velocity calculated. The additional afferent time from muscle to knee was then estimated on the basis of average measured distances of 2 cm for gastrocnemius, 3 cm for plantaris, 4 cm for soleus, 6 cm for tibialis anterior and 8 cm for extensor digitorum longus. The total afferent conduction time from muscle to dorsal root so derived, although neglecting afferent time within the muscle itself, was considered adequate for the present purpose, and when subtracted from the latency of the driven spike, gave the initiation time. It is evident from the histogram that most responses began in the first 2 msec after the onset of contraction and that the total spread was quite narrow. Yet the absolute

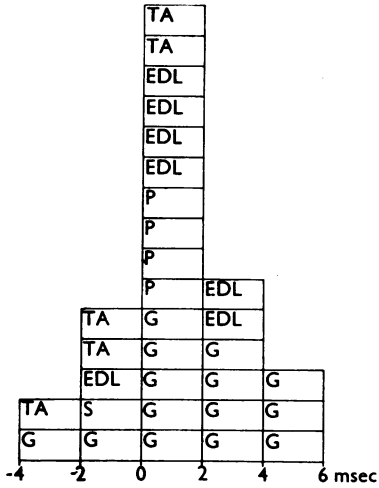

Fig. 5. Relation between time of initiation of spindle response and time of onset of contraction, in 31 cases of supraspinal stimulation. Time of initiation estimated by subtracting afferent conduction time from total latency, for each case. Abscissae represent differences between initiation time and time of onset of contraction, the latter set at zero. Class interval 2 msec. Abbreviations indicate muscle in each case (EDL, extensor digitorum longus; G, gastrocnemius; P, plantaris; S, soleus; TA, tibialis anterior).

latencies of contraction and spindle response had wide ranges, 11–24 and 12–29 msec, respectively. This may be taken to indicate that the spindle discharge in each instance has been evoked by some mechanism operating with approximately the same speed as that of the fibres exciting extrafusal muscle, i.e. α fibres. Without the added evidence of the short latencies of many driven responses, this in itself suggests that the γ loop was not here involved.

DISCUSSION

The fundamental result of the present study is that co-activation of extrafusal muscle contraction and spindle afferent discharge is readily observed on supraspinal stimulation. That is, when stimulation at one of several sites in

the brain elicits a contraction in an ankle muscle, many spindles in that muscle are activated and discharge when the contraction begins. This disclosure led to a re-examination of the early discharge of spindles to stimulation of ventral root or peripheral nerve (Granit *et al.* 1959). It proved possible to separate an ephaptic component (cf. Lloyd, 1942; Leksell, 1945), due to excitation of sensory fibres by the muscle action potential which precedes the measurable onset of contraction, from a genuine physiological activation making spindles discharge at the foot of the contraction, just as in the present observations. Our general conclusion is therefore that whatever the site stimulated, be it a place in the brain stem as in this work, or ventral root or nerve as in the second report, evidence for a fast process of spindle activation is obtained; and so it seems necessary to conclude that, essentially, it is one and the same process accessible from different sites. It is not found in all spindles of the leg muscles studied (see Granit *et al.* 1959) and often requires some γ bias or slight extension of the muscle, both procedures known to increase a spindle's phasic sensitivity (Granit & Henatsch, 1956; Lippold, Redfearn & Vučo, 1958). In the periphery, distal to the ventral root, fast spindle activation is conducted at α velocity (Granit *et al.* 1959).

Besides that of Granit & Holmgren (1955), several studies of spindle activation by supraspinal stimulation have been made in the past (Granit & Kaada, 1952; Eldred *et al.* 1953; Eldred & Fujimori, 1958) in which activation has been attributed to excitation of γ fibres. Latency was not measured in the latter studies and the response was described as slowly recruiting in character and was followed by a long-lasting after-effect, although Granit & Kaada (1952) pointed out that activation of spindles from the pyramid caused a quick burst. However, in the experiments of Granit & Holmgren (1955) particular attention was paid to the question of latencies. By stimulating the mesencephalic tegmentum with single shocks they activated the γ loop selectively without producing any contraction. Their average values were of the order of 22 msec (range 20–26) with conduction time to ventral roots L7 and S1 of the order of 7–12 msec. We have confirmed their results in similar experiments. However, we have now demonstrated spindle activation at latencies as short as 14 msec by stimulating the mid-brain at the same site. The difference between the shortest latencies of the two studies can best be explained by the existence of a peripheral mechanism activating spindles at α conduction rates.

In selecting sites for supraspinal stimulation attention was given to regions which send descending fibres to the spinal cord. It was shown that stimulation of the pyramidal tract, which is known to be involved in the production of phasic movements, effectively activated this fast spindle mechanism. Stimulation of Deiters's nucleus and reticular formation, which on the other hand are known to take part in the regulation of postural tone, also evoked an early

spindle discharge. The cerebellum has access to these latter regions through fastigio-deitersian and fastigio-reticular connexions, and descending cortical projections to the brain-stem reticular formation have been demonstrated (Rossi & Brodal, 1956). The fast spindle mechanism, then, should be available to several higher centres whose functions are related to regulation of motor activity.

Our results have the further interest that they provide fresh evidence for the existence of a peripheral mechanism facilitating centrally induced muscle contraction. This was demonstrated (Granit, 1950) by using monosynaptic testing to study the excitability of ventral horn cells in response to both shocks and slowly rising currents applied to the peripheral stump of a cut ventral root. Contraction was accompanied by an early rise of motoneurone excitability followed by suppression of excitability as muscular tension increased. The present work and its sequel (Granit *et al.* 1959) suggest that the mechanism behind this brief, early facilitation accompanying contraction is a specific process of spindle activation based on α fibres.

It is not yet known whether the α control of spindles also extends to spinal segmental reflexes. One striking fact seen in work on these reflexes, as pointed out by Hunt (1951), Granit *et al.* (1952), Eldred & Hagbarth (1954) and Hunt & Paintal (1958), is the overwhelmingly strong and well maintained γ effect on extensor spindles from skin receptors. They are clearly organized with a large margin of safety for γ activation and involve enough synaptic delay to make the fast α mechanism less important than the slower γ mechanism. For this reason, even if there be α activation of the spindles at the foot of such reflex contractions, they would be submerged in the powerful discharge set up by the γ system.

SUMMARY

1. The effect of supraspinal stimulation upon the discharge of hind-limb spindle afferents isolated from dorsal roots was studied in decerebrate or anaesthetized cats; tension myograms were simultaneously obtained.

2. Consistent afferent driving was obtained from pyramid, Deiters's nucleus, brain-stem reticular formation and medial longitudinal bundle, using 2–3·5 msec square pulses at one per second.

3. The latency of the spindle afferent response to pyramidal stimulation was generally less than the sum of the average latencies of ventral root response to pyramidal stimulation plus peripheral γ loop from ventral to dorsal root.

4. In almost all cases muscular contraction accompanied afferent driving and the initiation of the spindle response in each case was closely related in time to the onset of the evoked contraction.

5. In view of the temporal relationship between extrafusal contraction and afferent spindle discharge, and the brief latencies observed, it is considered

unlikely that spindles have here been excited by γ motoneurones. Instead, it is suggested that these effects have been mediated by α motoneurones.

6. The physiological significance of fast supraspinal and spinal control of spindles is discussed.

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