have to be considerable and consequently the reflex very easy to elicit. This, however, is by no means the case. The monosynaptic response is often far more difficult to elicit than the stretch reflex. The two may even behave as if there were some competition. The stretch reflex tends, for instance, to disappear in light anesthesia when the monosynaptic response may be better than before (cf. similar observations by Brooks and Fuortes, 1952; Alvord and Fuortes, 1953). Park, Teasdall, and Magladery (1951) and Dott and Gohl (1952) point out that for man the monosynaptic response (their H-reflex or Hoffmann-reflex) may often be absent in patients who to all appearances have excellent muscular control.

Liddell and Sherrington (1924, 1925) and Lloyd (1943b) held the stretch reflex to be highly autogenous. Granit and Ström (1951a) found that despite light anesthesia some individual ventral horn cells were fired by both the medial and lateral gastrocnemius nerve provided that some facilitation by stretch was added. Job (1953a), in our laboratory, made a special study of this question by recording from both severed ventral roots and severed peripheral nerves and proved that synergists could fire each other's motoneurones under a variety of conditions, all defined by sufficient facilitatory support from themselves or other systems. This has been confirmed independently by Roberts (1952), Cohen (1953), and Alvord and Fuortes (1953).

Many of the questions dealt with in this chapter closely concern the physiology of the spinal cord. It has been necessary, however, to delimit the subject and make a halt somewhere as an alternative to writing a chapter on the spinal cord. The latter subject will be found extensively treated by Lloyd in Howell's textbook of physiology, edited by Fulton (1946), as well as by Eccles (1953) in a recent monograph (cf. Creed et al., 1932).

Chapter 7

Spinal and Supraspinal Control of Posture and Movement by the Loop to the Muscle Spindles. Rigidity. Spasticity

1. Introduction

It appears that Rossi (see below) in 1927 was the first to envisage a role for the spindle innervation corresponding to the ideas prevalent today. Leksell (1945) realized that his work required completion with a study of reflex effects of the γ fibers but did not himself attempt experimentation along these lines. Granit (1950a) and Hagbarth and Naess (1950a) next published the experiments already mentioned and were surprised to find inhibition with supramaximal stimulation of the ventral root of sufficient strength to bring in γ efferents. On Hunt's (1953) recent evidence this inhibition may well have arisen in the myotube endings of the muscle spindles.

Granit and Ström (1951b, 1952), studying the stretch reflex at light initial tension in decerebrate animals, found earlier facilitation if the external loop was left intact than after de-efferentation and concluded that the spindles were tonically innervated by the γ fibers. Sommer (1940) and Hoffmann (1951) suggested that activation of the tendon jerk in man by Jendrassik's well-known method was due to spindle activation because it was found to take place without an increase of tension in the muscle concerned.

However, most of the new information on reflexes and supraspinal control in terms of spindle afferents and γ efferents has come from the direct approach of Hunt (1951, 1952a, 1953), Kobayashi et al. (1952), Granit and Kaada (1952), Granit, Job, and Kaada (1952), Eldred, Granit, and Merton (1953), Eldred and Hagbarth (1954), and Granit, Holmgren, and Merton (1954). In presenting the results I shall try to build up a synthetic view based on the results of Hunt, the Japanese authors, and our group, all of which deal with the functional interpretation of records from γ fibers and spindle afferents.
Fig. 110 presents a schematic diagram of the experimental arrangement used in this kind of work unless the records are taken directly from $\gamma$ efferents. The nuclear bag afferent in a root filament serves as indicator of spindle activation. The advantage of studying the spindle afferent rather than the $\gamma$ efferent is that the mechanical muscular events are integrated into the picture.

Fig. 110. Diagram illustrating arrangement of experiment for reflex work with simultaneous spindle control. Muscle with parallel intrafusal fiber containing spindle connected to strain gauge. Afferent fiber discharge from spindle isolated in dorsal root and projected on oscilloscope. Destination of $\alpha$ and $\gamma$ fiber from ventral root of spinal cord shown. (Granit, Holmgren, and Merton, 1954.)

2. The tonic discharge and its effect on extensor spindles

Tasaki and his collaborators appear to have been the first to study the activity of individual $\gamma$ fibers, and their work from 1944 onward has recently been summarized in English (Kobayashi, Oshima, and Tasaki, 1952). Having been ignorant of Leksell's (1945) simultaneous work, they did not realize that the small efferents in mammals were the motor fibers of intrafusal muscle (cf. preceding chapter), but they did record their discharge. It is perfectly clear from Fig. 111 that they noted the tonic firing in the fibers, found by Kuffler, Hunt, and Quilliam (1951), Hunt (1951), and Granit and Kaada (1952), which firing, indeed, is such a very striking feature of this system. The tonic resting frequencies are high. Even in his spinal animals Hunt (1951) recorded values from 20 to 60 per sec.

Fig. 111. Cat under urethane. Action currents recorded from three myelinated fibers of below 5 $\mu$ in diameter innervating the medial head of gastrocnemius. A: spontaneous efferent discharge from the spinal cord, B: increase in the frequency of discharge by decerebration, C: record taken about 10 min. after decerebration, D: increase of the frequency by repetitive induction shocks applied to the contralateral sciatic nerve (started at the arrow). Time: 10 msec. (Kobayashi, Oshima, and Tasaki, J. Physiol., 117, 152. 1952.)

As shown by Fig. 111, Kobayashi et al. found the discharge to increase after decerebration and to accompany reflex action. Their results with the well-known spinal reflexes agree with those of Hunt insofar as $\gamma$ activity is concerned, but their interpretation is that these fibers are tonic motor fibers capable of supporting decerebrate rigidity by themselves. This conclusion is based on the observation that the large $\alpha$ fibers were found to be silent in decerebrate rigidity. However, long ago Dusser de Barenne (1911) and Buytendijk (1912) showed that string galvanometer records of the electromyogram in decerebrate rigidity indicated persistent activity, for some time afterward spoken of as the Dusser de Barenne-Buytendijk vibrations, and so it is rather improbable that their view can be correct even if, as pointed out above, functions to some extent will overlap in caliber spectra. Long ago
Denny-Brown (1929) and Adrian and Bronk (1929) studied this tonic activity in single motor units. Granit and Kaada (1952) isolated a large number of small and large fibers in ventral roots. In general it seems true that most small fibers discharge tonically while most large fibers are silent, but even in barbiturate anesthesia there will be active α fibers. Recently Gernandt (1952) has studied vestibular reflexes (cf. Adrian and Bronk, 1929) in decerebrate animals and has had no difficulties in finding persistent α activity.

In order to make clear what the tonic γ discharge signifies in terms of spindle activity Fig. 112,B, compares, for a decerebrate animal, the spontaneous activity of the spindle with intact innervation with C, the same baseline discharge after de-efferentation. When here, as elsewhere, I speak of spindle activity I refer to a nuclear bag afferent as indicator because the single fibers have been isolated in the roots (Fig. 110) in which myotube afferents are but rarely obtained. The excited spindle exhibits a persistent irregular discharge, often grouped, while the nonexcited spindle (which is identical with the purely peripheral muscle-nerve preparation hitherto discussed) has a very much lower rate of spontaneous firing. This also is characteristically regular unless too low. A spindle discharging at a rate below some five impulses per second does not seem to be able to fire regularly (cf. Matthews, 1933). Also in barbiturate anesthesia there is irregular firing in excited spindles. In Fig. 112,A, stretch has been applied and the grouping of the spindle discharges may well indicate synchronous rhythmic γ outbursts to the intrafusal fibers. For convenience I shall speak below of excited and nonexcited spindles when comparing discharges before and after de-efferentation. In our work de-efferentation has been used as a standard of comparison for describing effects of γ efferents against a reference point of zero γ control.

The two upper records of Fig. 113 illustrate a 10 mm. stretch of the muscle for an excited spindle with a spontaneous rate as high as 40/sec. at the zero initial tension used, the lower ones the same experiment after de-efferentation. The strain gauge myograph had been mounted on rollers and movement started with the muscle just slack. There is clearly a considerable stretch reflex in the intact preparation A–B (decerebrate cat) as can be seen by comparing the myograms of, respectively, the upper and lower sets of records. The nonexcited spindle C–D was silent at zero tension when stretch started. While stretch is maintained, some adaptation takes place, as has been shown by Adrian and Zotterman (1926a) and Matthews (1933) for the nonexcited spindles they always used, even though these organs belong to the category of receptors which have little adaptation compared with rapidly adapting ones. Part of this adaptation will be due to the viscoelastic properties of the stretched tissues but—as in other
receptors—there must be a genuine adaptive mechanism superimposed upon the effects of the mechanical factors. Adaptation in stretch receptors has been studied by Bronk (1929) and Matthews (1931). Now, when comparing the adaptive process in excited and nonexcited spindles, we found that the impulse frequencies, though throughout very much higher for the excited spindle, tend to drop along roughly parallel curves in both instances, but for the excited spindles this curve is displaced upward in a coordinate system of frequency plotted against tension or length. This means that $\gamma$ bias still must be considerable at a time, late in stretch, when the nonexcited spindle fires very slowly or may even have ceased altogether to respond. The same shift upward in the general level of activity was also noticed at all degrees of initial tension from zero upward. While it is quite common at zero tension to find nonexcited or de-efferentated spindles silent, those of the intact decerebrate (excited) preparations in good condition are practically always firing. As a consequence the threshold of excitation generally is considerably lower in the excited spindle than in the nonexcited one, a fact of great physiological importance. These observations on decerebrate preparations refer to Eldred, Granit, and Merton (1953).

The Japanese authors found more $\gamma$ activity in decerebrate preparations than after spinalization, and Granit and Kaada (1952) also reported their impression that the spindles were particularly active in their decerebrate animals. Since that time our very much extended experience has made it possible to state that in cats decerebrated by pre- or intercollicular sections the spindles uniformly fire at exceptionally high rates and do so even in the absence of rigidity ($\alpha$ activity). Hunt noted that when, in decerebrate animals, a spontaneous increase of tension took place, this too was accompanied by efferent $\gamma$ firing, and Granit and Kaada confirmed this, using the spindle as afferent indicator.

In order further to elucidate this question an experiment was devised, based on the principle of the anemic decerebration of Pollock and Davis (1930). The basilar artery of the cat (chloralose) was tied under ether at the operating table and slings placed around the common carotids. When the strings were pulled, anemic decerebration took place. As soon as the rise in tension began, or at the latest when it was maximal, the slings were released and the animal allowed gradually to return to the status quo ante. This kind of decerebration has the advantage that it can be repeated several times.

Fig. 114 is an evaluation of spindle frequencies and myograph values during this procedure. It is seen to have taken 20 seconds of carotid occlusion to release the formidable rise of tension which is the initial phase of anemic decerebration. The soleus muscle was used, and it has apparently contracted to the maximum obtainable (cf. the maximal tetanic contraction values for this muscle given by Eccles and Sherrington, 1930 and in Chapter 6). The interesting point, however, is that this activity not only is initiated in the spindles (cf. Hunt, 1951) but that in addition the spindle discharge is maintained high throughout the slow tonic contraction. This would hardly be possible against

![Graph](image-url)

**Fig. 114.** Cat. Chloralose 20 mg/kg. Permanent clamp on basilar artery. Slings around carotids. The two ordinates refer to myogram ($T$ and filled circles) and spindle frequency ($S$ and open circles). At zero abscissa, carotids occluded and released when tension reached maximum. Compare curves $S$ and $T$.  

If the carotids are left occluded, there is a fall in tension after the
strong initial effect described above. When later on smaller postural contractions spontaneously return and disappear, the same sequence of events is observed. It will be shown below that after permanent anemic decerebration of animals left to recover from the ether narcosis without additional anesthetics, a curious disintegration of $\alpha$ from $\gamma$ activity takes place. In fact, decerebration by the anemic and trephine methods respectively produces two different types of rigidity. The latter method alone can be relied upon to elicit with great regularity a high level of spindle activity.

Sherrington (1898) pointed out that the anomalous state which he called decerebrate rigidity may not be the only kind of rigidity and it is clear from very satisfactory evidence that states of the same general type may occur in animals deprived by de-afferentation of both $\gamma$ loop and postural limb reflexes (see for references the recent review by Moruzzi, 1953). I shall return to this question below. Sherrington used to speak of the state of decerebrate rigidity as exaggerated posture. Apparently the spindles through their facilitatory effects on the ventral horn cells contribute their full share of this exaggeration.

3. Inhibition of $\gamma$ fibers in stretch. Integration of $\alpha$ and $\gamma$ in the "lengthening reaction"

One of the most important observations made by Hunt (1951) on $\gamma$ fibers is recorded in Fig. 115. Records 1 and 2 from a spinal cat show a few efferent $\alpha$ and $\gamma$ fibers in isolation. In record 1 the baseline or tonic discharge, as usual, consists of pure $\gamma$ activity. When the muscle is stretched (2), reflex $\alpha$ activity appears but the $\gamma$ outflow is inhibited. This, at the moment, is the only known proprioceptive reflex on the $\gamma$ motoneurones. Biologically the purpose of the $\gamma$ inhibition must be to suppress excessive spindle stimulation at a time when the spine already is being stimulated by stretch, one more example of a reflex self-regulation which is similar to the autogenetic inhibition from the Golgi tendon organs. It is not yet known whether the inhibition of $\gamma$ activity also is initiated by the tendon organs and thus is strictly parallel to the autogenetic $\alpha$ inhibition described in the previous chapter. Possibly the effect derives from the myotube endings. Nevertheless it seems clear that both inhibitions are likely to be coordinated in reflex self-regulation of muscle activity and for this reason it is of interest to examine the "lengthening reaction" with, if possible, simultaneous records from spindle and Golgi afferents.

The lengthening reaction, as originally described by Sherrington (1909), cannot be wholly autogenetic. To be sure, the true autogenetic inhibition from the Golgi tendon organs must on the evidence of Chapter 6 be one of its essential components but actually Sherrington's experiments were performed with otherwise intact decerebrate animals and it does not succeed very well with muscles in isolation after proper denervations of other limb muscles. The sudden clasp-knife cessation of muscular resistance is well developed only if the extensive synergist inhibition set up by the tendon organs in response to muscular tension (Granit, 1950a and Chapter 6, sec. 6) is allowed free play.

![Fig. 115. Spinal cat. Ventral root filaments containing one large fiber and small fibers. 1: small fibers show continuous activity while large fiber is silent. 2: during stretch reflex excitation of large fiber and reflex inhibition of small fibers. (Hunt, J. Physiol., 115, 456. 1951.)](image-url)
spike the tendon organ increase of spike frequency to the increase in tension during the twitch. This identification of the small spike as a spindle was confirmed (records on the extreme right) by its behavior in the pinna reflex. Granit, Job, and Kaada (1952) showed that there are very active pinna reflexes (see Fig. 120) on the γ fibers, often without any effect on the motor contraction, and this method of identification we generally use in our laboratory, in addition to testing with a twitch. There was a good response in this case (see records N and O). The Golgi tendon organ, which was silent as long as the limb was held straight, did not fire to twisting of the cat’s pinna.

The experimenter, then, to elicit the lengthening reaction, grasped the animal’s leg with one hand, steadying its knee with the other. After a while he started to bend the leg slowly, thus stretching the ankle extensors, and the records from B onward are taken during this act of bending the leg up to its minimal angle. The spindle firing as directly recorded, and the stretch reflex, as felt, increase steadily from record to record and ultimately the discharge frequency reaches the exceedingly high maintained value of 300 impulses per second in G. The greatest tension is in H, where the Golgi tendon organ has its peak frequency. The latter picked up tension relatively late (in D) owing to its characteristically high threshold. Then, quite suddenly in I, the spindle discharge is inhibited and this inhibition must have been very strong to suppress its activity to such a low level despite the increased pull due to continued bending of the leg. At the same time the muscle relaxes, as is clearly demonstrated objectively by the slowing of the Golgi tendon organ. This sudden drop of tension is Sherrington’s lengthening reaction. There is thus perfect cooperation between spindle inhibition and tendon autogenetic inhibition in preventing excessive states of tension in stretch, a self-regulation run with a double safety mechanism comparable to the triple safety arrangements in the silent period. This double safety mechanism is supported by the extensive inhibitory overlap to synergists described above (see Chapter 6), by means of which it can overcome the tremendous facilitatory background of stretch combined with spindle cramp (decerebrate animal). Sherrington’s lengthening reaction has thus been satisfactorily explained and has also served to lay bare the details of an important integrative mechanism in reflex self-regulation of muscle activity.

Attention should also be called to the steady and very high rate of firing of the excited spindle in the intact limb (Fig. 116), hardly to be expected in view of Hunt’s inhibition of the γ efferents by stretch. (Fig. 115. Probably Hunt carried out this type of experiment only on spinal animals.) A frequency of 300 per second can be obtained with nonexcited spindles only in the very beginning of sudden, heavy stretch. Inhibition of the γ discharge by stretch in a decerebrate animal apparently requires a considerable amount of tension. It behaves in this respect like the autogenetic inhibition from the Golgi tendon organs (cf. Job, 1953b). Both inhibitions are probably suppressed in the decerebrated state by hyperexcitation from higher sources, direct as well as indirect through the γ loop.

These high frequencies are interesting from many other points of view. Thus one may well ask what is achieved in the centers by such high rates in view of the low firing frequency of the motoneurones (Adrian and Bronk, 1929; Denny-Brown, 1929). Do they mobilize other systems more
effectively than the monosynaptic one? The discharge frequency of the motoneurones is apparently regulated within narrow limits by the Renshaw feedback, but the high frequency effect may well be piled up elsewhere—for instance in the reticular structures, which to high frequencies set up lasting states of excitation (see below). High frequencies are by no means restricted to muscle spindles. In the retina it is common to find maintained rates of discharge up to 400/sec. (Granit, 1944) and for short times values between 800 and 900 per second have been recorded by Eneroth (1952) and Kuffler (1953). They also present an interesting problem from the point of view of impulse generation. How can the generator potential maintain such high frequencies in the face of accommodation and cathodal depression?

With stretch mobilizing excitatory and inhibitory afferents for the α motoneurones as well as inhibitory ones for the γ motoneurones, one may well ask what the sum total will turn out to be in terms of reflex contraction. There is no general answer to this question. It will vary with type of preparation, state of excitability in motor and premotor neurones, as always is the case with reflex effects. The simplest way of attacking this question is by means of monosynaptic (heterosynaptic) testing, because it is possible to cut a number of sample filaments in the ventral root for permanent recording of the effect of the monosynaptic test volley while the rest are (a) left intact and (b) afterwards severed. The principle of this mode of approach may be studied in Fig. 117, and it has been tried by Granit and Ström (1951b, 1952) on decerebrate animals. Their intention was to study the excitability of the ventral horn cells of the ankle extensors with excited and non-excited spindles. At low initial tension it was actually possible to demonstrate that in stretch monosynaptic facilitation started earlier before de-erefferentation than after, but the difference was small and later on in stretch not at all definite. However, when high initial tension was used, there was no such difference early in stretch but, later on, actually more inhibition with the γ loop through the intact muscle. Thus, as soon as initial tension is sufficiently high, the sum total in the balance of excitatory and inhibitory reflexes, even in the decerebrate preparation, is in favor of inhibition. This does not seem difficult to understand. In the de-erefferented state there is no reflex motor contraction. However, with the loop intact there is a stretch reflex which augments the sum total of tension enough to mobilize autogenetic inhibition for both α and γ motoneurones.

Fig. 117. Diagram illustrating semisections of spinal cord at the segmental levels of L7 and S1, and arrangement of experiment. Test shock to severed lateral gastroc. nerve (GL), recording of monosynaptic reflex response from filament of ventral root L7 as well as the whole of S1 ventral root connected with gastroc. muscle through medial gastroc. nerve (GM). (Granit and Ström, Acta physiol. scand., 27, 255. 1952.)
our reflexes: (1) facilitation from nuclear bag endings upon the ventral horn cells, (2) inhibition from Golgi tendon organs upon the ventral horn cells (α inhibition), and (3) inhibition from unknown endings upon the γ cells (γ inhibition), with consequent indirect removal of excitation upon the α motoneurones from nuclear bag endings. Also (4), the myotube endings, as stated, will add inhibition to the extensors and excitation to the flexors (Hunt, 1953).
4. Some skin reflexes on the γ system

Hunt (1951) as well as the Japanese authors (Kobayashi et al., 1952) described the spinal γ reflexes in very similar terms. By carefully grading stimulation in the flexion reflex it was shown that the γ system responded more readily to touch of the skin than the α system. With increasing stimulus strength both systems went off. Fig. 118 is an illustration from Hunt's paper, reproducing α and γ reflexes together with the electromyogram. Fig. 119, by the Japanese authors, demon-

---

Fig. 118. Spinal cat. Simultaneous recording from central end of cut upper nerve branch to tenuissimus and from lower end of muscle with intact innervation. Note difference in amplification. A: baseline in “resting” state. Note discharge in nerve giving impulses of small potential, while no potentials are recorded from the muscle surface. B: ipsilateral foot touched. Small-nerve discharge increased and activity set up in fiber giving large potentials. Each large-nerve impulse is accompanied by propagated potentials recorded from the muscle surface. C: contralateral foot touched. Background small-nerve discharge completely inhibited. Diagram illustrates leading conditions. (Hunt, J. Physiol., 115, 456. 1951.)

Fig. 119. Inhibition of contralateral extension reflex by induction shocks applied to the ipsilateral peroneal nerve. Action currents were led from five fibers, between 20 and 5 μ, innervating the lateral head of gastrocnemius of a decerebrated cat. The crossed reflex was maintained by continued stimulation of the contralateral peroneal nerve. Only one fiber of 5 μ is active in the crossed reflex. Time: 10 msec. (Kobayashi, Oshima and Tasaki, J. Physiol., 117, 152. 1952.)

---

strates with a γ efferent fiber the inhibition of a contralateral extension reflex by ipsilateral electrical stimulation. In the well-known spinal reflexes it appears that there is strict correlation between α and γ activation. The typical response will therefore be intra- and extrafusal cocontraction. Hunt, in particular, emphasized that the γ fibers have receptive fields from a large variety of end organs.

Granit, Job, and Kaada (1952) studied Sherrington's pinna reflex with both γ efferents and muscle spindle afferents. This reflex has a very strong γ component. Upon touching the ear sometimes pure excitation is obtained, sometimes inhibition which is later followed by a vigorous excitatory rebound when the pinna is released. An example
of the first type is shown in Fig. 120. Very often the $\gamma$ reflex is obtained in isolation; sometimes it leads up to a contraction (isolated limb muscle) during which the intrafusal fibers are co-activated to such an extent

![Image](image_url)

**Fig. 120.** Effect of twisting ear on muscle spindle afferent from gastrocnemius. Dial-chloralose. Initial tension 35 g. Myogram (M) in record 1, horizontally; in the successive sweeps, 2–20, vertically. Distance between M and baseline (B) corresponds to 15 g. Contraction of 118 g. in record 1 to demonstrate spindle-character of ending. 2–7: control, 8: twist of ear, (marked "Pinna"), 9–20: acceleration of spindle discharge in pinna reflex from a baseline discharge of about 7/sec. to about 36/sec. Interval between sweeps 2 sec. (Granit, Job, and Kaada, *Acta physiol. scand.*, 27, 161. 1952.)

that the effect of extrafusal unloading is more than neutralized. As with onset of rigidity (Hunt, 1951; Kobayashi *et al.*, 1952, and Fig. 114 above) both $\gamma$ and spindle discharges generally precede the $a$ discharge. In the pinna reflex on the hind limb the $\gamma$ action apparently serves to

![Image](image_url)

**Fig. 121.** Spinal cat. Records from central end of cut branch of medial gastrocnemius nerve. Vertical lines to the right indicate the approximate duration and strength of pinches applied to the skin at the sites indicated by arrows. $\gamma$ fiber activity, represented by the short spikes, is inhibited from the toe-pads (a) but facilitated from the skin on the dorsal aspect of the leg (b). With stronger stimulus at the latter site, tall spikes of an $a$ fiber appear together with a deflection of myograph (M). Initial tensions in this and succeeding illustrations about 40 grams. (Eldred and Hagbarth, *J. Neurophysiol.*, 17, 59. 1954.)

prepare the ground for the postural and phasic changes leading up to a scratch reflex (cf. Sherrington, 1917).

The muscle-skin organization of reflexes, discovered by Hagbarth (1952), is particularly well suited for analysis of $\gamma$ reflexes because of its strict reciprocal organization. Hagbarth (cf. Chapter 2, sec. 4) found that independently of whether limb flexors or limb extensors were studied, the receptors in the skin above any particular muscle facilitated the motoneurones of this muscle and inhibited those of
antagonists. Eldred and Hagbarth (1954) then investigated Hagbarth's system with a view of correlating \( \alpha \) and \( \gamma \) activity. Their results uniformly fell out as illustrated by Fig. 121. Co-excitation and co-inhibition were precise and strictly reciprocal in both types of efferents. The \( \gamma \) neurones had a lower reflex threshold than the \( \alpha \) fibers and generally started discharging before the latter.

Even when needles are inserted into the brain for electrical stimulation or when cortical structures in the cerebrum and cerebellum are stimulated electrically (Granit and Kaada, 1952), the \( \gamma \) fibers are commonly found to go off in advance of the \( \alpha \) fibers, and it is comparatively easy to stimulate them in a selective way. All this can only mean that connections to this system are profuse in the spinal and supraspinal centers in the same way as in the muscles where \( \gamma \) innervation is found to be profusely distributed over the spindles (cf. Hunt, 1951).

In every instance hitherto analyzed the \( \alpha \) and \( \gamma \) reflexes have proved to be linked, co-excited, and co-inhibited, often with the \( \gamma \) reflexes leading. All experimenters have been struck by this fact. The significance of \( \alpha-\gamma \) linkage may now be preliminarily assessed in general terms: excitation of the \( \alpha \) motoneurones over the \( \gamma \) loop through nuclear bag afferents is sufficiently important to be organized for cooperation with direct \( \alpha \) excitation. Is it important enough to have a decisive influence on motor performance?

In order to reply to this question it is necessary to study \( \alpha \) and \( \gamma \) reflexes before and after de-afferentation. Clearly the reply to our question will be largely dependent upon the amount of tonic or permanent activity going on in the \( \gamma \) system and the spindles. Suspecting that this was controlled from cortical centers in the brain stem elsewhere, we (Granit and Kaada, 1952) took up this problem first. The next step in our research involved de-afferentation. Below, in presenting the results, I shall follow the same order of procedure.

5. Supraspinal control of the muscle spindles

It proved particularly easy to obtain selective \( \gamma \) excitation from many places within the brain stem reticular system. In Fig. 122 are shown some records from a few fibers in the ventral root \( S_1 \). In \( A \) a 3 msec. shock to the motor cortex is seen to have activated only the small \( \gamma \) efferent at low strength, while a somewhat stronger shock also activated the large spike of the \( \alpha \) fiber. These records are given merely to show that there was one \( \alpha \) and one \( \gamma \) fiber in the filament that had been picked up. Then the mesencephalic tegmentum was stimulated repetitively in \( B \) between "Stim on" and "Stim off." The \( \alpha \) fiber remained silent but the \( \gamma \) fiber's firing frequency gradually rose from 8 to 40/sec. and very slowly fell back to the resting value. The

![Fig. 122. Effect of stimulation of motor cortex (A) and mesencephalic tegmentum (B) on discharges in ventral root \( S_1 \). Dial-chloralose: A: single shock to motor cortex, as marked by large shock artifact (point)—1: relative strength 5, only small fiber responds; 2: relative strength 6, large fiber is also brought in. \( B \) same experiment directly continued with tegmental stimulation—3–4: spontaneous rate of firing of the small unit; 5–9: tegmentum stimulated at a rate of 32/sec. for 19 sec. Timing of sweeps marked on records. "Driving" of small-fiber discharge at the stimulus rate in 7 and 8. 10–12: after stimulation, at times marked on records.

Note: gradual recruitment of discharge rate of small spike during stimulation from originally around 8/sec. to maximally 40/sec. without a large spike activation. Note also after-discharge. (Granit and Kaada, \textit{Acta physiol. scand.}, 27, 130. 1952.)

spindle counterpart of this experiment is shown in Fig. 123 for a nuclear bag afferent from the gastrocnemius. Above is the test with a motor twitch to demonstrate the pause of the spindle. The myograph was then shifted to \( M \) alongside the record and 4 sweeps 2 seconds apart are given to illustrate the baseline discharge. Stimulation of the midbrain tegmentum (between arrows) gradually excited the spindle, which still fired at maximum frequency 20 seconds after cessation of
stimulation. The muscle was silent; hence the stimulus was again highly selective. Such recruitment and long-lasting after effect are typical for the brain stem and diencephalic reticular system and are comparable to the recruitment and after effect seen by facilitation of reflex and cortically induced movements as a result of stimulation of the same structures. We generally tested for cortically induced movement when stimulating the reticular structures, and the outcome was practically always positive.

It seems likely that all along the motor path, from the cortex downward, fibers are directed to \( \gamma \) centers in this region. In one instance we also stimulated the pyramidal tract with a needle electrode. There was some selective activation of the spindle but it did not have the slowly recruiting character of the typical reticular response. Since Brodal and Walberg (1952) and Brodal and Kaada (1953) recently have demonstrated afferents in the pyramidal path by histological and electrophysiological methods, we thought it necessary to make a double-sided resection of the motor cortex in this experiment. The pyramidal effect proved to be uninfluenced. So far this is the only exception to the rule that \( \gamma \) effects rise and fall slowly.

Magoun and his collaborators (Magoun, 1944; Magoun and Rhines, 1945, 1946; Niemer and Magoun, 1947) have described a diffuse bulbo-recticular inhibitory system. Inhibition of stretch reflexes and tonus have been obtained from the anterior limbic gyrus (Smith, 1945; Kaada, 1951; Hodes, Peacock, and Heath, 1951). Cerebellar inhibition of rigidity is well known from early papers by Loewenthal and Horsley (1897) and Sherrington (1898). These three inhibitory sites were stimulated in the experiment of Fig. 124, in which some \( \alpha \) and \( \gamma \) fibers were isolated in the ventral root \( L_\gamma \). Complete inhibition of both \( \alpha \) and \( \gamma \) discharge was obtained in all three cases. Similar experiments were also carried out with isolated spindle afferents.

In view of the fact that onset of decerebrate rigidity is marked by \( \gamma \) excitation, it is of particular interest to perform the classical experiment on cerebellar inhibition of rigidity in order to see if it can be done with the \( \gamma \) system alone. It is actually possible to make inhibitory stimulation highly selective. The experiment of Fig. 125 was carried out on a decerebrate animal slightly clonic, as shown by the response (record 1) to the shock for the test twitch. There follows the baseline discharge (2-4) of the isolated spindle afferent. Stimulation of the anterior lobe of the cerebellum between records 5 and 10 gave complete inhibition of the spindle with some escape at the end. Nothing hap-

---

Fig. 123. Effect of brain stem reticular (midbrain tegmentum) stimulation (between sweeps 4 and 12) on a gastrocnemius muscle spindle afferent. Above: contraction of 134 g. at low myograph sensitivity to demonstrate pause of large unit. Initial tension throughout: 52 g. Dial-chloralose. 1-4: control before reticular stimulation; 5-11: during stimulation at a frequency of 37/sec.; 12-31: after stimulation. Consecutive sweeps at 2-sec. intervals. Myograph \( M \) along-side film. Distance \( M-B \) (baseline) corresponds to 10 g. (Granit and Kaada, *Acta physiol. scand.*, 27, 130. 1952.)
pended in the muscle. The effect was readily reproducible. It was, indeed, quite a striking experience to watch the screen of the cathode ray and the wholly quiet animal and listen to the sudden cessation of detonations in the loudspeaker when this long-range control of a sense organ was put into operation. It is of some interest to note that a

cerebello-bulbo-reticular pathway for inhibition has been found by Snider, McCulloch, and Magoun (1949).

Cerebellar excitation may also be obtained by electrical stimulation (e.g. Moruzzi, 1950). In some cases we succeeded in stimulating the spindles from the cerebellum.

It is hardly necessary to adduce further examples to illustrate the main results of Granit and Kaada, which were that (1) there is close correlation between \( \alpha \) and \( \gamma \) activity in the various systems in the brain known to be engaged in motor activity; (2) it is often easy in Dial

---

**Fig. 124.** Inhibition of ventral root discharges (L) to stimulation of (A) the bulbo-reticular inhibitory system (at arrow on section), (B) the anterior lobe of cerebellum, and (C) the anterior limbic (cingular) area. Nembutal. 1 (in each column): control before stimulation (note small and large spikes); 2–3: during stimulation at 120/sec. for 10 sec. Time from onset of stimulation marked on records. 4–5: 1 and 10 sec. respectively after cessation of stimulation. Note the practically complete inhibition in records A3 and B3 and the rebound in B4 after cessation of cerebellar stimulation. (Granit and Kaada, *Acta physiol. scand.*, 27, 130. 1952.)

**Fig. 125.** Inhibition of muscle spindle discharge from anterior lobe of cerebellum (culmen). Decerebrate animal. Gastrocnemius. Initial tension 66 g. Myograph at maximum sensitivity (see record 12) except in 1, in which (clonic) contraction to single shock to the gastrocnemius nerves demonstrates silent period. 2–4: controls before stimulation, 5–10: during cerebellar stimulation at 140/sec. with 1-msec. shocks for 26 sec., 5–7: after 18–20 sec., 8–10: after 24–26 sec., 11–12: immediately after cessation of stimulation. Note: drop in spindle frequency from about 20/sec. to an irregular discharge frequency of about 5/sec. (Granit and Kaada, *Acta physiol. scand.*, 27, 130. 1952.)
with great regularity obtained from the excitatory brain stem and diencephalic reticular formation as well as corresponding inhibitory ones from those parts of it which inhibit motor performance.

In view of the low threshold to stimulation, the \( \gamma \) system also in these regions must be provided with rich diffuse connections, but somewhere there ought to be a collecting network for them. It seems very likely that the reticular formation from diencephalon down to the spinal cord serves in this capacity. In the bulb and the brain stem this extensive system has lately attracted a great deal of attention (cf. Chapter 3). It includes parts of the bulbar reticular formation, the pontile tegmentum, the central grey matter and tegmentum of the mesencephalon (Magoun, 1944; Rhines and Magoun, 1946), the ventral diencephalon—sub- and hypothalamus—(Murphy and Gellhorn, 1945; Rhines and Magoun, 1946), parts of the midline and intralaminar group of thalamic nuclei, and certain of the specific thalamic nuclei as well (Murphy and Gellhorn, 1945; Jasper, 1949; Austin and Jasper, 1950; Peacock and Hodes, 1951). This facilita-

Fig. 126. Effect of stimulation of leg area in chloralose (20 mg/kg.). Each set of records taken with two parallel, double-beam oscilloscopes. On the left, electromyogram and time in 100 cy/sec.; on the right, tib. ant. spindle and myogram of tib. ant. muscle. 1: single shock, 2: stimulation at 15/sec. during 3 sec., 3–5: rate of stimulation reduced to 1/sec. Note effects on spindle discharge.


tory system of large dimensions has properties characteristic of \( \gamma \) activity, such as long duration, broad front of attack, and great range, and may therefore play a leading role in \( \gamma \) activation, even when the \( \gamma \) neurones are excited over the motor cortex.

With sufficiently long shocks it is possible, even in the modestly developed cat's motor cortex, to elicit differentiated single contractions in single leg muscles, particularly from the tib. ant., which then responds in the twitchlike fashion illustrated in Fig. 126, record 1. This is very much of a pure \( \alpha \) contraction, as seen by the pause of the spindle discharge. Yet the stimulus activates the \( \gamma \) system too (Granit and Kaada, 1952), as can be seen by making it repetitive, as in record 2. Its destination may be by extrapyramidal paths to the similarly extrapyramidal activating centers in the reticular formation, because the effect does not look at all like the differential \( \alpha \) outbursts setting up the rhythmic contraction in record 2. Characteristically, the \( \gamma \) activation lasts for a long time, as seen when the original firing rate of once per second was reinstalled. The pause is filled out in record 3, which is a definite sign of intrafusal contraction by \( \gamma \) activity, but gradually returns in records 4 to 6.

An interesting aspect of this result is its possible significance for Hughlings Jackson's well-known "march of movement," which signifies that the effect from a cortical point stimulated slowly at constant strength gradually spreads from muscle to muscle, just as does the focalized epileptogenic fit. Part of this spread may well also be indirect, facilitation by diffuse \( \gamma \) action of the ventral horn cells of muscle after muscle through the spindle loop. This question deserves to be investigated.

The notion that the general facilitatory and inhibitory systems of the brain stem are instrumental in determining the level of tonic facilitation through the spindle loop as well as in switching it on and off receives some support also from our attempts to determine the range of the effect, from maximum excitation to maximum inhibition. This question implies that two places must be found in the brain, one of which excites, another which inhibits the same sensitive spindle selectively. Fig. 127 illustrates an experiment with a low-threshold muscle spindle afferent in soleus which could be selectively excited from the contralateral inferior colliculus and similarly inhibited from a place in the contralateral internal capsule alongside the caudate nucleus. The sections showing the actual needle tracks are given in Fig. 128. The whole experiment was carried out with the same soleus spindle, which
was very sensitive and at the same time stable, so that it could ultimately be tested in the nonexcited state also, after de-efferentation. The central foci remained constant for hours and were highly selective. Fig. 127 illustrates this selectivity with myographic control during inhibition and excitation at stimulus rates and strengths which then were

![Diagram](image)

**Fig. 127.** Spindle in soleus. Effect of stimulation of the inhibitory and excitatory loci shown in Fig. 128. *A:* base-line, *B:* first record during stimulation (note shock artifacts), *C:* during stimulation, *D:* last record before cessation of stimulation, *E,* *F:* immediately afterward. Myograph record on lower trace; initial tension 55 g. Cat under chloralose and dial. (Eldred, Granit, and Merton, *J. Physiol.*, 122, 498. 1953.)

preserved throughout the whole experiment. In this test it is necessary to be able to assert that the effects observed did not depend on mechanical events in the muscle set up by a activation. Very high myograph sensitivity was therefore used. There is, during inhibition, a slight fall of tension of 0.1–0.2 g. which may or may not have been accidental. If it had been due to concomitant inhibition the spindle would have been pulled upon and hence accelerated. Actually it was inhibited down to zero. Therefore the fall in tension is inconsequential.

In Fig. 129 the same excitatory and inhibitory foci have been studied at different initial lengths increasing downward and shown to the left in the figure. The first vertical row illustrates the baseline discharge with loop intact, the second and third during supraspinal excitation and inhibition as in Fig. 127, the third the baseline of the de-efferented nonexcited spindle with which the first vertical row of the excited spindle should be compared. At 13 mm. extension a good initial ten-

![Image](image)

**Fig. 128.** Sections to show the position of the stimulating needles in the experiment illustrated in Figs. 127, 129, 130. *A:* the inhibitory point in the contralateral internal capsule, *B:* the excitatory point in the contralateral inferior colliculus. The scale applies to both sections. (Eldred, Granit, and Merton, *J. Physiol.*, 122, 498. 1953.)

sion was developed—in fact 450 g. Again it can be seen that spindle excitation is sufficient to overcompensate for the $\gamma$ inhibition to stretch, even though stimulation of the excitatory focus still is capable of causing further increase of the discharge. The initial effect of inhibition is actually to suppress the rate of firing below that of the nonexcited spindle, but this is certainly due to the sudden unloading which was shown by Matthews (1933) to cause a pause of several seconds, during which excitability was built up to the level characteristic for the new length (cf. Chapter 1, Katz's positive terminal potential, Figs. 6 and 7). This recovery can actually be seen in Fig. 127, which traces the inhibitory effect for several sweeps, while in Figs. 129 and 130 only the maxima of excitation and inhibition have been picked out.
The main results of the experiment are summarized in Fig. 130. The high rate of firing of the excited spindle should be noted. It reached a peak value of as much as 215/sec., averaged over a fifth of a second. The maximum range, which is the difference between spindle frequencies during central excitation and inhibition, is reached at an extension of about 8 mm. and is of the order of 160 impulses per second. It should further be noted that spindle excitation is considerable also at zero tension.

Eldred, Granit, and Merton (1953) have introduced the notion of excitatory spindle bias in terms of equivalent length. The bias is that shortening of the muscle which reduces the rate of discharge of the biased (excited) spindle to that of the unbiased (nonexcited) de-efferented spindle at the original length. I mention this concept not in order to elaborate its significance in detail, but merely to point out that at zero tension extrapolation of the curve for the excited spindle would give a bias as high as 5 mm. below the length of the slack muscle. The result suggests that a spindle under command from the supraspinal centers, and thus excited by natural means, would work also in isotonic contraction. The supraspinal commands clearly possess extreme range and potency. On the one hand it was possible to abolish normal $\gamma$ bias completely; at the opposite end of the scale a state of spindle excitation was obtained which was so intense that it becomes doubtful whether further increase serves any practical purpose in the normal life of the animal.

The fact that the $\gamma$ loop is at the disposal of powerful supraspinal mechanisms should also be considered in the light of the observations on the arousal reaction from the reticular activating system in the brain stem, discussed in Chapter 3, sec. 6, from other points of view. The spindle loop integrates motor and sensory performance in a curious and fascinating manner. The brain drives and sensitizes end organs, which in their turn are capable of driving the muscle which contains these end organs as well as its synergistic muscles. Now, muscle is the instrument of action, and so it seems natural that it should be made to feel the arousal reaction of an animal aroused. Again, considered from the sensory point of view, a pure extrafusal a arousal without concomitant $\gamma$ arousal of the intrafusal fibers of the muscle spindle would make the sense organ pause and consequently be incapable of serving as an "internal measuring instrument" and hence useless for the animal at the very moment when it is needed.
6. Reflexes before and after de-afferentation

One of Sherrington's best known experiments proved that in the decerebrate animal rigidity of a limb could be abolished by acute severance of the dorsal roots. The remaining ventral roots could not maintain this state of activity unless the ventral horn cells received the facilitatory influx from the limb afferents. The level of excitation of the \( \alpha \) system isolated from the proprioceptive inflow was too low. Do the \( \gamma \) cells share with the \( \alpha \) cells this state of depression? Or are they relatively independent, despite \( \alpha-\gamma \) linkage?

In the experiment of Fig. 131 (Eldred, Granit, and Merton, 1953) the tonic neck reflex of Magnus (1924) has been used to test this point. The receptors have been found to be in the ligaments of the joint (McCouch et al., 1951). A spindle afferent has been isolated and in \( A \) some tendon jerks have been elicited to show that it pauses during the muscle contraction. The experimenter then grasped the animal's head firmly and waited until the \( \gamma \) reflexes to touch and pressure had disappeared. In \( B \) is found the baseline discharge of the spindle together with the myograph record of tonic \( \alpha \) activity, indicated by irregular small movements. The head was next turned upward to elicit the characteristic Magnus inhibition of hind limb tonus (cf. myograph), which also is reflected in the slowed rhythm of the spindle afferent (record \( C \)). During the interruption in the record the head was bent downward and held there (\( D \)). There followed in the muscle a violent contraction, carrying the cathode ray off the face of the tube, and a no less violent discharge of the spindle. In the lower half of Fig. 131

![Fig. 131. Reflex activation of \( \alpha \) and \( \gamma \) systems by head movement in the vertical plane. Rigid decerebrate cat with brisk ankle jerk and spontaneous \( \alpha \) activity (record \( A \)). Myograph shows tendon tap succeeded by jerk. Records from soleus spindle with head level (record \( B \)), flexed backward (\( C \)), and suddenly (at the interruption of the traces) flexed downward and held there (\( D \)). After de-afferentation the same sequence (\( E-G \)) produces \( \gamma \) response but no \( \alpha \) discharge. Initial tension approximately 85 g. (Eldred, Granit, and Merton, \( J. \) Physiol., 122, 498. 1953.)](image)

the same procedures were repeated at higher myograph sensitivity after de-afferentation. \( E \) is the baseline discharge. The muscle was silent throughout but the spindle (in \( F \)) repeated its previous performance (as in \( C \)). The motoneurones of the \( \alpha \) system were thus greatly depressed by de-afferentation, but the \( \gamma \) motor cells, though slightly less active than before, were fully capable of responding to the stimulus in the normal way.

Similar experiments were successfully carried out with other reflexes as indicators. Fig. 132 illustrates the response to rhythmic movement of the head from right to left in the horizontal plane. Intraspinal spindle and extraspinal motor contraction go off together. After de-afferentation (lower record) the spindles alone respond as before, while the muscle is quiet.

The effects of central stimulation at different initial tensions of the muscle in the manner of Granit and Kaada were compared before and after de-afferentation. The \( \gamma \) effects studied in the spindles were in the main independent of whether the limb was intact or de-afferented.
At low tensions tonic spindle activity tended to be somewhat reduced. If a place was selected from which both $\gamma$ and $\alpha$ activity could be obtained, the threshold for the latter effect was generally found to have risen a great deal after de-afferentation, while the $\gamma$ system was practically as sensitive as before the operation.

The interpretation of all these experiments is that the $\gamma$ system is there not only to improve the performance of the sense organ but also as an “ignition mechanism” to initiate movement as well as to maintain tonus. When the loop through the muscle to the ventral horn cell has been interrupted on its afferent side, the $\gamma$ system still operates to carry out its task in the activation of the ventral horn cells, but the nuclear bag impulses are prevented from reaching the latter, and so the $\alpha$ reflexes do not come off. A consequence of this interpretation is that the muscles possessing spindles actually are provided with two motor systems. This being so, $\alpha-\gamma$ linkage, in which mostly $\gamma$ activity is leading, means that a very large number of motor acts do not at all take place the way one imagined and held to be self-evident, namely that the $\alpha$ contraction simply was put on by whatever circuits happened to be activated. In many if not most natural contractions hitherto studied the $\gamma$ loop was first started, the nuclear bag afferents then facilitated, and the appropriate $\alpha$ motor neurones and direct $\alpha$ activation came last or together with $\gamma$ activity. With this arrangement the sense organs in the muscle are immediately ready to “measure” during the ensuing contraction.

For the first time this makes the existence of a monosynaptic reflex from muscle afferents intelligible. Half a millisecond one way or another can hardly as such be of any significance whatever for large limb muscles and bones of considerable inertia and momentum. But for the cerebral command to the loop it is essential that it be carried straight to the ventral horn cells by a fast path not subject to complex polysynaptic influences. Their role is a later modulation.

This should not be interpreted to mean that direct $\alpha$ action, such as seen by electrical stimulation of the brain by single shocks or in tendon jerks, is excluded. It does mean, however, that the relative significance of $\alpha$ and $\gamma$ activation must be elucidated case by case. Merton (1951), investigating the servo-loop in the human subject, found, for instance, that sudden movements could always break through, presumably by direct $\alpha$ activation. Tendon jerks and single shocks to the motor cortex do the same.

The results on de-afferentation also mean that the $\alpha$ and $\gamma$ systems are fundamentally independent. De-afferentation, as we have seen, treated them very differently. Their respective motoneurones are converged upon by different influences. This being so, it is clear that the $\alpha-\gamma$ linkage is maintained by some property of organization. If it were possible to destroy the linkage experimentally, one could from such experiments derive some notion of where coordination takes place. Apparently such organizations exist at different levels in the neanaxis, to judge from the fact that $\alpha-\gamma$ linkage is found also in spinal animals. We have studied this question in the decerebrate preparation.

It is interesting to note that insofar as tonic firing is concerned, Rossi (1927) deduced an essentially correct picture of the role of spindle innervation. He thought of tonic firing of muscle spindles at various lengths of the muscle as a fixation of the intrafusal fibers at appropriate lengths by specific motor fibers to them. Thus, he said, it would become possible for the higher centers to be at rest while charging lower centers with the duty of keeping up a suitable amount of spindle or intrafusal contraction to maintain postural tonus. Now, twenty-five years later and unaware of his deductions, we have ultimately succeeded in proving him right, in the sense that tonic facilitation of the ventral horn cells is maintained by the spindle loop.

7. Experimental destruction of the $\alpha-\gamma$ linkage.

The $\alpha$ animal

It is well known that the preparation obtained by anemic decerebration (Pollock and Davis, 1930), in which half the cerebellum and a considerable part of the pons is destroyed, is intensely rigid, despite de-afferentation (Pollock and Davis, 1931). Moruzzi (1953) and Kaada (1953) have recently reviewed the literature in this field and in Moruzzi's laboratory Terzuolo and Terzian (1953) have made a comprehensive study of this preparation after both acute and chronic de-afferentation. Rigidity was preserved in both cases, despite lack of support of the $\gamma$ loop. Both inhibition and excitation of fore limb muscles could be obtained by appropriate electrical stimulation (cf. Moruzzi, 1950) of the cerebellum.

Here, then, is a state representing an exaggeration of standing which must be maintained by pure $\alpha$ activity. This, of course, does not exclude the possibility that the $\gamma$ fibers might be as heavily biased as after intercollicular decerebration, or that they actively participate in both postural and phasic reflexes. The results mentioned show merely that $\alpha$ activity by itself is sufficient for rigidity in this particular case.

However, when we began to make anemic decerebrations, taking
care to tie both the internal and external carotids in addition to the basilar artery (adding intercollicular decerebration if the animals were restless), we were struck by the circumstance that though the spindles were excited, this bias generally was modest, particularly by comparison with the \( \alpha \) activity as simultaneously recorded myographically by electrodes in the extensor muscles of the hind limb. Also, the \( \alpha-\gamma \) linkage was broken. It is well known that the reflex behavior of this preparation is frequently erratic (Pollock and Davis, 1930, 1931), suggesting that something has gone wrong in the coordination of the events leading up to a reflex contraction. In the Sherrington decerebrate animal one hardly ever fails to find both onset and cessation of rigidity as well as permanent high rigidity accompanied by the appropriate spindle adjustments as discussed above. This is not so in the Pollock-Davis animal. These behave like “cats.”

In the reflex responses, illustrated in Fig. 133, the spindle bias is obvious, to judge by the signs that by now should be familiar. Yet both the reflex contractions displayed—and they are big ones (cf. calibration)—begin with \( \alpha \) activity. In the upper there is a very small increase of spindle discharge, in the lower practically pure \( \alpha \) discharge, as shown also by the electromyogram. In Fig. 134 the experiment of Fig. 131 with the neck reflexes is repeated in an \( \alpha \) animal, before and after de-afferentation. The spindles behave in a wholly passive manner, pausing

---

Fig. 133. Precollricular decerebration and section of cerebellar vermis removing culmen and lobulus med. Soleus muscle. Spindle discharge, myogram, electromyogram, and time in 100 cy/sec., recorded by four cathode ray beams.

Upper records: fast movement of head up. Lower records: same at slower rate with two taps on tendon of synergist gastrocnemius muscle. Note in both reflexes \( \alpha \) activity, indicated by myogram and electromyogram, with little if any \( \gamma \) activity. Silent period in soleus, following taps on gastroc. tendon. (Observations by Granit, Holmgren, and Merton.)

Fig. 134. Anemic decerebration. Soleus muscle before and after de-afferentation. Neck reflexes as indicated above records. Note that spindle fires on falling phase of reflex contraction. Time in 1/5 sec. (Observations by Granit, Holmgren, and Merton.)
during the onset of the contractions and firing when tension drops. Therefore the preparation obtained by anemic decerebration, despite some spindle bias, is lacking the very characteristic $a$-$y$ linkage of other preparations, such as the Sherrington type of decerebrate animal, the spinal animal, and the barbiturate or chloralose animals studied in the previous sections.

It is not easy to give a wholly satisfactory answer to the many questions raised by these observations on destroyed $a$-$y$ linkage. Suspecting that the anterior part of the cerebellum was involved, we carried out a considerable number of experiments to test this hypothesis. Essentially it implies that $a$-$y$ linkage has an important part of its organization run by circuits passing through the cerebellum. Cooling and removal of the anterior part of the cerebellum were tried.

In the experiment of Fig. 135 the animal was originally decerebrated by precollicular section. Then under trilene a section was made, removing vermis, culmen, and lobulus med. The trilene anesthesia rapidly disappeared and the muscle isolated went into spontaneous slow clonus. This is seen to be a pure $a$ clonus. The spindles are passive and respond on the falling instead of on the rising phase of the contraction (cf. Fig. 132). In the experiment illustrated in Fig. 136 the left tentorium was removed from the inside and a piece of frozen saline (record in the middle) placed on the corresponding anterior lobe, ipsilateral with respect to the muscle isolated. The spindle activity disappeared completely, some increase of $a$ activity occurred. When ultimately (bottom record) the cerebellar surface was warmed up again, spindle activity reappeared. The necessity of carrying out these experiments on hind limb muscles in order to have good fixation and long root filaments often makes the results less striking than they would be if fore limb muscles had been used, the latter responding more actively to destruction or cooling of the anterior lobe. However, when a definite effect is observed, it is in the direction illustrated by the experiments of Figs. 135 and 136.

For this reason it seems likely that the cerebellum does play an important role in organizing $a$-$y$ linkage. Essentially the results presented signify that these types of preparation cannot use their “internal measuring instruments” in the spindles in the normal way because normal behavior is based on $a$-$y$ linkage. They are therefore to be regarded as objective evidence in favor of dysmetria, well known in connection with cerebellar disturbances.

8. Rigidity, spasticity

The gist of this chapter has been to underline the realization that the ventral roots contain two motor systems, those that have been called
a and γ. This has compelled some revision of our concepts. Clearly much work still remains to be done before we are ready for a final assessment of the relative significance of a and γ components for movement in relation to muscular receptivity and central control. Thus, for instance, when the reflex effects of the myotube afferents have become fully worked out, a number of new facts will have to be incorporated into the picture. Even at the present stage, however, the clinician will be interested in what the new knowledge might mean for concepts such as rigidity and spasticity (for recent literature see Fulton, 1949b; Denny-Brown, 1950; Magoun and Rhines, 1947; Stella, 1944a,b; Ward, 1947; Cardin, 1952; Sprague and Chambers, 1953).

With regard to “rigidity” it is clear that the two types studied above, one with strongly active γ loop, the other with a hyperactivity, represent only limited aspects of rigidity regarded as a clinical proposition (cf. Denny-Brown, 1950). The new information, as far as it goes, raises more questions than it solves, but it does show that both systems should be taken into account. And it demonstrates in precise terms a number of factors that have to be considered in a test as simple as a pull on a muscle. Both physiological varieties of rigidity, studied above, are really better characterized in clinical terms as spastic states (cf. Hoefer and Putnam, 1940; Sprague and Chambers, 1953), i.e. by their exaggerated stretch reflexes. Whatever the ultimate cause of the γ hyperactivity in the ordinary decerebrate preparation, the ensuing afferent discharge must help toward keeping up some depolarization of the ventral horn cells and thus facilitate the elicitation of the stretch reflex. Yet this type of preparation may often lack persistent rigidity in the isolated hind limb muscles which have been used above for isolation of the factors concerned. The a cat, however, is always intensely rigid and spastic, even despite virtual absence of γ bias.

I have also tried to evaluate the tendon reflexes from these points of view, but at the moment it is perfectly clear that we do not understand why tendon reflexes are sometimes absent, sometimes enhanced. Even at the spinal level they cannot be explained in terms of a concept as simple as “excitability of the ventral horn cells.” In a general way some increase of a excitability facilitates the appearance of tendon reflexes, and they are nearly always present in the a cat. But it may happen that if this preparation is given sufficient pentobarbitone to stop persistent a activity and active stretch reflexes, the tendon jerk suddenly springs into existence in supernormal size. When stimulating various regions in the brain stem, one can easily demonstrate that under maintained iterative stimulation of long duration the tendon jerk may come and go seemingly independent of the amount of spindle firing. It is true that it does tend to appear when a slow tonic contraction becomes visible in the muscle as a sign of increased excitability of the a cells. However, even this simple rule is not without exceptions, and after cessation of stimulation I have actually seen tendon jerks at their best when both a and γ activity to all appearance have been completely in abeyance. The tendon jerk is thus quite capable of surprising the experimenter just as much as is its nearest electrical equivalent, the monosynaptic reflex. In both cases it is best to admit that we do not yet understand all aspects of what constitutes “motoneurone excitability.”

An exaggerated importance has in the past been attached to individual components in motor action and their topology. Yet Adrian and Moruzzi (1940) found impulses traveling in the pyramidal tract without corresponding motor contractions. In the light of the results by Brodal and Walberg (1952) and Brodal and Kaada (1953) one might suggest that some of them may have been sensory impulses, but we have also in the course of the present work seen several examples of intense spindle firing without motor action. Unless stimulation in any one system is highly synchronous, it is likely to be rather ineffective without support from some other system. And in all this there may well be unknown factors of strategic approach to the cell to be fired. Clearly motor, just as sensory, integration always involves the collaboration of several systems, general or unspecific as well as specific ones. I fail to see any fundamental necessity for excluding the possibility of specific action from what nowadays are often called systems for widespread diffuse action, such as those described by Magoun and discussed in Chapter 3 and above. The retina is a good example: there are some cells which integrate vast areas into a final common path of discharge, others which restrict themselves to picking up effects from highly circumscribed areas. In this vein I interpret the recent demonstrations by, e.g., Austin (1952), Gernandt (1952), and Sprague and Chambers (1954) that the brain stem reticular system, held to possess generalized action, also contains structures for differentiated action upon specific muscle groups.

9. Sensory aspects

Throughout my presentation of the muscle receptors the “muscle sense” has been deliberately kept in the background. This is because it would be premature at the present stage to venture much beyond
276  RECEPTORS AND SENSORY PERCEPTION

general statements. We are lacking detailed information about the central projections of the joint receptors which in this connection can hardly be neglected. On the muscle receptors the information is controversial. Thus, for instance, Mountcastle, Covian, and Harrison (1952), on the one hand, find only the smallest fibers of muscle nerves represented in the cerebrum, while McIntyre (1953), on the other, states that so-called Group II afferents containing what we have called myotube afferents definitely have such projections. Both agree that the nuclear bag afferents pass only to the cerebellum. These statements are subject to the limitations of the technique of evoked potentials and raise the question of whether a representation might not be found if one knew what systems it would be necessary to facilitate in order to make the technique more sensitive.

With regard to the muscle receptors being "private measuring instruments," it seems clear that the Golgi tendon organs would serve as tension recorders, while the impulses from the spindles probably would be appraised by a differential determined by the relative spike patterns in nuclear bag and myotube endings. Of the latter we know too little to say anything definite. They may well be in a state of rest when the contractile myotube portion is contracted and pulls on the passive nuclear bag. On the servo-theory it is possible to describe the nuclear bag endings as "length recorders" or misalignment detectors measuring the difference in length between intrafusal and extrafusal fibers. Sherrington (1900b, 1924) also thought of them as length recorders. In this capacity the nuclear bag endings have the property of discharging with a frequency roughly proportional to the length of the intrafusal fiber (Eldred, Granit, and Merton, 1953).

New information on stretch receptors in muscles other than those mentioned has been obtained by Cooper, Daniel, and Whitteridge (1951, 1953) from the intrinsic eye muscles of the goat. Cooper (1953) has recently described stretch receptors in the intrinsic muscles of the human tongue.

Chapter 8

Sensory Discrimination and Integration

1. General anatomical principles

By discrimination is meant the capacity to distinguish one sensory experience from another. Primarily this property is laid down as a differentiation in anatomical space and has culminated in the topographical map of projections on the cerebrum of the higher species, which have greatly developed special fields for special senses and motor performance. However, within the definition of topography also falls any single path or loop in a synaptic network by which the impulses from one point are carried along a route different from that of any other. A good example of the significance of the topographical factor is provided by the fovea of the primates, which is projected on the cortical striate area on a vastly enlarged scale. Another example is the map of somatic sensory projections of the body on the thalamus, worked out by Henneman and Mountcastle (1948) with the aid of the technique of evoked potentials. I shall return below to sensory projections. This brief introduction serves merely to emphasize the fundamental topographical principle. If we refuse to admit that discrimination is in some way based on different anatomical constituents differently located in the brain, we may as well give up altogether.

Whatever the nature of the central mechanisms, they must be capable of interpreting the frequency code. We first face the general problem of how uniqueness is established by these means, because if two adjacent touch spots on the skin can be discriminated, the frequency code must have transmitted "uniqueness" for each of them. Wherein are they unique? In the early chapters we had to give up the 1:1 relation of skin organ: nerve: brain cell which, if it had existed, might have been adduced in favor of uniqueness wholly anatomical. This would have been a solution of the problem similar to the one applied in photography and very generally in the technique of reproduction and based on what was called fineness of grain. The image is projected piecemeal for corresponding parts of prototype and reproduction, the