

CHAPTER XII

Concluding Remarks

Lo The preceding chapters have served to prepare an answer to questions of biological significance such as: how do we employ our muscle spindles in the control of movement and posture, and why do we need this potent and highly differentiated fusimotor-spindle apparatus? These questions should be seen against the background of general sensory physiology. In vision, for instance, it is possible to cross the borderland of enquiry from "how" to "why" by considering the significance of any well-defined physiological mechanism for the act of seeing whose ultimate purpose is to make it possible for the living organism to discriminate one thing from another. In the present context it is equally sensible to ask: what are the tasks of the muscle spindles, or of the tendon organs?

A reply stating that the muscle spindles measure muscle length and the tendon organs muscle tension means that something has been understood, albeit at a very elementary level. This reply neglects the essential aspect of control by fusimotor fibres and of such aspects the coordinated muscular act is the final interpreter, just as in vision the act of seeing is the definitive interpreter of the experimental findings in that field.

Tone. The Stretch Reflex

An early attempt at interpretation was Rossi's (1927) notion that postural tone might be maintained by contractions of the intrafusal fibres causing stretch reflexes (cf. also the stabilization theory of Hultkrantz, 1931). Rossi's idea had been forgotten, probably because it lacked experimental support. It turned up spontaneously twenty-five years later (Granit & Kaada, 1952), this time, however, as a deduction from experimental work and formulated in the following manner: "when more experience has been accumulated, the notion of tonus as a postural reflex may well have to make room for a new concept in which the postural reflex is merely the last link in a system determining spindle activity" (p. 156). This system has since been studied extensively and

the balance of evidence seems to warrant a general conclusion to the effect that activity across the gamma-loop is essential for the maintenance of normal tone and normal postural reflexes.

A basic contribution to tone as such—if one wants to distinguish it from postural reflexes—is provided by the tonic activity of the fusimotor gamma fibres in the states of wakefulness (Chap. X) and arousal (Granit, 1955a, p. 264). The need for fusimotor support of stretch reflexes was pointed out in the previous chapters in several places (Chaps IV, VII and X). It has also been emphasized that the role of the stretch reflex, studied from the aspect of the motoneuron as its “final common path”, requires that these cells be at or above their firing level.

At this stage it should be recalled that there are at least three types of stretch reflexes corresponding to the three types of receptor, primaries, secondaries and tendon organs, as emphasized by the author (Granit, 1955a, p. 249) and recently again by Matthews (1969, 1970). There may also be postural reflexes on the fusimotor neurons. Both tendon organs and spindle secondaries have long been known to make use of polysynaptic circuits and it has been shown above that the tonic component of the action of primaries in the stretch reflex also is modulated by interneurons. The polysynaptic circuits are facultative in the sense that they may be open or closed dependent on central adjustments often beyond experimental control. Recently Matthews (1969, 1970) has suggested that the spindle secondaries are facultative to the extent of being dependent on “switchboards” wholly changing their sign, from inhibition to excitation. This is one way of describing his assumption that the well-established inhibition of the secondaries on extensor motoneurons reverts to excitation in the stretch reflex of the decerebrate animal (it may not do so normally). His hypothesis is based on the observation that vibration at controlled frequencies and amplitudes can be made to mobilize all the primaries of a muscle and yet not be able to elicit as much isometric tension per impulse per sec as does the natural stretch reflex at very much lower rates of discharge, calculated on impulses per mm extension. The secondaries, likewise mobilized by the stretching, are the only end organs that can make the stretch reflex produce tension in excess of what the low firing rates of the primaries can account for. Some critical comments to this hypothesis were made above (p. 176). It might be added that a conclusive experiment in support of this view would be to demonstrate the persistence of an excitatory stretch reflex after blocking the Group Ia spindle afferents. Some experiments (Granit, 1950) by monosynaptic testing making use of a compression block and a cold block only showed inhibition of extensor

motoneurons afterwards but because they were carried out in light anaesthesia they cannot be regarded as decisive in this particular case.

The complexities of the states of neural balance obtained after brain stem sections are well known. The author (Granit, 1969) found it a striking fact that the insignificant stretch reflex of the precollicular cat could be greatly increased by "self-facilitation" as induced by rapidly repeated brief tendon jerks. These facilitated states were of long duration. A subsequent intercollicular section released the characteristic rigidity of that type of preparation. Matthews (1969) has emphasized the need for experiments aiming at a quantitative separation of the contributions from the three kinds of receptor participating in the stretch reflex. While such results would be of great interest for the analysis of this reflex in the decerebrate state—or any other type of preparation for that matter—it can be questioned whether they ever would be valid beyond the particular "state of neural balance" from which they were derived. Besides, in the "normal" animal the central settings are likely to be biased in a different and probably more "normal" way blending movement and posture in well-co-ordinated volitional or "automatic" acts.

The grossly abnormal decerebrate preparation is of chief interest as a state of neural balance in which it is possible to illustrate some of the inherent resources of the gamma-loop as well as its behaviour in one particular state of unbalance. The concept of a gamma type of rigidity was derived from this preparation and we have since learned about the decisive importance of the static gamma fibres for the characteristic decerebrate extensor reflex to stretch. Furthermore, it has been demonstrated in this preparation that a variation in the level of the static fusimotor activity produces a family of parallel tension-extension curves (Fig. 91) suggesting an elegant mechanism for maintaining a constant tension at different lengths. By pure alpha regulation the same operation would have to be carried out on the basis of tension-extension curves varying greatly in slope and thus involving a great deal of "reshuffling" of motor units.

Liddell & Sherrington (1924, 1925) had established the stretch reflex as a negative feedback for the maintenance of one particular constant length dependent on the amount of stretch. The gamma-loop adds to this operation a new and important degree of freedom determined by the amount of loop activity the organism is in need of for the task in hand.

The maintenance of a constant length with the aid of a given amount of gamma bias has been clarified by a number of recent experiments. One factor of importance is the greater sensitivity of the primary end

organ at small rather than at large changes of length. This is shown in Fig. 120 based on the work of Matthews & Stein (1969) with sinusoidal stretching as the stimulus. The response amplitude of a primary and a secondary ending are plotted for different amplitudes of stretching. Clearly the primary end organ is most sensitive at small amplitudes such as those required for the regulation of a length setting by the feedback mechanism of the stretch (cf. also Poppele & Terzuolo, 1968).

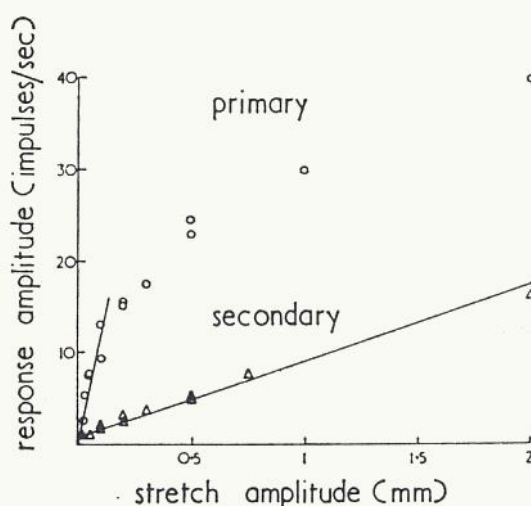


FIG. 120. The responses of a primary and of a secondary spindle ending as a function of the amplitude of stretching. Measurements made in the decerebrate cat with intact ventral roots on stretching the muscle sinusoidally at 1 Hz. (Matthews & Stein, *J. Physiol.*, 1969).

Motoneuron properties, which are generally neglected in discussions of the role of the gamma loop, are of importance in this context. It was pointed out in Chap. VI that to a sudden onset of stimulation the motoneuron responds with a fast rate of discharge within the secondary range exhibiting considerably higher gain across the cell membrane than the "adapted" discharge of the steady state in the primary range of activity studied in most papers on the stretch reflex. To this property of their motoneurons the muscles are adapted, because the initial velocity of contraction (Chap. I, p. 24) is favourably influenced by rates of discharge far in excess of those required for maintained action. The dynamic fusimotor gamma and alpha fibres serve to increase the sensitivity to the small rapid stretches that are involved in the maintenance of any given length setting. Inasmuch as the stretch reflex leads to a contraction and thus to shortening of the muscle, the fundamental biasing of the intrafusal musculature controlling primaries would always have to involve the static gamma fibres (Lennerstrand & Thoden, 1968d). In the decerebrate animal both the static and dynamic

fibres appear to be released (Chap. X). In a process as normal as respiration the dynamic and static fusimotor fibres have also been shown to be simultaneously active. They are likely to be so, whenever the nervous system is faced with the task of maintaining muscles at given lengths.

One consequence of the biological operations contributing to the maintenance of a length setting will be an oscillating muscular response. This may be slightly caricatured in decerebrate rigidity. It is easily demonstrated in that state by increasing myographic sensitivity as in Fig. 121.

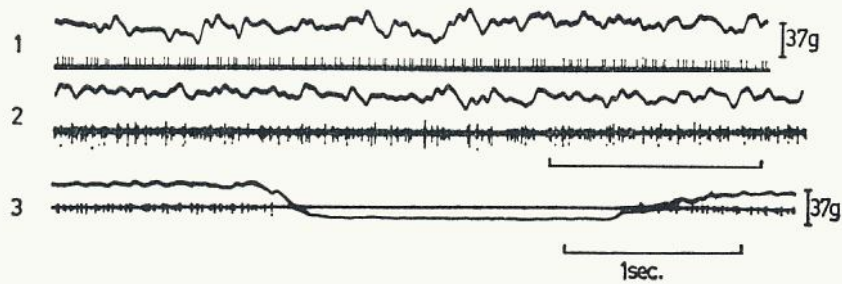


FIG. 121. Cat, decerebrate. 1 and 2 show large soleus stretch reflex at 6 mm extension; continuous record, spindle discharge in 1 having been exchanged for electromyogram in 2. 3, soleus stretch reflex (at 6 mm extension) and electromyogram. Inhibition in the middle of the record by pulling slowly on the tibialis anterior tendon. Stretch reflex recovers when tibialis anterior released. Time, 1 sec. (Granit, *J. Physiol.*, 1958).

The basic independence of control by static or dynamic fusimotor fibres respectively has often been pointed out above. There is, however, very little experimental information about the specific situations in which a motor act is controlled by exclusive emphasis on either of the two fibre types. The only case known is that of the spinal animal with its dominating spontaneous fusimotor activity of the dynamic type (Chap. X). Papers from the period preceding the separation of static and dynamic fibres (1962) tend to be dealing in the main with static fusimotor action.

The stretch reflex in the clinic has mostly been regarded as a pathological sign, because it has been found difficult to elicit this response in normal subjects, except in the form of a jerk. The tenor of recent work on the motoneurons (Chap. VI) is that the stretch reflex is a governor in contraction and insignificant in silent motoneurons. The reflex is of considerable magnitude in the firing motoneuron or in motoneurons at the threshold of firing. The fusimotor component is activated automatically in alpha-gamma linkage when muscles take part in functionally organized movements, volitional (Chap. VII), respiration

(Chap. VIII), walking (Chap. IX), vestibular (Chap. X) etc. Meaningless pulling on muscles evokes un-linked spindle firing of the passive type incapable of supporting stretch reflexes other than the largely monosynaptic burst of spikes eliciting a "tendon" jerk. However, if cessation of stretching is followed by a spindle burst, it is likely that some dynamic gamma bias had been present.

The Servo-Hypothesis

This interpretation of the role of the muscle spindles, as elaborated by Merton (1951, 1953a) and Hammond, Merton & Sutton (1956), infused a new element into our thinking of problems in this field, going as it did beyond the concept of Liddell & Sherrington (1924, 1925) which dealt with a negative feedback counteracting gravity by the stretch reflex. The missing fusimotor control of this feedback mechanism was inserted in the previous section. The new element of servo-theory was the assumption that the gamma motoneurons control muscle length on the principle of a "follow-up-length" mechanism, meaning that the length at which a muscle is going to act is set by the contraction of the intrafusal muscle fibres under gamma influence. The extrafusal musculature is then forced by the stretch reflex to "follow up", until functional equality of length in the two muscle types silences the spindles. The ideas of Rossi, Granit & Kaada, discussed above, could be fitted into this notion but did not necessarily require it. The servo-hypothesis, though limited to the action of spindle primaries alone, has been a valuable stimulus for the development of research in this field.

Inasmuch as the proprioceptive reflexes are three in number and the servo-theory only considers one of them there will be limitations to its applicability unless it can be developed to take account of plus and minus terms derived from the effects of tendon organs and secondaries on the motoneurons. A fundamental objection, namely that motoneurons cannot be fired across the gamma loop, has been removed by the experiments presented in Chap. V showing them to fire to this mode of stimulation against the twofold antagonism of unloading of the spindle and tension-sensitive inhibition. The early experiments of Eldred, Granit & Merton (1953) were interpreted on the servo-theory (Chap. VII, p. 165) though these were originally begun only in order to find out whether the stretch reflex was in need of gamma bias to occur at all. The theory requires that spindle activity should lead alpha activity and in reflex action this often, though not always, is seen to be the case. It seems entirely possible that in pathological states involving active motoneurons and strong fusimotor activity a follow-up length

servo may play a decisive role. There is no need to exclude the possibility of such servo-action in normal movements before we have seen examples of spindle control other than the ones at the moment available. For criticism of the servo-hypothesis, see Hunt & Perl (1960) and Matthews (1964, 1969).

An important argument in this criticism is that the gain across the "servo" is insufficient for the task attributed to the loop. However, the gain as tested by the stretch reflex refers to a very specific state of hypertonus involving tonic motoneurons with small slope constants (Chap. VI; Fig. 80). These cells are subject to recurrent inhibition in addition to the complications stemming from co-activation of tendon organs and spindle secondaries. It has been pointed out (Chap. VI) that the highly stabilized firing of these motoneurons curtails the "true" input. While it is possible in a general way to speak of gain of a reflex producing tension in response to an input defined as extension, this term is then used in a way implicating a large fraction of the central nervous system with the net result of all the interactions involved. Restricting the term "gain" to the precisely defined slope constant of a motoneuron, one knows what particular process is being measured. Because of the algebraical additivity of plus and minus terms at the synapses of the motoneuron, the firing rate will in the end be determined by the slope constant. The maintained discharge frequency can never become high in the small tonic motoneurons of the stretch reflex and regulation is thus bound to be carried out by recruitment of fresh motoneurons from the subliminal fringe (or "decrutment") in the way it is being done by the organism. The pseudo-stretch reflexes of the alpha rigidities are based on the additional release of phasic motoneurons and, consequently, may be very large. Some alpha-involvement caused by the operation should always be suspected when the stretch reflexes of a decerebrate animal are in excess of the normal range.

Thinking of locomotion in a general way means turning to motoneurons with greater slope constants than in tonic alphas. For such motoneurons we have the information that at or above their firing threshold they respond to postsynaptic potentials by 2.28 imp/sec/mV. This value refers to steady state firing. The figure would be considerably higher at the moment of initiation of a contraction, before the slope constant has fallen as a consequence of "adaptation" at the membrane. However, restricting the discussion of gain to the known figure of about 23 imp/10 mV, it is by no means impossible for spindle impulses to elicit an EPSP of this order of magnitude (cf. Fig. 77). Regrettably we do not know in what particular situation the large increases in the spindles' position sensitivity of the Type II take place, reported to be

of about seven times the resting value in the eye muscles (Chap. XI). The types of normal movement so far analysed are extremely few and restricted in force and velocity. Fast motor units capable of producing large contractions have hardly been studied at all in natural movements and these motoneurons are the ones employed for versatility of action. Alpha control is likely to be dominant in many rapid and strong movements. The scale of muscular movement, in both force and velocity, ranges from heavy manual labour to the playing of elaborate musical instruments. Maximal efforts would push the motoneurons into the secondary range with a very large increase in gain (that is slope constant).

These considerations again emphasize that the idea of a follow-up-length servo should not be finally struck from the list of potential resources of the fusimotor alpha and gamma interactions until withdrawal of it is enforced by more definite evidence than is now at our disposal.

However, so far the most commonly observed effect of fusimotor fibres on spindles in the modest range of "normal" movements that have been studied, is undoubtedly their remarkably precise co-activation with the alpha activity in what has been briefly referred to as alpha-gamma linkage. In the amphibia such co-contractions of extra- and intrafusal partners are the inevitable corollary of a common innervation, the two kinds of motor fibres being branches of the same stem fibre. If stereotyped alpha-gamma linkage were the ideal goal realized, why then is this arrangement not perpetuated as the dominant one in higher species? Clearly, because a more flexible system is a biological asset. It has added new degrees of freedom to the linkage, based on the fundamental independence of the measuring instruments with their static and dynamic control (Chap. X). We are badly informed about how and when these are invoked independently by the organism in motor activity. However, the normal movements in which alpha-gamma linkage has been studied are best described as servo-assisted rather than as servo-controlled by the loop (Matthews, 1969). In most cases the role of the spindles in these movements can be understood intuitively and expanded experimentally without any reference to servo-theory. An exception is the damping by derivative feedback as an example of a servo-assisted contraction.

It was pointed out by Merton (1953a) that the response to velocity on the part of the primary end organ compensates for transport lag in the stretch reflex by behaving in this respect like derivative feedback in a servo-operated process. The impulses elicited by stretching have to travel round the feedback circuit to exert their ultimate effect on the muscle. The contraction of the latter will consequently be delayed and

out of phase with the signal and this causes a tendency of the system to oscillate which is counteracted by the velocity-sensitive burst preceding the contraction, especially when the dynamic response is speeded up by the action of the appropriate fusimotor alpha and gamma fibres. The theory of Matthews (1964) to the effect that the dynamic gamma fibres act by increasing the viscosity of the intrafusal muscle (the nuclear bag muscle on present evidence) implies that the fusimotor damping of the system is ultimately a regulation of viscosity. Since that time Lennerstrand and Thoden (1968a and Fig. 37) have separated a "quick" component of velocity sensitivity from velocity-dependent gain by a "slow" one. The fusimotor effect on the quick component is apparently the one most useful in producing the anticipatory response which engenders the phase advance required for compensation of transport lag. How the two components of the velocity response relate to the actual development of viscosity is at the moment unknown. Their separation indicates that damping cannot be the sole purpose of dynamic fusimotor action. Besides, its alpha fusimotor component need also be taken into account. In this context it is of interest to recall the finding of Henatsch (1966) that tremor occurs after an intracerebral injection of tubocurarine. This procedure was shown to shift the ratio of static to dynamic activity in favour of the former and thereby to lessen the damping in the system.

Structures as complex as the motoneurons should not be considered in terms of gain alone. They also have to maintain constant activity. It has been pointed out (Chap. VI) that slow dendritic changes of synaptic potential may have an important role to play in this regard. They could (as in some other cells) serve to maintain an even depolarizing pressure while the firing soma membrane is forced to swing between the two extremes of spike potential and afterhyperpolarization. At least in tonic action the primary afferents reach the motoneurons across internuncial cells and these often synapse on dendrites. Thus the gamma-supported spindle activity may well be a major instrument in the postulated "maintenance function".

It is still possible to expect that more knowledge about the peripheral spindle mechanisms could throw light on control problems. Stiffness and viscosity of the two types of mammalian intrafusal fibres have yet to be determined, both in passive and active spindles. These quantities may be differently influenced by gamma plates and gamma trails, as well as by the degree and nature of the overlap of different fusimotor fibres. We also need more information on the way muscle spindles are inserted on muscle fibres, whether these fibres belong to different or virtually identical types of motor units. In the former case their task might be to smooth out inequalities of tension and rate of its develop-

ment in motor units of different mechanical properties (cf. Jones, 1969). This function they could subserve also to some extent even if restricted in localization to one particular motor unit (see next section). Most biological adaptations have different tasks to perform in the organism and there seems to be no reason for regarding the muscle spindles as an exception from this rule.

Velocity of Movement

The role of the muscle spindles in the organism has generally been considered in relation to the power supply to be controlled, that is the tension of the muscles in which they are located. An equally important property of the extrafusal musculature in locomotion is the velocity at which force is generated. In the extremities it seems likely that velocity control would depend to some extent on information from joints and ligaments. The question as to whether the spindles also contribute something invites speculation. The easiest case to discuss is a muscular action controlled by alpha-gamma linkage and performed at constant speed which at a given moment is opposed by an obstacle to be overcome because of a (centrally determined) demand for the particular speed at which it was begun. No new concepts are needed for a discussion of this situation.

Phillips (1969) has treated such a case in a speculative diagram shown in Fig. 122. It illustrates an intended movement proceeding at a uniform velocity from *a* to *c* (in (a)) and carried out by parallel recruitment of alpha and gamma motoneurons, the latter antagonizing the unloading effect on the spindles. An unexpected resistance is encountered at *b*. This reduces the unloading effect (bottom) and thus excites the spindles (fusimotor effect in (a)) dynamically and statically. The primaries act as in *p*, the secondaries as in *s* below it, to oppose the obstacle by load compensation which also produces velocity compensation. "The prompt increase in force at the instance of deviation, and its further increase will only be checked if the movement is brought back to its proper course towards the target *c*. (The compensated responses are not shown in the diagram.) The secondary endings (*s*) are also supposed to be under static fusimotor influence, and would signal the increasing discrepancy between the 'intended' and actual movements, but would differ from the primaries in transmitting no information of the velocity of the deviation. The secondaries do not excite the alpha motoneurons, but their information, as well as that supplied by the primaries, may well be important at cerebral and cerebellar levels" (pp. 157-158). *Mutatis mutandis* the same reasoning is applied to a sudden reduction of resistance in the right half of the diagram.

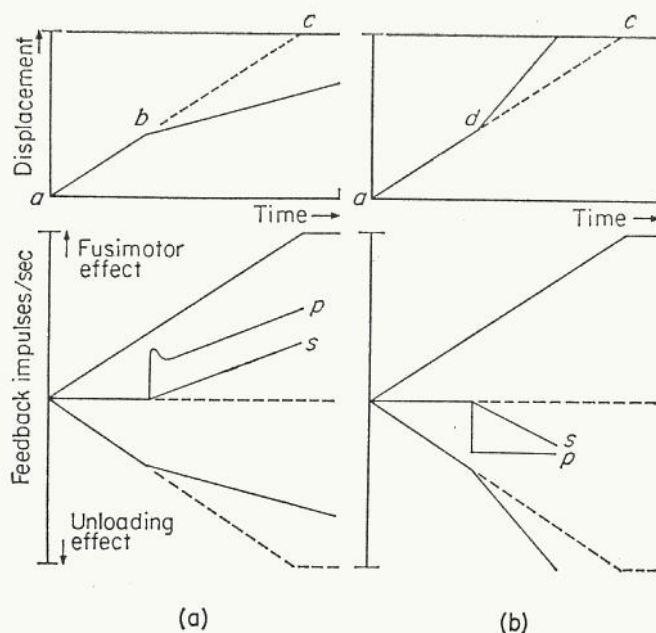


FIG. 122. Diagram of tentative fusimotor contribution to an intended movement. (a) Movement is supposed to proceed from *a* to *c* at uniform velocity all the while recruiting motoneurons of alpha and gamma type (fusimotor effect), linked in parallel, the latter compensating for spindle unloading effect. The unexpected resistance at *b* reduces unloading and increases spindle feedback so that the primaries (*p*) and secondaries (*s*) are induced to fire along curves *p* and *s* to the resistance and bring the curve back to its target trajectory provided that *s* is excitatory as is *p*. This, at least, is the case in flexors. (b) Represents the reasoning on the assumption that there is an unexpected reduction of resistance at time *d*. The spindle discharges will then reflect the increase of unloading, as the extrafusal fibres' contraction becomes stronger than intended. The primaries and secondaries are reduced in firing rate along the curves *p* and *s* respectively leading to a reduction of excitability in the alpha motoneurons. (Phillips, *Proc. Roy. Soc., B.*, 1969).

It is more difficult to discuss cases in which no special obstacles occur to alter the speed of a commanded movement. How to reason in this case will be shown for a demanded movement beginning slowly and then accelerating towards its end. The movement, which carries a modest load, begins by recruiting small motoneurons which activate slow motor units and produce modest amounts of force. The movement would be servo-assisted and in addition to recruitment an increase in firing rate of the recruited motoneurons is allowed. The slow motor units would have force-velocity curves of the kind shown for soleus in Fig. 11 and thus could not meet the demand for an acceleration of the movement. Under the circumstances they would not have enough power at their disposal to satisfy the equation stating that mass times acceleration equals force. They would, however, have been powerful enough to unload the fast motor units during the slow phase of the contraction. The fast motoneurons would thus have been in a state of

relative hyperpolarization or, at least, of less depolarization. In conjunction with the slackness of the unloaded motor units this would have caused a jerky acceleration of the movement by steps of recruitment unless some process existed to smooth out discrepancies of level of activity in mechanically different motor units. It is suggested that in a servo-assisted movement the overlapping central projections of the muscle spindles on different motoneurons serve this very purpose of facilitating smooth transitions from slow to fast action. It should not be too difficult to investigate these theories experimentally.

Linked and Independent Action

The emphasis on linked alpha-gamma discharges in the interpretation of the role of the fusimotor regulation of spindle activity is not meant to convey the impression that alpha-gamma linkage is the only possible mode of operation of the loop through the muscles. It is merely the one best understood and most systematically analysed, evidently because it has been regularly encountered in experimental work. This is also why some caution should be exercised in judging about exceptions from the rule. They may signify that the stimulus situation by chance has favoured either motor component, alpha or gamma, at the expense of the other, simply as a consequence of the employment of artificial stimuli. While these are useful for the detection of possible pathways of excitation or inhibition, they do not show how such pathways are engaged by the organism in motor control, unless subsequently identified in supplementary experiments on movement or posture.

So far the most clear-cut exception from the rule of alpha-gamma linkage is the spindle response to passive stretch in one phase of stepping, mentioned in the previous chapter. Proprioceptive reflexes on fusimotor neurons may likewise belong to the category of true exceptions. Most of these reflexes are curiously elusive (p. 168) and still require to be regularly demonstrated with natural stimuli. Recently, again, such reflexes, suggesting that extensor primaries from the gastrocnemius muscle excite primaries in ipsilateral antagonists and contralateral homologous muscles, have been reported by Haase & Vogel (1969) and Schlegel & Sontag (1969). The role of these reflexes in movement and posture is not yet understood.

Results on the boundaries of a field of research may not be ripe for a synthesis of the kind that has been attempted in these chapters. Their role is to indicate new openings for future investigations. They are mentioned for this reason and also in order to emphasize that two short decades of experimentation in a new area of research can hardly be expected to have solved more than a fraction of the problems facing us

in interpreting the role of proprioceptors in motor control. The deficiencies in our knowledge about the secondaries is another item worth mentioning in this connection. In the end the complexities are perhaps most obvious when attempts are made to apply the new knowledge in the clinic. The motor disturbances seem to involve problems of balance in the activity of the various systems concerned. In the near future the method of direct recording from spindle afferents (Chap. VII) is likely to shed new light on the diseases of motor control.