CHAPTER XI

Concluding Remarks

The preceding discussion has served in no part to 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 two distinct and highly differentiated fusimotor-spindle systems? These questions cannot be seen against the background of general sensory physiology. In vision, for instance, it is possible to state the technical task as requiring from "lines" to "edges" by some rather close step-by-step series of so-defined physiological mechanisms. So far as all seeing whose ultimate purpose is to make it possible for the living organism to discriminate out things from ensuing in the present context it is equally sensible to ask what are the "aims" in the muscle spindles, or of the tendon organs?

It is worth noting that the muscle spindles measure muscle length and the tendon organs muscle tension means that something has been understood, albeit in a very elementary kind. This reply makes the essential sense of control by intrafusal fibres and of each separate type of efferent muscular act in the final interpretive, but as in vision can not of course in the distinctive interpretive of the experimental findings in that field.

Tone. The Stretch Reflex

An early attempt at interpretation was Rood's (1917) notion that postural tone might be maintained by contraction of the intrafusal fibres causing stretch reflexes of the type the stabilization theory of Hubbard (1959). Rood's idea had been forgotten, partially because it lacked experimental support. It turned up spontaneously twenty-five years later (Gerard & Kandel, 1959), this time, however, as a deduction from experimental work and formulated in the following manner: "After a tonic excitation has been examined for the action of muscle 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. 126). This system has since been studied extensively and

(Chaps. VIII, yielding (Chap. IX), contractile (Chap. X) see. Mecklenburg calling on muscle nodes on record specific firing of the passive type *incapable* of supporting steady reflexes other than the largely monosynaptic burst of spikes evoking a "twitch" (p. 34). However, if condition of stretching is followed by a spindle burst it is likely that some dynamic gamma has had been present.

The Servo-Hypothesis

This interpretation of the role of the muscle spindles as discussed by Merton (1951, 1953a) and Granit, Henatsch & Steiner (1954), without a new element into our thinking of problems in the field, giving as it does a well-known reflex (the stretch reflex of Sherrington, 1910) a definite role with its neural feedback concentration, namely for the muscle reflex. The guiding formative concept of this feedback mechanism was borrowed in the previous section. The true interest of servo-theory was the assumption that the gamma motoneurones 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 motoneurons of the intrafusal muscle fibres under various influences. The contractile tension there is then forced by the muscle reflex to "follow up", and functional capacity of length is in two words equal all over the spindles. The idea of these, Granit & Kaada, discussed above, could be fitted into the system 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 deep approach 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, in this respect, of plus and minus terms derived from the effects of tendon organs and nociceptors on the motoneurons. A fundamental objection, namely that tendon organs cannot be fitted into the gamma loop, has been removed by the experiments presented in Chap. V, showing them so far in this mode of examination against the cocktail assumption of attributions of the spindle and tension receptors (Hubbard). The early experiments of Hubbard, Granit & Matthews (1955), were interpreted on the servo-theory (Chap. VII, p. 165) through them were originally begun only in order to find out whether the stretch reflex was in need of gamma bias to serve at all. The theory requires that tonically active muscle feed signal activity and in reflex action like other, though we always, it seem to be the case. It seems currently possible that as pathological states involving motor phenomena are raising fusimotor activity a follow-up length

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

A basic contribution to aim to 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 (Chaps. X) and anesthesia (Section, 1953a, p. 264). The need for fusimotor support of stretch reflexes was pointed out in the previous chapters in several cases (Chaps IV, VII and X). It has also been emphasized that the action of the muscle reflex, studied from the aspect of the movements as its "final common path", requires that muscle be set as shown during living movements.

As has already been indicated there are at least three types of muscle reflex corresponding to the three types of receptor, primaries, secondaries and tendon organs, as emphasized by me since (Granit, 1955a, p. 719) and more so again by Matthews (1959, 1931). There may also be postural reflexes from the Golgi neurons. Both muscle reflexes and spindle secondaries have long been known in static act of proprioceptive stretch and it has been shown there that the tonic component of the action of primaries in the stretch reflex also is established by fusimotors. The polysynaptic circuits are facilitative in the sense that they may be open or closed dependent on central adjustments after lowered experimental control. Recently Matthews (1960, 1957) has suggested that the spindle secondaries are facilitative to the extent of being dependent on "fusimotors" wholly disengaging their signals from fusimotors on excitation. This is one way of describing his assumption that the stretch-reflex of cats by that of the secondaries on excitation motoneurons seems to excitation in cats secondaries of the decerebrate animal. It may not do so normally. His hypothesis is based on the observations that vibration or controlled impressions and amplitudes can be made to reinforce at the secondary of a muscle and not was able to elicit in such isometric tension per muscle per se as does the natural stretch reflex as were upon lower most of Granit's experiments on impulses per unit extension. The secondaries, it seems would tend by the stretching are the only receptors that can make the muscle reflex positive section in excess of what the less firing rates of the primaries can account for. Section of all fusimotors in the hypothesis were made above (p. 178). It might be added that a corroborative experiment in support of this view would be to disconnect the primaries of the ordinary stretch reflex after blocking the Group Ia spindle afferents. Since experiments (Section, 1955) by monosynaptic testing rendering use of a monosynaptic block and a cold block only proved inhibition of extensor

motoneurons after-reds but because they were carried out in lean anaesthesia they cannot be regarded as decisive in this particular case.

The complication of the states of normal balance obtained after brain or cord lesions are well known. The earliest (Granit, 1930) found it a striking fact that the insignificant stretch reflex of the decerebrate cat could be greatly increased by "self-facilitation" as induced by rapidly repeated knee tendon taps. These facilitated states were of long duration. A subsequent anaesthetized section released the characteristic opposite of this type of preparation. Matthews (1959) has emphasized the need for experiments arising of a qualitative separation of the contributions from the three kinds of receptor participating in the stretch reflex. While more recent work has of great interest for the analysis of the reflex at the decerebrate state or any other type of preparation, it is clear that the ideal conditions for such theory first would be found in the so-called "state of equilibrium" (p. 178) in which they were derived. Besides, in the "normal" animal in the natural settings are likely to be found to a different and probably the most "normal" way blending nociceptive and postural in well-co-ordinated volitional or "automatic" acts.

The greatly increased discontinuous preparation is of chief interest as a state of neural balance in which it is possible to fix the error of the inherent resonance of the gamma-loop as well as its behaviour in one particular state of stabilization. The concept of a gamma type of rigidity was derived from this preparation and we have since learned about the decerebrate hyperactivity of the same gamma fibres for the discontinuous decerebrate contracture reflex in stretch. Furthermore, it has been demonstrated in the preparation that a resistance to the load of the static fusimotor activity produces a family of parallel tension-extension curves (Fig. 81), supportive as regards mechanism for maintaining a constant tension at different lengths. By pure alpha regulation the same equivalent would have to be carried out on the basis of certain extension curves varying greatly in slope and thus involving a great load of "controlling" 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 spindle. The gamma loop adds to the mechanism a new and important degree of freedom determined by the control of loop activity the organism is in some of the the two to load.

The maintenance of a constant length with the aid of a more constant of gamma load has been described by a number of recent experiments. One factor of importance is the greater sensitivity of the primary end

organ is small rather than of large changes of length. This is shown in Fig. 120 based on the view of Matthews & Stein (1960) with myocardial stretching as the stimulus. The response amplitude of a primary and a secondary of firing are plotted for different amplitudes of stretching. Clearly the primary end organ is more sensitive at small excursions and, as those required for the regulation of a length setting by the feedback mechanism of the stretch (cf. also Poppele & Terzuolo, 1960).

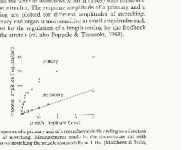

Fig. 120. The response of a primary and a secondary spindle to sinusoidal stretches of the amplitudes of 0.1 mm. and 0.5 mm. respectively. The stimulation was made by the myocardium and the response recorded from the muscle nerve. (Matthews & Stein, *J. Physiol.*, 1960).

Motoneurone 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 in a motoneurone of intermediate discharge rate (Fig. 81) supportive or negative mechanism for maintaining a constant tension at different lengths. By pure alpha regulation the same equivalent would have to be carried out on the basis of certain extension curves varying greatly in slope and thus involving a great load of "controlling" of motor units.

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of about 0.001. Since the resting value in the cat muscles (Chap. XI). The type of tension "recovery" is for analysed are extremely fast and are used in force and velocity. Fast motor unit is capable of producing large contractions at a relatively low rate of stimulation, available, and these motoneurones are the ones employed for the smaller contractions. The fusimotor system is assumed to be slow and strong motoneurones. The fusimotor system is assumed to be slow and strong motoneurones. The fusimotor system is assumed to be slow and strong motoneurones