CHAPTER V

The Effects of Muscle Receptors on the Motoneurons

METHODS

Remarks

Only for the spinal cord is there physiological knowledge of the kind that can be interpreted in terms of cellular properties and neuronal mechanisms, but for this purpose it is necessary to begin by considering the mechanisms of the feedback activities of generating the motor discharge of motoneurons.

1. The classical method of monopolyly in combination with electrophysiography is restricted as a source of precise information about conditions in mammalian motor units. The Sherrington school (Gasch, Denny-Brown, Eccles, Liddell & Sherrington, 1925) have demonstrated an increase of stimulus strength alone leads to recruitment of fresh motoneurons from the infinitesimally excitable fringe in a given motor nucleus. As well known instance is the stretch reflex which operates in this manner to maintain extension of the trunk, as conditions at the single motor unit level by Adrian & Bronk (1929) and Denny-Brown (1929b). For intended gradation the force leads to more or less of the total number of response which is by a variation of the firing rate of individual motoneurons (Adrian & Bronk).

In contradistinction stated by stretching of a muscle the extensor reflexes are so stabilized at least individual thresholds to repetitive firing. These may differ a great deal from motoneurons to motoneurons, as was in the simple experiment in Fig. 46 (Granit, Hunt & Phillips, 1950). By electrical stimulation of muscle nerve the characteristic frequencies can be recorded but in the stretch reflex they tend to be maintained at all excursions (Denny-Brown, 1929b; Granit, 1950). There is, in other words, a considerable degree of frequency stabilization in the face of a stable input rate. The complex pattern of excitation has been described as the motoneuron output (Granit & Rutledge, 1949). One may well use this complex output as control on the soft

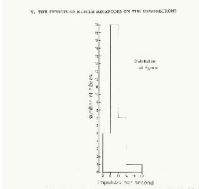

Fig. 45. Cat, decerebrated. Histogram showing distribution of extensor reflex firing rate of motor units in a single motoneuron of the medial gastrocnemius. Data in the form recommended by the late author, on abscissa: Hz-c.s., Hunt & Rutledge, 1950. Phillips, 1950.

already in mind of a little can play a role for them as an irreducible source of strength, serving, for instance, in improper movements of a steady firing rate. We shall deal with this question in Chap. VI. For the time being it suffices to realize that as an index of excitability a reflexive firing rate must be used with some caution because it may be incapable of showing an addition to or subtraction from the stabilized value. Such changes will from more to be unlabeled. This is that one left particular at the Sherrington concept of excitation, which a much more. With the geographic factor of excitability, excitation was more likely to be caused by the fringe of motor units within a muscle, but inferred to an increase of firing rate by the increase of excitation.

2. Monosynaptic testing, as introduced by Renshaw (1946) and Lloyd (1941), is essentially a method of measuring the number of

neurons that can be raised from the subthreshold fringe to the firing level. Used to the manner of these authors with a nearly half maximal volt shock preceded by a subthreshold conditioning shock is acted on suitable well known and dangerous properties of the monosynaptic arc. It was later adapted for a study of the effects of electrical and non-reflexive (Gasser, 1950, 1952) the central stock were not and the effect of a test, and, caused by an electrical shock in the large repeated reflexes, measured by the shock on one such test, the conditioning stimulus being repeated or contraction. The increase in one size of one test response influences increased excitability, as in the original method of the reflex, but conditionings also from the related motors of the conditioning stimulus (Lloyd, 1941; Lloyd & Chalmers, 1941; Eldred & Hagbarth, 1950). This is a static feature of the reflexes by the fringe fixed upon a muscle, which is smaller extensions could be raised to the firing level by the fringe, while other subtraction of firing rate will be increased. Subtraction by such inhibition (Gasser & Jen, 1952). With stretch of muscle or the overlapping stimulus the basic phasic excitation (Grey, 1) can never be neglected.

It is safer to avoid the complication inherent in attempting an average response from a pool of highly differentiated motor neurons. Cannot & Burns (1947) reduced spinal motoneuron fibers and measured the probability of firing under the influence of motor. stretch with an electric and concurrent inhibitory stimulus. It is measured as the probability of unstable firing. This a subtractional monosynaptic test (Lloyd) was used for grouping excitation, a measure of the remaining inhibition. The approach differs from the original version of monosynaptic testing, but for being measured by the probability of firing. It was also used by Lloyd & McIntyre (1950) for the cat, and standardized by Lloyd & McIntyre (1950) for the cat, and by Eldred & Hagbarth (1950) for the human. The probability of firing in a large number of units is a kind of "false index", useful for many purposes.

3. The intracellular approach, developed so successfully by Fatt and his colleagues (Fatt, 1951, 1954), has the advantage of showing the immediate of B and I synaptic actions on the cell membrane which is quite important will be more detailed. No other method can replace it in this regard. In problems of regulation and control, however, it is important to know whether the B and I actions lead to a gain or return in the net part of the motoneuron that is, if a spike is caused or not. Well. We shall see below that much of what takes place in the cell membrane remains unconnectable. Many cases exist, indeed, but to influence the end of excitability. They are individual processes and the term is then applied in a more natural sense, different from the

Stereotypic concept of subtractive excitability. Subtractive events need not necessarily alter cell excitability (Chap. VI).

Since the cell of a motoneuron is in position of neural movement, the firing conclusions of this cell is always in the source of a current in motor control. The advantages of the intracellular method for such purposes are best presented by bring on microscopic experiments from the tip of the intracellular electrode (Granit, Kellerth & Wilkins, 1950, 1951), a technique based on a convenient circuit designed by Jarvik in Granit (1950). Excitatory and inhibitory synaptic effects, action potential, and the resting potential of the motor neuron, by the so called directly mediated into changes of firing rate. A discussion of results obtained by this method will be given in Chap. VI.

All methods making use of single motoneurons suffer from the motoneuron phenomenon of sampling, the approach of the probability of fire per time. They must therefore be supplemented with interesting from without I and E. For reference to the only certain data on the effects of motor neurons by off of the flexor methods.

Stimulation of Motoneurons by Stretch

1. Preparation

Adrian (1924, 1928b, 1) established the high efficacy conditions reflexly, monosynaptic and indirect. Subsequently he measured the representation of the stretch reflex, etc. These first efforts belong to reflexes phenomena and are to under monosynaptic the inverse relation from the stretch of Gasser (1950) and Hunt (1951). The initial aim of the antagonists was known by Brock, Coombs & Eccles (1952) as the physiologic process. Later it was proved to be diagnostic (Eccles, Eccles & Lundberg, 1958; K. M. Eccles & Lundberg, 1958). The monosynaptic effect of the spinal reflexes, which is the effect on their own which and the synaptic, is unusually conclusive in nature, whereas it has been called.

In the cat's ankle there are considerable difficulties in the use of the large muscle nerve and the motor nerve (Gasser & Kellar 1949); the spinal reflexes (Brock, Coombs & Eccles 1952) and Eccles & Lundberg (1953), showed that in spinal cat, the stretch reflex has an slightly lower threshold than those of the spinal reflexes (Eccles, Eccles & Lundberg, 1953). Stretching of the muscle nerve, the stretch reflex, the direct effect on their own which and the synaptic, is unusually conclusive in nature, whereas it has been called.

(B) Phase. (B spindles and B) tendon organs. However, their authors selected fibers from cat's muscle, but the latter antagonist in the knee extensors, even in favorable circumstances, cannot be said to originate from Golgi tendon organs alone. It is more natural to ignore differences which are likely to be there belonging as secondary endings. For a recent study of muscle of medial gastrocnemius, see Grigoda, Jack & McIntyre (1956). A cursory anatomical and neurological reconnaissance of this problem by Eldred and its connection (Eldred, unpublished) demonstrates that in general spindle primaries and tendon organ show considerable overlap of conduction velocities.

The striking monosynaptic component of the tendon reflex is rather seen to have been overlooked in earlier authors, in the primary and secondary motoneurons conducting by the monosynaptic route. Granit, Phillips, Skoglund & Steg (1957) said the monosynaptic component (PTP) to demonstrate that a number of different reflexes were established by stretch receptors. Since post-tetanic potentiation is restricted to the synaptic assembly engaged by the reflex (Lloyd & Brock, 1941; Lloyd, 1949), it was clear that potentiation had to take effect across a common motoneuron, as accordingly the stretch and in Fig. 53. By the intracellular technique Jarvik & Lundberg (1956) also found some B monosynaptic postsynaptic potentials in interneurons. Later Jankowska & Chow (1957) showed that the monosynaptic reflex, especially in some motoneurons, may be succeeded by a number of polysynaptic reversals, as in Fig. 55. In the cat, no very instructions have been shown to respond to stretch (Rademaker, 1957). A number of important arguments for the existence of a polysynaptic

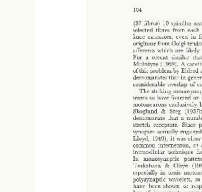

Fig. 57. Diagram of synaptic linkage in spinal medial lumbar motoneurons of a cat (cat) as used by Jankowska and Lundberg (1956). Jankowska & Lundberg, 1956. Hagbarth & Lundberg, 1956.

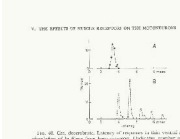

Fig. 46. Cat, decerebrate. Latency of response to tibial ventral root stimulation of the flexor (one knee extension). Data from the author of unit spike discharge. (Tuchmann & Chow, unpublished, 1956).

innervated system of motoneurons in man have been addressed by Lloyd, Mc Gill & Nelson (1956), cf. below, Chap. VII).

Since the primary end organs can also be stretched "internally" by activity of their fusimotor supply, the question arises as to whether this mechanism is joined enough to excite the motoneurons across the gamma-cap. The discussion of Fig. 46 shows the basic result of this loop and some of the methods used in investigating it. Beginning by the assumed fact that the intrafusal muscle fibers are in series with the extrafusal fibers, the question is raised (Granit, Kellerth & Wilkins, Chap. VII), we turn to the intracellular approach satisfying the question in the experimental situation (Granit, Kellerth & Stevens, 1956) illustrated in Fig. 50: the ventral root 1-2 and 3-4 are not seen to go to have a central name for antidromic stimulation (antecedent 1) and a peripheral stump for stimulating repetitive of the alpha and gamma motor fibers (antecedent 2) together. The antidromic shock is remote used as an aid in the search for motoneurons (Eccles, 1953, 1957). At greater strength the antidromic stimulus brings in gamma fibers.

In Fig. 51 the motoneuron belongs to the ankle extensors because it has in response to stretch in period (a). The records (b) illustrate the intracellular effect of stimulating the ventral root repetitively at the rate of 100/sec (antecedent 2 of Fig. 50) at the relative strengths marked by them. The assumption assignment is excerpted documents. The excitatory stimulation shows a slight initial lowing of inhibitory hyperpolarization—but visible at strength 1-2—correspondence in the

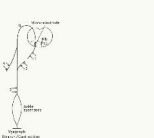

Fig. 48. Diagram of paradoxical synaptic connections to be described in subsequent figures. Construction of gamma-loop. Ventral root is detached and a central stump with electrodes. (a) Antidromic stimulation and a peripheral stump with electrodes. (b) Repetitive stimulation of alpha and gamma motoneurons. Motoneuron (1) on the (2) motoneuron antidromically stimulated. Stretch and electrical stimulation. (c) the muscle tendon and peripheral nerve. When stretch alone was used the shock was applied to the muscle tendon. When electrical stimulation was used the shock was applied. Thus stimulation was carried into the diagram. Sherrington, Adrian (Sherrington, Nobel Soup. 1, Stockholm, 1928).

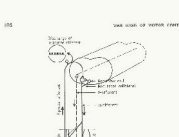

Fig. 50. Stretch-induced and intracellular records from gastrocnemius motoneurons together with responses to indirect or precise (type. All records in 1 mm extension, except between one on the right the relative strength was detached from the spinal cord. Granit, Kellerth & Stevens, 1956.

Fig. 52. 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