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LECTURES

MUSCULAR TONE (*)

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Some of the most important studies on the terminal muscle apparatus are still, as we all know, those of Ruffini and Golgi, published towards the end of last century. Ruffini's special concern was with the muscle fibres but he wrote also on the Golgi tendon spindles.

Around 1949 I realized that although we had extensive knowledge of the reflexes of the muscular afferents, thanks largely to Sherrington and his school, and had important data on the properties of the terminal muscle apparatus, due to the work of Adrian and Zottermann and of Bryan Matthews, we knew practically nothing of the role of these sensory organs in motor regulation.

What are the muscle spindles for and what is the role of the Golgi tendon spindles?

It was thus that I started on my experimental researches.

It is impossible to give a complete account of the studies conducted in our laboratory and elsewhere, so I will confine myself to some observations of a general character.

We began by showing that the Golgi tendon spindles are regulators of tension in the extensors, acting as a brake upon contraction and at the same time preventing these large muscles from producing undue tension. Their discharge simultaneously stimulates the flexor antagonists to contract. The same function would be ensured by facilitating the critical moment of entry into operation (of suitable mucles). The muscle fibres seemed to be more interesting. Sherrington, with his experiments on degeneration in 1894 had shown that the large fibres of mammalian muscle spindles are afferent. The first to demonstrate, with convincing experiments on degeneration, that the muscle spindles also have a nerve supply, was Cipollone in 1897. "We find that the fine myelinated fibres and the endplates degenerate while the thick myelinated fibres and the rich terminations of the fusiform swelling are perfectly conserved. It may therefore be asserted with safety that the former are motor fibres and endings and that the latter are sense fibres and endings".

In 1945 at our laboratory Leksell obtained definitive physiological proofs of the fact that the muscular polar regions of spindles contract in response to selective stimulation of the slim fibres, which he called "gamma fibres" because of their speed of conduction (on the Erlanger-Gasser scheme). These researches were further developed by Kuffler *et al.* The new problem that presented itself was this: what use does the organism make of such a complicated system?

The muscle fibres are parallel to the principal muscle and hence are relaxed and rested by the latter's contractions. Is it possible that their own motor nerve supply exists only to make them contract with the principal muscle, as Kuffler and Hunt had thought?

That such a complex mechanism should serve such a simple purpose seemed too elementary.

Prof. Rossi of Florence had considered the problem in 1927 and had come to the

(*) Lecture presented at St. Vincent (Turin, Italy) on occasion of the International Medical Meetings, 1961.

conclusion that the main task of the muscle fibres in motor regulation was to coordinate the postural reflex.

Let us try to understand what this means.

The hypothesis was based on the postulate that the muscle spindles and not the Golgi tendon spindles produce the stimulus for the stretch reflex. We proved this to be so in 1950. The work of Liddell and Sherrington had shown that the elongation of the muscle such as occurs under the influence of gravity reflexly contracts the muscle to counterbalance stretching. And this is how an animal maintains its erect position. Rossi's idea, about which we were unaware at the time of our observations, was that the nerve centres, through the gamma efferent fibres of the spindles slightly contracted the polar muscular regions of these sense organs, rendering them more sensitive to slight stretching. Thus, if the spindles are sufficiently sensitive, they can automatically start up their own reflex, which is necessary to counteract gravity. This ingenious hypothesis thus indicated that the purpose of the spindles is posture control. I think we may say we have confirmed this. One of the important implications of Rossi's hypothesis was that it was possible to show that the muscle spindles are under the control of the central motor centres. This evidence was provided in a work of Birger Kaada and myself in 1952. Our demonstration of cerebral control over the sense organs has led several laboratories to investigate the general question of descending control of the sense organs, a question which is now becoming an interesting field of research.

It has long been known that the brain stem contains important centers for the control of tonus, since sectioning of the stem produces decerebrate rigidity.

Moruzzi and Magoun in their classic work of 1949 called attention to the importance of the brain stem in the genesis of the complex phenomenon known as "waking".

Actually, this same part of the brain strongly influences the activity of the gamma-efferent fibers, as has been demonstrated by the researches of C. von Euler and Söderberg at our laboratories, from which it is clear that, when an animal is awakened, the gamma-efferent fibers come into play automatically, thus touching off postural tonus, whereas when the animal falls asleep, the gamma-efferent fibers cease to discharge impulses.

Another assumption underlying Rossi's hypothesis is that the postural reflexes should be absent when the ring passing through the muscle spindles is interrupted, that is, if it is true that these reflexes depend on the control exerted by the gamma-efferent fibers.

In 1953 Eldred, Merton and myself were able to establish that the assumption is founded in the case of postural reflexes produced by head movements.

In order to check one particular aspect of our conclusions and one deriving from Rossi's hypotheses, that is, that a major factor in the genesis of rigidity from decerebration is the exaltation of the control exercised by the gamma-efferent fibers with consequent hyperactivity of the muscle spindles, Peter Matthews, in conjunction with Rushworth, in 1958 selectively treated the gamma-efferent fibers of the soleus muscle in the decerebrate animal, thereby causing disappearance of the hyperactivity in the reflex of the same muscle due to stretching. Many years earlier Sherrington had demonstrated that the rigidity of the decerebrate animal disappears with deafferentation. Theories of the central origin of rigidity from decerebration were unable to account for this fact, whereas today we know that the disappearance of rigidity is a direct consequence of the severing of the gamma loop. In fact, we found that an important element in decerebration is cramp of the spindles induced by overactivity of the gamma-efferent fibers.

Used as we are to thinking of muscle contractions only as direct effects of pyramidal or extrapyramidal paths on the motoneurons or on their premotor cells, the view that centrally caused muscle contraction depends upon a length-detector arrangement, such as the muscle spindle, lying within the muscle itself may seem to constitute a breakaway from classical concepts. But this mechanism is certainly not only a highly sensitive means of control over postural tonus but also of making a muscle capable of adapting itself to a wide range of tasks, from weightlifting to piano playing.

For every task there must be an optimal spindle-length, which must be adjustable, otherwise this organ could have been independent and arranged parallel to the other muscle fibers.

For obvious reasons we cannot go further into this problem, but there is no doubt that the muscle spindle may be important in many other connections as yet unknown.

I think that these results and ideas are of some interest for analysis of studies on locomotion as, for instance, in various forms of spasticity and rigidity, and a great deal of clinical work has since been done along these lines in several countries. There is no doubt that it will be very helpful to know that such disorders may involve two motor systems rather than one, that is, the ordinary motor fibers and the ring that is set up through the gamma-efferent fibers of the spindle.

With regard to our experimental animal, the decerebrate cat, we set ourselves the question of whether the motoneurons of the main muscle were all of the same type or whether perhaps those concerned with postural tone formed a special system. In this animal the second hypothesis proved to be the right one, for the tonic motoneurons have finer axons and a slower conduction rate and, further, they are very plentiful in red muscle, such as the soleus and the crural.

These motoneurons tend to discharge impulses tonically at low frequency, as Denny-Brown noted in Sherrington's laboratory in 1929.

From the facility with which impulses are discharged in the tonic motoneurons as a result of stretching, we deduced that they have dense connexions with the efferent fibers of the spindles, a fact confirmed by the demonstrations with Ecles and Lundberg intracellular recordings. These Authors have proved that the tonic motoneurons possess long-lasting posthumous positive potential, a property which presupposes a long-lasting depression of excitability. Ecles and Lundberg consider that the long-lasting posthumous potentials explain the low frequency of discharge of tonic motoneurons. This may be true, but we considered another possibility: studying Golgi's recurrent collaterals, which are a kind of negative "feed-back" with an effect on the efferent axons of the motoneurons, we found that recurrent inhibition was particularly marked on the motoneurons, a fact confirmed later by others, including the Canberra laboratory. Hence, we thought that this fact might account for the low frequency of discharge of these neurons.

The most likely interpretation seems to be that there is cooperation between recurrent inhibition and posthumous hyperpolarisation, with the result that the discharge declines in frequency. A third factor, which has come out of the researches of Frank and Fuortes as well of our own Institute, is that, in all probability, the tonic motoneurons require strong depolarisation to produce relatively small effects on the frequency of discharge.

All in all, it is interesting to see the great number of efferent and muscular physiological mechanisms that have been developed to integrate and adapt to one another in alternation for the performance of the tasks involved in postural control.

I have mentioned only some of them, but enough to show the creative value of the intellectual premises, and the whole thing seems to hang together very cogently.

For example, the presence of Golgi recurrent collaterals, if they could be found, in the gamma-efferents could be defined as a technical error, for these collaterals have to perform their action at high frequencies.

We studied this point with Pascoe in 1957, but we were never able to demonstrate recurrent inhibition for any of the gamma-efferent fibers.

Golgi's recurrent collaterals have been the subject of study for the past two years, but our experiments have been done on a strictly quantitative basis and so it is rather difficult, without the aid of slides and a blackboard, to explain the results.

Some of you may be familiar with the phenomenon of lateral inhibition in the eye of the Limulus crab, as elucidated by Artline and his co-workers at the Rockefeller Institute.

If an ommatidium is illuminated, it inhibits its neighbours by a process strictly proportional to the frequency of its impulses. We have found that exactly the same law applies to motoneurons under the effect of the recurrent inhibition which they themselves produce naturally when discharging. Just as happens with the Limulus, in which it can be demonstrated that inhibition is a means of producing a contrast mechanism, so with the motoneurons recurrent inhibition ensures a type of motor contrast as it suppresses the frequency of discharge around an active zone.

And at this point, Mr. Chairman, I think I had better close, otherwise I shall strain the patience of this august gathering.

It is difficult to deal fully with a subject when the results are so specific, and if I were to expound the whole fascinating problem of Golgi recurrent collaterals I should need to go into the greatest detail. These collaterals have come to be recognised as important formations since Ramon y Cajal proved their presence in a number of nerve centers. The tonic motoneurons appear to us to be in a steady state of reflex discharge necessary for a quantitative study of recurrent inhibition.

We have now reached the point when circuits of the type to which I have alluded can be studied quantitatively.