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Self-Activation of Muscle Spindles in the Precollicular Cat*

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IT is generally, and also correctly, assumed today that the spindle afferents themselves do not exert a definitely measurable influence on the gamma outflow to their own muscles—in other words, that there is no wholly convincing demonstration of autogenetic gamma reflexes. This is based on work in many laboratories with decerebrated, anesthetized, and spinal animals. With isotonic recording in the precollicular decerebrate cat apparent exceptions from this rule occur which deserve to be briefly reported. As will be shown in the Discussion, they have a direct bearing upon Denny-Brown's [1] early work on clonus.

Methods

Cats were decerebrated in the usual manner, but by a precollicular instead of an intercollicular section. Laminectomy was performed to lay bare the lumbosacral region of the spinal cord, and a large spindle afferent was functionally isolated in a thin root filament containing gastrocnemius-soleus fibers. Otherwise the dorsal and ventral roots were left undisturbed. The limb was denervated with the exception of the gastrocnemius-soleus muscles which were to be used in the experiment. These were freed and separated.

The animal and its limbs were rigidly fixed in the usual way and a steel hook pushed through the chip of bone of the tendon of the muscle to be stretched. The latter was joined directly, or by a spring of known stiffness, to a strain gauge placed in a myograph on a sliding stand. Zero length of the muscle was taken to be the length at which it resisted further elongation as read off within an excursion of the myograph corresponding to maximally 20 gm. As all readings refer to static conditions, it was possible to adjust extension by shifting the stand and

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waiting for equilibrium. A sliding pointer provided with a scale was set to correspond to a mark on the chip of bone in such a manner that it was possible to compare isotonic and isometric muscle lengths.

Results

If in this simple arrangement one produces a static stretch reflex by shifting the myograph stand, tension values should be the same in the isotonic and isometric arrangements, provided that zero setting and length measurements are correct. To put it simply, muscle is machinery for translating length into tension along a curve that is determined by the motor alpha output applied. If under the circumstances a systematic difference is obtained between isometric and isotonic reflexes to stretch, then some change of output must be responsible for it.

In the intercollicular preparation with its good stretch reflex it is generally possible to verify these postulates, subject only to the variability one expects with the decerebrate preparation. More often than not, the precollicular preparation behaves in a different manner. Its stretch reflex is normally weak, and the curves relating frequency of discharge of the indicator spindle to muscle extension are singularly flat; in fact they are often so flat that one must suspect some inhibitory influence at work on the gamma motoneurons. Nevertheless, beyond a certain extension self-activation very often takes place in the isotonic arrangement so that the stretch reflex improves, and with it the indicator spindle's firing rate.

In order to visualize all this in a single graph in both the precollicular and intercollicular state, the firing rate of the indicator spindle was plotted against tension in grams per millimeter, isometric extensions of 6, 8, 10, and 12 mm being used (Fig. 7-1). For the isotonic experiments with a weak spring the extensions were read off by means of the pointer. The curve shown in Figure 7-1 begins on the left with the four isometric readings at the four extensions (open circles) in the precollicular state; very little tension in gm per millimeters was present at the four lengths, and all of it was passive tension. The open triangles demonstrate that under isotonic conditions there was active tension and also higher spindle-firing frequencies; thus self-activation occurred. In spite of not extending the muscle isotonically more than about 8 mm when the stand was shifted 12 mm, there is more tension per millimeter. The next step was to suck away the superior colliculi. The broken line merely serves to indicate that it is the same experiment which continues. The four isometric readings, when now repeated (solid circles), show the considerably increased stretch reflex in gram per millimeter as well as the similarly increased impulse ac-

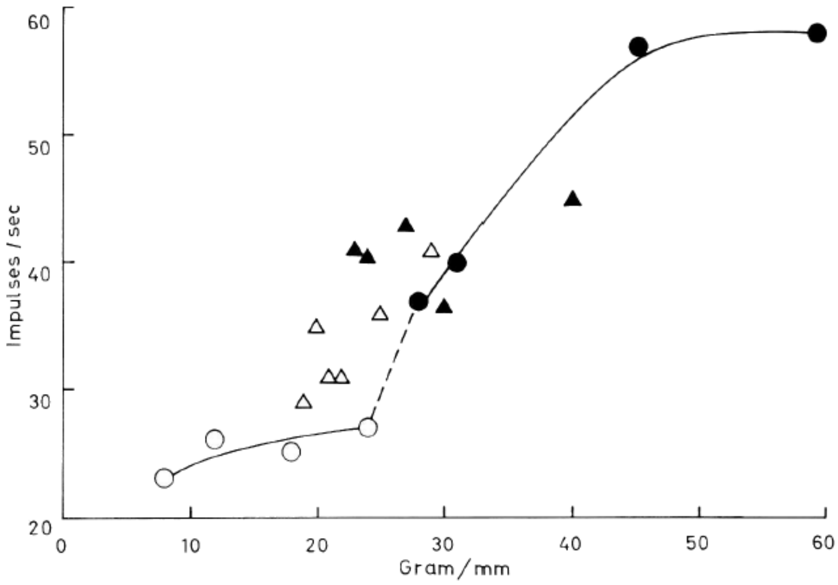

Fig. 7-1

Impulse frequency of a soleus spindle plotted against gram tension per millimeter in an experiment on stretch of the isolated soleus muscle in the precollicular (open circles and triangles) and intercollicular (solid circles and triangles) states. The experiment consisted in stretching the muscle 6, 8, 10, and 12 mm. In the isotonic state, with spring with a stiffness of 10 gm per millimeter inserted, this implied much less extension depending upon reflex contribution. Averages of two or three repetitions. Abscissa obtained by dividing total tension by length at that tension. Having obtained the isometric and isotonic values in the precollicular state, the superior colliculi were sucked away and the experiment repeated (see text).

tivity of the spindle, both being effects to be expected from the well-known gamma release in the intercollicular decerebrate preparation (as described elsewhere [2]). When at 12 mm extension the isometric reflex produces a total tension of 60 gm per millimeter, the firing rate of the spindle has flattened out. Why this occurs remains a matter of conjecture. A real inhibition of the gamma motoneurons from tendon organs is possible. The solid triangles are readings from the corresponding isotonic experiment. The shortening of the muscle makes the spindle frequencies stay practically constant. In such cases it is often seen that a good stretch reflex contracts the muscle to lengths below the set zero; how much depends on the stiffness of the spring or the weight used, in cases when the spring is replaced by a weight or a weight is added to pull on the spring.

At a certain extension the self-activation mostly occurs spontaneously, but in some precollicular cats it was necessary to start this process by some taps on the tendon of the synergistic muscle which was stretched out and fixed to a second stand well secured to the

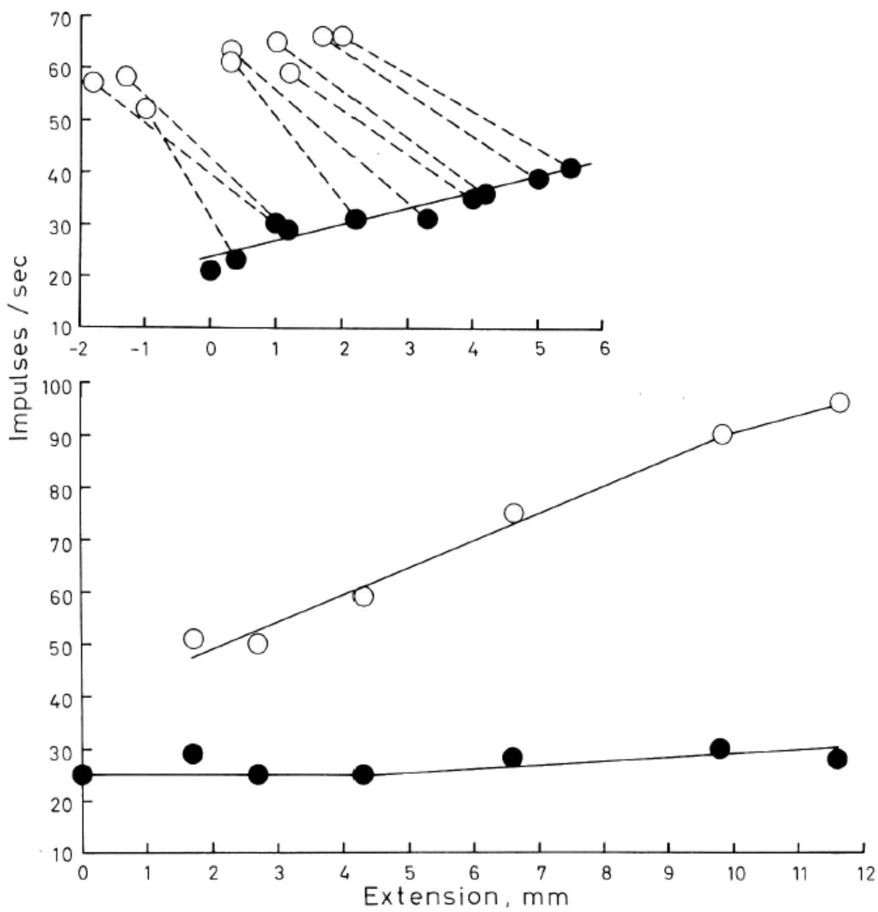

Fig. 7-2

Soleus muscle and soleus spindle of precollicular cat, with firing rate of the spindle plotted against extension (length) of muscle. Lower graph: Isometric recording *before* (solid circles) and *after* (open circles) having given ten taps to the tendon of the synergist gastrocnemius muscle fixed to a separate stand. Upper graph: Same experiment repeated in isotonic recording after insertion of spring with a stiffness of 9 gm per millimeter between tendon and myograph. The broken lines joining measurements before activation with those obtained afterward show the amount of shortening that the activated reflex engendered.

experimental table. This procedure was used in the experiment shown in Figure 7-2, the soleus muscle of a precollicular cat being tested with the synergistic gastrocnemius fixed to a separate stand. In the isometric experiment (lower graph), the lower curve (solid circles) illustrates an extreme case of slackness in the spindle taken from the soleus of the precollicular preparation. Its rate of discharge hardly changed at all between zero and 12 mm of extension, suggesting a tandem spindle. After activation by a series of tendon taps to the synergistic gastrocnemius, the soleus spindle became responsive (open circles). At zero length it then fired at a rate of approximately 40 impulses per second; the slope of the curve is of the order of 5 impulses per millimeter. There was now a stretch reflex, as can be seen from the upper graph in which the same experiment was repeated isotonically after insertion of a spring (stiffness, 9 gm per millimeter). Again the solid circles represent the inactivated isotonic state. A little self-activation may have been present because in this state there is a rise in the curves as compared with its isometric counterpart. A stiffness of 9 gm per millimeter means a weak spring, and so 6 mm is the limit of extension of the muscle. After activation (open circles), it is doubtful whether there is much of a change in the firing rates of the spindle beyond the basic increase caused by the after-effect of the tendon taps on the gastrocnemius. The reason for the small effect of extension on the spindle is likely to be unloading because the muscle has contracted reflexively in compensation. The readings now obtained for spindle firing have been joined by broken lines to their counterparts before activation. On an average the reflex contraction shortened the muscle by 2 mm, but the actual effect varies with the extension imposed. The points near the set zero embodying small extensions have now become negative.

In many cases, sometimes *with,* at times *without,* activation, the process that has been described ended in a long-lasting clonus, provided that isotonic recording was used [1]. The series elasticity of the isometric muscle was never large enough to support the clonic response which could so easily be produced by inserting weights or springs of various stiffness. A certain amount of stretch was needed to start the clonus, but once it was well under way the muscle could be cautiously brought back to zero tension without disturbing it, even though the rhythm then became a little slower. The observations on clonus have been published elsewhere [3]; they essentially confirm Denny-Brown's [1] findings. The most important new observation came from simultaneous spindle records which showed that in clonus the spindles reached very high firing rates—of the order of 400 per second—in the bursts they delivered in the extension phase. Denny-Brown, at the time, thought of the tendon organs and in terms of tension. Since it is the spindles that get active, it is a matter of length (extension).

Discussion

The self-activation in the stretched extensor muscles of the precollicular preparation is of a reflex character and involves the gamma-spindle loop. I consider it as a forerunner to a fully developed clonus. In the muscles the Horsley-Schäfer rhythm of 9 to 10 per second [5] is always present. This is identical with the rhythm of clonus, and the natural firing rates of the soleus alpha motoneurons are not very far from it either; 5 to 15 per second in stretch according to Denny-Brown [1]. Some stretch and a chance for the muscle to shorten is all that seems to be required for the Horsley-Schäfer rhythm to synchronize a smaller or greater number of neurons into a hardly noticeable or fully developed clonic response. Self-activation may be no more than the intermediate stage. It requires a certain basic rate of spindle firing. If it is too high there is not much of a chance for the synchronizing process because a durable stretch reflex takes over; if too low, there is not enough depolarization of motoneurons.

Apparently the precollicular preparation is in a suitable labile state, and the spindles behave as if there was very little static but some dynamic gamma activity in the sense of Matthews [7] and Jansen and Matthews [6]. Judging by the high spindle rates in full clonus, mentioned above, the dynamic gamma component seems to be the one involved in self-activation, if this process is regarded as a step on the way toward a clonic response. By tendon taps it is possible to activate for a while even a deefferented muscle spindle [4], but for the long-lasting events described above this serves merely as a starting device.

References

1. Denny-Brown, D. On the nature of postural reflexes. *Proc. Roy. Soc.* [Biol.] 104:252, 1929.
2. Granit, R. *Receptors and Sensory Perception.* New Haven: Yale University Press, 1955.
3. Granit, R. Observations on clonus in the cat's soleus muscle. *An. Fac. Med. Montev.* 44:305, 1959.
4. Granit, R., Homma, S., and Matthews, P. B. C. Prolonged changes in the discharge of mammalian muscle spindles following tendon taps or muscle twitches. *Acta Physiol. Scand.* 46:185, 1959.
5. Hammond, P. H., Merton, P. A., and Sutton, G. G. Nervous gradation of muscular contraction. *Brit. Med. Bull.* 12:214, 1956.
6. Jansen, J. K. S., and Matthews, P. B. C. The effects of fusimotor activity on the static responsiveness of primary and secondary endings of muscle spindles in the decerebrate cat. *Acta Physiol. Scand.* 55:376, 1962.
7. Matthews, P. B. C. The differentiation of two types of fusimotor fibre by their effects on the dynamic response of muscle spindle primary endings. *Quart. J. Exp. Physiol.* 47:324, 1962.