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Prolonged Changes in the Discharge of Mammalian Muscle Spindles Following Tendon Taps or Muscle Twitches.

By

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Abstract.

GRANIT, R., S. HOMMA and P. B. C. MATTHEWS. Prolonged changes in the discharge of mammalian muscle spindles following tendon taps or muscle twitches. *Acta physiol. scand.* 1959. *46*. 185—193. — The muscle spindle is a very sensitive recording instrument and is here found to change its level of excitability, despite de-efferentation, after tendon taps or submaximal contraction, as shown by prolonged changes in its frequency of discharge. It is suggested that this effect often is due to mechanical displacement, but since it is influenced by injection of Flaxedil, the intrafusal end plates may well be spontaneously active in the normal state. Flaxedil causes full paralysis of extrafusal motor end plates at a time when intrafusal gamma end plates are far less influenced.

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It is well known that the release of a stretched muscle is often followed by a period of silence in the discharge of its muscle spindles (MATTHEWS 1933). We were therefore surprised when, in the course of other work, we found that a brief tap to the tendon of a muscle might sometimes initiate a prolonged increase in the discharge of the muscle spindles from it. This paper describes investigations into the phenomenon, unfortunately without coming to any definite decision as to its origin. A major difficulty has been that the effect has sometimes been more easily elicitable with tendon taps, sometimes with twitches below the strength necessary for stimulating gamma motoneurones. However, some factors have been experimentally excluded.

Methods.

The results to be described have been obtained from muscle spindles lying in the ankle extensor muscles of both cats and rabbits. The cats were anaesthetized with ether and decerebrated by suction, usually just in front of the anterior colliculi. In some cases they were then made spinal by cutting the spinal cord at the level of Th12. The experiments were performed when the effect of the ether had worn off. Some rabbits were similarly decerebrated and made spinal under ether anaesthesia. Other rabbits were anaesthetized by the intravenous injection of a mixture of 1 % chloralose and 10 % urethane (5—6 ml/kg), and not decerebrated. A little ether was also usually given during the operation but not during the experiment. The anaesthetized rabbits had little if any tonic gamma activity but gamma reflexes to pinna manipulation and to painful stimuli could be elicited.

Single muscle spindle afferents were isolated by splitting dorsal rootlets into fine filaments and recording from their peripheral ends. Fuller details have been given in many preceding publications from this laboratory (*cf.* GRANIT and KAADA 1952, ELDRED, GRANIT and MERTON 1953, GRANIT 1958). The leg studied was firmly fixed, and the nerves other than those to the extensor muscles were cut. Sometimes the whole triceps surae was used, but mostly the gastrocnemius and soleus muscles were separated. In the rabbit the gastrocnemius is firmly attached to a portion of the soleus in the lower half of it. Separation therefore entails some mutilation of either muscle. The experiments were usually performed under both isometric and isotonic conditions for recording the response of the muscle. For isometric recording the muscle was connected by metal links to a strain gauge myograph on a movable stand. For 'isotonic' recording one of these metal links was replaced by a light spring (stiffness either 40 g/mm or 9 g/mm), thus allowing the responses of the muscle-spindle to be followed after the muscle had shortened.

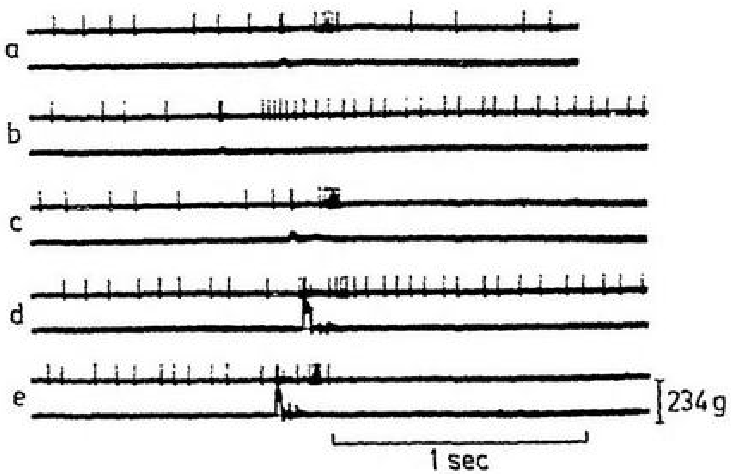

Fig. 1. The effect of tendon taps on the discharge of a muscle spindle in the soleus muscle of a decerebrate cat (pre-collicular). For each pair of records: above, the discharge of the muscle spindle recorded from a small filament of dorsal root; below, myograph record obtained from an isometric myograph connected to the soleus muscle by a weak spring (stiffness 9 g/mm). The records are arranged in order of increasing size of tap. Note that the discharge after the tap is in some cases above the resting level, and in some cases below.

Spindle afferents were identified as such by the pause in their discharge during the contraction of the muscle produced by stimulating the muscle nerve electrically. In rabbits the conduction velocity of the afferent fibre studied was always roughly estimated by determining the time interval between a shock to the muscle nerve and the arrival of the action potential of the single afferent in the dorsal rootlet. The conduction distance was about 15 cm and the conduction times ranged from 1.2 to 3 msec, giving conduction velocities ranging from 125 to 50 m/sec. Some of the slower afferents presumably originated in the myotube endings, but in our tests there have been no obvious differences between the behaviour of the larger and the smaller spindle afferents, and both appeared to be influenced by the gamma motoneurones (*cf.* Hunt 1954). In cats previous experience has shown that the technique of root splitting almost always isolates fibres of high conduction velocity, and we have only occasionally measured it in the present experiments.

Results.

1. *General description.* The prolonged effect which a tendon tap may have on the discharge of a muscle spindle is shown in Fig. 1. The spindle lay in the soleus muscle of a decerebrate cat,

and, except for the removal of a small filament of dorsal root from which the spindle afferent was isolated, the innervation of soleus was intact. Soleus was connected to an isometric myograph through a light spring (stiffness 9 g/mm) making the recording approximately isotonic. A series of taps were then delivered to the hook connecting the spring to soleus and the records of Fig. 1 obtained (for each pair of records the spindle discharge is above and the myograph tension below). In every case there is an initial rapid discharge from the spindle at the same time as the initial mechanical deflection produced by the tap. This is followed by a silent period in the spindle discharge, presumably while soleus contracted in the tendon jerk reflex — though because of the isotonic conditions there is very little increase in tension. The silent period is terminated by another rapid discharge. These are classical findings; what is perhaps surprising is the variation in the discharge of the spindle later in the records, where sometimes the frequency of discharge is above the initial level and sometimes below. There appeared to be no correlation with the strength of the tendon tap, and the records are arranged in order of increasing strength of tap as judged by the mechanical record (the taps were delivered by hand). In this particular experiment the excitatory effect was no longer found when the spring was removed and the soleus connected to the myograph isometrically instead of isotonically; instead the spindle discharge was uninfluenced by the tap. In other experiments the increase in discharge has been found under isometric conditions and this is shown in Fig. 2 a. Here, after two tendon taps, the discharge has increased, above the initial level. In general, however, the prolonged increase in discharge has been more easily obtained under isotonic recording conditions. With isometric registration demonstration of the effect often required careful adjustment of muscle length. It was seen at one length (tension) but not at another. Some stretch was necessary. The effect has been found with afferents conducting at 50—70 m/sec, presumably coming from the myotube endings, as well as with larger afferents from the nuclear bag endings.

A prolonged decrease in the discharge has been particularly marked when the previous discharge rate has been high, especially if it has been raised either by stimulating the muscle nerve at about the strength required to excite the gamma fibres, or if the gamma motoneurones have been excited by a pinna reflex or by

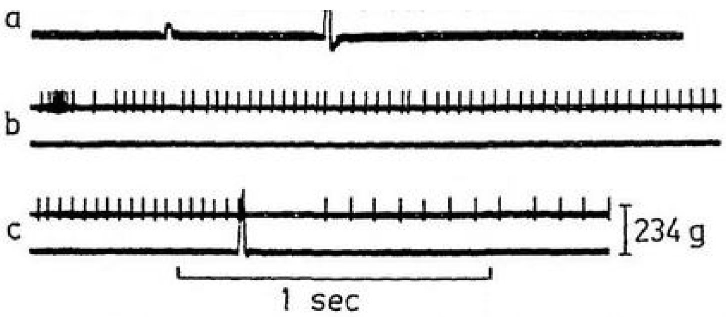

Fig. 2. The effect of tendon taps on the discharge of a muscle spindle in the triceps surae of an anaesthetized rabbit. For each pair of records: above, the discharge of the muscle spindle; below, the tension in the muscle recorded directly with an isometric myograph.

In *a*: the second of two tendon taps increases the discharge.
In *b*: the brain stem was stimulated electrically thereby increasing the frequency of discharge of the spindle.
In *c*: a further tendon tap now reduces the discharge to its original level (spikes retouched).

stimulating in the mid brain. This last effect is illustrated in Fig. 2 b where the effect of mid brain stimulation is shown and in Fig. 2 c where is shown the effect of a subsequently applied tendon tap. This may be compared with Fig. 2 a where is shown the previously excitatory effect of a tendon tap.

In all these cases the stimulus to the muscle spindle system is complex. Initially the tap stretches the muscle, but the ensuing reflex contraction, when present, shortens it again. (With 'isotonic' recording the muscle may shorten to below its initial length, when it will be re-extended by the spring as it relaxes.) In either isometric or isotonic recording the muscle, and its included muscle spindles, will then return gradually to their previous length (this may involve internal redistribution of displacement). Possibly the final level of muscle spindle discharge will depend upon whether the muscle reaches its initial length again by being pulled out, or by shortening. A further complicating factor in the interpretation of the records is that in the intact animal the gamma motoneurones might be affected reflexly either by the initial stretch of the muscle or by its subsequent contraction. However, we shall proceed to demonstrate (section 3) that all the essential features of the prolonged discharge are seen in animals devoid of all reflexes.

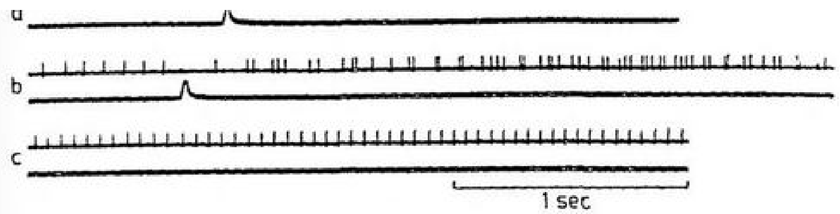

Fig. 3. The effect of weak stimuli to the muscle nerve on the discharge of a muscle spindle in the soleus muscle of an anaesthetized rabbit. For each pair of records: above, the discharge of the spindle; below, the tension in the soleus recorded isometrically.

In *a*: the third shock started the spindle discharging;
in *b*: is shown the ninth shock;
in *c*: is the steady discharge built up after many seconds stimulation (spikes retouched).

2. *Contraction.* The effect of the contraction was investigated by stimulating the nerve to the muscle electrically with weak shocks, submaximal for the contraction of the muscle and therefore considered to be below threshold for the gamma fibres and probably also of the smaller afferent fibres. The shock could also sometimes be set so as to be below the threshold of the spindle afferent studied, but presumably some other spindle afferents or Golgi tendon organ afferents were excited as well as some of the motor fibres. Such an experiment is shown in Fig. 3 taken under isometric conditions. The spindle was initially silent, after the third shock it began to discharge (shown in *a*), the sixth shock is shown in *b*, and in *c* is shown the semistationary discharge established after several seconds of stimulation. Often only one shock was needed but otherwise these were fairly typical results and at that stage suggested that the prolonged excitatory effect of the tendon tap may be partly dependent upon the muscle contraction rather than directly on the initial tap. As some afferent fibres were also excited electrically it is possible that this (reflexly) was the cause of the alteration in spindle discharge. This possibility was next tested by de-efferentation.

3. *De-efferentation.* The effect of a reflex through the gamma motoneurones was initially investigated by giving Flaxedil intravenously in order to paralyse neuromuscular transmission and produce a reversible de-efferentation. In general the prolonged excitatory effects were less marked after this though they could still occur. However by this method it proved impossible to

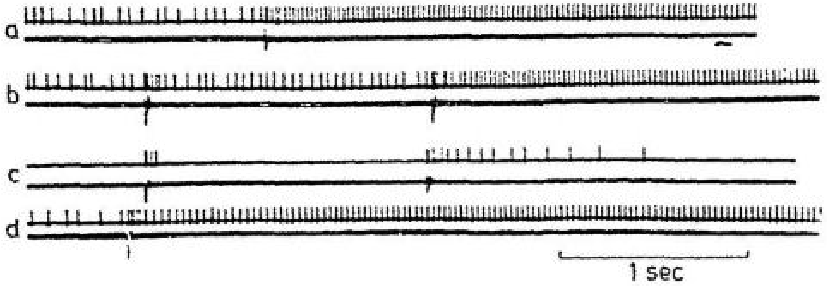

Fig. 4. The effect of tendon taps on the discharge of a de-efferented muscle spindle in the gastrocnemius muscle of a decerebrate cat. For each pair of records: above, the spindle discharge; below, myograph record from isometric myograph connected to the gastrocnemius via a spring of stiffness of 40 g/mm.

a, *b*: show the increase in discharge produced by tendon taps;
c: is after an intravenous injection of Flaxedil (6 mg), discharge decreased;
d: after extending gastrocnemius by 2 mm when the effect of tendon tap was restored (spikes retouched).

produce a complete gamma block at the time of complete alpha block. Interestingly the gamma end plates were far more resistant to this blocking agent than the alpha end plates on extrafusal muscle, as has also independently been found by HENATSCH and SCHULTE (1958) in the frog. Complete de-efferentation was next employed. In some cases after this the excitatory effect could no longer be obtained, yet in most cases it was still strongly present provided that the length of the muscle was correctly set. An example is shown in Fig. 4, where the recording is again under isotonic conditions. Here *a* and *b* show the effect of three tendon taps and again illustrate the variability of the reactions (note, however, that tendon taps were delivered manually). It seemed of interest to try blocking the end plates in this case also, so Flaxedil was then given, with the result that the resting discharge and the response to tendon tap decreased — Fig. 4 c. Stretching soleus by 2 mm restored both to near their previous level — Fig. 4 d. Further injections of Flaxedil produced the same effect at the increased length, and again the discharge could be restored by stretching. This effect of Flaxedil was regularly found in the completely de-efferented preparation and so cannot be ascribed to the progressive deterioration of the preparation. Also it was seen half an hour after de-efferentation when it seems unlikely that any injury discharges would be persisting. Thus partial paralysis of the end plates in the completely denervated prepara-

tion can alter the behaviour of the muscle spindle, and the end plates therefore appear to be in some way spontaneously active.

Thus though the prolonged excitation may apparently be produced by muscle contraction, it is not essentially dependent upon reflex contraction as it is still found following a tendon tap in the de-efferented preparation. Similarly a brief twitch, as in Fig. 3, may elicit prolonged excitation after de-efferentation, provided that proper attention had been given to the adjustment of muscle length.

Discussion.

In pursuing these experiments it had been hoped to uncover a proprioceptive reflex from contracting muscle to its gamma motoneurones. Though this may occur the present experiments provide little evidence for it, but they do serve to emphasize the lability of muscle spindles after mechanical disturbance. A possible explanation for these results is that after a mechanical displacement the part of the muscle spindle lying beneath the sensory ending does not return to precisely the same length as before. This would make our effect analogous to the prolonged increase in discharge sometimes found by KUFFLER, HUNT and QUILLIAM (1951) after stimulation of the gamma motor fibres. However, it is not quite clear on this view why more basic stretch is required after Flaxedil to elicit the same phenomenon and why it had a lower threshold before the intrafusal end plates were partially paralyzed. The essential effect may therefore be a variation in the spontaneous rate of discharge of gamma motor end plates. The alpha motor end plates have been found to discharge miniature potentials at a faster rate when stretched (FATT and KATZ 1952, HUTTER and TRAUTWEIN 1956). The sensory portion of the muscle spindle may well be a sensitive detector of such spontaneous variations in its motor end plates, some of which, besides, on anatomical evidence (see *e. g.* BARKER 1948) belong to fibres of the alpha group.

Summary.

1. When a tap is given to the tendon of a leg extensor muscle it may be followed by a prolonged (many seconds) increase or

decrease in the discharge in a single afferent coming from a muscle spindle in the muscle.

2. Similarly after one or several brief twitches from a shock to the large muscle efferents a prolonged increase of the discharge of an isolated spindle afferent may ensue.

3. In both cases this increase in discharge may still be found after cutting the ventral roots. This effect is not therefore necessarily dependent upon reflex activation of the gamma motoneurones, but its cause has not been discovered.

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