

## Stretch Reflexes Before and after De-Efferentation.

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In the Proceedings of the Scand. Physiol. Soc. (GRANIT and STRÖM 1951) we reported some results of work on decerebrate cats in which, by monosynaptic testing, stretch reflexes of the gastroc. muscle were studied before and after de-efferentation of the appropriate ventral roots. It was found that the early phase of facilitation during stretch was diminished by section of the ventral roots provided that the muscle had been under light initial tension. Since the effects referred to were encountered within the first 5 msec. of stretch, it was clear that a tonic influence on the muscle spindles had been removed by de-efferentation. This was ascribed to the small gamma efferents of LEKSELL (1945). Both HUNT (1951) and GRANIT and KAADA (1952) have since, by more direct methods, proved that the gamma fibres, indeed, are tonically active.

Our results, though presented in full at a meeting of the Physiol. Soc. of Stockholm in April 1951, remained unpublished because GRANIT and JOB (1952) found that monosynaptic testing and electromyography do not always agree in defining reflex excitability. It is clear now that their criticism of the monosynaptic method would only apply to later phases of stretch. Therefore the emphasis will be laid on the early phase which also is the one of greater interest. This is so because in the first 5 msec. of stretch there has not yet been re-excitation of the muscle by its

own (autogenetic) stretch reflexes. Consequently, conditions before and after de-efferentation refer to the study of tonic excitation prevailing in the centres as well as in the muscle spindles (HUNT and KUFFLER 1951 a, b, HUNT 1951, GRANIT and KAADA 1952) at the time of onset of stretch.

To know, as we do now, on the evidence mentioned, that the gamma fibres controlling the muscle spindles are tonically excited, does not yet mean that we know whether or not their tonic discharge, even when it discharges the afferents of muscle spindles, necessarily succeeds in elevating or depressing reflex excitability. The work by both HUNT (1951) and GRANIT and KAADA (1952) was carried out in terms of single fibre responses. Our experiments, now to be reported in full, supplement them with a comparison of reflex excitability before and after de-efferentation. It will be shown that de-efferentation not always succeeds in altering the reflex excitability in spite of the fact that the external loop over the gamma fibres through the muscle spindles always has been removed by this operation.

### Methods.

Decerebrate cats were mostly used but also animals in light Dial anaesthesia (around 0.4 ml/kg) and spinal cats under Dial. Denervation of both limbs was carried out, leaving the limb to be used with its gastroc. nerves intact. On this side the ileopsoas muscle was cut. The gastroc.-soleus tendon was freed and connected to the stretching device (GRANIT 1950), the medial and lateral branches of the gastroc. nerve isolated and each provided with a pair of light shielded electrodes. These were for the supramaximal test shock. After laminectomy, threads were passed around the ventral roots which were to be severed in the second phase of the experiment. A filament of L<sub>1</sub>VR or S<sub>1</sub>VR was isolated and severed peripherally to serve for the recording of the monosynaptic test response (Fig. 1).

Monosynaptic controls and responses during stretch are found in Fig. 4, recorded on the upper beam of a double cathode ray oscillograph, the lower beam being used for timing (1,000 or 100 cy/s) or the recording of muscle stretch (GRANIT 1950). We hardly ever went beyond 3 mm of stretch and mostly used modest or light initial muscle tension. The test shock for the monosynaptic response was shifted temporally along the stretch period and each position tested five to ten times to give reliable mean values. Monosynaptic controls without stretch were repeated now and then to measure a slow change of control level, usually of small magnitude, but occurring in most preparations. The responses in a given position during stretch sometimes varied a great deal but there were also experiments in which both the mono-

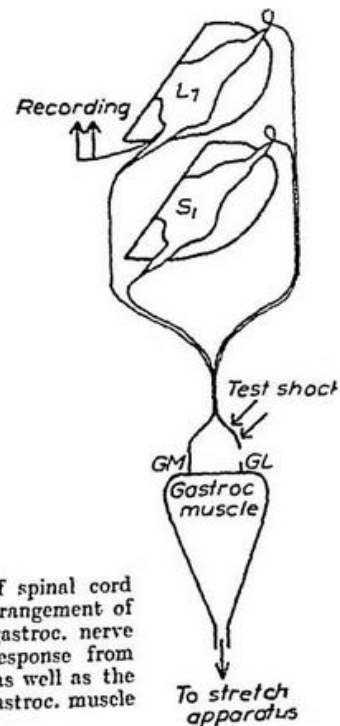


Fig. 1. Diagram illustrating semisections of spinal cord at the segmental levels of  $L_7$  and  $S_1$ , and arrangement of experiment. Test shock to severed lateral gastrocnem. nerve (GL), recording of monosynaptic reflex response from filament of ventral root  $L_7$ . The rest of  $L_7$ , as well as the whole of  $S_1$  ventral root connected with gastrocnem. muscle through medial gastrocnem. nerve (GM).

synaptic control and the effects of stretch upon it were very regular. The experiments selected for the illustrating figures were all highly satisfactory ones from this point of view. Some 100 msec. were necessary for completion of a 3 mm stretch in our apparatus. In each experiment the earlier phases of stretch were first studied with a fast sweep (covering 40 msec.). Then a slower sweep was used (covering 120 msec.) in order to repeat testing during earlier phases and to study later phases as well. In some experiments merely the slow sweep was used. Muscle stretch was applied every 5 sec. in a testing series.

The stretching device was connected to a Brown-Shuster myograph and provided with a microswitch which triggered the cathode ray a few msec. in advance of the beginning of pull on the myograph lever (see Fig. 4).

### Results.

*The external loop.* It will make interpretation easier to consider, at this stage, the time factors involved in the external loop: ventral horn cell — spindle — ventral horn cell (see Fig. 1). Afferent impulses initiated by muscle stretch may produce reflex contraction in the stretched muscle within 5 msec. This time

includes large afferents, one synaptic delay, large efferents and peripheral junctional delay. The time for a full turn may be considerably longer, however, if small afferents and polysynaptic transmission are important for facilitation during muscle stretch. Conduction in small efferents will increase the total circuit delay with 1.5 msec. or more (assuming the conduction rate of the fastest spindle efferents to be half of maximum conduction rate for muscle-fibre efferents) (LEKSELL 1945, KUFFLER et al. 1950). Reflex changes in spindle responsiveness will therefore not occur earlier than 6.5 msec. after the onset of stretch.

It is now possible to predict what would happen if, in this particular experiment, the muscle spindles acted 'in parallel', with the muscle fibres. If a muscle is stretched to a slight initial tension, sufficient to elicit a small static stretch reflex, the severance of its ventral roots should slacken the tension caused by reflex contraction and, if the isometric myograph lever is allowed to yield, the passive pull on the spindles should increase. Hence, the influence of de-efferentation, if any, should be in the direction of giving a greater and earlier effect of stretch than before. Exactly the opposite result was obtained.

*Effect of de-efferentation.* Fig. 2 illustrates the typical effect of de-efferentation. In a decerebrate cat the motoneurone facilitation produced by stretch of the gastrocnemius muscle (medial gastroc.

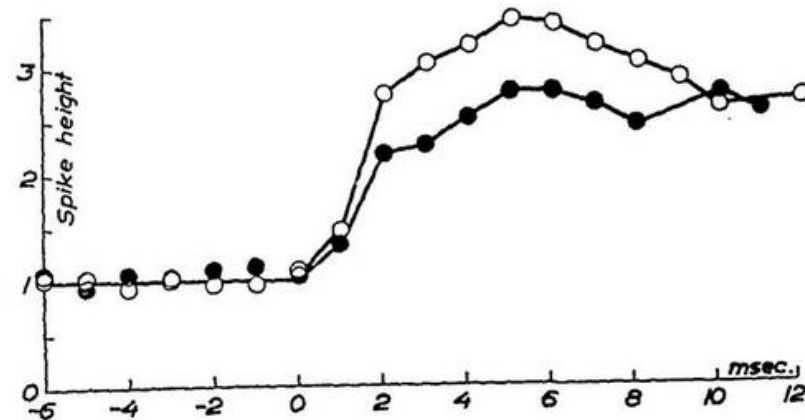


Fig. 2. Facilitation during stretch before (open circles) and after (filled circles) de-efferentation. Decerebrate cat. Test shock on severed lat. gastrocnem. nerve, recording of monosynaptic reflex response from filament of  $L_7$  ventral root. Light initial muscle tension, 2 mm stretch. Abscissa: time in msec. after onset of muscle stretch. Ordinate: monosynaptic test reflex in units of control size.

nerve intact) was determined by monosynaptic testing ('heterosynaptic' test, electrodes on severed lateral gastroc. nerve- see Fig. 1. cf. BROCK, ECCLES and RALL 1951 and GRANIT and JOB 1952). After de-efferentation the early facilitation during stretch is less than before, and, not until 10 msec. after the onset of stretch, do the two curves coincide. In this experiment the myograph lever was not allowed to yield, and the control size of the monosynaptic test reflex (without muscle stretch) remained approximately unchanged during the whole experiment. The facilitation curves in Fig. 2 represent the mean values of a large number of single values (160 before, 177 after de-efferentation) and therefore possess considerable fidelity.

In different experiments in most of which no steps were taken to prevent slight yielding of the myograph the influence of de-efferentation showed some variations: sometimes the early facilitation was delayed and decreased, sometimes no change was apparent, but on no occasion was any increase observed. It soon became apparent that differences in initial muscle tension were responsible for the variation.

*Influence of initial muscle tension.* Fig. 3 illustrates the effect of de-efferentation in three decerebrate cats, with light (Fig. 3A), moderate (Fig. 3B) and high (Fig. 3C) initial tension of the stretched gastrocnemius muscle. As to the early part of the facilitation curve, the effect of de-efferentation is obviously more pronounced at light than at high initial tensions, and this was a constant feature of our experiments.

As to the later part of the facilitation curve, it was often quickly curtailed in the intact animal, while in the de-efferented, it might continue at considerable amplitude throughout the stretch period. The effect of de-efferentation is more pronounced at high than at moderate initial tensions in the experiments of Fig. 3, but in this respect our results varied a great deal (cf. Fig. 4).

*Relation of reflex discharge to monosynaptic test response.* Fig. 4 shows the actual recordings of the experiment of Fig. 3B, photographed before (Fig. 4A) and after (Fig. 4B) de-efferentation. In the early part of the stretch period a group of reflexly evoked impulses can be seen, as recorded at low (A: 2) or high (A: 3) amplification. The destination of these impulses is assumed to be the stretched gastrocnemius muscle. After de-efferentation the early impulses are seen to have disappeared (B: 11, 12) to a large extent. On the other hand, there is an increased reflex discharge

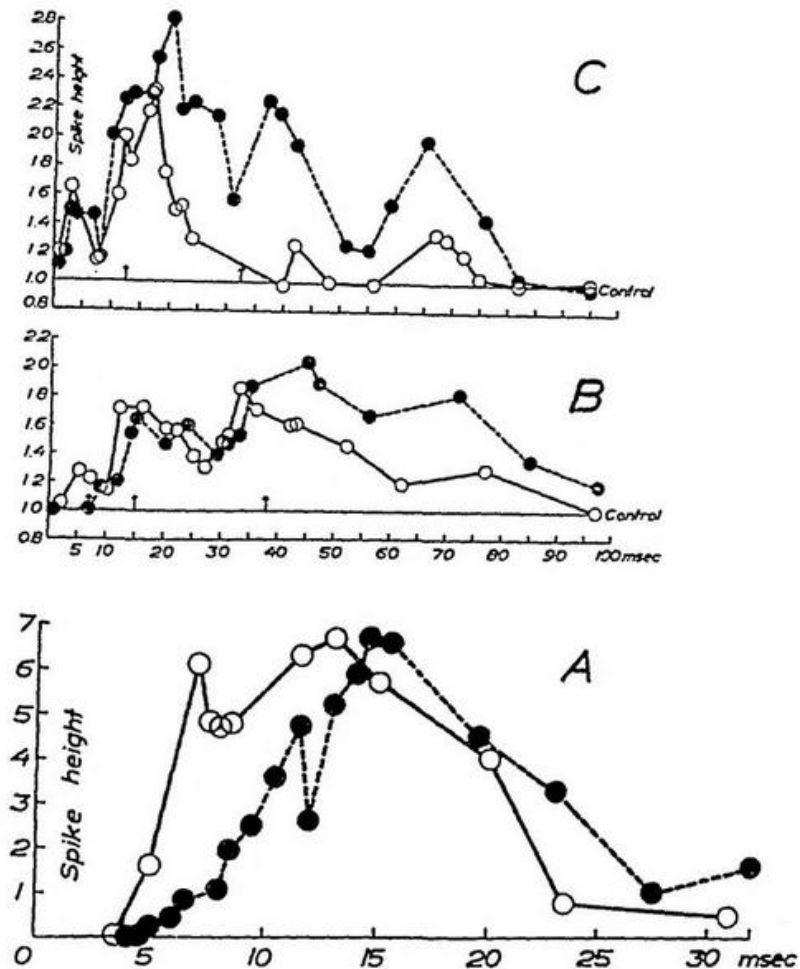


Fig. 3. Facilitation during stretch before (open circles) and after (filled circles) de-efferentation, with varying initial muscle tension (A: light, B: moderate, C: high). Three decerebrate cats. Test shock on severed medial gastroc. nerve, recording of monosynaptic reflex response from filament of L<sub>1</sub> ventral root. Abscissa: time in msec. after onset of muscle stretch. Ordinates: monosynaptic test reflex in units of control size (B and C), and in absolute units (A).

of impulses in the late part of the stretch period (cf. A: 8, 9 with B: 17, 18). The effect of de-efferentation on the reflex discharge of impulses is therefore closely similar to its effect on the facilitation curve as measured with the monosynaptic test method.

*Observations on Dial cats and spinal Dial cats.* The effect of de-efferentation, as described above for decerebrate animals, could also be observed in Dial cats. They often showed a large

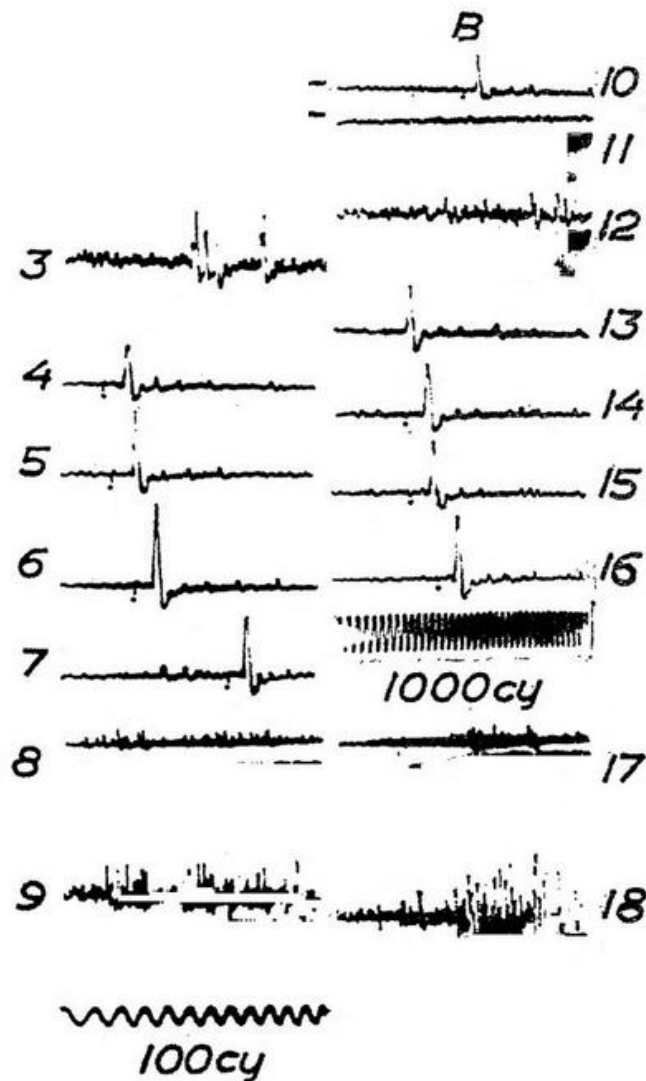


Fig. 4. Original records from experiment analyzed in Fig. 3 B. Series A before, series B after de-efferentation. 1 and 10, monosynaptic control; 2, 3, and 11, 12, stretch alone, the lower pair at 16 times higher amplification; 4—7 and 13—16, monosynaptic test in different phases of stretch. Comparable intervals have to be compared in A and B. 8—9 and 17—18, stretch alone as in upper pair of records, at two amplifications but with slower time base.

change in size of the control monosynaptic reflex after de-efferentation, a fact which tends to obscure the significance of the experimental result. Nevertheless, as stated, the effect was present.

In some experiments performed on spinal Dial cats, de-efferentation did not, however, produce any significant change of the facilitation curve during stretch (neither in the early nor the late parts of the stretch period).

#### Discussion.

It was pointed out by HUNT (1951) that the discharge of the gamma fibres had "approximately the same background activity in spinal and decerebrate cats". This suggests that the de-efferentation in both cases should 'desensitize' the muscle spindles in approximately the same manner, at least in light initial tension. In our experiments spinalization, in addition to initial muscle tension, proved to influence the amount of facilitation lost by de-efferentation.

Assuming the afferent mass discharge actually to have been the same in our decerebrate and spinal animals, despite the Dial anaesthesia in the latter case, the afferent stretch impulses might have struck a less facilitated centre in the spinal cats. On the other hand, GRANIT and KAADA (1952) found the spindle afferents more active in their decerebrate than in their Dial-chloralose cats. The difference may have been due to the anaesthesia or due to decerebration producing facilitation of gamma efferents. There was, however, considerable tonic gamma activity also in their Dial animals. Further experiments will be needed to explain the absence of our effect in the spinalized Dial animals.

The disappearance, at high initial muscle tension, of the difference in early facilitation before and after de-efferentation is probably accounted for by the assumption that the distended muscle spindle in the stretched muscle were ready to fire at the slightest provocation, as, indeed, seems to be true for the frog muscle spindle (KATZ 1950).

The later phases of the facilitation curve represent a very complex innervation pattern, which cannot be explained in detail on the present evidence alone. Reflex changes in spindle responsiveness (HUNT 1951) take part in it as well as the arrival in the spinal cord of impulses from all the autogenetic excitatory and inhibitory sources. In addition, the method of testing also has

the short-comings elucidated by GRANIT and JOB (1952). It would have been valuable to have been able to use electromyographic testing to supplement the monosynaptic approach. This was now precluded by the necessity for de-efferentation. On the other hand, the reflex discharge in ventral roots was sampled in all our experiments. This indicates (Fig. 3A, B and C and Fig. 4) that the monosynaptic facilitation curve actually reflected the course of events in the ventral horn cells with some fidelity. The later phase was depressed before de-efferentation, therefore the total balance of a maintained external loop to the muscles would seem to have favoured autogenetic inhibition in the later phases of stretch. This is in agreement with HUNT's observation that stretch inhibits the gamma efferents (1951).

### Summary.

1. The excitability of motoneurons in Dial cats, spinal cats under Dial and decerebrate cats consequent up on stretch of the muscle which they innervate, has been measured by the method of monosynaptic testing.

2. In the decerebrate and Dial cats, the early facilitation to onset of stretch was greater before than after de-efferentation. This effect could not be demonstrated in spinal cats under Dial. Since the effect took place before re-excitation of the reflex centre by the stretch reflex could have had time to develop, it was explained by tonic innervation of the muscle spindles on the part of the gamma efferents of LEKSELL. The effect disappeared at high initial tension of the muscle.

### Acknowledgment.

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