

EFFECTS OF STRETCH ON DYNAMIC FUSIMOTOR AFTER-EFFECTS IN CAT MUSCLE SPINDLES

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(Received 7 August 1984)

SUMMARY

1. Conditioning stimulation of dynamic fusimotor axons leaves persistent after-effects which increase the responses of primary endings to test dynamic stimuli. Such after-effects are abolished by muscle stretch.

2. Destruction of these after-effects depends on the following. (a) Amplitude of stretch: with symmetrical triangular stretches of moderate velocity, an extension of soleus by 4–5 mm totally abolishes the after-effects. Lesser stretches cause a graded reduction. (b) Velocity of relaxation: for a given amplitude of stretch there is greater destruction of after-effects when it is followed by a slow rate of relaxation than after rapid relaxation. (c) After-effects tested late in ramp stretch are more resistant to destruction by stretch than those increasing test dynamic responses early in ramp stretch.

3. Stretch itself produces after-effects which enhance test responses to dynamic but not to static fusimotor stimulation. Interactions between conditioning dynamic stimulation and stretch suggest that both these effects occur in the same intrafusal elements, the bag₁ fibres.

INTRODUCTION

In mammalian muscle spindles, prior stimulation of either static or dynamic fusimotor axons leaves an after-effect which produces an increase in the modulation of discharge frequency of a primary ending by small amplitude sinusoidal stretch superimposed on a slow ramp stretch (Baumann, Emonet-Dénand & Hulliger, 1983*a*). Such after-effects are abolished by a large stretch of the muscle. As shown in the preceding paper (Emonet-Dénand, Hunt & Laporte, 1985), the after-effect of dynamic fusimotor stimulation enhances the response of primary endings to test stimulation of dynamic axons during slow ramp stretch. This effect, reflecting residual changes in the bag₁ fibre, is also destroyed by a large muscle stretch.

In the present study we have examined the factors which determine the abolition of after-effects by stretch. It will be shown that the persistence of after-effects depends

not only on the amplitude of stretch but also on the speed of subsequent relaxation. Further, the extent of destruction of after-effects by a given stretch appears greater when tested by dynamic fusimotor stimulation early in ramp stretch than later. Stretch itself can produce after-effects which also increase the responses of primary endings to test dynamic, but not static, fusimotor stimulation. This appears to result from activation of the bag₁ fibre by stretch.

Preliminary reports of a portion of this work have appeared (Emonet-Dénand & Hunt, 1984; Emonet-Dénand, Hunt & Laporte, 1983).

METHODS

The methods were the same as reported in the previous paper (Emonet-Dénand *et al.* 1985). The data were obtained from the same set of experiments on the soleus muscle of the anaesthetized cat.

RESULTS

The effects of stretch on the persistence of after-effects produced by dynamic fusimotor stimulation

The after-effects produced by stimulating static or dynamic fusimotor axons, with the muscle at short or intermediate resting length, are abolished by stretch of moderately large amplitude (Baumann *et al.* 1983*a, b*; see also preceding paper). In the present study, we have found that the persistence of dynamic fusimotor after-effects depends upon several factors, in addition to amplitude of stretch and initial length of the muscle, namely the speed of relaxation following the extension and the position of test dynamic stimulation during subsequent ramp stretch. Accordingly, there is no unique amplitude of stretch which causes destruction of dynamic after-effects. However, it is possible to give an idea of approximately how much stretch is required. With symmetrical triangular stretches of moderate velocity (around 5 mm/s) and the soleus muscle set initially at 6 mm less than maximal physiological length, it usually required a stretch of 4–5 mm to abolish completely the dynamic fusimotor after-effects (see Fig. 1 of preceding paper). These after-effects showed no reduction following similar stretches up to 1.5 or 2 mm in amplitude, but between amplitudes of 2 and 4 mm there was a graded reduction in the dynamic after-effect.

The amplitude of a symmetrical triangular stretch which will abolish the dynamic after-effect in soleus (4–5 mm) represents an increase of about 10% of the extrafusal muscle fibre length (Rack & Westbury, 1969). Furthermore, the reduction in after-effect is graded over a considerable range of stretch amplitude. Neither of these results would be expected if the after-effects were due to the persistence of an increased number of cross-bridges between thick and thin filaments, equally distributed along the bag₁ fibre length. It is necessary to suppose that there is a considerable non-homogeneity in the numbers of cross-bridges in sarcomeres along the fibre length if the cross-bridge hypothesis is valid (see Discussion).

The effect of relaxation velocity. The destruction of after-effects by stretch was strongly dependent on the velocity of relaxation which followed extension. An asymmetrical triangular stretch with a rapid rate of relaxation was most favourable

for the persistence of after-effects. A typical example of the effect of relaxation velocity is shown in Fig. 1. In the upper record (A), conditioning stimulation of a γ_d -axon at 130/s was followed by a large after-effect to test stimulation during a 2 mm ramp stretch. The relaxation which ensued was at a slow rate (about 0.17 mm/s) and test stimulation during the subsequent ramp showed that the after-effect was almost

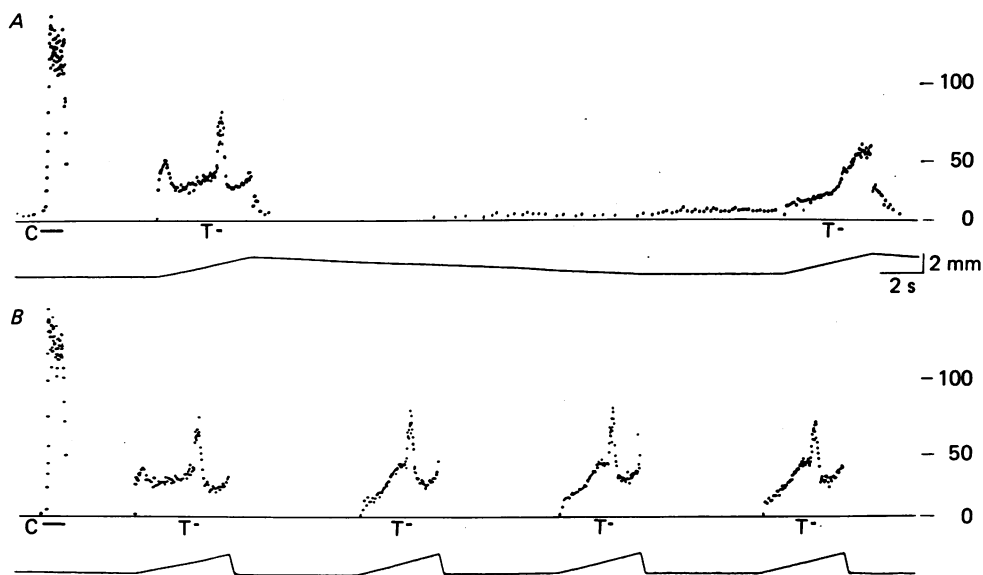


Fig. 1. Responses of a primary ending to test stimulation of a dynamic γ -axon following conditioning stimulation of the same axon at 130/s (C). Test stimulation (T) at 30/s. In upper records (A) the 2 mm stretch is followed by slow relaxation. In the lower records (B), relaxation is rapid. Upper traces: ordinate, discharge frequency of primary ending; calibration in impulses/s on right.

completely abolished. The conditioning stimulation also caused a large initial burst at the onset of ramp stretch; this too was abolished by the stretch. In the lower record (B), similar conditioning stimulation produced a large after-effect during the stretch which was now followed by a much more rapid rate of relaxation (about 10 mm/s). Under these conditions test stimulation during subsequent ramp stretches showed no significant reduction in the after-effect. In contrast, the initial burst showed a considerable reduction following the first stretch.

The dependence of the persistence of dynamic fusimotor after-effects on the velocity of relaxation is shown in further detail in Fig. 2, in which the percentage of the control after-effect amplitude persisting after a stretch of 2 mm is plotted as a function of relaxation velocity. A relaxation velocity of 0.1 mm/s completely eliminated the after-effect. As the velocity of relaxation was progressively increased, the amplitude of the after-effect which persisted became larger, reaching 80% of the control value at 2 mm/s and about 90% at 5 mm/s.

Conditioning stimulation during the relaxation phase of a large symmetrical stretch leaves after-effects which increase the response of primary endings to

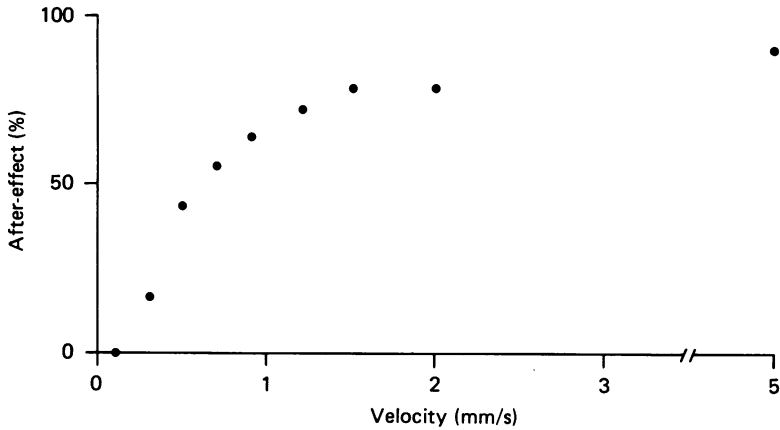


Fig. 2. Relation between percentage of after-effect amplitude and velocity of relaxation following a 2 mm stretch.

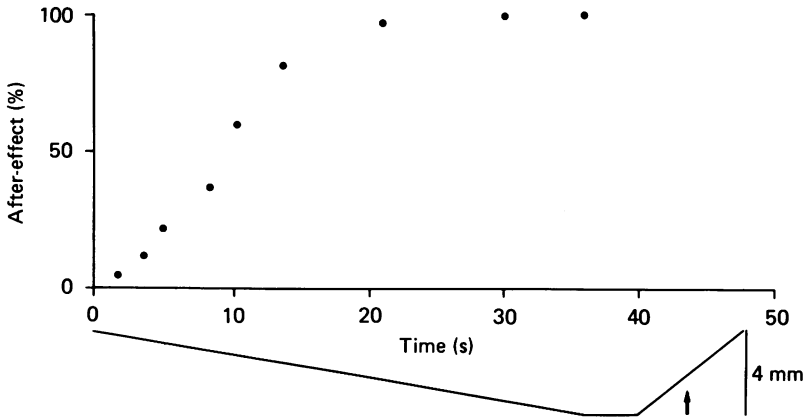


Fig. 3. Variation in dynamic fusimotor after-effect produced by changing the position of conditioning stimulation during relaxation. Plot shows percentage of maximal after-effect following conditioning stimulation (100/s for 1.6 s) of a γ_d -axon. Points represent the time of onset of the conditioning stimulation. After-effect amplitude was measured as the increment in discharge frequency of the primary ending produced by test stimulation (six shocks at 30/s) of the same γ_d -axon during ramp stretch. Change in muscle length shown below including, on right, ramp stretch and time of onset of test stimulation (arrow).

combined sinusoidal and ramp stretch (Baumann *et al.* 1983*a*) and to test dynamic fusimotor stimulation given during ramp stretch (see preceding paper). In the present study, we have given brief periods of dynamic fusimotor conditioning stimulation at varying times during the relaxation phase of a triangular stretch and found that such conditioning stimulation is not equally effective during the entire relaxation period. An example is shown in Fig. 3. Conditioning stimulation early in the relaxation phase left very little after-effect. As the stimulation was moved later during relaxation, the amplitude of the after-effect progressively increased and during the latter half of the relaxation phase was nearly as great as at constant muscle length. These findings

indicate that decreases in muscle length can influence the persistence of dynamic after-effects, presumably by reducing the increase in short-range elasticity that follows conditioning stimulation.

The effect of position of test stimulation during ramp stretch. The response of primary endings to test dynamic fusimotor stimulation varies with the position of this

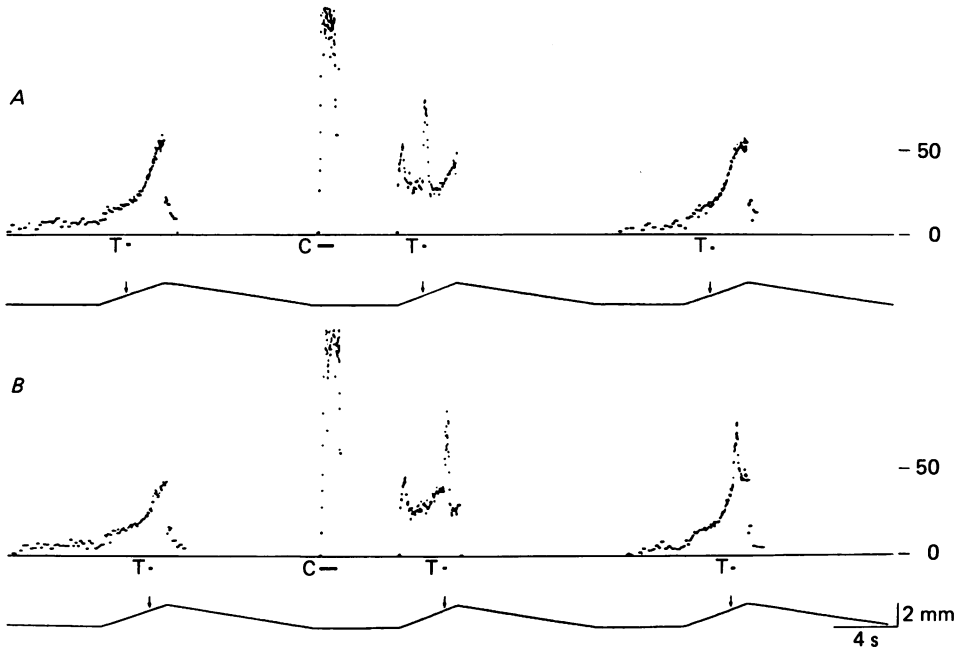


Fig. 4. Effect of position of test stimulation (T) during ramp stretch on the persistence of after-effects. Conditioning stimulation (C) at 130/s to the same dynamic γ -axon. Stretch and conditioning stimulation are identical in A and B, but test stimuli are given earlier in the ramp in A than in B. Test stimulation at 30/s. Upper traces show frequency of discharge of primary ending; calibration in impulses/s on right. Lower traces: muscle length. Amplitude of stretch 2 mm.

stimulation during slow ramp stretch. Test stimuli early in the ramp are relatively ineffective; as they are moved later in the ramp they become progressively more effective. After-effects of prior dynamic fusimotor stimulation are also greater when tested later during ramp stretch. Furthermore, the after-effects tested by dynamic fusimotor stimulation late in ramp extension can persist after a stretch which eliminates the response to test stimuli early in the ramp. An example is shown in Fig. 4.

In the upper record (A), test γ_d stimulation during the control ramp had no evident effect. After conditioning stimulation of the same axon, there was a large response to the test γ_d stimulation as well as a prominent initial burst. The subsequent ramp stretch showed that the initial burst had been abolished and the after-effect destroyed. In the lower record (B) the test stimulation was delivered later in the ramp; otherwise conditions were identical. In this case the after-effect persisted after the ramp stretch. However, the initial burst was abolished.

After-effects produced by stretch

Stretch alone produces significant after-effects which augment the responses of primary endings to test stimulation of dynamic fusimotor axons, but not of static axons, as illustrated in Fig. 5. In this experiment, a static and a dynamic axon were isolated to the same spindle. During ramp stretch, a brief period of stimulation was given, first to the static γ -axon and then to the dynamic γ -axon. In the absence of

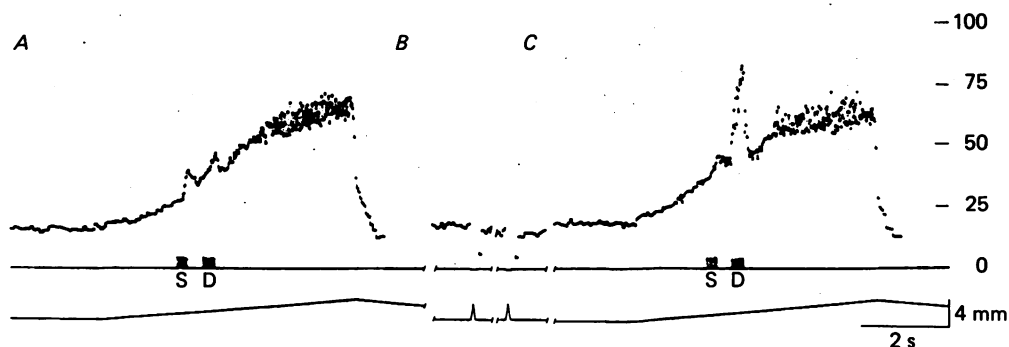


Fig. 5. Response of primary ending to test stimulation of a static (S) and a dynamic (D) γ -axon during ramp stretch. *A*, control responses. *B*, ten rapid stretches of soleus (only the first and last of which are shown). *C*, test stimulation after stretch. Note the after-effect on dynamic but not on static test response. Calibration in impulses/s on right.

any conditioning stimulation, each gave only a small increase in the primary discharge frequency. Both the static and dynamic test responses showed considerable after-effects when their axons were given conditioning stimulation (not shown). The control responses are shown in *A*. The soleus muscle was then subjected to ten identical brief stretches of 4 mm amplitude (*B*), only the first and last of which are shown. During the subsequent ramp stretch there was a large increase in the response to test dynamic fusimotor stimulation, but there was no significant change in the response to static test stimulation (*C*). The result was the same if the order of stimulation was reversed, that is if the dynamic stimulation preceded the static. It was regularly observed that stretch left after-effects to test dynamic stimulation but not to static test stimulation (with the muscle at low initial length). This suggests that, under these circumstances, the after-effect of stretch results principally from residual changes in the bag₁ fibre, presumably following some type of stretch excitation (see Poppele & Quick, 1981).

This is further indicated by the interaction between stretch and dynamic conditioning stimulation on the responses to test dynamic fusimotor stimulation. If submaximal after-effects of both stretch and conditioning dynamic stimulation are added, summation of their effects occurs as may be seen in Fig. 6. However, if maximal effects produced by both conditioning dynamic stimulation and by stretch were added, occlusion was observed (not illustrated).

The after-effects of stretch can be graded by the number of stretches as is seen in Fig. 7. The after-effect builds up to some maximal value as the number of repetitive

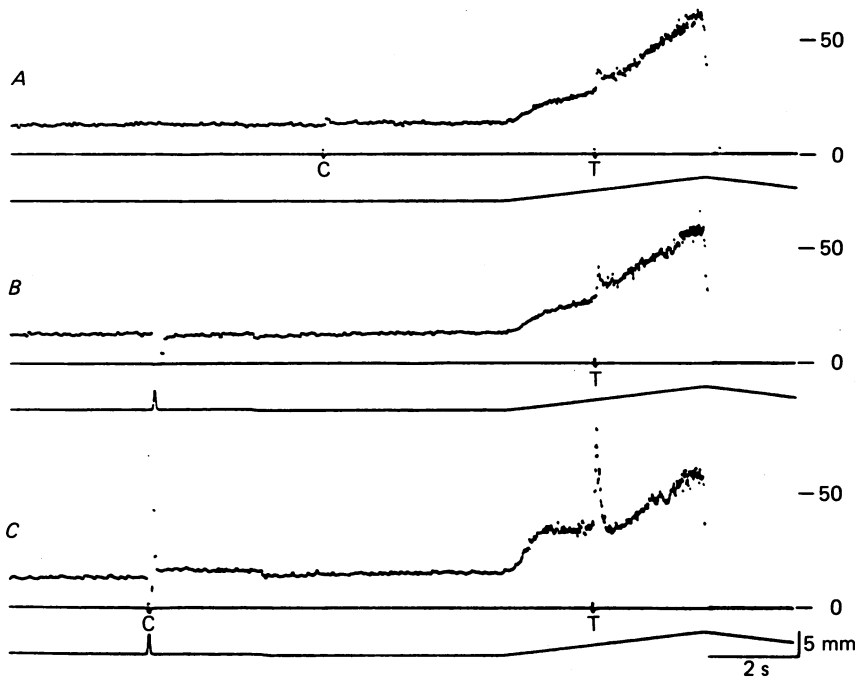


Fig. 6. Interaction between after-effects produced by dynamic γ conditioning stimulation and stretch. *A*, response to test stimulation (50/s) following conditioning stimulation of same dynamic γ -axon. *B*, test response following muscle stretch. *C*, following combined muscle stretch and conditioning fusimotor stimulation. Upper traces: discharge frequency of primary ending; calibration in impulses/s on right. Lower traces: muscle length.

stretches is increased. This was seen after about ten brief stretches to soleus, 4 mm in amplitude. However, even single stimuli could be quite effective (see below). The minimal amount of stretch needed to evoke a demonstrable after-effect on a test dynamic fusimotor response is probably in the order of only a few millimetres. We do not know if there is a definite threshold for stretch-evoked after-effects. Our method of detection may not be sufficiently sensitive to detect residual changes which follow only small amounts of contractile activation.

The persistence of after-effects produced by stretch, like those following dynamic fusimotor stimulation, depends on the velocity of relaxation. Thus, asymmetric triangular stretches with rapid rates of relaxation are most effective in producing stretch-evoked after-effects. In some preparations a single stretch followed by rapid relaxation produced a large after-effect, as illustrated in Fig. 8. In the upper trace (*A*), a symmetrical triangular stretch of 4.5 mm left no detectable after-effect as tested by γ_d stimulation during a subsequent ramp. In the lower record (*B*), a similar stretch followed by rapid relaxation left a large after-effect as shown by the response to test stimulation during the following ramp stretch.

Responses to repeated γ_d test stimulation, delivered during small ramp stretches followed by rapid relaxation, often showed a progressive build up in the responses of the primary ending to test γ_d stimulation. Fig. 9 shows an example of repeated

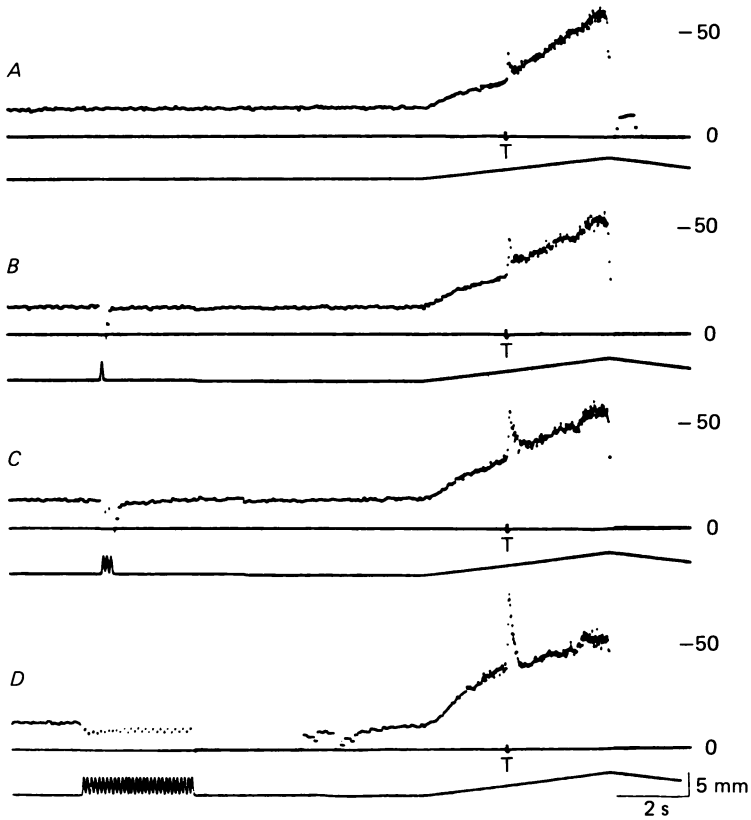


Fig. 7. Effect of the number of stretches on the amplitude of the after-effect they produce. Upper traces: primary ending discharge frequency; calibration on right. Lower traces: muscle length. *A*, control test response. *B*, after one stretch. *C*, after three stretches. *D*, after thirty stretches.



Fig. 8. Responses of primary ending to test stimulation (*T*) of a dynamic γ -axon during ramp stretch. In *A*, relaxation velocity is slow, in *B* it is rapid. Note the after-effect of stretch in *B* but not in *A*.

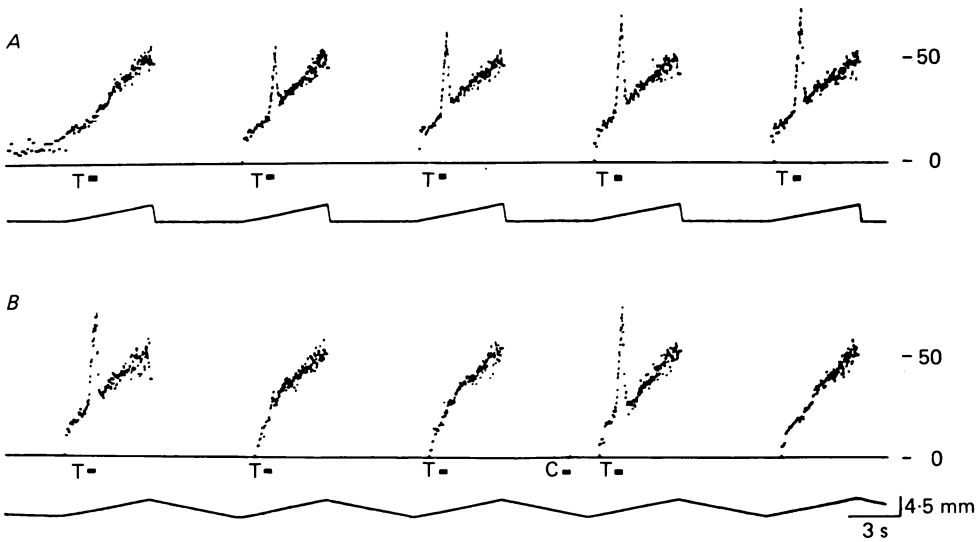


Fig. 9. Responses to test dynamic fusimotor stimulation (T) given during repeated ramp stretches. Upper traces: primary ending discharge frequency; calibration on right in impulses/s. Lower traces: muscle length. In *A*, the relaxation velocity is rapid and there is a build up of after-effects. In *B*, relaxation velocity is slow and the after-effect is destroyed. Record *B* immediately follows record *A*. Before the 4th stretch in *B*, conditioning stimulation (C) was given to the dynamic γ -axon during relaxation from the previous stretch and an after-effect resulted. Last stretch in *B* shows response to stretch alone.

4.5 mm ramp stretches during each of which a γ_d -axon was briefly stimulated. When the relaxation velocity was high (*A*), the response increased with successive stretches until reaching a maximum. If relaxation velocity was then slowed as in *B*, the effect was abolished.

Two factors play a role in such a build up of response: (1) each test stimulus may leave an after-effect which can accumulate and (2) each stretch may leave an after-effect which can also be cumulative. In some preparations it could be seen that stretch without γ_d stimulation produced only a small after-effect when tested by subsequent γ_d stimulation, whereas the after-effect built up rapidly when each stretch was accompanied by brief γ_d test stimulation. In others, particularly when stretch amplitude was relatively large, stretch alone produced considerable after-effects when given repetitively. Probably both stretch and dynamic fusimotor after-effects usually contribute to such a build up of response.

DISCUSSION

The after-effects produced by fusimotor stimulation appear to result from residual changes in the intrafusal fibres themselves, as discussed in the preceding paper. These changes are likely to be due to a persistent increase in the number of cross-bridges between thick and thin filaments following activation of the fibres. Such cross-bridges would produce a short-range elasticity, rendering the fibre, or a portion thereof, less

compliant and augmenting the effect of stretch on the sensory terminals. The residual cross-bridges would also increase the response to subsequent fusimotor stimulation.

Stretch destroys after-effects, but the magnitude of stretch required to do so is well beyond that expected on the cross-bridge hypothesis if one assumes the fibre to be a uniform structure and the cross-bridges evenly distributed along its length. The bag₁ fibre is not uniform and the nucleated equatorial region is more compliant than its striated portions. Stretch may be expected to extend the sensory region to a greater extent than the rest of the fibre. However, the amount of muscle stretch required to abolish the after-effects is much too large to be explained on this basis alone. The amount of sarcomere length change which would be expected to break cross-bridges is about 0.2% (Hill, 1968). In soleus, a stretch of about 4 mm abolishes most of the after-effect. This is about 10% of the extrafusal muscle fibre length (Rack & Westbury, 1969). We do not know whether the spindles which are approximately 1/5 of the extrafusal muscle fibre length, are stretched proportionately. Assuming they are, a 7 mm long spindle would be extended 0.7 mm by such a stretch. If this increased the length of the equatorial region by 100 μ m, a substantial increase, the rest of the fibre would undergo an increase in length of 0.6 mm or about 9%, far beyond the limit expected for the short-range elasticity. To sustain the cross-bridge hypothesis, it is necessary to assume that the residual cross-bridges are not evenly distributed among the sarcomeres along the muscle length. Since the bag₁ fibre is activated locally, one can imagine that the after-effects, and hence cross-bridges, occur in the region activated and that these are in series with others that are more compliant. Such sarcomere non-homogeneity could explain why such a large stretch is required to abolish the after-effects.

The rate of relaxation following extension is found to have a major influence on the persistence of after-effects. It is not known whether this is an effect of velocity of relaxation *per se* or whether the time the fibre is at a more extended length is responsible. Morgan, Prochazka & Proske (1984) have shown that when the soleus muscle is subjected to a series of stretches and then returned to its original length, there is a large response to test dynamic fusimotor stimulation during a subsequent ramp stretch. However, if the muscle is held at the longer length for some time and then returned to the original length, the response to the test dynamic stimulation is reduced or abolished.

Their interpretation of the after-effects following stretch differs from ours. They regard stretch as abolishing cross-bridges which then reform spontaneously, at the length at which the muscle is held following stretches, and assume that such 'stable' cross-bridges produce the response to test dynamic fusimotor stimulation during the subsequent ramp stretch. In our view, such large responses to test dynamic fusimotor stimulation do not develop spontaneously but result from some type of stretch excitation of the bag₁ fibre. Stretch is known to abolish the short-range elasticity of the intrafusal fibres, associated with the initial burst. This short-range elasticity redevelops spontaneously after several seconds. However, the after-effects produced by conditioning fusimotor stimulation or stretch appear to depend on the formation of a considerably larger number of cross-bridges than develop spontaneously. Our finding that, at short muscle length, stretch produces a large after-effect to test dynamic stimulation, but that the response to static stimulation is changed very little, is hard to reconcile with the interpretation of Morgan *et al.* (1984).

Stretch itself leaves an after-effect which is similar to that produced by conditioning stimulation of dynamic fusimotor axons. It enhances the response to test stimulation of dynamic but not static axons. Therefore, the stretch-evoked after-effect appears to result from an action on the bag₁ intrafusal muscle fibre. In the isolated spindle, Poppele & Quick (1981) found evidence for a stretch-evoked activation of the bag₁ fibre. Sarcomere spacing in the juxta-equatorial region of the bag₁ fibre initially increased and then decreased during ramp stretch. The mechanism for this activation, or excitation, is not known. While there could be a stretch activation at the myofilament level, similar to that seen in insect flight muscle (Pringle, 1972), other possibilities need to be considered. Stretch might have an effect on the motor nerve terminals, the muscle membrane of the bag₁ fibre or on some subsequent stage of the excitation-contraction process.

Proske (1975) found that repeated stretches ('alternating movements') produced a facilitation of the response of the primary ending to dynamic fusimotor stimulation, but this decayed quite rapidly, returning to the control level within about 3 s. The relation of this phenomenon to the present results is not clear for the after-effects reported herein persist for a long time, certainly for many minutes.

The response of primary endings to dynamic fusimotor activity is much greater during ramp stretch than at constant muscle length (Emonet-Dénand & Laporte, 1981). Further, the effectiveness of dynamic stimulation becomes greater when it is given later during ramp stretch. These phenomena may depend on the passive properties of elements which are in series with the portion of the bag₁ fibre activated by fusimotor stimulation. At greater length, the local bag₁ contraction could produce a larger extension of the sensory region due to changes in the series compliance. However, since stretch itself excites the bag₁ fibre it is necessary to consider the possibility that interactions between ramp stretch and dynamic fusimotor stimulation might depend, at least in part, on stretch-excitation of the bag₁ fibre. The effect of changing the position of dynamic fusimotor stimulation during ramp stretch on after-effects is suggestive that this may be the case. If the contraction produced by a given stimulation of a dynamic axon during ramp stretch occurred in an otherwise passive spindle, one might expect the same set of sarcomeres in the bag₁ fibre to be activated, even if the position of the stimuli during the ramp were changed. Hence, a maximal after-effect following stimulation at one position might be expected to be maximal when shifted to another position. This does not appear to be the case. On the contrary, when stimulation is shifted during the ramp from one associated with a maximal after-effect, the after-effect at the new position is at first less than maximal and then builds up to a maximal value (F. Emonet-Dénand & C. C. Hunt, unpublished observations). This suggests that a partially different set of sarcomeres may be activated at two different positions during ramp stretch. This could result if, during ramp stretch, stretch excitation of somewhat different sets of sarcomeres occurred at different levels of stretch. This excitation might then combine with that produced by fusimotor stimulation to leave after-effects which varied with position of stimuli during the ramp.

It is interesting to speculate on the possible physiological importance of the effects of stretch in producing after-effects or in diminishing those resulting from prior fusimotor activity. During slow muscle movements, stretch of large amplitude would be expected to diminish any residual effects resulting from prior fusimotor activity.

More rapid movements might be expected to preserve such residual effects and to add after-effects of stretch on the bag₁ fibre.

In the case of large rhythmic alternating movements in which flexors and extensors are alternatively active, one may imagine that the phase of flexor activity, associated with fusimotor activation of spindles in a flexor muscle, would produce after-effects in those spindles. In the subsequent extensor phase of movement, after-effects in the flexor muscles would enhance the responses of their spindles to stretch, but if the stretch were sufficiently large would also lead to abolition of these after-effects. At the same time, fusimotor activity in extensor muscles would occur, leaving behind after-effects which would be manifest in the next flexor phase of the cycle. Thus, with large alternating movements after-effects would be produced with each phase of the repetitive cycle and carried over to the next half-cycle but not from one cycle to the next (see Baumann, Emonet-Dénand & Hulliger, 1982). If the alternating movements are small, however, stretch will not destroy the after-effects and they can build up to some maximum. In the case of dynamic fusimotor activity not only will there be a persistence of after-effects resulting from prior dynamic fusimotor activity but after-effects will also accumulate as a result of the action of stretch itself on the bag₁ fibre.

This research was supported by grants from the Fondation pour la recherche Médicale Française and from the U.S. Public Health Service, NS 07907. We thank Mrs Ginapé for technical assistance.

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