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THE AFTER-EFFECTS OF STRETCH AND FUSIMOTOR STIMULATION ON THE RESPONSES OF PRIMARY ENDINGS OF CAT MUSCLE SPINDLES

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SUMMARY

1. These experiments explore the after-effects of repetitive movements and dynamic fusimotor stimulation on the responses of primary endings of soleus muscle spindles in the anaesthetized cat.

2. If immediately following a series of conditioning stretch and shortening movements, the muscle was held at the stretched length for 3 s before being returned to its rest length, the subsequent response to a brief dynamic fusimotor tetanus given during a slow test stretch produced only a small increase in spindle firing. If, on the other hand, the muscle was returned to its rest length immediately after the movements, the fusimotor tetanus evoked a much larger afferent burst.

3. This difference in the size of the burst could only be observed if the fusimotor tetanus was given soon after onset of the test stretch. If it was delayed and given at a time when the test stretch passed through the length at which the muscle had been held stretched after the movements, there was no difference in the size of the afferent burst.

4. If following the movements the muscle was held stretched for less than 3 s, the response to the subsequent tetanus was not fully depressed. Once the depressed condition had been achieved, the muscle had to be left undisturbed for up to half an hour before the response had recovered its original fully undepressed size.

5. Conditioning repetitive stimulation of the fusimotor fibre was just as effective as using alternating movements in producing the effects.

6. If the test tetanus, which was normally ten shocks in 50 ms, was made longer, the change in size of the impulse burst became a change in latency of onset of the response to the tetanus. Holding the muscle stretched at the end of the conditioning movements/tetanus produced a delay in onset of the response to the test tetanus without significantly altering its size.

7. These observations have been interpreted as arising from development of stable cross-bridges between actin and myosin filaments in the intrafusal fibres. During repetitive movements or fusimotor stimulation, stable bridges become detached and during the subsequent 3 s they re-attach, at the length at which the muscle is being

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held after conditioning. Once attached, if the muscle is left undisturbed the bridges will detach and re-attach spontaneously but very slowly, taking up to half an hour. It is proposed that the delay in onset or depression of the response to a test fusimotor tetanus, when the muscle is held stretched after movements, is because the stable cross-bridges have all formed at the stretched length. When subsequently the muscle is returned to its rest length, slack must be taken up before the intrafusal contraction can effect an increase in afferent firing.

INTRODUCTION

It has long been known that repetitive stimulation of the fusimotor supply of a muscle spindle is followed by a period during which the spindle's response to a subsequent single fusimotor volley is enhanced, and that such 'post-excitatory facilitation' can be abolished by a brief stretch (Hunt & Kuffler, 1951). A phenomenon which is probably based on the same underlying mechanism is that observed by Brown, Goodwin & Matthews (1969), who found that the responses of muscle spindles to stretch of the passive muscle showed an initial high-frequency peak, the initial burst, which was greatly increased in size if the stretch was preceded by a period of fusimotor stimulation. The authors proposed that the initial burst arose from the formation of stable cross-bridges (Hill, 1968) between actin and myosin filaments within sarcomeres of the intrafusal fibres. According to this hypothesis, stable bonds were formed following repetitive stimulation of a fusimotor axon, so that the intrafusal fibres became 'stuck' at the length at which stimulation had been applied. This was manifested by a burst of impulses during a stretch which passed through the length at which the intrafusal fibre had been stuck.

In recent years, interest in 'after-effects' has continued to grow, and some effort has been made to incorporate them into considerations of the role of spindles in motor control (Baumann, Emonet-Dénand & Hulliger, 1982, 1983). Another important development is that after-effects can be detected following a series of rapid alternating stretches and releases (Proske, 1975), and the effects resemble those following fusimotor stimulation (Emonet-Dénand, Hunt & Laporte, 1983; Emonet-Dénand & Hunt, 1984). In both studies, dynamic fusimotor fibres were stimulated. In the experiments of Emonet-Dénand *et al.* (1983) a brief burst of fusimotor stimulation was applied soon after the onset of a slow stretch; the response of the spindle was enhanced by conditioning stimulation or stretch.

We have extended the explanation of Brown *et al.* (1969) to encompass these observations as well as those using a simple stretch as the test. One important consideration which has emerged is the previous history of stimulation, be it stretch or fusimotor stimulation, that has been applied to the spindle. Another is the time course of the effects. As a result of our findings we now believe that most, if not all, of the phenomena included under after-effects can be explained in terms of the development of stable cross-bridges in intrafusal fibres.

METHODS

The experiments were carried out on seven cats in the weight range 2·5–4·0 kg. Animals were anaesthetized with sodium pentobarbitone. An initial dose of 40 mg/kg was given, and this was supplemented with additional doses during the course of the experiment whenever a flexor withdrawal reflex could be elicited. All of the experiments used the soleus muscle. This was freed from surrounding connective tissue and its tendon of insertion attached to a servo-regulated electromagnetic stretcher (with Shaevitz LVDT length transducer). The hind limb was extensively denervated, including hip muscles, but sparing the soleus nerve. A laminectomy was performed to expose dorsal and ventral roots L6–S2, all of which were cut at their point of entry into the spinal cord. Bipolar platinum electrodes were used for stimulating and recording.

Dorsal roots L7 and S1 were dissected into fine filaments, each small enough to contain only a single functional afferent fibre. Primary endings of soleus spindles were identified by the silencing of discharge during a muscle twitch and by their afferent conduction velocity. The ventral roots were similarly dissected until they contained a functionally single dynamic fusimotor axon. This was achieved in the following manner. The muscle was subjected to large amplitude, ramp-and-hold stretches and the response of the spindle monitored during the stretch. At the same time a ventral root filament was stimulated, and if on stimulation it increased the dynamic response of the spindle, the filament was dissected further until the effect could be tracked down to a filament containing only one axon from soleus conducting within the gamma velocity range, 20–50 m/s.

The experiments were carried out at muscle lengths which did not exceed maximum body length as measured with the muscle *in situ*. Typically, what was called the slack length was 2–3 mm short of the length at which a maximal muscle twitch could be elicited, a length at which there was no detectable passive tension.

The animal's body temperature was maintained at 38 °C with a servo-regulated electric blanket and rectal probe. The exposed soleus muscle and spinal cord were covered by pools of paraffin, the temperature of which was maintained in the range 35–38 °C.

RESULTS

Since the effects of alternating movements had been described for primary endings of spindles, using test bursts of dynamic fusimotor stimulation (Emonet-Dénand *et al.* 1983), this combination was used in these experiments. In a total of seven experiments, eight primary endings were studied, each together with at least one dynamic fusimotor fibre. It was a common finding that soleus spindles were supplied with at least two dynamic fusimotor fibres, one of which was typically more powerful than the other. It was our practice to choose the fibre with the more powerful action, but when, on occasions, the weaker was used the effects observed were qualitatively the same.

The first pitfall with these experiments, and one which it took some time to learn to avoid, was that a spindle, apparently in a resting state, could already be significantly conditioned by earlier activity since the effects of previous activity could be very long-lasting. It was therefore necessary to devise a standard conditioning procedure, one where the previous history no longer exerted any influence. Failure to use a standard conditioning procedure does not produce an unconditioned state, but one conditioned by the previous test.

In Fig. 1 is illustrated the effect of alternating stretch–release movements on the response of the spindle to a brief fusimotor burst during a slow stretch. In the upper set of records the muscle is held at the short length following the movements, in the lower set it is held at the long length for 3 s before being returned to the short length. Only when the muscle is kept short at the end of the movements is there a large

response to the fusimotor burst. It is therefore not the movements themselves, but what happens to the muscle immediately afterwards which is important. Notice that the response of the passive spindle to the slow stretch is altered as well as the response to the fusimotor burst. The response in the upper record shows a clear peak (initial

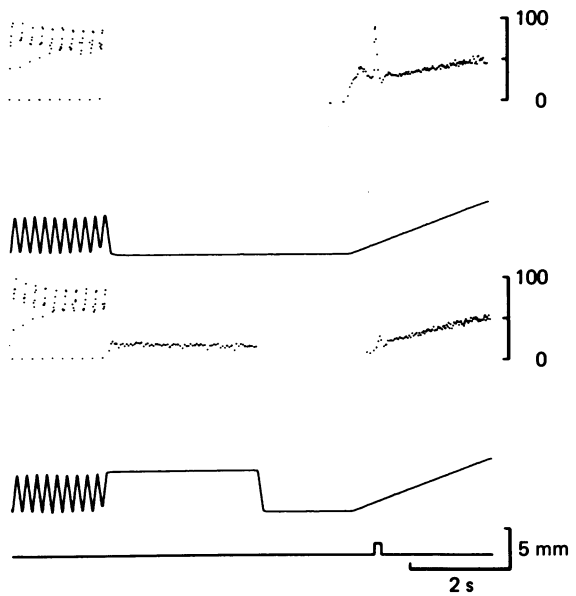

Fig. 1. The effect of a conditioning sequence of movements on the response of the primary ending of a soleus spindle to a brief fusimotor tetanus applied during a slow stretch. The test stretch was 6 mm at 2·2 mm/s and the fusimotor tetanus, ten shocks in 50 ms, was given 0·4 s after the onset of the stretch. The conditioning movements consisted of a sequence of nine alternating stretches and shortenings each of 5 mm amplitude and at a rate of 100 mm/s. At the end of the movements the muscle was either held in the shortened position for 5 s before the test stretch was applied (upper set of traces) or held stretched for 3 s and then short for 2 s before the test stretch was applied (lower traces). Increasing the 'hold-short' time to 5 s did not significantly alter the result (see Fig. 4). In both pairs of recordings the upper trace represents the instantaneous firing rate of the spindle (calibration on the right), the lower trace the length record. At the bottom of the Figure are shown the time-location of the stimulus burst as well as time and length calibrations.

burst) and a higher firing rate throughout most of the stretch. When the muscle was held at the long length for a few seconds after the movements (lower traces, Fig. 1), firing of the passive spindle increased only gradually during the test stretch and did not show an initial peak. Furthermore, the response to the fusimotor burst was small.

The difference in the response of the passive spindle is shown more dramatically in Fig. 2, where two responses are superimposed: one which shows an initial burst, the other with no burst and a lower firing rate. However, the main point of this Figure is to show the effect of applying the fusimotor test tetanus later, at a time when the test stretch passed through the length which corresponded to the stretched length following the alternating movements (dashed line). Here the passive firing rates

had converged to the same value and the two responses to the fusimotor tetani superimposed precisely.

So it emerged from our experiments that a critical factor was what happened to the muscle after the movements: was it held at a long or short length? We then asked the question: how long did the spindle need to be held at a particular length before

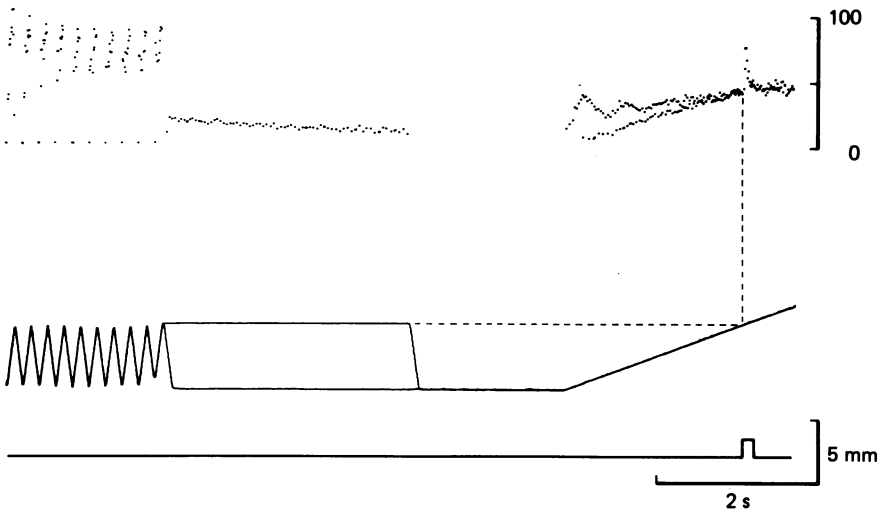

Fig. 2. The effect on the response of the spindle of the same sequence of conditioning movements as shown in Fig. 1, but with the fusimotor tetanus given later during the test stretch, at a time when the stretch passed through the length corresponding to the stretched position following the movements (dashed line). The two sets of responses and length traces are shown superimposed. The spindle was silent while the muscle was held short, and during the slow stretch the higher discharge rate corresponds to the 'hold-short' condition. The response to fusimotor stimulation was the same regardless of whether the muscle had been stretched or kept short at the end of the movements.

the effect characteristic for what length manifested itself? The answer is provided by the experiment shown in Fig. 3. The control response is represented by the lowest of the four afferent discharge displays. Here the test fusimotor tetanus was applied 0·5 s after onset of the slow stretch with the muscle held at the slack length for 5 s after the movements and before the test stretch was applied. The afferent burst in response to the fusimotor stimulus represents an increase in discharge above the passive level of 62 impulses/s. In the trace immediately above, at the end of the alternating movements the muscle was briefly held stretched (0·5 s) before it was slackened off again. This resulted in a slight fall in the response to the fusimotor tetanus to give an increase of 56 impulses/s. In the second trace from the top, the muscle was held at the stretched length for 1·5 s and this reduced the response further to 26 impulses/s. In the top trace is shown the smallest response which was achieved with the muscle held for 2·5 s at the stretched length. In this experiment it was found that the time the muscle was held short following the movements and before the beginning of the test stretch did not change the size of the test response. The critical

factor always was how long the muscle had been held stretched immediately following the movements.

A detailed plot of development of this 'depression' is shown in the upper graph of Fig. 5. It can be seen that for this spindle the depression was complete after 3 s. The open circles show the time course of decay of the 'potentiation' observed by Proske (1975).

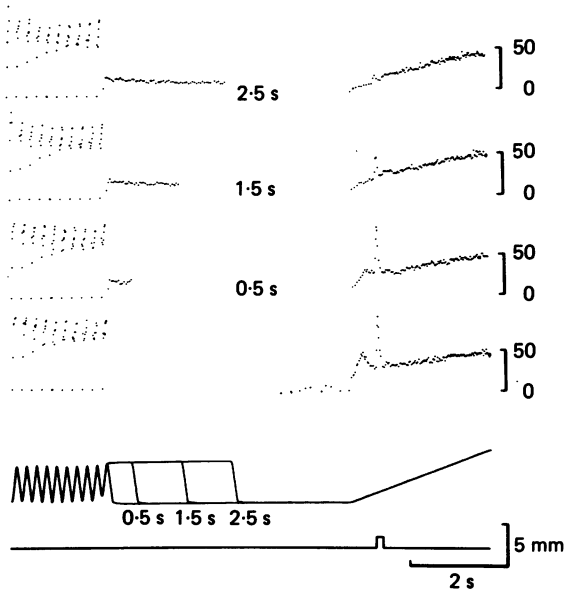

Fig. 3. The effect on the size of the test response of holding the muscle in the stretched position for different periods of time following a series of movements. The response to the fusimotor tetanus becomes progressively smaller as the duration of the hold-time at the stretched length is increased, from 0 to 2·5 s. The length records from the four sets of responses have all been superimposed.

Up to this point, it was not clear whether indeed we were dealing with a depression of the response due to holding the muscle stretched after the alternating movements, or a potentiation when holding it short. We also wanted to know whether, once a particular condition had been established, it would persist indefinitely. The experiment which explored this point is shown in Fig. 4. Here, following the alternating movements, the muscle was held short to give a large response to the fusimotor burst (bottom discharge trace) or held long for a sufficiently long time to produce a small response (second trace from the bottom). In this record the test fusimotor burst was applied 2·5 s after release from the long length. In the upper traces the same procedure was carried out – i.e. movement plus hold at stretched length – but the onset of the test stretch was further delayed. Gradually, as the time between the release from the long length and the onset of the test stretch was increased, the spindle redeveloped a resting discharge, an initial peak in the passive response to stretch reappeared, and the response to the fusimotor tetanus became progressively larger. With a wait of 900 s (top trace) the response was nearly equal to that seen when the muscle was held

short after the conditioning movements (bottom trace). This experiment suggests that if the condition where the muscle is left undisturbed for long periods represents the unconditioned state, then it would be appropriate to refer to a depression of the test response following the movements and 'hold-long' rather than a potentiation

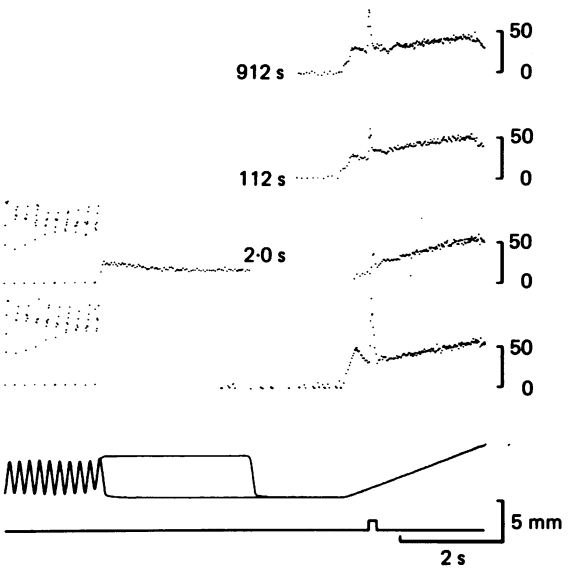

Fig. 4. The persistence of effects following a series of conditioning movements. Four sets of responses have been shown but only two of the length traces (superimposed), corresponding to the bottom two frequency traces, are shown. The bottom frequency trace represents the response to the test fusimotor stimulation with the muscle held short for 5 s after the conditioning movements and before the start of the test stretch. In the trace above it, the muscle had been held stretched for 3 s after the movements and was returned to the rest length for a further 2·5 s before the test stretch was applied. On each occasion, the test tetanus was given 0·5 s after the start of the test stretch (which had a velocity of 2·4 mm/s). In the second trace from the top, the time interval between release from 3 s of hold after the movements and the onset of the test stretch was 112 s. In the top trace it was 912 s. When the muscle is kept still for long periods, the depression produced gradually disappears.

after the movements and 'hold-short'. The time course of the reappearance of a large response to fusimotor stimulation is shown in the lower graph of Fig. 5. It can be seen that one needs to wait up to half an hour for complete disappearance of the depression – that is, to obtain a response no longer conditioned by previous actions.

All of the effects described above have been conditioned by alternating rapid stretch and shortening. However, it is possible to see much the same kind of after-effect using a conditioning burst of fusimotor stimulation. This is shown in Fig. 6. Here, for the response shown in the upper trace, the conditioning fusimotor tetanus was given at the stretched length, and immediately on cessation of stimulation the muscle was brought back to the slack length. The response to the fusimotor burst during the test stretch was large. If, however, the stretched length was maintained for 3 s

after the end of the conditioning tetanus (lower trace) the response to the test burst was depressed. We have used a whole range of test procedures following a conditioning fusimotor tetanus and, qualitatively at least, the after-effects closely resemble those seen with alternating movements. For example, conditioning stimulation could be

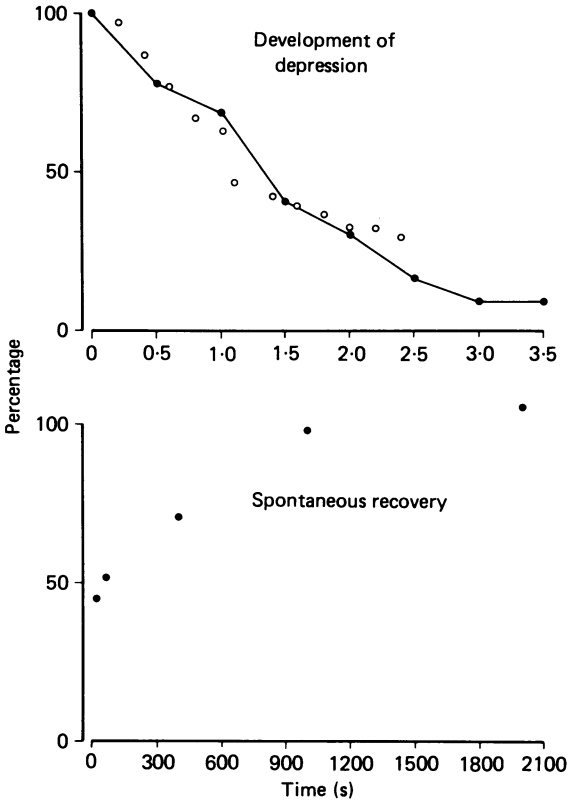

Fig. 5. The time course of development and recovery of after-effects. The filled circles in the upper graph represent the amount of reduction of the response to the fusimotor tetanus by increasing the period of 'hold-long' following alternating movements (see Fig. 3). The open circles are data taken from Proske (1975) to show the decline from 'potentiation' of a fusimotor response following alternating movements. The lower graph shows the recovery from a depressed response. The depression was produced by alternating movements and then holding the muscle stretched for 3 s before returning it to its rest length for varying periods of time (Fig. 4). For full recovery it is necessary to leave the muscle at its rest length for more than half an hour.

applied at the short length and the muscle immediately afterwards stretched and held for a few seconds. This was just as effective in producing a depression, i.e. the determining factor was not the length at which the muscle was stimulated, but the length at which it was held immediately after stimulation.

In their report Emonet-Dénand *et al.* (1983) mentioned that the combined effects of conditioning stretch and fusimotor stimulation were additive. This too we have been able to mimic in our experiments. It was necessary here to use only one small

stretch–release, and a very brief conditioning fusimotor tetanus so that each had a clearly submaximal effect on the test response. When the two were applied one after the other the test was more than doubled in size.

Throughout the experiments described up to now, the test consisted of a brief burst of dynamic fusimotor stimulation applied shortly after onset of a slow stretch. We used this test partly because others have done so (Emonet-Dénand *et al.* 1983) and we arrived at it partly by trial and error. Its advantage is that it is a very sensitive test.

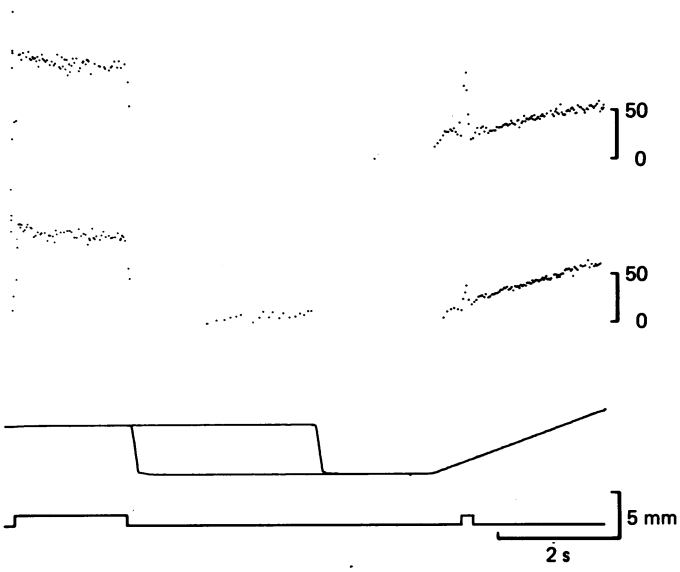

Fig. 6. The effect of a conditioning fusimotor tetanus (200 pulses/s; 1·8 s duration) on the response to a test tetanus applied during a slow stretch 5 s later. The conditioning fusimotor tetanus is given with the muscle held at the stretched length. At the end of stimulation the muscle is returned to its rest length (upper frequency trace) or kept for a further 3 s at the stretched length before being returned to the rest length and application of the test stretch 2 s later (lower trace). The two length traces are shown superimposed below the frequency records while the periods of stimulation are shown at the bottom of the Figure.

However, more insight into the possible mechanism of the phenomenon can be obtained by using tetani of longer duration. The result is illustrated in Fig. 7. In *C* are shown superimposed the responses to alternating movements with the spindle then held at either the stretched or the short length. During the subsequent slow test stretch, a long-duration fusimotor tetanus was used rather than a brief burst. Although the responses to passive stretch, before stimulation commences, are clearly different, the increase in spindle firing during fusimotor stimulation differs only in its time of onset, the response at the short length rising earlier. This is shown more clearly on an expanded time scale in *B*. The difference in time of onset is about 90 ms, which is slightly more than the 80–85 ms usually seen. We concluded that what we were seeing was a shift in the latency of onset of the fusimotor-evoked response. That this could be made to look like a potentiation/ depression is shown in Fig. 7*A*. Here,

still on an expanded time scale, the duration of fusimotor stimulation had been reduced to 90 ms and the response appeared as a burst of impulses resembling those illustrated in the earlier Figures. To achieve a large difference in peak firing rates, it was necessary to use tetanic durations which did not exceed the duration of the latency shift.

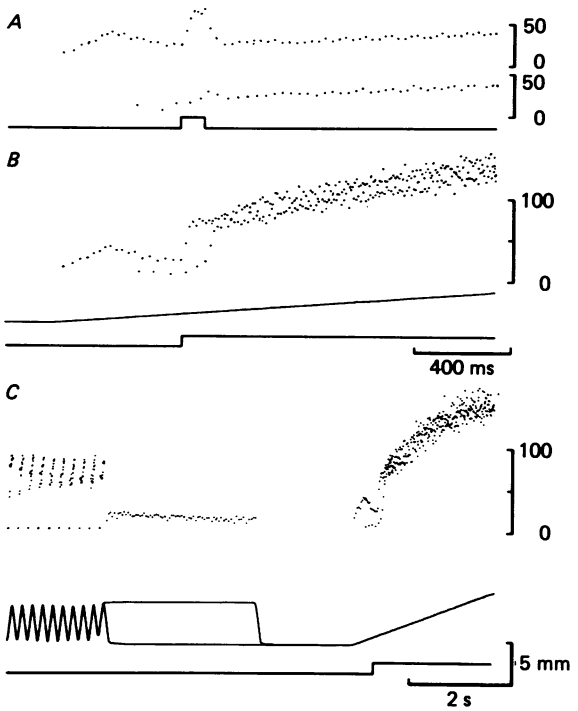

Fig. 7. The response to a brief fusimotor tetanus becomes a shift in latency of onset when the duration of the tetanus is made longer. In *C* is shown the same experiment as illustrated in previous Figures where the conditioning movements are followed by a test stretch with a fusimotor tetanus (100 pulses/s) applied 0·5 s after stretch onset but with the tetanus maintained throughout the rest of the stretch. When the muscle is held stretched for 3 s at the end of the movements, the subsequent response to the fusimotor tetanus rises above the passive value later than when the muscle is returned to its rest length immediately after the movements. This shift in latency of the fusimotor-evoked increase in firing is shown on an expanded time scale in *B*. If then the duration of the test tetanus is reduced to 100 ms (*A*) the latency shift becomes potentiation/depression of a burst of impulses. Records in *B* and *C* are each a pair of superimposed traces, with the length trace and stimulus bar below the frequency record. In *A*, the length trace has been omitted and the two frequency records have been separated for clarity.

DISCUSSION

To summarize our observations, the after-effects of repetitive stretch or fusimotor stimulation represent a shift in latency of onset rather than a potentiation/depression of the response to a fusimotor tetanus during a test stretch. The latency is long when the muscle is held stretched for 3 s or more immediately after conditioning.

This appears as depression of an impulse burst if a brief test tetanus is used. The latency is short if after conditioning the muscle is immediately returned to its rest length. The change in responsiveness following conditioning takes up to 3 s fully to establish itself and hundreds of seconds to revert to the rest state. We have been able to incorporate all of these phenomena in an explanation based on the hypothesis put forward by Brown *et al.* (1969).

Our interpretation of the experiment illustrated in Fig. 1 is that alternating rapid, large-amplitude movements break any pre-existing stable cross-bridges between actin and myosin filaments (Hill, 1968) within the intrafusal fibres and that immediately after the movements new stable bridges rapidly re-form at the length at which the intrafusal fibre is held. Subsequent fusimotor stimulation at this or longer lengths will produce a rapid rise in intrafusal tension and a large burst of afferent discharge. In the lower records of Fig. 1, the intrafusal fibre was 'stuck' at a long length so that when the muscle was re-shortened and stimulated, the fibre had to shorten actively and take up the slack before generating any tension. The time taken to do this resulted in the longer latency of onset or depressed response depending on the duration of the test tetanus. In other words, we believe that following movements the intrafusal fibre will always form stable bridges; when this is at a long length the fibre on returning to its rest length will be (stiff but) slack; when at a short length it will be (stiff and) taut. These conditions give rise to the difference in response to the fusimotor burst during the test stretch. The same kind of explanation can be applied to all of our observations.

Recently, considerable interest has centred on the possibility that the intrafusal fibres innervated by dynamic fusimotor axons, the dynamic nuclear bag_1 fibres (Arbuthnott, Ballard, Boyd, Gladden & Sutherland, 1982) may show stretch activation, i.e. the stretch acts to produce active tension in the intrafusal fibre (Poppele & Quick, 1981). While that may well be true under certain conditions the kind of apparent potentiation we observe after stretches or after fusimotor stimulation can be entirely attributed to the influences of stable cross-bridges. Furthermore, Fig. 4 shows that these after-effects are better described as reversal of an apparent depression and not a potentiation.

Comparison of the upper trace in Fig. 6 with, for example, the bottom trace in Fig. 4 shows that conditioning with a fusimotor tetanus is not quite the same as with alternating movements. When using conditioning stretches, the response of the passive spindle during the slow test stretch rose steeply to produce a sharp initial peak (the 'initial burst'). A conditioning fusimotor tetanus, on the other hand, produced an initial burst which was much less well defined. We do not have a simple explanation for this difference, but several possibilities come to mind. The most likely is based on the fact that stretch exerts its effect on the whole intrafusal bundle while stimulation of the dynamic fusimotor axon engages only a single muscle fibre, the dynamic nuclear bag fibre. It is conceivable that following stimulation the tension rise during stretch of stable bridges in the bag fibre is slowed by interconnexions with adjacent fibres which are not stuck at the same length. Another possibility concerns the distribution along the intrafusal fibre of stable cross-bridges. It still remains uncertain whether a dynamic fusimotor tetanus engages the contractile machinery along the entire length of the intrafusal fibre or whether there are contraction foci, with other parts of the fibre remaining passive (see for example Arbuthnott *et al.* 1982). If the latter is true then it is possible that following a fusimotor tetanus, stable cross-bridges re-form only in those regions which have been recruited by the tetanus, the condition of the remaining parts of the fibre depending on the previous history of stimulation. The rise in intrafusal tension during the test stretch may therefore depend on the relative stiffness of the different parts of the fibre. When the conditioning stimulus is alternating

movements, stable bridges along the whole length of the intrafusal fibre are likely to be detached so that re-formation would occur in all parts and the stiffness (of the contractile parts of the intrafusal fibre at least) would be uniform. It may be this uniform engagement of the whole intrafusal fibre which gives rise to the large initial burst.

Throughout this paper we have made the tacit assumption that stable cross-bridges do exist in intrafusal fibres and that in general terms they behave like stable bridges in extrafusal muscle. The existence of stable cross-bridges was first postulated by Hill (1968) to account for the short-range elastic component and filament resting tension in frog muscle. Since then, a similar short-range elasticity has been described for mammalian skeletal, cardiac and smooth muscle (see, for example, Joyce, Rack & Westbury 1969; Moss, Sollins & Julian, 1976; Siegman, Butler, Mooers & Davies, 1976) and evidence has been obtained that the time course of redevelopment of an initial burst of muscle spindles is similar to that of extrafusal short-range elasticity (Proske & Gregory, 1977). Direct evidence of an intrafusal short-range elasticity which correlates closely with the initial burst has been obtained for single isolated cat spindles by Hunt & Ottoson (1976).

There is an apparent discrepancy between the time course of stable cross-bridge formation described here and that measured as reappearance of the 'initial burst' by Proske & Gregory (1977). They found that full recovery of the amplitude of the initial burst required 10 s, while here we were able to produce maximal 'depression' in 3 s. The difference is, of course, in the nature of the measurement. When we held the muscle at the stretched length, full depression was manifest as soon as the intrafusal fibre had become stiff enough not to be able to take up the slack on shortening the muscle. That, however, would not prevent the formation of further stable bridges. It is likely therefore that the 10–20 s measured by Proske & Gregory is closer to the true time required for all stable bridges to form.

The potentiation of responses to brief dynamic fusimotor tetani after alternating movements (Proske, 1975) has a time course of decay which closely resembles the time required to develop a 'stuck' intrafusal fibre (Fig. 5). A simple explanation of the potentiation would be that when all stable bridges are broken by the series of stretches the intrafusal fibre becomes compliant and the weak contraction produced by the short fusimotor burst is readily able to distend the region of fibre supporting the sensory ending. Once the stable cross-bridges have been formed, the contraction has to detach these bridges, by compression from nearby actively cycling bridges before any movement of the fibre becomes possible. A further contributing factor may be that following the movement there may still be some slow yielding of series elastic elements so that as the stable bridges form the fibre becomes stiff but slack The fusimotor tetanus must take up this slack before it will begin to modulate the afferent discharge.

When we used a long-duration fusimotor tetanus during the test stretch the latency of onset to stimulation after the condition 'hold-stretched' was 80 ms later than after 'hold-short'. This presumably represents the time required by the contracting intrafusal fibre to take up the slack and raise the tension sufficiently to increase afferent firing above the passive level. Assuming that the contraction is only lightly loaded and uniformly engages the whole intrafusal fibre, an approximate value of maximum shortening velocity can be calculated. The length of muscle spindles is typically about one-third of the length of extrafusal fibres and the intrafusal fibres attach at their ends to connective tissue rather than to tendon, making for a compliant connexion.

Extrafusal fibres in soleus are about 26 mm long (Walmsley & Proske, 1981) while bag_1 fibres of spindles are about 8 mm long (Boyd, 1981). A 5 mm stretch applied to soleus would stretch the spindle by only 1·7 mm. Shortening over 1·7 mm in 80 ms (using a stimulation rate of 100 pulses/s) would therefore represent a shortening speed for the bag_1 fibre of 2·6 muscle lengths/s.

In conclusion we believe that for many of the known after-effects of stretch and dynamic fusimotor stimulation, one can usefully look for explanations based on the existence of stable cross-bridges. Whenever these effects are studied, it is important always to be sure that the condition of the spindle at the start of each test has been returned to a comparable state. This is because of the unusually long time course of the phenomenon.

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