Interactive report

Summing responses of cat soleus muscle spindles to combined static and dynamic fusimotor stimulation

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Abstract

This is a study of the summation of responses of primary endings of muscle spindles to combined static and dynamic fusimotor stimulation in the soleus muscle of the anaesthetised cat. Summation, expressed as a summation coefficient, \( K \), was measured under a variety of conditions including (1) at several, fixed muscle lengths using steady rates of stimulation, (2) using ramp-shaped increases in stimulation rates, (3) during passive stretches after muscle conditioning, and (4) during combined stretch plus stimulation. The predominant effect observed was occlusion, that is, the combined response was less than the sum of the two individual responses. The calculated mean \( K \) value for responses at fixed length was 0.156 (±0.005 S.E.M.). It was hypothesised that summation arose from electrotonic spread of generator current between the afferent terminals, either directly, or as a result of mechanical interactions between the contracting intrafusal fibres. Summation for responses from pairs of static fusimotor fibres gave a larger mean \( K \) value, 0.340 (±0.020 S.E.M.). These findings were interpreted in terms of a model of the muscle spindle where responses to dynamic fusimotor stimulation arise at one impulse generating site, and static fusimotor responses arise at another.

Theme: Sensory systems

Topic: Somatic and visceral afferents

Keywords: Muscle spindle; Fusimotor; Electrotonic; Stretch; Contraction; Summation

1. Introduction

Mammalian muscle spindles, as stretch receptors, are remarkably complicated structures. They consist of a bundle of intrafusal fibres, each supplied with terminals of a Ia axon and by terminals of one or more group II axons. Added to that is a motor innervation for each intrafusal fibre and an enclosing, fluid-filled connective tissue capsule. Muscle spindles have been studied intensively over the last 40 years and much new knowledge has been gained. Why spend so much effort on this receptor and its internal workings? We believe the spindle plays a major role in motor control and understanding how it works will give us important clues about central nervous strategies in the control of posture and movement.

Anatomical considerations [2] as well as some physiological observations have led to the conclusion that the mammalian spindle is a two compartment receptor [14]. One compartment contains the bag\(_1\) fibre, its Ia terminal and a \( \gamma_{\text{dynamic}} \) fusimotor supply. The second compartment comprises the bag\(_2\) and chain intrafusal fibres, their Ia terminals and a \( \gamma_{\text{static}} \) fusimotor supply. So the spindle can be thought of as responding to dynamic and static fusimotor inputs from separate compartments which are served by branches of the one afferent.

The experiments described here are concerned with the interactions that can occur between the two compartments of the spindle. Over the years evidence has accumulated in support of the idea that afferent impulses may be generated at more than one site in the spindle. That has raised the possibility of interactions, within the spindle afferent tree, between several, converging impulse streams. The current view is that the bag\(_1\) terminal is one source of impulses, the other being the terminals on bag\(_2\) and chain fibres. Since the Ia axon supplies both compartments, it has been
postulated that there is mixing of impulse traffic from these two sources, leading to pacemaker switching when one input is at a higher rate than the other [3,6,11]. These considerations have led to models of impulse initiation in the spindle [4,12]. When discharge rates from different pacemakers are similar, it has been proposed that there may be probabilistic mixing of the two impulse streams [7]. Finally, on the basis of the amount of summation of Ia responses to combined static and dynamic fusimotor stimulation, it has been proposed that generator current from one impulse generator may spread along the peripheral afferent tree to influence rates of firing at the second generator [1].

But does it actually matter whether there is leakage of receptor currents between generators? More generally, does it matter what kinds of interactions take place between different spindle compartments? In a recent study of the responses of spindles during treadmill locomotion of the decerebrate cat, patterns of fusimotor activity were deduced from discharge profiles of the Ia afferents [17]. The aim was to obtain insight into central nervous strategies making use of the fusimotor system during locomotion. One complication considered was the electrotonic interaction from receptor currents between impulse generators. It was found that when allowance was made for this kind of interaction, the response profiles predicted from known intrafusal activation patterns could be identified. In other words, understanding the processes within the spindle allows interpretation of its afferent responses in terms of an underlying motor strategy.

Here we re-examine the evidence for electrotonic spread of current from one generator to the other. In the main, we agree with the earlier conclusions that response summation seen with combined static and dynamic fusimotor stimulation is due to electrotonic effects [1]. However, we view this interaction not just as a simple spillover of current from one generator site to another, between spindle compartments which remain independent of one another in all other respects. Some of the observed behaviour is consistent with the idea that the amount of current generated at one site is influenced by transmission of forces between adjacent contracting intrafusal fibres.

2. Methods

All experiments were approved by the local Standing Committee for Ethics in Animal Experimentation. The experiments used the soleus muscle of the anaesthetised cat. A total of 15 cats was used, with weights ranging from 3.5 to 7.0 kg. Anaesthesia was induced with pentobarbitone sodium (nembutal, Boehringer Ingelheim) 40 mg/kg i.p. and maintained via a cannula in the cephalic vein, 12 mg/ml to effect. Anaesthetic depth was monitored using end tidal CO₂ levels (Datex Normocap) via a tracheal cannula as well as checking for the presence of blink and withdrawal reflexes and assessing the level of muscle tone. The animal’s body temperature was monitored using a rectal probe, and maintained in the range 38±1°C using a thermal blanket.

A laminectomy was performed exposing the lumbo-sacral spinal cord from L6 to S2. Dorsal and ventral roots were cut where they entered the cord and the peripheral portions dissected into small filaments to obtain functionally single afferent and motor axons. The left soleus muscle and its tendon were dissected free and the tendon attached via a fragment of calcaneum to an electromagnetic muscle stretcher regulated by feedback. Muscle lengths were referred to the maximum in situ physiological length (Lₘ). Muscle tension was monitored using an in-series strain gauge placed between the stretcher and the muscle. The left hindlimb was extensively denervated, including the hip, but sparing the nerve to soleus. Skin flaps of the hindlimb and back were fashioned into pools filled with mineral paraffin oil and warmed with radiant heat.

Action potentials were converted to TTL pulses and recorded digitally using a commercial analog to digital converter (PCI-MIO-16E-4, National Instruments Corp., Austin, Texas, USA) and a Power Macintosh computer. The recording and analysis were done using the software package Igor Pro (WaveMetrics, Lake Oswego, Oregon, USA).

Afferent axons, dissected in filaments of dorsal root, were identified as lying in the group I range by their conduction velocity. This was calculated from the latency of the recorded action potential in the root filament in response to stimulation of the muscle nerve and the conduction distance between stimulating and recording electrodes. Afferents were identified as coming from muscle spindles by their ‘in parallel’ behaviour, interruption of their discharge during a muscle contraction. Fusimotor axons were isolated in filaments of ventral root and were identified by the excitatory effect of their stimulation on spindle afferents in the absence of extrafusal tension. They were classified as static or dynamic by the effect of their stimulation at 100 pulses per second (pps) on spindle afferent responses to a ramp-and-hold muscle stretch of 5 mm at 10 mm/s [8].

Fusimotor axons were stimulated, alone and in pairs, in a pseudo-random sequence, so that the minimum interval between successive stimulation epochs was 20 s. Fusimotor stimulation was at 100 pps unless otherwise stated. Typically, summation coefficients were measured using 4 s duration tetani.

Spindle responses to fusimotor stimulation were quantified by averaging, using a backfill method. Here, instantaneous rates in each response were joined to create a continuous record and average rates were calculated for successive 200-ms segments of each record. This yielded approximately 20 data points for each 4-s period of stimulation.
Summation of responses of spindles to combined fusimotor stimulation was quantified using the summation coefficient, $K$ [9], defined as:

$$K = \frac{\text{Combined response} - \text{Larger individual response}}{\text{Smaller individual response}}$$

The value of $K$ therefore represents the fraction of the smaller individual response that would be needed to be added to the larger response to produce the observed combined response. A negative summation coefficient indicates that the response on combined stimulation is less than either of the two individual responses. A value of $K$ between 0 and 1 means that there is some summation, if less than algebraic, between pairs of responses. A value of $K > 1$ implies some, mutual, potentiation between responses.

For measurement of length effects, the 4 s of stimulation was done at a rate sufficient to produce a near-maximum fusimotor response, typically 200–250 pps. The order in which fusimotor fibres were stimulated, singly or in combination, was pseudo-randomised in each of nine trials, representing three sets of comparisons. A series of such measurements was carried out at each muscle length. The order of selection of each length was also pseudo-randomised.

Ramp stimulation was carried out at or near $L_m - 10$ mm, using a similar protocol to the length–effect measurements. One of the constant rate tetani was replaced with a frequency ramp stimulus that rose from 0 to 140 pps in 4 s. Experiments using combined stretch and fusimotor stimulation were done from an initial length of $L_m - 16$ mm and consisted of a 3-mm stretch at 0.5 mm/s during fusimotor stimulation at 100 pps. Again, stimulation order was pseudo-randomised.

The passive ramp stretches were performed at a test length of $L_m - 16$ mm. The muscle was stretched by 5 mm, a conditioning whole-muscle contraction carried out and the muscle held at this length for a further 5 s. The muscle was then returned to the test length and a further conditioning contraction (1 s at 100 pps) was used to selectively remove slack in intrafusal fibres (see Fig. 4). A pseudo-random order was used for fusimotor stimulation. Then the test stretch of 3 mm at 0.5 mm/s was imposed.

2.1. Statistical analysis

A comparison of values of summation coefficients for 20 pairs of static:dynamic and 13 pairs of static:static responses was carried out using an ANOVA (Data Desk; Ithaca, NY, USA), since some pairs were from the same animal.

3. Results

All of the observations were made on the responses of spindle primary endings to stimulation of pairs of fusimotor neurones, in all but one experiment, identified static and dynamic neurones. In the remaining experiment pairs of static fusimotor responses were compared.

3.1. Intrafusal isometric contractions

Here we refer to afferent responses to fusimotor stimulation when muscle length was held constant. Our working hypothesis was that if impulses were set up at separate and independent sites within the spindle afferent tree, representing the static and dynamic fusimotor pacemakers, there should always be total occlusion between them. In other words, for a pacemaker-switching model the combined response should never be bigger than the larger individual response, yielding a $K$ value of zero. We viewed a $K$ value of more than zero as a degree of response summation. Comparisons were made between responses to stimulation of 20 pairs of static and dynamic fusimotor fibres belonging to 16 different spindles. The findings were in line with our earlier observations [3] and those reported by others [1]. There was almost always some response summation, above the values for the individual responses, but with the combined response reaching less than the algebraic sum. The amount of summation varied between different response pairs. On some occasions the combined response was little bigger than the larger individual response, giving a $K$ value close to zero. Other responses showed substantial summation yielding $K$ values of 0.5 or more (Fig. 1). When values obtained from the 20 pairs of units were pooled, (Fig. 5), the mean $K$ value was 0.156±0.005 (S.E.M.).

Another measure of response summation made under isometric conditions was to keep the stimulation rate to one fusimotor fibre, either the static or the dynamic fibre, constant while a ramp increase in stimulation rate was applied to the other. An example is shown in Fig. 2. Notice that stimulating the $\gamma_{\text{dynamic}}$ fibre alone did not produce any response from the spindle over the range of stimulation rates between 0 and 20 pulses/s. Yet during combined stimulation over this range the response was consistently slightly above the $\gamma_{\text{static}}$ response alone. It suggests that even though the spindle was not generating impulses to the low rates of $\gamma_{\text{dynamic}}$ stimulation, it did produce a sub-threshold response which could make a contribution to the combined response. In general, response summation under these conditions, studied for four pairs of fusimotor responses, was the same as when both fusimotor fibres were stimulated at constant rates (Fig. 5).

3.2. Effect of muscle length

Our aim in these experiments was to try to obtain some insight into the mechanism responsible for response summation. The predominant effect expected from combined stimulation of a fusimotor pair was occlusion, as one generator, that firing at the higher rate, dominated the parent axon discharge, suppressing all activity from other
generators by re-setting [10]. To explain the summation seen on many occasions we considered two possibilities. One was that some of the current from the suppressed generator is able to spread through the afferent tree to sum with current at the dominant site [1]. That is, while re-setting may suppress propagated impulses in the second generator, this generator is still able to manifest its influence by virtue of spreading generator current. The second is that mechanical interactions between contracting intrafusal fibres can lead to response summation [3]. Here the idea is that summation results, not from current from a second generator, but as a result of forces exerted by contraction of adjacent intrafusal fibres acting to increase current at the pacemaker.

In an attempt to distinguish between these two alternatives we examined the effect of changing muscle length on summation of fusimotor responses. The rationale was that electrotonic spread of current should be essentially independent of muscle length. However, if summation was largely due to mechanical interactions between contracting intrafusal fibres, values of $K$ were likely to show some length dependence. At longer lengths, where intrafusal contractions were stronger and passive tension began to rise, the nature of any mechanical effects might be expected to change.

An example of responses at different muscle lengths is shown in Fig. 3. For this afferent there was a small, progressive increase in $K$ at longer lengths. The experiment was repeated for three other afferent fibres and mean ($\pm$ S.E.M.) $K$ values are shown in Fig. 3. An ANOVA carried out on the data showed that for lengths longer than $L_m - 14$, there was a significant length dependence for $K$ values ($P < 0.001$). There was a large amount of variability in calculated $K$ values over the length range $L_m - 20$ to $L_m - 14$. However, inspection of the actual records (upper traces, Fig. 3) shows that for each unit there was not very much variability within responses. The large standard error of values arose from comparisons between units. In other words, at short muscle lengths there were large differences between units in calculated $K$ values. Since electrotonic effects would be expected to be independent of muscle length, this variability between units was interpreted as suggesting that mechanical factors were playing a role.

### 3.3. Responses to passive stretch

While up to this point interactions were studied between spindle responses to fusimotor stimulation, impulses in spindles can also be initiated by stretch. Here, we have examined stretch responses with one or more intrafusal fibres contributing to generation of the responses.

We had shown earlier that because of muscle’s thixotropic property it is possible by conditioning the muscle to introduce slack into intrafusal fibres [16]. A spindle with slack intrafusal fibres shows a depressed response to muscle stretch. Furthermore, we showed that slack introduced into intrafusal fibres could be taken up selectively.
Fig. 3. Effect of muscle length on fusimotor response summation. Summation during combined static and dynamic fusimotor stimulation, measured at different muscle lengths. Symbols as in previous figures. Responses were recorded at 11 lengths beginning at \( L_m = 20 \) mm and incrementing in 2-mm steps. The continuous trace in the middle of the figure represents the \( K \) value calculated from the mean of three successive responses. For each of four units, this data was used to derive a single-value mean for \( K \) at each length. At the bottom are shown mean (±S.E.M.) values for \( K \) at each length calculated from a total of four units that is, a total of 12 responses. In all three traces, dashed lines indicate zero.

by fusimotor stimulation [15]. Stimulating a dynamic fusimotor fibre to a slack spindle should therefore lead to the selective take-up of slack in the bag\(_1\) fibre. The response to a subsequent test stretch should therefore be dominated by afferent activity arising in the bag\(_1\) fibre.

In this experiment, our hypothesis was that if response summation was the result of spread of generator current, this should also apply to passive stretch responses. Comparisons between stretch responses generated by only bag\(_1\) or only bag\(_2\) + chain sensory terminals, should show evidence of summation when terminals on all intrafusal fibres were contributing. It was thought unlikely that any mechanical effects would be involved since passive forces were likely to be low over the range of lengths through which the muscle was stretched.

An example is shown in Fig. 4. The stretch response of the spindle, with all intrafusal fibres slack, was depressed. Slack had been introduced by previously stretching the muscle to a longer length. When a dynamic fusimotor fibre was stimulated to take up some of the slack in the spindle, the subsequent stretch response increased significantly. When, instead, a static fusimotor fibre was stimulated, the stretch response was larger again. Conditioning the muscle with combined dynamic and static stimulation led to a further increase in stretch response. Comparing the effects of dynamic, static and combined fusimotor conditioning allowed calculation of \( K \) values. These were remarkably variable for rather small differences in the individual response rates (Fig. 5).

We also looked at summation of responses generated by stretch combined with fusimotor stimulation. The stretch was rather slow, similar to that illustrated in Fig. 4 (0.5

Fig. 4. Response summation to passive stretches after different forms of muscle conditioning. The diagram at the top indicates the conditioning sequence. The muscle was stretched by 5 mm at 10 mm/s, contracted using fusimotor-strength stimulation (filled bar) and then 5 s later returned to the test length. Then in some sequences a fusimotor fibre was stimulated at 100 pulses per second (second filled bar) before a slow test stretch of 3 mm at 0.5 mm/s was applied. Response in the absence of any fusimotor stimulation (crosses), \( \gamma_{\text{dynamic}} \) conditioning (open triangles), \( \gamma_{\text{static}} \) conditioning (open circles), conditioning by combined \( \gamma \) stimulation (filled squares). At the bottom of the figure is shown the calculated \( K \) value from \( \gamma_{\text{static}}, \gamma_{\text{dynamic}}, \) and \( \gamma \) combined conditioning. The trace above indicates the muscle length change. Notice that in the absence of \( \gamma \) conditioning, the spindle does not respond to the stretch until it has undergone nearly 2 mm of length change. Starting length \( L_m = 16 \) mm.
Fig. 5. Distribution of summation coefficients in different experiments. In each of the four experiments shown, $K$ values, averaged over 200 ms of record, for combined responses to static and dynamic fusimotor stimulation were plotted against the mean difference in discharge rates between the contributing individual responses. Values were plotted for summation during fusimotor stimulation at a constant rate with the muscle held at a fixed length (ISOMETRIC), where one fusimotor fibre was stimulated at a steady rate, the other at an increasing rate (FREQUENCY RAMP), after various forms of conditioning (PASSIVE STRETCH) and during combined stretch and fusimotor stimulation (STRETCH & STIMULATION). Notice that one afferent could generate up to 20 values for each of the conditions tested. For the ISOMETRIC and FREQUENCY RAMP responses, the open squares indicate values for a single afferent showing strong interaction and therefore a large $K$ value. The open triangles in the isometric responses were for units measured at short muscle lengths (less than $L_{0}-14$, highlighting the increase in variability of $K$ values.

$K$ values for responses from 13 measured at short muscle lengths (less than $L_{0}-14$), highlighting them pairs of static axons gave a mean of $0.340 \pm 0.020$ S.E.M. for a single afferent showing strong interaction and therefore a large $K$ value. The open triangles in the isometric responses were for units measured at short muscle lengths (less than $L_{0}-14$), highlighting the increase in variability of $K$ values.

mm/s). Here calculations gave $K$ values which spanned a range comparable to that seen with isometric contractions (Fig. 5). Thus, there appears to be something different about passive stretch responses when compared with active stretches or isometric responses. It is concluded that when $K$ values are calculated for passive stretch responses, the summing process cannot be interpreted simply in terms of summation of generator currents.

### 3.4. Comparisons between static fusimotor responses

The two-compartment model of the spindle envisages the bag fibre together with its afferent ending as one compartment, the bag plus chain fibres with their endings as the other. Models of this kind predict that there should be more summation between different static fusimotor responses than with static plus dynamic responses, since each static response would be acting on the same pacemaker. However, some examples of occlusion would also be expected, since there is the possibility of tension saturation when both fusimotor axons act on the one intrafusal fibre [4]. We have included here a number of comparisons between isometric contractions of individual static fusimotor responses and their sum. $K$ was plotted against the absolute rate difference, that is the rate difference regardless of sign, between the two responses (Fig. 6). The calculated $K$ values for responses from 13 pairs of static axons gave a mean of $0.340 \pm 0.020$ S.E.M. For the 20 pairs of static and dynamic axons, $K$ was $0.156 \pm 0.005$ S.E.M. There was a significant dependence of the $K$ value on pair type ($P < 0.001$) with values for static:static coefficients being larger than for static:dynamic coefficients (ANOVA). As can be seen in Fig. 6, another feature of static summations was the scatter in $K$ values. The coefficient of variation for the 13 response pairs was 1.39 compared with 0.67 for the static–dynamic pairs.

### 4. Discussion

When a fusimotor fibre to a spindle is stimulated, the intrafusal fibres it innervates contract to initiate impulses in the associated pacemaker. When a pair of fusimotor fibres is stimulated, several intrafusal fibres contract and there is the opportunity for activity to arise at several pacemakers. The experimental observation is that during combined stimulation the response is almost always a little larger than either of the individual responses. The question is what is the origin of this additional activity. We argue below that the competitive interaction, probabilistic mix-
ing, between several pacemakers cannot account for it. It has recently been proposed that even though one pacemaker may be suppressed by resetting, it remains a source of generator current which spreads throughout the Ia afferent tree to influence activity at the dominant generator [1]. We propose that under some conditions an additional mechanism may be operating. The amount of generator current at the dominant site may also be increased mechanically by forces transmitted from adjacent contracting intrafusal fibres [3]. Our general conclusion is that our data does not allow us to assign precise values to contributions from either mechanism and the most parsimonious view would be that both are operating. The precise contributions from each are likely to change, depending on the prevailing mechanical conditions in the spindle, as suggested by the increase in variability in $K$ values between afferents at short lengths and the trend towards larger $K$ values at longer lengths (Fig. 3).

When we combined all of the $K$ values for isometric contractions of dynamic:static pairs, including those measured at different muscle lengths, we arrived at a mean of 0.156 ($\pm$ 0.005 S.E.M.). This is rather lower than the range of 0.25–0.5 reported by Banks et al. [1]. The explanation for this difference probably relates to differences between muscles. Tenuissimus is a notoriously difficult muscle from which to obtain reproducible Ia responses, because of compliant connections between spindles, extrafusal fibres and tendon. Responses from soleus are more consistent. In any case, the $K$ value of 0.156 for soleus is rather low and emphasises that the overriding phenomenon during combined fusimotor stimulation is response occlusion.

Another mechanism, one which has been invoked repeatedly in the past to account for response summation, is that of probabilistic mixing [1]. If, as we believe, there are two separate impulse generators within the spindle, then the parent axon will have convergent impulse streams at the branch point which serves the two generators. Interactions between two impulse generators lead to complete dominance by one generator provided its mean rate is significantly higher than that of the other generator. This is because its impulses travel backwards down the other branch and re-set the discharge from that generator [10]. If, however, the impulse rates in the two streams are similar and both discharges exhibit a degree of variability then the opportunity for impulse mixing arises. For example, a chance long interval in the dominant generator may allow impulses from the second generator to briefly access the discharge in the parent axon. Probabilistic mixing is therefore a regularising process, leading to a small increase in mean rate and a reduced variability of the discharge in the parent axon [7].

In discussing the range of summation coefficients obtained from trapezoidal stretches, stimulus rate modulation and isometric responses, Banks et al. [1] assigned most of the effects to electrotonic interactions. The observed dependence of the $K$ value on the difference between the contributor rates they attributed to the mechanism of probabilistic mixing. While in this study we did not see such a rate dependence (Figs. 2 and 5), we also argue that as a mechanism to account for response summation probabilistic mixing is likely to be trivial.

To test for a contribution from probabilistic mixing to response summation, Eagles and Purple [7] generated a series of artificial impulse trains, adjusted to have a degree of inter-impulse variability determined by a given coefficient of variation. The interval distributions were generated for the two trains with the same variability and on combining them a distribution was calculated which was predicted by probabilistic mixing [7]. So, to achieve a $K$ value of 0.156, using a mean rate for each fusimotor response of 30 impulses per s, would require a coefficient of variation in the individual responses of 0.25. This is the degree of irregularity exhibited by a spindle under random fusimotor activity [13]. The coefficient of variation during constant fusimotor stimulation will be much lower. So under the conditions of our experiment, responses do not show sufficient inter-impulse variability for probabilistic mixing to make a significant contribution. Some more direct calculations, based on actual responses, have led to a similar conclusion [3,5]. None of this, however, excludes the possibility that in the freely moving animal conditions may arise where the influence of probabilistic mixing may become more important.

If response summation was a simple matter of spread of generator current from a suppressed generator to the generator responsible for the recorded activity, the degree of summation should change little as the spindle is stretched out to a range of different lengths. This is because the nerve endings themselves are not likely to stretch very much, and there should be little change in electrotonic path length between generators. Yet at short lengths $K$ values were very different for different pairs of responses while at long lengths there was much less variability (Fig. 3). Our interpretation of this finding is that at short lengths, where passive tensions are low, forces transmitted by adjacent contracting intrafusal fibres are more likely to reach the pacemaker to influence its rate of discharge. The size of the influence varies unpredictably between fusimotor responses for different spindles. At longer lengths as passive tension rises, forces in the spindle are more likely to be longitudinally directed, leading to less cross-transmission between intrafusal fibres (see Ref. [3]).

An unexpected finding was that summation coefficients calculated for passive stretch responses after static, dynamic or combined fusimotor conditioning gave a wide scatter of values (Fig. 5). By contrast responses to combined stretch and fusimotor stimulation gave $K$ values comparable to those measured under isometric conditions. We do not have a satisfactory explanation for this difference in behaviour. Since the stretches were applied at an initial length of $L_m$=16 mm, this variation in $K$ values is
reminiscent of that seen at short muscle lengths, under isometric conditions (Fig. 3).

In addition to measuring summation of static and dynamic responses, we have made some observations on interactions between pairs of static fusimotor responses. Here we anticipated significant summation between receptor currents since our model had bag2 and chain intrafusal inputs both acting on the same pacemaker [4]. Consistent with that view, the calculated mean value of $K$ was significantly higher than for static:dynamic summation. However, some $K$ values within the sample of responses were quite low. We interpret these as the result of intrafusal tension saturation. So, for example, if a particular intrafusal fibre was activated near-maximally by stimulation of one fusimotor fibre and the intrafusal targets of a second fusimotor fibre overlapped with those of the first, a partial saturation of tension responses might be expected on combined stimulation [4]. Such a mechanism presumably accounted for the relatively low $K$ values obtained in a recent study of static:static summations [3].

Inspection of the Ia afferent tree topology [1] shows that distances between terminals on bag2 and chain fibres are smaller than between bag1 terminals and the rest of the tree. It means that based on the electrotonic spread of current mechanism larger $K$ values would be expected for static:static interactions. Such an effect will have to be taken into account when interpreting the scatter of measured $K$ values.

To conclude, it is not possible to attribute to any single mechanism the summation of fusimotor responses measured in the way described in these experiments. There are various underlying assumptions about the stimulus:tension relationship and linearity of tension to current and current to impulse relationships. Despite these uncertainties the general conclusion is that when dynamic and static fusimotor responses are summed, one largely occludes the other. The remnant summation is the result of summing currents from electrotonic spread between pacemakers as well as from currents arising from mechanical interactions between the contracting intrafusal fibres. There is less occlusion for responses to pairs of static fusimotor fibres. All of this means that the spindle cannot be seen as a simple, two-compartment structure since there are influences exerted across compartments. However, whenever there are competing sources of impulse traffic within the receptor, only one will predominate at any one time. Which generator dominates is likely to change as conditions in the spindle change.

References