

## THE RESPONSE OF DE-EFFERENTED MUSCLE SPINDLE RECEPTORS TO STRETCHING AT DIFFERENT VELOCITIES

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It has long been known that when a muscle is stretched from one length to another its muscle spindle endings discharge more rapidly during the dynamic phase of stretching than they do subsequently at the new length (Matthews, 1933; Granit & Homma, 1959). More recently it has been shown under a variety of conditions that the primary endings, supplied by Group I afferents, are appreciably more sensitive to such dynamic stimuli than are the secondary endings, supplied by Group II afferents (Appelberg, 1962; Bessou & Laporte, 1962; Cooper, 1959, 1961; Harvey & Matthews, 1961; Jansen & Matthews, 1962*a*; Lundberg & Winsbury, 1960). Together these experiments provide a fairly comprehensive picture of the differences between primary and secondary endings, but in any one set of these experiments the effects of only a comparatively limited range of velocities of stretching were investigated, and the experiments also differed in the muscle used and as to whether or not the fusimotor nerve fibres were active. The present experiments were performed to compare the responses of the primary and secondary endings of de-efferented muscle spindles of a single muscle to a wide range of velocities of stretching.

### METHODS

The experiments were performed on ten cats anaesthetized with pentobarbitone sodium (Nembutal, Abbott Laboratories). The methods were similar to those used in previous studies (Jansen & Matthews, 1962*a*; Matthews, 1962) which give fuller details.

*Recording.* The discharge from single afferent fibres from muscle spindles lying in the right soleus muscle was recorded from dorsal root filaments. The soleus muscle was completely isolated from the spinal cord by cutting the L6, L7, S1 and S2 dorsal and ventral roots. The amplified action potentials were used to trigger a circuit which gave a direct display of the instantaneous frequency of discharge of the ending. With it each action potential caused a momentary brightening of a cathode-ray tube spot, and the height of the spot above zero was proportional to the reciprocal of the time interval since the preceding action potential. In the ranges normally used this display was accurate to 5 impulses/sec or better. Changes in frequency were, in general, more accurately recorded with it than the absolute frequency, as in a few of the experiments the display developed a slight zero error (less than 5 impulses/sec). Mean frequencies of discharge could, however, also be obtained from a subsidiary display on the same cathode-ray tube. This consisted of a linear vertical

sweep at 10 c/s and after photography was equivalent to a conventional record at 10 cm/sec, but with the action potentials represented by dots instead of by spikes.

The length of the muscle and the tension in it were recorded on a separate cathode-ray tube. The two cathode-ray tubes were photographed together on slowly moving paper. During the dynamic phase of stretching the spot of the cathode-ray tube with the frequency display was swept to the right to permit better observation of the dynamic behaviour of the ending. This was done by applying to the X plates of the cathode-ray tube a voltage proportional to the extension of the muscle (the linearly increasing control voltage corresponding to the required position of the stretcher was actually used, see Matthews, 1962). The effective recording speed during the dynamic period of stretching therefore increased linearly with the velocity of stretching. The spots of the cathode-ray tube recording length and tension were not so swept to the right, consequently these records were not in vertical register with those displaying the frequency of discharge; this made the records slightly confusing at first sight. The records of length and tension have therefore been omitted from the figures, and in the period of dynamic stretching has been indicated by ink bars drawn in afterwards.

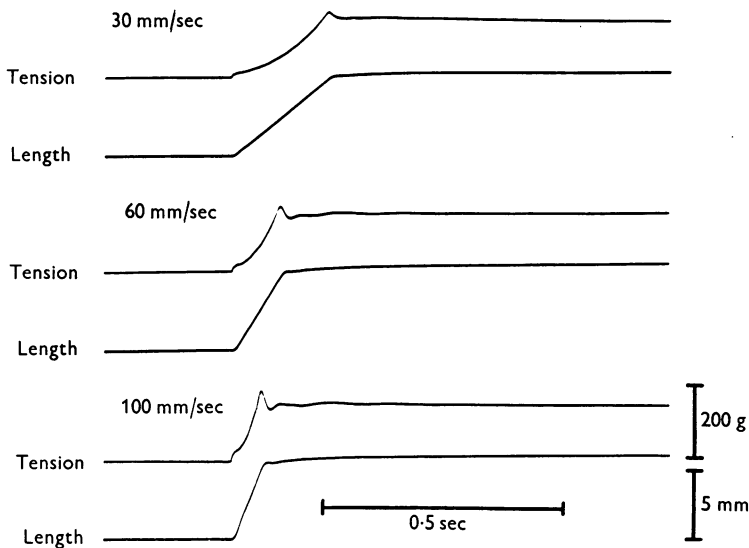


Fig. 1. Records showing the movement of the 'stretcher' and the tension in soleus on extending soleus by 6 mm at three different velocities.

*Application of stretch.* The soleus muscle was stretched by an electro-magnetic servo-mechanism (Matthews, 1962) which was used to apply stretches at velocities from 0.1 to 100 mm/sec. Most of the observations were made by using stretches of 5 or 6 mm which were maintained for 1-5 sec and which were repeated every 10 or 15 sec. This relatively high repetition rate did not always allow the endings to regain their normal discharge at the initial length in between stretches (cf. B. H. C. Matthews, 1933), but tests suggested that this had little effect on the results to be described. The final length of the muscle corresponded approximately to the greatest length that the muscle could take up *in situ*. The tension at the initial length was usually under 50 g wt. At velocities of stretching above about 30 mm/sec the performance of the 'stretcher' deteriorated. There was a slight oscillation in velocity at the beginning of the stretch, and in position on completing the dynamic phase of stretching (amplitude < 0.1 mm). In addition, for all velocities of

stretching there was a slight creep of extension at the end of stretching. It was approximately exponential, with a time constant of about 0.1 sec, and an amplitude proportional to the velocity of stretching (30 mm/sec stretching gave a creep of about 0.2 mm). These effects are shown in Fig. 1, where it will be seen that the oscillations are very much more prominent in the tension record than in the length record. This is probably mainly due to the visco-elastic properties of the muscle causing appreciable tension changes for very small length changes, but it is also possible that some of the oscillations occurred not in the 'stretcher', but in the linkage connecting it to the muscle (tendon, detached piece of calcaneum, tendon hook, 5 cm long wire connecting linkage). It is clear that even if an ideal mechanical wave form is generated it may be distorted in its transmission to the receptors in the muscle. Such distortion may also occur inside the muscle if its mechanical properties are not homogeneous longitudinally. It is felt, however, that the apparatus, though capable of improvement, was adequate for the present investigation, as it permitted comparison of the response of an ending at the end of the period of dynamic stretching, when the velocity was constant, with its response at the final length shortly afterwards when the oscillations and creep had ceased. The transient response of the ending on starting and stopping stretching could not, however, be confidently studied for the more rapid stretches.

*Measurement of conduction velocity.* Muscle spindle afferents were identified on the basis of their behaviour during a twitch of the muscle elicited by stimulating the muscle nerve (B. H. C. Matthews, 1933). The conduction velocity of their afferent fibres was measured by stimulating the muscle nerve and recording the impulse thereby evoked in the dorsal root filament. The conduction distance was sometimes determined by dissecting out the conduction pathway in its entirety, but sometimes the roots were not dissected through the intervertebral foramina and the length of this portion was estimated by measurements over the bones; the two methods applied to the same animal gave results differing by less than 0.5 cm (in approximately 15 cm total conduction distance).

## RESULTS

The two distinct kinds of sensory ending which can be distinguished inside the muscle spindle by histological study are now generally called the primary and the secondary ending (Ruffini, 1898; Barker, 1948; Boyd, 1962). Measured at the spindle, the axon of the primary ending is larger than that of the secondary ending, and it is widely considered that in the muscle nerve the afferents from the primary endings fall into Group I (diameter  $> 12\mu$ ) and those from the secondary endings into Group II (diameter  $4-12\mu$ ). Thus in an electrophysiological experiment an ending may be classified as a primary or secondary ending depending upon whether the conduction velocity of its afferent fibre is above or below 72 m/sec (Hunt, 1954). But until some other means can be found for identifying an ending functionally, it is impossible to decide whether this dividing line is correctly placed, whether it is sharp, and how far it is consistent from muscle to muscle and from animal to animal. For this reason and to simplify the description of the results the 75 endings studied in the present experiments have been divided into three groups: 34 with afferent fibres conducting at over 80 m/sec, which have been assumed to be primary endings; 27 with afferent fibres conducting

at below 60 m/sec, which have been assumed to be secondary endings; and 14 with afferent fibres with intermediate conduction velocities, upon which judgement may be reserved. The actual distribution of the conduction velocities of the different afferent fibres may be seen from Fig. 12.

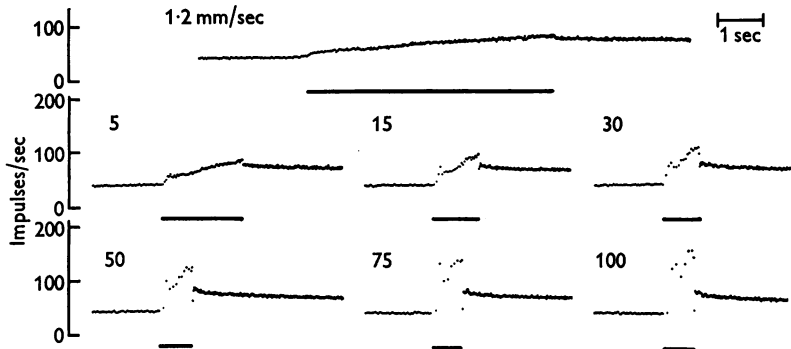


Fig. 2. The response of a secondary ending (afferent fibre conduction velocity, 50 m/sec) to an extension of 6 mm applied at velocities ranging from 1.2 to 100 mm/sec. The records show the frequency of discharge of the ending; each spot represents an action potential and its height above zero (see scale) is the reciprocal of the time interval since the preceding action potential. The bars beneath the records indicate the periods of stretching; on completion of the dynamic phase of stretching, the final extension was maintained until the end of the record (see Fig. 1). The time calibration (top right) does not apply to the dynamic periods of stretching, which are on more open time scales different for each record (the recording speed increases linearly with the velocity of stretching, see Methods). The velocity of stretching is shown (mm/sec) above the beginning of each record.

### *Secondary endings*

The secondary endings were, in comparison with the primary endings, rather insensitive to the dynamic stimulus of stretching. This led to a simpler pattern of behaviour which will be described first. The responses of a fairly typical secondary ending on applying a stretch of constant extent (6 mm) at a series of different velocities are shown in Fig. 2. After an initial increase in the frequency of discharge at the beginning of the stretching, the frequency of discharge of the ending increased progressively as the stretch increased. At the end of the dynamic phase of stretching the frequency fell by about the amount it increased at the beginning of the stretching. The higher the velocity of stretching the greater was the maximum frequency of discharge, and the greater the rise at the beginning and the fall at the end of the dynamic period of stretching. The discharge rate at the final extension, measured 0.5 or 1 sec after completion of the dynamic phase of stretching was, however, approximately independent of the velocity of stretching used to reach the final extension.

The muscle spindle ending may be considered as an instrument responding to both the length of the muscle and the velocity at which it is being stretched. A measure of its velocity response may be obtained by measuring the fall in its frequency of discharge at the end of the dynamic phase of stretching; for this is the change in the response of the ending when the velocity changes from a finite value to zero, while the length of the muscle remains the same. Figure 2 shows that while most of this fall in frequency occurred abruptly, part occurred more slowly; for some

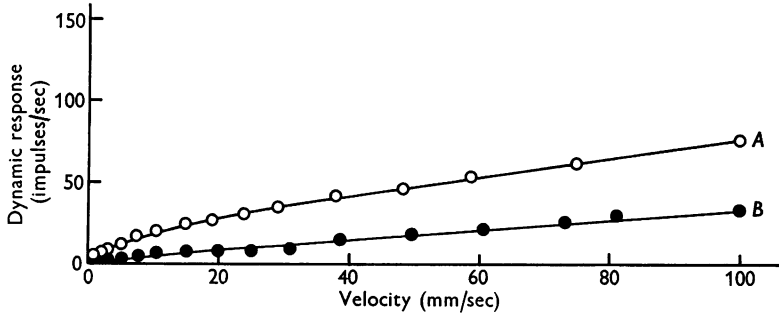


Fig. 3. The relation between the dynamic response and the velocity of stretching for two different secondary endings (*A*, *B*). *A* is the ending of Fig. 2. *B* is the ending of Fig. 4*B*. The dynamic response is the difference between the frequency of discharge just before the end of the dynamic period of stretching (mean of frequencies of last two action potentials) and that occurring 0.5 sec later. (Where more than one observation was made the mean has been plotted.)

endings this slow fall was more prominent. The relative magnitudes, and the time course, of the fast and slow falls in frequency would be important for any detailed quantitative analysis of the behaviour of an ending (Pringle & Wilson, 1952; Davey & Roberts, 1958). In the present experiments, partly because of the limitations of the 'stretcher', the dynamic behaviour of an ending has been assessed solely by measuring the difference between its frequency of discharge at the end of the dynamic phase of stretching and that at the final extension half a second after the end of the dynamic phase of stretching, when the creep and oscillations of the 'stretcher' had ceased. Jansen & Matthews (1962*a*, *b*) called this measurement the 'dynamic response' of the ending and this term of convenience will continue to be used here. Figure 3 shows graphically the dependence of the magnitude of the dynamic response upon the velocity of stretching for the ending of Fig. 2 (upper curve) and for another secondary ending from a different preparation (lower curve). The points for the higher velocities of stretching have only limited significance, because there were so few action potentials during the dynamic phase of stretching and their interspike intervals varied somewhat irregularly. For the more rapid stretches

the dynamic responses of both endings increased approximately linearly with the velocity, but for velocities below 20 mm/sec the upper line is slightly curved. For these endings, and for most of the other secondary endings, the size of the dynamic response for any particular velocity of stretching was approximately independent of the final extension and the amplitude of stretching within physiological limits.

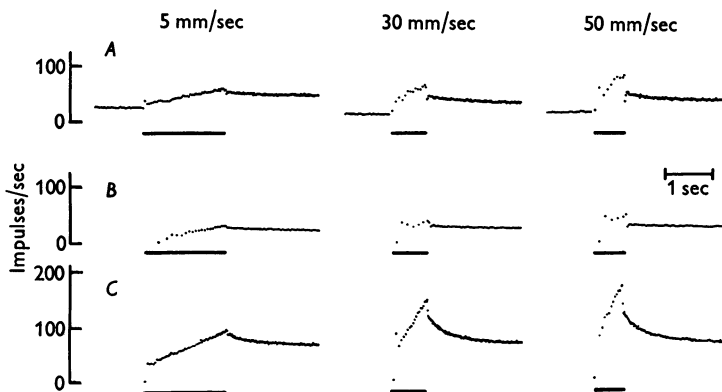


Fig. 4. Records illustrating the variation of behaviour of different secondary endings. Endings *A* and *B*, which were typical, were in the same preparation; ending *C*, which was atypical, was in another preparation. Endings *B* and *C* had no discharge at the initial length of the muscle. Method of recording the same as in Fig. 2. The extension was 6 mm. The velocity is shown above the records. The conduction velocities of the afferent fibres of *A*, *B*, and *C* were 46, 27 and 37 m/sec respectively. Periods of stretching shown by bars. (Some isolated spots re-touched.)

Figure 4 illustrates further the range of behaviour found with different secondary endings. The upper ending *A* is similar to that of Fig. 2, though from another preparation. The middle ending *B* had no discharge at the initial length used, though it was in the same preparation as *A*, and had a rather small dynamic response, which has been plotted as the lower curve of Fig. 3. The bottom ending of Fig. 4*C* from another preparation had an unusually large dynamic response for a secondary ending and much of the fall of frequency on completion of the extension occurred slowly, rather than rapidly; the initial rapid fall in frequency was only slightly larger than that of ending *A*.

#### *Primary endings*

During the dynamic phase of stretching the primary endings usually discharged at much higher frequencies than did the secondary endings, even though the maintained discharge of the two kinds of ending at the final length was often not very different. Figure 5 shows the behaviour of a primary ending which had a large response to the dynamic stimulus of

stretching, and which was not discharging at the initial length. At the beginning of the stretching there was an 'initial burst' of three to five impulses, as already described by Jansen & Matthews (1962*a*) for slow stretching. For velocities of stretching up to 50 mm/sec the frequency of discharge then tended to increase progressively as the muscle was extended,

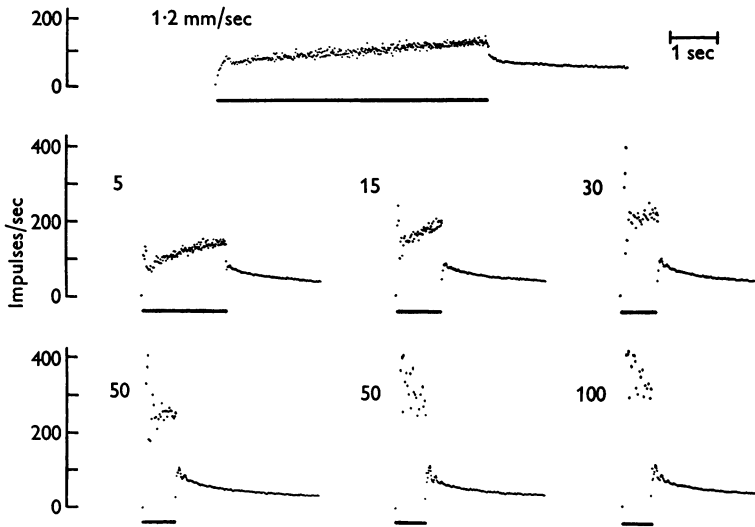


Fig. 5. The response of a primary ending (conduction velocity of afferent fibre, 103 m/sec) to an extension of 6 mm at velocities ranging from 1.2 to 100 mm/sec. Method of recording the same as in Figs. 2 and 4. Periods of stretching shown by bars; velocity of stretching in mm/sec shown above each record. (One or two high-frequency spikes may have failed to be recorded at the beginning of the two fastest stretches; they were observed in other records taken at a lower sensitivity. Some isolated spots retouched.)

while at higher velocities of stretching it tended to fall (see B.H.C. Matthews, 1933, Figs. 6 and 7). In all records there was an abrupt fall in frequency on completion of the dynamic period of stretching, followed by a smaller slow fall, which was complicated after the higher velocities of stretching by the response of the ending to the oscillations of the 'stretcher'. In the upper curve of Fig. 6 the dynamic response of this ending, calculated as before, is plotted against the velocity of stretching.

Not all primary endings, however, gave responses during the stretching which were of as simple time course as those illustrated in Fig. 5. One example is illustrated in Fig. 7, in which the discharge of the ending, after increasing only slightly at the beginning of the stretching, increased suddenly in the middle of the period of stretching, and appeared to show an 'initial burst' here, for the frequency then fell again although the stretching continued. Such endings do not lend themselves to any simple quantitative

treatment, but for reasons which will be outlined later it is felt that these irregularities do not deserve emphasis. The dynamic response, that is the decrease in the discharge of the ending on completion of the stretching, has therefore still been used as a measure of the dynamic behaviour of the ending. But it has only been determined for the lower velocities of stretching for which the frequency of discharge at the end of the stretching had

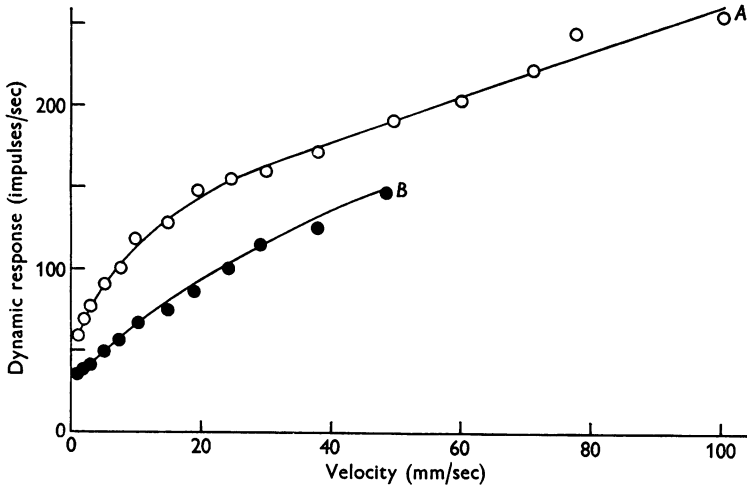


Fig. 6. The relation between the dynamic response and the velocity of stretching for two different primary endings (*A*, *B*). *A* is the ending of Fig. 5. *B* is the ending of Fig. 7. The dynamic response is the difference between the frequency of discharge just before the end of the dynamic period of stretching (mean of frequencies of about the last four action potentials) and that occurring 0.5 sec later. (Where more than one observation was made the mean has been plotted.)

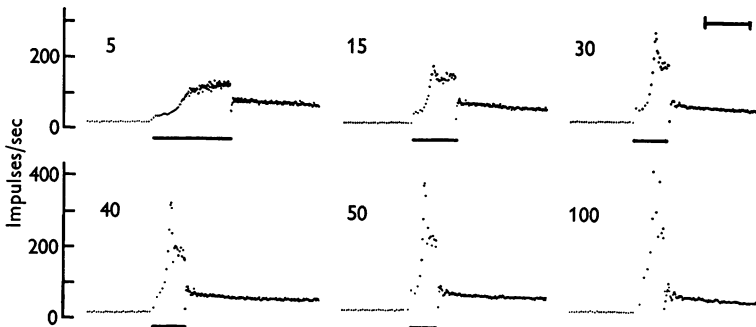


Fig. 7. The responses of a primary ending (afferent fibre conduction velocity, 97 m/sec) which gave its highest frequency of discharge in the middle of the period of stretching, if the velocity of stretching was high. Method of recording the same as in Fig. 2. Periods of stretching shown by bars; velocity of stretching (mm/sec) shown above each record. Extension 6 mm. (Some isolated spots retouched.) Time calibration, top right, 1 sec.



settled to a nearly constant value, as measured over 4–5 inter-spike intervals. The lower curve of Fig. 6 shows the plot of dynamic response against velocity for the ending of Fig. 7.

The two curves of Fig. 6 show certain common features, which were also found for the other primary endings studied (see also Fig. 11). First, the initial part of the relation between dynamic response and velocity appears to be convex upwards. This was clearly so for the upper curve of Fig. 6, but rather less definitely so for the lower curve, many of the points of which would have been reasonably fitted by a straight line. For a certain number of other endings a linear relation would also have fitted most of the points which could be reliably determined; but the finding of endings such as *A* of Fig. 6 and the strong tendency for all deviations from linearity to be in this direction discouraged any attempts to fit straight lines to experimental points such as those of Fig. 6*B*. The relation between the absolute value of the frequency of discharge at the end of the stretching and the velocity of stretching was also usually non linear (as follows from the approximate constancy of the frequency of firing at the final length when the velocity of stretching was varied). Figure 6 shows, secondly, that both endings still had an appreciable dynamic response on stretching at 1 mm/sec, and that if a straight line had been fitted to the points in the lower range of velocities (say 1–20 mm/sec), then it would not have passed through the origin on extrapolation.

The actual effect of stretching at velocities below 1 mm/sec was, for practical reasons, studied with an extension of 1 mm instead of 6 mm. Figure 8 illustrates the usual finding, that a detectable dynamic response persisted down to stretching at 0.1 mm/sec, the slowest velocity used. At the slowest rates of stretching, however, the fall in the frequency of discharge did not occur as abruptly at the end of stretching as it did on stretching more rapidly. (Indirect arguments suggest strongly that this slow fall did not merely reflect a slow cessation of the stretching, but the matter could not be checked experimentally. The slight differences in the discharge at the final length after the different velocities of stretching did not occur regularly.) The relation between the dynamic response and the velocity, though no doubt slightly non-linear, could usually be approximately fitted by a straight line from 3 mm/sec down to 0.2 or 0.3 mm/sec, and the slope in the range below 1 mm/sec was about the same as that from 1 to 3 mm/sec. There was sometimes a rather smaller response at 0.1–0.2 mm/sec than would have been expected from the linear approximation, but the matter was not investigated in detail.

*Threshold length for the dynamic response.* The magnitude of the dynamic response of primary endings was usually approximately independent of the initial length, the final length and the amplitude of stretching, when

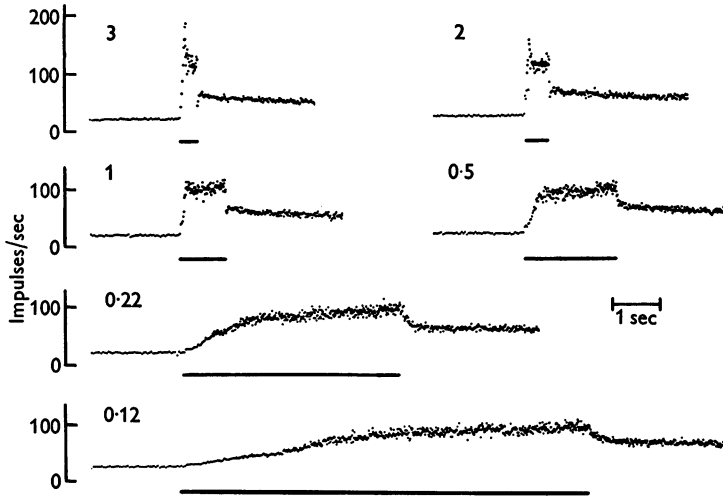


Fig. 8. The responses of a primary ending to 1 mm stretches applied at velocities from 3 down to 0.12 mm/sec (velocity, mm/sec, shown above each record). Same ending as Fig. 7 and final length approximately the same as in Fig. 7. Method of recording the same as in Fig. 2, except that unlike Fig. 2 the 1 sec calibration applies to the whole of the present figure, including the period of stretching (again indicated by bars).

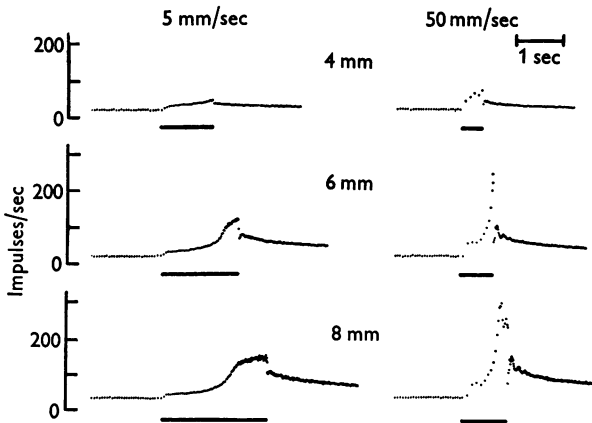


Fig. 9. The responses of a primary ending (afferent fibre conduction velocity, 91 m/sec) which only gave an appreciable dynamic response when the final length of the muscle was above a certain threshold value. Method of recording same as in Fig. 2. Periods of stretching shown by bars. The initial length was the same for all records; the final length was increased from above downwards so that the extensions applied were 4, 6 and 8 mm. Left-hand extensions applied at 5 mm/sec; right-hand extensions applied at 50 mm/sec.

these were varied so that the final length of the muscle was in the last 6 mm or so of the maximum possible length of the muscle in the body. This was best seen for the slower velocities of stretching when the discharge during the stretching consisted of an appreciable number of impulses (Jansen & Matthews, 1962*a*, Figs. 4 and 6 illustrate this for 3 mm/sec stretching). Occasionally, however, the dynamic response increased markedly on increasing the final length of the muscle above a critical value. An example is shown in Fig. 9 (a similar effect was also shown by the ending of Fig. 7). For an extension of 4 mm the ending behaved like a secondary ending and gave little dynamic response, whether the velocity of stretching was 5 or 50 mm/sec; for larger extensions it gave an appreciable dynamic response, typical of that of other primary endings. A similar threshold muscle length was found for the dynamic response when such endings were tested with extensions of 1 or 2 mm, starting from different initial lengths. The occurrence of a threshold for the dynamic response is very unlikely to have been due to failure of transmission of the extension through the muscle to the muscle spindle, because in other similar experiments (Matthews, 1962, Fig. 4*B*, and unpublished) stimulation of single fusimotor fibres caused the dynamic response to appear at lengths of the muscle otherwise below the threshold length.

*'Burst' responses.* Those endings which only gave a dynamic response when the length was increased above a certain threshold value tended to give a burst of impulses when stretched through the length at which the dynamic response appeared. The burst was, however, only marked for the higher velocities of stretching. Such behaviour appeared to be shown by the ending of Fig. 7. The reason that such irregular discharges and 'initial bursts' were earlier minimized is that both the threshold length for the dynamic response and the initial burst are probably not found when the intrafusal fibres are contracting and are therefore probably both physiologically unimportant. This effect of fusimotor activity was seen in the experiments of Jansen & Matthews (1962*a*) in which the activity was that occurring 'spontaneously' in the decerebrate cat, and has also been seen on stimulating single fusimotor fibres (Matthews, unpublished). Jansen & Matthews (1962*a*) also showed that 'bursts' were not responses to acceleration, for they were not found when the velocity of stretching was increased from 1 to 3 mm/sec in the middle of stretching. In any case the burst responses, whether at the beginning or in the middle of the period of stretching, did not lend themselves to quantitative analysis both because they were inconstant in magnitude on repeating the same stretch, and because the time intervals between the successive action potentials of the burst often differed so much that it was not clear what could usefully be measured. It may be seen, however (Figs. 5, 7 and 8), that the frequency of the impulses in the burst increases with the velocity of stretching. The burst tended to be seen best when the initial length of the muscle was fairly great, and when the muscle was stretched by successive increments (see Jansen & Matthews, 1962*a*, Fig. 7*c*). Secondary endings hardly ever showed an appreciable initial burst, though sometimes the first impulse during the stretching was at a slightly higher frequency than those immediately following it. The difficulty created by the occurrence of the burst is one reason why the velocity sensitivity of the endings has been assessed by their behaviour at the end of the stretching rather than at the beginning. Another reason for this is that there may be some hysteresis in spindle behaviour, so that the discharge of an ending at the beginning of stretching is different

depending on whether the muscle had previously been stretched up to the initial length or had been released from a longer length, as occurred in the present experiments (see B. H. C. Matthews, 1933).

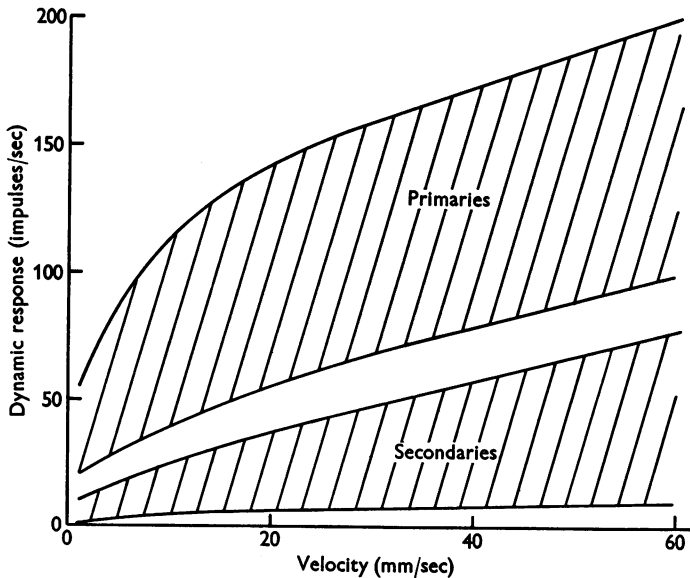


Fig. 10. Comparison of the relation between the dynamic response and the velocity of stretching for primary endings and for secondary endings. The graphs for 31 out of 34 primary endings (classified on the basis of the conduction velocity of their afferent fibres), fell into the upper shaded area. The graphs for 23 out of 27 secondary endings fell into the lower shaded area. The graph has not been extended beyond 60 mm/sec because the dynamic responses of some endings could not then be reliably determined.

#### *Comparison of the responses of different endings*

In the series of ten experiments, the dynamic responses of endings with large axons (conduction velocity  $> 80$  m/sec, the presumed primary endings) were consistently greater than those of endings with small axons (conduction velocity  $< 60$  m/sec, the presumed secondary endings) for all velocities of stretching. This is illustrated by Fig. 10 which shows that distinct regions of the graph of dynamic response against velocity were occupied by the responses of most of the presumed primary endings and by those of most of the presumed secondary endings. These areas included the responses of all but three of the 34 presumed primary endings studied, and all but four of the 27 presumed secondary endings; the responses of the 14 endings with axons conducting at 60–80 m/sec have, however, been omitted.

The three atypical presumed primary endings gave responses just at the top of the secondary region of Fig. 10. The four atypical presumed secondary endings had typically

small dynamic responses for velocities of stretching below 5 mm/sec, but above this their dynamic response increased unusually fast with velocity, so that their responses fell into the primary region for velocities of stretching of 50 mm/sec and above. The response of three of these endings was, however, qualitatively unlike that of the primary endings, as slightly over half their dynamic response (measured over 0.5 sec) decayed slowly, whereas most of that of the primary endings decayed abruptly. The response of one of these endings has been shown in Fig. 4C. If their dynamic behaviour had been assessed by measuring the fall in frequency occurring in the first 0.1 sec after completing the stretching, they would have fallen into the secondary region of Fig. 10 (in contrast, if their dynamic response had been measured over 1 sec rather than 0.5 sec it would have been still larger). These three atypical presumed secondary endings were found in a single experiment, and they also gave larger than average static responses at the final extension when it was maintained. (This experiment also contributed two of the atypical primary endings, but other endings behaved normally.) The conduction velocities of the axons of the secondary endings were not near the arbitrary border line of 60 m/sec, but were 29, 33, and 37 m/sec. The conduction velocity of the axon of the fourth atypical presumed secondary ending was 50 m/sec, and this ending did not show a slow fall of frequency on completion of the extension.

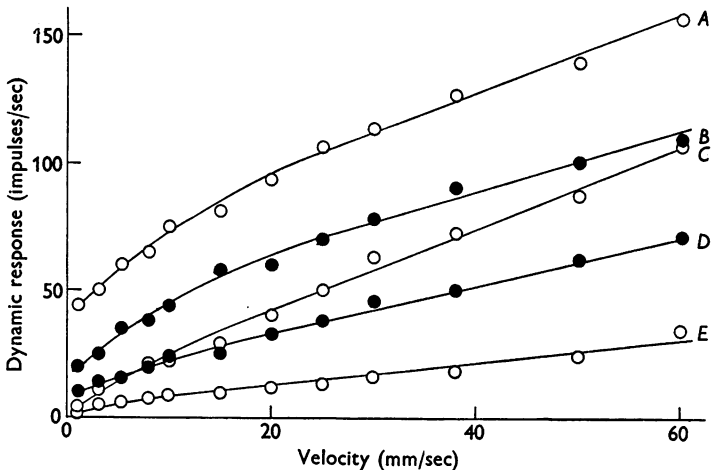


Fig. 11. The relation between the dynamic response and the velocity of stretching for five afferent endings (*A*, *B*, *C*, *D*, *E*), all studied in a single preparation. The response of ending *C* moved from the secondary ending region to the primary ending region of Fig. 10 as the velocity of stretching increased. (Conduction velocities of afferent fibres of *A*, *B*, *C*, *D*, and *E* were 104, 61, 80, 58 and 44 m/sec, respectively.)

Bearing in mind these exceptions, it may provisionally be suggested that if the dynamic responses of a soleus ending fall wholly into the primary or secondary regions of Fig. 10 then it is likely to be a primary or a secondary ending. This functional classification was applied to the 14 endings studied which, on the basis of the conduction velocities of their afferent fibres alone (60–80 m/sec), might not perhaps be confidently classified as primary or secondary. Five behaved as primary endings and three behaved as secondary endings; their dynamic responses were not all on the

border lines of their respective classes (see also Fig. 9, Harvey & Matthews, 1961*b*). The remaining six endings, however, were not immediately classifiable on this basis, as they showed intermediate behaviour. This is illustrated by Fig. 11, which shows graphically the dynamic responses of five endings, all studied in a single experiment. Ending *A* was a typical primary ending (afferent fibre conduction velocity, 104 m/sec). Ending *E* was a typical secondary ending (afferent fibre conduction velocity, 44 m/sec). Ending *B*, though it had a relatively slow axon (conduction velocity 61 m/sec), was just at the bottom of the primary region of Fig. 10, while ending *D* with a similar sized axon (conduction velocity, 58 m/sec) was at the top of the secondary region. Ending *C*, however, with a larger axon (conduction velocity, 80 m/sec) passed from the secondary region to the primary region as the velocity of stretching increased. Thus not every ending could be sharply classified as a primary ending or as a secondary ending on the basis of its response at the end of the dynamic phase of stretching.

Previous work has left it uncertain how far muscle spindle endings fall into two functionally distinct groups, and how far they form a single population with certain properties varying continuously with the conduction velocities of their afferent fibres. The over-all results of the present experiments would probably be compatible with either type of distribution. This is further shown by Fig. 12, which for each ending studied relates the magnitude of its dynamic response to the conduction velocity of its afferent fibre. Scatter diagram *A* for 3 mm/sec stretching would not be well fitted by a single straight line, while scatter diagrams *B* for 30 mm/sec and *C* (the difference between *A* and *B*) would be more readily so fitted. These possible correlations have not been examined statistically.

Figure 12*A* and *B* also serves to confirm the differences, which have already been described, between the dynamic responses of endings with large axons and endings with small axons. Figure 12*C* shows further that the slope of the relation between the dynamic response and the velocity in the range 3–30 mm/sec tends to be much less for endings with small axons than for endings with large axons (differences in slope above 30 mm/sec tended to be less marked). It might be suggested that it is the value of the dynamic response relative to the magnitude of the maintained discharge at the final extension which is important, rather than the absolute value of the dynamic response. If this was so it would make little difference to the comparison of the dynamic behaviour of different endings, for there was relative uniformity in the static behaviour of the endings at the final extension. This is shown by Fig. 12*D*, in which the frequency of discharge at the final length, measured 0.5 sec after completing a stretch of 5 mm/sec, is plotted against the conduction velocity of the afferent fibre of

each ending. The final length was usually the same for the different endings studied in a single experiment, and in the different experiments lay within the last 4 mm of the maximum length of soleus possible in the body. Figure 13 shows a tendency for the maintained discharge of the primary endings to be greater than that of secondary endings, as might be expected from their lower threshold of extension for maintained firing (Hunt, 1954; Harvey & Matthews, 1961; Bessou & Laporte, 1962); but the difference is

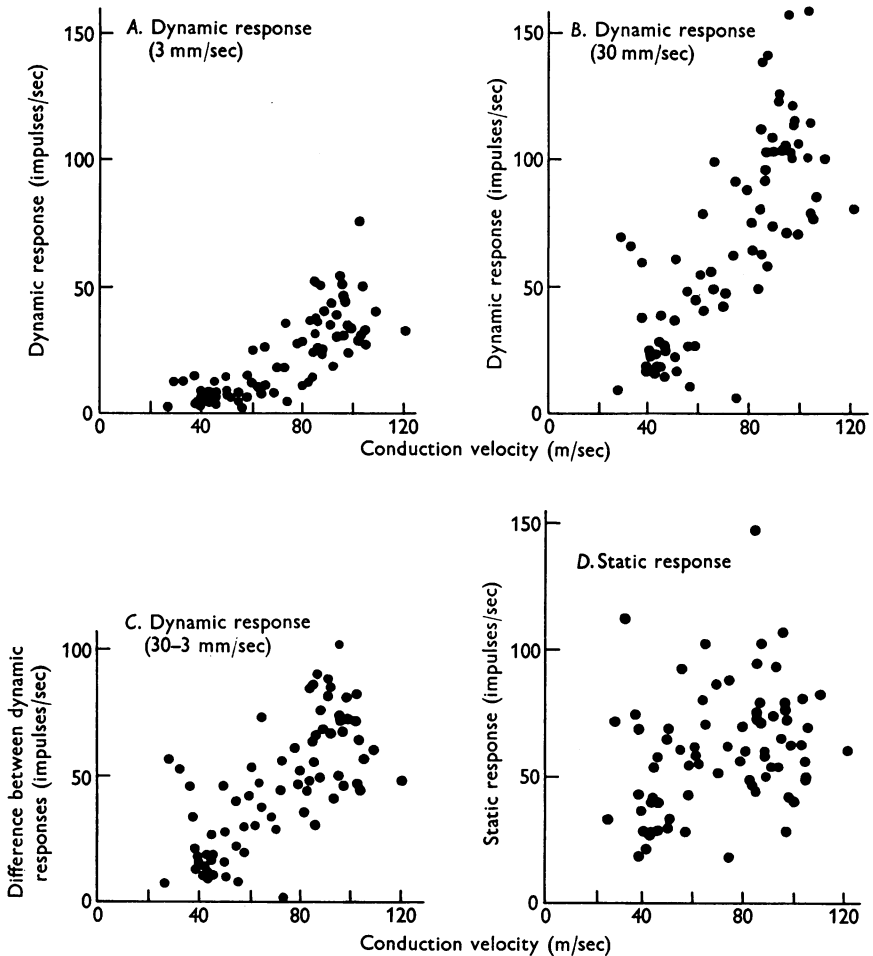


Fig. 12. Scatter diagrams relating various responses of 75 endings to the conduction velocities of their afferent fibres. *A*, *B*, *C*, show dynamic responses; *D* shows static responses. The velocity of stretching was 3 mm/sec for *A* and 30 mm/sec for *B*. *C* shows for each ending the difference between its dynamic responses on stretching at 3 mm/sec and 30 mm/sec. *D* shows the frequency of discharge at the final extension (static response), measured 0.5 sec after completing a stretch at 5 mm/sec.

too slight to be taken as the cause of the differences in their dynamic responses. Nor does the slope of the frequency-extension relation, as measured either by slow stretching or 0.5 sec after completion of stretching, differ greatly for the primary and the secondary endings of the soleus (Harvey & Matthews, 1961; Jansen & Matthews, 1962*b*), so that expressing the dynamic responses of the endings in relation to their slopes would not have abolished the difference between the primary and the secondary endings.

#### DISCUSSION

The present results extend previous work by showing that the greater response to dynamic stimuli of the primary than of the secondary ending of the muscle spindle is found at all velocities of stretching likely to be of physiological significance. They also show that in the range 3–30 mm/sec the effect of increasing the velocity is greater in primary than in secondary endings. The difference between primary and secondary endings is perhaps most marked at velocities of stretching of 1–2 mm/sec, as the dynamic response of secondary endings is then only a small proportion of their total response, while that of primary endings is then still appreciable. Many endings could be identified as primary or secondary endings as certainly on the basis of their dynamic behaviour as on the conduction velocity of their afferent fibres. The fact that a few of the endings had intermediate properties is hardly surprising in view of the complexity and variability of the structure of the spindle. Primary endings may occur in simple, complex or tandem spindles, and the number of intrafusal fibres of either kind in the spindle may vary. Secondary endings may lie at various distances from the equatorial region of the spindle, and besides their terminations on the nuclear-chain fibres, may also have terminations on the nuclear-bag fibres. It is possible that all endings would have been functionally classifiable if different testing conditions had been used, and if their intrafusal fibres had been contracting, for a muscle spindle which is de-efferented cannot be considered to be behaving normally. In view of the histological distinctiveness of primary and secondary endings (Boyd, 1962) it seems more useful at the moment to emphasize the functional distinctiveness of most of the primary and of most of the secondary endings, rather than to concentrate attention on endings with transitional properties under the present limited range of experimental conditions.

It may be concluded, in agreement with previous workers (Laporte, 1962; Jansen & Matthews, 1962*b*), that primary and secondary endings signal different information to the central nervous system, the former measuring length plus velocity and the latter mainly length. But the secondary endings were not completely insensitive to the velocity of



stretch, though for many of them the dynamic response only became appreciable at velocities of stretching so high that there was time for only a very few impulses to be discharged during the actual stretching (see Fig. 4*B*). This effect would, of course, have been even more marked if stretches of smaller amplitude had been used, which would further have emphasized the functional differences between primary and secondary endings (Bessou & Laporte, 1962).

The finding that some primary endings had a threshold length, below which their dynamic response was inappreciable even though the ending was discharging in the absence of stretching (static response), is readily explained by the hypothesis of Jansen & Matthews (1962*a*). They suggested that the dynamic response of the primary ending was mainly derived from its branches on the nuclear-bag intrafusal muscle fibres, while the maintained static response was derived in addition from its branches on the nuclear-chain intrafusal fibres. If the minimum length of the muscle required to activate the nuclear-chain branches of the primary ending was less than that required to activate the nuclear-bag branches, the present findings would be explained, and such hypotheses can be developed whatever the nature of the mixing of the signals from the different terminals of the primary ending. Other explanations are, however, also possible, so the present results cannot be taken as proving the hypothesis of Jansen & Matthews (1962*a*).

The sensitivity of the primary ending to the velocity of stretching is of interest in relation to its role in the 'servo control of movement' and the reflex regulation of muscle contraction, for its dynamic sensitivity tends to counteract the effects of the time delays involved in transmitting activity round the stretch reflex loop (Merton, 1951, 1953; Pringle & Wilson, 1952; Partridge & Glaser, 1960). The present experiments show that the velocity sensitivity of de-efferented primary endings, as crudely assessed by their dynamic responses, differs in two ways from that which would be given by a system linear in the servo-engineering sense (one in which doubling the input doubles the output). First, the relation between the dynamic response and the velocity is slightly curved (though this could be true of a linear system with exponential time lags). Secondly, on extrapolation of the approximately linear lower portion of the curve it does not pass through zero, but gives a positive dynamic response for zero velocity of stretching, which is to say that doubling the velocity of stretching does not double the dynamic response. These non-linearities contrast with the approximately linear measure of the length of the muscle (above an arbitrary zero) given by the frequency of discharge of both primary and secondary endings, recorded under either static conditions, or during slow stretching (Bessou & Laporte, 1962; Eldred, Granit

& Merton, 1953; Harvey & Matthews, 1961). The non-linearities may perhaps have depended upon using large stimuli, for though the stretches were in the physiological range they may have been much larger than the movements which the primary endings are used to control in the body. Also, it is possible that the non-linearities, like the initial burst at the beginning of stretching, are a property of the de-efferented ending only and are not found for endings influenced by physiologically occurring fusimotor activity. Many secondary endings, however, behaved approximately linearly. If the non-linear behaviour of the primary ending is also found under more physiological conditions, then the question of its significance for reflex mechanisms will be raised. Meanwhile it is sufficient to note that these non-linearities suggest that the response of primary endings to sinusoidally varying extensions may be non-sinusoidal (harmonic distortion) and thus complicate the analysis of spindle and reflex properties by this otherwise attractive form of mechanical input.

#### SUMMARY

1. The discharge of single afferent endings of de-efferented muscle spindles in the soleus muscle of the anaesthetized cat was studied on stretching the muscle at velocities from 0.1 to 100 mm/sec.

2. Endings with afferent fibres conducting at over 80 m/sec were assumed to be primary endings. They were all markedly sensitive to the dynamic stimulus of stretching and their frequency of discharge during the stretching increased progressively with the velocity of stretching.

3. Endings with afferent fibres conducting at below 60 m/sec were assumed to be secondary endings. Some were very insensitive to the dynamic stimulus of stretching, and only a few of them were as sensitive as the least sensitive of the primary endings. This difference was found at all velocities of stretching. The maintained discharges of the two kinds of ending at the final length differed comparatively little.

4. Endings with afferent fibres conducting at 60 to 80 m/sec sometimes showed properties intermediate between those of the main masses of primary and secondary endings, as defined above.

5. These results, which were obtained while using a wider range of velocities of stretching than has been used previously, confirm the greater dynamic sensitivity of the primary than of the secondary ending of the muscle spindle.

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