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THE RESPONSE TO STRETCH OF HUMAN INTERCOSTAL MUSCLE SPINDLES STUDIED *IN VITRO*

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SUMMARY

1. The discharge properties of human muscle spindles have been studied *in vitro* in a preparation based on the biopsied external intercostal muscle.

2. The static and dynamic responsiveness of thirty-six endings in twenty visualized and histologically identified spindles have been investigated using amplitudes and velocities of stretch likely to encompass those occurring *in vivo*.

3. The dynamic index, measured at a stretch velocity of 3 mm/sec, ranged from 3 to 40 impulses/sec and was distributed bimodally, consistent with the presence of primary and secondary endings.

4. The relationship between the dynamic index and the velocity of stretch was approximately linear both for primary and secondary endings up to the maximum velocity tested (10 mm/sec).

5. The frequency/extension relationship was approximately linear for both primary and secondary endings. The mean values of the slope for primary and secondary endings were $16{\cdot}1 \pm 8{\cdot}3$ S.D. of the observation and $12{\cdot}1 \pm 6{\cdot}5$ impulses/sec per five per cent extension.

6. The slopes of the frequency/extension relationship for endings lying in the same spindle were positively correlated, significant at the 10 % level.

7. It was estimated from the results *in vitro* that the position sensitivity of human intercostal spindles *in vivo* ranges from 2 to 21 impulses/sec per millimetre.

INTRODUCTION

A functional role for the muscle spindle in the control of movement in man has been demonstrated now by a number of experimental studies. Motoneurone excitability during a voluntary contraction, for example, has been shown to depend on spindle afferent discharge, both for limb muscles (Hansen & Hoffman, 1922; Angel, Eppler & Iannone, 1965) and for intercostal muscles (Newsom Davis & Sears, 1970) by the occurrence of a 'silent period' in the electromyogram when the mechanical load is

suddenly reduced. Conversely, sudden stretching of the contracting muscle causes an excitatory response whose characteristics are consistent with autogenetic excitation from spindle afferents (Hammond, Merton & Sutton, 1956; Newsom Davis & Sears, 1970; Marsden, Merton & Morton, 1972). The potential effectiveness in man of spindle Ia afferent discharge is illustrated by the response of a muscle to vibration which, by analogy from animal studies, is assumed to act selectively on spindle primary endings. Such stimulation causes a tonic reflex contraction of the muscles (Hagbarth & Eklund, 1966) and with repeated application can produce an almost maximal motor response (Marsden, Meadows & Hodgson, 1969). In addition, a sensory role for spindle afferents in man is suggested by the distortion of joint position sense which occurs when vibration is applied to the muscle (Goodwin, McCloskey & Matthews, 1972).

These human studies, relying in part on evidence from animal work, have drawn attention to the need for direct information about the discharge properties of the individual spindle. Such information has recently become available with the development by Hagbarth & Vallbo (1968) of a technique for recording from human muscle afferents with a microelectrode inserted percutaneously into peripheral nerve. This technique has already provided a valuable insight into the functional role of the spindle (Vallbo, 1970, 1971, 1974*a*, *b*). But as Vallbo (1970) himself pointed out, even under optimal conditions there is some uncertainty about the nature of the receptor generating the afferent discharge. Furthermore, for technical reasons only weak mechanical stimulation or small passive joint movements are possible (Vallbo, 1970, 1974*a*).

An *in vitro* preparation has therefore been developed, based on the biopsied external intercostal muscle, which allows detailed investigation of a visualized and histologically identified human muscle spindle (Newsom Davis, 1973*a*), and which can thus provide information about spindle discharge characteristics to complement that obtained with the percutaneous method. Such information will also be needed for any future study of the direct effects of neuromuscular disease on receptor function. In the present study, the static and dynamic responsiveness of human spindle afferents to ramp and hold stretches have been investigated using amplitudes and velocities of stretch likely to encompass those occurring *in vivo*. Some of the features distinguishing primary from secondary endings are described. A brief report of part of these results has already appeared (Newsom Davis, 1973*b*). An *in vitro* study of another aspect of the behaviour of human spindle afferents, namely the response to small sinusoidal stretches, has recently been described in a short report by Poppele & Kennedy (1974), who obtained their material from biopsy of a finger extensor muscle.

METHODS

Material. Intercostal muscle biopsy was undertaken in patients undergoing thoracotomy for chest or heart disease. Permission for the biopsy was obtained after the nature of the procedure had been explained. The patients' ages ranged from 41 to 70 and none had clinical evidence of neuromuscular disease.

Technique. The preparation is based on the biopsied external intercostal muscle which others have used in the study of neuromuscular transmission in man (Creese, Dillon, Marshall, Sabawala, Schneider, Taylor & Zinn, 1957; Elmqvist, Johns & Thesleff, 1960). A segment of the muscle was excised from a site usually in the fifth or sixth interspace over the lateral aspect of the chest wall. The muscle was

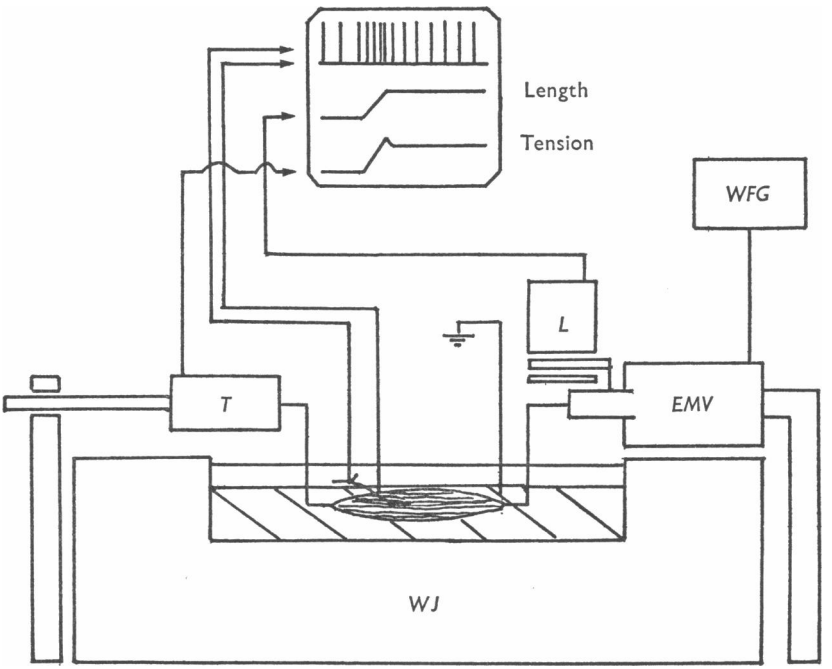

Fig. 1. Diagram to illustrate the experimental arrangement. The muscle spindle, either lying in its fascicle or isolated, is mounted in a Ringer bath. A nerve branch is shown lifted into paraffin oil. One end of the fascicle or spindle is attached to the tension transducer (*T*), and the other to an electromagnetic vibrator (*EMV*) which can be driven by a wave form generator (*WFG*). Length changes are recorded by a displacement transducer (*L*) in parallel. The temperature of the bath is thermostatically controlled by a surrounding water jacket (*WJ*).

then immediately placed in a modified Ringer solution, as used by Hubbard (1961), of the following composition: NaCl, 137 mM; KCl, 5·0 mM; $CaCl_2$, 2·0 mM; $MgCl_2$, 1·0 mM; NaH_2PO_4, 1·0 mM; $NaHCO_3$, 12·0 mM; glucose, 198 mg/100 ml. 5 % carbon dioxide in oxygen was continuously bubbled through the solution giving a pH

7·35–7·4. The specimen was taken from the Chest Hospital to the laboratory (a journey of about 20 min) and set up in a small preparation bath (Fig. 1). The Ringer solution was changed regularly during the course of the experiment.

The initial dissection was carried out at room temperature. When the muscle fascicle containing the receptor had been isolated, the temperature of the solution was gradually raised and maintained at 34–35° C by means of a thermostatically controlled water jacket surrounding the bath.

Under the dissecting microscope, small nerve branches could be identified. One of these was dissected free, brought up into a layer of liquid paraffin and placed on a fine platinum electrode for monophasic recording; the other electrode was placed on the muscle. The source of any afferent discharge was located by selective stretching of bundles of muscle fibres until an obvious change in the discharge was elicited. Careful dissection then usually revealed the receptor. Where more than one receptor was contributing to the discharge, nerve branches were cut until the discharge from only a single receptor remained, as judged by the response to a stretch applied close to the pole of the visualized receptor. The muscle fascicle in which the receptor lay was then isolated or in some experiments the spindle itself was isolated. One end was tied with a silk thread to a fine steel rod connected to a tension transducer (Devices UF1 or RCA 5734) and the other end was attached similarly to an electromagnetic vibrator which, by means of a wave form generator, could impose ramp and hold length changes on the spindle. The length changes were measured by a displacement transducer in parallel. The length and tension signals together with the afferent discharge were displayed on a CRO and recorded on magnetic tape for later analysis. A pulse height discriminator enabled single populations of spikes to be fed separately to a frequency meter whose voltage output was proportional to the instantaneous spike frequency.

The available length of afferent nerve from which recording was made usually exceeded 3 mm. The distance between the recording electrodes was arranged so that spike amplitudes were maximal in order to facilitate discrimination between individual spike populations.

Satisfactory responses could be obtained from the spindle with this preparation at 15 hr or more after biopsy. At the end of the experiment, the receptor was marked, when necessary, for later histological identification.

RESULTS

The receptor generating the afferent discharge was visualized during the experiment (see Methods). Muscle spindles were usually recognized from their *in vitro* appearance and location in the muscle. In addition, a silent period could be elicited in the afferent discharge when a twitch was evoked in the muscle by nerve stimulation, as shown for three units in Fig. 2*A*. For comparison, Fig. 2*B* shows a response of two tendon organ afferents to a muscle twitch. An increase in the discharge is evident during the phase of rising tension.

Satisfactory recordings were obtained from a total of thirty-six endings from twenty spindles. Two afferent units could be recorded from about half the spindles, distinguished by their spike amplitudes, while from a third only a single afferent could be recorded. From a few spindles, three

afferents were recorded. In three instances, afferent units showed atypical responses. These are described separately and are not included in the main analysis.

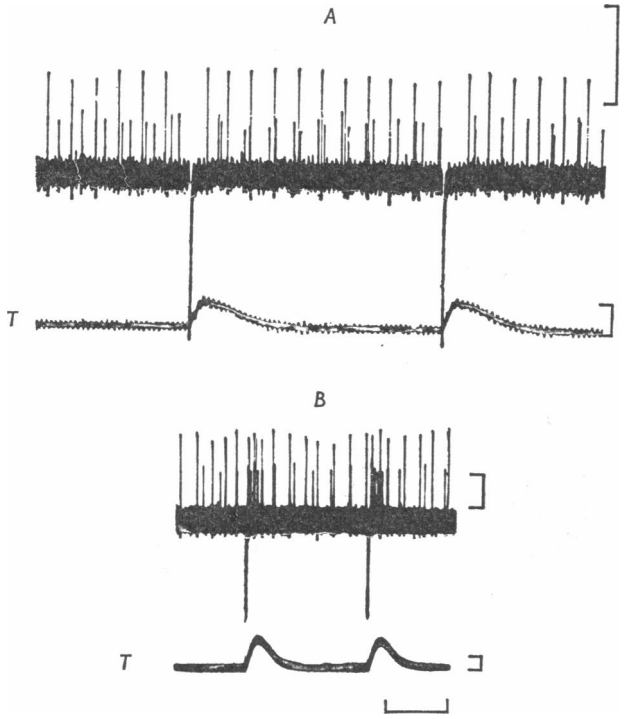

Fig. 2*A*. Three afferent units, distinguished by their spike amplitudes, recorded from a single spindle of a 64 yr old man. Note the 'silent period' in the afferent discharge during the phase of rising tension, shown on the tension record (*T*), when a twitch is induced in the muscle by nerve stimulation.
Fig. 2*B*. Two afferent units from a tendon organ of a 39 yr old woman. Both units increase their firing frequency when a twitch is elicited in the muscle by nerve stimulation.
Calibrations: 50 μV, 1 g; time scale, 250 msec in *A*, 500 msec in *B*.

Dynamic sensitivity

Fig. 3 illustrates the responses of three endings lying in the same spindle of a 60 yr old man. The spindle was subjected to a ramp and hold stretch of constant amplitude (1 mm) but at two different velocities (2 and 6 mm/sec). The resting length was set close to that at which the unit with the lowest threshold just began to fire ('threshold length'). Three populations of spikes can be distinguished by their amplitudes, those of the two smaller spikes showing some overlap which results in occasional gaps in the

instantaneous frequency displays. For both velocities of stretch the large spike ('*a*') shows a greater dynamic sensitivity than either of the others. The dynamic index, i.e. the decrease in firing frequency occurring in the first 0·5 sec after the end of the stretch (Jansen & Matthews, 1962; Crowe & Matthews, 1964), at 6 mm/sec, for example, was 29·7 impulses/sec for spike '*a*', 9·3 for spike '*b*' and 6·2 for spike '*c*'.

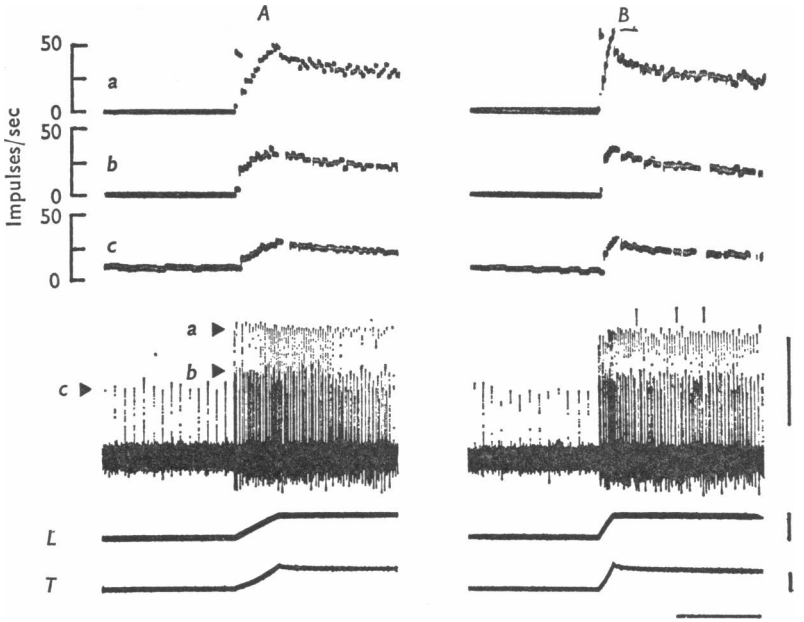

Fig. 3. Response to stretch of three afferent units recorded from a single spindle of a 60 yr old man. Amplitude of stretch 1 mm; velocity of stretch 2 mm/sec in *A* and 6 mm/sec in *B*. The instantaneous frequency is shown for each of the three units identified as *a*, *b* and *c*. Slight overlap in the amplitudes of *b* and *c* and simultaneous occurrence of spikes cause occasional gaps in the instantaneous frequency display. The greater dynamic responsiveness of unit *a* is evident at both velocities of stretch. This unit also shows an initial burst of two impulses. Note the similarity of response between units *b* and *c*.
L, length; *T*, tension. Calibrations: 100 μV, 1 mm, 2 g, 1 sec.

The dynamic index was measured at a stretch velocity of 3 mm/sec in all afferent units. Values ranged from 3 to 40 impulses/sec, and had a bimodal distribution as shown by the histogram in Fig. 4.

Classification of endings

Morphological studies of human intercostal muscle spindles have shown that the primary endings are innervated by a single group I*a* afferent fibre

and the secondary endings by one or two group II afferent fibres (Kennedy, 1970). The usual means of distinguishing group I*a* from group II afferents has been by measuring their conduction velocities (Hunt, 1954), but this method cannot be used in the *in vitro* preparation where the length of the afferent nerve is short. The bimodal distribution of the dynamic index, evident in Fig. 4, is consistent with the presence of two groups of endings,

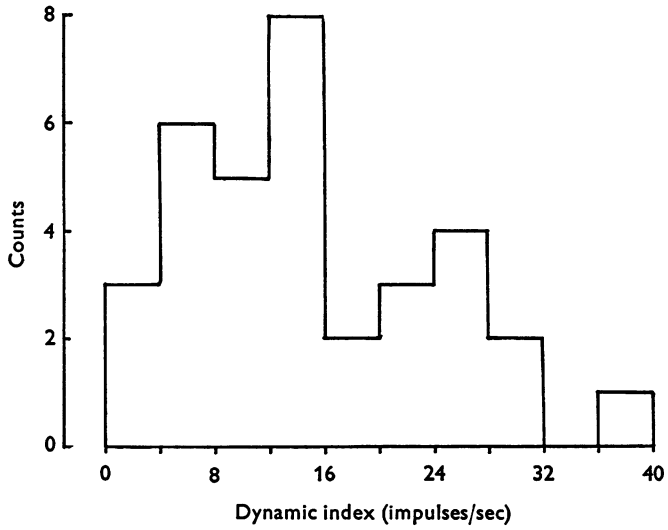

Fig. 4. Histogram illustrating the distribution of the dynamic index measured at a stretch velocity of 3 mm/sec in thirty-three afferent units.

and provides a basis for classification similar to that used by Andersson, Lennerstrand & Thoden (1968) in their study of cat intercostal spindles *in vivo*, where measurement of the afferent conduction velocity is also not practical (Euler & Peretti, 1966). Studies of endings lying in the same spindle have helped to resolve uncertainties about the extent of the overlap between the two groups. Pairs of afferent units in which spike amplitude differed by more than one third also showed clear differences in their dynamic sensitivities, the larger spike having the greater dynamic responsiveness as shown, for example, in Fig. 3. Although the distance between the recording electrodes could not always be made optimal for differentiating spike amplitudes (see Methods) this relationship between spike amplitude and dynamic responsiveness was, with one exception, a consistent finding and is illustrated for eight pairs of endings in Fig. 5. In this figure, the velocity of stretch was 3 mm/sec in each case, and spike amplitude has been normalized by expressing the amplitude of the smaller spike as a percentage of the larger. It can be seen that the larger spike in

any pair has the greater dynamic index, consistent with its origin from the primary ending. These observations accord with the expected relationship between spike amplitude and nerve fibre diameter (Hunt, 1951) from which one would expect the large spike to be generated by a large diameter (group I*a*) fibre innervating the primary ending.

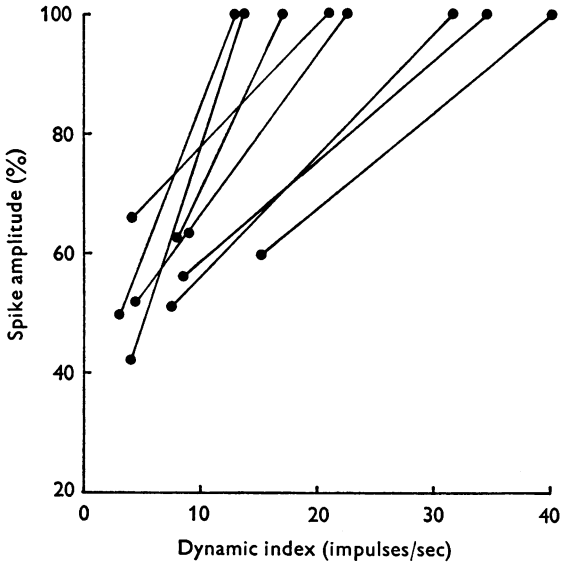

Fig. 5. Plot of spike amplitude against dynamic index for pairs of endings lying in the same spindles in which spike amplitudes differ by more than one third. Spike amplitude has been normalized by expressing the smaller as a percentage of the larger. Velocity of stretch is 3 mm/sec in each case.

For afferent units from the same spindle, therefore, of the type shown in Fig. 5, large spikes have been attributed to the primary ending and small spikes to the secondary ending (cf. Hunt & Ottoson, 1973). The observations made in these spindles were also used to classify single afferent units, or pairs of units showing differences in spike amplitude of less than one third. From Fig. 5 it can be seen that no primary ending had a dynamic index of less than 10 impulses/sec and no secondary ending greater than 15 impulses/sec. These values were therefore used as the lower and upper limits respectively for primary and secondary endings. By these criteria, a further seven units were classified as arising from primary endings (total = 15) and seven from secondary endings (total = 15), with three units which were unclassified in that their dynamic index at this velocity of stretch lay between 10 and 15 impulses/sec.

When endings were classified according to these criteria, the mean value

for the dynamic index at a stretch velocity of 3 mm/sec was 22·6 ± 7·1 S.D. of the observation impulses/sec for primary endings, and 6·2 ± 3·5 S.D. impulses/sec for secondary endings.

Endings classified in this way also behaved consistently during release from stretch. Secondary endings continued to fire during release from stretch, in the same manner as de-efferented secondary endings in cat limb muscles (Harvey & Matthews, 1961). Primary endings, on the other hand, showed two patterns during release from stretch at a velocity of 3 mm/sec: some units ceased firing at the onset of release (unit *A* in Fig. 8*a*) while others continued to fire (Fig. 6) in a manner analogous to Lennerstrand's (1968) 'intermediate' sub-group of primary endings.

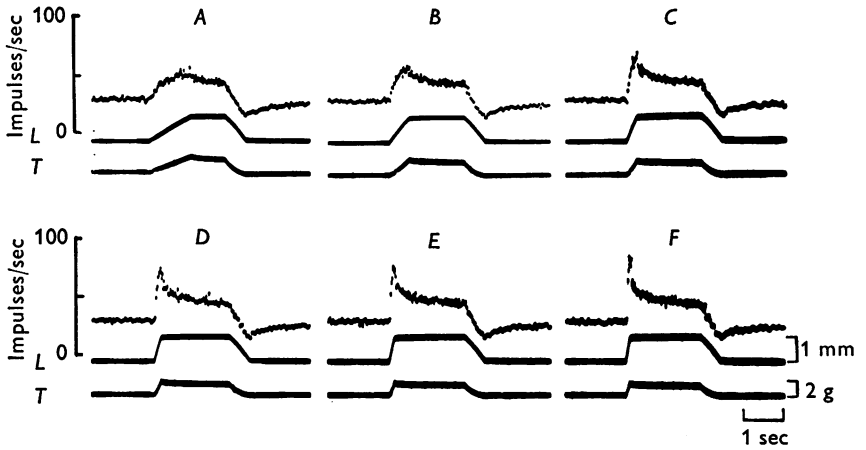

Fig. 6. Response of a primary ending from a spindle of a 62 yr old man to a series of stretches of constant amplitude but increasing velocity from *A* to *F*. (The velocity of release from stretch was the same in each case.) Note the progressive increase in the dynamic response and the consistent firing pattern on release. *L*, length; *T*, tension. Calibrations: 1 mm, 2 g, 1 sec.

Dynamic sensitivity as a function of velocity of stretch

Responses of a primary ending to a ramp stretch of constant amplitude and increasing velocity are shown in Fig. 6. The progressive increase in the dynamic response is apparent as the velocity of stretch is increased from *A* through to *F*, and is further shown plotted in Fig. 7. For comparison, a similar plot is shown for a secondary ending from another spindle. Over the range of velocities studied, the dynamic index is an approximately linear function of the velocity of stretch for both primary and secondary endings. The slope of the relationship is characteristically steeper for primary endings than for secondary endings.

An initial burst was seen in a few primary endings and in one secondary

ending. The peak frequency of the initial burst increased with the velocity of stretch (cf. Fig. 3). In Fig. 3, the primary ending was silent at the resting length but this was not necessarily the case in other endings showing an initial burst.

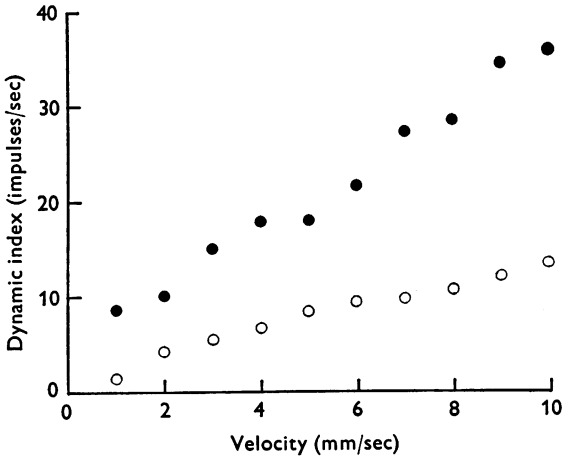

Fig. 7. Plot of dynamic index against the velocity of stretch for the primary ending illustrated in Fig. 6 (filled circles) and for a secondary ending from a 55 yr old man (open circles). Note the steeper slope of the relationship for the primary ending.

Static responsiveness

The frequency–extension relationship was investigated by subjecting the spindle to a sequence of ramp and hold stretches of increasing amplitude. The static firing frequency was measured 0·5 sec after the completion of the stretch; at this interval, the dynamic component of the stretch had little influence on the firing frequency (e.g. Fig. 6). Unavoidably, the length of the muscle fascicle or of the isolated spindle varied between experiments. Extension has therefore been normalized by expressing it as a percentage of threshold length (see above). Extensions were normally limited to about 7·5 % of the threshold length for a spindle studied *in situ* in its muscle fascicle in order to avoid possible disruption of the mechanical coupling of the spindle or over-stretching brought about by differential compliance in series with the receptor. In spindles which had been fully isolated, however, extensions of up to about 15 % were investigated.

The frequency–extension relationship has proved to be approximately linear for both primary and secondary endings over the range studied. Fig. 8*a* illustrates the type of records from which measurements were made for a primary ending from a spindle of a 51 yr old woman (*A*) and

for an unclassified ending from the spindle of a 65 yr old man (*B*). The spindle in *A* was studied *in situ* in its muscle fascicle, while that in *B* had been completely isolated. The instantaneous frequency records demonstrate the consistent manner in which both endings signal the static length charge. The dynamic overshoot of the primary ending, however, is much more pronounced, and in addition this ending ceases firing close to the

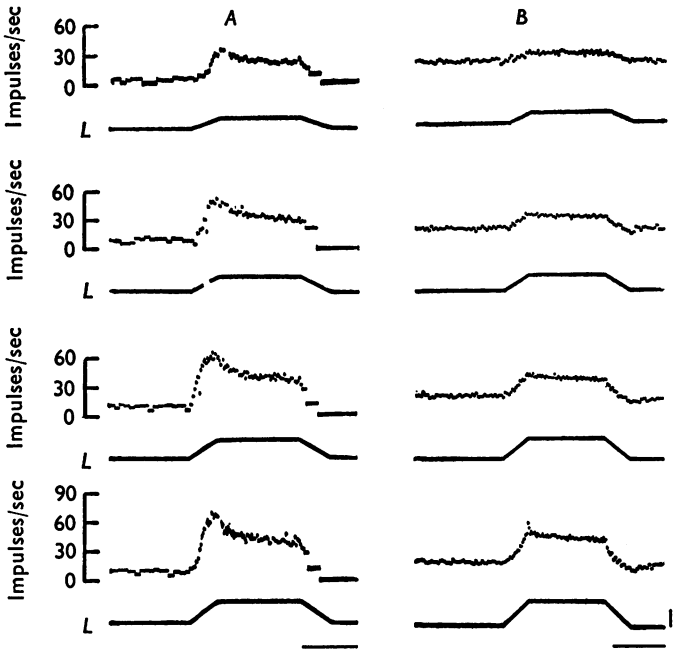

Fig. 8*a*. Responses of a primary ending in a spindle of a 51 yr old woman (*A*) and of an unclassified ending (see text) in a spindle of a 65 yr old man (*B*) to ramp stretches of increasing amplitude. The spindle in *A* was studied *in situ* in its muscle fascicle. In *B*, the spindle had been completely isolated. The figure has been arranged so that the extensions, expressed as a percentage of threshold length, are approximately the same for the two spindles in each of the four pairs of runs. In the upper pairs of traces, for example, the length change (660 μm in *A* and 180 μm in *B*) represented a 3 % extension for both spindles. The greater dynamic responsiveness of the primary ending is evident. *L*, length. Length calibration = 5 % extension; time, 1 sec. (Note that the frequency meter automatically resets to zero at interspike intervals of greater than 200 msec.)

onset of release. The pattern of activity of the unclassified unit in *B* suggests that it is either a secondary ending or an 'intermediate' primary ending (see Lennerstrand, 1968).

The static discharge frequencies are plotted against extension for these two units in Fig. 8*b*; the linearity of the relation is evident. Static

responsiveness, i.e. the change in firing frequency per unit change in length, has been expressed in terms of a 5% extension. For the units *A* and *B* in Fig. 8*a* the values were 32 and 20 impulses/sec per five per cent extension respectively. (A 5% extension was represented by a length change of 1·1 mm in *A* and 0·3 mm in *B*). It may be noted in *B* that the linear relationship extended over the full range (16%) of extension studied, implying that measurements made over smaller extensions as in *A* provide a true indication of the over-all static sensitivity.

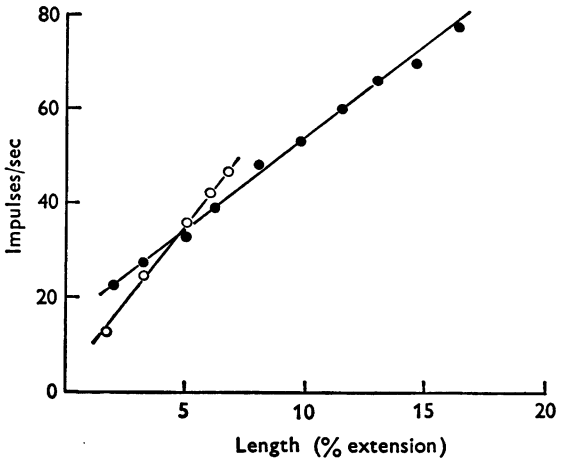

Fig. 8*b*. Plot of discharge frequency against length expressed as percentage extension of threshold length, for the two units illustrated in Fig. 8*a*. Note linear relationship for extensions of up to 16% of threshold length (open circle, unit *A*; filled circle, unit *B*).

The values obtained for primary and secondary endings are compared as a histogram in Fig. 9, which also shows the values for the three unclassified units. The distributions of the two main groups were similar. The mean value for the primary endings (16·1 ± 8·3 S.D. of the observation impulses/sec per five per cent extension) was slightly larger than that for secondary endings (12·1 ± 6·5 impulses/sec per five per cent extension) but the difference did not reach significance at the 10% level.

Comparison of responses of endings lying in the same spindle

The two small units illustrated in Fig. 3, which have been classified as secondary endings, showed considerable congruity in their responses, as is evident from the Figure. This is illustrated further for a ramp and hold series of stretches in Fig. 10 where the instantaneous frequency plots for the two units have been traced and superimposed. The amplitude and

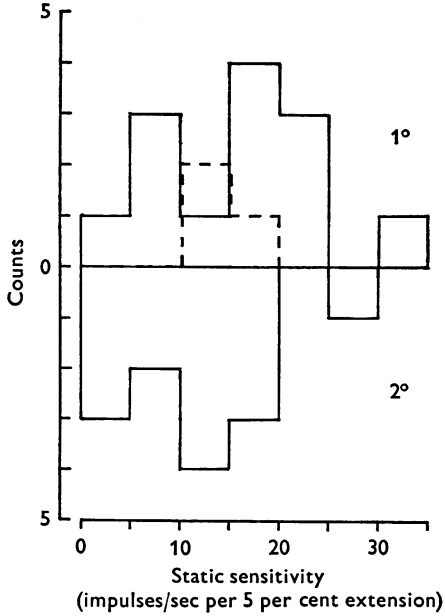

Fig. 9. Histogram illustrating the distribution of values for the slope of the frequency/extension relationship for primary and secondary endings and for three unclassified units expressed as change in firing frequency for a 5% extension of threshold length. The distribution of the unclassified units is shown by the dashed line.

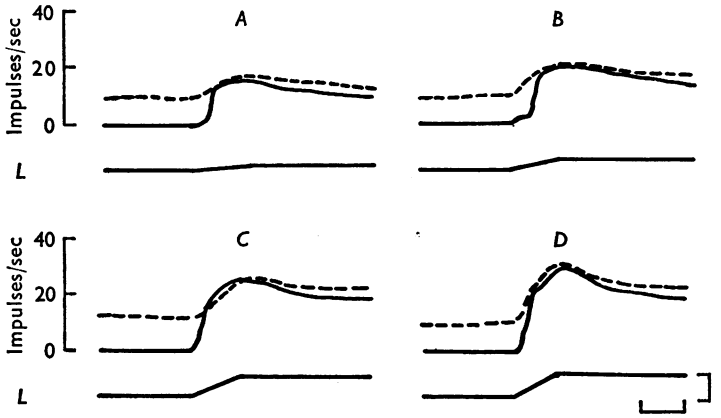

Fig. 10. Responses of two secondary endings lying in the same spindle to a ramp stretch of increasing amplitude (same units as in Fig. 3). Instantaneous frequency records have been traced and superimposed. Note the similarity of the responses.

velocity of stretch was increased from *A* to *D*. The dynamic and static responsiveness of the two endings maintain their similarity at all velocities and amplitudes of stretch, although one unit had a slightly lower threshold than the other.

The dynamic sensitivity of primary and secondary endings lying in the same spindle showed, of course, a clear difference as has already been described. Static responsiveness, on the other hand, tended to be the same. The values for eight pairs of endings have been plotted in Fig. 11. The coefficient of correlation was +0·83, which is significant at the 5% level. The slope of the regression was 0·91.

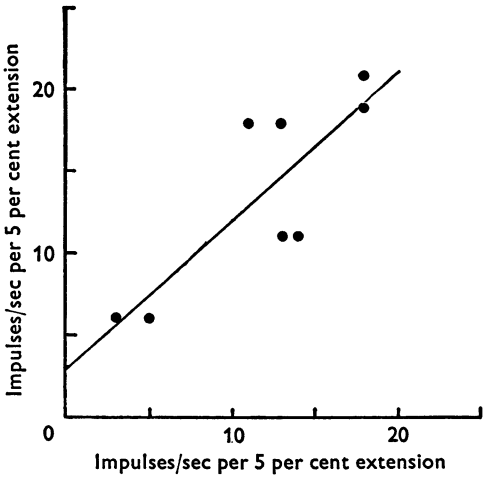

Fig. 11. Plot of static responsiveness for pairs of endings lying in the same spindle. The spike of largest amplitude is plotted on vertical axis. Note the positive correlation ($r = +0{\cdot}83$, significant at the 5% level). The regression line has a slope of 0·91.

Effects of age

Over the range in which it was studied here, age does not appear markedly to influence the frequency-extension relationship or the dynamic sensitivity of either primary or secondary endings. The absence of any clear trend with age implies that the present results would be applicable to younger adult subjects.

In a few instances, usually in the more elderly subject, endings were encountered whose responses were clearly atypical. These responses were characterized either by their inconsistency to a repeated ramp and hold stretch or, in the case of three primary endings, by step rather than graded changes in firing frequency in response to extension. These atypical responses, which will be described fully elsewhere (Bendeich, E. & Newsom

Davis, J., unpublished), were usually associated with morphological abnormalities. A spindle with an ending exhibiting an atypical response commonly contained another ending whose response was normal.

DISCUSSION

On the evidence of the present study, the human spindle can be studied *in vitro* as satisfactorily as other mammalian spindles (cf. Lippold, Nicholls & Redfearn, 1960; Boyd, 1966; Poppele & Bowman, 1970; Poppele & Kennedy, 1974). The range and velocity of the length changes used in the *in vitro* preparation first require comparison with those occurring *in vivo*. The resting length of the intercostal muscle at the site where it was usually biopsied was 2·8–3 cm but it was not possible to obtain satisfactory measurements of the length changes occurring during spontaneous breathing or during passive inflation of the lungs. However, the length changes during quiet breathing are unlikely to be less than the 1–2 mm reported for the cat (Andersson & Lennerstrand, quoted by Andersson, Lennerstrand & Thoden, 1968) where intercostal muscle length is about half that in man. An estimate based on these figures would give a length change in the external intercostal muscle of about 15 % in a vital capacity manoeuvre, and a stretch velocity of less than 1 mm/sec during quiet breathing and about 8 mm/sec during a forced expiration, for example, when flow rates of 7 l./sec or more may occur. These figures indicate that the extent and velocity of stretch studied here probably encompass the physiological range.

The demonstration of two functionally distinct groups of human intercostal spindle afferents with properties conforming to those of primary and secondary endings is consistent with the findings in cat intercostal spindles studied *in vivo* (Euler & Peretti, 1966; Andersson *et al.* 1968). The 'limit' values of the dynamic index chosen by Andersson *et al.* (1968) for the classification of primary and secondary endings were the same as those in the present study. These authors derived the index in a slightly different way from Jansen & Matthews (1962), measuring the static value 30 sec rather than 0·5 sec after the end of the stretch. This would tend to increase the value of the dynamic index and might in part account for the fact that a number of their primary endings had larger values than any encountered here.

Lennerstrand (1968) has defined an 'intermediate' group of endings which he regards as a sub-group of primary endings. These endings differ from other primary endings in continuing to fire during release even when the velocity of muscle shortening is relatively high. This characteristic is influenced by the degree of initial extension. Units of this type in the cat were found more frequently in spindles from intercostal muscles than in

those from leg muscles (Andersson *et al.* 1968). In the present study, units classified as primary endings have sometimes shown 'intermediate' characteristics (e.g. Fig. 6). But the true incidence of units of this type could not be assessed because the *in vivo* resting length of the spindle was not known.

An approximate figure for the position sensitivity of human intercostal spindles *in vivo* can be obtained from the present results. Static responsiveness *in vitro* has been expressed in terms of a 5% extension. If one assumes a value of 3 cm for the *in vivo* length of the intercostal muscle, a 5% extension would represent a length change of 1·5 mm. The position sensitivity, based on the findings *in vitro*, would then range from 2 to 21 impulses/sec per millimetre stretch (mean 10·7 for primary endings and 8·0 for secondary endings). These values are similar to those of 10·4 and 5·9 impulses/sec per millimetre for primary and secondary endings respectively found in cat intercostal spindles studied *in vivo* (Andersson *et al.* 1968), although in the present study the difference between the means of the two groups was not statistically significant, a finding that accords with observations in other animal muscles (Harvey & Matthews, 1961; Lennerstrand, 1968). But when allowance is made for the fact that the length of the cat intercostal muscle, as given by Andersson *et al.* (1968) is about half that in man, the static sensitivity of the intercostal spindle itself would appear to be greater in man than in cat.

The results obtained here *in vitro* need to be considered in relation to those obtained in man by the *in vivo* technique of recording from muscle afferents with a micro-electrode inserted percutaneously into peripheral nerve. With this latter method the velocity and range of movement has to be limited because of the risk of losing contact with the unit. Thus no quantitative information is apparently yet available for the dynamic sensitivities of units studied *in vivo* with which the present results could be compared, nor has it yet proved possible to examine the relationship between dynamic responsiveness and the velocity of stretch. But Vallbo (1974*a*) has recently investigated the position sensitivity *in vivo* of human spindle receptors lying in a relaxed finger flexor muscle of the forearm. Over an intermediate range of muscle length, representing less than a quarter of the full range, the static discharge frequencies were low, and relatively few units were active. This implies insignificant fusimotor driving under these conditions (Vallbo, 1974*a*), and simplifies comparison with the *in vitro* results. As in the present study, the position sensitivity for secondary endings was less than that for primary endings, although the difference was not statistically significant. But the absolute values were considerably lower than those for intercostal muscle spindles *in vitro*, the values for primary endings, for example, ranging from 0·6–0·9 impulses/sec

per millimetre. When, however, the length change in each case is expressed as a proportion of the resting length of the muscle (which differs for these two muscles by a factor of ten) rather than as an absolute length change, the values prove to be similar. Thus if one assumes a length of 310 mm for the forearm finger flexor muscle, the position sensitivity for a 5 % extension (15·5 mm) would range from 9·3 to 14·0 impulses/sec, values which are of the same order as those found here for intercostal spindles. The similarity of the position sensitivities when expressed in this way suggests that, for the spindle itself, the inherent relationship between discharge frequency and length is much the same whether it lies in an intercostal or a forearm finger flexor muscle.

The relationship between firing frequency and joint extension was linear in Vallbo's (1974*a*) study, although for practical reasons it could only be investigated over a small range of movement. A similar relation exists for the intercostal spindle *in vitro* for extension up to the maximum that probably occurs in the body, so that one might expect this also to be true for finger flexor muscles.

It is interesting that the slope of the frequency/extension relationship for endings lying in the same spindle tended to be the same not only for pairs of secondary endings but also for primary and secondary endings. At first sight, this appears to be of functional importance for it would mean that length information from any individual site within the muscle would be signalled by locally consistent rates of change of firing frequency and would facilitate central comparison of information signalled from primary and secondary endings in individual spindles. The significance of the observation must, however, be questioned because although static fusimotor fibres exert qualitatively similar actions on the position sensitivity of primary and secondary endings lying in the same spindle, this is not so in the case of dynamic fusimotor fibres (Appelberg, Bessou & Laporte, 1966).

The values for the dynamic and static responsiveness of human intercostal spindles are of interest in relation to the proprioceptive control of these muscles. Newsom Davis & Sears (1970), using a semi-quantitative electromyographic technique, demonstrated short latency excitatory responses to stretch of the human intercostal muscle which were consistent with autogenetic excitation from intercostal spindle afferents. The maximum velocity of stretch to the inspiratory intercostal muscles in their study would be about 3 mm/sec. This is well within the range over which, within the present study, the relationship between discharge frequency and velocity of stretch has been found to be linear, and suggests that the excitatory responses shown in the earlier study, although often large, were not necessarily the maximum of which the system is capable.

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