J. Physiol. (1979), **291**, *pp.* 277–290
With 8 *text-figures*
Printed in Great Britain

THE REGULARITY OF MUSCLE SPINDLE DISCHARGE IN MAN

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(*Received 28 July 1978*)

SUMMARY

1. The variability of discharge of thirty-nine muscle spindle afferents from the pretibial muscles of normal human subjects was determined for spike train sequences recorded with the ankle joint fixed in 25° plantar flexion, during further stretch and during graded voluntary contractions of the receptor-bearing muscle.

2. In non-contracting muscles with the ankle joint in 25° plantar flexion, a sustained discharge was maintained by twenty-four of the thirty-nine endings. The mean discharge frequency for the active endings was 11·1 Hz (range 4·8–22·1 Hz), the mean coefficient of variation 0·073 (range 0·021–0·183). With further stretch, the discharge of endings maintaining frequencies below 10–12 Hz became more regular. For endings maintaining higher frequencies, changes in the coefficient of variation were small and occurred in either direction. All secondary endings maintained a highly regular discharge, but, at these frequencies, there was no statistically significant difference in the variability of primary and secondary endings.

3. It is considered that these findings are comparable to those of Matthews & Stein (1969) for de-efferented feline spindle endings, and support the view that there is no functionally effective background fusimotor drive to non-contracting muscles of normal human subjects.

4. A voluntary contraction sufficient to accelerate a spindle ending invariably decreased the regularity of its afferent discharge. During voluntary contractions, coefficients of variation up to 0·345 were recorded. However, coefficients as low as 0·1 were not uncommon, and thus the absence of fusimotor drive cannot necessarily be inferred from a regular afferent discharge pattern.

5. With contractions of different strength, the increase in the coefficient of variation did not parallel the increase in discharge frequency. It is concluded that not all fusimotor influences acting on a spindle ending are translated into variability, and that measurements of the variability of discharge do not accurately reflect the level of fusimotor drive.

6. The discharge frequency of some spindle endings decreased slightly in some contractions and this was accompanied by an increase in the variability of discharge. It is suggested that contracting extrafusal muscle fibres can modulate the discharge pattern of spindle endings and contribute to the variability of discharge during a voluntary contraction.

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7. In contracting muscles the irregular fusimotor-driven spindle discharge contained a 'hidden' periodicity, but this was not as extensive as has been reported for the cat. No such periodicity could be demonstrated for spindle endings in non-contracting human muscles.

INTRODUCTION

Matthews & Stein (1969) have reported that, in the cat, muscle spindle afferents have a regular discharge pattern when not subjected to a fusimotor influence and a more irregular pattern when subjected to the fusimotor drive present in the decerebrate preparation. In both situations, the variability of discharge of secondary endings is less than that of primary endings.

With human subjects Vallbo (1970) has used the variability of discharge of spindle afferents in a relaxed muscle as one of a set of criteria for the differentiation of primary and secondary endings. However, no detailed study on the regularity of spindle discharge has been made in man even though such information would be of value, particularly since classification of human spindle endings is hampered by the absence of conduction velocity measurements for the afferent fibres.

In man, spindle endings in relaxed muscles are not subjected to functionally effective fusimotor influences (Vallbo, 1970, 1974*a*; Burke, Hagbarth, Löfstedt & Wallin, 1976*b*), but during isometric voluntary contractions their discharge frequencies tend to increase in proportion to contraction strength (cf. Vallbo, 1974*b*) once a threshold level has been exceeded (Burke, Hagbarth & Skuse, 1978). These findings provide the rationale for the present study which was undertaken to quantify the regularity of discharge of human spindle endings when deprived of significant fusimotor drive and when subjected to graded degrees of fusimotor drive as judged by the changes in discharge frequency that occur in voluntary contractions. A preliminary report of some of the findings has been presented to the Australian Physiological and Pharmacological Society (Burke, Skuse & Stuart, 1978).

METHODS

Data were obtained from fourteen experiments on seven healthy adult subjects all of whom gave informed consent to the experimental procedures.

Experimental procedures. Unitary recordings from afferent axons were made at the level of the fibular head from fascicles of the peroneal nerve innervating tibialis anterior, extensor digitorum longus and extensor hallucis longus. The details of the recording technique have been described in full previously (Vallbo, 1970; Hagbarth, Wallin & Löfstedt, 1975; Burke, Hagbarth, Löfstedt & Wallin, 1976*a*). Subjects reclined supine on a couch with one foot secured by straps to a footplate attached to a rigid metal bar. A four-arm strain gauge bridge was bonded to the bar to provide a measure of contraction strength. The position of the footplate was fixed so that the ankle joint was in 25° plantar flexion (+25°). The electromyogram (e.m.g.) of the receptor-bearing muscle was recorded with surface electrodes 5 cm apart orientated longitudinally along the belly of the muscle, usually on either side of the receptor. These data were monitored during the experiments and were recorded on magnetic tape for subsequent analysis. The recording and replay speeds of the tape-recorder were constant, the degree of jitter over a 2–3 hr period being $< 0{\cdot}2\,\%$.

Afferents from thirty-nine muscle receptors were identified as being of muscle spindle origin on the basis of their responses to electrically induced muscle twitch contractions of the receptor-bearing muscle (Hagbarth *et al.* 1975; Burke *et al.* 1976*a*). Classification of spindle endings as 'probably primary' or 'probably secondary' was based on the presence or absence, respectively, of a dynamic response to stretch and a pause in discharge on shortening (cf. Fig. 1 *C–E*). For these tests muscle stretch was produced by the abrupt application of pressure to the tendon of the receptor-bearing muscle. The regularity of afferent discharge was not used as a criterion for classification.

Spike trains of 1–2 min duration were recorded: at rest with the ankle at +25°; during maintained stretch produced by sustained pressure on the muscle tendon or occasionally by direct pressure over the spindle ending; and during graded 'isometric' voluntary contractions of the receptor-bearing muscle. To attain complete muscle relaxation, subjects viewed the e.m.g. of receptor-bearing muscle on one beam of a dual beam oscilloscope. To sustain a steady voluntary contraction subjects viewed the level of contractile tension on the second beam of the same oscilloscope. Unless the afferent discharge rate was particularly low, spike train sequences longer than 1–2 min were not sought, because of the difficulty in maintaining a steady contraction for periods longer than 2 min and because of the possibility that the recording conditions would deteriorate before a full series of tests could be completed.

Computational procedures. The data obtained were processed by a digital computer. The afferent spike trains were amplified from the replayed tapes and filtered as described previously (Hagbarth *et al.* 1975; Burke *et al.* 1976*a*). They were then converted into pulses of standard amplitude. To reduce background noise this procedure involved use of a discriminator level which was often deliberately set so that not every afferent spike from a single unit reached threshold. Thus, from time to time, the computed interspike interval would appear to be double the true interval (cf. Fig. 1 *C–E*). This discrepancy does not affect significantly a non-sequential interval histogram or computations based on that histogram since the spurious values produced a second peak in the histogram at double the true mean interval. This peak could be recognized easily and the relevant values excluded from subsequent calculations. Such measures precluded computations based on successive interspike intervals as were made by Matthews & Stein (1969).

The afferent pulse trains were converted into interspike interval histograms computed to the nearest 500 μs. The pulses were monitored simultaneously on an instantaneous frequency meter to ensure that the overall discharge frequency was stationary for each analysis sequence. This control was particularly important, both for passive muscle stretch, when a slow adaptation is not uncommon following the abrupt component of the stretch, and for voluntary contractions, when subjects sometimes have difficulty maintaining a steady contraction level or when a slow decline in afferent discharge frequency may occur even when the level of contractile torque remains steady. All non-stationary recordings were rejected.

For each spike train sequence, the mean interval and its standard deviation, the coefficient of variation (standard deviation divided by mean interval) and the mean discharge frequency were calculated. To compare interspike interval histograms from different endings or from different sequences for the same ending, each histogram was normalized for the number of entries and plotted as a probability density function. To determine the extent to which these plots of probability density as a function of interspike interval approached a normal distribution, cumulative probability functions were plotted on a cumulative probability scale (on which scale a truly normal distribution produces a straight line).

All measurements in this paper were based on spike train sequences involving a minimum of 150 afferent spike intervals. In some instances 1000–2000 consecutive intervals were analyzed, but the usual number was 400–600.

RESULTS

Recordings were obtained from thirty-nine muscle spindle endings of which seventeen were classified as probably primary and six as probably secondary. The remainder were unclassified, often not so much because of intermediate characteristics but because the recorded activity did not contain stretching and shortening sequences appropriate for the classification criteria described above.

Spindle behaviour in non-contracting muscles

Activity at +25°. With the ankle joint fixed in the standard position of 25° plantar flexion, the discharge frequencies of the spindle endings in non-contracting muscles were low (Fig. 1*A*). Sustained discharge was maintained by only twenty-four of the

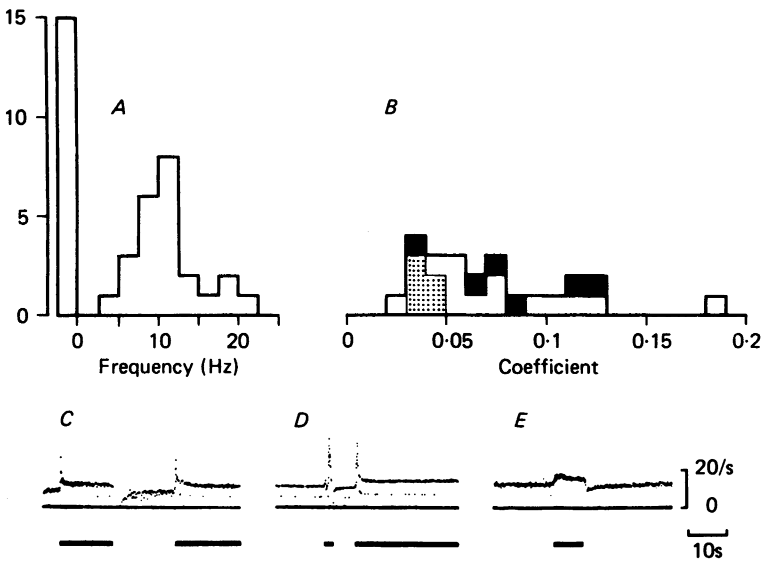

Fig. 1. Discharge characteristics of spindle endings in non-contracting muscles. *A*, histogram of discharge frequencies at +25°. *B*, histogram of the coefficients of variation for the twenty-four endings active at +25°. White: primary endings (n = 13); dotted: secondary endings (n = 5); black: unclassified endings (n = 6). *C–E*, classification of three spindle endings using steady pressure applied to the muscle tendon (indicated by horizontal bars). Endings *C* and *E* show typical characteristics of primary and secondary endings, respectively. Ending *D* had the most regular discharge pattern of any ending in the study (coefficient 0·021 at +25°) but responded to stretch in an extremely dynamic manner.

thirty-nine endings (thirteen of the seventeen identified primary endings; five of the six identified secondary endings). Discharge frequencies ranged from 4·8 to 22·1 Hz (mean 11·1 Hz). The high percentage of silent endings (39 %) and the low discharge rates of the active endings indicate an absence of effective fusimotor drive to non-contracting muscles (Vallbo, 1970, 1974*a*; Burke *et al.* 1976*b*).

Probability density functions of the interspike intervals for individual endings approximated normal distributions, but most had a mild positive skew towards longer interspike intervals (Fig. 2). For one primary ending a negative skew was present due to modulation of the discharge by the arterial pulse (cf. Fig. 4). These modest departures from normality were ignored for the computation of coefficients of variation.

For the twenty-four endings active at +25°, the coefficients of variation were 0·021–0·183, mean 0·073 (Fig. 1*B*). The five active secondary endings maintained a mean discharge frequency of 12·5 Hz with a mean coefficient of variation of 0·040. The thirteen active primary endings maintained a mean discharge frequency of

9·5 Hz with a mean coefficient of variation of 0·078. The difference between the coefficients for primary and secondary endings was not statistically significant ($P > 0{\cdot}2$). Furthermore, there was no evidence of a bimodal distribution of the coefficients of variation; rather, the values for the secondary endings were concentrated towards the lower end of the range, while those for the primary endings were

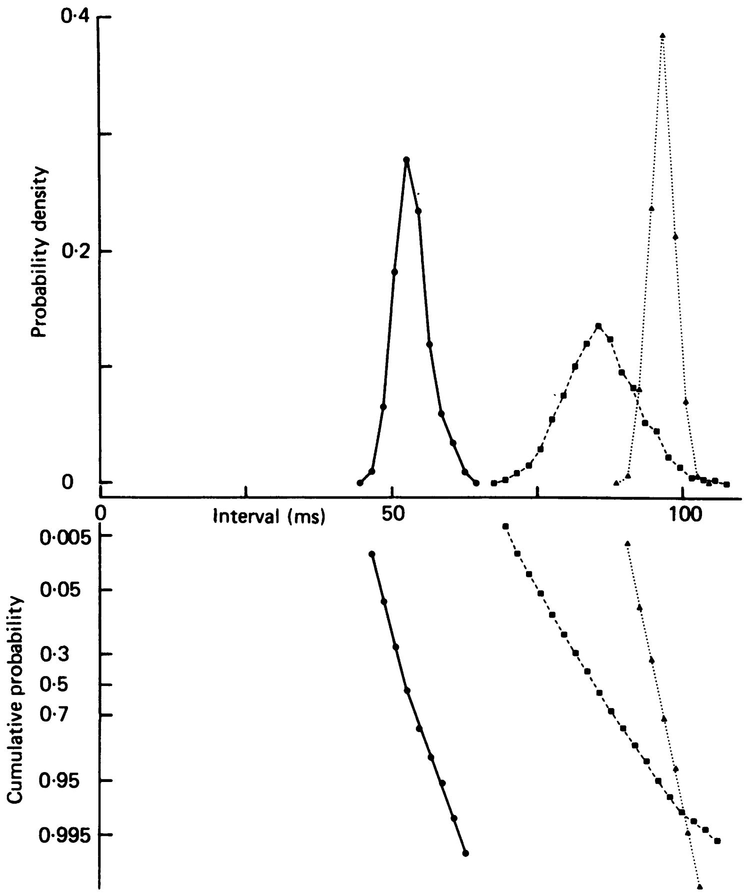

Fig. 2. Probability functions for three primary endings (from three different experiments). Upper graphs: probability density functions (normalized interspike interval histograms). Lower graphs: cumulative probability functions, plotted to a cumulative probability scale, on which a truly normal distribution will produce a straight line. The abscissa is interspike interval. The histograms from left to right are based on 575 discharges (mean discharge frequency 19·0 Hz; coefficient of variation 0·056), 1024 discharges (mean frequency 11·5 Hz; coefficient 0·071), and 866 discharges (mean frequency 10·5 Hz; coefficient 0·021).

spread over the entire range. Indeed, a primary ending had the lowest recorded coefficient (0·021, cf. Figs. 1*D* and 2).

Effects of further stretch of passive muscle. Further stretch of passive muscle was applied to twenty spindle endings, including five which had been silent at +25°. Discharge parameters for at least two different muscle lengths could be calculated for sixteen endings. In general, spindle endings with initially low discharge frequencies (below 10–12 Hz) tended to fire more regularly with further stretch whereas, for endings with higher discharge frequencies, changes in the coefficient of variation were small and occurred in either direction (Fig. 3*B*). Skewed probability density functions generally became more normal with increasing stretch of the passive muscle (cf. Figs. 4 and 7).

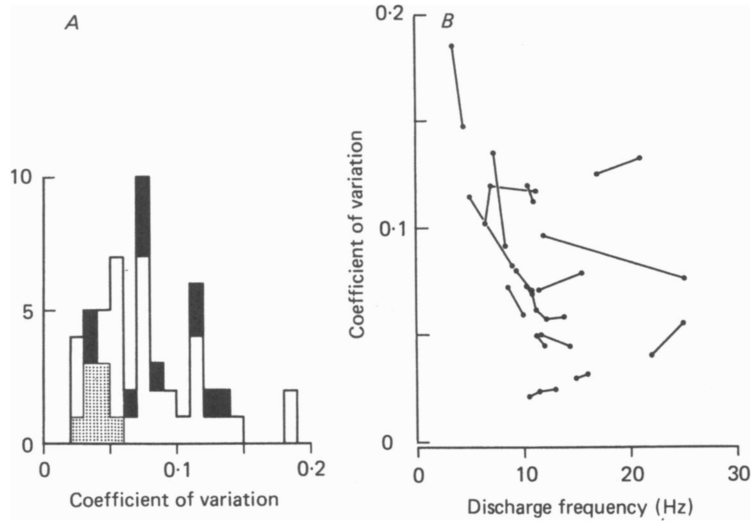

Fig. 3. Effects of passive stretch of non-contracting muscles. *A*, histogram of all computations of the coefficient of variation obtained for spindle endings in non-contracting muscles: fifty-two values for twenty-nine spindle endings. White: primary endings; dotted: secondary endings; black: unclassified endings. *B*, effects of passive stretch on the coefficient of variation for individual endings. Results for sixteen spindle endings.

By pooling all data from non-contracting muscles, independently of the extent of passive muscle stretch, fifty-two computations of the coefficient of variation were available for twenty-nine spindle endings (Fig. 3*A*). The distribution of these values was surprisingly close to the more limited sample presented in Fig. 1 at +25°. Discharge frequencies were 3·5–25·2 Hz (mean 11·3 Hz). Coefficients of variation were 0·021–0·183 (mean 0·076). The eight values for the six secondary endings were among the lowest values obtained but their mean of 0·041 was not significantly lower than 0·084, the mean of the thirty-three values obtained from the seventeen primary endings ($P > 0{\cdot}1$). It may be concluded from the data presented in Figs. 1*B* and 3*A* that if the discharge of a spindle afferent in a relaxed muscle is irregular, the afferent is probably from a primary ending, but if the discharge is quite regular, it can be from either a primary or a secondary ending.

Pulse-synchronous modulation of spindle discharge. One spindle primary afferent displayed an intermittent increase in discharge which occurred at 80/min, time locked to the arterial pulse and unaccompanied by e.m.g. activity or a detectable change in torque. This pulse-synchronous modulation of the discharge frequency produced a negatively skewed probability density function, with a coefficient of variation of 0·074. Computation of only the values from the normally distributed component of the histogram provided an estimate of 0·039 for the 'true' variability. With increasing stretch, the discharge frequency increased and the pulse-synchronous modulation diminished, thus decreasing the extent of skew (Fig. 4). Whether calculated on the entire histogram or only the 'normal' component, the coefficient of variation for this particular ending decreased when it was subjected to stretch.

Spindle behaviour in contracting muscles

Voluntary contractions of different strength were performed by the subjects while recordings were made from twenty spindle endings, nine of which had no activity at $+25°$. Fifteen of the twenty endings displayed an increase in discharge rate in the

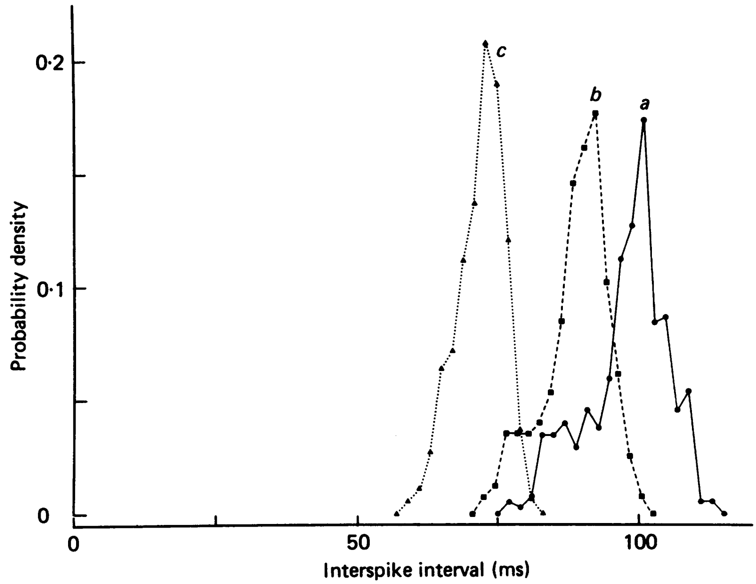

Fig. 4. Modulation of discharge of a primary ending by the arterial pulse. Probability density functions at three muscle lengths. *a* is based on 367 discharges (mean frequency 10·3 Hz; coefficient of variation 0·074), *b* on 388 discharges (mean frequency 11·1 Hz; coefficient 0·063), and *c* on 791 discharges (mean frequency 13·8 Hz; coefficient 0·058).

test contractions, presumably because the accompanying increase in fusimotor drive had a greater effect on the endings than the unloading attributable to contraction of adjacent skeletomotor fibres. The remaining five afferents underwent a decrease in discharge frequency during weak contractions suggesting that extrafusal unloading was the dominant influence. For three of these five afferents a further increase in the strength of contraction resulted in spindle acceleration, but with only one was the discharge during the stronger contraction sufficiently stable to be suitable for the computational procedures. Thus, for five afferents (two primary, two secondary, one unclassified) it was possible to compute the coefficient of variation during contractions which produced a deceleration in discharge while for sixteen afferents (eight primary, one secondary, seven unclassified), the coefficient of variation could be computed for forty-six contractions which produced spindle acceleration.

Weak contractions. Voluntary contractions which resulted in a change in spindle discharge rate invariably increased the irregularity of the discharge, irrespective of whether the discharge rate increased or decreased. The five spindle afferents which underwent a slight reduction in discharge during weak contractions maintained a mean rate of 11·1 Hz in the passive muscle. Weak contractions reduced the mean discharge rate by 1·3 Hz and the coefficient of variation increased from a mean of 0·047 to a mean of 0·097. In contrast, the six other afferents active in the passive muscle at +25° (mean discharge rate 8·5 Hz) increased their firing rates by a mean

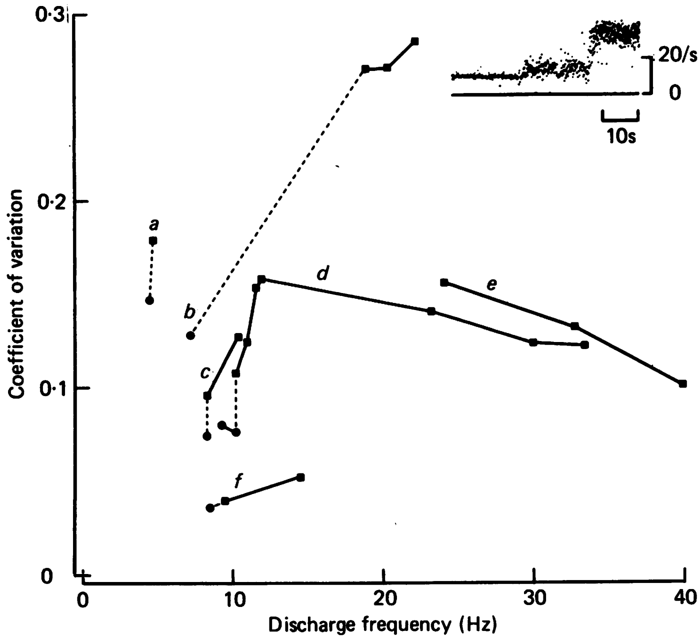

Fig. 5. Effects of different strengths of contraction on coefficients of variation for six spindle endings. Symbols for the endings are ■: values obtained during voluntary contractions; ●: values obtained in non-contracting muscles (for five endings only). Endings *a*, *b* and *c* are primary endings, ending *d* and *e* unclassified endings, and ending *f* a secondary ending. The inset shows the instantaneous frequency of discharge of a primary ending, in an initially non-contracting muscle, during a weak contraction, and during a strong contraction.

of 2·9 Hz in response to weak contractions, and their coefficients of variation increased from a mean of 0·086 to 0·130 (cf. Fig. 5, endings *b*, *d* and *f*). Of this sample, the one secondary ending had the most regular discharge. As shown in Fig. 5 (ending *f*) its discharge frequency increased from 8·6 Hz in the passive muscle (+25°) to 9·6 Hz and then to 14·5 Hz. The coefficient of variation showed corresponding increases from 0·036 to 0·039 and 0·051, respectively.

Stronger contractions. Once an afferent was activated, the discharge frequency and the irregularity of discharge generally increased together in stronger contractions (Fig. 5, inset). However, the change in the regularity of discharge did not parallel the changes in contraction strength and discharge frequency except over a limited range (cf. Fig. 5, endings *b*, *c*, *d* and *f*). With contractions resulting in increases in discharge frequency greater than 5–10 Hz there was commonly little further increase in irregularity. Rather, a plateau was reached or the coefficient of variation decreased slightly (Fig. 5, endings *d* and *e*). In the forty-six contractions, weak and strong, which resulted in spindle acceleration, the coefficients of variation ranged from 0·039 to 0·345 (mean 0·156). The highest discharge frequency was 40·2 Hz, associated with a coefficient of 0·108. The highest coefficient (0·345) was associated with a discharge frequency of 9·4 Hz.

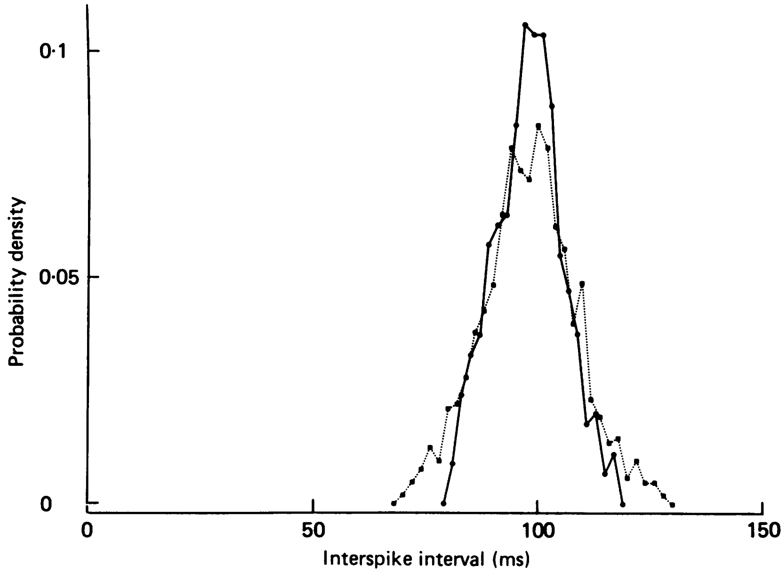

Fig. 6. Probability density functions of a primary ending with discharge maintained at the same frequency by passive stretch (●——●; based on 452 discharges) and by a weak voluntary contraction (■. . . . ■; based on 1023 discharges). For both sequences the mean discharge frequency is 10·3 Hz. Coefficients of variation are 0·077 and 0·108, respectively.

Comparison of irregularity in active and passive muscles. At a given frequency, the variability of afferent discharge was higher if firing was maintained by voluntary contraction rather than by passive stretch (Fig. 5, endings *a*, *c* and *d*; Fig. 6). Furthermore, for afferents initially discharging at less than 10–12 Hz, voluntary contraction had the opposite effect to passive stretch on the variability of discharge; there was a slight decrease in the coefficients of variation in response to passive stretch and a prominent increase in response to contraction (Fig. 7, cf. also Fig. 5, ending *d*).

The shape of the probability density functions generally departed from normality as discharge frequency rose in response to a voluntary contraction (Fig. 7). A pronounced positive skew was not uncommon. For four afferents, the probability functions had broad peaks, and for two others some computations revealed a slight tendency towards a double peak, possibly because the seemingly irregular spike trains contained a hidden periodicity (see below).

Hidden periodicity in fusimotor-driven spindle discharges. In the cat, fusimotor-driven spindle discharges have an inverse relationship between successive interspike intervals, so that a relatively short interval will probably be followed by a relatively long interval and vice versa (Eldred, Granit & Morton, 1953; Matthews & Stein, 1969). A consequence of such a periodicity is that the discharge will be less variable when the sums of pairs of successive intervals are considered. For six spindle afferents of the present study, periodicity in the presumed fusimotor-driven (i.e. contraction-driven) discharge was demonstrated using a technique similar to that of Matthew & Stein (1969). A series of binary counters was used to trigger the computer and the instantaneous frequency meter by every spike, every second spike or every fourth

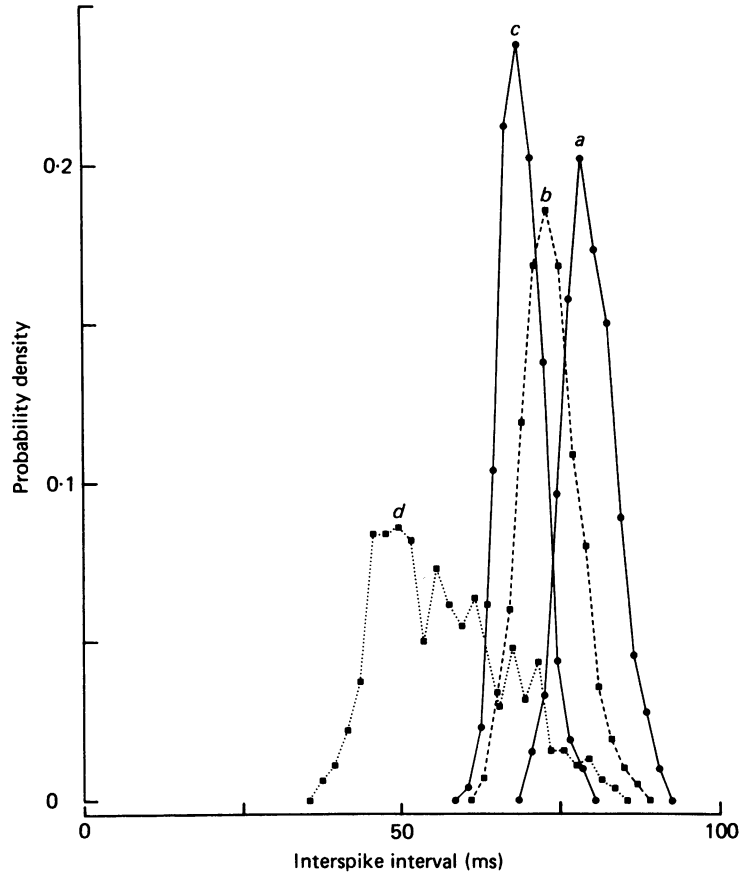

Fig. 7. Contrasting effects of passive stretch and voluntary contraction on the probability density function of a primary ending. *A*, non-contracting muscle at + 25° (mean discharge frequency 12·7 Hz; coefficient of variation 0·050; based on 393 discharges). *B*, contraction producing torque of 1·6 Nm at + 25° (mean frequency 13·5 Hz; coefficient 0·059; 1622 discharges). *C*, non-contracting muscle subjected to further stretch (mean frequency 14·3 Hz; coefficient 0·044; 682 discharges). *D*, contraction producing torque of 2·9 Nm at + 25° (mean frequency 17·5 Hz; coefficient 0·168; 437 discharges).

spike in the recorded sequence. An example is shown in Fig. 8 for a spindle afferent which was quiescent in the passive muscle at + 25° but active during a voluntary contraction. At first glance, the instantaneous frequency plots reveal an impressive improvement in the regularity of discharge when every second or fourth discharge triggered the frequency meter.

The coefficients of variation for the three sequences in Fig. 8 were 0·086, 0·051 and 0·036 and their variances were 12·896, 18·281 and 35·665 ms^2. The decrease in variability resulting from compiling the histogram using alternate spikes is statistically significant ($P < 0·01$; comparison of actual and expected variances using F-distribution). However, even though there appears to be a further improvement in regularity on computing the interval distribution using every fourth spike, this improvement is no greater than would occur if a truly irregular distribution were subjected to similar processing. The variance of every second spike will be the sum of the

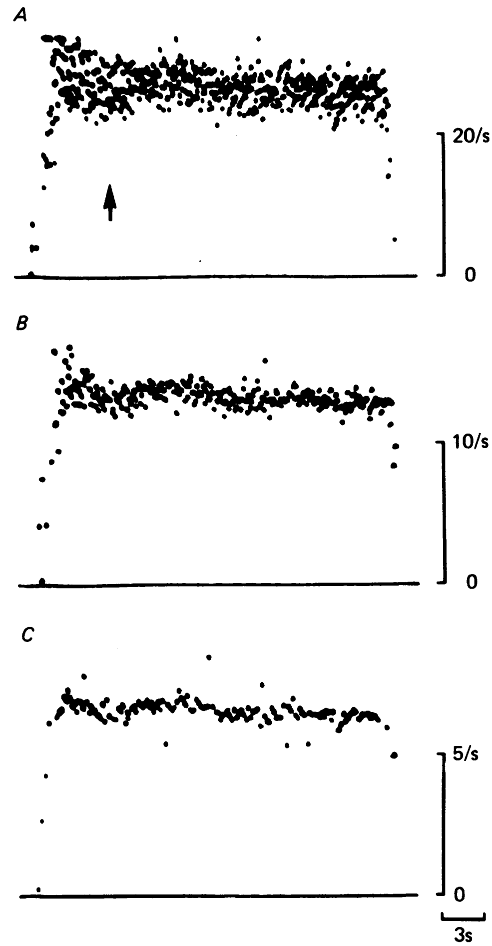

Fig. 8. Reduction in the variability of discharge of a fusimotor-driven spindle ending on summing successive interspike intervals. Response of an initially silent spindle ending at $+25°$ during an isometric voluntary contraction. Instantaneous frequency plots of the resulting discharge, triggering the meter with every spindle discharge (upper trace), every second discharge (middle trace) and every fourth discharge (lower trace). The computations of the discharge parameters for each trace were begun at the vertical arrow, by which time the frequency appeared stable.

variances of the two spike intervals, and, for a truly irregular distribution, this would be approximately double the variance of the original interspike interval. In the example shown in Fig. 8, the variance of every fourth spike is approximately double that for every second. With a truly irregular distribution, the coefficient of variation for every second spike will be $\sqrt{2}/2$ times the coefficient of variation for every spike. The decrease in the coefficient of variation on taking every second spike for the Fig. 8 data exceeds this value, but the further reduction on taking every fourth spike does not. Similar results were found with the other five spindle endings subjected to this analysis. It is concluded that there is a significant serial correlation between successive interspike intervals in fusimotor-driven spindle discharges, but that this correlation does not appear to extend beyond the second interval. When the same computational procedure was applied to spike train sequences from spindle afferents active in non-contracting muscles, the decrease in variability that occurred on computing every second spike rather than every spike did not exceed that which would be expected if the discharge pattern was truly irregular. Thus, there was no evidence of a correlation between successive interspike intervals, a finding consistent with the beliefs that such a correlation results from fusimotor innervation (cf. Matthews & Stein, 1969) and that there is no background fusimotor drive to non-contracting muscles in man.

DISCUSSION

Non-contracting muscles. From the present study, it appears that spindle afferents in non-contracting muscles of human subjects maintain discharge patterns of comparable regularity to those of de-efferented feline spindle afferents (cf. Matthews & Stein, 1969). The ranges for the coefficients of variation of primary endings are similar in man and cat (0·021–0·183 in man; 0·027–0·160 in the cat). The mean coefficient of 0·078 for man is higher than the mean of 0·058 for the cat, but this difference probably results from the lower, non-standardized discharge frequencies of the present study (cf. Gregory, Harvey & Proske, 1977). Matthews & Stein (1969) based their measurements on a standard discharge frequency of 25–33 Hz, producing this frequency by varying the extent of passive muscle stretch. A sustained discharge of such frequency is rarely seen in man if the receptor-bearing muscle is not contracting. The present observation that, despite the low discharge frequencies of human spindle afferents, they display comparable regularity to that of de-efferented feline afferents supports the view that in man there is no functionally significant background fusimotor drive to non-contracting muscles. Furthermore, the present values for man are likely to be of practical value for future human studies since they reflect the range of variability seen at a standard muscle length, regardless of discharge frequency.

The effect of passive stretch on the regularity of spindle discharge was found to depend on the discharge frequency. Muscle stretch *per se* was reported to have no consistent effect on the regularity of feline receptors discharging at reasonably high frequency (Matthews & Stein, 1969) but with stretch receptors discharging at relatively slow rates Gregory *et al.* (1977) reported the afferent discharge to be more regular the higher the discharge frequency. As such, the present findings in man are consistent with both of these studies.

Differences between primary and secondary endings were seen in the present study but whereas Matthews & Stein (1969) reported that the coefficients of variation for the two types of spindle ending did not overlap at all in the cat, such was not the case here. This, too, probably results from differences in discharge frequency, in that Matthews & Stein (1969) reported that de-efferented secondary endings '*invariably* fire more regularly than do the primary endings for all frequencies above about 25/sec', but they only '*usually* do so also for lower frequencies of discharge' (our italics). The present study emphasizes that, in man, an afferent with a low variability of discharge could come from either a primary or a secondary ending whereas an afferent with a relatively high variability of discharge is likely to be from a primary ending.

Changes in the regularity of spindle discharge accompanying voluntary contraction. Matthews & Stein (1969) found that fusimotor drive sufficient to increase the discharge rate of spindle afferents also increased the variability of discharge. In the present study, a coefficient of > 0·2 was not seen for spindle discharge in non-contracting muscles, but values up to 0·345 were recorded during voluntary contractions which produced spindle acceleration and thereby indicated a significant fusimotor influence. It is probable that much of the contraction-induced irregularity of afferent discharge does result from fusimotor activity, but, as discussed in the next section, there is evidence that other factors are also important. In intact man it is difficult to isolate the factors, a necessary prerequisite if the irregularity of discharge is to be used as an indication of the *presence* of fusimotor drive. Furthermore, since contractions sufficient to accelerate a spindle ending resulted in coefficients of variation as low as 0·039 (identified secondary ending in Fig. 5) and 0·059 (identified primary ending in Fig. 7), the *absence* of fusimotor innervation cannot be established conclusively for an individual spindle ending solely on the basis of a relatively low variability of discharge.

The contraction-induced increases in discharge frequency and discharge variability did not parallel one another except within a limited range, after which a frequency increase was not necessarily accompanied by an increase in variability. Although there are presumably some common mechanisms, the increase in discharge frequency is probably determined by factors additional to those determining the increase in variability. Assuming that the increase in discharge frequency results from fusimotor influences, this implies that not all fusimotor influences are translated into variability. This too, supports the viewpoint that measurements of the variability of the spindle discharge cannot be used to assess the extent of fusimotor activity.

Factors affecting discharge regularity during voluntary contractions. During a voluntary contraction spindle endings are subjected not only to fusimotor influences but also to the modulating effect of asynchronous twitch contractions of anatomically related muscle units (Binder, Kroin, Moore, Stauffer & Stuart, 1976; Windhorst & Meyer-Lohmann, 1977; Binder & Stuart, 1978). From the present results, it seems likely that asynchronous twitching of adjacent muscle fibres can affect the variability of spindle discharge significantly.

Five spindle endings appeared to be unloaded in weak contractions, and this was accompanied by a more variable discharge pattern. The greater variability could have resulted from a fusimotor influence too weak to accelerate the spindle ending or from the modulating effect of contracting muscle fibres. The latter alternative seems more likely since, in isometric contractions, each spindle ending has a specific threshold for activation, a threshold which probably reflects a recruitment threshold for the innervating fusimotor neurones (Burke, Hagbarth & Skuse, 1978). That the five endings were not activated in weak contractions suggests that the contractions were subthreshold for relevant fusimotor neurones and that the spindle endings were therefore not subjected to a significant increase in fusimotor drive.

It is concluded that, in the human situation, factors such as motor unit activity can contribute significantly to the variability of spindle discharge during a voluntary contraction. Since it is not possible to activate human fusimotor fibres with certainty except by contracting the muscle voluntarily, it is not possible to dissociate the fusimotor effects on the regularity of spindle discharge from the extrafusal effects. Thus, no estimate can be given of the relative importance of these factors.

This study was carried out under a grant from the National Health and Medical Research Council of Australia. The authors are grateful to Drs J. W. Lance and A. K. Lethlean for support during the study, to Drs M. D. Binder, K.-E. Hagbarth, D. I. McCloskey and R. A. Westerman for reviewing a draft manuscript and to Mr B. B. McKeon for assistance with some of the computations.

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