Discharge of human muscle spindle afferents innervating ankle dorsiflexors during target isometric contractions

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1. There are discrepancies in the literature about the reproducibility of forces at which human muscle spindle afferents accelerate their discharge during isometric voluntary contractions. The aim of this study was to determine for single muscle spindle afferents both the reproducibility of the 'acceleration threshold' and the factors contributing to variability of 'acceleration threshold'.
2. Microneurographic recordings were made from muscle spindle afferents innervating tibialis anterior while subjects performed isometric ankle dorsiflexions. Subjects matched the force of their contractions with a visually displayed 'ramp-and-hold' template. Template parameters were determined by the force of maximal isometric ankle dorsiflexion (MVC), and expressed as per cent MVC. The required 'ramp' rate and 'hold' force was adjusted between trials (range, 0·5–5 % MVC s^{-1} and 0·5–20 % MVC, respectively). The duration of the hold phase was 4 s and, following each contraction, stretch was applied transversely to the tendon to minimize the influence of any 'after-effects' on spindle afferent responses in subsequent contractions.
3. For each contraction, the force at which the rate of muscle spindle discharge increased was defined as the 'acceleration threshold'. Of twenty-six muscle spindle afferents innervating tibialis anterior, all but two increased their discharge in the test contractions. In 90 % of contractions, acceleration thresholds were less than 3·2 % MVC (range, 0·01–11·9 % MVC).
4. Individual muscle spindle afferents increased their discharge at similar but not identical forces in repeated contractions. There was a positive correlation between the rate of contraction and the acceleration threshold ($P < 0{\cdot}001$), but the strength of the target contraction had no effect on the threshold, and there was no trend for thresholds to change over time.
5. The results suggest, first, that most muscle spindle endings in the human pretibial muscles receive a significant increase in fusimotor drive during relatively weak isometric efforts and secondly, that when fusimotor after-effects are controlled, much of the residual variability in 'acceleration threshold' for any one spindle in repeated contractions is due to extrafusal factors, particularly variability in contraction rate.

Direct recordings from human motor units have shown that recruitment order is reproducible and that recruitment threshold increases with motor unit size (Milner-Brown, Stein & Yemm, 1973) in accordance with Henneman's size principle (Henneman, Somjen & Carpenter, 1965). Data on γ-motoneurone recruitment are comparatively sparse, but there are no data to suggest similar reproducibility of recruitment. Indeed, the recruitment order of reflexly activated γ-motoneurones may be quite variable, although when recruitment order *is* constant, the size principle applies (Murphy, 1981). Because of the difficulty of recording directly from human fusimotor axons, their activity must be inferred from changes in muscle spindle afferent discharge rates. In human subjects, muscle spindle afferent activity often increases during voluntary contractions (Vallbo, 1971, 1974; Hagbarth, Wallin & Löfstedt, 1975). Although the increased muscle spindle activity during a voluntary contraction could be explained by skeleto-fusimotor (β)

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activation alone, experiments with pressure block suggest that γ-motoneurone activity contributes to the increased spindle afferent activity during voluntary effort (Burke, Hagbarth & Skuse, 1979).

During voluntary isometric contractions, the onset of discharge of α-motoneurones usually precedes the acceleration of muscle spindle discharge (Vallbo, 1970, 1971). This suggests that fusimotor activation occurs at the same time as or after α-motoneurone activation, but the precise temporal relationship has been the subject of debate (see Burke, Hagbarth & Skuse, 1978; Edin & Vallbo, 1990*a*). It has been argued that each muscle spindle afferent has a reproducible 'threshold' at which its discharge rate increases during isometric voluntary contractions and that this can be expressed in terms of the level of skeletomotor activity (Burke *et al.* 1978). However, for individual afferents innervating the extensors of the fingers, the force at which the discharge of muscle spindles accelerated 'varied considerably' between contractions (Edin & Vallbo, 1990*a*). In the same study, there was a small but significant reduction in threshold from the first to the third contraction, a finding that was unexplained but may have been due to after-effects of fusimotor drive on intrafusal fibres (e.g. Morgan, Prochazka & Proske, 1984; Baumann & Hulliger, 1991; Proske, Morgan & Gregory, 1993; Wilson, Gandevia & Burke, 1995). Other factors affecting the acceleration threshold for individual muscle spindle afferents have not been investigated, and it is not clear whether reproducible thresholds exist for either muscle spindle afferents or fusimotor neurones. Edin & Vallbo (1990*a*) also suggested that there may be two groups of spindle afferents, those that do and those that do not receive increased fusimotor drive during voluntary efforts. However, an alternative explanation is that the mechanical unloading produced by the extrafusal contraction outweighs any increase in fusimotor drive for some spindle afferents. The present study has sought evidence for this.

This study was undertaken to re-evaluate the behaviour of human muscle spindle endings in isometric contractions and to determine the variability of the acceleration threshold for individual spindle afferents, as well as for a population of afferents. In particular, the effects of sequential contractions (ensuring that the test muscle was stretched between contractions), the rate of contraction and the size of contraction have been assessed. Implications for the fusimotor system have been extrapolated where possible. A preliminary account of some findings has been presented (Wilson, Gandevia, Inglis & Burke, 1996).

METHODS

Studies were conducted on twenty-two healthy adult volunteers of either sex, aged 19–39 years. Muscles investigated were tibialis anterior and toe dorsiflexors. The subjects gave written, informed consent to the experimental procedures, which were approved by the appropriate institutional ethics committee.

Data collection

Subjects were seated in an adjustable chair with the ankle fixed in 95–105 deg dorsiflexion and the knee in 45–55 deg flexion. Throughout the experiment, subjects maintained this position and tried to relax all muscles except the test muscle. The foot of the test limb was immobilized by strapping it to a metal plate, and the torque about the ankle joint was monitored at high gain using a load cell (linear to 250 N). All contractions were as close to isometric as is possible in human experiments. Surface electrodes were placed to record EMG activity from tibialis anterior, long toe extensors and soleus. The inter-electrode distances were 6, 5 and 4 cm, respectively. Surface EMG was recorded continuously at high gain (×50000–100000; bandwidth 3·2–3·2 kHz). Due to the high gain, EMG signals were clipped during some voluntary contractions. To help relax the relevant muscles when required, subjects could monitor the EMG recordings on a large oscilloscope. All data were recorded on tape for off-line analysis.

Microelectrode recordings

Insulated tungsten microelectrodes were inserted percutaneously into the common peroneal nerve just proximal to the fibular head. Afferents from muscle spindles and Golgi tendon organs were identified by their response to maximal muscle twitch (produced by intrafascicular stimulation), to ramp stretch applied to the tendon and to voluntary muscle contraction with abrupt relaxation (McKeon & Burke, 1980; Burke, Aniss & Gandevia, 1987; Edin & Vallbo, 1990*b*). No attempt was made to distinguish between primary and secondary muscle spindle afferents. The filtered neural recordings were discriminated through a dual time-amplitude window discriminator (model DDIS 1, BAK) and reprocessed off-line using a CED 1401 interface running Spike2 software to reconfirm all unit shapes and to generate instantaneous frequency plots. The ramp stretches used in the identification of muscle spindle afferents were delivered via a servo-controlled vibrator (Cordo, Gandevia, Hales, Burke & Laird, 1993). Tendon taps were delivered transversely to the distal tendon with a background force of 3 N, an amplitude of 2·7 mm and one of three indentation velocities (6·75, 13·5 and 27 mm s^{-1}).

Contraction protocol

Prior to the study, all subjects underwent a training session for 20–40 min during which they practised controlled isometric contractions of the dorsiflexor muscles of the ankle and toes. For each subject, forces produced by maximal ankle dorsiflexion and toe dorsiflexion were recorded. Maximal force was determined from the best of three attempted maximal voluntary contractions (MVCs) during which the subject received verbal encouragement and visual feedback of the force. In three additional studies, these values were used to generate the target contraction forces. During each test, voluntary force was superimposed on a computer-generated 'ramp-and-hold' profile of the required force. Subjects relaxed completely between contractions, as verified by EMG and force recordings, and stretch was applied to the tendon 5–10 s prior to each contraction. The stretch was applied by indenting the tendon with a finger for 3 ± 1 s using a median applied force equivalent to 14 N (range 10–60 N). Stretches of this amplitude are sufficient to eliminate after-effects of preceding contractions on spindle discharge (see Wilson *et al.* 1995). In the first of two series of contractions, subjects increased the contraction at a constant rate (either 1 or 2% MVC s^{-1}), to peak forces that varied across trials (0·5, 1, 2, 3, 5, 8, 10 or 20% MVC; Fig. 1*A*). In the second series of contractions, the target force remained constant (either 5, 10 or 15% MVC), while the rate of increase of contraction varied across trials (0·5, 1, 2, 3 or 5% MVC s^{-1}; Fig. 1*A*). In both series the peak forces were held for 3–5 s, after which the subjects were required to relax the muscle completely. The rate of force reduction was controlled specifically in only a few trials. The first trials were usually of low force and rate (1 % MVC s^{-1}), and the target was varied from trial to trial in a pseudo-random sequence, although sequences of three identical trials were also included. The antagonist EMG was recorded at high gain and trials in which subjects co-contracted triceps surae were discarded.

In three subjects, additional experiments were performed to assess the extent to which toe extensor muscles and peroneus longus contributed to the ankle dorsiflexion torque. Intramuscular wire electrodes were inserted into tibialis anterior, extensor digitorum longus, extensor hallucis longus, and peroneus longus (75 μm stainless-steel wire, 1 mm insulation exposed, bandwidth 80 Hz to 3·2 kHz). The subjects then performed ankle dorsiflexion efforts, contracting to reach target forces as in the main study. The subjects did not receive feedback about the levels of EMG in the individual muscles, so that conditions were comparable to those in the main study.

Definition of acceleration threshold

Given that spindle acceleration occurs *after* the onset of EMG in a voluntary contraction (Vallbo, 1971; Hagbarth *et al.* 1975), the mean interspike interval for 5 s immediately prior to the onset of EMG was used to calculate the 'pre-contraction' discharge rate. The force recorded when the instantaneous firing rate exceeded the pre-contraction rate was defined as the acceleration threshold for that contraction (Fig. 1*B*).

Muscle spindle afferent discharge rates

The mean discharge rate of muscle spindle afferents during the hold phase of each contraction was measured. The mean discharge rates during the ramp phase of contractions were not assessed because marked fluctuations in discharge rate throughout the ramp were associated with small irregularities in the contraction (e.g. Hagbarth & Young, 1978; Wessberg & Vallbo, 1995).

Statistics

Non-parametric statistical tests were generally used for data on acceleration thresholds (i.e. Wilcoxon's signed rank, Friedman's analysis of variance by ranks, and Mann–Whitney *U* test) as appropriate. To assess the significance of correlations, Spearman's coefficients were used. Unless indicated, values are given as medians ± interquartile ranges, with the exception of muscle spindle afferent discharge rates, for which values are given as means ± S.D. The χ^2 test with Yates correction was used for comparing the observed discharge rates with those in other afferent samples. Significance was set at the 5 % level.

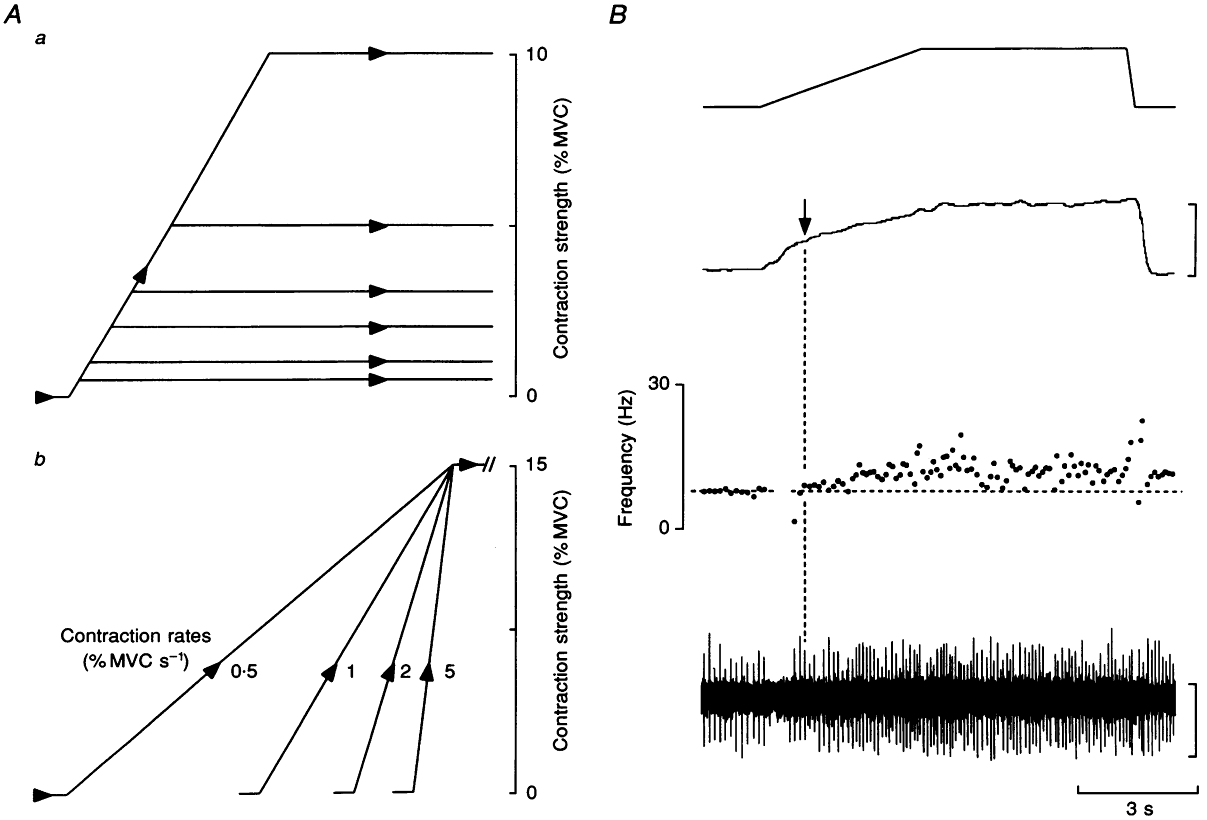

Figure 1. Contraction protocol and acceleration threshold for a muscle spindle afferent innervating tibialis anterior

Aa, first contraction protocol: the required contraction rate was constant (usually 2 % MVC s^{-1}), with variable peak contraction strengths; *Ab*, second protocol, with fixed contraction strength (5 or 15 % MVC) but variable contraction rate. *B*, traces from the top represent the visually displayed target ramp, ankle torque, instantaneous frequency of discharge of a muscle spindle afferent with a background discharge of 6·5 Hz, and the neurogram. The arrow and vertical line indicate acceleration threshold. Note the initial spindle unloading before its acceleration. Vertical calibrations: 800 μV and 3 % MVC.

RESULTS

Background discharge rates

Recordings were made from forty-three muscle spindle afferents innervating tibialis anterior ($n = 26$), extensor digitorum longus ($n = 14$), extensor hallucis longus ($n = 2$) and extensor digitorum brevis ($n = 1$) during voluntary isometric contractions. The total number of contractions studied was > 500. Five muscle spindle afferents were studied during only one target contraction and five during more than twenty-five contractions. The same proportion of endings innervating both tibialis anterior and toe extensors had no background discharge at rest (17/26 and 11/17). This contrasts with findings in the upper limb, in which spindle afferents innervating wrist extensors have a background discharge significantly more often than those in finger extensors (Gandevia, Wilson, Cordo & Burke, 1994). The mean discharge rate of the fifteen endings active in relaxed muscle was 7·3 ± 1·9 Hz, and the mean frequency for all forty-three afferents was 2·6 ± 3·7 Hz (range, 0–11·4 Hz).

Ankle torque

For three subjects, intramuscular wire electrodes were inserted into toe extensors, peroneus longus and tibialis anterior, and recordings made while the subjects performed voluntary ankle dorsiflexions, attempting to contract tibialis anterior selectively. In all three subjects, there was minimal or no activity in peroneus longus in deliberate ankle dorsiflexions of up to 10% MVC. In extensor digitorum longus and extensor hallucis longus motor unit recruitment occurred even in the weakest efforts (0·5 and 1% MVC) in all three subjects. In only 9% of the weakest contractions was activity limited to tibialis anterior.

Acceleration threshold

The contractions were performed in two series in which subjects matched the force of ankle (or toe) dorsiflexion with a target force. Contractions were made at a fixed rate to different target strengths (first series), or to a fixed target force at different rates (second series; see Fig. 1*A*). Acceleration threshold was measured as the force at which the instantaneous discharge rate of the afferent exceeded the pre-contraction rate (see Methods). Figure 1*B* illustrates the acceleration threshold for a spindle afferent innervating tibialis anterior, discharging at 6·5 Hz. All except two spindle afferents innervating tibialis anterior and one innervating extensor digitorum longus were activated in at least some voluntary contractions. For fourteen of fifteen actively discharging endings there was invariably a transient reduction in discharge rate (unloading) before the unit accelerated (Fig. 1*B*). This is not a feature of spindle endings in forearm extensor muscles (Edin & Vallbo, 1990*a*).

The variability in the acceleration threshold for two typical spindle afferents is shown in Fig. 2*A*. The distribution of thresholds was usually positively skewed, and this was the reason for recording median rather than mean values. Accordingly, there was a tendency for median thresholds to be closer to the 10th than the 90th percentile (Fig. 2*B*). The majority of afferents accelerated their discharge at low forces but because of the difficulty in performing isolated

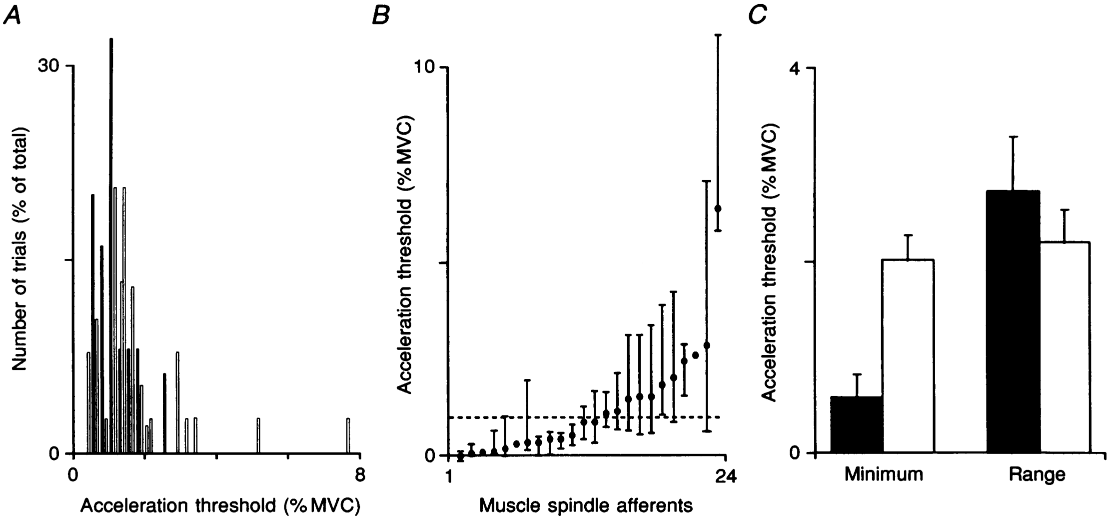

Figure 2. Acceleration thresholds for two spindle afferents, for all twenty-four afferents innervating tibialis anterior whose discharge increased during contractions and for these afferents compared with finger extensors

A, distribution of acceleration thresholds for two muscle spindle afferents (filled and open bars) in repeated contractions. *B*, median values (●) and 10th to 90th percentiles (error bars) for acceleration threshold for all 24 tibialis anterior afferents that accelerated in voluntary contractions. The afferents are ranked in order of increasing acceleration threshold. *C*, comparison of both the minimum acceleration thresholds, and the range of acceleration thresholds for tibialis anterior afferents in this study (■) with that for finger extensors (□) recorded by Edin & Vallbo (1990*a*).

contractions of toe dorsiflexors, acceleration thresholds were only quantified as a percentage of MVC for the afferents innervating tibialis anterior. Threshold was measured for twenty-six spindle afferents in sixteen subjects in > 400 contractions. For twenty-four afferents, discharge rates increased during the contractions, and median acceleration thresholds ranged from 0·02 to 3·99% MVC, with most < 1% MVC. It is unlikely that inter-subject variability produced the range of thresholds in the afferent sample because, for example, four afferents studied in one subject included two afferents with thresholds always < 1% MVC and two with thresholds as high as 6·7% MVC. There was a tendency for variability in the threshold to be greater for spindle afferents that accelerated at higher thresholds (Fig. 2*B*).

A comparison of the acceleration thresholds for spindle afferents innervating tibialis anterior with those for afferents innervating finger extensors in the study by Edin & Vallbo (1990*a*) is shown in Fig. 2*C*. Minimal acceleration thresholds were lower for afferents innervating tibialis anterior than for those innervating the finger extensors (medians of 0·22 and 1·64% MVC, respectively; Mann–Whitney rank sum test: $P < 0.001$).

Three of forty-three spindle afferents innervating tibialis anterior and toe extensors did not have increased discharge rates in the weak voluntary contractions used in the present study. This represents less failure of acceleration than that occurring for afferents innervating finger extensor muscles in contractions of comparable strength (Edin & Vallbo, 1990*a*; 23 of 84 not recruited, χ^2: $P = 0.014$). Of the three afferents not activated during voluntary contractions, one innervating extensor digitorum longus had a background discharge. During contraction, the discharge rate declined, but there was a sustained elevated post-contraction discharge after subsidence of the relaxation burst (Fig. 3*A*). This behaviour was reproducible in seven contractions and suggests that increased fusimotor activity had been directed to the spindle during the contractions (see Wilson *et al.*

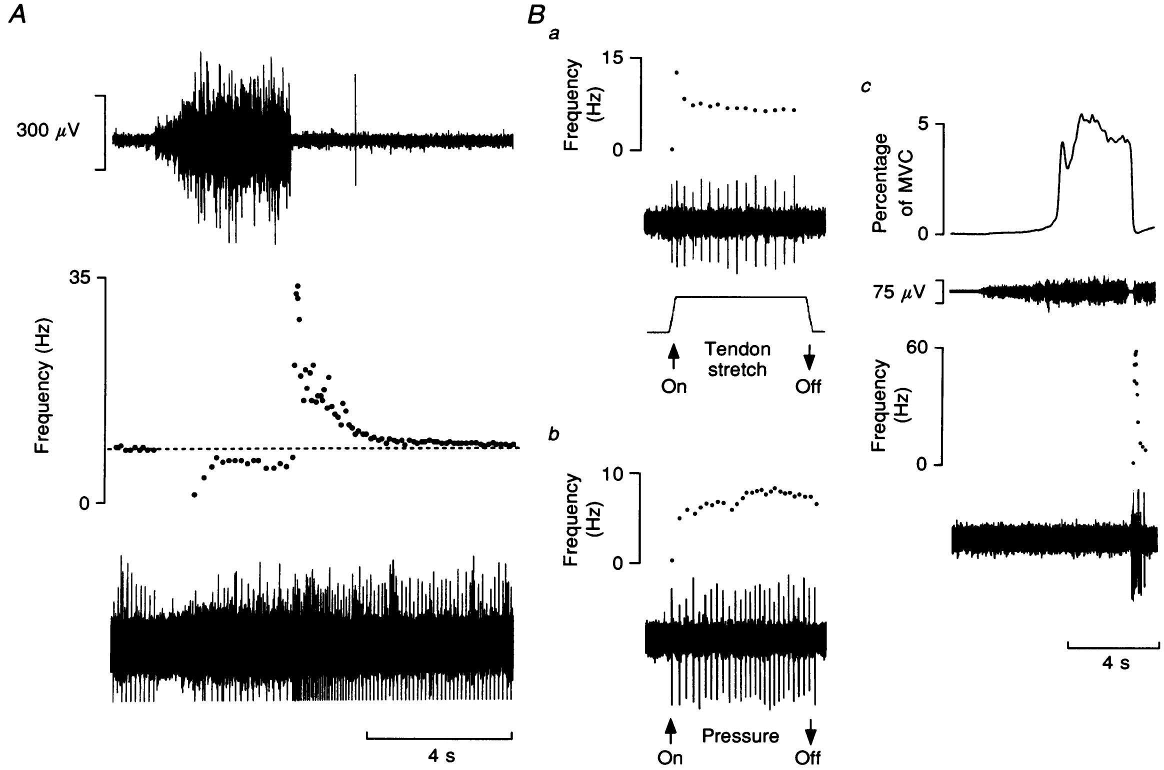

Figure 3. Two muscle spindle afferents, one with and one without background discharge, whose discharge rates did not change during voluntary contractions

A, data from a toe extensor afferent that had a background discharge of 5·4 Hz. It was unloaded during contraction and had an elevated post-contraction discharge rate at 7·6 Hz. Traces from the top are: EMG, instantaneous frequency for the afferent and neurogram. *B*, data from an afferent innervating tibialis anterior that did not discharge during contraction. *Ba* shows the response to stretch applied transversely to the tendon (2·7 mm at 27 mm s^{-1}; see Methods). From the top, traces are instantaneous frequency, neurogram and probe position. *Bb* shows the afferent response to abrupt sustained pressure applied (indicated by arrows) over the receptive field. Traces are instantaneous frequency and neurogram. *Bc* shows the afferent discharge during and after a contraction at 5% MVC. The afferent did not discharge during the contraction but produced a high-frequency burst of impulses with relaxation. Panels are as in *A* with addition of a top panel representing torque.

1995). One afferent innervating tibialis anterior did not discharge in a 5% MVC (Fig. 3*Bc*), but had a prominent relaxation burst (peak frequency ~60 Hz). The dynamic response of the afferent to stretch applied transversely to the tendon under passive conditions was relatively low: the dynamic index was 5 Hz with the fastest stretch and the peak instantaneous frequency was less than 15 Hz (Fig. 3*Ba*). This difference in response could be dismissed as being due to differences in the stretch reaching the spindle ending, but the afferent also showed little dynamic response to abrupt pressure applied directly over the receptor (Fig. 3*Bb*). Although alternative explanations cannot be excluded (e.g. passive lengthening of the spindle due to pull by series elastic elements; Vallbo, 1970; Edin & Vallbo, 1990*a*), the contrast between the low stretch responsiveness and the prominent relaxation burst would be consistent with a contraction-associated increase in dynamic fusimotor drive that was insufficient to produce spindle afferent activity during the contraction. The third afferent did not discharge during contraction (20% MVC) and had no post-contraction discharge to suggest that it had been subjected to fusimotor drive during the contraction.

Factors affecting acceleration threshold

Effect of contraction speed. In the second series of contractions, the rate of contraction varied between trials (0·5–5% MVC s^{-1}; Fig. 1*A*). In general, subjects could track the target quite well, but there were inevitably deviations from the goal of a smoothly increasing contraction. Correlations between acceleration thresholds and the mean rate of increase of force over different time intervals were sought. The intervals over which mean contraction speeds were calculated included the time from the onset of the contraction until acceleration, time from onset of contraction until onset of the hold phase (at the peak force), and also time intervals of 100, 200 and 400 ms immediately prior to acceleration. Correlations between threshold and contraction speed were consistently highest for the average speed from onset of contraction until acceleration, and this value is used as the index of contraction speed unless otherwise indicated. For fifteen spindle afferents innervating tibialis anterior, recordings were made during more than five contractions, and for ten, there was a significant positive correlation between contraction rate and threshold, as illustrated in Fig. 4 for two spindle afferents. No negative correlations were observed. For the population of fifteen afferents there was a positive correlation between contraction rate and acceleration threshold for contractions of similar strength (e.g. contraction strength < 1·5% MVC, $P < 0{\cdot}001$). This positive correlation between threshold and speed of contraction would not be expected if increased spindle discharge were directly related to the drive to α-motoneurones, because motor units are recruited earlier in faster contractions, i.e. there is a negative correlation between contraction rate and the threshold for α-motoneurones (e.g. Büdingen & Freund, 1976).

In contractions of similar target strength performed at different rates, there was a negative correlation between the latency for acceleration after the contraction began and the contraction rate (Spearman's rank: −0·41, $P < 0{\cdot}001$). In other words, spindle acceleration occurred later the slower the contraction but, as discussed in the preceding paragraph, the threshold force at which afferents were activated was lower. Overall, the time to acceleration varied between 0 and 12·6 s, with median and interquartile range of 0·84 s and 1·3 s, respectively.

Effect of contraction strength. In contrast to the effect of contraction speed, a significant positive correlation between the strength of the target contraction and acceleration threshold was seen for only two of the fifteen afferents recorded in more than five contractions ($P = 0{\cdot}013$ and $P = 0{\cdot}047$). Overall, for the population of fifteen afferents, there was no significant correlation between contraction strength and acceleration threshold for contractions of similar speed. Thus knowledge of the strength of the

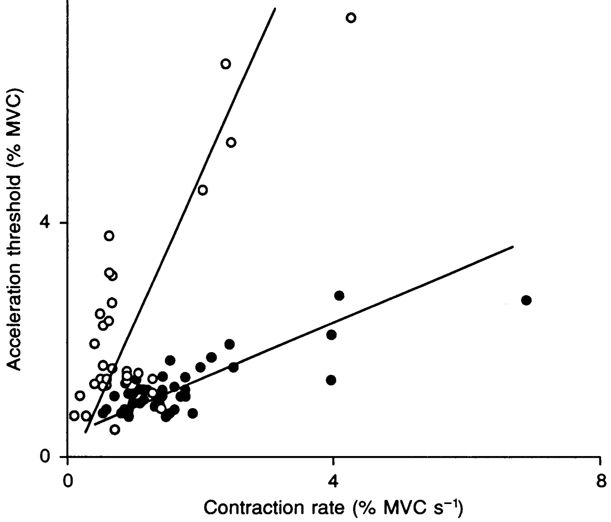

Figure 4. Effect of contraction rate on acceleration threshold

Acceleration thresholds recorded in contractions of different speed are shown for two afferents innervating tibialis anterior (○ and ●). For illustration, regression lines for the two data sets are drawn. Spearman's rank correlation was significant for data from both afferents ($P < 0{\cdot}01$).

required contraction did not influence the 'α–γ balance' at the onset of the contraction.

Effect of contraction sequence. The long-term effects of repeated voluntary contractions on acceleration thresholds were assessed by comparing the acceleration threshold in the first and last contractions. Comparisons were only made between contractions of similar rate and strength (26 pairs of contractions, 8 spindle afferents). The first and last contractions of each pair were separated by a variable number of contractions (median 9; range 6–36) and by a variable time period (median 17 min; range 5–55 min). There was no difference in acceleration threshold (see Fig. 5*A*; Wilcoxon signed rank, $P = 0{\cdot}26$).

In three consecutive contractions of similar rate and strength, there was also no significant change in the acceleration threshold ($P = 0{\cdot}25$, Friedman's ANOVA, 12 spindles; 39 data sets; Fig. 5*B*). The discrepancy between these results and those of Edin & Vallbo (1990*a*) may be because, in the present study, stretch was applied to the tendon between contractions to minimize spindle after-effects that may alter the responses in subsequent contractions (see Discussion).

Factors affecting muscle spindle afferent discharge rates

For the fifteen afferents studied in over five contractions, the increase in the mean discharge rate from the pre-contraction period to the hold phase of contraction was 6·6 ± 4·1 Hz (i.e. inclusive of the full range of contraction strengths). The maximal increase in discharge rate during contractions was 14·9 ± 8·6 Hz. To detect whether the discharge rate during the first part of the hold phase differed substantially from the mean discharge rate for the entire phase (usual duration, 4 s), the mean discharge frequency during the first second of the hold was determined. In individual trials afferent discharge rates varied during the first second and during the entire hold, but the mean increase in discharge frequency during the first second of the plateau phase was not different from the mean frequency for the entire plateau phase ($P = 0{\cdot}57$).

Effect of contraction strength. The effect of the strength of contraction on spindle discharge rate (during the plateau) is illustrated in Fig. 6 for five of the fifteen afferents innervating tibialis anterior for contractions of 1–10% MVC. For four of the fifteen afferents there was a positive correlation between the mean discharge frequency during the hold phase of contraction and contraction strength (Fig. 6*A–D*). For the remaining eleven afferents, there was no significant correlation between discharge rate and contraction strength (e.g. Fig. 6*E*). However, when the fifteen afferents were considered together, there was a strong positive correlation between the contraction strength and mean afferent discharge rate ($P = 0{\cdot}005$).

Effect of contraction speed. Mean discharge rates were not significantly affected by the speed of contraction ($P = 0{\cdot}817$, $P = 0{\cdot}122$).

Effect of contraction sequence. In three consecutive contractions of similar rate and strength, there was no significant change in mean afferent discharge rates during the hold phase of contraction (Fig. 5*C*).

Combined response

To assess the overall input to the nervous system during contractions of different strength, the data from fifteen

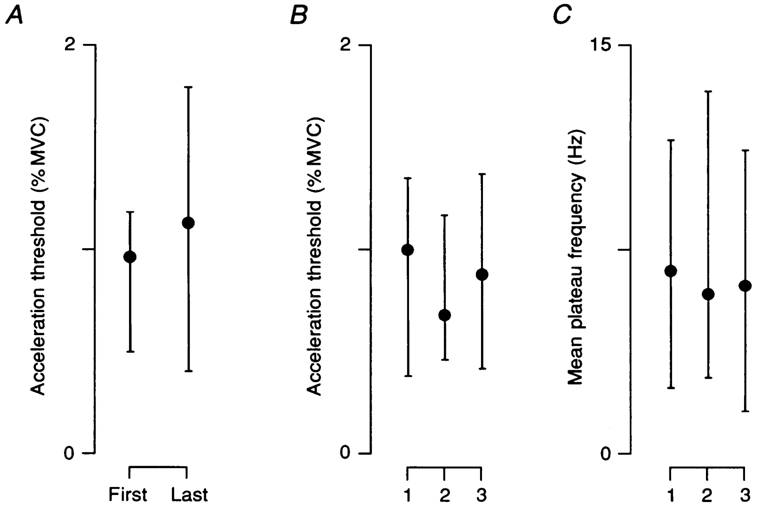

Figure 5. Effect of order of contractions on acceleration threshold and afferent discharge rates

A, median acceleration thresholds for the first and last contractions (26 data sets) recorded during a series of contractions with ≥ 6 contractions separating the first and last contraction for each data set, and with a similar strength and rate of contraction for both the first and last contractions of each data set (median and interquartile range). *B* and *C*, the median acceleration thresholds and the mean discharge rates, respectively, during the plateau phase of the contraction for the first, second and third of three identical consecutive contractions (39 data sets). Error bars represent the interquartile ranges.

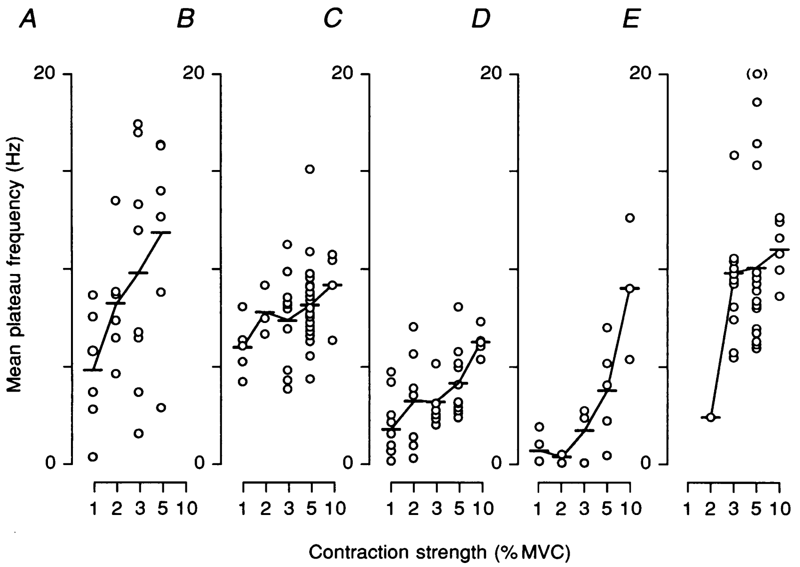

Figure 6. Mean discharge rates during contractions for five muscle spindle afferents

A to *E*, the data for five muscle spindle afferents. The increase in mean discharge rate during the hold phase of contraction above the mean discharge rate at rest is represented (○) for each contraction. The increase in discharge rates for contractions of different strengths are compared for each afferent, with contractions arranged in order of increasing strength from left to right (1, 2, 3, 5 and 10% MVC). The symbol enclosed in parentheses in *E* represents a discharge rate of 21 Hz. The horizontal bars represent median values for each group of data points, and horizontal bars across the range of contraction strengths are linked to indicate the trend in discharge rate with contraction strength.

spindle afferents were pooled. The total increase in spindle input during contractions of different strength will be the result of both the number of afferents recruited during contraction and the increment in their individual discharge rates. The growth of the combined spindle discharge as contraction strength increases is illustrated in Fig. 7. The combined afferent response was estimated as the cumulative sum of the mean increase in discharge rate during the hold phase for each of the fifteen afferents. For each afferent, the increase in discharge rate was entered into the cumulative response at the acceleration threshold of that afferent. This relationship underestimates the true population response because it does not take into account the further increases in discharge rate of spindle endings as contraction strength increases, a factor that is significant even if small (see previous section). If this factor was included in the

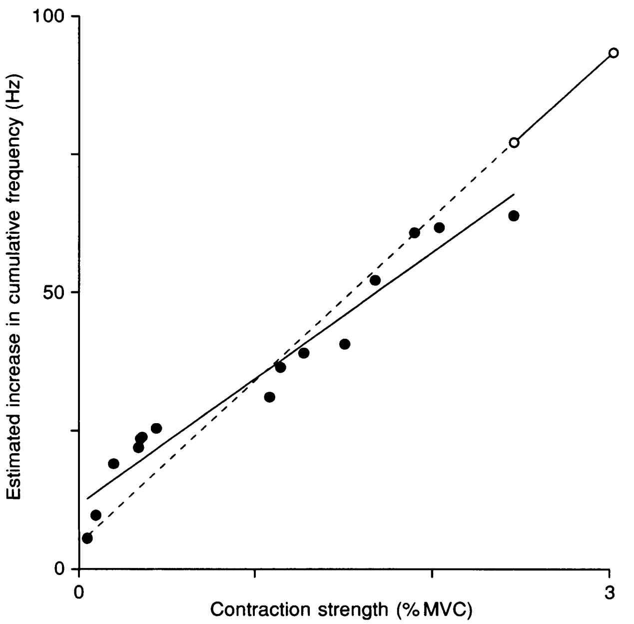

Figure 7. Cumulative sum of the increase in mean afferent discharge rates with increasing contraction strength due to acceleration of muscle spindle afferents

The change in the mean discharge rate for a population of fifteen afferents is represented by a cumulative sum. Each afferent is positioned along the horizontal axis (●) at its acceleration threshold. For each afferent, the contribution to the cumulative sum was the increase from its mean discharge rate at rest to the mean rate during the hold phase of the contraction (< 3% MVC). The linear regression is represented by the continuous line and is significant ($r = 0{\cdot}98$; $P < 0{\cdot}01$). The two open symbols (○) represent adjustments to the cumulative sum of the overall discharge rate, correcting for the additional increments in discharge rate due to progressive increases in discharge rate for each afferent between acceleration threshold and the final contraction strength (either 2·44 or 3% MVC). These data points are joined by a continuous line and this is projected back as a dashed line. There is little difference between the relationships.

estimation, there would be a comparable relationship with a slightly steeper slope: the open symbols (○) in Fig. 7 represent data in which the increases in discharge rates of individual afferents with increasing contraction strength were considered (up to 2·44 and 3% MVC, respectively, for each point). Either way, it can be concluded that, in weak contractions, the input from a population of spindle afferents grows in proportion to contraction strength ($P < 0{\cdot}01$).

DISCUSSION

The present study has shown that the discharge of most muscle spindle afferents increases at low forces in isometric contractions, and that acceleration thresholds for individual muscle spindle afferents exhibit some variability. These findings extend those of Burke *et al.* (1978) by quantifying the range of acceleration thresholds for both the afferent population and individual afferents and by demonstrating that muscle spindle afferents from the pretibial flexors accelerate at relatively low forces, similar to that occurring with forearm extensors (see Edin & Vallbo, 1990*a*). The findings of the present study also extend those of Edin & Vallbo (1990*a*) by demonstrating that contraction rate, but not target contraction strength, influences the acceleration threshold. The data from recordings of acceleration threshold in sequential contractions (three contractions) differ from those of Edin & Vallbo (1990*a*), in that a sequential reduction in acceleration threshold was not observed when the after-effects of the preceding contraction were minimized. Mean muscle spindle discharge rates during contraction in this study were similar to those previously recorded in human studies.

Contribution of different muscles to ankle dorsiflexion torque

The production of maximal voluntary ankle dorsiflexor torque involves a number of muscles, and the contribution from tibialis anterior can be estimated to be about 55% of the maximal ankle dorsiflexor torque (e.g. Fukunaga *et al.* 1992). An initial assumption in this study was that tibialis anterior contributed most of the ankle dorsiflexor torque at the range of contraction strengths used and this would also then imply that there was a proportionately greater contribution from tibialis anterior to ankle torque in the contractions used to assess acceleration thresholds than in the maximal ankle dorsiflexion efforts. The net effect of an unequal contribution from tibialis anterior to ankle torque in maximal and test contractions would be an underestimation of thresholds (in terms of per cent maximum tibialis anterior contraction). Given that recordings from intramuscular electrodes showed that there was often activity in toe extensors with even the weakest deliberate ankle dorsiflexion efforts, the exact extent of the bias would be difficult to quantify. Importantly, variability in the extent to which different muscles contribute to the force produced when tracking the target force would result in variability in acceleration thresholds (see below).

Low acceleration thresholds

In a study of the acceleration of spindle endings during voluntary isometric contractions of ankle dorsiflexors (Burke *et al.* 1978), eighteen of nineteen afferents were activated in contractions of up to 4 N m, a force equivalent to about 8% MVC (see Adams, Gandevia & Skuse, 1990). A failure to increase spindle discharge during contractions was similarly rare in the present study, with only three of forty-three afferents not activated in contractions of up to 20% MVC. However, for finger extensors, the failure of muscle spindle afferent discharge to increase in weak isometric contractions appears to be more common: twenty-three of eight-four afferents in contractions up to 10% MVC (Edin & Vallbo, 1990*a*). There was also a significant tendency for acceleration thresholds, although low in all three studies, to be higher for afferents innervating the finger extensors than for those innervating the pretibial muscles. Acceleration thresholds were usually < 5% of MVC for finger extensor afferents (Edin & Vallbo, 1990*a*) and < 3·2% MVC in the present study. A number of factors could contribute to the tendency for lower acceleration thresholds and the acceleration of a greater percentage of spindle endings in tibialis anterior than in finger extensors. First, there could be greater mechanical unloading of spindles in the finger extensors during isometric contractions, possibly resulting from contraction of components of the muscle that act on fingers adjacent to the test finger (Vallbo, 1974), as has been found with digital flexors in contractions as low as 2·5% MVC (Kilbreath & Gandevia, 1994). However, if there is greater spindle unloading for finger extensor spindles than for pretibial spindles, it is perhaps surprising that in actively discharging finger extensor spindles, the discharge rates did not undergo a transient reduction prior to their acceleration (Edin & Vallbo, 1990*a*), something that was almost invariable with pretibial spindles. This could have been due to differences in the muscle architecture and in the patterns of muscle contraction in the forearm such that, when significant, unloading could not be overcome. A second factor that could contribute to differences in acceleration thresholds in the two muscle groups is their architecture. The compliance of tendinous structures 'in series' with the muscle spindles and the ratio of the lengths of tendon to total muscle length, for example, may significantly influence spindle discharge. Thirdly, there may be differences in the $\alpha-\gamma$ balance in voluntary contractions of the pretibial flexor and finger extensor muscles. Finally, as discussed above, pretibial muscles other than tibialis anterior will contribute to maximal voluntary force, thus increasing the possibility of the present thresholds being low. However, it is likely that this problem is also important with finger extensors. Accordingly, it would be prudent not to assign too much weight to differences in acceleration thresholds for spindles in different muscles.

Variability of acceleration thresholds

Edin & Vallbo (1990*a*) emphasized that acceleration thresholds for spindle afferents can vary considerably (Fig. 2*C*; see also Vallbo, 1974). On the other hand, it has been claimed that the acceleration thresholds for ankle dorsiflexors were relatively constant (Burke *et al.* 1978; Burke, McKeon & Westerman, 1980), though its variability was not specifically quantified. The present study reveals that the force at which a spindle afferent is recruited *is* variable in repeated contractions, as was noted for muscles in the upper limb (Vallbo, 1974; Edin & Vallbo, 1990*a*). However, the variability is not random: it seems to be related to differences in the way in which repeated contractions are performed. This will presumably result in subtle trial-to-trial variations in the loading and unloading seen by individual spindle endings caused by variability in the activity of motor units near the spindle. In the present study, the variability cannot be explained by contraction-dependent after-effects due to 'stiction' within the intrafusal fibres (see Brown, Goodwin & Matthews, 1969), because all contractions were preceded by stretch designed to break actin–myosin bonds in intrafusal fibres, so that the spindle was reset similarly prior to each contraction (for review, see Proske *et al.* 1993). This precaution was not included in previous study protocols (Burke *et al.* 1978; Edin & Vallbo, 1990*a*).

Factors affecting acceleration threshold

The positive correlation between the acceleration thresholds of muscle spindle afferents and the speed of contraction recorded in this study contrasts with the negative correlation between acceleration thresholds and contraction speeds of α-motoneurones (e.g. Büdingen & Freund, 1976). Inevitably, there will tend to be more mechanical unloading of muscle spindle endings for any given force as the contraction speed increases, except when the contractions are fast enough to recruit spindle endings before the mechanical events produced by the extrafusal contraction (Vallbo, 1971; Hagbarth *et al.* 1975). The increase in threshold is consistent with fixed elements in the latency between onset of effort and fusimotor activation of the spindle ending in the face of more rapid development of force. This does not imply that skeleto- and fusimotor drives are necessarily dissociated by changes in contraction speeds; indeed, there is evidence that γ-motoneurone activity does increase with contraction speed, i.e. the tendency as contraction speed increases, for reduced time from the onset of contraction until spindle afferent acceleration.

For contractions performed at the same rate, acceleration thresholds were not affected by the target contraction strength. This suggests that fusimotor drive is not predetermined according to the target force. In other words, at least for the type of contractions performed here, subjects do not adopt a different fusimotor 'strategy' depending on whether the intended contraction is weak or strong (see Prochazka, Hulliger, Zangger & Appentang, 1985). There was also no evidence from acceleration thresholds for a change in the fusimotor strategy between the first and subsequent contractions. In addition, although not studied formally, when the target contraction rate was changed by the experimenter unknown to the subject, the first contraction under the new conditions was not associated with an earlier or more intense spindle discharge. These findings are consistent with the absence of any effects of practice or learning on muscle spindle discharge in voluntary contractions (Al-Falahe &Vallbo, 1988).

Most afferents accelerated at low forces, but because the contractions were slow, the fastest at 5% MVC s^{-1}, the delay between the onset of contraction and afferent acceleration was as long as 12·6 s. This emphasizes that the contractions studied, while 'weak' when expressed as a percentage of MVC, still covered a range over which subjects could maintain considerable fine control. The amount of effort required to overcome the weight of the foot is about 0·3 N (see de Leva, 1996), within the range of the contraction strengths tested in this study (e.g. if MVC is 60 N, then 0·3 N $\approx$ 0·5% MVC). The sequential acceleration of individual afferents during the slow rise in force of these ramp contractions, even with only a small difference between individual afferent thresholds, can effectively provide an afferent signal encoding contraction strength (see Fig. 7). Whether the information encoded in the population response is unique will, however, depend on other confounding factors, such as the rate of contraction, the variability in its performance and whether overt movement occurs.

The idea that there may be two subgroups of spindle afferents, accessed differently by fusimotor activity in weak isometric contractions (see Edin & Vallbo, 1990*a*), is not supported by this study. For two of three pretibial spindle afferents that did not accelerate during contraction, there was suggestive evidence of an increase in fusimotor drive (e.g. post-contraction changes in spindle discharge). When this is taken into consideration, it is likely that few, if any, pretibial spindle afferents received no fusimotor drive during the comparatively weak contractions tested in this study.

Muscle spindle afferent discharge rates

The mean discharge rates recorded during isometric contractions in this study rarely exceeded 20 Hz, a finding comparable to other human studies (e.g. Vallbo, 1974; Edin & Vallbo, 1990*a*), but considerably less than in awake cats, typically 100–300 Hz (Prochazka, Westerman & Ziccone, 1977). The low firing rates of human spindle endings, whether at rest or during a voluntary contraction, prompts questions about which aspects of the afferent discharge are biologically important. The cumulative sum of the increment in mean afferent discharge rate during isometric contractions of up to 3% MVC for the fifteen afferents (Fig. 7) shows a combined increment in discharge rate of ~70–100 Hz. The total number of muscle spindles in tibialis anterior is ~284 (Voss, 1971), greatly exceeding the number sampled in this study. This suggests that the total spindle afferent input at contraction levels of 3% MVC would be about 1700 impulses s^{-1} (assuming that 11·5% (3 of 26) are not activated). The cumulative increment in muscle spindle afferent discharge rate for a population of afferents can be calculated for stronger contractions (of 30% MVC) from data collected in a previous study of isometric contractions of the pretibial muscles (Macefield, Hagbarth, Gorman, Gandevia & Burke, 1991). Using their data, the calculated cumulative increment in discharge rate for a sample of fifteen afferents would be about 225 impulses per second, i.e. only about two to three times the cumulative increase in frequency recorded in the 3% MVC in the current study (~4260 impulses s^{-1} for the total population of tibialis anterior spindles). Combined with the evidence of low acceleration thresholds for the majority of muscle spindle afferents, these findings suggest that there will be proportionately greater growth in muscle spindle afferent support across weak efforts.

Observations on the rates of 'deafferented' motor units in graded voluntary efforts suggest that there is normally significant reflex support to a contraction throughout the range of isometric contraction strengths (Gandevia, Macefield, Burke & McKenzie, 1990; Macefield, Gandevia, Bigland-Ritchie, Gorman & Burke, 1993). Matthews (1986) has emphasized that, even if the afferent feedback during a contraction is constant, the reflex effects increase proportionately with voluntary force through the mechanism of 'automatic gain control'. Graded increase in muscle spindle discharge rates across the low force range would constitute an additional mechanism for grading the reflex support to these weak contractions, perhaps allowing more flexibility in tasks requiring fine motor control.

ADAMS, R. W., GANDEVIA, S. C. & SKUSE, N. F. (1990). The distribution of muscle weakness in upper motoneuron lesions affecting the lower limb. *Brain* **113**, 1459–1476.

AL-FALAHE, N. A. & VALLBO, B. (1988). Role of the human fusimotor system in a motor adaptation task. *Journal of Physiology* **401**, 77–95.

BAUMANN, T. K. & HULLIGER, M. (1991). The dependence of the response of cat spindle Ia afferents to sinusoidal stretch on the velocity of concomitant movement. *Journal of Physiology* **439**, 325–350.

BROWN, M. C., GOODWIN, G. M. & MATTHEWS, P. B. C. (1969). After-effects of fusimotor stimulation on the response of muscle spindle primary afferent endings. *Journal of Physiology* **205**, 677–694.

BÜDINGEN, H. J. & FREUND, H.-J. (1976). The relationship between the rate of rise of isometric tension and motor unit acceleration in a human forearm muscle. *Pflügers Archiv* **362**, 61–67.

BURKE, D., ANISS, A. M. & GANDEVIA, S. C. (1987). In-parallel and in-series behavior of human muscle spindle endings. *Journal of Neurophysiology* **58**, 417–426.

BURKE, D., HAGBARTH, K.-E. & SKUSE, N. F. (1978). Recruitment order of human spindle endings in isometric voluntary contractions. *Journal of Physiology* **285**, 101–112.

BURKE, D., HAGBARTH, K.-E. & SKUSE, N. F. (1979). Voluntary activation of spindle endings in human muscles temporarily paralysed by nerve pressure. *Journal of Physiology* **287**, 329–336.

BURKE, D., MCKEON, B. & WESTERMAN, R. A. (1980). Induced changes in the thresholds for voluntary activation of human spindle endings. *Journal of Physiology* **302**, 171–181.

CORDO, P. J., GANDEVIA, S. C., HALES, J. P., BURKE, D. & LAIRD, G. (1993). Force and displacement-controlled tendon vibration in humans. *Electroencephalography and Clinical Neurophysiology* **89**, 45–53.

DE LEVA, P. (1996). Adjustments to Zatsiorsky-Seluyanov's segment inertia parameters. *Journal of Biomechanics* **29**, 1223–1230.

EDIN, B. B. & VALLBO, B. (1990*a*). Muscle afferent responses to isometric contractions and relaxations in humans. *Journal of Neurophysiology* **63**, 1307–1313.

EDIN, B. B. & VALLBO, B. (1990*b*). Classification of human muscle stretch receptor afferents: A Bayesian approach. *Journal of Neurophysiology* **63**, 1314–1322.

FUKUNAGA, T., ROY, R. R., SHELLOCK, F. G., HODGSON, J. A., DAY, M. K., LEE, P. L., KWONG-FU, H. & EDGERTON, V. R. (1992). Physiological cross-sectional area of human leg muscles based on magnetic resonance imaging. *Journal of Orthopaedic Research* **10**, 928–934.

GANDEVIA, S. C., MACEFIELD, G., BURKE, D. & MCKENZIE, D. K. (1990). Voluntary activation of human motor axons in the absence of muscle afferent feedback: the control of the deafferented hand. *Brain* **113**, 1563–1581.

GANDEVIA, S. C., WILSON, L. R., CORDO, P. J. & BURKE, D. (1994). Fusimotor reflexes in relaxed forearm muscles produced by cutaneous afferents from the human hand. *Journal of Physiology* **479**, 499–508.

HAGBARTH, K.-E., WALLIN, G. & LÖFSTEDT, L. (1975). Muscle spindle activity in man during voluntary fast alternating movements. *Journal of Neurology, Neurosurgery and Psychiatry* **7**, 625–635.

HAGBARTH, K.-E. & YOUNG, R. R. (1978). Sensitivity of normal human muscle spindles to small spontaneous changes in muscle length during voluntary contraction. *Transactions of the American Neurological Association* **103**, 1–4.

HENNEMAN, E., SOMJEN, G. & CARPENTER, D. O. (1965). Functional significance of cell size in spinal motoneurones. *Journal of Neurophysiology* **28**, 560–580.

KILBREATH, S. L. & GANDEVIA, S. C. (1994). Limited independent flexion of the thumb and fingers in human subjects. *Journal of Physiology* **479**, 487–497.

MACEFIELD, V. G., GANDEVIA, S. C., BIGLAND-RITCHIE, B., GORMAN, R. B. & BURKE, D. (1993). The firing rates of human motoneurones voluntarily activated in the absence of muscle afferent feedback. *Journal of Physiology* **471**, 429–443.

MACEFIELD, G., HAGBARTH, K.-E., GORMAN, R., GANDEVIA, S. C. & BURKE, D. (1991). Decline of spindle support to α-motoneurones during sustained voluntary contractions. *Journal of Physiology* **440**, 497–512.

MCKEON, B. & BURKE, D. (1980). Identification of muscle spindle afferents during *in vivo* recordings in man. *Electroencephalography and Clinical Neurophysiology* **48**, 606–608.

MATTHEWS, P. B. C. (1986). Observations on the automatic compensation of reflex gain on varying the pre-existing level of motor discharge in man. *Journal of Physiology* **374**, 73–90.

MILNER-BROWN, H. S., STEIN, R. B. & YEMM, R. (1973). The orderly acceleration of human motor units during voluntary isometric contractions. *Journal of Physiology* **230**, 359–370.

MORGAN, D. L., PROCHAZKA, A. & PROSKE, U. (1984). The after-effects of stretch and fusimotor stimulation on the responses of primary endings of cat muscle spindles. *Journal of Physiology* **356**, 465–477.

MURPHY, P. R. (1981). The acceleration order of γ-motoneurones in the decerebrate rabbit. *Journal of Physiology* **315**, 59–67.

PROCHAZKA, A., HULLIGER, M., ZANGGER, P. & APPENTANG, K. (1985). 'Fusimotor set': new evidence for α-independent control of γ-motoneurones during movement in the awake cat. *Brain Research* **339**, 136–140.

PROCHAZKA, A., TREND, P., HULLIGER, M. & VINCENT, S. (1989). Ensemble proprioceptive activity in the cat step cycle: towards a representative look-up chart. *Progress in Brain Research* **80**, 61–74.

PROCHAZKA, A., WESTERMAN, R. A. & ZICCONE, S. P. (1977). I a afferent activity during a variety of voluntary movements in the cat. *Journal of Physiology* **268**, 423–448.

PROSKE, U., MORGAN, D. L. & GREGORY, J. E. (1993). Thixotropy in skeletal muscle and in muscle spindles: a review. *Progress in Neurobiology* **446**, 1–19.

VALLBO, B. (1970). Discharge patterns in human muscle spindle afferents during isometric voluntary contractions. *Acta Physiologica Scandinavica* **80b**, 552–566.

VALLBO, B. (1971). Muscle spindle response at the onset of isometric voluntary contractions in man. Time difference between fusimotor and skeletomotor effects. *Journal of Physiology* **218**, 405–431.

VALLBO, B. (1974). Human muscle spindle discharge during isometric voluntary contractions. Amplitude relations between spindle frequency and torque. *Acta Physiologica Scandinavica* **90**, 319–336.

VOSS, H. (1971). Tabelle der absoluten und relativen Muskelspindelzahlen der menschlichen Skelettmuskulatur. *Anatomischer Anzeiger* **129**, 562–572.

WESSBERG, J. & VALLBO, B. (1995). Coding of pulsatile motor output by human muscle afferents during slow finger movements. *Journal of Physiology* **485**, 271–282.

WILSON, L. R., GANDEVIA, S. C. & BURKE, D. (1995). Increased resting discharge of human spindle afferents following voluntary contractions. *Journal of Physiology* **488**, 833–840.

WILSON, L. R., GANDEVIA, S. C., INGLIS, J. T. & BURKE, D. (1996). Human muscle spindle afferent recruitment in isometric contractions. *Proceedings of the Australian Neuroscience Society* **7**, 196P.

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