THE DEPENDENCE OF THE RESPONSE OF CAT SPINDLE Ia AFFERENTS TO SINUSOIDAL STRETCH ON THE VELOCITY OF CONCOMITANT MOVEMENT

By T. K. BAUMANN* AND M. HULLIGER†

From the Brain Research Institute, University of Zürich, CH-8029 Zürich, Switzerland, and the Department of Clinical Neurosciences, University of Calgary, Calgary, Alberta, Canada T2N 4N1

SUMMARY

1. The responses of de-efferented soleus muscle spindle primary afferents to 1 Hz sinusoidal stretches, which were superimposed on triangular background movements of intermediate amplitude (1·2 mm, half peak-to-peak) and widely varying speed, were recorded in anaesthetized cats.

2. Compared with control responses to the same sinusoids applied at fixed mean muscle length, the sensitivity to small (50 and 100 μm, half peak-to-peak), but not to large (1000 μm), sinusoidal movements was dramatically reduced during concomitant stretching, unless the background movements were extremely slow (well below 0·005 resting lengths per second).

3. For small stretches (50 and 100 μm) the reduction of sensitivity caused by background movement depended on the speed of this movement. For the highest velocity studied (1·6 mm s^{-1}, corresponding to about 0·03 resting lengths per second) sensitivity dropped to below 10% of the control values.

4. The functional implication is that the sensitivity of spindle Ia afferents to small irregularities of voluntary movements (of any but the slowest speeds) may well be very much lower than it has hitherto been inferred from the striking sensitivity to minute disturbances at fixed mean muscle length. The present finding clearly puts extra demands on the gain of any spinal or central reflex actions of the sensory feedback from spindle afferents.

5. The effect is interpreted in terms of the widely accepted cross-bridge hypothesis of spindle small-movement sensitivity. The result suggests that in de-efferented intrafusal muscle fibres, which are subjected to imposed stretches, connected cross-bridges (conveying a friction-like property to the contractile fibre poles) may exist not only in a state of permanent attachment, but also in a dynamic equilibrium

* Present address: Department of Surgery, Division of Neurosurgery, Oregon Health Sciences University, School of Medicine, L-472, 3181 SW Sam Jackson Park Road, Portland, OR 97201, USA.

† To whom all reprint requests should be sent at the Department of Clinical Neurosciences, University of Calgary, Health Sciences Centre, HMRB 106, 3330 Hospital Drive NW, Calgary, Alberta, Canada T2N 4N1.

between stretch-induced detachment and reattachment. Indirect evidence further suggests that the duration of this disruption and reattachment cycle is of the order of 1 s.

INTRODUCTION

Primary muscle spindle afferents are known to be much more sensitive to small than to large movements, both under passive conditions and when they are subjected to static or dynamic fusimotor drive (Matthews & Stein, 1969; Poppele & Bowman, 1970; Hasan & Houk 1975 *a, b*; Hulliger, Matthews & Noth, 1977 *a, b*). This has led to the view that they should be particularly suited to monitor, with high sensitivity, small variations of muscle length, such as deviations from the planned trajectory of a voluntary movement, rather than the overall course of this movement. By doing so they might contribute to automatic servo-like correction of movement irregularities, provided that central reflex gain was suitably high (Matthews, 1972, 1981 *a, b*; Stein, 1974; Marsden, Merton & Morton, 1976).

The high sensitivity of passive primary afferents has been attributed to friction arising from the existence of stuck cross-bridges between intrafusal actin and myosin filaments. By enhancing the stiffness of intrafusal fibre poles, this would expose the spindle's sensory region to a relatively greater proportion of externally applied stretch and so sensitize its afferents (Brown, 1971; Matthews, 1972; Hasan & Houk, 1975 *b*; cf. also Hill, 1968, and Brown, Goodwin & Matthews, 1969). The progressive decay of the afferents' sensitivity with increasing amplitude of stretch can then be ascribed to a disruption of an increasing fraction of these cross-bridges. This interpretation has been supported by direct measurements of intrafusal tension in isolated spindle preparations (Hunt & Wilkinson, 1980), since the amplitude-dependent reduction of afferent sensitivity was closely paralleled by an amplitude-dependent reduction in intrafusal stiffness (gain compression).

A pronounced small-movement sensitivity of passive I a afferents becomes manifest within a few seconds after a large stretch has been applied to the parent muscle. Such resetting of I a sensitivity has been observed over a wide range of mean muscle lengths (Matthews & Stein, 1969; Goodwin, Hulliger & Matthews, 1975; Hasan & Houk, 1975 *b*). Since sufficiently large stretches (5–10 mm in cat soleus muscle) are likely to disrupt most (if not all) cross-bridges in passive intrafusal fibres, it has to be postulated that cross-bridges can reattach even in non-contracting intrafusal muscle tissue. Moreover, it is conceivable that cross-bridge detachment is not contingent upon muscle stretch and that the bridges might undergo a continual turnover of detachment and reattachment even at constant muscle length.

The high sensitivity of primary spindle afferents has so far been described only for responses to small stretches which were applied at constant mean muscle length, often close to the maximum physiological extension. This left open the question whether this pronounced sensitivity would persist, if small stretches were superimposed on movements of large amplitude. Given the ability of I a afferents to reset their sensitivity at different mean lengths it was to be expected that a high sensitivity to small disturbances might still be present during on-going movement, provided that this was not too fast. The present study was undertaken to investigate this issue. It emerged that a high sensitivity of primary spindle afferents was

maintained only during very slow movements. For faster movements, with speeds still well within the physiological range, sensitivity was reduced to below 10 % of the control values measured at corresponding mean muscle length.

Preliminary accounts of this work have been published previously (Baumann & Hulliger, 1981, 1984; Hulliger, 1981, 1984).

<div align="center">METHODS</div>

The methods followed those described by Goodwin *et al.* (1975) and Hulliger *et al.* (1977 a), except for the type of signals used to drive the muscle stretcher and certain aspects of data analysis.

Animals and preparation

The experiments were performed on the soleus muscle of twelve cats weighing between 2·4 and 3·3 kg. These were anaesthetized with pentobarbitone (40 mg kg^{-1} I.P. initially, repeated injections of 10 mg I.V. subsequently, to maintain deep and areflexic anaesthesia). The left hindlimb was widely denervated except for the nerve supplying the soleus muscle. In addition, in the later experiments the soleus muscle was partly denervated by cutting fine intramuscular branches, in order to facilitate isolation of single afferent units in the dorsal roots (see below). The muscle and its tendon were dissected free by first exposing and then removing the gastrocnemius and plantaris muscles. A fine thread was tied into the deep connective tissue close to the lateral malleolus. This provided a stationary reference marker of maximum physiological length. With the ankle maximally dorsiflexed a second marker was placed on the tendon, aligned with the reference marker. The tendon and part of the calcaneus were then detached to be tied to the muscle stretcher later on. A laminectomy was performed and the dorsal and ventral roots (between L6 and S1) were dissected free and cut close to the cord. Subsequently the animal was transferred from the operation table to a stereotactic frame and the left hindlimb was rigidly fixed using horizontal steel pins inserted into the bones of the hip, knee and ankle region.

Functionally single afferents from the soleus muscle were isolated in fine dorsal root filaments (L7 and S1), which were dissected with watchmaker's forceps. Primary spindle afferents were first selected on the basis of a high dynamic sensitivity for sinusoidal stretch of the parent muscle (1 Hz, 1–2·5 mm, half peak-to-peak amplitude). They were further identified by their characteristic response to a maximum twitch contraction of the parent muscle, a conduction velocity in the group I range (greater than or equal to 80 m s^{-1}) and an appropriately high dynamic index (mostly greater than 40 impulses s^{-1}) in response to a ramp-and-hold stretch (10 mm s^{-1}, 4 mm half peak-to-peak amplitude).

Mechanical stimulation

An electromagnetic puller, operated in length servo mode, was used to apply longitudinal stretches to the muscle. The characteristics of the device were nearly identical to those of the apparatus used by Hulliger *et al.* (1977 a). Its frequency response was flat within 10 % up to 400 Hz, the internal noise level was below 0·5 μm (above 10 Hz), and its stiffness was above 60 N mm^{-1}.

The command signals were taken from a specially developed hybrid signal generator (Frei, Hulliger & Lengacher, 1981). In this apparatus a range of different signals were permanently stored in digital memories (EPROMs, with a resolution of 1024 $(X) \times 4096$ (Y)). For signal generation regular pulse trains, provided by a clock with adjustable frequency, were used to read the contents of successive memory registers. These values were then passed through a D–A converter and the resulting staircase function was smoothed, using a second-order Bessel low-pass filter whose corner frequency was about 50 times the signal repeat frequency. Sinusoids (1, 2 or 4 Hz) and triangles or rectangles of lower frequencies (between 0·01 and 0·66 Hz) were generated simultaneously, in two parallel channels, at strict integer ratios of their repeat frequencies. This was achieved by a counter which divided a master clock signal (which was also used to generate the sinusoids) by the appropriate integer number (fast/slow signal repeat frequency ratio, $R_{f/s}$), to provide a clock pulse train for the slower function. The period pulse of the latter (occurring at the end of each cycle) was used to synchronize the channel generating the sinusoids, to set up and, if necessary, maintain defined phase relationships. The sinusoidal signals always started in the direction of muscle release (i.e. they were phase-lagged by 180 deg), in order to reduce the size of any transient response at the

beginning of the extension phase of a triangle or after a step change in muscle length (rectangles). During data collection (see below) the laboratory computer verified for each individual measurement that strict integer ratios of signal repeat frequency, which the apparatus was designed to provide, indeed were generated.

Triangles of decreasing velocity were generated, for a given sine frequency, simply by increasing the fast/slow signal ratio ($R_{t/s}$) of the dividing counter. For a triangle amplitude of 1·2 mm, $R_{t/s}$ figures of 96, 72, 48, 36, 24, 18, 12 and 6 gave triangle velocity values of 0·05, 0·066, 0·1, 0·133, 0·2, 0·266, 0·4 and 0·8 mm s^{-1}. To generate stretches at 1·6 mm s^{-1} the triangle amplitude had to be set to 2·4 mm ($R_{t/s} = 6$). The $R_{t/s}$ values were selected so that even each half-cycle of the slower function contained an integer number of sinusoids.

When two functions were generated simultaneously, they were attenuated separately and then summed to provide the input signals to the stretcher. The amplitudes of stretch, always expressed as half peak-to-peak values, were 1·2 or 2·4 mm (for triangles and rectangles) and multiples of 50 μm up to 1000 μm (for sinusoids).

Data collection and analysis

Amplified and filtered unitary action potentials (recorded in dorsal root filaments) were passed through a Schmitt trigger and, together with the sine- and slow-function period markers, sampled on-line by a laboratory computer (LSI 11/03). All data were stored in raw form (as inter-impulse intervals) on computer diskettes. Data acquisition always covered an integer number of slow-function cycles and (given the integer fast/slow signal ratios, above) an integer number of sine cycles. Within practical constraints the total sampling time was kept comparable for different triangle velocities, by increasing the number of triangle cycles collected in proportion to their repeat frequency. However, in practice this was strictly adhered to only for the faster movements (to keep the period of total data acquisition within reasonable limits). Hence sampling time ranged from 96 s (at 0·05 mm s^{-1}, single cycle) to 48 or 24 s (from 0·1 or 0·2 mm s^{-1} upwards).

The analysis was performed off-line by constructing averaged cycle histograms both for the slow (triangle or rectangle) and for the faster (sinusoidal) stretches. Up to four non-overlapping windows, each based on an integer number of sine cycles and each spanning a selected portion of the slow-function cycle, could be displayed simultaneously. The histogram resolution was 24 bins per sine cycle and up to 1000 bins per slow-signal cycle (for the latter: No. of bins = $R_{t/s} \times 24/n$, where $n = 1,2$ or 4 depending on $R_{t/s}$). The responses were routinely expressed and analysed as average frequency estimates of afferent discharge (Matthews & Stein, 1969). However, control computations were also performed using the probability density method. These fully validated the use of the average frequency method, since for 1 Hz sinusoids the estimates of sensitivity were identical, whilst for the phase the average frequency method introduced a small error (average phase lag 5–10 deg; M. Hulliger & T. K. Baumann, unpublished observation; see also Matthews & Stein, 1969).

The responses to combined sinusoidal and triangular stretch contained an approximately triangular as well as superimposed sinusoidal components (see Figs 1 and 2). In sine-cycle histograms the triangular component was manifest as a modest drift with positive or negative slope (see Fig. 2, row 5, and Fig. 7C). In order to obtain unbiased estimates of the magnitude and phase of the sinusoidal response the drift component had to be removed. To this end an algorithm for inherent slope correction was used, which permitted first the extraction and then the subtraction of the slope component from the compound response (M. Hulliger & T. K. Baumann, unpublished observation). Briefly, the algorithm relied on the half-cycle repeat properties ('symmetry') of a single sinusoid, in that for all arguments separated by 180 deg the function value (modulation) has the same size but the opposite sign. Thus for compound signals consisting of sinusoids superimposed on some background drift component the summation (across the cycle) of paired values (all 180 deg apart) reduces the sinusoidal modulation to zero, whilst the drift component is magnified (by a factor of 2). In the present application the summation of pairs of bins (of a 24 bin histogram) separated by 180 deg gave a 12 point plot, from which the slope value could be computed using linear regression analysis and appropriate scaling (division by 2). The values of slope obtained from sine-cycle histograms of a given repeat frequency were further normalized and expressed as change in discharge rate (impulses s^{-1}) per second (impulses s^{-1} s^{-1}). The algorithm of inherent slope correction was not applicable when sine-cycle histograms contained an appreciable number of empty bins (clipped histograms; in the present data mainly in responses to 1000 μm sinusoidal

stretch). Since empty bins are likely to reflect undefined rather than true zero values of firing rate (Chapman & Duckrow, 1975; Hulliger *et al.* 1977*a*) they were excluded for curve-fitting purposes. Such bin exclusion had more restrictive consequences for the slope correction than for the sine-fitting algorithm (see below), since a figure of 50% empty bins could reduce the number of valid bin pairs available for slope correction to zero, whilst still leaving 50% of the bins (i.e. those containing positive values of firing rate) for the sine-fitting procedure.

Control computations using forced slope correction, which relied on estimates of slope from responses to triangular stretch alone, were also performed. This was partly to ascertain that the results were not seriously affected by the particular method of slope correction that was used. Such considerations were important, when the inherent slope correction algorithm was not applicable, owing to extended periods of silence (see above), or when the combined responses to sinusoidal stretch strongly deviated from the requisite sinusoidally modulated profile (see e.g. 'distorted histograms' in Fig. 7*C*). Whilst in such situations the two methods of correction often gave different values of slope, the differences were small enough not to affect the sensitivity estimates. This was true in particular for clipped responses, when the sinusoidal modulation of the response was large compared with the size of the slope. Omission of slope correction then was hardly noticeable. In contrast, the values of phase computed from compound response histograms tended to be more sensitive to variations in the value of slope, which was subtracted (M. Hulliger & T. K. Baumann, unpublished observation). In view of the above assessment all quantitative analysis of the responses to combined sinusoidal and triangular or rectangular stretch was performed either with inherent drift correction or with no drift correction at all. Responses to sinusoidal stretch alone (at constant mean length) were analysed without any slope correction.

For the assessment of the effects of the velocity of stretch on Ia sensitivity to 1 Hz sinusoids the rising phase of each triangle was divided into three windows, each covering one-sixth of the entire triangle cycle. For triangles of decreasing velocity these contained increasing numbers of sinusoids, but they were always centred around the same levels of mean muscle length (2·2, 3 and 3·8 mm below maximum physiological extension; see Fig. 2). For convenience, these windows are referred to as 'short', 'intermediate' and 'long', according to the range of muscle length from which the data were collected. Within each window the afferent response to successive sinusoidal stretches was averaged to give a single sine-cycle histogram. Whilst in the second and third window all sine cycles were analysed, the first cycle of the window at 'short' length was routinely excluded. This first cycle often contained bursts (acceleration response at the beginning of muscle lengthening) which, if included, would have unduly distorted the results of the analysis. Each cycle histogram was fitted with a sinusoid of the same frequency, using a least-squares algorithm which automatically ignored empty bins (Hulliger *et al.* 1977*a*).

The goodness of sinusoidal fit was assessed by computing an r.m.s. error term (root-mean-square deviation between the response and the fitted sine). For a given response profile the r.m.s. error is proportional to the residual harmonic power contained in all Fourier coefficients beyond the fundamental (fitted sine; Hulliger *et al.* 1977*a*; Hulliger, 1979). The r.m.s. figures are high in the presence of high levels of random noise (unsynchronized with stimulus) or of response components whose description requires higher order Fourier terms of significant magnitude. The latter is the case for any deviation from a predominantly sinusoidally modulated response, i.e. for distortions such as asymmetries, step changes, multiple peaks due to phase locking etc. The contribution of random noise to the error term is limited by the amount of averaging and by histogram resolution (cut-off at repeat frequency × No. of bins/2), and for recordings from Ia afferents it tends to slightly increase with repeat frequency (reflecting the power distribution of noise in these recordings; for documentation see Hulliger, 1979, on a closely related application of r.m.s. error estimates). For the present data, repeat frequency (1 Hz) and sine-cycle histogram resolution (24 bins) were constant, yet the amount of averaging increased for very slow background movements (see above). However, it is unlikely that this contributed significantly to the velocity-dependent variations of the error estimates (Fig. 3, 'long' length: Fig. 4*B*), since it was repeatedly noted that graphs of r.m.s. error *vs.* velocity could be largely flat, regardless of variations in the amount of averaging (as illustrated in Fig. 3*B*, 'short', 'intermediate' and in Fig. 3*D*, 'short').

The absolute measure of r.m.s. error (e_1), rather than some relative measure (Like e_1/m_1; where m_1 is the magnitude of the fundamental of the response), was chosen because the former, but not the latter, is defined even when m_1 approaches zero. For further detail see Hulliger (1976, 1979) and Hulliger *et al.* (1977*a*).

The time course of recovery of sensitivity to 4 Hz sinusoidal stretch after an abrupt rectangular stretch (Fig. 8) was estimated by first computing the values of sensitivity for successive sine cycles (using inherent slope correction) and by then fitting these data with an exponential with a single time constant (Fig. 9), using a Marquart–Levenberg-type non-linear iterative least-squares algorithm (Procedure Fitfun, Research System 1; Bolt, Beranek & Newman, Cambridge, MA, USA).

In order to obtain estimates of trends in scatter diagrams (Figs 4, 5 and 7) a 'robust locally weighted regression' procedure was used ('locally weighted scatterplot smoothing'; Cleveland, 1979, 1981). This provided smoothed curves describing, in approximation, the course of weighted means ('middle smoothing') and upper and lower 'quartiles' ('upper' and 'lower smoothing'). For 'middle smoothing' the algorithm computed, for each value of x-co-ordinate, a weighted mean, by attaching more importance to near than to remote neighbours, and by giving reduced weight to outliers (using iterated weighted least-squares and a bisquare robust estimation function). 'Upper' and 'lower smoothing' was performed by applying the same algorithm to the upper and lower residuals (i.e. the data points above or below the weighted mean obtained by the 'middle smoothing').

RESULTS

Small-movement response during concomitant larger movement

Single-unit behaviour

Figure 1 shows responses of three primary spindle afferents (from three separate experiments) to small sinusoidal stretches (1 Hz, 50 μm). In A the sinusoids were applied at constant mean muscle length, 3 mm below maximum physiological extension, whereas in B they were superimposed on a slow triangular stretch (amplitude 1·2 mm, velocity 0·266 mm s^{-1}), which was centred around the same mean length. Although the responses to the small sinusoidal stretches during concomitant triangular movement were appreciable (Fig. 1B), they were smaller than at constant mean muscle length. This was true especially for units 1 and 2 (in Fig 1A), since for these the modulation of the receptor response was only partly visible at constant mean length (clipped firing profiles in A), whereas during concomitant triangular movement their firing rate was continuously modulated (Fig. 1B). This difference was clearly borne out by quantitative analysis. The values of sensitivity for afferents 1–3 were 777, 605 and 426 impulses s^{-1} mm^{-1} with sinusoidal stretch alone, whilst during combined stretch they were 260, 386 and 329 impulses s^{-1} mm^{-1} at corresponding mean muscle length (average values for cycles 4–6 during the lengthening phase of the triangle). Thus the sensitivity to sinusoidal stretch was reduced by 67, 36 and 23%, respectively.

The responses of Fig. 1 were representative for the effects of large background movements of intermediate velocity on the sensitivity to superimposed small movements, as studied in seventeen primary muscle spindle afferents (with conduction velocities ranging from 80 to 111 m s^{-1}). The term 'intermediate' refers to the present range of velocities of muscle stretch. Clearly, in absolute terms, the speeds of the triangular movements studied were very low: 0·05–1·6 mm s^{-1}, corresponding to 0·001–0·032 resting lengths per second, assuming a muscle belly length of 50 mm for the soleus muscle (see also Discussion).

Response profiles. The firing patterns of primary afferents during triangular stretch varied widely between units. Although these need not form distinct groups (with non-overlapping clusters of response properties), three broadly defined types may be

described: 'accelerating', 'linear' and 'decelerating'. An example of the 'accelerating' firing profile during ramp stretch is illustrated in Fig. 2 (upper diagrams), where the time course of discharge rate curved upwards as the stretch progressed. The 'linear' type of response was characterized by a proportional, and the
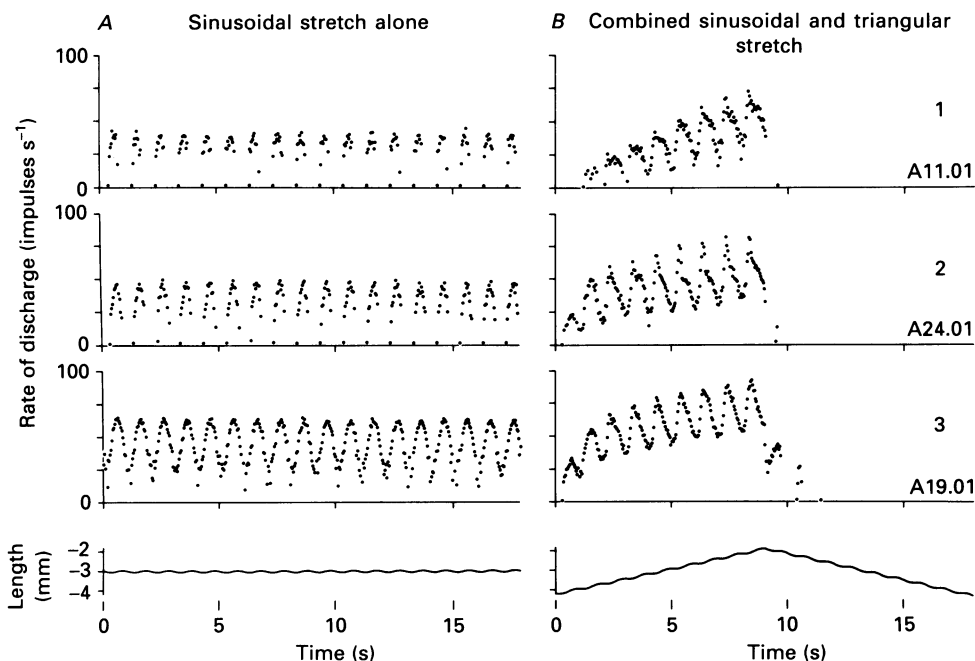

Fig. 1. Small-movement response of primary spindle afferents in the absence and presence of larger movement. *A*, 50 μm, 1 Hz sinusoidal stretch alone, applied at a mean length which was 3 mm below the physiological maximum (see bottom diagram). *B*, 50 μm sinusoids (1 Hz) superimposed on slow triangular stretch (0·266 mm s^{-1}). Single-sweep average frequency display of the responses of three Ia afferents from three separate experiments (note unit codes: A(fferent) experiment number.unit number). The bottom curves are schematic drawings of the time course of stretch on a length scale relative to maximum physiological extension (0 mm).

'decelerating' type by a steep initial and then progressively diminishing, increase in firing rate throughout the lengthening phase of a triangular stretch (both not illustrated). These profiles were closely reflected in the build-up of sensitivity to small sinusoidal movements when such stimuli were superimposed on a slow triangular stretch. The 'accelerating' type showed an accelerating increase in small-movement sensitivity during a ramp stretch (Fig. 2, bottom diagrams), whilst for the 'linear' and 'decelerating' type the increase in sensitivity with length was also linear (Fig. 1*B*1) and decelerating (Fig. 1*B*2 and 3) respectively.

The reduction in sensitivity to small sinusoidal stretches was strongly dependent on the velocity of the background movement and was only seen at relatively high velocities. Figure 2 illustrates the responses of another primary afferent to triangular
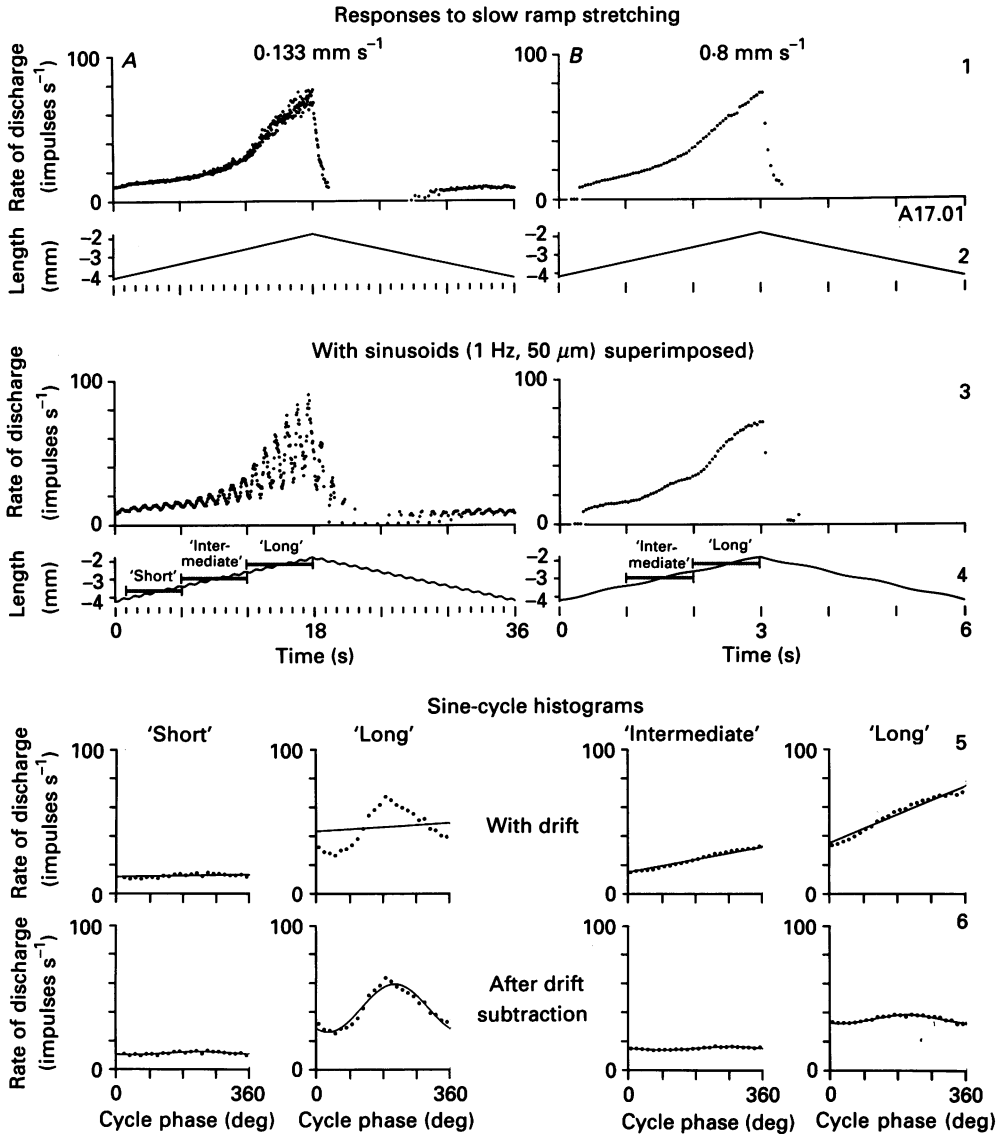
Fig. 2. The effects of velocity of large movement on the Ia response to superimposed sinusoids. Rows 1 and 3, triangle-cycle histograms showing Ia firing rate (average frequency display) during triangular stretch alone (row 1) and during combined triangular and sinusoidal stretch (row 3) (in A, single-response cycle; in B, eight cycles averaged). The velocity of the ramp stretch was 0·133 mm s^{-1} in column A, and 0·8 mm s^{-1} in column B. Sine frequency and amplitude were 1 Hz and 50 μm in either case (note compressed time scale in A). Rows 2 and 4, schematic illustrations of the time course of stretch (same scale as in Fig. 1), with the horizontal bars in row 4 delimiting the analysis windows ('short', 'intermediate' and 'long') which were routinely used for quantitative analysis. Note that the very first sine cycle during triangle lengthening was excluded from quantitative analysis (see Methods). For fast to slow signal repeat frequency ratios ($R_{t/s}$ values) greater than 6 the window at 'short' length was therefore shorter (by one sine cycle) than the remaining windows. For $R_{t/s} = 6$ it was not available at all (as in B), since the entire lengthening phase then encompassed only three sine cycles. Rows 5 and 6, sine-cycle histograms constructed from the responses to combined sinusoidal and triangular

stretch at two different velocities (in A, 0·133 mm s^{-1}; in B, 0·8 mm s^{-1}). These are shown as normalized triangle-cycle histograms (note compressed time scale in A) in order to emphasize the similarity in the response trajectories to triangular stretch alone (A1 and B1). The diagrams in A3 and B3 illustrate the responses to the same triangular stretch, but now with superimposed 1 Hz sinusoids (amplitude 50 μm). Whilst at the lower velocity of stretch (A3) the size of the sinusoidal response was large (if only at longer mean muscle length), it was strongly reduced at the higher velocity of stretch (B3). During the last third of the triangle lengthening phase (analysis window at 'long' length, see A4 and B4) the value of sensitivity fell from 330 impulses s^{-1} mm^{-1} (at 0·133 mm s^{-1}; see A6 'long') to 60 impulses s^{-1} mm^{-1} (at 0·8 mm s^{-1}; B6 'long'). This effect was not attributable to any major change in the response to the triangular stretch *per se*, since the profiles of firing rate (A1 and B1; normalized display) remained very similar. The sine-cycle histograms of rows 5 and 6 show averaged responses (to the small sinusoidal stretches) within selected analysis windows (see A4 and B4). The histograms were constructed from the same data as in panels A3 and B3. In A5 and B5 they illustrate 'raw' responses, prior to subtraction of the drift component (which is very manifest in the responses of B5). In A6 and B6 the same data are shown after subtraction of the background drift component (using the inherent slope correction algorithm; see Methods). They illustrate that after drift correction responses could satisfactorily be fitted with simple sinusoids (but cf. Fig. 7). In contrast, especially for small sinusoidal modulation superimposed on large drifts, omission of drift correction would have introduced large errors (not illustrated; M. Hulliger & T. K. Baumann, unpublished observation).

Firing during release. Figure 2 also illustrates another finding which is of considerable practical importance. During the slow and passively imposed triangular movement (A1) the afferent discharged impulses not only during muscle lengthening but also during the second half of the shortening phase. This was not due to exceptional properties of the particular primary afferent illustrated (conduction velocity 89 m s^{-1}). Its general stretch response characteristics fell in the normal range of Ia behaviour, in that small-movement sensitivity at the end of the linear range (see Goodwin *et al.* 1975) was 235 impulses s^{-1} mm^{-1} (for 50 μm sinusoidal stretch at 1 Hz, 3 mm below maximum physiological extension). Moreover, the unit showed the familiar silence during muscle release at higher velocities (B1). A further example of this phenomenon is illustrated in Fig. 7B for another Ia afferent with equally normal properties.

The behaviour of the afferents of Figs 2 and 7 was representative for the present sample of seventeen Ia afferents. Recovery of afferent firing during release of triangular stretch alone was observed at a velocity of 0·05 mm s^{-1} in ten units, at 0·2 mm s^{-1} in nine, at 0·4 mm s^{-1} in three units, and at 1·6 mm s^{-1} in one afferent. The

stretch (row 3) within selected analysis windows (cf. with row 4). Row 5, raw histograms prior to correction for baseline drift (response component attributable to background triangular stretch), with superimposed lines indicating the size of this drift component (as estimated with the inherent-slope correction algorithm; see Methods). Row 6, same responses after subtraction of drift. The superimposed curves are the best-fitting sinusoids (after correction), which were computed with the least-squares algorithm described in Methods. For further detail, see text.

conduction velocities of the afferents concerned ranged from 80 to 111 m s^{-1} and their sensitivity to 50 μm sinusoids varied between 165 and 804 impulses s^{-1} mm^{-1} (see also below, *Pooled data* and Fig. 4).

The dependence of sensitivity to sinusoidal stretch on the velocity of concomitant triangular movement was systematically investigated for all seventeen units of the
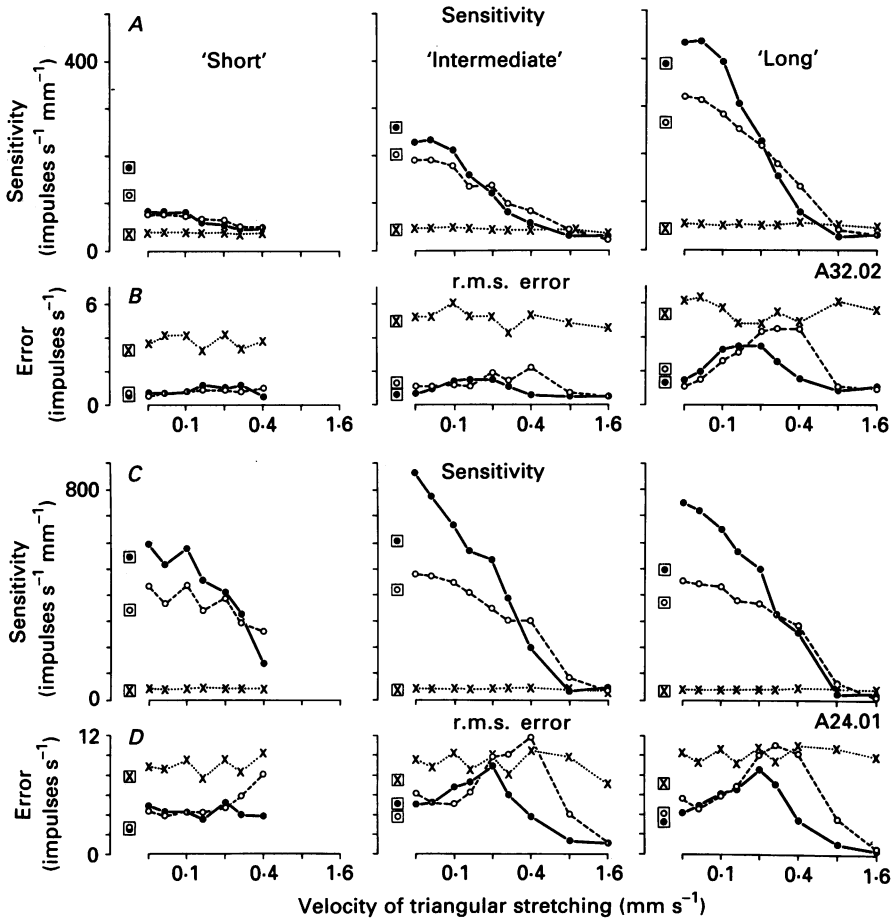

Fig. 3. Dependence of Ia sensitivity to sinusoids on the velocity of underlying triangular movement. Data from two representative primary spindle afferents are shown in *A* and *B*, and in *C* and *D*, respectively. Sensitivity (*A* and *C*) and r.m.s. error (measuring goodness of fit, *B* and *D*) are plotted against the velocity of triangular stretch, illustrating the results of quantitative analysis obtained for three separate amplitudes of 1 Hz sinusoids (●, 50 μm; ○, 100 μm; ×, 1000 μm). Average-frequency sine-cycle histograms were constructed for each of the three analysis windows described in Methods and illustrated in Fig. 2, and the analysis was based on the 'inherent slope correction' algorithm (see Methods). Note that at 'short' length reliable data were not available for the highest two velocities (see Methods and legend to Fig. 2). Symbols enclosed by boxes illustrate data from control measurements at constant mean muscle length. The data in *C* and *D* are from the same afferent as illustrated in Fig. 1, row 2.

present sample. Three amplitudes of sinusoidal stretch (50, 100 and 1000 μm) were regularly used, in addition to controls with triangular stretch alone. Triangle velocities ranged from 0·05 to 1·6 mm s^{-1} (see Methods).

Figure 3 shows the results of quantitative analysis for two representative units. The values of sensitivity to sinusoids and of r.m.s. error (goodness of sinusoidal fit; see Methods) are plotted against the velocity of triangular stretch for each of the three windows of analysis (see Methods and Fig. 2). In both cases the sensitivity to small movements (50 and 100 μm, ● and ○) declined with increasing velocity of concomitant stretch. In C this was manifest for all three segments of the triangle lengthening phase, whereas in A this effect was pronounced at 'long' length, smaller but clearly present at 'intermediate' length, whilst almost absent at 'short' length (cf. also Fig. 2, row 3). In contrast, the sensitivity to sinusoidal movements of much larger amplitude (1000 μm, graph symbol ×) was virtually independent of the velocity of concomitant triangular stretch. This was true for both units and for all analysis windows.

Control responses to sinusoidal stretches of the same amplitudes were also collected in the absence of triangular stretch, at corresponding levels of mean muscle length. The parameters computed from these data are shown on the left of each panel in Fig. 3 (same symbols, enclosed by boxes). The values of small-movement sensitivity (50 and 100 μm) at fixed mean length were much closer to those obtained during slow than during faster triangular stretch. In contrast, for larger sinusoidal stretches (1000 μm, graph symbol ×) the sensitivity of the afferents not only was independent of the velocity of the concomitant triangular movement, but it also was virtually identical with that measured at fixed mean length. Taken together, the findings of Fig. 3 then show that small- but not large-movement sensitivity of Ia afferents declines, from its high value at fixed mean length, with increasing speed of concomitant movements of larger amplitude.

For the data of Fig. 3 the goodness of sinusoidal fit (as first judged by eye) was by and large better for the responses to small (50 and 100 μm) than to large (1000 μm) stretches. In accordance with this the values of r.m.s. error were about five times higher for the latter than for the former. This agrees with measurements taken at constant mean muscle length (Hulliger *et al.* 1977a). However, the curves of r.m.s. error had distinct peaks at intermediate velocities of triangular stretch, especially at 'long' (B and D), but also at 'intermediate' (D), mean length. High values of r.m.s. error often are indicative of distortions (non-sinusoidal response; see Methods). In line with this, histograms with unusually high error values in Fig. 3 indeed showed marked asymmetries (see Fig. 7). The error curves of Fig. 3 were typical of the entire sample of afferents, as can be judged by comparing the example of the pooled data of Fig. 5B (50 μm responses at 'intermediate' length) with the corresponding 50 μm data of Fig. 3 ('intermediate').

Pooled data

In order to illustrate the generality of the findings of Figs 1–3, data from all seventeen units were pooled and displayed as scatterplots of response parameters *vs.* velocity of triangular stretch. Examples are shown in Figs 4 and 5.

For the entire sample of afferents velocity dependence of sensitivity to small sinusoidal stretches was equally pronounced as in the examples of Fig. 3. The values

computed from responses to 50 μm stretches are shown in Fig. 4*A* for the three analysis windows described above (Fig. 2; Methods). In spite of the considerable scatter in *A*, it can be seen that at long length the sensitivity to 50 μm stretches was reduced by more than 90 % (median: from 576 impulses s^{-1} mm^{-1} at the slowest, to
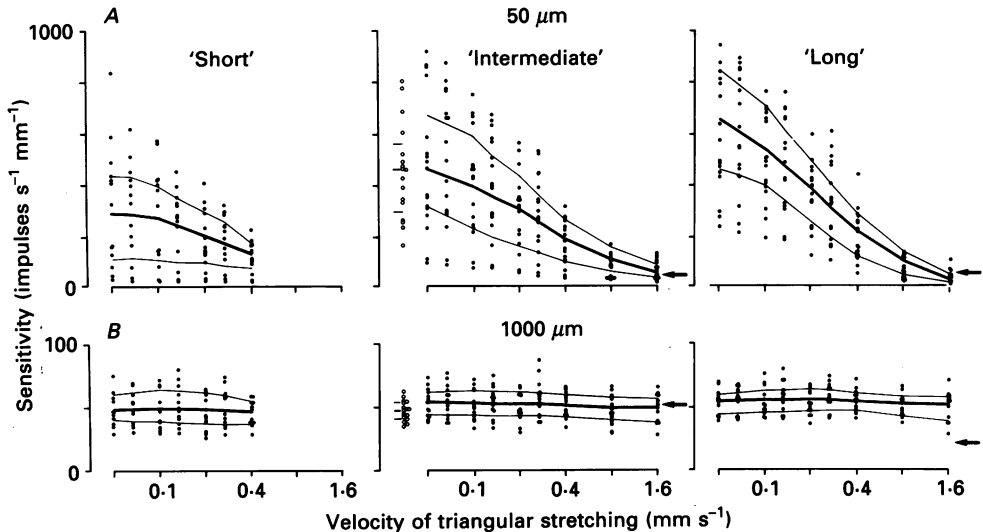

Fig. 4. Pooled data from the entire sample of seventeen I a afferents to illustrate the effects of velocity of underlying movement on afferent sensitivity to 1 Hz sinusoids. 50 μm sensitivity in *A* and 1000 μm sensitivity in *B*; measurements from averaged responses from the three analysis windows illustrated in Fig. 2. ●, responses to combined sinusoidal and triangular stretch; ○ ('intermediate' length), responses to sinusoids alone (controls at constant mean length). The short horizontal lines ('intermediate' length) give the values of median and quartiles for control measurements at constant length. The drawn-out lines are the middle (thick) and upper and lower 'quartile' (thin) smoothings of the pooled data (from measurements during concomitant triangular stretch). Note that for clarity the sensitivity scale is enlarged in the panels of the lower row (*B*). In order to ease the comparison of values between *A* and *B*, the arrows to the right of the intermediate and long length panels indicate, in *A*, the medians of 1000 μm sensitivity (from *B*) and, in *B*, the medians of 50 μm sensitivity (from *A*), in either case for the responses to sinusoids at the fastest velocity of background movement (1·6 mm s^{-1}). For further details see text.

36 impulses s^{-1} mm^{-1} at the fastest velocity; mean: from 587 ± 221 to 39 ± 22 ($\pm$s.d.)). At intermediate muscle length the reduction in sensitivity was slightly less than 90 % (median: from 461 impulses s^{-1} mm^{-1} at the slowest to 51 impulses s^{-1} mm^{-1} at the fastest velocity; mean: from 473 ± 261 to 61 ± 36 ($\pm$s.d.)). This is further borne out by the drawn-out lines which represent the middle, and upper and lower 'quartile', smoothings of the data (see Methods). It may also be noted that the decline in small-movement sensitivity with increasing large-movement velocity was progressive and did not reveal conspicuous discontinuities or steps (cf. also Fig. 3*A* and *C*). Fifty per cent of the overall reduction in sensitivity (i.e. about 55 % of the control values at the lowest background velocity) was attained around a velocity of 0·25 mm s^{-1}. This was estimated from the curves of middle smoothing of Fig. 4*A* ('intermediate' and 'long' length). Further, the values of sensitivity to sinusoids

obtained at the lowest velocities of triangular stretch were almost identical with the figures derived from responses at fixed mean length. This was systematically assessed only at intermediate (fixed) mean length and is illustrated in the middle panel of Fig. 4A by open symbols. The fine horizontal lines indicate the level of the median (463 impulses s^{-1} mm^{-1}, as opposed to 461 impulses s^{-1} mm^{-1} during the slowest movement, above) and of the upper (563) and lower (287) quartile (mean 452±186 (±S.D.) as opposed to 473±261 impulses s^{-1} mm^{-1} during slow background movement, above).

Almost identical, but slightly scaled-down plots were obtained for the responses to 100 μm sinusoids (not illustrated). At fixed intermediate length and during slow background movement the reference values of 100 μm sensitivity were 322 and 299 impulses s^{-1} mm^{-1} (median and mean), about 30 % lower than corresponding 50 μm figures. In the presence of faster background movements 100 μm sensitivity fell to 9 % (at 'long' length) and 12 % ('intermediate' length) of the reference figures.

Higher speeds of movement. For technical reasons higher velocities of triangular stretch than those illustrated in Fig. 4 were not systematically studied. However, in a related study on dynamic fusimotor action on Ia sensitivity in the presence of background movements it has since been found (for a large sample of passive afferents) that both small- and large-movement sensitivity to 4 Hz sinusoids remained low (and declined much less steeply than in Fig. 4 up to 1·6 mm s^{-1}) for background movement velocities up to 12·8 mm s^{-1} (Hulliger & Sonnenberg, 1985, and R. Kohen-Sonnenberg & M. Hulliger, unpublished observation).

In striking contrast to the smaller amplitudes, sensitivity to 1000 μm sinusoidal stretches was practically independent of the velocity of concomitant movement (Fig. 4B) and uniformly low. For instance at the lowest velocity the median of the sensitivity at intermediate length was 53 impulses s^{-1} mm^{-1} (quartiles 62 and 42) and at the fastest velocity of background stretch it was 51 impulses s^{-1} mm^{-1} (quartiles 59 and 37). In addition, these values were nearly identical with the figures from control measurements at intermediate fixed mean length (Fig. 4B, middle panel, $\bigcirc$: median 45, upper quartile 52, lower quartile 41 impulses s^{-1} mm^{-1}). Moreover, at intermediate length, the sensitivity to 1000 μm sinusoids was virtually identical with the values of small-movement sensitivity during fast (1·6 mm s^{-1}) triangular stretch, whilst at long length it even exceeded the sensitivity figures obtained during the fastest background movement. These relationships are indicated by the arrows (in the 'intermediate' and 'long' length panels): in A (50 μm) these give the medians from B (1000 μm), and in B vice versa (note compressed scale in A compared with B). Thus velocity-dependent reduction of sensitivity to sinusoids was very pronounced for small, but negligible for large movements, to the extent that the gain compression non-linearity, which is characteristic for measurements taken at constant mean length, was virtually abolished (see Fig. 6).

Length dependence. The data of Figs 3 and 4 are displayed in tripartite form, since it was evident from the outset that the phenomena described depended on mean muscle length. A clear example is shown in Fig. 2A3 (cf. also Fig. 1B1, and *Response profiles*, above). Especially for the lower velocities of triangular stretch the values of small-movement sensitivity increased from one analysis (i.e. length) window to the next, although the mean increments in length were less than 1 mm (cf. the three

panels of Fig. 4*A*). At the lowest velocity of concomitant stretch (0·05 mm s^{-1}) the medians and means were: at 'short' length, 325 impulses s^{-1} mm^{-1} and 316±37 (±s.d.); at 'intermediate' length, 461 impulses s^{-1} mm^{-1} and 473±261 (±s.d.); and at 'long' length, 567 impulses s^{-1} mm^{-1} and 587±221 (±s.d.). Since for higher velocities of triangular stretch length dependence of sensitivity to sinusoids was practically absent, the manifestation of the phenomenon of velocity-dependent reduction of sensitivity to small movements was most pronounced at 'long' and least pronounced at 'short' mean length. In striking contrast, the sensitivity to larger sinusoids was entirely independent of mean muscle length. This is illustrated in Fig. 4*B*, where the data points and the middle and 'quartile' smoothings cover widely overlapping ranges. The maximum difference between mean values of large-movement sensitivity at different mean lengths (but at comparable speeds of background movement) was less than 5 impulses s^{-1} mm^{-1}.

These observations confirm earlier reports of a pronounced dependence on length of I a sensitivity to small movements (Matthews & Stein, 1969; Goodwin *et al.* 1975; Hulliger, 1976; Hunt & Ottoson, 1977; Poppele, Kennedy & Quick, 1979; Hunt & Wilkinson, 1980; see also Kirkwood, 1972, for a related phenomenon in the frog). Although the present data only bear on a narrow range (about 2 mm), average small-movement sensitivity more than doubled. Whilst the earlier reports on this phenomenon often were based on rather limited data, the present observations on a sample of seventeen I a afferents studied in considerable detail clearly demonstrate that length dependence of small-movement sensitivity is a general, non-linear property of primary spindle afferents. It also bears emphasis that such length dependence is not restricted to stationary muscle length, since it was seen in the presence of background movements of velocities up to 0·4 mm s^{-1}. This is in line with preliminary reports on this matter from slightly different experimental protocols (Emonet-Dénand, Laporte & Tristant, 1980*a*; Baumann, Emonet-Dénand & Hulliger, 1982, 1983).

The uniform decline in sensitivity to small sinusoidal stretches with increasing velocity of background movement was not paralleled by equally uniform behaviour of other response parameters. Figure 5 shows pooled data from responses to 50 μm sinusoidal stretch (at 1 Hz) at 'intermediate' length. Whereas modulation declined in a monotonic fashion (*A*), r.m.s. error (*B*), phase (*C*) and underlying slope (*D*) all went through an absolute or relative maximum in the intermediate range of velocities. This is emphasized by the curves of the middle and 'quartile' smoothings. The r.m.s. error (see above, and Methods) was generally low compared with the sinusoidally modulated (fundamental) component of the response (*A*). Yet goodness of fit was more satisfactory for slow and fast velocities than for intermediate velocities (cf. also the single-unit data of Fig. 3*B* and *D*), where responses to sinusoids showed consistent distortions (see Fig. 7). These were also influential in causing the peaks in the plots of phase (Fig. 5*C*) and slope (Fig. 5*D*).

At fixed frequency of stretch, phase advance tends to go hand in hand with reduction of sensitivity. This is typical of the amplitude-dependent reduction in sensitivity at constant length (Hulliger *et al.* 1977*a*) and it was also observed for the present velocity-dependent reduction in sensitivity in the presence of background movement. Formally this is explicable in terms of a phase-dependent break-down of

sensitivity (see below, *Distorted response*), conceivably due to break-down of stuck intrafusal cross-bridges. In a stretch cycle break-down would occur the earlier, the more rapidly critical strain is reached with larger stretch or faster background movement. In a distorted profile (with an early, curtailed peak and a drop in carrier
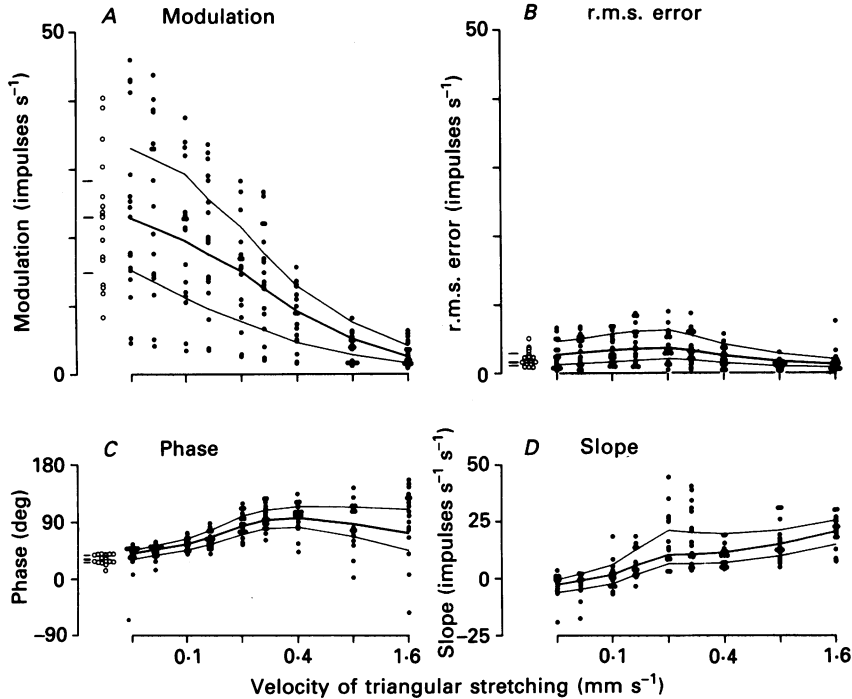

Fig. 5. Dependence of parameters of response to sinusoids on the velocity of triangular stretch. Pooled data from the entire sample of seventeen Ia afferents, derived from measurements at 'intermediate' muscle length (3 mm below maximum physiological extension). The frequency of sinusoidal stretch was 1 Hz and the half peak-to-peak amplitude 50 μm. Same analysis as for Fig. 4. ●, responses to combined sinusoidal and triangular stretch; ○, responses to sinusoids alone (controls at constant mean length). Drawn-out lines, middle smoothing (thick), and upper and lower 'quartile' smoothings (thin). Horizontal lines on the left of each panel, medians and quartiles for data obtained at constant mean length. *A*, modulation of response to sinusoidal stretch, expressed as half peak-to-peak value of the fitted sinusoid (same data as in Fig. 4*A*, 'intermediate' length, but plotted on different scale). *B*, r.m.s. error to describe the goodness of sinusoidal fit. *C*, phase of the fitted sinusoid, relative to the sinusoidal command signal generating the stretch. *D*, value of slope (triangle response component) as estimated with the aid of the 'inherent slope correction' algorithm (see Methods); cf. also text.

rate with reduction of sensitivity; see Hulliger *et al.* 1977*a*) a fitted sinusoid would peak earlier, compared with an undistorted response (with fully exposed peak of response), thus introducing phase advance.

The modest increase in computed slope with the velocity of triangular stretch is in broad agreement with the fractional power relationship between Ia firing and the velocity of stretch (Houk, Rymer & Crago, 1981). The peak and scatter at intermediate velocities (Fig. 5*C*) were mainly attributable to the asymmetric

distortions of response (Fig. 7) and to limitations of the 'inherent slope correction' algorithm, which relies on symmetry (see Methods), since they were absent when slope values were computed from responses to triangle stretch alone, using the same algorithm (not illustrated).
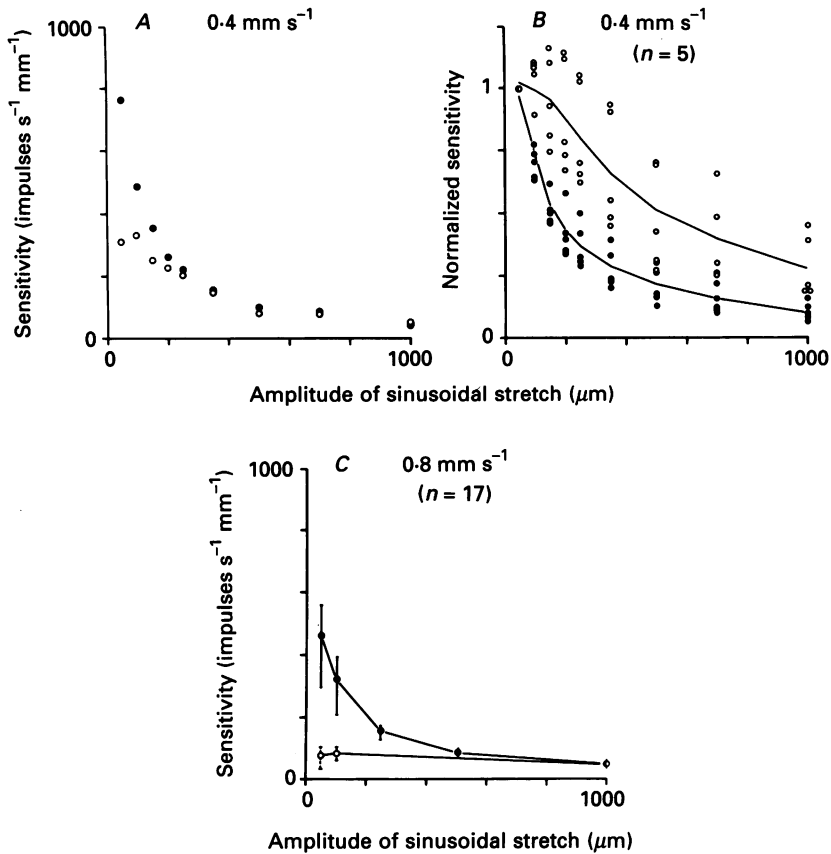

Fig. 6. Tendency for linearization of I a response to sinusoids provoked by concomitant triangular stretch. Values of sensitivity are plotted against amplitude of sinusoidal stretch. ○, measurements from responses to combined sinusoidal and triangular stretch ('intermediate' length window); ●, data from responses to sinusoidal stretch alone (at corresponding mean length, −3 mm). *A*, data from a representative primary afferent. *B*, pooled data from five units studied extensively (display normalized to the 50 μm values). *C*, pooled data from the entire sample of seventeen I a afferents studied for a limited number of sine amplitudes. The drawn-out lines in *B* are 'middle smoothings' describing, in approximation, median behaviour. The drawn-out lines in *C* connect median values, and the vertical lines describe the range between upper and lower quartiles.

Linearization of spindle response

The reduction in the degree of amplitude dependence (gain compression, see Fig. 4) of the responses to sinusoidal stretch (in the presence of triangular stretches of sufficient speed) was studied in more detail in five units of the present sample. The responses of these afferents to sinusoidal stretches of progressively increasing
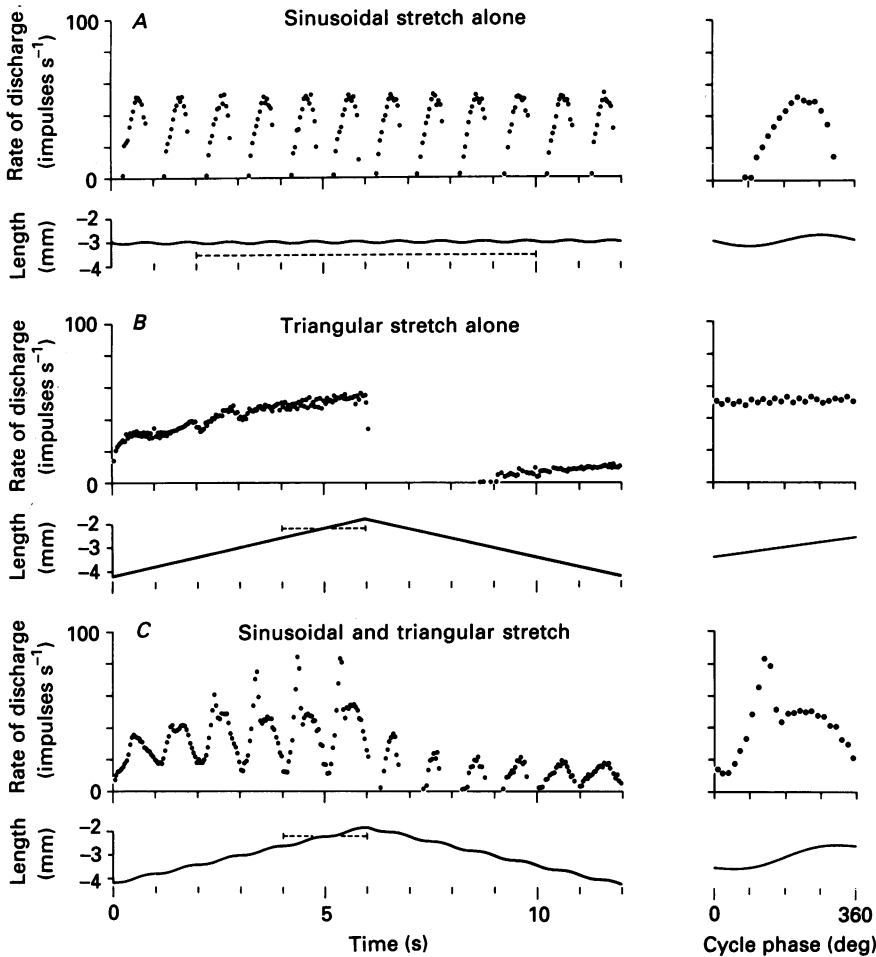
Fig. 7. Events accompanying sensitivity reduction in the region of intermediate velocities of triangular stretch. Left, segments of Ia response to sinusoidal, triangular, and combined sinusoidal and triangular stretch. Right, averaged sine-cycle histograms (all based on eight cycles of Ia response to 1 Hz sinusoidal stretch). Averaging was performed within the windows indicated by dashed horizontal lines (lower traces of each panel on the left): in A, eight consecutive sine cycles; in B and C, four pairs of adjacent sine cycles from successive triangle stretches. Upper diagrams of each panel (A, B and C), average frequency display of Ia firing rate; lower diagrams, schematic drawings of time course of stretch (same scale as in Figs 1 and 2). Triangles: 0·4 mm s⁻¹ (0·0833 Hz, 1·2 mm half peak-to-peak amplitude); sinusoids: 1 Hz, 50 µm (A and C), 0 µm (B). A, left, single-sweep display of response to twelve consecutive sinusoidal stretches applied at fixed mean length (−3 mm). B, left, triangle-cycle histogram showing averaged response to four consecutive triangular stretches centred around same mean length (−3 mm; cycle duration 12 s). C, left, triangle-cycle histogram displaying averaged (four cycles) response to combined sinusoidal and triangular stretch (same stretch parameters as in A and B).

amplitude (nine values) were recorded both at constant mean length (corresponding to the 'intermediate' window, Fig. 2) and during combined sinusoidal and triangular stretch of intermediate velocity (0·4 mm s⁻¹). A representative example is shown in

Fig. 6*A*. Gain compression (decline in sensitivity with increasing amplitude) was clearly more pronounced at constant length (●) than during triangular movement (○; Fig. 6*A*). This was true for all five units of this sub-sample (Fig. 6*B*, normalized display, see legend). Yet it is notable that in both diagrams the amplitude dependence was reduced, but not abolished, during triangular movement. However, at faster velocities the degree of gain compression was further diminished. This is shown in Fig. 6*C* (for 0·8 mm s^{-1}), which illustrates data from the entire sample of seventeen Ia afferents, but only for the three sine amplitudes which were routinely studied both in the presence and absence of triangular stretch.

Distorted response at intermediate velocities

The responses of Fig. 7 illustrate a phenomenon which was prominent in the region of intermediate velocities of concomitant stretch, where sensitivity to superimposed sinusoids declined. For sixteen out of seventeen afferents the cycle histograms of responses to 50 and 100 μm sinusoidal stretches revealed marked distortions. The one exceptional unit was also the least sensitive of the present sample (sensitivity to 50 μm sinusoid 165 impulses s^{-1} mm^{-1}). A particularly clear example of a distorted response is shown in Fig. 7*C* for a triangular stretch with 0·4 mm s^{-1} velocity. Both in individual sine cycles (left) and in the averaged cycle histogram display (right), afferent firing rate rose steeply initially, but then fell suddenly to a lower level, as if an abrupt switch from a high to a low level of sensitivity had occurred. This was not attributable to any inherent irregularities in the discharge properties of the unit illustrated, since its responses to sinusoids at constant mean length were smooth and nearly sinusoidal, although clipped (Fig. 7*A*), and since its response to triangular stretch alone also was inconspicuous (Fig. 7*B*), at least over the range of length where the distortions were most prominent. Other examples of distorted responses, with fast downward transients in mid-stretch, are illustrated in Fig. 1 (*B*1 and *B*2). In the present data such distortions were much more common at 'long' (sixteen units) and 'intermediate' (fifteen units) than at 'short' length (four units). They were seen almost exclusively at intermediate velocities where decline in sensitivity was particularly pronounced and where – now quite understandably – goodness of sinusoidal fit was relatively poor and r.m.s. error high (cf. Methods).

Small-movement sensitivity at constant mean length

Small-movement sensitivity of Ia afferents is very high when a muscle is held at constant mean length, even after a large and rapid pre-stretch (e.g. 10 mm at 10 mm s^{-1}; Matthews & Stein, 1969; Goodwin *et al.* 1975). On the evidence above one should therefore expect that such stretches would drastically reduce the sensitivity of Ia afferents to smaller movements and that, upon completion of pre-stretch, their responsiveness would first have to recover. Observations in the present experiments indeed indicated that such recovery took place and that its time course was relatively fast. To assess this with sufficient resolution, 4 Hz (less successfully 2 Hz) sinusoidal test stretches (25, 50 and 100 μm) were superimposed on larger rectangular stretches (1·2 mm) which encompassed between twenty and eighty sine cycles.

Examples of Ia responses (two units) to rectangular variation of muscle length are shown in Fig. 8, in *A* without, and in *B* with superimposed 4 Hz sinusoids (25 μm).

The responses to step changes in length alone (*A*) showed a transient burst followed by slow adaption of firing rate. When small sinusoidal stretches were superimposed, the depth of modulation of I a firing rate increased gradually, over a period of 1–2 s, subsequent to the abrupt stretch of large amplitude.
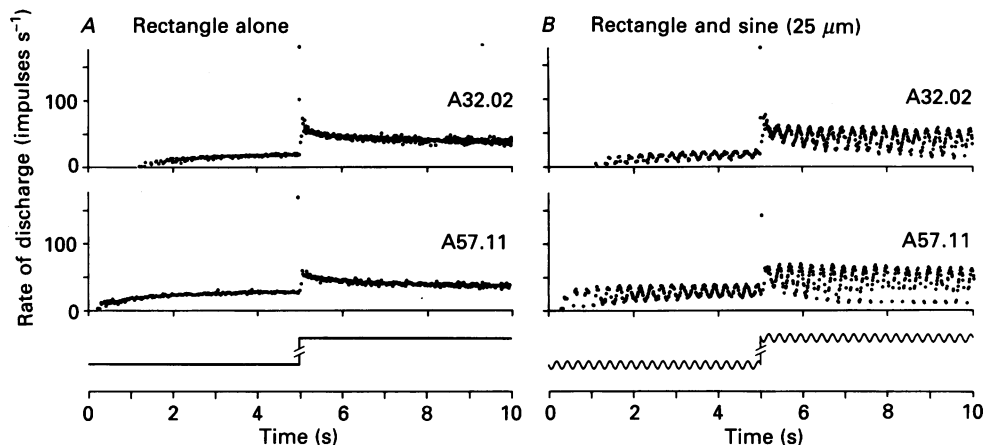

Fig. 8. Recovery of small-movement sensitivity following abrupt change in muscle length (1·2 mm). Illustration of responses of two representative primary afferents to rectangular stretch alone (*A*), and to combined rectangular and sinusoidal (4 Hz, 25 µm) stretch (*B*). Upper records, rectangle-cycle histograms (average frequency display, four cycles averaged); bottom traces, schematic drawings of time course of stretch (note that the step change in length is not drawn to size, since rectangle amplitude was 48 times sine amplitude). Given that each rectangle encompassed forty sinusoids, the recovery of small-movement sensitivity after the sudden step change in length could be followed over twenty successive sine cycles; cf. Fig. 9 for quantitative analysis of the raw data of the two afferents illustrated.

Quantitative analysis of the time course of recovery of small-movement sensitivity confirmed the qualitative impression gained from Fig. 8. 'Inherent slope correction' (see Methods) was used to remove the slow adaptive drift component, and a cycle-by-cycle analysis was then performed using the sinusoidal fitting procedures described in Methods. The first sine cycle after the step increase in length often showed particularly small modulation, but it had regularly to be discarded, since high-frequency bursts made sinusoidal analysis meaningless. The results for the two units of Fig. 8 are shown in Fig. 9*A*, together with the data from a third afferent. It is evident that the range of sensitivity values covered by individual units during recovery varied widely, but even when it was minimal (illustrated in the two bottom curves of Fig. 9*A*) some reconstitution still was detectable. The largest effect encountered is illustrated in the upper trace of Fig. 9*A*.

In order to obtain an estimate of the time constant of the recovery process the single-sine-cycle data (as in Fig. 9*A*) were fitted with a single exponential (see Methods). The best-fitting curves obtained for eight I a afferents (which all belonged to the main sample of seventeen units described above) are illustrated in Fig. 9*B*. The time constant estimates ranged from 0·16 to 2·06 s. The median was 1·43 s.

DISCUSSION

The findings of this study confirm earlier reports on the high sensitivity of spindle primary afferents to small movements (see Introduction). For the present sample of I a afferents the mean value of sensitivity at the end of the linear range (50 μm,
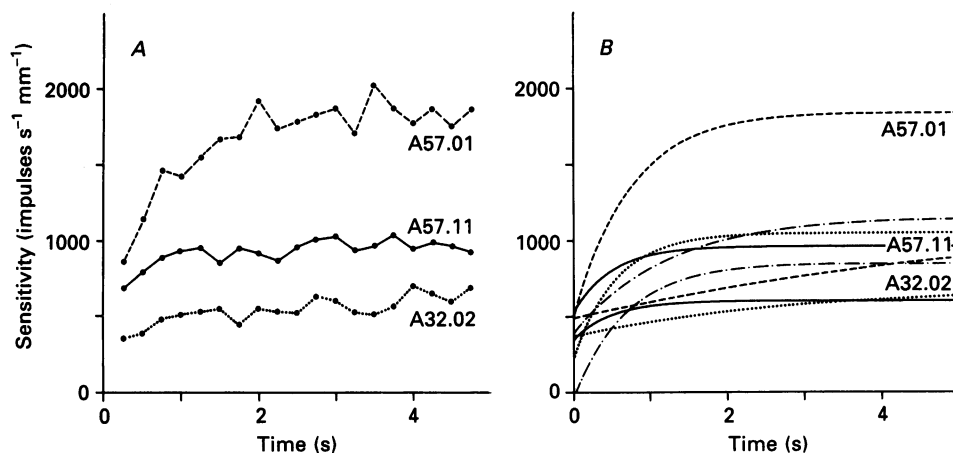

Fig. 9. Time course of recovery of I a sensitivity to small sinusoidal stretch following an abrupt stretch of large amplitude. *A*, estimates of sensitivity during sine cycles 2–20 after the rapid stretch (see Fig. 8), as obtained from three separate I a afferents, two of which are illustrated in Fig. 8 (note unit numbers; analysis using 'inherent slope correction'). *B*, trajectories of best-fitting exponential functions describing the time course of recovery of small-movement sensitivity (for details see text and Methods).

Goodwin *et al.* 1975) was 452 impulses s^{-1} mm^{-1}, when measured with 1 Hz sinusoidal stretches at constant mean length, 3 mm below the maximum physiological extension of the soleus muscle. This compares well with the figure of 465 impulses s^{-1} mm^{-1} reported by Goodwin *et al.* (1975) for nearly identical experimental conditions. Together with other observations of familiar I a properties (see Results), this suggests that the present sample of primary afferents was not unduly dominated by units with unusual properties.

The main new observation of this report is that the sensitivity to small stretches is strikingly reduced when the same sinusoidal stretches are superimposed on triangular movements of larger amplitude, unless these are very slow. For extremely slow triangular movements (0·05 mm s^{-1}) the sensitivity to small sinusoids during simultaneous stretch is the same as when it is measured at constant mean length. Yet when the velocity of the underlying movement is progressively increased, then the sensitivity to sinusoidal stretches falls steadily along a smooth sigmoid curve. At the highest velocity studied (1·6 mm s^{-1}) the sensitivity to small movement was reduced to less than 10% of the control values (at constant length and during the slowest triangular movements). Fifty per cent of the overall reduction was reached around a velocity of 0·25 mm s^{-1}. Faster velocities (up to 12·8 mm s^{-1}) have since also been investigated, indicating that velocity-dependent reduction of sensitivity (to 4 Hz

sinusoidal stretches) also applies to movements of higher speed (see Results: *Higher speeds of movement*). However, the range of frequencies, for which velocity-dependent sensitivity reduction is documented, at present still is limited (1–4 Hz).

Functional significance

The velocities of triangular stretch of the present experiments were very slow when compared with the highest speeds of natural movement. Normalized in terms of muscle resting length (l_r; Prochazka, Stephens & Wand, 1979) the velocity of stretch ranged from 0·001 to 0·032 l_r s^{-1} (see Results). This clearly is well below the highest speeds attained during physiological movements, since figures up to 5 l_r s^{-1} have been reported (see Prochazka, 1981). Yet, even if sensitivity reduction were limited to intermediate velocities, the present findings still have important implications for general considerations of motor control mechanisms.

The possibility has been considered that primary spindle afferents, by virtue of their high sensitivity to small movements, significantly contribute to servo-assisted correction of undesired irregularities of voluntary movement (Matthews, 1972, 1981a, b; Stein, 1974; Marsden *et al.* 1976). Yet, the results of the present investigation indicate that for a wide range of velocities of natural movement spindle Ia sensitivity to small disturbances is much lower than was hitherto assumed. For velocities between 0·005 and 0·25 l_r s^{-1} small movement sensitivity dropped to between 50 and less than 10 % of the values measured at fixed muscle length (around 500 impulses s^{-1} mm^{-1} for cat soleus muscle). This then puts extra demands on the gain required for any spinal or central reflex action involved in such automatic compensation of unexpected perturbations. On the other hand, in postural tasks or during slow swaying movements a pronounced sensitivity of Ia afferents may still be preserved, provided that either the parent muscle is taut (in the absence of fusimotor action), or that appreciable and almost selective dynamic fusimotor drive is present (cf. Hulliger *et al.* 1977b). Neither condition need be met during ordinary movements, first, since these movements rarely extend into the region of muscle length where passive Ia sensitivity indeed is high (i.e. close to the physiological maximum; cf. Results, *Length dependence*) and second, since routine movements in general may well be dominated by static fusimotor action, as indeed has been demonstrated for normal locomotion in freely moving cats (see Hulliger, Zangger, Prochazka & Appenteng, 1985; Prochazka, Hulliger, Zangger & Appenteng, 1985).

Ia firing during muscle shortening

The occurrence of afferent firing during muscle shortening in natural movements is commonly interpreted as a manifestation of (mainly static) fusimotor action. However, the present observation that primary afferents deprived of fusimotor drive were capable of maintaining a background discharge even during imposed muscle shortening must strike a note of caution. Although the speeds of the movement for which this occurred were very low, it should be noted that the likelihood of passive afferent firing during the release of background stretch is further enhanced, when this is accompanied by small oscillatory perturbations (see Fig. 2; also Baumann *et al.* 1982; Emonet-Dénand, Hunt & Laporte, 1985a). Therefore, relatively low discharge

rates during slow shortening movements, as they may be encountered in microneurographic recordings from human subjects or in chronic recordings from behaving animals, are not necessarily reliable indicators of concomitant fusimotor action.

Receptor mechanisms

The high sensitivity of primary spindle afferents to small movements is commonly attributed to the persistence of stuck cross-bridges between intrafusal actin and myosin filaments (Brown, 1971; Matthews, 1972) which, over a limited range of imposed stretch, would enhance polar stiffness of intrafusal muscle fibres (short-range elasticity; Hill, 1968). On this view the reduction in sensitivity to larger movements (gain compression) would arise from an amplitude-dependent break-down of these bridges. In general, the present observations are compatible with this notion, but their interpretation along these lines suggests further refinements of the concept. In particular, it indicates that, even in passive intrafusal muscle, cross-bridges, rather than being permanently attached or detached, may be subjected to relatively slow turnover, undergoing a cycle of stretch-induced detachment and reattachment. Three related aspects are considered below.

Non-linear distortions

Although sensitivity (estimated by fitted sinusoids) declined smoothly with increasing velocity, the effect was accompanied by a number of non-linear features (see Results, Figs 5 and 7). In particular, the majority of afferents exhibited conspicuous distortions in their response to 50 μm stretches, but only for background movements of intermediate (but not of fast or slow) velocity. In the extreme such distortions led to a rapid fall in firing rate during the lengthening phase of a sinusoidal stretch. Formally this appeared as a sudden drop of the afferent's sensitivity from a high to a lower level. In terms of the cross-bridge hypothesis this would indicate that disruption of the bonds between actin and myosin filaments depends not only on the amplitude of a movement but also on its velocity, i.e. on the speed with which a large movement makes its potentially disruptive effect 'felt'. Earlier reports have described similar, if less striking, examples (Cabelguen, 1979; Emonet-Dénand, Laporte & Tristant, 1980b), yet in these the importance of movement velocity and its implications for cross-bridge kinetics was not evident.

Large-movement sensitivity

For larger sinusoidal stretches (1000 μm) sensitivity was uniformly low, in-dependent of the velocity of concomitant stretch, and practically identical with the values at constant mean length. Thus, when sensitivity was already low in the absence of background stretch, then adding such background stretch did not further reduce it (as might have been the case, had the reduction of sensitivity been due to some saturation, e.g. of mechano-electrical transduction). The implication for the cross-bridge hypothesis would be that primary afferents' sensitivity to movements of intermediate size is no longer borne by stuck cross-bridges or, if it were, then by a subset of bonds which was not susceptible to disruption by concomitant large movements. In line with this is the observation that at the highest velocities of

background stretch the amplitude dependence (gain compression) of the Ia response was nearly abolished. However, this may only apply for muscle lengths close to the physiological maximum (present data), since equally indirect evidence from experiments performed at intermediate lengths seems to indicate that under these conditions cross-bridges can bear the strain of considerably larger movements (Emonet-Dénand, Hunt & Laporte, 1985b).

Turnover of bonds in passive intrafusal muscle

There was a broad agreement between the time course of recovery of small-movement sensitivity after a large and abrupt rectangular stretch and the value of velocity for which concomitant triangular stretch provoked half-maximum reduction in sensitivity. Assuming a first-order exponential process, the time constant of recovery after abrupt stretch was estimated to be of the order of 1·5 s (median 1·43 s). This suggests that after 1 s, 50% (after 1·43 s, 63%) of the cross-bridges capable of reattachment had reattached. Thus the median reattachment time was approximately 1 s.

Turning now to the much slower triangular movements, the evidence of Fig. 4 suggests that on average also 50% of the cross-bridges were attached at a triangle velocity of 0·25 mm s^{-1}, since at this critical velocity the half-maximum reduction of sensitivity to superimposed small sinusoids was reached (Fig. 4). This interpretation rests on two assumptions: first, that the subpopulation of cross-bridges capable of reattachment in the passive state had approximately uniform elastic properties and second, that apart from a likely difference in the degree of synchronization of cross-bridge cycles there were no other major differences in cross-bridge kinetics between fast (rectangular) and slow (triangular) disrupting stretches.

At the break-even point of triangular stretch (0·25 mm s^{-1}) individual bridges would on average spend the same amount of time in the attached and in the detached state. As a first approximation the reattachment time (estimated from the recovery of sensitivity after abrupt stretch, above and Fig. 9) may be taken as an estimate of the time spent in the detached state. Therefore, at the critical triangle velocity the intervals which cross-bridges spent in the detached and the attached state were on average both 1 s. In this condition, the amount of stretch, which the 50% of connected cross-bridges were subjected to since their formation, must have been less than their short-range elastic limit. Thus, for a velocity of 0·25 mm s^{-1} (i.e. 250 μm s^{-1}) and an average attachment period of 1 s, the median of this elastic limit would appear to be 250 μm ('median' simply implying that the cross-bridge limit is a distributed property). This deduced value of 250 μm for the cross-bridge limit is in broad agreement with the value of 100 μm for the extent of the small-movement linear range measured from responses to sinusoidal stretches in the absence of background movements (50 μm half peak-to-peak sine amplitude, Matthews, 1972; Goodwin *et al.* 1975; see also Hasan & Houk, 1975b). The discrepancy (100 *vs.* 250 μm) is less serious than it might appear, since the end of the linear range (the first detectable deviation from proportionality) is likely to reflect the beginning rather than the 50% break-even point of the process of cross-bridge break-down.

In conclusion, the present data suggest that in passive intrafusal muscle, which is subjected to imposed length changes, the cross-bridges between actin and myosin

filaments may not only persist in stuck form, but that they may also exist in a state of dynamic equilibrium between break-down and reattachement, with the equilibrium depending on the velocity of stretch which is imposed on a muscle spindle.

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