Motoneuronal pre-compensation for the low-pass filter characteristics of muscle. A quantitative appraisal in cat muscle units

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1. The relevance of motoneurone dynamic sensitivity in compensating for the low-pass filter properties of muscle was assessed by stimulating cat muscle units (MUs) with impulse discharges generated by two current-to-rate converters: (i) a spinal motoneurone, sensitive to both the input intensity and its first derivative, and (ii) a linear current-to-rate converter, i.e. a neurone model with the same static sensitivity as the motoneurone but lacking dynamic sensitivity.

2. Discharges generated by injection of sine-wave currents in three motoneurones of the 'fast' type and in the three related model versions were applied to the axon of forty-six MUs. The MU isometric tension was modulated at the frequency of the current sine wave (0·5–20 Hz). Phase and gain of the current-to-force transduction were measured.

3. When MUs were driven by the model, the force lagged the current by 90 deg at 1 Hz in slow MUs and at around 5 Hz in fast MUs. Under motoneurone drive, the 90 deg phase lag was attained at frequencies about twice as high.

4. The gain of the transduction (peak-to-peak force modulation/peak-to-peak current modulation) decayed when the modulation frequency was increased. In all but five units, the cut-off frequency, F_{co} (gain attenuated by -3 dB), was higher when the unit was motoneurone driven (F_{co}Cell) then when it was model driven (F_{co}Mod). In both conditions, F_{co} was inversely correlated with the MU's time-to-peak. The advantage conferred by the motoneurone dynamic sensitivity was expressed by the F_{co} ratio (F_{co}Cell/F_{co}Mod). Across the MU population this ratio ranged from 0·6–2·8, was inversely correlated with the time-to-peak, and was directly correlated with the half-tension rate, i.e. the impulse rate at which MUs develop 50% of their maximal tetanic force. The largest improvement (F_{co} ratio $> 2·0$) was found in units with mechanical features similar to those presumably coupled '*in vivo*' to the motoneurones utilized for stimulation.

5. This estimate was confirmed in experiments in which trains of pulses, generated by injection of ramp currents in another motoneurone and the related model, were used to activate eight MUs, selected for being similar to that connected '*in vivo*' to the motoneurone. As expected, for any given current slope the rising phase of isometric tension was steeper when units were motoneurone driven than when they were model driven. The gain (force slope/current slope) was plotted against the ramp slope to identify the cut-off slope, S_{co}, at which the gain was attenuated by -3 dB. In this homogeneous MU sample, the ratio expressing the advantage of the motoneurone drive (S_{co}Cell/S_{co}Mod, equivalent to the F_{co} ratio), ranged from 2·62–2·97, values comparable with those observed in sine-wave experiments when the motoneurone and muscle units were properly matched.

Sherrington's motor unit (the motoneurone and the muscle fibres innervated thereby) may be described as the elementary interface between the central nervous system and the environment: the motoneurone encodes supra-liminal synaptic currents into firing rates and these impulse trains are converted into levels of force by the innervated muscle fibres (the muscle unit).

In response to steady inputs, the motoneurone current-to-rate relation is linear over an extension ('primary range', Kernell, 1965) which covers the straight portion of the rate-

to-force relation of the corresponding muscle unit (Baldissera & Parmiggiani 1975; Kernell 1979, 1983).

In response to time-varying inputs, the two components of the motor unit display different characteristics. The motoneurone behaves like a linear current-to-rate transducer, sensitive to both the input intensity and its first derivative (Baldissera & Campadelli, 1977; Baldissera et al. 1984a, b, 1987): when neurones are stimulated by sine-wave currents, the transduction sensitivity (i.e. peak-to-peak change in firing rate/peak-to-peak current) grows progressively as the modulation frequency rises above 1 Hz.

Conversely, when the isolated muscle is activated by impulse trains, whose rate is modulated sinusoidally, it behaves like a low pass filter. The amplitude of the response decreases as soon as the modulation frequency is higher than 0·5–1 Hz (Partridge, 1965; Partridge & Benton, 1981; see also Mannard & Stein, 1973 and Bawa & Stein, 1976). When discussing these limits of the muscle, Partridge (1979) stressed the need for their pre-compensation by neural control. Interestingly, since the motoneuronal response is amplified over the same frequency range (from 1 to 10–20 Hz) in which the muscle response is attenuated, the dynamic properties of the nerve cell may be one basic mechanism, built into the motor unit, which provides such compensation.

Theoretically, the extent of such a pre-compensation could be estimated by combining the neural with the muscular input–output relations. The studies quoted above, however, cannot be utilized for this aim: while neural transduction was analysed in single motoneurones, information transfer in muscle was described for the rate-to-movement transduction (thus including the effect of inertial and viscous resistances) in the whole muscle.

The extent of the pre-compensation, however, may be measured directly by comparing how one and the same muscle unit behaves when it is driven by a real motoneurone (whose firing rate is proportional to both the intensity and the first derivative of the stimulating current) and when it is driven by a sham motoneurone (a current-to-rate converter) with the same static sensitivity as the real motoneurone but lacking dynamic sensitivity. This goal was pursued by splitting the experiment into two parts, i.e. first, recording the motoneurone discharges to inputs of various shapes and intensity (Baldissera et al. 1984a, b) and then, in a second session, stimulating the axon of single muscle units with those discharges, as well as with the discharges generated by the linear encoder. At the end, the comparison between the force responses obtained in the two conditions will show which differences are introduced by the neural dynamic sensitivity in the input–output relation across the motor unit. This splitting procedure allowed us to bypass the significant technical difficulties of doing the whole analysis in undivided motor units by stimulating their motoneurone intracellularly, first with sine-wave or ramp-currents and then with trains of impulses artificially generated by similar

input currents fed into the linear converter. Moreover, this double-step procedure also gave the opportunity to apply the two stimulus patterns to a sample of muscle units with different contraction properties and thus to verify the importance of the proper coupling between the motoneurones and the muscle units ('rate-match', Kernell, 1990, 1992).

The first part of this paper will report results obtained when both the motoneurone and the converter were stimulated with sine-wave currents while the second part will illustrate results obtained with ramp-current stimulation.

METHODS

Experiments were performed on eight adult cats, anaesthetized with Nembutal (initial dose 30–40 mg kg^{-1} I.P. supplemented intravenously during the experiment as required to maintain fissured myosis and avoid reaction to ear pinching). Care and handling of animals was in accordance with international guidelines (NIH) and approved by the Animal Care Committee of the University of Milan. End-tidal CO_2, partial pressure, rectal temperature and arterial pressure were continuously monitored and maintained at their physiological levels. After lumbar laminectomy, which gave access to the L6–L7 ventral roots, the spine was clamped and immobilized. The tendon of one or more hind-limb muscles (gastrocnemius lateralis, tibialis anterior, peroneus longus and tertius) was dissected free and connected to an isometric force transducer (Grass FT03). Femur and tibia were firmly fixed and the exposed muscles covered with mineral oil. All the other muscles of the limb were denervated. The spinal cord was covered with mineral oil at 37 °C and the ventral roots were divided at their emergence from the cord. A flexible Ag–AgCl electrode was placed on the exposed muscle for EMG recording. Fine filaments were dissected free from the ventral roots' peripheral stump and mounted on stimulating wire electrodes. Dissection continued until a single muscle unit was isolated. This was judged by the all-or-none properties of the EMG action potential and of the mechanical response of the muscle (both single twitches and tetanic response to a short train of pulses at 40 Hz). During stimulation, the muscle was kept at the length giving the largest twitch responses.

Once isolated, each muscle unit was stimulated with the following protocols: (1) single stimuli; (2) trains of stimuli at constant rate (from 5 to 100 impulses s^{-1}) to develop tetanic fusion and to determine the steady-state rate-to-force relation (Cooper & Eccles, 1930); these trains, lasting 800 ms, were given in an order of ascending rate, separated by 1 min of pause. The force of incompletely fused contractions was measured at the peaks of the twitches; (3a) trains of pulses reproducing the discharge evoked by sine-wave current injection both in spinal motoneurones and in a linear current-to-rate converter; (3b) trains of pulses, lasting 300 ms, reproducing the discharge evoked by ramp current injection either in a spinal motoneurone or in a linear current-to-rate converter. The interspike intervals of these pulse discharges, recorded in previous experiments, were computer reproduced to drive a Grass S88 stimulator one-to-one, through the digital output of a DT 2801-A board (sampling rate 25 kHz). Again, the interval between each train was 1 min; (4) trains of pulses at 40 impulses s^{-1}, lasting 300 ms and repeated once every second for 3 min, to determine the 'fatigue index' (Burke et al. 1973). A total of forty-six muscle units were analysed with sine-wave stimuli. They belonged to the following muscles: tibialis anterior (7), gastrocnemius

lateralis (29), peroneus longus (10). A further eight muscle units were analysed with ramp stimulation (2 from peroneus longus, 3 from tibialis anterior, 3 from peroneus tertius).

The isometric tension developed in response to these stimulation protocols was recorded, digitized and stored for analysis. At the end of the experiment, the animal was killed by an i.v. injection of a Nembutal overdose (100 mg kg^{-1}).

Motoneuronal discharges evoked by sine-wave current injection

The motoneurone firing responses to sinusoidal stimuli utilized in this experiments were obtained in a previous experimental series (Baldissera *et al.* 1984*a*) from three spinal motoneurone (Cell1, Cell2 and Cell3) of the 'fast' type (Eccles *et al.* 1958, duration of the after-hyperpolarization (AHP) 50–60 ms). When stimulated by intracellular injection of rectangular currents, Cell1 displayed a linear current-to-rate relation at steady state ('primary range') whose slope (static sensitivity) was 1·57 impulses s^{-1} nA^{-1} (Fig. 2*A*, open circles); slope of the primary range was 2·12 impulses s^{-1} nA^{-1} in Cell2 and 1·43 impulses s^{-1} nA^{-1} in Cell3.

The three motoneurones had also been stimulated with sinusoidal currents, superimposed on current steps, whose frequency ranged from 0·5–1·0 Hz to 18–21 Hz in the three neurones. The firing responses of Cell1 to sinusoidal stimulation are illustrated in

Fig. 1*A*. Briefly, the amplitude of the motoneurone response (the peak-to-peak change in instantaneous firing rate) increased as the modulation frequency was raised above 2–3 Hz. After fitting the changes in firing rate with sinusoidal functions, sensitivity and phase of the current-to-rate conversion were determined. When increasing the sine-wave frequency, the response showed an increase in sensitivity as well as a phase advance, indicating (Baldissera *et al.* 1984*a*) that firing rate was proportional to both the stimulus intensity and its first derivative. The 'corner frequency', i.e. the frequency at which the sensitivity increased by 3 dB, was 5·3 Hz in Cell1, 7·4 Hz in Cell2 and 5·7 Hz in Cell3. Sensitivity and phase curves of Cell1 are illustrated in Fig. 2. Cell1 and Cell2 correspond to motoneurone 5 and 6 of Table I in Baldissera *et al.* 1984*a*, Cell3 was not included in that material.

Motoneuronal discharges evoked by ramp current injection

The neuronal discharges were obtained in a previous experimental series (Baldissera *et al.* 1987) from a gastrocnemius lateralis motoneurone (Cell4) with AHP duration of 90 ms. When stimulated by intracellular injection of rectangular currents, Cell4 displayed a primary range with a slope of 1·38 impulses s^{-1} nA^{-1}.

During that experiment, the motoneurone was also stimulated with trapezoidal currents reaching a final intensity of 32 nA through ramps of different slopes (from 0·2 to 2·5 nA ms^{-1}). Samples of those
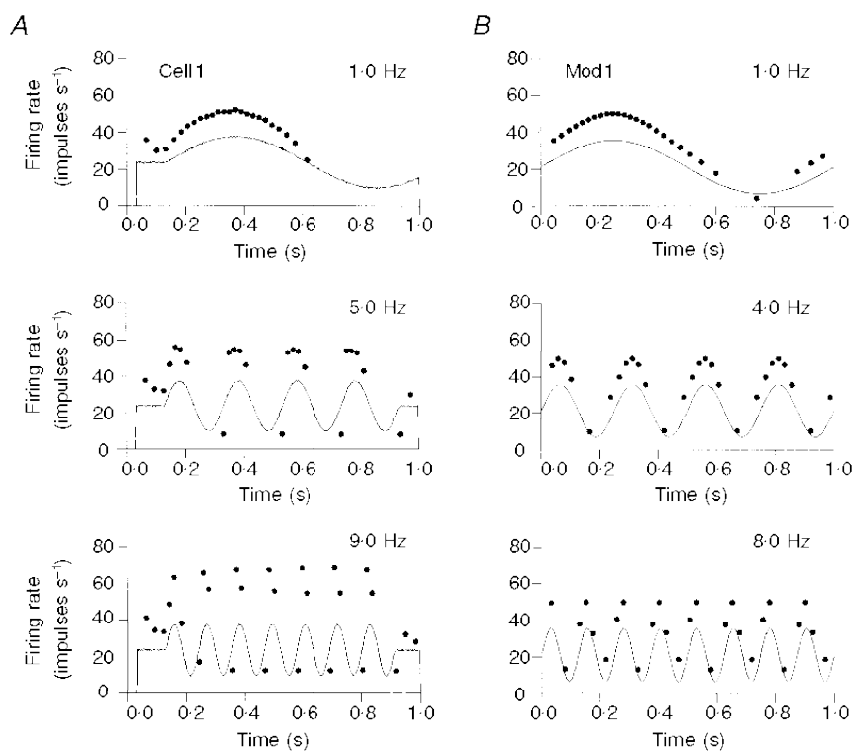

Figure 1. Firing response of motoneurone Cell1 and model Mod1 to sine-wave current stimulation

Injection of a sine-wave current (continuous line) in Cell1 (*A*) and in Mod1 (*B*) evoked a sinusoidally modulated discharge whose instantaneous firing rate is illustrated by dots. *A*, despite the current amplitude remaining constant (23 nA peak-to-peak, superimposed on a current step of 19 nA) the peak-to-peak amplitude of the motoneurone firing response increased when the sine-wave frequency was incremented (as indicated on each graph), revealing the dynamic sensitivity of the motoneurone. A phase advance of the firing rate on the current is also visible. *B*, both the amplitude of the firing rate modulation and the phase relationships remain constant when the modulation frequency increases. Amplitude of the sine-wave current and underlying step is the same as in Cell1.

discharges are illustrated in Fig. 9. The muscle unit innervated by Cell4 had the following mechanical characteristics: 'fatigue index', 80 (Burke et al. 1973); twitch time-to-peak, 27 ms; twitch duration, 90 ms; twitch isometric force, 0·9 g; maximal tetanic tension (F_{max}), 9·0 g; half-tension rate (HTR), i.e. the impulse rate at which 50% of F_{max} is developed, 23 impulses s^{-1}.

Discharges of the linear current-to-rate converter

A mathematical model of motoneurone repetitive firing was utilized as a linear current-to-rate converter. The model is based on the time course of the after-hyperpolarization refractoriness (Kernell, 1968; Baldissera & Gustafsson, 1974a, b) and simulates motoneurone dynamic properties by summating the after-hyperpolarization potassium conductance (g_K) changes. If the dynamic sensitivity is removed by omitting the g_K summation, firing rate becomes linearly related to the stimulus intensity over a wide range of current intensities.

For the sine-wave analysis, the model parameters were calibrated to generate three steady-state current-to-rate relations, each superimposed on that of one of the three motoneurones. Each model version (Mod1, Mod2 and Mod3) was then stimulated with sine-wave currents (and underlying step currents) of equal intensity to those originally injected into the three motoneurones and generated a sinusoidally modulated firing response (see Fig. 1B) which had the same amplitude as that of the related motoneurone at the lowest modulation frequency (0·5 Hz for Cell2 and 1 Hz for Cell1 and Cell3). When modulation frequency was increased, the amplitude of the model responses remained constant, because of the absence of any dynamic sensitivity (Fig. 1B and Fig. 2). Modulation of the firing rate remained in phase with the stimulating current over all the range of frequencies tested (Fig. 1B and 2).

For the ramp experiments, the model was calibrated to generate a steady-state current-to-rate relation superimposed on that of Cell4 and thereafter stimulated with ramp currents rising to a final intensity of 32 nA, through slopes ranging from 0·1–2·5 nA ms^{-1}. During the ramp, firing rate increased linearly to the steady-state value (46 impulses s^{-1}) without correlation with the ramp slope.

RESULTS

Part I: response of muscle units to sine-wave current stimulation of motoneurone and models

For the sake of clarity, in the following text the term 'frequency' will indicate the modulation frequency of the sine-wave stimuli, whereas impulse firing frequency, of both motoneurones and models, will be denoted as 'rate'.

Force modulation by motoneurone and model discharges

Contraction of each muscle unit was induced by activation of the motor axon, isolated within a ventral root filament, with trains of electric shocks. The pattern of train pulses reproduced the repetitive firing evoked by stimulating with sine-wave currents of different frequencies: (i) three spinal motoneurones (Cell1, Cell2 and Cell3); and (ii) three versions (Mod1, Mod2 and Mod3) of a linear current-to-rate converter, each calibrated to the corresponding motoneurone.

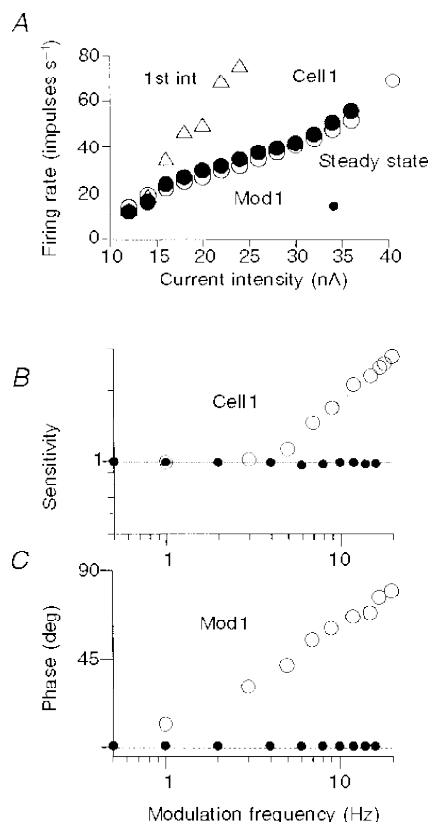Figure 3A shows the isometric tension generated by one protocol unit, MU84, when it was activated by the

Figure 2. Sensitivity and phase of the motoneurone and model transduction

A, current-to-rate relations obtained from responses to injection of current steps in Cell1 (△, 1st int, first interspike interval; ○, steady state) and in the related model (Mod1) lacking dynamic sensitivity and thus developing only steady-state firing (●). *B*, Bode plot representing sensitivity and phase of the current-to-frequency transduction operated by Cell1 (○) and Mod1 (●) when the modulation frequency was increased. Sensitivity is normalized to that of the response at 0·5 Hz. For phase measurements, Cell1 instantaneous rate was referred to the mid time of the related interspike interval. The sensitivity and phase of the model are unaffected by changes of the modulation frequency.

sinusoidally modulated discharges of Cell 1. The force generated changed periodically at the same frequency as the stimulating current, the tension profile becoming neatly sinusoidal above 3 Hz. Note that increasing the modulation frequency produced a progressive decrease of the amplitude of force modulation.

Observe, however (Fig. 3*B*), that the amplitude was reduced to a much greater extent when the same muscle unit was activated by the discharges generated by Mod 1, lacking dynamic sensitivity.

Estimate of the motor unit gain

The term gain, used here in its broader sense of output/input ratio, will indicate the change in isometric force of the muscle unit (output) produced by a unitary change of the current stimulating the motoneurone (input). It therefore has the dimension of $g\,nA^{-1}$.

In the sine-wave experiments, the gain was calculated between the mean peak-to-peak amplitude of force modulation (excluding the first peak, if it was affected by the initial response to the step) and the peak-to-peak amplitude of the sinusoidal current. In those responses at the lowest modulation frequencies (0·5 and 1 Hz) in which

the lower peak of the force variation was undetermined, the gain was evaluated on the upper half-cycle. In each muscle unit (MU), the gain was normalized to that of the response to the model at 0·5 Hz, whose value should correspond to the static gain.

The model-driven responses of MU 84 (Fig. 4, filled circles) display a regular decay which is well fitted (continuous line) by the equation of a simple resistance–capacitance (RC) low-pass filter (gain, $G(j\omega) = 1/(1 + j\omega RC)$) and reaches a -3 dB attenuation at 3·6 Hz, the 'cut-off' frequency', F_{co}. When the same muscle unit was motoneurone driven, responses were always higher than those obtained when it was model driven and the corresponding curve (open circles) was characterized by a slower decay and a higher cut-off frequency (9 Hz).

Muscle unit 84 was also stimulated by the discharges of the second motoneurone (Cell 2) and of the related current-to-rate converter (Mod 2). The general features of responses to Mod 2 were at all similar to those obtained with Mod 1, but cut-off frequency was somewhat higher (4·8 Hz, Fig. 4*B*). In responses to Cell 2, the gain curve was different from that obtained in response to Cell 1 in one detail, i.e. between 0·5 and 2 Hz, the gain rose from 1·0 to 1·6. When the frequency
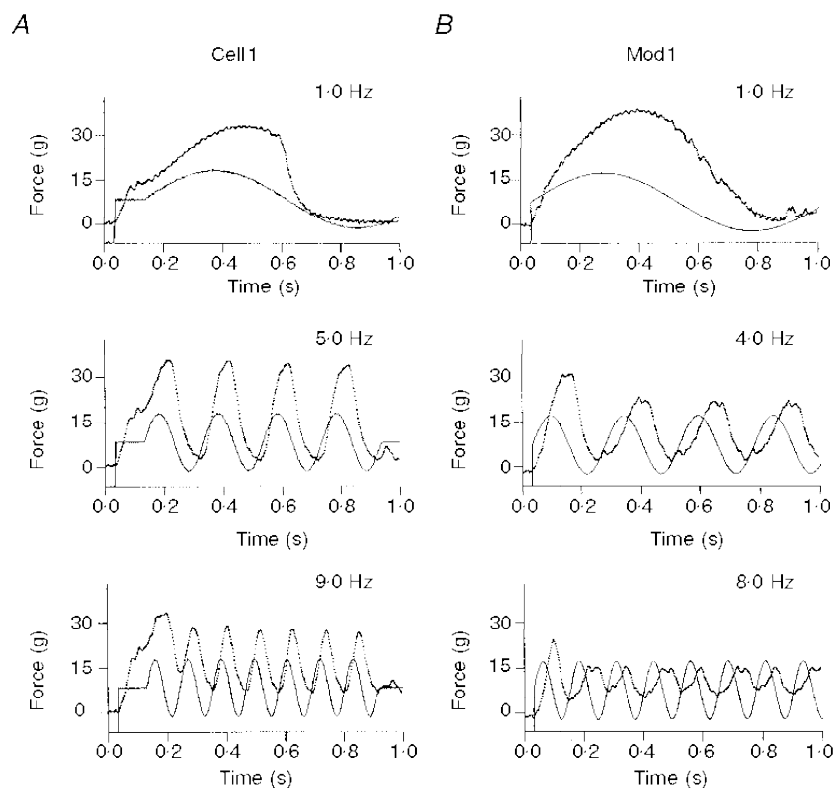

Figure 3. Current-to-force transduction in a motoneurone driven and model driven muscle unit

The isometric force developed by a muscle unit (MU 84) in response to sinusoidally modulated discharges of Cell 1 (*A*) and Mod 1 (*B*) illustrated in Fig. 1, is displayed together with the current itself. In this way, the electrical input and the mechanical output of the 'artificial' motor unit are visually correlated with each other. Note the stronger attenuation and larger phase lag of the muscle response when the unit is model driven.

was raised further, the response amplitude declined, although it remained higher than unity up to 6 Hz, and the cut-off frequency was reached at 10 Hz. In conclusion, when either Cell 1 or Cell 2 replaced the corresponding model, the cut-off frequency of MU 84 was increased by 2–2·5 times.

In other muscle units, however, changing from the model to motoneurone discharges did not lead to an improvement. An example is illustrated in Fig. 4C and D and Fig. 5. Figure 5 shows responses of a muscle unit of the slow type (MU 89) to Cell 1 and Mod 1 discharges. Impulse rates developed by both the model and the motoneurone saturated the force response at low frequency (compare with MU 84, Fig. 3), making evident the hysteretic properties described by Partridge (1965, 1979) and Binder-Macleod & Clamann (1989), i.e. the slow decay of force, compared with the decay of the stimulus rate, during the descending phase of the sine wave. Note, moreover, that force modulation is rapidly attenuated when the modulation frequency is increased.

The gain curves obtained in MU 89 when activated by Mod 1–Cell 1 and Mod 2–Cell 2 are depicted in Fig. 4C and D. The responses to the models (filled circles) had a faster decay (cut-off frequency around 2 Hz) than those obtained in MU 84. Changing to the motoneurone drive did not improve the mechanical responses (open circles): they were similar to, or even lower than, those obtained with the models.

Comparison of the motoneurone and model responses in motor units of different type

When operating the rate-to-force transduction, muscle behaves like a low-pass filter (Partridge 1979) because of the rounded profile and long-lasting decay of the force recruited by each nerve impulse. Filter properties should depend on features related to the time course of the single twitch and to the mechanisms of force summation during repetitive impulse stimulation. Thus, one may reasonably argue that the differences between the dynamic responses of MU 84 and MU 89 may be related to parameters which quantify the above mentioned features. Two of such parameters are: (i) the time-to-peak (TTP) of the single twitch and (ii) the half-tension rate (HTR), i.e. the impulse rate at which 50 % of the maximal tetanic force is recruited. These parameters are correlated with each other by a relation of inverse proportionality.

With respect to these parameters, MU 84 and MU 89 are clearly distinct. MU 84 is a fast muscle unit with a time-to-peak of 25 ms and a half-tension rate of 57 Hz. Conversely, MU 89 is a slow muscle unit with time-to-peak of 64 ms and half-tension rate of 14 Hz. Combining these features with the gain curves illustrated in Fig. 4 suggests that 'fast' motoneurones are well suited to enhance the dynamic response of motor unit of the fast type, like MU 84, but are
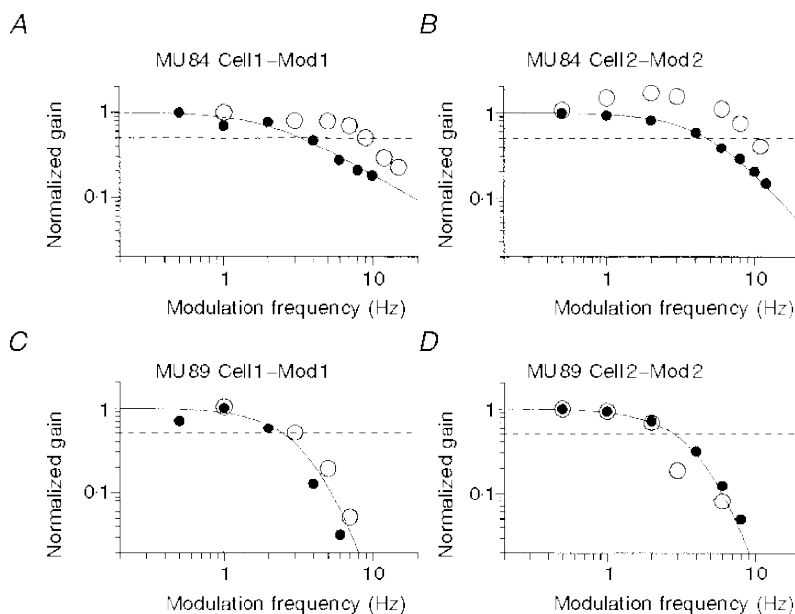

Figure 4. Input–output relations in fast and slow muscle units when driven by the motoneurone and by the model

The graphs refer to one fast (MU 84) and one slow muscle unit (MU 89), each driven by two different motoneurones (Cell 1 and Cell 2) or by the related model versions (Mod 1 and Mod 2). The gain of the motor unit transduction (amplitude of force modulation/amplitude of current modulation) was normalized to that of the response to the model at 0·5 Hz and plotted against the modulation frequency. Horizontal dashed lines indicate −3 dB with respect to unity. In the fast muscle unit (A and B) the gain of responses to both motoneurones (O) remains higher than the gain of responses to the related models (●). In the slow muscle unit (C and D) the gain difference between motoneurone and model drive is strongly reduced (C) or even reversed (D).

ineffective in improving the response of slow motor units like MU89.

It was, therefore, of interest to investigate whether the mechanical advantage provided by the motoneurone drive was systematically correlated with the distribution of TTP and HTR in a large population of the muscle units of both fast and slow types.

The experiment described above was repeated by activating forty-four muscle units with Cell1 and Mod1, twenty-five muscle units with Cell2 and Mod2 and on twenty-one muscle units with Cell3 and Mod3. The cut-off frequency (F_{co}) was determined in the two different conditions (model driven or motoneurone driven) for each muscle unit and it was correlated with the time-to-peak (TTP) and the half-tension rate (HTR) of that unit.

Results obtained in the MU sample stimulated by Cell1 and Mod1 are illustrated in Fig. 6. In this population, the cut-off frequency increased when TTP diminished. This occurred both when muscle units were driven by the model (Fig. 6A, filled circles) and when they were driven by the motoneurone (Fig. 6A, open circles). In slow MUs (TTP > 50 ms), F_{co} ranged between 2·2 and 2·8 Hz when they were model

driven and was only slightly higher (3·2–3·9 Hz) when they were activated by the motoneurone. As TTP decreased below 30 ms, F_{co} increased up to 7·6 Hz under the model drive and up to 17 Hz under motoneuronal drive.

The advantage conferred by the motoneurone dynamic sensitivity was quantitatively evaluated by the F_{co} ratio, i.e. the ratio between the cut-off frequency of the response to the motoneurone and the cut-off frequency of the response to the model. In this same MU population (Fig. 6B), the F_{co} ratio was lower than 1·5 in the four slow units and reached 2·75 as the TTP decreased towards its lowest values.

A clear-cut difference between motoneurone and model drive is also visible when F_{co} is plotted against the half-tension rate (Fig. 6C). When considering the response to the model firing (filled circles), it appears that F_{co} was low in the four slow MUs having HTR < 20 Hz, while it ranged between 3·5 and 7·5 Hz in the other units, without apparent correlation with HTR. Conversely, when considering the motoneurone driven responses (open circles), a positive correlation between F_{co} and HTR becomes evident (Fig. 6C), as is also shown by the continuous rise of the F_{co} ratio as HTR increased (Fig. 6D).
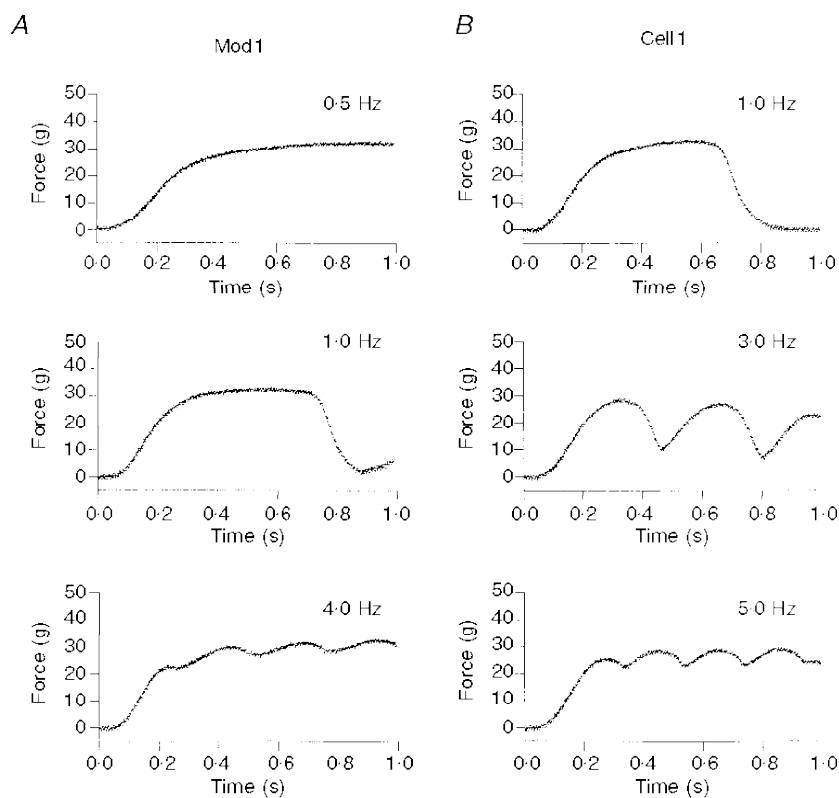

Figure 5. Tension responses to motoneurone and model drive in a slow muscle unit

Tension responses of a slow muscle unit (MU 89) to discharges evoked by sine-wave stimulation of Mod1 (*A*) and Cell1 (*B*). Note how the saturation of the tension responses and the prolonged persistence of force, despite the decline of the sine-wave current, strongly reduce force modulation. Time course of the stimulating current as in Fig. 1 *A* (Cell1) and *B* (Mod1), respectively.

Differences in the response to the three motoneurones

Analysis of the responses to Cell2–Mod2 (27 muscle units) and to Cell3–Mod3 (21 muscle units) gave similar results, which are plotted together in Fig. 7. With these two Cell–Mod combinations, however, the F_{co} ratio was lower than 1 in a number of motor units with HTR < 20 Hz, indicating that the introduction of the motoneurone dynamic properties led to a slight reduction in the mechanical dynamic response. This group includes MU89, illustrated in Fig. 6.

It may be argued that motoneurone dynamic sensitivity can compensate for muscular losses if it develops in parallel with, or earlier than, the attenuation of the muscle response; while it is ineffective if it develops at frequencies where the muscle response has already been cut off. Such a match may be evaluated by comparing the 'corner frequency', F_c, of motoneurone transduction (i.e. the frequency at which a 3 dB increase in sensitivity is reached) with the 'cut-off' frequency of muscle units.

The three cells employed here had different corner frequencies: in ascending order, 5·3 Hz (Cell1), 5·7 Hz (Cell3) and 7·4 Hz (Cell2). Thus one would expect, should these differences be significant, that when the three motoneurones are connected to a sample of MUs with a widespread range of cut-off frequencies, their relative effectiveness in improving the MU dynamic response should be higher the lower the 'corner' frequency. To verify this

prediction, the efficacy of the different motoneurones was compared by plotting the F_{co} ratio obtained with Cell1–Mod1 against that produced by Cell2–Mod2 or Cell3–Mod3 (Fig. 7B). With this representation, equivalence of effects should be revealed by a symmetric distribution of points on the two sides of the diagonal. In fact, the plot shows that Cell1 ($F_c = 5·3$ Hz) was slightly more effective than Cell3 ($F_c = 5·7$ Hz) (2/3 of the open circles lying below the diagonal) and considerably more effective than Cell2 ($F_c = 7·4$ Hz) (all filled circles but one lying below the diagonal). The differential efficacy of the three cells is confirmed when the four slow MUs (cut-off frequency < 3) are considered. Among these units (plotted to the left of the vertical dashed line in Fig. 7A), Cell1 increased the gain (F_{co} ratio > 1) in all units, Cell2 in 3/4, and Cell3 in none (F_{co} ratio always < 1). Conversely, those units which had an F_{co} ratio between 2 and 3 when coupled with one motoneurone, also had similar values when they were coupled with the others.

Input–output phase relations

When the whole muscle is activated by sinusoidally modulated impulse trains, the muscle output (force or movement) is essentially in phase with the input at low modulation frequency and lags the input as soon as the frequency rises, the phase shift occurring in parallel with the amplitude attenuation (Partridge 1965, 1979). Here, phase relations were measured in part of the motor units
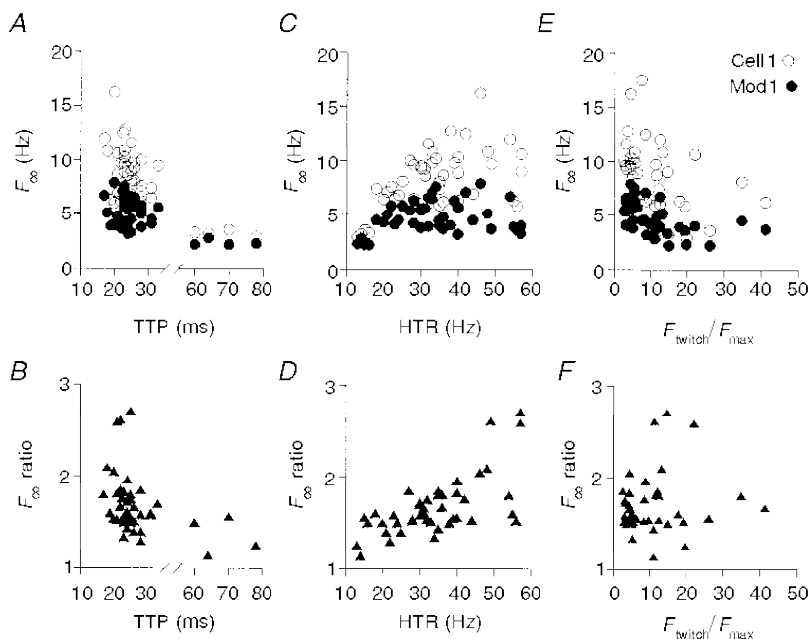

Figure 6. F_{co} and F_{co} ratio in different muscle units, when driven by the motoneurone and by the model

The cut-off frequency (F_{co}) of the responses of 45 muscle units to Cell1 (○) and Mod1 (●) is correlated to the time-to-peak (TTP, A), the half-tension rate (HTR, C) and the single twitch fractional force (F_{twitch}/F_{max}, E). In B, D and F, the F_{co} ratio, i.e. the ratio between cut-off frequencies (F_{co} Cell/F_{co} Mod), is correlated to the same three mechanical parameters.
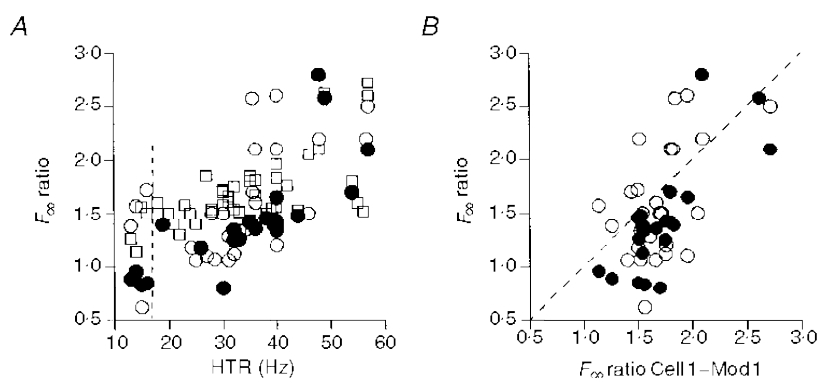
Figure 7. Activation of muscle units by different motoneurones

A, the F_{co} ratio obtained by stimulation of twenty-five muscle units with Cell2–Mod2 (●) and twenty-one muscle units with Cell3–Mod3 (○) are plotted against the muscle units half-tension rate (HTR). Values referring to Cell1–Mod1 are also superimposed (□). *B*, for each unit tested with more than one Cell–Mod couple, the value of the F_{co} ratio obtained with Cell2–Mod2 or Cell3–Mod3 is plotted against the value provided in the same unit by Cell1–Mod 1 (same symbols as in *A*).

activated by Cell1 and Mod1. For this measure we choose four MUs of the fast type (F_{co} ratio 1·85, 2·06, 2·62 and 2·72) and two MUs of the slow type (F_{co} ratio 1·1 and 1·2). For each frequency, phase differences were measured between the peaks of the force and current cycles and, when cycles were multiple, averaged. Delays include the time spent for impulse conduction from ventral roots.

Independently of their type, when MUs were model driven the phase shift was fundamentally similar to that found in the whole muscle, i.e. the lag reached 90 deg at about 5 Hz in fast MUs (Fig. 8*A*, filled circles), as in the gastrocnemius muscle (Partridge 1965), and at 1 Hz in slow MUs (Fig. 8*B*, filled circles), as in the soleus muscle (Partridge 1965). When the same units were driven by the neuronal discharges, the phase lag was consistently reduced. In slow MUs (Fig. 8*B*

open circles) 90 deg crossing occurred at about 2 Hz; in fast MUs (Fig. 8*A*, open circles) phase lag never went beyond 80 deg, within the range of modulation frequencies tested. Thus, in these latter units, the neural discharge, compared with the model discharge, effectively reduced the phase lag by an amount which progressively increased from 15–20 deg at 1 Hz to around 70 deg at 10 Hz, a reduction of about 50%.

Effects on the gain of the single-twitch fractional force

The dynamics of force summation during tetanic fusion, as expressed by the cut-off frequency value, were found to correlate with another parameter, i.e. the fractional contribution of the single twitch to the maximal tetanic tension (F_{twitch}/F_{max}). It may be argued that force can be extensively modulated by rate changes if each impulse
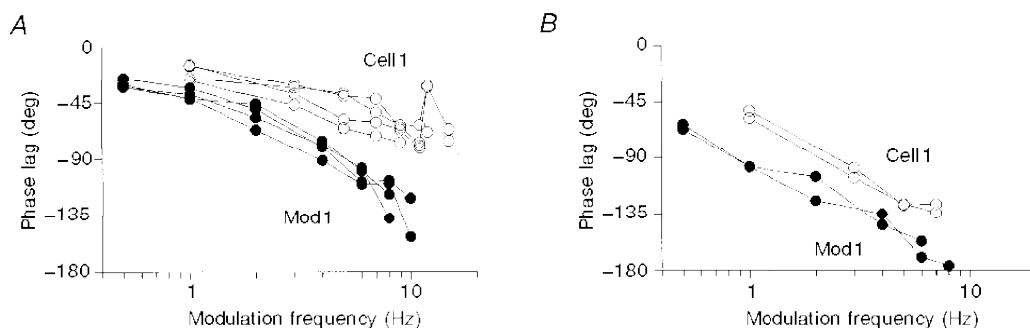

Figure 8. Phase lag of the force response in fast and slow muscle units

A, phase lag between the peaks of the force response and the peaks of the stimulating sine-wave current in four fast muscle units stimulated by Cell1–Mod1. The large phase lag developed by the model response (●) when modulation frequency increased to 10 Hz was about halved when the units were driven by the motoneurone (○). In the two slow muscle units illustrated in *B*, which underwent the same stimulation, the phase lag was much higher than in the fast units and was compensated to a lesser extent by the motoneurone drive.

recruits only a small fraction of F_{max}; at the opposite extreme, if tension of a single twitch corresponds to F_{max}, then rate changes will result in little or no force modulation. This suggests that the higher the fraction, the lower the force modulation, and therefore the cut-off frequency. Plotting the F_{co} against the fractional value of F_{max} delivered by a single twitch (Fig. 6E) shows this to be the case. In fact, units with a low value of F_{twitch}/F_{max} display high cut-off frequencies when responding both to the model (filled circles) and to the motoneurone (open circles). Instead, the F_{co} ratio does not show any clear-cut correlation with F_{twitch}/F_{max} (Fig. 6F), suggesting that the advantage brought about by the small fractional value of the single twitch apparently affects the force recruitment independently of the type of neuronal drive.

Muscle unit dynamic response and fatigue resistance

The improvement in the muscular dynamic response conferred by motoneurone dynamic sensitivity shows no apparent dependence upon the fatigability of muscle units, as expressed by the fatigue index, i.e. the percentage residual force developed by the unit after 2 min of stimulation according to Burke (1981). It should be underlined, however, that the threshold for a clear-cut sign of fatigue was never reached with the present experimental protocol.

Part II: response of muscle units to ramp current stimulation of motoneurone and model

In this second part of the experiment, muscle unit contraction was induced by a train of pulses reproducing the repetitive firing evoked by stimulating with ramp currents of different slopes: (i) one spinal motoneurone (Cell 4); and (ii) a linear current-to-rate converter (Mod 4), calibrated to generate a steady-state current-to-rate relation superimposed on that of the motoneurone. Since features of the muscle unit naturally connected to Cell 4 (Cell 4MU) were known, the proper match between Cell 4 and MUs was easily met by selecting a sample of eight muscle units which were similar to Cell 4MU with respect to those features (see Methods) which characterize tension recruitment.

Muscle units characteristics

All muscle units belonged to the fast type (TTP ranging between 23 and 28 ms); the fatigability test distinguished two fatiguing (FF), three fatigue resistant (FR), and three intermediate (FI) muscle units. In all units, the steep portion of the rate-to-tension curve lay between 15 and 45 Hz. Half-tension rate (HTR) ranged between 24 and 33 Hz, with most values concentrated between 24 and 29 Hz, i.e. all slightly higher than that (23 Hz) of the muscle unit
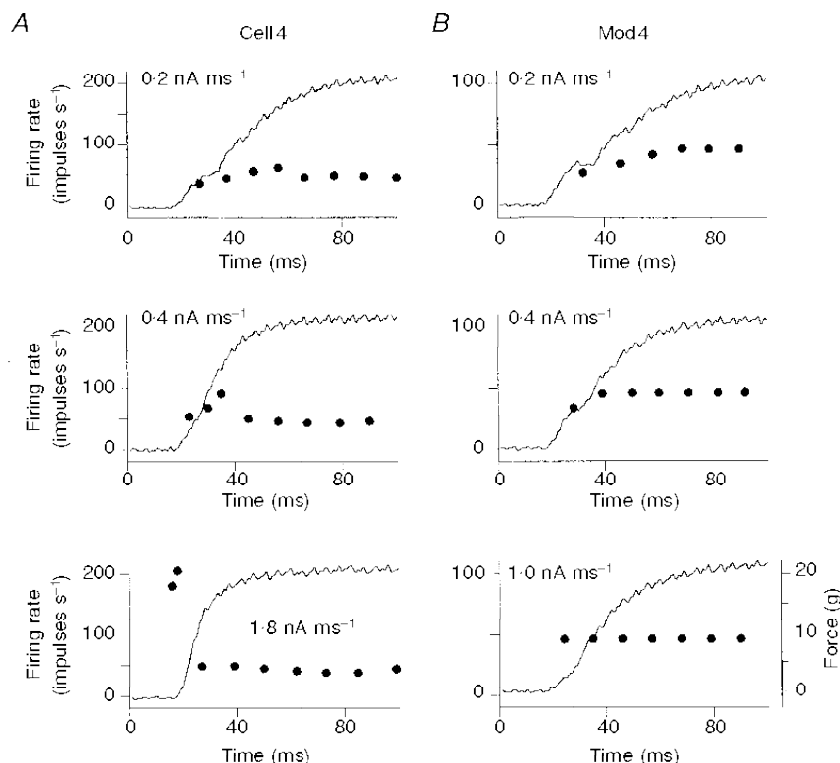

Figure 9. Tension responses of MU 46 to the discharges evoked by ramp current injection in motoneurone Cell 4 and Mod 4

The instantaneous firing rate (●) of the motoneurone (*A*), and model (*B*) discharges evoked by intracellular injections of ramp currents of different slope, as indicated on each diagram, is plotted together with the isometric force developed by MU 46 (mechanical features indicated in Table 1) in response to those discharges. Note the absence of any dynamic component in the model discharge during transients. In response to slopes exceeding 1.0 nA ms^{-1}, the model produced constant rate firing.

innervated by Cell4. However, in the latter unit HTR was measured from responses to step current injection in the motoneurone. Due to the initial high frequency burst, in this situation the tension developed is higher, in the first 300–500 ms, than that recruited by rhythmic stimulation at the constant rate; this results in a shift to the left of the rate-to-force relation, which decreases the HTR (Baldissera & Parmeggiani, 1975). Thus, if tested with trains at a constant rate, HTR of the unit innervated by Cell4 would have been high enough to fall within the values of the muscle units investigated.

Muscle unit response to motoneurone and model discharges

Ramp currents stimulating Cell4 and Mod4 reached the final intensity of 32 nA, corresponding to a steady-state firing rate of 46 impulses s^{-1}. Thus, in all eight units, the firing rates generated by the model during ramp stimuli spanned the range in which the maximal rate of tension recruitment per unitary change in firing rate was produced.

The responses obtained from one and the same muscle unit (MU46) when stimulated with Cell4 and Mod4 are illustrated in Fig. 9A and B. Ramp currents injected in Cell4 had slopes varying between 0·2 nA ms^{-1} and 2·5 nA ms^{-1}. Increasing the ramp slope produced a proportional increase of the ramp-related firing rate, well above the values attained at steady state (Fig. 9A, filled circles); as a consequence, the speed of tension development also increased (Fig. 9A, continuous line).

Firing responses to ramp currents of the linear converter Mod4 (filled circles) and the tension evoked thereby in the same MU46 are shown in Fig. 9B. In the absence of the initial high rate burst characterizing the neuronal dynamic response, tension was recruited by the model discharge much more slowly than by the motoneurone (compare responses with the same ramp slopes in Fig. 9A and B). At a ramp slope of 1 nA ms^{-1}, the model discharge attained the steady-state rate from the very first interspike interval

(Fig. 9B) and subsequent slope increase did not produce any further change either in firing or in the time course of force development.

Estimate of the motor unit gain during transients

On each tension diagram, the rate of force development was estimated by fitting with a straight line (by the least squares method) that portion of the tension curve which was produced by the ramp-related discharge.

The changes in the force slope (dF/dt) produced by increasing the current slope (dI/dt) are described in Fig. 10 for two motor units. The curves showing the responses to motoneurone discharges (open circles) are similar to those obtained in motor units by ramp current injection into their own motoneurones (Baldissera & Campadelli, 1977; Baldissera *et al.* 1987). After an initial phase of quasi-linear growth, the curves bend and the growth saturates. Correspondingly, the gain of the motor unit (dF/dI, the ratio between the linearized force slope and the current slope) is initially constant and progressively decreases as the ramp becomes steeper.

Calculating the instantaneous force/current ratio gives a precise estimate of gain only for that part of the mechanical response where the force grows linearly but it remains, anyhow, a reliable indicator of the dynamic response.

Curves referring to the model-evoked responses (Fig. 10, filled circles) have a similar shape but, at each ramp slope, the force slope is always lower than when the same unit is activated by the motoneurone. This confirms the positive effect of motoneurone dynamic response on the speed of tension development. A quantitative estimate of the advantage procured by the neural dynamic sensitivity can be expressed through the ratio between the maximal values of the force slope which are reached under the motoneurone and model drive, respectively. In the present sample, this ratio (FS_{max} ratio, Table 1) ranges between 1·63 and 2·80, with a mean of 2·22 ± 0·41.
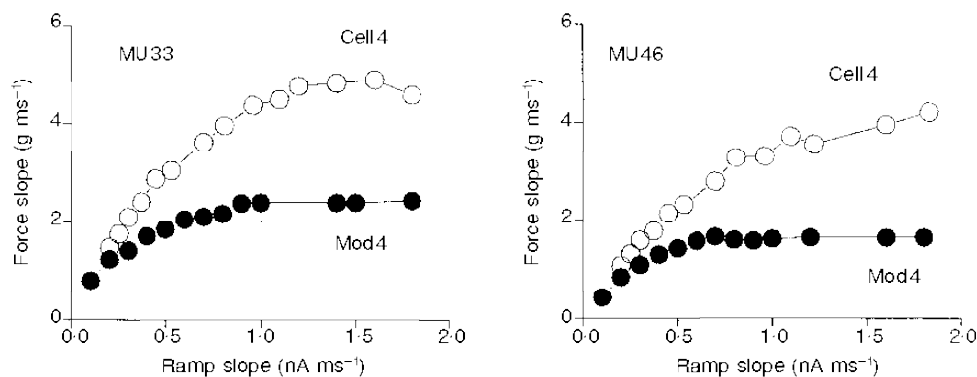

Figure 10. Ramp slope to force slope correlation under motoneurone and model drive
Relation between the slope of the ramp current and the slope of the isometric force developed by the ramp evoked discharge in two muscle units (MU33 and MU46), when they were activated by the motoneurone (O) and by the linear converter (●).

However, in Part I, muscle unit responses to sinusoidal stimulation have been displayed on Bode plots (gain *versus* sine-wave frequency) and the advantage conferred by the motoneurone dynamic properties defined by the ratio between cut-off frequencies (F_{co} ratio). In order to allow a quantitative matching of the present results with those findings, the gain (dF/dI) was plotted against the ramp slope (dF/dt). Gain was normalized with respect to that obtained with the slowest ramp ($0·1$ nA ms^{-1}), which should approach the gain in static conditions. This procedure allowed us to determine the cut-off slope (S_{co}), i.e. the ramp slope at which gain was attenuated by -3 dB, an equivalent of the cut-off frequency measured in sine-wave analysis. In turn, the difference between motoneurone and model activation was expressed by the ratio between the corresponding cut-off slopes (S_{co} ratio).

The gain-to-slope plots of the eight muscle units are illustrated in Fig. 11. In response to the model discharges, gain decayed in all units in a regular way when the ramp

slope was increased (Fig. 11, filled circles). As after sine-wave stimulation, the decay was well fitted (continuous line) by the transfer function of an RC low-pass filter; cut-off slope corresponded to $0·68$ nA ms^{-1} in MU46 and $0·48$ nA ms^{-1} in MU33. Similar features characterized the gain decay in all eight muscle units, when driven by the model. The S_{co} varied between $0·37$ and $0·81$ nA ms^{-1}, with a mean of $0·63 \pm 0·15$ nA ms^{-1}.

When the muscle units were driven by the motoneurone discharges, the maximal gain was higher than unity in 7/8 units, and close to 1 in MU33 (Fig. 11, open circles). In all cases, the gain decayed at a slower rate than when the same units were model driven, the cut-off slope varying between $1·0$ and $2·2$ nA ms^{-1}, with a mean of $1·73 \pm 0·42$ nA ms^{-1}.

These results confirm that the dynamic properties of the motoneurone consistently favour the conversion operated by the motor unit during transients, producing a substantial increase in the cut-off slope. When considering the different motor units (Table 1), one can appreciate that the cut-off
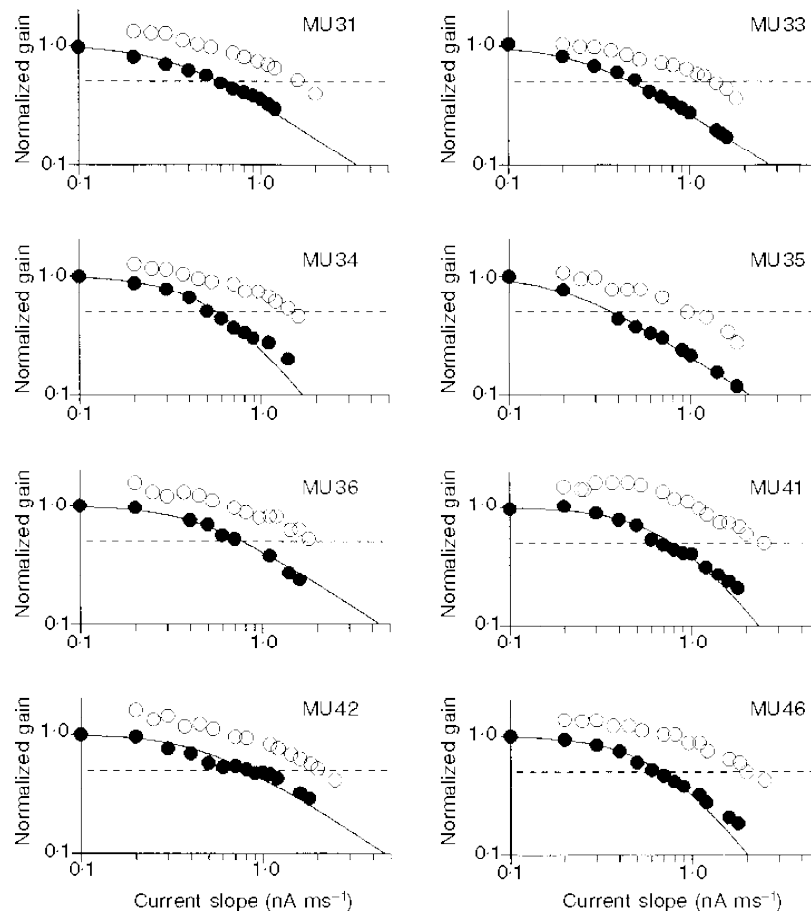

Figure 11. Cut-off slope (S_{co}) of the muscle unit response under motoneurone and model drive

The gain (force slope : current slope) of the responses of 8 muscle units to the motoneurone (O) and to the model (●) discharges is plotted on double logarithmic axes against the slope of the ramp current. Unitary gain is that of the model-driven response to the slowest ramp ($0·1$ nA ms^{-1}). Continuous lines fitting the model responses represent the attenuation produced by a simple RC filter. Horizontal dashed lines on each graph indicate -3 dB attenuation.

Table 1. Dynamic responses of eight muscle units to motoneurone and model discharges

	S_{co}Cell (nA ms^{-1})	S_{co}Mod (nA ms^{-1})	S_{co} ratio (Cell/Mod)	FS_{max} ratio (Cell/Mod)
MU 31	1·61	0·59	2·71	1·71
MU 33	1·28	0·48	2·66	2·12
MU 34	1·50	0·56	2·68	2·60
MU 35	1·00	0·37	2·70	2·00
MU 36	2·02	0·77	2·62	2·50
MU 41	2·21	0·78	2·83	2·80
MU 42	2·19	0·81	2·70	1·63
MU 46	2·02	0·68	2·97	2·46
Mean ± s.d.	1·73 ± 0·42	0·63 ± 0·15	2·73 ± 0·10	2·22 ± 0·41

S_{co}Cell, cut-off slope when motoneurone driven; S_{co}Mod, cut-off slope when model driven; S_{co} ratio, S_{co}Cell/S_{co}Mod; FS_{max} ratio, force slope$_{max}$Cell/force slope$_{max}$Mod.

slopes of model and motoneurone responses change in parallel and that the ratio between the two values (S_{co} ratio) remains almost unchanged throughout the sample, ranging between 2·62 and 2·97 (mean 2·73 ± 0·10).

DISCUSSION

The comparison between motoneurone and model drive allowed us to quantify the physiological relevance of motoneurone dynamic sensitivity in the information transfer through the motor unit, revealing that the attenuation of input transients (which is due to the low-pass filter characteristics of muscle) is efficiently pre-compensated for by the high dynamic sensitivity of the motoneurones.

Response of muscle units to the linear current-to-rate converter

The simple model for motoneurone firing (Kernell, 1968, Baldissera & Gustafsson 1974*a*) used as a linear encoder, granted linearity of transduction of sine waves of the intensity utilized here, up to 16 Hz. When muscle units were driven by the model discharges, modulation of muscle contraction underwent a rapid attenuation when the frequency of the stimulating sine wave increased, as described long ago by Partridge (1965). In those experiments attenuation was described as starting at around 0·2 Hz both for soleus and gastrocnemius muscles, while in most of the units investigated here the responses to the linear converter (i.e. to a stimulus pattern analogous to that used by Partridge, 1965) were substantially identical at 0·5 and 1 Hz and attenuation appeared when frequency rose above 1 Hz. The earlier decay may have been due to the fact that muscle shortening, not isometric force, was recorded. Only in the four slowest muscle units of our sample was attenuation found to occur between 0·5 and 1 Hz, as the result of a 'rate mismatch' (see below) occurring between the impulse encoders (motoneurones and models) and the rate-to-force relation of the muscle units.

Matching of motoneurone and muscle properties

Rate modulation is the physiological mechanism utilized by the nervous system to regulate force output of muscle units. In steady-state conditions, an increment of firing rate induces a proportional increase of force when it occurs within a defined range of firing rates ('regulatory range') covering the steep portion of the muscle rate-to-force relation. Since this steep portion has a different location in the various types of muscle units – it covers a narrow range between 8 and 20 Hz in slow muscle units and a wider range between 20 and 50 Hz in fast muscle units – matching of the muscle regulatory range with the range of motoneurone repetitive firing ('rate match', Kernell, 1990, 1992) is required. Such a match is granted because in each motor unit the motoneurone AHP has the same duration as the muscle-single twitch, so that the two values co-vary across the motor pool. By this correspondence, fusion of single twitches and force summation start at the minimal rate of motoneuronal repetitive firing.

The three motoneurones employed in sine-wave experiments had AHPs lasting 50–60 ms, suggesting that they were coupled '*in vivo*' with muscle units located at the upper border of the 'fast' type population (Eccles *et al.* 1958). Their sinusoidally modulated discharge was applied to a large sample of muscle units, whose speed of contraction covered almost the whole range of physiological values. Within this sample, the higher dynamic responsiveness, as quantified by the value of the cut-off frequency (F_{co}), was displayed by muscle units with short time-to-peak (TTP) and high half-tension rate (HTR): i.e. muscle units of the fast type. These findings, however, do not in themselves highlight the role of the neural dynamic sensitivity, but rather underline the relevance of certain muscle properties in determining the mechanical responsiveness to fast transients. As a matter of fact, when the same units were stimulated by the model, devoid of dynamic sensitivity, a similar correlation was found between the F_{co} and TTP. Similarly,

the F_{co} value was high, both under motoneurone and model drive, in those units where the single twitch delivered only a small fraction of the maximal tetanic tension, and low when the single twitch represented a large fraction of F_{max}. Since single twitch potentiation may increase this fractional value, on such occasions a concomitant reduction of the dynamic response has to be expected.

A direct clue to the relevance of motoneurone dynamic sensitivity in the development of muscle force is offered by the value of the F_{co} ratio, which expresses the increase of F_{co} that each muscle unit displayed when passing from the model to the motoneurone drive. This value shows a large variability within the sample but increases progressively and continuously when TTP diminishes or HTR rises. In contrast, F_{co} ratio did not show any significant correlation with the fractional value of the single twitch.

For each of the three 'fast' motoneurones employed here, sharing an AHP duration of 50–60 ms, the highest values of the F_{co} ratio, between 2 and 3, were found among the fastest muscle units, i.e. those characterized by TTP around 20 ms, HTR > 40 Hz and a twitch duration of 50–60 ms, which gave a correct rate match with the three motoneurones. When the latter cells were coupled with slow muscle units, the muscle dynamic response underwent an early cut-off and the benefit produced by the intervention of motoneurone dynamic properties was little or nil (F_{co} ratio close to, or lower than, unity). This inefficient coupling was apparently caused by the 'rate mismatch' occurring between the muscle unit 'regulatory range' (5–15 impulses s^{-1}) and the range of motoneurone and model firing (12 to 46 impulses s^{-1}). This high rate caused saturation of the tension response and the appearance of hysteresis (the force developed by a given impulse rate is larger when rate is decreasing than when it is increasing, Partridge, 1979, Partridge & Benton, 1981; Binder-Macleod & Clamann, 1989). Saturation and force persistence, despite the rate decrease, were responsible for the flat tension response of slow MUs at low modulation frequency and for the early attenuation of force modulation as soon as the modulation frequency was increased. The hysteresis that appears during time-varying rate stimulation of muscle seems therefore to signal the presence of a rate mismatch between the impulse generator and the mechanism of tetanic fusion, which interferes with the physiological use of muscle by depressing its response to transients.

A 'rate match' should be achieved in slow MUs when they are coupled with 'slow' motoneurones (AHP duration > 150 ms) whose primary range, starting at 5–6 impulses s^{-1}, covers the unit 'regulatory range'. In these conditions, motoneurone rate can be modulated without saturating the summation of force. In motoneurones of the 'slow' type, however, the primary range of firing extends well above the 'regulatory range' of the related muscle unit, implying that intense synaptic inputs may develop firing rates high enough to saturate the force production. This has been reported to occur during contractions evoked by electrical stimulation in

the brainstem (Tansey & Botterman, 1996; Tansey *et al.* 1996). The motoneurone discharge was recorded from single motor axons and used to re-stimulate the same axons in order to uncover the contribution of the related muscle unit to the generation of force. Under these conditions, in most of the early recruited units the firing rate was sufficiently high to develop tension levels close to maximum and to produce hysteretic loops.

It seems hard to decide how 'physiological' this way of activating motoneurones may be, also considering that, during voluntary contractions of increasing strength in man, the firing rate of motoneurones recruited first stops growing as force development proceeds (Monster & Chan, 1977; Monster, 1979; Bellemare *et al.* 1983). This difference, which may be due either to a distribution of the voluntary excitatory input to motoneurones different from that induced by the brain stem stimulation, or to inhibition of the early recruited motoneurones when the voluntary contraction proceeds, seems important because it avoids over-stimulation of the slow motor units and also avoids a prolonged persistence of muscle force when the neural drive declines.

With regard to those 'fast' muscle units where the F_{co} ratio was lower than 2, it remains to be seen whether such values reflect the real amount of neural pre-compensation or whether they result from a 'rate-mismatch' between the employed motoneurones and those units. An answer to this question may come from results of ramp experiments, in which the analysed muscle units all shared similar mechanical properties with the muscle unit innervated '*in vivo*' by the motoneurone. Within this homogeneous sample, the dynamic component of the motoneurone discharge produced a uniform improvement of the muscle response (S_{co} ratio, 2.73 ± 0.1). When, in sine-wave experiments, units with similar mechanical properties (TTP 25–30 ms, twitch duration 80–100 ms, HTR 25–30 Hz) were stimulated by any one of the three cells 1, 2 or 3, the F_{co} ratio fell to about 1.5. This lower value is possibly a consequence of the mismatch between the short-lasting AHP of motoneurones (50–60 ms) and the more prolonged duration (80–100 ms) of the muscle twitches.

It might therefore be suggested that, in the presence of the proper coupling between the motoneurone and the muscle unit, characterized by an equal duration of the AHP and the single twitch, the extent of the pre-compensation exerted by motoneurone dynamic sensitivity should indeed be represented by an increase of the cut-off frequency (or cut-off slope) by 2.5–3 times, independently of the unit's type.

In comparing responses to ramp and sine-wave experiments, it has to be considered that during ramp stimulation the initial response was measured, whereas during sinusoidal stimulation, force was estimated during cycles following the first one, and may therefore be influenced (see for instance Burke *et al.* 1976) by the past history of contraction. Finally, no apparent correlation was found between muscle resistance

to fatigue and the F_{co} ratio, except that implicit in the fact that slow units are fatigue resistant.

Phase relations

Phase measurements showed that motoneurone dynamic sensitivity not only reduced the frequency dependent attenuation of the muscular response but also shortened the temporal lag between the motor unit input, i.e. the synaptic currents acting on the motoneurone membrane, and the production of force. In motoneurones, the sinusoidally modulated firing rate leads the stimulating current (Baldissera *et al.* 1984*a*); conversely, muscle tension lags the sinusoidally modulated nerve discharges (Partridge, 1965, 1979). Thus, again, neural encoding tends to pre-compensate for muscle limitations. Comparison of the model with the motoneurone drive showed that, in the presence of a proper rate match between motoneurone and muscle unit, the muscle force lags motoneuronal input by only half of the delay which is introduced by the frequency response of the muscle. Translated into time, the phase lags found in model-driven MU of the fast type at 1, 5 and 10 Hz imply delays of 111, 50 and 37 ms, respectively, between the occurrence of a certain value of the stimulating current and the moment when the corresponding level of muscular force is reached. When the motoneurone drive was applied, the neurone dynamic sensitivity effectively shortened those delays to 56, 25 and 19 ms, respectively, in all cases including the axonal conduction time.

Similar estimates result from the response to ramp stimuli. When muscle units were motoneurone driven, the slope of tension rise in response to a given ramp slope was always higher than when they were model driven. This obviously means that a certain level of muscle tension is reached earlier in the first than in the second condition. The ratio between the maximal force slopes reached in the two

conditions had a mean value of $2 \cdot 22 \pm 0 \cdot 41$: thus, during the linear portion of the tension rise, the neuronal dynamic properties reduce by about one half the time lag introduced by the muscle.

Dynamic sensitivity and motoneurone central control

The utility of the motoneurone dynamic sensitivity in motor control can also be appreciated by briefly considering how the central drive to the final common path ought to be shaped if the same muscular performances obtained by spinal motoneurones were to be achieved through neurones lacking dynamic sensitivity, i.e. behaving like the model. In response to ramp-and-hold inputs, a linear transducer can be induced to develop the same pattern of discharge as motoneurones, and therefore the same tension time course in the muscle units, if it is stimulated with a current rising to an high intensity during the ramp period, and then suddenly decreasing to the steady-state value (dashed line in Fig. 12*A*). In real motoneurones, summation of the motoneuronal after-hyperpolarization automatically reduces the firing rate once the current has reached its steady value, thus relieving motor centres from the task of constructing such an input profile. The AHP summation process is also quite effective when repeated activation and releases are performed, as in response to a series of sine-wave or triangular stimuli. Due to its non-summated refractoriness, a linear converter receiving a triangular stimulus would also generate one or more impulses during the phase of current decay (Fig. 12 *B*, open circle). This (these) impulse(s) would prolong the force profile well beyond the command decay (Fig. 12*B*, dotted line, see Binder-Mcleod & Clamann, 1989) and strongly attenuate the amplitude of a successive contraction. Conversely, during the phase of the current decay, motoneurones stop firing (Fig. 12*B*, filled circles) because of the long-lasting refractoriness generated by AHP summation, a mechanism which also provides sensitivity to the negative slope of the

Figure 12. Different shapes of synaptic current necessary to evoke the same firing response in a real motoneurone and in a virtual neurone behaving like a linear converter

Schematic illustration of the different current shapes needed for evoking the illustrated firing responses (●) and the related force profiles when applied to a motoneurone (continuous lines) or to a virtual neurone lacking dynamic sensitivity (dashed lines). Responses to ramp-and-hold stimuli (*A*); responses to triangular currents (*B*). In *B*, the linear converter would generate an impulse pattern identical to that of the motoneurone only if the current is suddenly cut at the peak of the ramp (dashed line). If stimulated with the isosceles triangular current (continuous line), the converter would also generate an impulse during the current decay (O), which increases the force response, as depicted by the dotted trace, and strongly delays tension release.
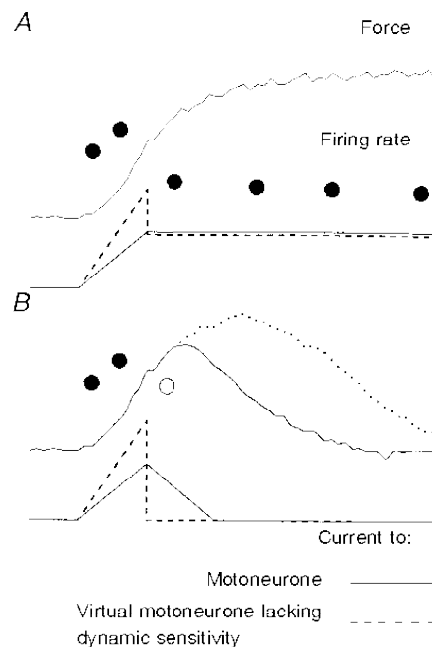
stimulus. In order to reproduce the motoneurone discharge and generate an impulse-free period for tension release, the current command to the linear converter should suddenly decrease after its peak, as indicated by the dashed line of Fig. 12*B*. In this way, the next contraction will be separated from the preceding one and can build up a large amount of force.

Thus, the membrane properties which provide motoneuronal sensitivity to input transients guarantee that the time course of the nervous command and that of the mechanical effect are similar even during fast and repeated contractions.

Functional implications

Thanks to the dynamic sensitivity of motoneurones, the fastest motor units of cat leg muscles may follow alternating activation up to 10–15 Hz; values like these have been described for fast ankle extensors (gastrocnemius) during paw shaking (Smiths *et al.* 1980). During physiological movement, however, other factors may intervene to limit the frequency response, like the neural organization which produces the instantaneous synaptic input to motoneurones and the mechanical characteristics of the moving segments. In man, one example of rapid alternating movement is represented by the musical figure known as trill ('a common and pleasing alternation of two neighbouring notes' as described on Leopold Mozart's 'Violinschule'). Trill is produced by alternately lifting and pressing a finger on a string or on the key of a wind instrument. Measurements obtained from commercial records indicate that its frequency may be as high as 8 Hz on the violin (Jascha Heifetz) and 6·5 Hz on the flute (Jean-Pierre Rampal, a lower value possibly due to interference of the key mechanics). Extrapolation of the findings described here to humans, whose muscle contraction tends to be slower than in cats, suggests that such musical performances would not be achieved if motoneurones were devoid of dynamic sensitivity.

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