Nonlinear Tension Summation of Different Combinations of Motor Units in the Anesthetized Cat Peroneus Longus Muscle

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Troiani, D., G. M. Filippi, and F. Andreasi Bassi. Nonlinear tension summation of different combinations of motor units in the anesthetized cat peroneus longus muscle. J. Neurophysiol. 81: 771–780, 1999. The purpose of this study was to examine the linearity of summation of the forces produced by the stimulation of different combinations of type identified motor units (MUs) in the cat peroneus longus muscle (PL) under isometric conditions. The muscle was fixed at its twitch optimal length, and the tension produced by the single MU was recorded during 24- and 72-Hz stimulation. The summation analysis was first carried out for MUs belonging to the same functional group, and then different combinations of fast fatigable (FF) MUs were added to the nonfatigable slow (S) and fatigue resistant (FR) group. The tension resulting from the combined stimulation of increasing numbers of MUs (measured tension) was evaluated and compared with the linearly predicted value, calculated by adding algebraically the tension produced by the individual MUs assembled in the combination (calculated tension). Tension summation displayed deviations from linearity. S and FR MUs mainly showed marked more than linear summation; FF MUs yielded either more or less than linear summation; and, when the FF units were recruited after the S and FR MUs, less than linear summation always occurred. The magnitude of the nonlinear summation appeared stimulus frequency dependent for the fatigable FF and FI group. The relationship between measured tension and calculated tension for each MU combination was examined, and linear regression lines were fitted to each set of data. The high correlation coefficients and the different slope values for the different MU-type combinations suggested that the nonlinear summation was MU-type specific. The mechanisms of nonlinear summations are discussed by considering the consequences of internal shortening and thus the mechanical interactions among MUs and shifts in muscle fiber length to a more or less advantageous portion of single MU length-tension curves.

INTRODUCTION

Assuming that activation of single motor units (MUs) always produces the same tension value and that each MU acts independently, a linear tension summation can be expected. However, the hypothesis of independence of MU activity can be questioned by the arrangement of the MU fibers within the muscle body (fibers belonging to different MUs are usually intermingled; Ariano et al. 1973; Donselaar et al. 1987; Emonet-Dénand et al. 1990; Kernell et al. 1983) by the presence of the viscoelastic matrix among muscle fibers (Demiéville and Partridge 1980) and finally by muscle tendon compliance (Griffiths 1991; Prosk and Morgan 1984; Rack and Westbury 1984; Zajac 1989). On these grounds, mechanical interactions can be expected, and the activity of a given MU may alter the mechanical conditions under which other MUs operate, thereby altering their response. In fact, various authors reported nonlinear summation of MU forces under isometric conditions (Claman and Schelhorn 1988; Emonet-Dénand et al. 1987, 1990; Lewis et al. 1972; Powers and Binder 1991). The results are contradictory, with more or less than linear summation, largely varying in magnitude, described even in the same muscle. The relevance of nonlinear tension summation is also controversial. It was suggested (Powers and Binder 1991) that deviations from linearity are absent during voluntary movements and that more or less than linear summation of MU forces may be observed only in muscles contracting isometrically. It can be argued that the generation of isometric force, which is the most commonly studied form of contraction, is of considerable importance for stabilizing joint complexes during locomotion and for maintaining posture (Sargeant and Jones 1995). In addition, many common voluntary movements against a load are performed under an isometric initial holding phase followed by a movement phase. Generally, progressive recruitment of new MUs according to Henneman’s rank order principle (Henneman and Mendell 1981; Henneman et al. 1965) and/or by increasing the motoneurone firing rate (Burke 1981) are used to optimize the desired force output (Kernell 1992).

This study was undertaken to analyze in peroneus longus muscle (PL) the isometric tension summation when an increasing number of MUs are recruited according to the following sequence: slow (S), fatigue resistant (FR), fast intermediate (FI), and finally fast fatiguable (FF) MUs (Burke et al. 1973; Zajac and Faden 1985). In our experiments increasing groups of S and then FR MUs were summed. Then FF unit contraction was superimposed on their background activity. Our results illustrate nonlinear tension summation in all the different combinations of type-identified MUs and suggest that the different magnitudes and signs of deviations from linearity can be attributed to MU type and to a lateral dispersion of energy (Emonet-Dénand et al. 1990; Powers and Binder 1991). Specifically, the different MU types have different length-tension curves (Filippi and Troiani 1992, 1994), and because of internal shortening muscle fiber lengths may be shifted to a more or less advantageous portion of their length-tension curves, thus producing different nonlinear summations. The simultaneous stimulation of groups of MUs may induce a relief of internal friction and produce nonlinear tension summation that may vary in function of muscle length and activation frequency.
Methods

General experimental procedures

Experiments were performed on adult cats of either sex weighing between 2.5 and 3.5 kg. All procedures for animal care and use were approved by the local ethics committee and were in accord with the principles of the Italian Physiological Society and the Society for Neuroscience. Initial anesthesia was induced by pentobarbital sodium (40–50 mg/kg ip), and intravenous maintenance doses were given during the course of the experiment to insure a deep level of anesthesia (constricted pupils, lack of corneal and pinna reflexes, absence of withdrawal reflexes to strong toe pinch, etc.). A tracheal cannula and intravenous and intraarterial catheters were inserted. Blood pressure (via carotid cannula) and rectal and muscle temperatures were monitored and maintained at ~80–140 mmHg and 37°C, respectively. Artificial ventilation was used, if required. The surgical procedures were described in detail in a previous work (Filippi and Troiani 1994). Briefly, a lumbosacral laminectomy was performed to expose the spinal cord from segment L4 to S2, and a paraffin oil filled pool was made by elevating skin flaps. The right hindlimb was fixed in a long-lasting stimulation (72 Hz for 2.5 s) of combinations of S + FR MUs. All tests were performed at the muscle twitch optimal length L0 (Petit et al. 1990), which corresponded to an ankle angle of 130° (Filippi and Troiani 1994). The control tension value of each MU was evaluated first, and then the developed tension of MU groups was calculated and individual MU responses were controlled again. Muscle tension was sampled at a rate of 10 kHz and stored and analyzed by an integrated hardware and software package (ISC-16 A/D card, Computerscope EGAA System R. C. Electronics USA). The contraction magnitude of each MU or MU combination was calculated by computing the active tension-time area. The tension produced by the MUs stimulated in combination was denominated “measured tension time,” and the algebraic sum of the tensions of the individual units (predicted sum of the combined MU responses) was named “calculated tension.” The magnitude of the nonlinear summation was expressed both as the difference between the measured and the calculated tension and as the percentage difference between the measured and the calculated tension [(measured − calculated) × 100/calculated]. The measured tension was further evaluated as a function of the calculated tension by means of linear regression analysis. Significance level was set to α = 0.05.

Results

Description of sample and of MU combinations

In 6 experiments, a total of 68 PL MUs were isolated; however, results were obtained from the complete analysis of 41 MUs that were functionally identified as 21 S, 12 FR, and 8 FF in the preliminary categorization always performed at the beginning of each experiment (Filippi and Troiani 1992, 1994). On completion of the experiment, the initial classification was confirmed by Burke’s fatigue test, and two of eight MUs belonging to the FF group were found to be FI type.

A total of 124 summation tests were performed on the 41 MUs grouped in various combinations on which the different stimulation patterns were applied. A consistent finding was that MU forces added nonlinearly (either more or less than linearly) and that in most combinations (64%) the combined force was greater (more than linear summation) than the algebraic sum of the forces of the separate units assembled in the combination. Specifically, as shown in Table 1, of 44 S combinations tested at 72 Hz, the majority (33 against 11) summed more than linearly; similarly, all 7 FR and 20 S + FR MU combinations produced more than linear summation. The 40 FF groups added both more than linearly (10 at 24 Hz and 10 at 72 Hz) and less than linearly (19 combinations). Only the S + FF combinations always added less than linearly (7 at 24 Hz and 7 at 72 Hz).
nonlinear summations of MU tension areas. For 80 MU combinations (64% of the total), a mean increase of $+30.6 \pm 16.5\%$ (range from 0 to 80% of the calculated value was found, and for the remaining 44 combinations (36% of the total), a mean decrease of $-34.4 \pm 28.4\%$ (range from 0 to $-100\%$) of the calculated value was obtained. The degree of nonlinear summation for both more and less than linear summations varied widely, and, as shown in the bar graph of Fig. 1A, the distribution of the more than linear summation was not uniform, most combinations being segregated in a bin centred at $\sim 30\%$ (bin value having mean increase of $22 \pm 8.7\%$). A greater dispersion of the degree of summation in the combinations producing less than linear summation was observed (range from 0 to $-100\%$). By analyzing the ratio between measured tension and calculated tension of all tested MU combinations (plot in Fig. 1B) a highly significant linear correlation was observed ($r^2 = 0.91, n = 124, P < 0.001; m = 1.07 \pm 0.02$). Interestingly, the two groups of combinations with opposing responses had equivalent ranges of tension values both regarding calculated (0–120 g $\times$ s) and measured tension data (0–130 g $\times$ s).

Distribution of summation according to MU functional categorization

The analysis of the degree and distribution of MU nonlinear summations is illustrated in the bar graphs of Fig. 2, where the tested combinations are pooled according to MU functional categorization.

The summation of S and FR MUs and of S + FR MUs (i.e., of MUs resistant to fatigue) was mainly more than linear. The majority (Fig. 2A) of tested S MU combinations (75%) added more than linearly, with a mean value of $32.2 \pm 15.6\%$. Less than linear summation occurred (mean decrease: $-21.8 \pm 16.7\%$) only in the remaining 25% of S MU tests (Fig. 2F). FR MUs (Fig. 2B), stimulated with pattern 1, showed more than linear summation; the mean increase was of $24.4\%$, with a comparatively small variation of $\pm5\%$; less than linear summation was never detected. FF MUs summed either less than linearly or more than linearly. Stimulation pattern 2 was applied to this population (which also included the FI units) to evaluate, by using 24-Hz stimuli, the summation response at a frequency considered within a physiological range for this group and by applying 72-Hz stimulation to test a homogeneous frequency in the S and FR groups. In neither condition was the summation uniform; however, the magnitude of summation was related to the frequency of stimulation applied. At 24 Hz (Fig. 2D) 50% of tested FF units showed an increase of $51.7 \pm 12\%$, whereas the remaining 50% (Fig. 2G) had a decrease of $-63.1 \pm 7\%$. At 72 Hz the magnitude of effects was less important, the increase (Fig. 2E) reaching $11.6 \pm 5\%$ in 48% of tested combinations and the decrease (Fig. 2H) amounting to $-11.7 \pm 4\%$ in 52% of trials.

Summation among MUs belonging to different functional groups was analyzed applying recruitment according to the size principle. The FR MUs were added to the S units (Fig. 2C), and in all 20 combinations studied more than linear summation (29 ± 13\%) was always observed. On the contrary, when the contractions of the larger FF MUs were superimposed on the preexisting tensions of the smaller MUs (S and FR), less than linear summations were always recorded (Fig. 2I and J). All the FR units were grouped with the S MUs and stimulated at 72 Hz for 2.5 s (stimulation pattern 3), and then sequential addition of FF and FI units was superimposed (latency 1.5 s, frequency 24 and 72 Hz, train duration 0.5 s). The superimposed...
FIG. 2.  Bar graphs showing the percent nonlinear summation for all slow (S) (bar plots A and F), fatigue resistant (FR) (B), fast fatigable (FF) (D, E, G, and H), S + FR (C), and R* + FF (I and J) MU combinations; R* includes S + FR MUs. The degree and sign of deviation from linearity and the stimulation frequency applied are illustrated for each MU type combination.
FIG. 3. Examples of more than linear and less than linear summations among type identified MUs. Original recordings are shown on the left and middle side of figure; bar plots of effects on the right. Ordinate, percent of summation; abscissae, MU combinations. A: 4 S MUs are combined according to increasing force pattern and stimulated at 72 Hz. B: 3 FR MUs are added according to decreasing strength protocol and stimulated at 72 Hz. C and D: 2 FF and 1 FI MUs are assembled according to filament isolation sequence and stimulated at 24 and 72 Hz.
sition of FF MU stimulation on the preexisting nonfatigable MU (S and FR) contraction (developing a tension-time area ranging between 40 and 100 g s) always induced less than linear summation of the fatigable MUs (mean decrease at 24 Hz: −44.8 ± 33%; mean decrease at 72 Hz: −32 ± 39%).

In sum, the magnitude of more than linear summation was greatest for the combinations of S, FR, and S + FR MUs at 72 Hz (Fig. 2, A–C) and of FF MUs at 24-Hz stimulation frequency (Fig. 2D). Regarding the degree of less than linear summation it was high and uniformly distributed only among the 10 FF MU combinations stimulated at 24 Hz (Fig. 2G); otherwise, it was modest (Fig. 2H) and/or variable (Fig. 2, F, I, and J).

Typical tension summations produced by combined stimulation of nonfatigable MUs and of fatigable MUs are illustrated in Fig. 3.

Four S MUs are assembled according to an increasing strength criterion in Fig. 3A; the single MU tensions (Fig. 3A, left) are aligned to allow immediate evaluation of their algebraic summation amplitude, whereas the three superimposed traces (middle trace) were obtained by stimulating the same MUs in different combinations. In spite of the different tension value for each MU, the magnitude of more than linear summation was similar in all combinations (histogram of Fig. 3A, right), amounting to 56% for combination S1 + S2, to 58.8% for combination S1 + S2 + S4, and to 44% for combination S1 + S2 + S4 + S6.

A typical example of FR unit combinations is shown in Fig. 3B, where more than linear summation, reaching a value of 28% in combination FR1 + FR3 + FR7, is illustrated (Fig. 3B, right).

The tension summation produced by combined stimulation of fatigable MUs at different frequencies is shown in Fig. 3, C and D. Important less than linear summation is shown in the example of Fig. 3C, whereas a modest more than linear summation can be seen after 72-Hz stimulation (Fig. 3D).

Subtetanic, unfused contractions are associated to evident less than linear summations (Fig. 3C), whereas more than linear summations (plots in Fig. 3, A and B) and nearly linear summations (Fig. 3D) are shown for MU combinations with almost complete fusion and relatively less complete fusion, respectively.

The magnitude of tension summation produced by combined stimulation of nonfatigable (S + FR MUs) with fatigable MUs (FF and FI) is shown in Fig. 4. Stimulation pattern 3 was applied, and less than linear summation always occurred. The test was carried out in two steps, 1) the control tension of an increasing number of FF MU combinations was determined by stimulating at 24 and 72 Hz and 2) a test combination of S + FR (usually 5–10 units) was stimulated at 72 Hz, and with a delay of 1.5 s the stimulation of the FF combinations previously tested was added. According to this pattern of stimulation (pattern 3, see Methods), the FF stimulation started with a delay of 1.5 s, and it was interrupted 0.5 s after the onset and before the end of S + FR stimulation, respectively.

In Fig. 4 the previously reported paradigm was followed, and the baseline of the thick trace represents the tetanic plateau of S + FR contraction, whereas the thin trace baseline is the

![FIG. 4. Tension summation between FR and FF MUs evaluated by applying stimulation pattern 3. The control tension of an increasing number of FF MUs was evaluated by 24-Hz stimulation (thin trace). Then the same combinations were stimulated (thick trace) with a delay of 1.5 s and duration of 0.5 s on the background tension (tension time-area: 114 g s, not shown) produced by S + FR MU 72-Hz stimulation. In each combination the baseline of the passive muscle tension (thin trace) is arbitrarily aligned for evaluation with the baseline of the S + FR MUs background force (thick trace). The original recording for each test is associated to the right with a bar plot, which illustrates the magnitude of less than linear summation. From A to D: 1–4 FF MUs are added progressively according to an increasing strength criterion.](http://jn.physiology.org/content/3/5/776/F4)

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passive muscle tension. The two baselines are arbitrarily superimposed to allow a better comparison between the FF tension value in the two conditions. The magnitude of the tension developed by the long-lasting stimulus (involving the nonfatigable MUs) was not influenced by the superimposition of the second stimulus (applied to the fatigable group), and the same level of tension (114 g \times s) was recorded both before and after the short train. The decrease of tension for the FF group ranged from 13 to 93%; in the example of Fig. 4 it was of 38–61%. In this case, as shown in Fig. 4, B–D, the magnitude of less than linear summation is not related to the amplitude of tension oscillations. The independence of the magnitude and sign of summations on the degree of fusion are also illustrated in the cumulative bar graphs reported in Fig. 2 in which less than linear summations are reported for relatively fused contractions (slow units, Fig. 2F), whereas more than linear effects are reported for FF MU combinations stimulated at low frequency (Fig. 2D).

**TABLE 2. Linear regression analysis**

<table>
<thead>
<tr>
<th>MU type</th>
<th>S</th>
<th>FR</th>
<th>S + FR</th>
<th>FF 24 Hz</th>
<th>FF 72 Hz</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slope, m</td>
<td>1.28</td>
<td>1.24</td>
<td>1.31</td>
<td>1.46</td>
<td>1.13</td>
<td>1.24</td>
</tr>
<tr>
<td>SD</td>
<td>0.02</td>
<td>0.01</td>
<td>0.03</td>
<td>0.03</td>
<td>0.02</td>
<td>0.02</td>
</tr>
<tr>
<td>$r^2$</td>
<td>0.99</td>
<td>0.99</td>
<td>0.98</td>
<td>0.96</td>
<td>0.99</td>
<td>0.98</td>
</tr>
<tr>
<td>$n$</td>
<td>33</td>
<td>7</td>
<td>20</td>
<td>10</td>
<td>10</td>
<td>80</td>
</tr>
<tr>
<td>$P$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
<td>$&lt;0.001$</td>
</tr>
</tbody>
</table>

**More Than Linear Summation**

**Less Than Linear Summation**

Regarding the more than linear summation, it is shown that the slope ($m$) values of the FR groups (Fig. 5A) are clearly different from those of the FF groups (Fig. 5B), and the stimulation frequency influences differently the FF MU more than linear summation. In fact, the slopes of FF MU combinations have a smaller value at 72 Hz and a larger one after the more physiological 24-Hz stimuli. Regarding the less than linear summations (Fig. 5, C and D), the slope values confirmed the discrepancies between S and FF combinations and the difference between the effects of 24- and 72-Hz stimulation for the FF group. However the slopes of the FF group superimposed on the background activity of S + FR MUs (Fig. 5D) show similar values both after 24 and 72 Hz, indicating a possible interaction of background muscle force on the tested units.

The linear trend obtained with data collected from different experiments underlines the reproducibility of effect that is not undermined by biological variability. The magnitude of contribution to the nonlinear summation effect appears constant. In fact the percent contribution to the effect by each MU assembled in the combination remains the same, and it is linked neither to the number of MUs assembled nor to the actual tension value of each MU present in the combination.

**DISCUSSION**

This study examined force summation among different MUs during progressive recruitment of new MUs based on the MU’s functional classification and/or MU firing rate modulation in the cat PL muscle (Burke 1981). Physiological conditions were partially approximated; PL was fixed at its operational length L0 (Filippi and Troiani 1994), single MUs were functionally identified, and then, mimicking recruitment (Henneman and Mendell 1981; Henneman et al. 1965), they were combined according to MU type and tension value. The experiments were...
confined to isometric conditions, one fixed muscle length and to two stimulation frequencies. PL was fixed at the whole muscle twitch optimal length, which corresponded to an ankle angle of 130°. Two test stimulation frequencies were chosen, that is, a standard tetanic frequency (72 Hz) for the nonfatigable MUs and, alternatively, a subtetanic (72 Hz) and a physiological range (24 Hz) stimulation for the fatigable units (Bigland and Lippold 1954; Edstro¨m and Grimby 1986; Thomas 1995).

The main findings of this study were deviations from linearity in force summation both among MUs belonging to the same functional category and among MUs combined according to the size principle recruitment order. Specifically, our results showed important more than linear summation for 75% of S MU combinations and for 50% of FF MU groups and less pronounced increments for all (100%) of the FR group. Less than linear summation was observed in 25% of S units and in the remaining 50% of the FF group. In all (100%) 20 combinations in which the FR units were added to the contraction of S MUs, more than linear summation was constantly observed; on the contrary, less than linear summation always occurred when FF and FI activity was superimposed on a background S + FR MU tension (combinations tested by stimulation pattern 3). The findings generally agree with those of previous studies (Claman and Schelhorn 1988; Demiéville and Partridge 1980; Emonet-Dénand et al. 1987, 1990; Powers and Binder 1991), which demonstrated that the tension produced by simultaneously active MUs does not equal the linear sum of the tensions produced by the individual units. However, our findings indicate a certain degree of MU-type specificity to the

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**FIG. 5.** Relationship between measured and calculated tension among all the tested MU combinations grouped according to their functional categorization, sign of nonlinear summation, and stimulation frequency. Linear regression lines are fitted to each set of data points collected from all the experiments. A and B: more than linear summations. C and D: less than linear summations. Symbols designate MU type combinations. A: filled squares and dotted line, type S; open squares and solid line, type FR. B: open down triangles and solid line, type S + FR; open circles and dotted line, type FF 24 Hz; filled circles and dash line, type FF 72 Hz. C: open circles and dotted line, type FF 24 Hz; filled circles and dash line, type FF 72 Hz; filled squares and solid line, type S. D: filled up triangles and dotted line, type (S + FR) + FF 24 Hz; open up triangles and dash line, type (S + FR) + FF 72 Hz. Equation, correlation coefficient, and significativity are reported in Table 2.
nonlinearity of summation. In fact our results permit distin-
guishing between the nonlinearities of summation (mainly
more than linear) of FR MU combinations and those of the
fatigable MUs (strongly more or less than linear especially
after the more physiological 24-Hz stimulation). In addition,
force decrease was constantly observed when the recruitment
was applied between nonfatigable and fatigable MUs. Appar-
ently, mechanical advantages can be obtained when the non-
fatigable MUs are progressively recruited or coactivated,
whereas negative deviations from linearity are present when
the fatigable MU groups are progressively recruited after the
smaller and FR MU population. Certainly these data, observed
under strict isometric conditions, need to be extended to dy-
namic conditions to confirm whether they hold true for a wide
variety of natural movements. However a prediction of this
work is that in the isometric initial and final part of movements
the motor system when graduating the muscle force by MU
recruitment and derecruitment and by MU firing modulation
has to take into account among other constraints (i.e., muscle
length and muscle-tendon compliances) the existence of non-
linear MU tension summation.

The experimental protocol of this work was not devised to
clarify the mechanisms by which the forces of MUs activated
simultaneously add nonlinearly; however, some considerations
can be advanced. In agreement with other authors (Emonet-
Dénand et al. 1990; Powers and Binder 1991) the nonlinear
summation of MU forces can be explained by mechanisms
involving the lateral interactions among adjacent active and
inactive fibers (Demiéville and Partridge 1980), changes of
muscle length (Hill 1953), and the relation between force and
velocity of shortening (Katz 1939). It can be suggested that
the common basis of these possible and complementary mecha-
nisms is represented by the presence of a muscle fiber short-
ening inside the muscle also in isometric conditions (De-
mieville and Partridge 1980; Griffiths 1991; Hill 1953; Joyce
et al. 1969; Rack and Westbury 1969; Scott et al. 1992). Such an
internal muscle shortening can be due to different factors, 1)
the extramuscular tendon compliance, which is high at low
applied forces and low when high forces are developed (Prosko
and Morgan 1984; Zajac 1989), and 2) the high compliance of
the intramuscular tendon portion (Rack and Westbury 1984;
Zajac 1989), which is very long in PL. It is conceivable that
the relative motion among adjacent active and passive fibers can
produce mechanical interactions through the connective link-
age and thus lateral dispersion of energy (Emonet-Dénand
et al. 1990). This effect is likely present in PL because different-
size fibers (i.e., fibers belonging to different MUs) are usually
intermingled and asymmetrically distributed (Ariano et al.
1973; Donselaar et al. 1987; Emonet-Dénand et al. 1988;
Kernell et al. 1983). It could be predicted that, when the force
production is increased by enhancing the number of the re-
cruited MUs, the internal fiber shortening caused by the tendon
stretching increases and the relative movement decreases be-
cause more adjacent fibers are active. This last condition
should lead to a decrease of the lateral dispersion of energy.
The resulting effects would be only more than linear summa-
tion for increasing MU combinations (Powers and Binder

Even if the lateral dispersion of energy can provoke only
more than linear summation at increasing numbers of stimu-
lated MUs, our data show both less and more than linear
summation. It follows that at least some other mechanisms
must be invoked to explain the results. The inverse relation
between force and velocity should lead to less than linear
tension summation particularly pronounced in conditions of
subfused tetani when the internal movement is probably larger
(see Fig. 3). In fact the decrease of isometric tension could be
due at least partly to a dispersion of energy produced by the
internal motion (Joyce et al. 1969; Rack and Westbury 1969).
However our results do not always speak in favor of this
interpretation because less than linear summation was also
observed for MU combinations showing relatively complete
fusion (Fig. 2F), and more than linear summation was evi-
denced for FF MU combinations with unfused contractions
(see Fig. 2D). On the other hand, internal movement can change
the fixed muscle length (the whole muscle optimal length L0)
and can generate both more and less than linear summation by moving the fixed muscle length along the ascen-
ding or the descending limb of the MU length-tension curve.
In a previous paper (Filippi and Troiani 1994) different
tetanic optimal lengths for single MUs were reported. In par-
ticular, the internal movement can move the operational point
of the single MUs along their length-tension curves, producing
more than linear (the operational point ascends the descend-


REFERENCES


