Nonlinear summation of force in cat tibialis anterior: a muscle with intrafascicularly terminating fibers

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Sandercock, Thomas G. Nonlinear summation of force in cat tibialis anterior: a muscle with intrafascicularly terminating fibers. J Appl Physiol 94: 1955–1963, 2003. First published January 10, 2003; 10.1152/japplphysiol.00718.2001.—The complex connective tissue structure of muscle and tendon suggests that forces from two parts of a muscle may not summate linearly, particularly in muscles with intrafascicularly terminating fibers, such as cat tibialis anterior (TA). In four anesthetized cats, the TA was attached to a servomechanism to control muscle length and record force. The ventral roots were divided into two bundles, each innervating about half the TA, so the two parts could be stimulated alone or together. Nonlinear summation of force (Fnl) was measured during isometric contractions. Fnl was small and negative, indicating less than linear summation of the parts, which is consistent with the predicted Fnl of muscle fibers connected in series. Fnl was more significant when smaller parts of the muscle were tested (21.8 vs. 8% for whole muscle). These data were fit to a model where both parts of the muscle were assumed to stretch a common elasticity. Compensatory movements of the servomechanism showed the common elasticity is very stiff, and the model cannot account for Fnl in cat TA.

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The purpose of this study was to 1) measure $F_{nl}$ in cat TA; 2) test the hypothesis that in cat TA the degree of $F_{nl}$ between two parts of the muscle can be accounted for by a simple common elasticity model; and 3) test the hypothesis that the intrafascicularly terminating fibers in cat TA will produce less than linear summation due to force transmission in series. Essentially, the study in cat Sol (20) was repeated in TA (a muscle with fibers that do not run the length of the muscle). The results showed that $F_{nl}$ in TA was quite small. However, unlike cat Sol, the nonlinearity is not accounted for by a stretch of a common elasticity. The less-than-linear summation may be explained by fibers effectively connected in series.

**METHODS**

The methods have recently been described in detail (20) and will be summarized here. The data were obtained from four cats (male and female). All surgical and experimental procedures conformed with the policies of Northwestern University and the National Institutes of Health. The cats were anesthetized with isoflurane during the surgical procedures and switched to pentobarbital sodium (intravenous) for data collection. The left hind legs were partially denervated and mounted in rigid frame. The nerve and blood supply to the TA was preserved. The complete TA tendon was freed. At its insertion on the medial side of the foot, three muscles were removed by using a dental drill. The bone chip was attached to a servomechanism (custom device with a compliance of 0.01 mm/N) that allowed the TA to be moved by computer while muscle force was simultaneously measured. The ventral roots were exposed via laminectomy and divided into two bundles. Each part innervated roughly half of the TA. They were placed on separate hook electrodes so that each part could be stimulated independently. The muscle force and length signals were generally sampled at 1 kHz. Passive tension was always measured and subtracted from active tension. $L_o$ is defined in this paper as the length where $P_o$ occurs during stimulation at 100 Hz.

$F_{nl}$ is defined as

$$F_{nl}(t) = F_{nh}(t) - F_h(t) - F_h(t)$$  \[1\]

where $F_{nh}$ is the force when both parts are stimulated together, $F_h$ is the force when part A is stimulated, $F_h$ is the force when part B is stimulated, and $t$ is time. $F_{nl}$ was measured under two experimental conditions: 1) isometric contractions with equal duration tetany to both parts of the muscle and 2) isometric contractions with unequal duration tetany simulating recruitment of new motor units to an already partially active muscle. These conditions were shown to produce the largest nonlinearities in cat Sol (20). Similar experiments were performed to estimate the common elasticity by using quick stretches to measure stiffness. All experiments share a common protocol. First, the whole muscle was stimulated by activating the ventral roots for parts A and B simultaneously. Then, then the ventral roots for part A and part B were stimulated individually, and muscle force measured. Because fatigue is a problem in TA, whole muscle force was measured again, allowing fatigue to be monitored. Fatigue was partially compensated for by averaging whole muscle force before and after stimulation of the individual parts. The length of the muscle-tendon complex was the same in each of the four trials.

In three experiments, $F_{nl}$ was measured between large and small parts of the muscle. These measurements were performed to simulate the recruitment of a large motor unit to an already active muscle. The large part had a force of approximately half the muscle. The ventral roots were sub-

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*Fig. 1. Muscle and tendon models. A: detailed model with elastic links between fibers and tendons. B: simplified model of the common elasticity. Part A and part B refer to the muscle fibers in groups A and B, respectively. The elasticity of part A is attributed to the cross bridges within the muscle fibers, as well as elastic links within the fibers and between fibers and tendon, that act independently from part B. Common elasticity $K$, any elastic component that is stretched by both the fibers in part A and part B.*

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$F_{nl}$ may be more important in cat TA and other muscles with serial fibers. In vivo, if two isolated muscle fibers are connected in series, the steady-state force from the two fibers will be the same as the force from a single fiber (when length-tension effects are ignored). In muscles with intrafascicular terminations, force transmission is not fully understood. However, if some of the force is transmitted serially, analogous to the two-fiber example above, the serial fibers will contribute less to total muscle force than the linear sum. Glycogen depletion studies have shown that intrafascicularly terminating fibers are not connected to fibers within the same motor unit. Thus, when additional motor units are activated, some of the fibers will be in series with already active units and less than linear summation may occur. Sheard et al. (21) have examined motor units in guinea pig sternomastoid and shown, on average, the opposite effect: greater than linear summation of force between motor units. However, when only two motor units are active, the random distribution of the fibers makes the probability of two active fibers in series relatively small, possibly underplaying $F_{nl}$ due to fibers in series. For this reason, summation of force needs to be studied with a larger portion of the muscle active.
divided so that the small piece produced a force from 2.0 to 0.7 N.

To determine whether the common-elastic lumped parameter model of Fig. 1B provided a reasonable account of the data, the puller was used to mimic stretch of the common elasticity. The common elasticity was assumed to be a linear element. When both halves of the muscle are active, the common elasticity will stretch by a distance \( L_{ab}(t) \) proportional to \( F_{ab} \)

\[
L_{ab}(t) = \frac{F_{ab}(t)}{K}
\]

where \( K \) is the stiffness of the common elasticity. When part A is stimulated alone, the muscle fibers will not shorten as much because now the common elasticity will only be stretched by the force from part A

\[
L_A(t) = \frac{F_A(t)}{K}
\]

Thus, for the muscle fibers of part A to shorten by the same amount when part A is stimulated alone, compared with when both parts of the muscle are active, the servomechanism needs to move by the difference between \( L_{ab}(t) \) and \( L_A(t) \). This movement can be approximated by

\[
L_A(t) = \frac{F_A(t)}{K}
\]

The force waveform measured during activation of part B was divided by the estimated stiffness of the common elasticity. The resulting waveform is an approximation of the elastic stretch attributed to part B. It was used to drive the puller during activation of part A, and the resulting force is referred to as \( F_{AM} \). Conversely, the force from part A was used to estimate the tendon stretch and drive the puller during activation of part B. The resulting force is referred to as \( F_{BM} \). These new waveforms can be used to determine the nonlinearity that would result from a linear common elastic element of magnitude of \( K \)

\[
F_{nl\text{model}}(t) = F_{ab}(t) + F_{AM}(t) - F_A(t) - F_B(t)
\]

where \( F_{nl\text{model}} \) is the \( F_{nl} \) of this model. In a previous paper (20), \( F_{AM} \) and \( F_{BM} \) were subtracted from \( F_{ab} \). That method worked well in cat Sol where, with the proper selection of \( K \), the resulting waveform approached zero, indicating that the model fit the data. That did not happen in TA with any value for \( K \). The waveform described by Eq. 5 is easier to interpret.

Quick stretches (0.5 mm in 5 ms) were used to measure muscle stiffness. Within this distance and time, the muscle acts as a linear spring, so the change in the force waveform is equal to the change in the length waveform multiplied by the stiffness (12). A computer program calculated the stiffness that minimized the difference between the force and scaled length waveforms for the 5 ms period after the initiation of the stretch. This procedure provided a more accurate estimate of stiffness than that obtained by using a single point measured 5 ms after stretch initiation. The three-element model in Fig. 1B, coupled with the experimental stiffness measurements, can be used to determine \( K \). An algebraic solution was obtained by assuming the common elasticity was linear over the range of forces measured (\( F_A \) to \( F_{ab} \))

\[
K = \frac{-s_A s_B - \sqrt{(s_A s_B)^2 + (s_{AB} - s_A - s_B) s_{AB} s_B}}{s_{AB} - s_A - s_B}
\]

where \( s_{AB}, s_A, \) and \( s_B \) are the experimentally measured stiffness of the muscle when parts AB, A, and B are respectively stimulated with the same stimulus train.

RESULTS

Stimulation with unequal length tetany. Stimulation with unequal length tetany is analogous to the recruitment of a very large motor unit in a partially active muscle. Typical results are shown in Fig. 2. First, consider the waveforms on the left side of Fig. 2. They...
show the experimental determination of \( F_{nl} \). The top panel shows the force when parts A, B, and AB were stimulated together. Part A was stimulated with a 100-Hz train beginning at 0.15 s and ending at 0.8 s. Part B was stimulated with a 100-Hz train beginning at 0.3 s and ending at 0.5 s. In this example, part B is about twice as large as part A. The middle panel shows \( F_{nl} \) as calculated by Eq. 1. Note that \( F_{nl} \) is fairly small. During the plateau (from 350 to 500 ms), \( F_{nl} \) is negative, indicating less-than-linear summation. \( F_{nl} \) is largest during the relaxation of part B, where it reaches +2.2 N (6.4% of \( P_o \)). This shape was typical of all four experiments.

The right side of Fig. 2 depicts the experimental determination of \( F_{nl} \) (Eq. 5). The model in Fig. 1B was assumed to be correct, and the puller was used to reproduce estimated stretch of the common elasticity. A value of \( K = 20 \) N/mm was used in Eqs. 3 and 4 to calculate the puller movements (see the bottom right panel of Fig. 2). Note that \( F_{nl} \) model is substantially different than \( F_{nl} \). It shows an initial negative spike, and the plateau region is much smaller. The results using \( K = 20 \) N/mm are shown because they provide the best match between \( F_{nl} \) model and \( F_{nl} \).

Figure 3 shows the results from another experiment using three different values for \( K \). \( F_{nl} \) model was calculated by using \( K = 10, 20 \), and 40 N/mm. The experimental protocol was the same as shown in Fig. 2 except the stimulus trains were longer. Here, part A was stimulated from 200 to 500 ms at 100 Hz, and part B was stimulated from 200 to 500 ms at 100 Hz. No values of \( K \) produce a \( F_{nl} \) model that accurately matches \( F_{nl} \). As \( K \) became more compliant, the initial negative spike and terminal positive spike of \( F_{nl} \) model became larger, but the overall shape is a poor fit.

Similar results were seen in all four experiments that used the unequal length isometric tetany. \( F_{nl} \) was never large, its maximum amplitude ranged from 5.1 to 6.8% of \( P_o \) (Table 1). All showed a negative plateau region in \( F_{nl} \) that was not matched by \( F_{nl} \) model. The size of the plateau ranged from about −1 to −2 N. The positive peak in \( F_{nl} \), resulting from the relaxation of part B, was seen in all four experiments but varied widely in both amplitude and duration. In two experiments, \( F_{nl} \) was best matched by \( F_{nl} \) model using \( K = 20 \) N/mm and in two others by \( K = 40 \) N/mm.

**Stimulation with equal length tetany: length-tension curves.** Next the protocol was altered so both parts of the muscle were stimulated with equal length tetany. Equal length tetany allows the construction of length-tension curves during partial and whole muscle stimulation. Figure 4 shows a typical example. Stimulation to both parts was applied from 0.4 to 0.6 s at 100 Hz while the muscle was held isometrically at \( L_o \). \( F_{nl} \) is initially negative when both parts are active and then becomes positive during relaxation. \( F_{nl} \) model was measured by using \( K = 20 \) N/mm and is plotted along with \( F_{nl} \). It is clearly a poor match to \( F_{nl} \). Figure 5 shows \( F_{nl} \) at different lengths. The data are from the same muscle, and the stimulation parameters are the same as in Fig. 4. \( F_{nl} \) decreased at shorter isometric lengths, becoming slightly positive at −12 mm with respect to \( L_o \). The decrease in \( F_{nl} \) with length means that the length-tension functions of the parts may have a different shape than the length-tension function of the muscle as a whole. The top plot in Fig. 6 shows data from the same muscle presented in Figs. 4 and 5. Rather than \( F_{nl} \), the digital summation of parts A and B are shown. Note that the sum is larger at \( L_o \) but becomes smaller by −15 mm. Similar results were seen in all four muscles. The mean difference at \( L_o \) was 4.1% of \( P_o \). In one experiment, the puller was adjusted to measure the length-tension data at longer lengths (Fig. 6, bottom plot). Here, \( F_{nl} \) became positive at a length of 7 mm. These data are inconsistent with a simple shift in the length-tension curve.

**Stiffness measurements.** Quick stretches were used to measure stiffness when parts A, B, and both A and B were stimulated together. The data from one experiment are shown in Fig. 7. The dotted line is simply a visual reference and was drawn from the origin to the largest data point. Note that the data points from part A and B are slightly above the reference line. This indicates that their normalized stiffness (stiffness over force) is just slightly greater than that from whole muscle. When the model of Fig. 1 is applied, Eq. 6 can

<table>
<thead>
<tr>
<th>Cat</th>
<th>( P_o )</th>
<th>( s_{AB} ) N/mm</th>
<th>( K ) N/mm</th>
<th>Dynamic Max ( F_{nl} )</th>
<th>Isometric Max ( F_{nl} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>30.0</td>
<td>14.7</td>
<td>46.2</td>
<td>5.3</td>
<td>−4.8</td>
</tr>
<tr>
<td>2</td>
<td>30.2</td>
<td>11.6</td>
<td>32.5</td>
<td>5.4</td>
<td>−3.4</td>
</tr>
<tr>
<td>3</td>
<td>25.2</td>
<td>12.7</td>
<td>47.8</td>
<td>6.8</td>
<td>−3.2</td>
</tr>
<tr>
<td>4</td>
<td>22.2</td>
<td>13.3</td>
<td>41.0</td>
<td>5.1</td>
<td>−4.9</td>
</tr>
</tbody>
</table>

\( \%P_o \), maximal tetanic tension; \( s_{AB} \), experimentally measured stiffness when parts A and B of the muscle are stimulated; \( K \), stiffness of the common elasticity; \( F_{nl} \), nonlinear summation of force; dynamic max \( F_{nl} \), largest error measured during isometric contractions with unequal tetany; isometric max \( F_{nl} \), largest difference between length-tension curves.
be used to estimate $K$. On the basis of four cats, whole muscle stiffness was measured at 13.1 N/mm and $K$ was measured at 41.9 N/mm (Table 1). By these calculations, about one-fourth of the whole muscle compliance can be attributed to the common elasticity.

$F_{nl}$ between smaller pieces of the muscle. In three muscles, $F_{nl}$ was also measured with smaller pieces of the muscle. A typical example is shown in Fig. 8. The experiment was similar to the unequal tetany protocol shown in Fig. 2. Because this experiment was very sensitive to fatigue, the complete protocol was repeated twice in each muscle. The larger piece of muscle (generating from $1/3$ to $1/2$ the total muscle force; see Table 2) was stimulated from 200 to 800 ms at 100 Hz. The smaller piece (generating 2–7% of the total muscle) was stimulated from 300 to 500 ms at 100 Hz, as shown in Fig. 8. The results are summarized in Table 2. $F_{nl}$ is expressed as a percentage of the smaller part of the muscle (Fig. 8B). The average $F_{nl}$ for the four trials in the two different muscles was 21.8%. The whole muscle data was expressed as a percentage of whole muscle $P_o$. For comparison, the whole muscle data should be normalized by one-half of $P_o$, which gives a mean $F_{nl}$ of 8.2%. Thus it appears that nonlinearity increases with small pieces of muscle.
DISCUSSION

This study examined $F_{nl}$ in cat TA. The muscle was divided into two parts by splitting the ventral roots. Division into two large pieces resulted in $F_{nl}$ that was quite small (less than 7% of $P_o$). $F_{nl}$ was negative except at the offset of stimulation of part of the muscle. When smaller pieces of the muscle were considered, $F_{nl}$ was somewhat larger (about 20% of the force from the small piece). In an attempt to account for the source of $F_{nl}$, common elasticity was measured in two ways: 1) by mimicking its effects by using the muscle puller and measuring the predicted $F_{nl}$; and 2) measurement of the change in short-term stiffness when part or all of the muscle was active. Both measures indicated the contribution of the common elasticity was small. $F_{nl}$ is, at best, only partially explained by stretch of the common elasticity. The data are consistent with the hypothesis that less than linear summation is produced in muscles with intrafascicularly terminating fibers.

Common elasticity can result in $F_{nl}$ because of the length-tension and force-velocity properties of a muscle. Consider Fig. 2 where part A of the muscle is active and part B is recruited. The additional force from part B will stretch the common elasticity, placing part A at a shorter length on its length-tension curve. This could produce more or less force depending on the start length. However, because TA has such a broad length-tension curve (Fig. 6) and the common elasticity is quite stiff, this effect is small. During the development of force in part B, the stretch of the common elasticity will transiently produce a shortening velocity in part A, leading to a reduction of force on the basis of the force-velocity properties. The opposite occurs during the relaxation of part B, where part A is transiently stretched, increasing force. These effects are apparent in $F_{nl,model}$ in Fig. 2, where stretch of the common elasticity was simulated. They are not readily apparent in $F_{nl}$ in Fig. 2. It is possible that these effects are present and masked by an additional nonlinearity. The initial decrease is similar, but $F_{nl}$ remains negative, and the length-tension properties do not account for this. The spike during relaxation is similar. The predicted effects of common elasticity are slightly more complicated when both parts of the muscle relax at the same time. The increased velocity of stretch when both parts are active can lead to a faster relaxation of the muscle, producing a negative $F_{nl}$ (3). This effect is

Table 2. Summary of $F_{nl}$ measured from a small piece of muscle

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Whole Muscle $P_o$, N</th>
<th>Force Part A, N</th>
<th>Force Part B, N</th>
<th>$F_{nl}$, N</th>
<th>$F_{nl}$ % of Force Part B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cat 2 trial 1</td>
<td>30</td>
<td>16</td>
<td>2.0</td>
<td>0.36</td>
<td>18</td>
</tr>
<tr>
<td>Cat 2 trial 2</td>
<td>30</td>
<td>16</td>
<td>0.8</td>
<td>0.22</td>
<td>28</td>
</tr>
<tr>
<td>Cat 3 trial 1</td>
<td>25</td>
<td>13</td>
<td>0.7</td>
<td>0.19</td>
<td>27</td>
</tr>
<tr>
<td>Cat 4 trial 1</td>
<td>22</td>
<td>11</td>
<td>1.1</td>
<td>0.16</td>
<td>14</td>
</tr>
</tbody>
</table>

Ventral roots were divided so that part A innervated $\frac{1}{2}$ the muscle and part B innervated a small piece.
apparent in $F_{nlmodel}$ in Fig. 4. Again, the effect is not observed in the measured $F_{nl}$.

Common elasticity was measured two ways. Each method is different and selected to determine how large parts of the muscle interact. It was hoped that a simple relationship would suggest how to mathematically represent recruitment in a muscle model. If the model in Fig. 1B was correct and the common elasticity was near linear, the two methods would have provided the same estimate of $K$. This was not the case. Unlike the direct measurement of tendon or aponeurosis stretch, the methods make no assumption about the location of the nonlinearity; rather, they measure the interaction between different parts of the muscle by using their length-tension or force-velocity properties. Each method had its own limitations. Quick stretches (Eq. 6) provide an estimate of common elasticity, provided the elasticity is linear over the range of forces studied. Thus the elasticity must be linear starting from the force produced by the smaller piece of muscle and extending to the force when both parts of the muscle are active (12, 20). An exponential stress-strain relationship over this range would lead to an underestimation of the common elasticity. Although isolated tendon is known to have a nonlinear stress-strain relationship over this range would lead to an underestimation of the common elasticity. Although isolated tendon is known to have a nonlinear stress-strain relationship, high forces levels it is often considered to be linear (1, 26). The mean $K$ was estimated to be very stiff at 42 N/mm, which by itself would produce small nonlinearities (see Fig. 3; $K = 40$ N/mm). The second method (Fig. 2) used the puller to mimic expected changes in the length of the common elasticity. Different values of $K$ were used because the value of $K$ estimated from the quick stretches was very stiff and was unable to match $F_{nl}$. More compliant values of $K$ did not fit the data either. Substitution of a nonlinear common elasticity was not tried since a range of physiological values was already tried and found lacking. In cat Sol, this method was successful because puller movements could account for most of $F_{nl}$, providing confidence in the common elasticity model as well as the value for $K$. Failure to match $F_{nl}$ in the TA provides little justification for the common elasticity model, which makes the value of $K$ determined with this method suspect.

Cat TA has a long tendon (~4 cm). Despite the length of the tendon, the measured common elasticity was very stiff, almost twice that of cat Sol. Although surprising, this is consistent with previous results in cat TA (19, 25). Roeleveld et al. (19) studied the mechanical properties of cat TA with and without its tendon. They found that removal of the tendon made little difference in the overall contractile properties of the muscle.

Few studies have examined $F_{nl}$ between large pieces of a muscle. $F_{nl}$ was initially examined to investigate polynuclear innervation of muscle fibers (8). The small degree of $F_{nl}$ was attributed to the stretch of the tendon (2). Sandercock (20), using the same techniques used in this study, measured $F_{nl}$ in cat Sol, finding the common elasticity explained a major part of $F_{nl}$. The shape of the $F_{nl}$ waveforms in the Sol study is very similar to $F_{nlmodel}$ measured in this study.

The common elasticity probably plays a minor role in the TA $F_{nl}$ for several reasons. First, the tendon in the TA is stiff, so large forces are necessary before there are substantial changes in fiber lengths. A change in fiber length will have two effects. The steady-state, or constant, length changes will affect the operating point on the length-tension curve. Faster changes in length will affect force through the force-velocity properties of muscle. The common elasticity in TA is ~40 N/mm compared with 20 N/mm in cat Sol. Second, the TA has a very flat length-tension curve (Fig. 6), so steady-state changes in fiber length need to be large before they will have much effect on force. Its length-tension properties are comparable to cat Sol. Finally, it has a relatively fast maximum velocity of shortening. The TA’s maximum velocity of shortening is 320 mm/s, which is almost twice as fast as cat Sol. Thus, when only the common elasticity is considered, TA should have half the steady-state $F_{nl}$ and a quarter of the dynamic effects on $F_{nl}$ observed in cat Sol.

If common elasticity cannot account for $F_{nl}$, what can? In cat TA, type F muscle fibers do not run the full length of the TA. These short fibers termnate short of the tendon and must somehow transmit their force to the tendon. The endomysial connective tissue matrix outside the muscle fibers (7, 14, 24) probably serves to transmitting the force (13). The intrasubcellular terminating fibers are likely to affect $F_{nl}$ in two ways: 1) increased compliance and 2) the serial transmission of force.

Serial fibers within a muscle may increase the compliance. Glycogen depletion studies on muscles with serial fibers have shown that the short fibers terminate near fibers of different motor units (10, 13). Thus the intrasubcellular terminating fibers probably transmit force to fibers that are not within the same motor unit. Because these fibers may not be active, the compliance seen by the motor unit may increase significantly. When a single motor unit is activated, its fibers must shorten farther. This may alter the operating point on the length-tension curve. Increased compliance, and hence shortening, may increase the nonlinearities due to friction between or the breaking of weakly bound crossbridges of neighboring fibers (see discussion of motor unit nonlinearities below). Sheard et al. (21) used this argument to explain greater-than-linear summation in the serial-fibered guinea pig sternomastoid muscle. There was little evidence of increased compliance is this study. Increased compliance would be expected to shift the peak of the length-tension curve to longer lengths when part of the muscle was active compared with the whole muscle. This was not observed.

The second possible effect of intrasubcellular terminating fibers is the serial transmission of force. Two fibers connected in series will theoretically produce the same force whether one or both of the fibers is active. Thus, when both parts of TA muscle are active, some fibers from each part will be effectively in series, so
they will not contribute additional force, resulting in less-than-linear summation. This may explain the less-than-linear $F_{nl}$ observed in whole muscle.

Fatigue was a problem with these experiments. Its significance varied between cats. The protocol required five experiments allowing additional controls. During stimulation, thus mitigating the fatigue effect. Some of the repetition of part AB allows an assessment of the fatigue of part A. Figures 2, 3, and 8 show small deviations that are less than the measured $F_{nl}$. Thus, when unequal parts of the muscle were stimulated (Fig. 8), it is unlikely that $F_{nl}$ results from the fatigue of part A. Because part B is small, its fatigue cannot contribute substantially to $F_{nl}$.

Substantial $F_{nl}$ has been demonstrated between single motor units (4, 15, 21). When a single motor unit is activated, its fibers must shorten slightly before force can be measured. Even in an isometric fixed end contraction, shortening cannot be avoided because there is some compliance in the force transducer as well as compliance in the tendon and aponeurosis. The endomysial connective tissue matrix suggests that fibers are coupled to their neighbors. Thus, for a fiber to shorten, it must drag its neighbors along. If the neighboring fibers resist shortening because of weakly bound cross bridges or other types of friction, then some of the potential force from the motor unit is lost and is not measured with the force transducer because it is used in the compression of neighboring fibers. A similar argument can be made if the muscle fiber must slide by its neighbors. If there is some friction preventing easy movement, force will be lost in the compression of its neighbors (17). This would explain the increase in force seen when pairs of motor units were stimulated together (positive $F_{nl}$). Emonet-Denand et al. (6) showed that, when $F_{nl}$ was measured between groups of motor units, it was smaller than between single motor units. Thus this mechanism would not play a major role when large portions of the muscle are active, such as in this study. Sheard et al. (21) studied $F_{nl}$ in serial- and parallel-fibered muscles and found greater-than-linear increases in force of 20 and 9%, respectively. The opposite was observed in this study. Troiani et al. (23) measured $F_{nl}$ between motor units in cat peroneus longus muscle. They found systematic differences between different motor unit types. In general, they found greater-than-linear summation between type S and FR units but less-than-linear summation between FF units. They noted that type S and FR motor units produce maximum force at shorter lengths than type FF motor units, thus they attributed the observed differences to steady-state changes in fiber length during single and multiple motor unit activation. Their results highlight the potentially complicated interactions between motor units. In this study, force from a small piece of muscle decreased when it was stimulated along with a larger piece. The reason for the greater negative $F_{nl}$ with a small piece of TA is not clear. It does not appear to be stretch of the common elasticity.

In summary, the interaction ($F_{nl}$) was measured between two parts of cat TA. This is a muscle with an unusual architecture in that some fibers do not run the full length of the muscle. The measured nonlinearities were generally small, but they could not be fully explained by the common elasticity. For motor control studies, the magnitude of the error is small enough that they probably do not need to be considered. However, although small, $F_{nl}$ is still of interest in understanding the structure of muscle.

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