Power Developed by Motor Units of the Peroneus Tertius Muscle of the Cat

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Petit, Julien, Marie-Agnes Giroux-Metges, and Maxime Gioux. Power developed by motor units of the peroneus tertius muscle of the cat. J Neurophysiol 90: 3095–3104, 2003; 10.1152/jn.01166.2002. The mechanical properties of motor units have been extensively studied under isometric conditions. Under dynamic conditions, the relationship between the force developed by single motor units and the muscle shortening velocity was determined for relatively high frequencies of activation. However, the interaction between the force-shortening velocity relation and the force-rate of activation relation was still unknown. We studied the power (which is the product of force and velocity) developed by single or groups of motor units during sinusoidal muscle stretches of 1-, 2-, 4-, 6-, and 8-Hz frequency. Motor units were stimulated with frequencies of 20, 40, 60, 80, 100, and 120 Hz during the shortening phase of the muscle stretch. The relationships, for different shortening velocities, between the power developed by single or groups of motor units and the frequency of stimulation were sigmoidal. However, these relations were not proportional to the shortening velocity. The relationships, for different frequencies of stimulation, between the power and the shortening velocity exhibited a maximum. The shortening velocity at which this maximum occurred increased with the frequency of stimulation. Slow motor units showed the lowest of those shortening velocities, whereas the fast fatigable motor units showed the highest. Groups of slow (or fast fatigue resistant) motor units had similar shortening velocities to those of single slow (or fast fatigue resistant) motor units. A mathematical function was fitted, using regression analysis, for all single and groups of motor units to the relationship among the power, the shortening velocity (F-V relation), and the frequency of stimulation. This function allowed examination, for different shortening velocity-frequency of activation combinations, of the relationship between the power developed by single and groups of motor units and the maximal isometric tetanic force they developed. These relationships were usually not monotonic but a monotonic relation could be obtained if slow, fast resistant, and fast fatigable motor units were activated at different frequencies. These results suggest that during a movement, the frequency of activation of motor units is mainly adjusted to the movement velocity and that the power developed by a muscle is mainly adjusted by the number of recruited motor units.

INTRODUCTION

An important element of motor control is the motor unit (MU). The number of activated MUs, their type, and their rate of activation are the main parameters that determine the force or the power developed by a muscle. Some models (Fuglevand et al. 1993; Heckman 1994; Heckman and Binder 1991) allow the calculation of the force developed by whole muscles using known firing properties of motoneurones and known mechanical properties of MUs. The muscle mechanical properties during activation of a single MU or groups of MUs have largely been studied under isometric conditions. Under these conditions, two relationships were mainly studied. The first is the relationship between the rate of activation of a MU and the force it develops (R-F relation). This relationship, which is sigmoidal (for a review, see Burke 1981), is characterized by a single parameter $f_{1/2}$, which is the frequency at which a MU develops half its maximal tetanic force. Slow (S) MUs have a lower $f_{1/2}$ whereas fast resistant (FR) and fast fatigable (FF) MUs have a higher $f_{1/2}$. The second, the relationship between the force developed by MUs and the muscle length (L-F relation), is similar to that observed during contraction of the whole muscle, but the MUs develop their maximal force at very different muscle lengths (Bagust et al. 1973; Filippi and Troiani 1994; Stephens et al. 1975).

Under dynamic conditions, the most important relationship is that between the force developed by a MU and the muscle shortening velocity (F-V relation). This relation is hyperbolic and depends on the type of MU activated (Devasahayam and Sandercoc 1992; Heckman et al. 1992; Petit et al. 1993). The interaction between the F-V and the L-F relationships has been examined (Heckman et al. 1992), whereas the interaction between the R-F and F-V relationships is still unknown.

To study this interaction, we measured during sinusoidal muscle stretches (1–8 Hz) the force developed by single MUs when stimulated at a constant frequency between 20 and 120 Hz. We calculated, using the force and the shortening velocity, the power developed by each MU because this parameter seems appropriate for expressing the efficacy of a MU under dynamic conditions. Because during normal activity several MUs are activated, the power developed by some groups of MUs of the same type was measured and compared with the power developed by single MUs.

METHODS

Experiments were carried out on three adult cats (2.7–4.4 kg body wt). The animals were anesthetized with an initial intraperitoneal dose of pentobarbital sodium (45 mg/kg), supplemented, as necessary, by additional intravenous doses to maintain full anesthesia. The nerve to the peroneus tertius muscle was freed, and the distal tendon of the muscle was attached to a force transducer (Kulite BG1000) fixed on
the shaft of a servo-controlled puller (LDS 201). All other muscles of the hind limb were denervated. The region containing the muscle was formed into a pool filled with paraffin oil. The pool and the body of the animal were maintained at 37–38°C by using heating elements controlled by thermosensors and regulators (Yellow Springs Instruments).

A laminectomy was performed between L3 and S2 to expose the lumbosacral cord, and the skin flaps were elevated to form a pool that was filled with paraffin oil. The dorsal and ventral roots were cut near their entry into the spinal cord. Ventral roots were split under oil into filaments and were raised onto a silver electrode that was used as the anode. A similar electrode, placed on the body mass near the root entry, served as cathode. Impulses in motor axons were detected by electrodes placed on the muscle nerve, which was elevated into oil. Potentials were amplified by Grass AC amplifiers and displayed on a Gould digital oscilloscope. A ventral root filament was shown to contain a single motor axon innervating the peroneus tertius muscle when its stimulation evoked a unique potential in the muscle nerve.

The muscle length-twitch force curve was determined during stimulation of the muscle nerve. The muscle length was then set to the optimal length for the muscle twitch force. Isometric contraction forces developed by single MUs were measured for six stimulation frequencies (20, 40, 60, 80, 100, 120 Hz). The MU type of each MU was determined according to the protocol of Petit et al. (1990). Briefly, the type of the MU is determined using the amplitude of the force oscillations and the mean level of the force developed by the MU during a stimulation at 20 Hz and a stimulation at 40 Hz. In the peroneus tertius of the cat, the classification of MUs obtained with this protocol is the same as that obtained with the protocol of Burke et al. (1973) because one of the authors (Petit) used in several studies, starting with Jami et al. (1982), the later protocol and made observations that led to the former protocol.

By simultaneously stimulating several isolated axons, the isometric forces developed by groups of MUs of the same type could be measured. In this study, two groups of two S MUs, two groups of three S MUs, two groups of two FR MUs, and two groups of three FR MUs were used.

Sinusoidal stretches (0.85-mm amplitude, frequencies: 1, 2, 4, and 6 Hz and 0.7-mm amplitude frequency: 8 Hz) were applied to the muscle. During these stretches, the measured maximal velocities were on average 5.4, 10.7, 20.6, 30.2, and 37.3 mm/s respectively.

Single alpha motor axons or groups of alpha motor axons were stimulated during the first part of every shortening phase, with trains of stimuli, phase locked to the sinusoidal stretch (see Fig. 1). During the four first cycles, the stimulation frequency was 20 Hz; then 40, 60, 80, 100, and 120 Hz were used successively for three succeeding cycles each. The first stimulus in the train led the maximum of the sinusoidal stretch by 10% of the sinusoidal period. The number of stimuli in a train was set such that the stimulation duration was close to 35% of the sinusoidal period. Consequently, the time of occurrence of the last stimulus was close to that of the maximal muscle shortening velocity.

The power developed by single MUs during the sinusoidal muscle stretches was calculated using the following procedure. 1) For each stretch frequency, frequency of stimulation combination an average active cycle force signal \( F_a(t) \) was calculated using the cycle force signals of the three succeeding cycles during which the stimulation frequency had a constant value (see Fig. 1, B and D). This average cycle force is the top trace in Fig. 2, A and B, top. 2) For the passive muscle, an average cycle force \( F_p(t) \) was obtained using the 3 corresponding cycles (middle traces in Fig. 2, top). 3) Similarly an averaged cycle muscle length \( L(t) \) was calculated (Fig. 2, bottom). 4) The cycle force developed by the MU (bottom traces in Fig. 2, top) was the difference between the average active cycle force and the average passive cycle force that is \( F_a(t) - F_p(t) \). 5) The cycle power signal \( P(t) \) (Fig. 2, middle) was the product of the cycle force developed by the MU and the cycle muscle length velocity (the 1st derivative of the average muscle length).

\[
P_w(t) = (F_a(t) - F_p(t)) \times \frac{dL}{dt}
\]

The force signal and the muscle length signal were digitized at 2,000 Hz and stored using a CED 1401 interface coupled to a PC computer running the Spike2 software.

RESULTS

In the course of three experiments, 45 single Alpha axons of MUs were isolated (10 S, 24 FR, and 11 FF). Single alpha axons were stimulated during the shortening phase of the sinusoidal muscle stretch. Examples of force and length signals recorded during 2- and 6-Hz sinusoidal stretches (amplitude: 0.9 mm) are shown in Fig. 1 (top and bottom, respectively), when the muscle was passive (Fig. 1, A and C) and during the stimulation of a FR MU (Fig. 1, B and D). It should be noted that the force was almost the same for the three succeeding stimulations at a same frequency. These signals shown in Fig. 1 were used to calculate the averages for passive muscle force \( F_p(t) \), active muscle force \( F_a(t) \) and muscle length \( L(t) \) as functions of time. These averages allowed calculation of the average force and the average power developed by the MU (see METHODS). These averages are shown in Fig. 2, A for a 2-Hz stretch frequency and in B for a 6-Hz stretch frequency. For both frequencies, the force developed by the FR MU stimulated at 120 Hz was minimal when the muscle shortening velocity was maximal (Fig. 2, - - - -). This is due to the hyperbolic force-velocity relation (Hill 1938).

The power (Fig. 2, A and B, middle) was non-zero during the duration of the activation of the MU muscle fibers, and, because of the mechanical delay and of the contraction relaxation, this duration was longer than the electrical activation of the alpha axon. For the 2-Hz stretch frequency (Fig. 2A), the power was negative during the muscle stretch and positive during the muscle shortening. For the 6-Hz stretch frequency (Fig. 2B), because of the short cycle period, the activation of the MU ended during the muscle lengthening and therefore the power was negative at the end of the cycle. The MU developed its maximal power when the shortening velocity was close to its maximum and the maximal power for the 6-Hz sinusoidal stretch (Fig. 2B) was about two times that for the 2-Hz sinusoidal stretch (Fig. 2A). By measuring the maximal power during a cycle and the corresponding shortening velocity for every stretch frequency and every stimulation frequency, we studied the dependency of the power developed by each MU on the stimulation frequency and on the shortening velocity.

The power developed by a S, a FR, and a FF MU as a function of the shortening velocity and of the stimulation frequency is presented in Fig. 3, A–C, respectively. The circles are the measured powers and the continuous lines are the regression lines fitting the following model to the experimental data

\[
w = ce^{d_v} e^{\frac{h_v}{f}} e^{\frac{g}{f}}
\]

v is the shortening velocity and f is the stimulation frequency. c, h, d, i, j, g, and k are constants different for each MU. The ranges were for c, 0.026–0.34; for h, 0.275–0.54; for d, −0.010 to −0.0001; for i, 1.87–4.16; for j, −1.65 to −0.209;
for $g = -9.662$ to $-557$; and for $k = -3.42$ to $-2.26$. Because the coefficient of correlation of all regression analyses was higher than 0.96, this function was suitable for calculating the power developed by all single MUs and all groups of MUs.

For the three types of MUs, the relationship between the power and the stimulation frequency for constant values of the shortening velocity (curves in planes parallel to stimulation frequency axis) was sigmoidal. This changed gradually with the increase in shortening velocity, that is, the corresponding curve was rather flat for low shortening velocities and steep for the highest velocities. For low frequencies of stimulation, the relationship between the power and the shortening velocity (curves in planes parallel to the shortening velocity axis) had a maximum, and the corresponding shortening velocity (optimal shortening velocity) depended on the value of the stimulation frequency. The above-mentioned model was used to calculate for every MU and every group of MUs stimulated at 20, 60, and 100 Hz, the optimal shortening velocity and the corresponding maximal power.

The relationships among the maximal power, the optimal shortening velocity, and the isometric tetanic force developed by each MU (or group) are shown in Fig. 4. The maximal isometric force developed by a MU was used as a measure of the size and strength of this MU. It should be noted that the force developed under isometric conditions by the MUs or the groups of MUs, stimulated at 120 Hz, is the maximal tetanic force for almost all the MUs of the peroneal muscles (see Jami et al. 1982; Kernell et al. 1983).

For the 20-Hz stimulation frequency (Fig. 4A), the maximal power and the optimal shortening velocity of single MUs increased roughly with the isometric force. The range of optimal shortening velocities was 15.6–25.5, 17.6–32.6, and 18.1–37.0 mm/s for S, FR, and FF MUs, respectively. Although an overlap existed, S MUs had, on average, the lowest optimal shortening velocities, FF MUs the highest, and FR MUs intermediate optimal shortening velocities. These differences were significant (test: Kolgomorov-Smirnov, $P < 0.05$). The optimal shortening velocities of the groups of FR (or S) MUs were in the range of those of single FR (or S) MUs and lower than those of FF (or FR) MUs that developed similar isometric tetanic forces (Fig. 4A). The power developed by the groups of FR MUs was much lower than that developed by FF MUs that developed similar isometric tetanic forces.

The optimal shortening velocities of S and FR MUs markedly increased when the stimulation frequency was increased to 60 Hz (Fig. 4B), whereas those of FF MUs increased only slightly. Therefore the S MUs had optimal shortening velocities close to those of FR MUs (range: 23.5–33.4 and 23.9–35.2 mm/s, respectively) and close to those of FF MUs (range: 27.9–37.1 mm/s). However, S, FR, and FF MUs had on average slightly different optimal shortening velocity (test: Kolgomorov-Smirnov, $P < 0.1$). The optimal shortening velocities of groups of MUs were again similar to those of single MUs of the same type and the maximal power developed by the groups of FR MUs was close to that of single FF MUs that developed similar isometric forces.
When the frequency of stimulation was 100 Hz (Fig. 4C), the optimal shortening velocity of some S and FR MUs was similar to that obtained with a 60-Hz stimulation because the maximal activation of these MUs was probably obtained with a stimulation frequency close to 60 Hz. This produced a rather large scattering of the shortening velocities of S and FR MUs. The power developed by the groups of FR MUs was again close to that developed by FF MUs that had similar isometric tetanic forces. The observed scattering probably explains that the optimal shortening velocities of S, FR, and FF MUs were not on average significantly different (Test Kolgomorov Smirnov P > 0.1).

During a movement, the power developed by a muscle may be adjusted by varying the frequency of activation of the MUs, but this process depends on the desired speed of the movement. To illustrate this point, we present in Fig. 5, for the S, FR, and FF MUs used in Fig. 3, the relationships between the stimulation frequency and the shortening velocity needed to maintain the power at different constant levels. These relations are the intersections of the surfaces presented in Fig. 3 with horizontal planes. The presented MUs were typical for each type of MU, but it should be noted that a continuum existed, that is, for example, FF MUs could have properties closed to those of FR MUs. For the three MUs, the curves obtained for the lowest values of power exhibited a first part that was almost parallel to the stimulation frequency axis. Therefore for low shortening velocities, it is ineffective to activate MUs with high frequencies because a desired power level is reached for rather low frequencies of activation. Then for higher shortening velocities, the shape of the second part of the curve depended on the type of the MU. The second part of the curves for the FF MU (Fig. 5C) was almost parallel to the shortening velocity axis; however, because the curves were close to each other, the power developed by the FF MU with a 20-Hz stimulation frequency and a shortening velocity of 30 mm/s was about three times that developed at 10 mm/s. The second part of the curves for S and FR MUs (Fig. 5, A and B) was not parallel to the shortening velocity axis (excepted for the lowest value of power) because the speed of contraction (the maximal shortening velocities) of the S and FR MUs were lower than those of the FF MUs (Devasahayam and Sandercock 1992; Heckman et al. 1992; Petit et al. 1993). To maintain the power almost constant over a wide range of shortening velocities, a noticeable increase in frequency was necessary.

The second way to adjust the power of a muscle is to recruit more or fewer MUs. Under isometric conditions, MUs are recruited according to the force they develop, and it is easy to predict the force developed by a group of MUs because this force is usually close to the sum of the individual forces of the MUs in the group (Powers and Binder 1991). To test if the same scheme of recruitment can hold under dynamic conditions, we studied the relationship between the power developed...
by single MUs and groups of MUs and their isometric tetanic forces for a known stimulation frequency and a known shortening velocity. For each MU, this power was calculated using the function previously determined for this unit (see preceding text). When the frequency of stimulation was 20 Hz and the shortening velocity was 10 mm/s (Fig. 6A) for the S, FR, and some FF MUs, the power tended to increase linearly with the tetanic force, whereas the power developed by groups of FR MUs and some FF MUs clearly did not follow this relation. When the shortening velocity was increased to 30 mm/s but the stimulation frequency was still 20 Hz, the power developed by some FR MUs and the FF MUs tended to increase linearly with the tetanic force, whereas that developed by the other FR, S, and groups of MUs did not follow the same relation. This could be expected because S and some FR MUs developed, at 20-Hz stimulation frequency, their maximal power for shortening velocities <30 mm/s (see Fig. 4A) and therefore developed relatively low power at 30 mm/s, whereas FF MUs developed nearly their maximal power (see Fig. 4A). The power developed by the groups of MUs when stimulated at 20 Hz were low compared with the power developed by single MUs especially for the 30 mm/s shortening velocity. This is not surprising because it is difficult to predict the power developed by a group of MUs from the power developed individually by the MUs and their maximal shortening velocity (Josephson and Edman 1988; Ranatunga and Thomas 1990). For example, a MU that develops a high power and that has a high maximal shortening velocity can unload MUs with lower maximal shortening velocities. It is probably the case in our experiments (Fig. 6, A and B) because the first group of FR MUs were made of two MUs that developed each an isometric force ≈0.3 N, and the second and third group were obtained by adding small MUs that developed each ≈0.04 N. When the stimulation frequency was 60 Hz, for a shortening velocity of 10 mm/s (Fig. 6C), the relationship between the isometric force and the power developed by single S, FR, and groups of MUs was linear and the power developed by FF MUs was slightly lower than that expected from this relation. When the shortening velocity was increased to 30 mm/s and the stimulation frequency maintained at 60 Hz, the power developed by S, FR, and groups of MUs again increased linearly with the isometric tension but the power developed by FF MUs was clearly larger than that expected from this relation. This could also be explained by the different shortening velocities at which the different MUs developed their maximal power but, at 60-Hz stimulation frequency, the differences were smaller than at 20 Hz (see Fig. 4B).

DISCUSSION

The aim of this study was to determine, for the first time, the interaction between the power-muscle shortening velocity relationship and the power rate of activation relationship for single or groups of MUs. We found that the power was a rather complex function of the shortening velocity and of the stimulation rate and not, as usually assumed, a simple product of two functions of each parameter.

In the present experiments, power developed by MUs was determined during sinusoidal muscle length changes because paw shaking or scratching in the cat, movements with high frequencies (~5 Hz) and relatively small amplitudes elicit similar muscle length changes (Abraham and Loeb 1985). Therefore sinusoidal muscle length changes of 1.5 mm applied to the peroneus tertius muscle (50% of in vivo maximal muscle
length change) with 1- to 8-Hz frequencies would include the maximal velocities encountered during natural movements.

The relationship between power and velocity could be determined using sinusoidal stretches with a single frequency, the maximal frequency used in our experiments, because the velocity varies during these stretches. Although we started the stimulation before the muscle length was maximal (and velocity null) to allow the activation of MUs to reach a constant level before muscle shortening, we observed that the power for the low velocities could not be determined accurately. Therefore we used several stretch frequencies and measured the power when the shortening stretch velocity was maximal. However, we mainly used this procedure because the maximal velocity always occurred at the same muscle length and, consequently, corrections to the measurements of the power for an effect of muscle length were not necessary.

Some factors could influence the measurement of the power developed by a MU during sinusoidal stretches. The first one is the elasticity of the tendon, but it was suppressed by tying the load cell near the insertion of the muscle fibers. Therefore only the in-series elasticity of the muscle must be considered. This elasticity is important for isometric contractions because the in-series elastic elements are put under tension. Then the shape of a twitch or of an unfused tetanus is determined by the

**FIG. 4.** Maximal power developed by single MUs or groups of MUs stimulated at the same frequency (A: 20 Hz, B: 60 Hz, C: 100 Hz) as a function of shortening velocity and of isometric tetanic force.
properties of these elements and by the “active state” of the muscle fibers. During shortening contractions, the in-series elastic elements are much less put under tension especially for moderate and high shortening velocities. It is why the amplitudes of the force oscillations are much smaller during shortening contractions than during isometric contractions. Therefore there is less uncertainty on the measurement of the force during the former contractions than during the later. The largest oscillations were obtained with a 20-Hz stimulation frequency combined with 1- and 2-Hz sinusoidal stretch frequency. For the 20- 2-Hz combination, because the fourth pulse of the stimulation (see Fig. 1D) occurred 25 ms before the maximal shortening velocity occurred (see METHODS) and because the mean contraction time of the fast and slow units
are 20 and 32 ms, respectively (Jami et al. 1982), the power measured for the maximal shortening velocity was very close to the maximal power that the MUs could develop at this velocity. From all these considerations, we can conclude that for all the stimulation frequency-shortening velocity combinations we measured, the power when each MU was fully activated. It is probably why the correlation coefficients obtained with the regression analysis were all $>0.96$.

Under isometric conditions, the relationship between the force developed by MUs and their rate of activation is sigmoidal (Kernell et al. 1983). During muscle shortening, we found that this relation had a similar shape (see Fig. 3; for constant shortening velocities the force is proportional to the power), but the function fitted to the data indicates that the curves for different shortening velocities cannot be deduced one from another by simply multiplying a single function of the stimulation frequency by a parameter that depends on the shortening velocity.

In the rat soleus muscle (Devasahayam and Sandeacook 1992), S and FR MUs (stimulated at 100 Hz) develop their maximal power for shortening velocity values scattered approximately $\pm 31$ mm/s (assuming a mean $L_0$, muscle fiber length of 17 mm), which is in agreement with the values we observed for S and FR MUs of the cat (see Fig. 4C).

It is known that a maximally activated muscle develops its absolute maximal power when it shortens at a velocity that is 20–30% of its maximal shortening velocity (Hill 1950). MUs of the soleus muscle of the rat, stimulated at 100 Hz, develop their maximal power for a velocity $V_{pp}$, which is between one-fourth and one-fifth of $V_{max}$, their maximal shortening velocity (Devasahayam et al. 1992). Using these ratios and the values of $V_{pp}$ observed for 100-Hz stimulation frequency in our experiments (Fig. 4C), the largest calculated range of maximal shortening velocities was 95–175 mm/s for S and FR MUs; this is in agreement with the range of values found in the superficial lumbrical muscle. In this small muscle, which has a size close to that of the peroneus tertius muscle (mean measured fiber length: 12 mm; estimated $L_0$, 16 mm) (Petit et al. 1990b), the range of $V_{max}$ was 25–120 and 90–200 mm/s for S and FR MUs, respectively (Petit et al. 1993), but this study included S MUs that had very small tetanic force, which explains some very low $V_{max}$ observed for S MUs.

To move a load with a defined velocity, a muscle develops a power that is the sum of the individual powers developed by the recruited MUs. Because a MU can develop a range of powers for a defined velocity (Fig. 5), a multitude of combinations of the number of activated MUs and frequencies of activation can produce a given muscle power. To understand...
motor control, it is necessary to understand why some combi-
nations are suitable for certain tasks.

During isometric contractions, it was shown that MUs are
recruited following the “size principle” (Henneman et al. 1965)
and that this recruitment allows the force developed by a
muscle to be precisely graded (Heckman and Binder 1991).
More precisely, because the sum of the forces developed by
the MUs increases exponentially with the order of recruitment
(Kernell 1992), the muscle force can be controlled with a
constant sensitivity. During nonisometric contractions the
“size principle” seems to be still valid (Desmedt and Godaux 1977)
although exceptions were observed. This scheme of recruit-
ment could be efficient to grade the power developed by the
muscle with a constant precision if the power monotonically
increases with the order of recruitment of the MUs. Because of
the almost exponential relationship between the sum of the
MUs’ forces and the order of recruitment, the relationship
between the tetanic force and the order of recruitment is also
exponential. Therefore the isometric tetanic force is a measure
of the order of recruitment, and if the power is graded with a
constant precision, the relationship between the power and the
tetanic force should be almost linear. We studied this relation-
ship for some shortening velocity-stimulation frequency com-
binations (Fig. 6), and we observed that usually it was not
monotonic. However, it is known that in the cat, during walk-
ing, MUs are activated at different rates (Hoffer et al. 1987)
and that those with the lowest thresholds (presumably S MUs)
have a peak firing rate ~40 Hz, whereas the MUs with the
highest thresholds (presumably FF MUs) have a peak firing
rate ~20 Hz. MUs of human arm flexor muscles during sinus-
oidal movements have the same range of activation frequen-
cies (Van Bolhuis et al. 1997). Therefore we plotted (Fig. 7)
the power-tetanic force relation with the S MUs activated at 40
Hz, the FR MUs activated at 30 Hz, and the FF units activated
at 25 Hz. These powers were calculated using the regression
equations determined in the preceding text.

For a shortening velocity of 10 mm/s (Fig. 7A), the power
developed by FF MUs was too small compared with that
developed by FR MUs, but at 20 mm/s (Fig. 7B), a rather good
relationship was obtained. A better relationship could be ob-
tained if the smallest FF MUs were activated at 30 Hz as FR
MUs to develop powers similar to those of FR MUs, and the
largest FF MUs were activated at 20 Hz to develop powers
similar to those of groups of FR MUs. By comparing the power
developed by groups of S MUs and single FR MUs, it can be
seen that the frequency of activation of FR MUs has to be
adjusted in a similar way to that used for FF MUs. More
generally it seems that the best power-tetanic force relation-
ship could be obtained if the MUs were activated with a frequency
that continuously decreases when the isometric tetanic force
increases.

Therefore our results suggest that to perform a movement
using the same scheme as that used under isometric conditions,
the range of rates of activation of the MUs is adjusted to the
desired speed of the movement. Then because the power de-
veloped by MUs is monotonically related to their isometric
tetanic force, the muscle power can be precisely regulated by
the number of MUs recruited. Such an adaptation of the rate of
discharge of motoneurons to the speed of movement (more
precisely to the walking speed), was observed in the cat (Hof-
fer et al. 1987). Furthermore an additional modulation of the
rate of discharge of motoneurons as a function of the move-
ment velocity could be provided, at least in leg muscles, by Ia
afferent discharges. These fibers are monosynaptically con-

nected to homonymous motoneurones (Lloyd 1947), and their
discharges are well known to be highly sensitive to muscle
stretch velocity. However, before forming general conclusions,
it will be necessary, in further studies of the power developed
by MUs to take into account the effect of the muscle length.

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DISCLOSURES

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