Catchlike property of human muscle during isovelocity movements

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Catchlike property of human muscle during isovelocity movements. J. Appl. Physiol. 80(6): 2051–2059, 1996.—This study examined the catchlike property of skeletal muscle during eccentric and concentric isovelocity contractions of fresh and fatigued quadriceps femoris muscles of 10 healthy subjects. During concentric contractions of fresh muscles, stimulation trains that elicited a catchlike response (CITs) produced greater force outputs and rates of rise force than comparable constant-frequency trains. These enhancements became more pronounced during fatigue. CITs were less effective in enhancing forces during eccentric contractions but did improve the rates of rise of force. Overall, the CIT that produced the greatest augmentation had a 5-ms initial interpulse interval. Proposed mechanisms for the catchlike property involve enhanced muscle stiffness for more efficient transmission of tension and increased calcium release. These results suggest that stimulation trains that take advantage of the catchlike property of skeletal muscle may be helpful during clinical applications where neuromuscular electrical stimulation is used to restore function in patients with damaged central nervous systems.

quadriiceps femoris; functional electrical stimulation; doublet; concentric; eccentric; paraplegia; isokinetic; fatigue

THE CATCHLIKE PROPERTY of skeletal muscle is the tension enhancement seen when an initial brief high-frequency burst of pulses at the onset of a subtetanic constant-frequency train is used to activate whole muscles (5,32) or single motor units (7,8,37). The force produced by the high-frequency burst is determined by the frequency and number of pulses within the burst (4). If the force produced by the initial high-frequency burst is less than or equal to the maximum force produced by the lower frequency train alone, no decline in force occurs when the frequency changes (3,4,7,8). If the force produced by the high-frequency burst is greater than the force that can be maintained by the lower frequency, however, an overshoot is observed and the force will decrease to the maximum force that the low-frequency portion can produce (4,35). The catchlike property is a fundamental property of muscle cells that is not due to properties of the motor axon or neuromuscular junction (1,7,35,37). This argument is supported by the observation that the amplitude of the compound muscle action potential in response to the second pulse of a high-frequency two-pulse train (doublet) is the same or smaller than the first response (1,7). Thus the tension enhancement by the catchlike property is not due to additional muscle fiber recruitment.

Doublets of motor unit electromyographic activity at the onset of a train of activity are reported to occur during volitional contractions in humans (11,18,26), controlled locomotion in cats (30), and free movements in rats (19). These observations suggest that the catchlike phenomenon may play a significant role during normal movement. Previous investigators propose that the catchlike property may allow an increase in the force output of a motor unit without a large change in the mean activation rate of the motoneuron (7,19). On the basis of the appearance of doublets during walking in high-decerebrate cats, Zajac and Young (38) suggest that if during normal locomotion there is a constraint on the number of pulses within a train to reduce fatigue, then a motor unit should fire with the activation pattern that optimizes the force. Other investigators have shown that doublets are seen in some subpopulations of motor units and not others in the rat hindlimb (19). These data suggest that there must be some functional advantages to using the catchlike property for some motor unit types and under some circumstances.

Recent work shows that the force augmentation attributed to the catchlike property varies as a function of the degree of potentiation and fatigue state of the muscle and with the type of contraction performed (1,3,4,9,29). As first reported by Burke and colleagues (7,8) and more recently confirmed by Bevan and colleagues (1), the augmentation seen with the catchlike property decreases as the muscle becomes potentiated during isometric contractions of fast-twitch cat single motor units. In contrast, during repetitive isometric contractions of cat single motor units or human whole muscle, the force augmentation produced by the catchlike property becomes more pronounced when the muscle is fatigued (1,3). A preliminary report by Sandercock and Heckman (29) shows that the force augmentation produced by the catchlike property decreases during shortening movements compared with isometric contractions for cat soleus whole muscle and single motor units. Callister and colleagues (9) report a slight decline in the force augmentation with the catchlike property during shortening and lengthening contractions compared with isometric contractions for the turtle external gastrocnemius muscle. Changes in the effects of the catchlike property during fatiguing shortening (concentric) or lengthening (eccentric) contractions have not previously been reported.

The purpose of this study is to examine the effects of the catchlike property on the force output of human quadriceps femoris muscles during nonisometric contractions. Specifically, the effects of the catchlike property on force and rate of force production were examined for concentric and eccentric movements during nonfatiguing and fatiguing contractions.
METHODS

Subjects. Ten healthy subjects (5 males, 5 females) ranging in age from 21 to 28 yr [23.7 ± 2.6 (SD) yr] voluntarily participated in this study, which was approved by the University of Delaware Human Subjects Review Board. All subjects signed informed consent forms.

Experimental setup. Subjects were seated on a computer-controlled dynamometer (KinCom II 500–11, Chattanooga, Chattanooga, TN) with hips flexed to ~75° (Fig. 1). The pelvis, right leg, and right thigh were stabilized with Velcro straps. The right knee joint axis was aligned with the dynamometer axis. The right quadriceps femoris muscle was stimulated using a Grass S8800 stimulator with an SIU8T stimulus isolation unit. All stimulation pulses were 600 μs in duration. Two 7.5-cm-diameter round carbon-rubber electrodes were secured to the thigh with elastic straps. Sponges, saturated with tap water, served as the conducting medium. The cathode was placed over the vastus medialis, and the anode was placed over the rectus femoris portions of the quadriceps muscle. The positions of the electrodes were adjusted to permit stimulation over the motor points (i.e., the point on the skin that produces maximum force from the muscle for a given stimulator intensity). A personal computer equipped with an analog-to-digital board digitized force and angle data on line at a rate of 200 samples/s.

Training session. All subjects participated in one training session. Each subject was familiarized with the experimental protocol and trained to refrain from voluntarily contracting the quadriceps femoris or hamstring muscles while the dynamometer controlled movements of the knee joint and during electrical stimulation of the quadriceps femoris muscle. The maximum voluntary isometric contraction (with the knee maintained in 60° of flexion) was then determined for each subject by use of a burst superimposition technique similar to that previously described (31).

Experimental sessions. Each subject participated in three experimental sessions. During the first experimental session, nonfatiguing concentric and eccentric contractions were produced from the muscle. Fatigue-inducing concentric and eccentric contractions were tested during the two subsequent sessions. Each experimental session was separated by ≥72 h.

All stimulation trains contained 10 pulses (9 interpulse intervals; Fig. 1). In the constant-frequency train, all interpulse interval durations were equal to 10 ms. The trains used to elicit a catchlike response (henceforth referred to as catchlike-inducing trains or CITs) had one initial brief interpulse interval (for details see below) followed by a constant-frequency portion with eight interpulse intervals of 70 ms.

For each experimental session, the stimulation intensity was set while the knee was held in 60° of flexion and the muscle was activated with constant-frequency trains. The stimulator amplitude was first adjusted to elicit a force equal to ~20% of the maximum voluntary isometric contraction of the muscle. Trains were then delivered once every 5 s until the muscle was potentiated (i.e., the force no longer increased with three successive trains), which required 5–10 trains for each subject. Stimulation was continued to allow the stimulation intensity to be readjusted to produce 20% of the maximum voluntary isometric contraction. Stimulation was then stopped, and the intensity was not changed for the remainder of the session to attempt to recruit a consistent population of motor units within each session.

Whereas it is unlikely that the same motor units within a subject were stimulated across sessions, it appears that this procedure recruited a consistent population of motor units within each session. If this were not so, we should have observed wide fluctuations in the force output during the fatigue test (see below) when the muscle was fatigued. During the fatigue test, motor units that were not recruited for the previous two to three cycles (6–8 s) should demonstrate marked force recovery. Thus, if we were not recruiting a relatively consistent population of motor units, we should have seen little fatigue, if the variability in the motor unit population recruited was large, or large fluctuations in the force output, if the variability was modest. This was not observed (see Figs. 6 and 7). Once a stable level of fatigue was reached during a fatigue test, the same stimulation train elicited force-time integrals and peak forces that were consistently and markedly attenuated compared with the fresh muscle.

Nonfatigue session. Within 30 s of adjustment of the stimulation intensity, the leg was placed in the starting position, 100° of knee flexion for concentric contractions and 0° for eccentric contractions, and the muscle was repotenti- ated (5–10 contractions) without a change in the previously set stimulation intensity. Within 5 s of repotentiation, data collection commenced. The dynamometer moved the leg between 0 and 100° of knee flexion while the muscle was electrically stimulated with a train of pulses; stimulation was initiated at an angle of 85° during concentric contractions and 15° during eccentric contractions to minimize the effects of

Fig. 1. A: schematic drawing of experimental setup used to test quadriceps femoris muscle. Rotational axis of dynamometer is aligned with axis of knee joint, and subject is secured to seat and force transducer (F) with straps. Dynamometer controls knee joint movement through a range of 0~100° of flexion, and the stimulator is triggered to activate quadriceps femoris muscle at 85° for concentric (con) or 15° eccentric (ecc) contractions. B: schematic representation of 3 of the 7 stimulation trains used during study. Top trace: constant-frequency stimulus train (CFT) with all interpulse intervals equal to 70 ms; middle trace: catchlike-inducing train (CIT) with a 30 ms initial interpulse interval; bottom trace: CIT with a 5-ms initial interpulse interval. Each pulse within a train is represented by a vertical line.
momentum during acceleration of the leg. A level detection circuit was used to trigger the stimulator at the 15° and 85° joint angles. The leg was moved at 100°/s in the test direction (extension for concentric contractions and flexion for eccentric contractions) and at 25°/s to return the limb to the start position. Thus, for even the longest stimulation trains (i.e., the constant-frequency trains), which last 630 ms, the stimulation terminated before completion of leg movement. The leg was then held in the start position for 11 s before the next movement cycle began to avoid fatigue.

During data collection, the first and the last two movement cycles were passive movements (i.e., no stimulation) and were used for gravity correction (see below and Fig. 2). Stimulation began during the second movement cycle with a constant-frequency train. During the next six movement cycles a random sequence of CITs with initial interpulse intervals of 5, 10, 15, 20, 30, or 50 ms was used. The next train was a second constant-frequency train followed by the six CITs presented in the reverse order to that previously used. The last train was another constant-frequency train. Because maximal voluntary eccentric contractions may compromise torque development of subsequent concentric contractions (14), eccentric testing followed concentric testing during the nonfatiguing session.

Fatigue session. Fatigue-producing sessions were similarly conducted with the following exceptions. The return speed of the dynamometer was set at 100°/s, and no rest period separated successive movement cycles, resulting in an ~2-s period between the start of successive stimulation trains. This brief rest period allowed the stimulation trains to fatigue the muscle. Five cycles of passive movement were recorded before the muscle was subjected to the fatiguing protocol. The stimulation trains tested were a constant-frequency train and CITs with initial interpulse intervals of 5, 10, 15, 20, or 30 ms. Ten random sequences of these six trains were used to form a block of 60 trains. Three blocks were used to form a stimulation protocol containing 180 trains. The same fatigue protocol (i.e., the same random sequence) was used for all subjects. Concentric and eccentric tests were performed in separate sessions. One-half of the subjects were randomly selected to perform concentric testing during the first fatiguing session and then eccentric testing in the second fatiguing session. The other half of the subjects performed eccentric testing first.

Data management. Records of passive movements (i.e., no stimulation) were used to determine the force exerted by the leg and foot due to gravity that opposed knee extension (i.e., the force attempting to flex the knee). This force changes as a function of the joint angle of the knee, being nearly zero with the knee flexed to 90°, and the weight of the leg and foot when the knee is fully extended (Fig 2). Because the quadriceps muscle must lift this force during each contraction, it was added to the forces recorded during stimulation to calculate the gravity-corrected forces generated by the quadriceps.

The dependent variables investigated were the gravity-corrected force-time integral, peak force, average force, and time to reach 80% of the peak force ($T_{80}$) in response to each train of pulses. The force-time integral is the area under the force trace; it is commonly used to quantify the force augmentation produced by the catchlike property (32, 37) and is a measure of the total work performed by the muscle. Peak force is the highest value relative to the baseline force occurring within the force trace and is another commonly used measure of force production. Average force is the force-time integral divided by the duration of the stimulus train and reflects the average power generated by the muscle. $T_{80}$ is the time from the onset of force to the time of the first occurrence of a value equal to 80% of peak force and is a measure of the rate of tension production (4). Linear interpolation between data points was used to estimate $T_{80}$.

To analyze the fresh data, first the difference in the force-time integrals produced in response to the first and second constant-frequency trains was compared with the difference in responses to the first and second third constant-frequency trains. The force responses of the two constant-frequency trains with the larger difference were averaged. This averaged constant-frequency train data and the responses to the intervening six CITs were then used for all further data analyses. This procedure was used to minimize the effects of any changes in the level of force potentiation of the muscle during the nonfatiguing protocol.

The fatigue data were calculated from the last 24 contractions of the 180-contraction fatiguing protocol and consisted of responses to four trains of each of the six stimulation patterns tested. The four contractions for each stimulation pattern were averaged and then analyzed. The four different

![Fig. 2. Typical force traces from an individual subject. A: force recordings during fresh eccentric condition](https://example.com/figure2a.png)

![Fig. 2. Typical force traces from an individual subject. B: gravity-corrected force trace during passive flexion with no stimulation. C and D: analogous gravity correction process for a concentric fresh contraction from same subject.](https://example.com/figure2b.png)
train sequences that were used to produce the last 24 contractions helped minimize any ordering effects. Percent improvement data for the force measurements for the concentric nonfatiguing, concentric fatiguing, eccentric nonfatiguing, and eccentric fatiguing conditions were calculated using Eq. 1

\[
\%\text{Imp}_{\text{CIT}} = \left( \frac{F_{\text{CIT}}}{F_{\text{CFT}}} - 1 \right) * 100
\]

where CIT is a CIT with 5-, 10-, 15-, 20-, or 30-ms initial interpulse interval and %\text{Imp}_{\text{CIT}} is the percent improvement in the force-time integral, peak force, and average force produced by each CIT. \( F_{\text{CIT}} \) is the force response to each CIT, and \( F_{\text{CFT}} \) is the force response to the constant-frequency train.

Improvement in \( T_{90} \) is represented by shorter durations (faster rate of rise) and was calculated by Eq. 2

\[
\%\text{Imp}_{\text{CIT}} = \left( 1 - \frac{T_{\text{CIT}}}{T_{\text{CFT}}} \right) * 100
\]

where \( T_{\text{CIT}} \) and \( T_{\text{CFT}} \) are the \( T_{90} \) values produced by the CIT and constant-frequency train, respectively.

Data analysis. First, the percent improvement data were used to determine the optimal CIT. The use of percent improvement data prevents the analysis from being biased by the stronger subjects. On the basis of prior experience with isometric contractions and pilot data using nonisometric contractions, we anticipated that the CIT with the 5-ms initial interpulse interval would produce the greatest augmentation (2, 22; unpublished observations). To test this assumption, one-way repeated-measures analyses of variance were used to compare the percent improvement data produced by the five CITs. If there was a difference in the augmentation produced between the CITs, paired t-tests were used to compare the 5-ms CIT with the “best” other CIT. Next, because the results showed that no CIT produced greater improvement than the 5-ms CIT, the 5-ms CIT was compared with the constant-frequency train by use of paired t-tests. For all analyses, an observation was significant if \( P \leq 0.05 \).

RESULTS

Complete data sets were collected for all 10 subjects. In all conditions the CITs produced a greater initial rate of rise of force than the constant-frequency trains (Fig. 3). Because all the trains contained the same number of pulses, the CIT response always terminated sooner than the response of the constant-frequency train. Thus, if a CIT is to demonstrate a greater force-time integral, any increase in force produced at the onset of stimulation must be greater than the area “lost” at the end of the train. The 50-ms CITs were omitted from the statistical analysis in the fresh condition. The 50-ms CITs were used only to verify the assumption that as the initial interpulse interval approached the duration of the constant-frequency train, the force measures would also approach those of the constant-frequency train. In reality, these observations did occur and were thus omitted from subsequent statistical analysis.

Differences among the five CITs in ability to produce improved forces or rates of rise of force occurred only during concentric fatiguing contractions (Fig. 4). In this condition, for all four measures, the percent improvements tended to decline with increasing duration of the initial interpulse interval. In general, the 5-ms CIT produced the greatest improvement for all measures (all \( P \leq 0.05 \)). Thus the 5-ms CIT was used in all subsequent analyses.

Concentric contractions. When the muscle was highly potentiated, but not fatigued, the 5-ms CIT produced \(-5, 6, 14, \) and \(35\% \) improvements in force-time integral, peak force, average force, and \( T_{90} \), respectively, compared with the constant-frequency train (all \( P \leq 0.05 \); Fig. 5).

Plots of the force-time integral, peak force, and average force produced in response to each train of the
fatiguing protocol for the concentric condition show that the muscle was fully potentiated at the onset of the test (i.e., no increase in force was observed), that all three force measurements declined linearly over approximately the first 40 contractions, and that there was no further decline in force after the 80th contraction (Fig. 6). As noted above, the 5-ms CIT produced the greatest percent improvements among the CITs (Fig. 4). When the muscle was fatigued, the 5-ms CIT produced 18, 30, 28, and 41% improvements in force-time integral, peak force, average force, and T80, respectively (all P < 0.01; Fig. 5).

Eccentric contractions. When the muscle was fresh, CITs did not show any significant improvement over the constant-frequency trains for any of the three force measurements. The CITs did, however, show improvement in T80. The 5-ms CIT produced 21% improvement in T80 (P < 0.01; Fig. 5).

In contrast to the concentric condition, plots of the force-time integrals, peak forces, and average forces produced in response to each train of the fatiguing protocol for the eccentric condition show that the muscle was not fully potentiated at the onset of the fatiguing protocol for the eccentric condition (Fig. 7).
During the fatiguing protocol the forces rose slightly over the first ~15 contractions and then declined steadily over the remaining 165 contractions. Interestingly, although the eccentric contractions produced ~2.25 times greater forces than the concentric contractions, the rate of decline in force production was greater for the eccentric contractions. That is, although the percent decline in force was comparable for both types of contractions (i.e., ~40%), the concentric condition required 80 contractions and the eccentric condition required 180 contractions to reach this level of fatigue.

For the eccentric contractions, when the muscle was fatigued the CITs only improved the average force and $T_{50}$ compared with the constant-frequency trains. The
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5-ms CIT produced -4 and 19% improvements in average force and $T_{50}$, respectively (both $P \leq 0.05$; Fig. 5).

In summary, 1) the 5-ms CIT was generally the best pattern for activation of the muscle, 2) the CITs produced marked increases in the rates of rise of force during eccentric and concentric contractions of the fresh and fatigued muscles, 3) the CITs produced increases in the force-time integrals and peak forces only during the fresh and fatigued concentric contractions, 4) the CITs produced increases in the average forces during the fresh and fatigued concentric contractions and during the fatigued eccentric contractions, and 5) the force increases produced by CITs were greater when the muscle was fatigued than when the muscle was fresh.

DISCUSSION

The purpose of this study was to examine the effects of catchlike property on the force production of fresh and fatigued human quadriceps femoris muscle during concentric and eccentric contractions. Similar to previously reported responses during isometric contractions, the CITs produced much greater force augmentation during concentric contractions when the muscle was fatigued than when the muscle was fresh and potentiated (1, 3; cf. Ref. 17). In contrast, even when the muscle was fatigued, the catchlike property produced little force augmentation during eccentric contractions. Quantitatively, the force augmentations presently observed during concentric and eccentric contractions are less than those previously observed for isometric contractions of the human quadriceps femoris muscle (2, 3) or other muscles (1, 4). These results are consistent with preliminary investigations by Callister and colleagues (9) and Sandercock and Heckman (29), who report diminished force augmentations for nonisometric contractions compared with isometric contractions.

Optimal augmentation with a CIT containing an initial doublet with a 5-ms interpulse interval is also consistent with previous studies using isometric contractions. For fast- (1, 8) and slow-twitch (8) cat motor units, fast- (19) and slow-twitch (4, 19) rat muscle, and human quadriceps femoris muscle (2; unpublished observations), an initial interpulse interval of 5-10 ms produced optimal force generation. Thus an initial interpulse interval of 5-10 ms appears to optimize force for a variety of muscles and for a variety of types of contractions.

The force augmentation seen with the catchlike property results from the greater rate of rise of force (4) and greater than linear summation of force produced by the initial doublet (12, 22, 32, 33, 37). Proposed mechanisms underlying these two causes of force augmentation include increased muscle stiffness and increased calcium release from the sarcoplasmic reticulum produced by the initial doublet.

Role of muscle stiffness. Parmiggiani and Stein (27) propose that one of the mechanisms for the catchlike property of skeletal muscle is enhancement of muscle stiffness. They liken the series elastic component to an elastic band held at slack length in which the first pulse delivered to the muscle must take up the slack in the series elastic component before force is produced; subsequent pulses in the stimulus train contribute primarily to increasing force (27). Recent work by Wilson et al. (36) during volitional exercise shows that a stiff musculotendinous system maximizes isometric and concentric performance by improving contractile component length, rate of shortening, and transmission of force from the contractile component to the skeletal structures. During the present concentric movements, the quadriceps femoris muscle is passively shortened during the electrical stimulation. This shortening movement may increase the effective series elastic component of the muscle and decrease its stiffness. Indeed, Curtin and Edman (10) demonstrate decreasing muscle fiber stiffness with increasing shortening velocity. The initial doublet, by rapidly increasing force and stiffness, would allow all subsequent pulses to produce greater forces.

As previously noted, the force enhancement by a CIT during concentric contractions is less than that reported during isometric contractions. This, in part, may be because the concentric movement continually increases the effective series elastic components and thereby decreases muscle stiffness. In contrast, during isometric contractions, after the slack is taken up initially by the doublet, the stiffness is maintained so that successive stimuli can more effectively increase force. Thus less augmentation in force is produced with concentric contractions than with isometric contractions, because a portion of the increased stiffness produced by the initial doublet is lost as a result of muscle shortening. Consistent with this suggestion is the observation by Ettema et al. (15) that force potentiation in rat gastrocnemius medialis muscle by prestretch is greater for isometric than for shortening contractions.

During eccentric movements the series elastic component is passively stretched as the knee is moved toward flexion. This movement stretches the cross bridges, causing them to operate higher on their stress-strain curves (10). If the stiffness of the muscle increases due to stretch, then there may be little additional slack to be taken up by the initial doublet. If CITs augment force by more efficiently taking up the slack in the series elastic component, then CITs should show little or no effect in enhancing force production during eccentric contractions. In fact, little or no augmentation was observed during eccentric contractions.

Changes in muscle stiffness may also explain the differences in augmentation seen during fatigue. Curtin and Edman (10) note a decrease in the stiffness of frog muscle fibers with fatigue and attribute the decrease in stiffness to fewer attached cross bridges. Thus, if stiffness decreases with fatigue, then improving muscle stiffness may be more efficacious in augmenting force in the fatigue state. In fact, Fig. 3 shows that for fresh concentric contractions the force produced by
the doublet equals the force produced by the first two pulses of the constant-frequency train; however, when the muscle is fatigued the doublet produces greater force than the first two pulses of the constant-frequency train. This difference may be due to increased muscle stiffness during the doublet stimulation as well as increased calcium release.

Role of calcium release. Another mechanism for the tension-enhancing property of CIT stimulation could be excitation-contraction coupling mechanisms related to Ca$^{2+}$ movements (13). Duchateau and Hainaut (13) showed that in fresh single barnacle muscle fibers the tension enhancement with doublets was due to augmented muscle stiffness and to changes in the ionized calcium concentration in the cell cytosol. The changes in Ca$^{2+}$ concentration reflected augmented Ca$^{2+}$ release by the second pulse and not summation of Ca$^{2+}$ transients, prolonged release of Ca$^{2+}$, or slowing of its reuptake. It is not clear what role augmented Ca$^{2+}$ release plays in the force augmentation presently observed. Similarly, we are not certain that greater summation of Ca$^{2+}$ transients, prolonged release of Ca$^{2+}$, or slowing of its reuptake is not working in the fatigued muscle. Westerblad and Allen (34) showed that the rate of decline in the free myoplasmic Ca$^{2+}$ concentration is reduced with fatigue. Thus it is possible that the greater than linear summation of the force produced by the doublet during the fatigued concentric contractions (Fig. 3) may be caused by greater summation of Ca$^{2+}$ produced by the closely spaced pulses than with the first two pulses of the constant-frequency train.

Effect of contraction type on rate of fatigue. As previously noted, the concentric contractions show a greater rate of fatigue than eccentric contractions (Figs. 6 and 7). This was somewhat surprising, because the initial force levels were more than two times greater for the eccentric than for the concentric contractions. Because the same stimulation intensity was used to elicit both types of contractions (see METHODS), we presume that comparable levels of motor unit recruitment were produced by both types of contractions. Thus greater forces were produced by the eccentric contractions, because stretching the muscle caused the cross bridges to operate higher on their stress-strain curves (10). Interestingly, for isometric contractions of the human quadriceps muscle, using a similar fatiguing protocol, we have seen initial force levels and rates of decline that are between the concentric and eccentric values (2; unpublished observations). Thus the rates of fatigue are related to the type of contraction being performed. Whereas it has been previously shown that, for any given force level, concentric contractions place greater metabolic demands on a muscle than eccentric contractions (16), we believe this is the first study to show greater fatigue rates for concentric than for eccentric contractions by use of comparable levels of motor unit recruitment.

Significance. The observations that CITs are capable of augmenting force during nonisometric conditions and during fatigue are important for clinical applications where neuromuscular electrical stimulation is used to restore function in patients with damaged central nervous systems (22). Walking assisted with the use of electrical stimulation requires repetitive activation of muscles during isometric, concentric, and eccentric conditions and is limited by the high energy costs (20, 21, 24) and rapid muscle fatigue that accompany its use (22, 23, 25). Pierrynowski (28) estimates that the quadriceps femoris exhibits peak activity $\sim 100$ ms after initiating eccentric loading at midstance and 100 ms after initiating concentric advancement of the leg during the swing phase of gait of a normal individual. Our work indicates that at these critical times a 5-ms CIT can markedly increase force over a constant-frequency train. At 100 ms, primarily because of the rapid rate of rise of force produced by the initial doublet, the force-time integrals were $\sim 80$ and 97% greater for the CIT than for the constant-frequency trains for the concentric, fresh, and fatigued conditions and 71 and 94% greater for the eccentric fresh and fatigued conditions, respectively (Fig. 3). Thus CIT stimulation may help augment forces during electrically assisted walking.

Summary. During concentric contractions, a CIT with initial interpulse interval of 5 ms produces greater force-time integral, peak force, and average force and a more rapid rate of rise of force than a comparable constant-frequency train. These enhancements are more pronounced during fatigue. In contrast, CIT stimulation is less effective in enhancing force production during eccentric contractions but did produce a marked enhancement in the rate of rise of force. Our observations may be explained by current proposed mechanisms for the catchlike property that appear to involve enhancing muscle stiffness for efficient transmission of tension or increased calcium release. These observations suggest that CIT stimulation may potentially improve the use of neuromuscular electrical stimulation to assist patients with damaged central nervous systems.

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