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Activation of human quadriceps femoris muscle during dynamic contractions: effects of load on fatigue

S. C. K. Lee, C. N. Becker and S. A. Binder-Macleod

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Effects of activation frequency on dynamic performance of human fresh and fatigued muscles

S. C. K. Lee and S. A. Binder-Macleod

J Appl Physiol, June 1, 2000; 88 (6): 2166-2175.

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Catchlike-inducing train activation of human muscle during isotonic contractions: burst modulation

SAMUEL C. K. LEE, CARA N. BECKER, AND STUART A. BINDER-MACLEOD
Department of Physical Therapy, University of Delaware, Newark, Delaware 19716

Lee, Samuel C. K., Cara N. Becker, and Stuart A. Binder-Macleod. Catchlike-inducing train activation of human muscle during isotonic contractions: burst modulation. *J. Appl. Physiol.* 87(5): 1758–1767, 1999.—Stimulation trains that exploit the catchlike property [catchlike-inducing trains (CITs)] produce greater forces and rates of rise of force than do constant-frequency trains (CFTs) during isometric contractions and isovelocity movements. This study examined the effect of CITs during isotonic contractions in healthy subjects. Knee extension was electrically elicited against a load of 10% of maximum voluntary isometric contraction. The stimulation intensity was set to produce 20% of maximum voluntary isometric contraction. The muscle was tested before and after fatigue with a 6-pulse CFT and 6-pulse CITs that contained an initial doublet, triplet, or quadruplet. For pre-fatigue responses, the greatest isotonic performance was produced by CITs with initial doublets. When the muscles were fatigued, triplet CITs were best. CITs produce greater excursion, work, peak power, and average power than do CFTs, because CITs produced more rapid rates of rise of force. Faster rates of rise of force enabled the preload on the muscle to be exceeded earlier during the stimulation train.

human quadriceps femoris muscle; catchlike property; isotonic; fatigue; functional electrical stimulation

FUNCTIONAL ELECTRICAL STIMULATION (FES) is the use of electrical stimulation of skeletal muscle to produce functional movements in individuals with central nervous system problems (33). Most applications of FES, such as stimulation-assisted ambulation, require repetitive activation of paralyzed muscle. One primary limitation to the widespread implementation of FES is muscle fatigue (31, 34). Most improvements in FES applications have involved technological improvements in system design and implementation, but little systematic investigation of the most appropriate stimulation frequencies or patterns for activating the muscle has been performed (8). Stimulation frequency affects force production of muscle (19, 30) and influences fatigue (2, 6, 28). High stimulation frequencies are associated with higher forces and greater fatigue than are low stimulation frequencies (2, 6, 28). Thus, although the use of low frequencies may reduce the rate of fatigue, they may not generate sufficient forces for all FES applications. Optimal stimulation trains, therefore, need to be identified.

Investigation of stimulus patterns to optimize force production from skeletal muscle has been a long-standing interest of our laboratory (3–5). Recent work

suggests that optimal stimulation may consist of a train of pulses containing more than one instantaneous frequency (10). By using trains that exploit the catchlike-property of skeletal muscle (catchlike-inducing trains), higher forces can be elicited than if traditional constant-frequency stimulation trains are used (1, 9, 10, 14). The catchlike property of skeletal muscle is the tension enhancement produced when an initial brief high-frequency burst of pulses (2–4 pulses) is used at the onset of a subtetanic constant-frequency train to activate the muscle (4, 5, 14, 15). The catchlike property is a fundamental property of muscle that is not due to properties of the motor axon or neuromuscular junction (1, 14, 29).

Our previous investigations of the human quadriceps femoris found that, during isometric contractions with the knee at 90° of flexion, catchlike-inducing trains were highly effective in augmenting force compared with comparable constant-frequency trains when the muscle was in a fatigued state (9–11). When the muscle was fresh, however, catchlike-inducing trains generally produced about the same force as did comparable constant-frequency trains, with the only added advantage of producing faster rates of rise of force (9, 10).

We have recently also investigated the use of catchlike-inducing trains during isovelocity movements (7). During concentric isovelocity movements, catchlike-inducing trains produced greater force-time integrals, peak forces, average forces, and more rapid rates of rise of force than did comparable constant-frequency trains when the muscle was fresh, and these enhancements were more pronounced during fatigue. In contrast to concentric contractions, catchlike-inducing trains were less effective in enhancing force production during eccentric isovelocity contractions but did produce marked enhancements in the rate of rise of force. Interestingly, no studies to date have identified the effects of catchlike-inducing trains to produce isotonic contractions, which are more similar to movements produced during FES than to those types of contractions previously studied. Most studies investigating the catchlike property during isovelocity conditions used force as the primary indicator of muscle performance (7, 38); few have reported values of excursion, work or power when studying the effects of catchlike-inducing train stimulation (cf. Ref. 41) from either fresh or fatigued muscle. The use of force as the only measure of functional impairment during dynamic fatiguing contractions, however, may lead to incomplete and even misleading results (21, 22, 27). The study of work and power is important, because measuring only the changes in force production may be incomplete and even misleading when functional performance of dynamic contractions is evaluated (21, 22, 27). Fatigue has been shown

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to develop more rapidly in isotonic contractions than in isometric contractions (36, 39). Additionally, a greater loss in the power produced during shortening contractions has been observed than the loss in force during isometric contractions (21, 22, 27, 39). Thus assessment of fatigue on the basis of loss of isometric force can seriously underestimate functional impairment of isotonic contractions (21, 27). The purpose of this study, therefore, was to determine whether catchlike-inducing trains could augment excursion, work, peak power, and average power vs. comparable constant-frequency trains from both fresh and fatigued human quadriceps muscles during isotonic contractions. Additionally, the high-frequency burst characteristics of catchlike-inducing trains were investigated to determine the number of pulses and the interpulse intervals required to produce optimal performance.

METHODS

Subjects. Data were obtained from 11 healthy volunteer subjects (6 men, 5 women) ranging in age from 19 to 31 yr old [22.64 ± 4.08 (SD) yr], with no history of lower extremity orthopedic problems. This study was approved by the University of Delaware Human Subjects Review Board, and all subjects signed informed consent forms.

Experimental setup. Subjects were seated on a computer-controlled dynamometer (KinCom III, Chattecx, Chattanooga, TN) with hips flexed to $\sim 75^\circ$ (Fig. 1). The trunk, pelvis, left leg, and thigh were stabilized with Velcro straps. The dynamometer axis was aligned with the knee joint axis, and the force transducer pad was positioned ~ 3 cm proximal to the lateral malleolus and placed against the anterior surface of the leg. The left quadriceps femoris muscle was stimulated by using a Grass S8800 stimulator with a SIU8T stimulus isolation unit. All stimulation pulses were 600 μ s in duration. Two self-adhesive, 3×5 -in. electrodes were used to stimulate the muscle. With the knee positioned at 90° , the anode was placed proximally over the motor point of the rectus femoris portion of the quadriceps femoris muscle. Because the skin over the thigh shifts with respect to the quadriceps femoris muscle as the knee moves into extension, the knee was then placed at 15° of flexion, and then the cathode was placed distally, over the motor point of the vastus medialis portion of the quadriceps. This electrode placement produced consistent force responses when the muscle activation produced knee extension. The stimulator was driven by a personal computer that controlled all timing parameters of each stimulation protocol. Force, angle, and velocity data were digitized on-line at a rate of 200 samples/s and stored for subsequent analysis.

Training sessions. Before the commencement of the experimental sessions, all subjects participated in one training

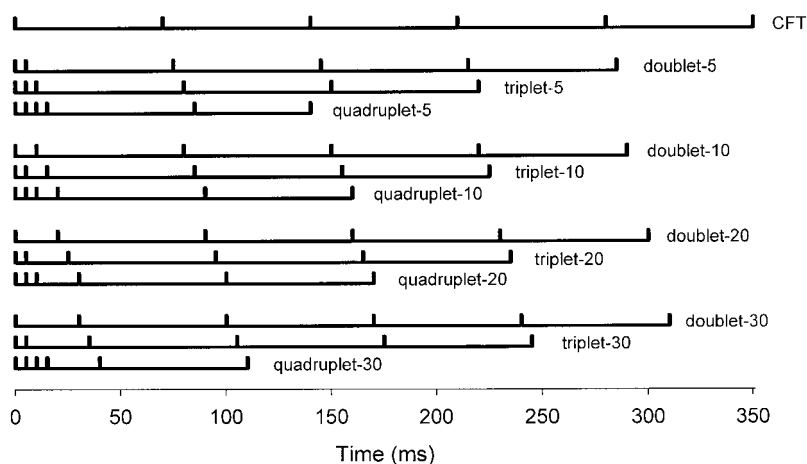
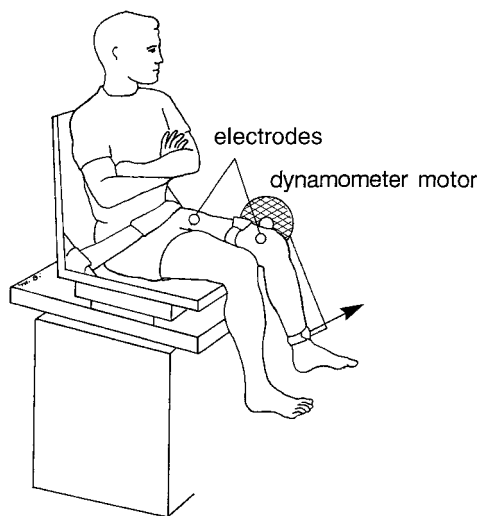


Fig. 1. *Top:* experimental setup showing a subject seated on computer-controlled dynamometer. Self-adhesive electrodes were placed over rectus femoris (anode) and vastus medialis (cathode) portions of left quadriceps femoris muscle. *Bottom:* schematic representation of each stimulus train. Vertical lines, each stimulation pulse within each train. Each train contained 6 pulses. Constant-frequency trains (CFTs) had all interpulse intervals (IPIs) equal to 70 ms. Each of the 12 catchlike-inducing trains (CITs) had an initial burst that contained 2, 3, or 4 pulses (doublets, triplets, and quadruplets, respectively). For doublet CIT, initial IPI was varied from 5 to 30 ms (designated as doublet-5, doublet-10, doublet-20, and doublet-30, respectively). For triplet and quadruplet CITs, first 1 IPI and first 2 IPIs, respectively, were 5 ms, whereas last IPI of initial burst varied from 5 to 30 ms (designated as triplet-5, triplet-10, triplet-20, triplet-30, and quadruplet-5, quadruplet-10, quadruplet-20, quadruplet-30). For all CITs, IPIs after the initial burst of pulses were 70 ms.

session. Subjects were familiarized with the experimental protocol and trained to relax during stimulation of their quadriceps muscle during both isometric and isotonic contractions. For each subject, the maximum voluntary isometric contraction (MVIC) was determined by using a burst superimposition technique (40) in which a 100-Hz, 10-pulse train at supramaximal stimulation intensity was delivered to the quadriceps muscle during an attempted maximal volitional contraction. If the stimulation produced a <5% increase in force, the force produced by the subject was determined to be the subject's MVIC. Conversely, if the stimulation produced a >5% increase in force, the subject rested 5 min before attempting another MVIC. All subjects produced MVICs within three trials during the training session. For all subjects, a minimum of 24 h elapsed between the training session and their experimental sessions.

Experimental sessions. All subjects were instructed to refrain from strenuous activity for at least 24 h before testing. Each of the 11 subjects participated in 1 experimental session that consisted of a prefatigue-testing sequence, a fatigue-producing sequence, and a fatigue-testing sequence (Fig. 2).

Before the experimental session, MVIC testing was conducted. The session was conducted only if the subject could perform an MVIC that was $\geq 95\%$ of the MVIC produced during the training session. If a subject was unable to meet this MVIC standard within approximately three attempts, the experimental session was rescheduled for another day.

For gravity correction purposes, the subject's leg was positioned at 0, 30, 45, and 60° of knee extension. The subject was encouraged to relax, and the leg was weighed at each angle by using the dynamometer's force transducer. Ten seconds of force data were collected at each angle, and the average force was used to calculate the limb's weight at each angle. For each knee joint angle, the weight of the limb was determined by using a cosine function that reflected the angle of the leg with respect to the ground. All four estimates of the limb's weight were averaged and used for gravity correction during data analysis.

Next, with the knee positioned at 90°, a 6-pulse, 100-pulses/s (pps) train was delivered to the muscle once every 5 s, first to potentiate the muscle and then to set the stimulation intensity. Stimulation intensity initially was adjusted to elicit

an isometric force $\cong 20\%$ of the subject's MVIC. Stimulation was continued until the force did not increase over three successive trains, which usually required ~ 10 stimulation trains. After force potentiation, the intensity was lowered and readjusted as necessary to produce a force equal to 20% of the subject's MVIC. The intensity was then kept constant throughout the remainder of the session in an attempt to recruit a consistent population of motor units from each subject's muscle.

After the stimulation intensity was set, the dynamometer was set in the isotonic mode by using the maximum available velocity setting (250°/s). Inspection of the velocity data revealed that the maximum velocity setting of 250°/s was never reached. The dynamometer settings were adjusted so that all movement began at 90° of knee flexion and provided resistance to knee extension that was equal to 10% of the subject's MVIC. The dynamometer's hydraulic system dampens the rate of acceleration at the turn points of movement. The dynamometer has three available accelerations: "low," "medium," and "high." The medium setting was used as a trade-off to reduce the dampening effects while maintaining system stability. Any dampening effect due to the dynamometer's hydraulic system is thought to be inconsequential because fluctuations in velocities that coincide with fluctuations in force could clearly be discerned.

Prefatigue-testing sequence. Immediately before the pre-fatigue-testing sequence, the muscle was repotentiated isometrically by using ten 6-pulse, 100-pps trains delivered once every 5 s. Within ~ 5 s after the last potentiating train, the dynamometer's isotonic mode was enabled, and the pre-fatigue-testing sequence commenced. The pre-fatigue-testing sequence consisted of a 70-ms interpulse interval constant-frequency train and 12 different catchlike-inducing trains (Fig. 1B). The 12 catchlike-inducing trains had an initial burst that contained 2, 3, or 4 pulses (i.e., a doublet, triplet, or quadruplet, respectively). For the doublet catchlike-inducing trains, the initial interpulse intervals were 5, 10, 20, or 30 ms. For triplet and quadruplet trains, the first one and first two interpulse intervals, respectively, were always 5 ms, whereas the last interpulse interval in the burst was 5, 10, 20, or 30 ms. The interpulse interval for all the pulses of the catchlike-inducing trains after the initial doublet, triplet, or

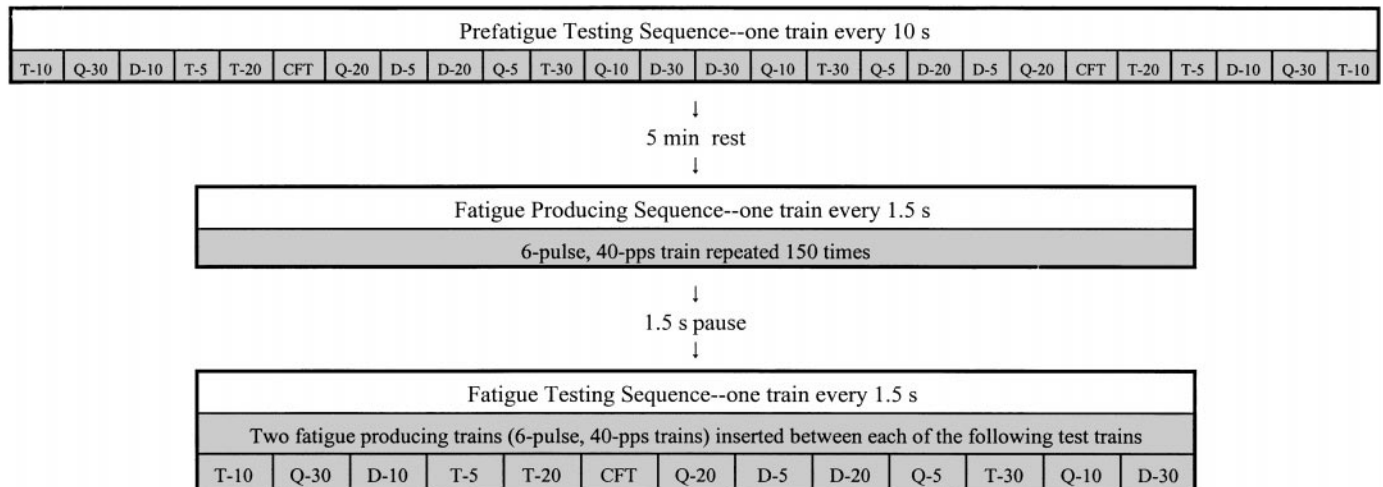


Fig. 2. Flow sheet illustrating prefatigue-testing, fatigue-producing, and fatigue-testing sequences that comprised the experimental protocol. During testing sequences, subjects were stimulated with a random order of trains that included CFT and 12 different CITs (see Fig. 1 for details). D, doublet CIT; T, triplet CIT; Q, quadruplet CIT; pps, pulses/s. Train order for an individual subject is shown. Each subject received his or her own random sequence. See text for additional details.

quadruplet was 70 ms (see Fig. 1B for additional details). One train was delivered every 10 s to prevent muscle fatigue. The order of the 13 trains was randomized for each subject and was repeated in reverse order for a total of 26 trains (Fig. 2).

Fatigue-producing sequence. The fatigue-producing protocol followed the prefatigue testing protocol after a 5-min rest. Before commencement of the fatigue-producing protocol, the muscle was repotentiated isometrically, and then the isotonic mode was enabled. A modified Burke's fatigue protocol (13) consisting of 6-pulse, 40-pps trains delivered to the muscle once every 1.5 s for a total of 150 contractions was used to fatigue the muscle. Unlike Burke's fatigue protocol that used isometric contractions, all contractions were isotonic. Six-pulse trains were used to allow the stimulation to end before the knee reached full extension. Additionally, short-stimulation trains were used because short bursts of activity typify activation patterns used to produce functional movements (26). Hennig and Lomo (26) showed that motor units typically fire in short bursts (up to 6 pulses) during normal activity in rats. Stimulators in cardiomyoplasty, a procedure in which a skeletal muscle is wrapped around the heart and stimulated to assist systole, all use 6-pulse trains (17) because the duty cycle is constrained by the cadence of the heartbeat. Finally, we anticipate that, as FES technology becomes more sophisticated, such applications will use shorter duration stimulation trains that more closely resemble physiological patterns of activation. The 1.5-s period allowed sufficient time for the leg to return to the start position.

Fatigue-testing sequence. Fatigue testing began immediately (1.5 s) after the last fatigue-producing train was delivered. All trains continued to be delivered in 1.5-s intervals. The subject's same prefatigue sequence (13 testing trains) was delivered with the exception that two fatigue-producing stimulation trains (6 pulse, 40 pps) were delivered before the presentation of each testing train. This was done to control for prior activation history and to ensure a stable level of fatigue during the fatigue-testing sequence.

Data management. All force responses were gravity corrected, and the four dependent variables were calculated by using custom-written software (Labview 4.0). The dependent measures of muscle performance were joint excursion, work, peak power, and average power produced during the shortening portion of each contraction. All performance measures were calculated by using the force, angle, and velocity data from the dynamometer during the period between force onset and maximum shortening (Fig. 3). Excursion was calculated as the maximum knee-joint displacement in degrees; work was calculated as the numerical integration (trapezoidal method) of force with respect to excursion over the time interval of force onset to the time of maximum shortening of the muscle; peak power was the maximum instantaneous power (force \times velocity); and average power was calculated by dividing the work by the time interval from force onset to maximum shortening of the muscle (Fig. 3). The prefatigue data analysis used the responses of the constant-frequency train and 12 catchlike-inducing trains collected during the prefatigue-testing protocol. The two occurrences of each train were averaged to help to control for previous muscle activation history. The responses to each train in the fatigue-producing sequence were recorded, and the percent decline for each dependent measure of muscle performance was calculated from the maximum response and the average response of the last three fatiguing trains. The fatigue data analysis used the responses of the 70-ms constant-frequency train and each catchlike-inducing train during the fatigue-testing sequence.

Data analysis. Separate analyses were performed for each dependent measure and for prefatigue and fatigued responses. First, the data were inspected to determine for which condition (fresh or fatigued) and for which performance measures the catchlike-inducing trains augmented performance. For each performance measure for which the catchlike-inducing trains produced augmentation, a one-way repeated-measures ANOVA was used to determine the optimal

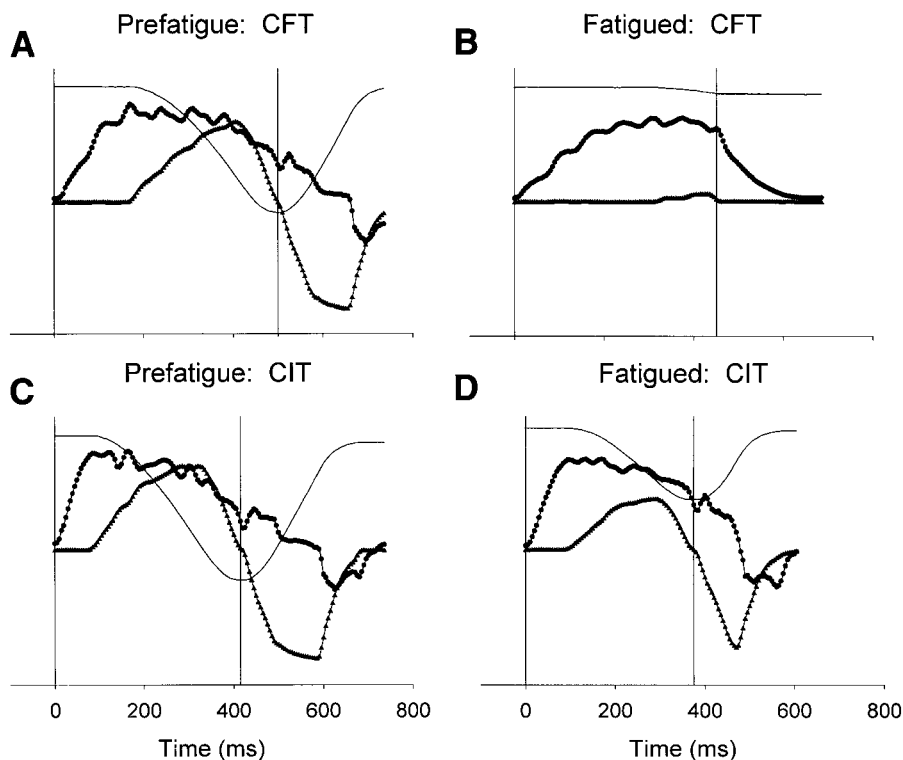


Fig. 3. Prefatigue (left) and fatigued (right) raw data traces from a representative subject. Gravity corrected force (\bullet), angle (line), and velocity (\blacktriangle) data in response to CFTs (A and B) and CITs (C and D). For prefatigue condition, CIT (C) had 1 brief initial IPI (doublet) equal to 5 ms. For fatigued condition, CIT (D) had 2 brief initial IPIs (triplet) equal to 5 ms. Excursion, work, peak power, and average power were calculated over the period of force onset to maximum shortening of the muscle (between vertical lines). Relative scales for force, excursion, and velocity are the same across all panels. Note that CITs produced peak excursions before CFTs and that they were able to maintain the rate of rise of force when fatigued.

interpulse interval duration within each group of catchlike-inducing trains (i.e., doublet, triplet, or quadruplet). As an example, if the doublet catchlike-inducing trains appeared to augment performance, a one-way ANOVA would be used to compare the four interpulse interval durations tested (5, 10, 20, and 30 ms). If the one-way ANOVA was significant, post hoc testing was used to identify the best interpulse interval. On the basis of prior studies (7, 9), an a priori assumption was made that the 5-ms interpulse interval for each catchlike-inducing train group would produce the best performance for all measures. Post hoc tests, therefore, used paired *t*-tests to compare the 5-ms duration with the 10-, 20- and 30-ms durations within each catchlike-inducing train group. Because this assumption was upheld (i.e., no interpulse interval produced greater augmentation than did the 5-ms interpulse interval), paired *t*-tests were used to compare the 5-ms catchlike-inducing trains with the constant-frequency train to determine whether the catchlike-inducing trains augmented force. If only one of the three catchlike-inducing trains (i.e., the doublet, triplet, or quadruplet) was significantly greater than the constant-frequency train, that catchlike-inducing train was designated as the optimal catchlike-inducing train. If more than one catchlike-inducing train type produced greater performance than did the constant-frequency train, then appropriate paired *t*-tests were used to determine the best overall catchlike-inducing train across catchlike-inducing train groups. For all analyses, an observation was significant at $P \leq 0.05$.

RESULTS

Fatigue-producing sequence. Complete data sets were collected for all 11 subjects. All of the muscle performance measures showed potentiation from the onset of the fatiguing protocol until approximately the 15th to 20th contractions, after which a steady decline was observed until approximately the 80th contraction (Fig. 4). After the 80th contraction, fatigue for each measure was relatively stable with ~ 42 , ~ 47 , ~ 50 , and $\sim 51\%$ decline, respectively, in excursion, work, peak power, and average power,

and average power from their respective maximum potentiated responses.

Burst interpulse interval. Overall, for the pre-fatigue data, only 6-pulse doublet and triplet catchlike-inducing trains produced greater excursion and work than did the 6-pulse constant-frequency trains. For peak and average power, however, all variable-frequency trains produced greater responses than did the constant-frequency trains (see Fig. 5). Although, whenever the catchlike-producing trains produced greater performance than did the constant-frequency trains, the 5-ms interpulse interval generally produced the greatest performance. No significant differences were noted in any of the performance variables as a function of varying the last interpulse interval within the burst of the catchlike-inducing trains (Fig. 5).

For fatigue-testing data, all catchlike-inducing trains produced greater responses than the constant-frequency trains for all performance measures. Significant differences were noted for the duration of the varied interpulse interval for some responses to doublet and triplet catchlike-inducing trains (Fig. 5), but for all dependent muscle performance variables, the 5-ms duration was as good as, if not better than, all other interpulse-interval duration. Thus our a priori assumption that the best interpulse interval was 5 ms was supported for both the pre-fatigue- and fatigue-testing conditions.

Number of pulses in the burst. For pre-fatigue data, the doublet catchlike-inducing train produced ~ 17 , ~ 21 , ~ 27 , and $\sim 38\%$ greater excursions, work, peak power, and average power (all significant at $P \leq 0.05$), respectively, than did the constant-frequency train (Fig. 6). Although augmentations produced by the optimal triplet catchlike-inducing train were also significant for the peak and average power measures, the

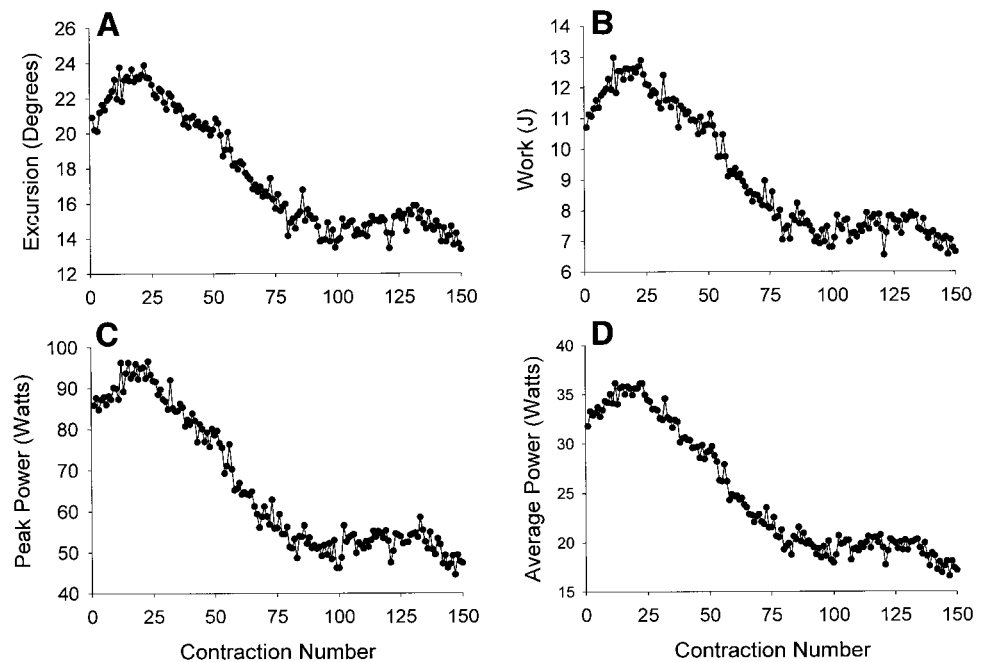


Fig. 4. Group excursion (A), work (B), peak power (C), and average power (D) in response to each train of fatigue-producing sequence. To produce fatigue, quadriceps femoris muscle was repetitively activated 150 times at a rate of 1 train/1.5 s by using 6-pulse, 40-pps trains. $n = 11$ Subjects. See text for additional details.

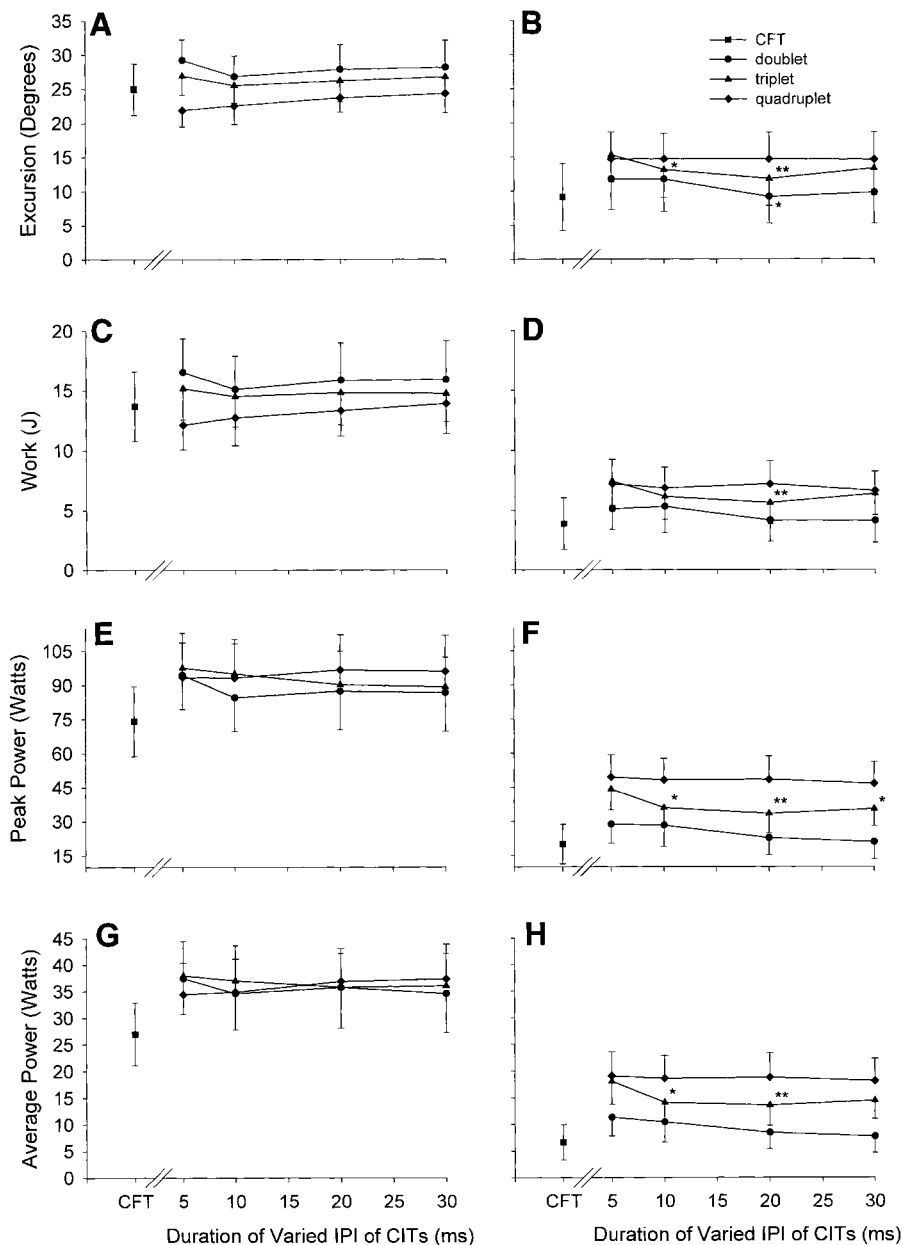


Fig. 5. Group prefatigue (left) and fatigued (right) excursion (A and B), work (C and D), peak power (E and F), and average power (G and H) in response to CFT and CITs. Values are means \pm SE; $n = 11$ subjects. CITs had 1, 2, or 3 brief initial IPIs (doublet, triplet, or quadruplet, respectively). For all performance measures in prefatigue condition, 1-way repeated-measures ANOVAs for each CIT type did not show an effect for IPI duration. Fatigued muscles showed that, for excursion, doublets and triplets showed a significant effect for IPI duration ($F = 3.576$, $P = 0.025$; $F = 5.508$, $P = 0.004$, respectively); for work responses, triplet CITs showed an effect for IPI duration ($F = 3.790$, $P = 0.020$); for peak power, triplet CITs showed an effect for IPI duration ($F = 4.701$, $P = 0.008$); and for average power, triplet CITs demonstrated an effect for IPI duration ($F = 4.079$, $P = 0.015$). Comparisons to 5-ms IPI within each CIT type: * $P \leq 0.05$; ** $P \leq 0.01$. See text for additional details.

relative augmentations were not significantly different from the optimal doublet catchlike-inducing trains. Because only the doublet catchlike-inducing train showed significant augmentations for all performance measures, the doublet catchlike-inducing train was chosen as the overall optimal catchlike-inducing train to produce isotonic contractions when the muscle was fresh.

For fatigued muscle, however, the doublet catchlike-inducing train did not produce significant augmentations over the constant-frequency train. Augmentations were nearly significant for excursion and average power (Fig. 6). In contrast, triplet and quadruplet catchlike-inducing trains consistently produced significantly greater excursion, work, peak power, and average power than did the constant-frequency train. The triplet catchlike-inducing train produced 67, 91, 121,

and 173% greater excursion, work, peak power, and average power, respectively, than did the constant-frequency train. Similarly, the quadruplet catchlike-inducing train produced 64, 86, 147, and 188% greater excursion, work, peak power, and average power, respectively, than did the constant-frequency train. No significant differences in the relative amount of augmentation were noted between the optimal 5-ms interpulse interval triplet and quadruplet catchlike-inducing trains.

DISCUSSION

The present study demonstrated that catchlike-inducing train activation was effective in augmenting joint excursion, work, peak power, and average power over constant-frequency train activation when isotonic contractions are elicited from the human quadriceps

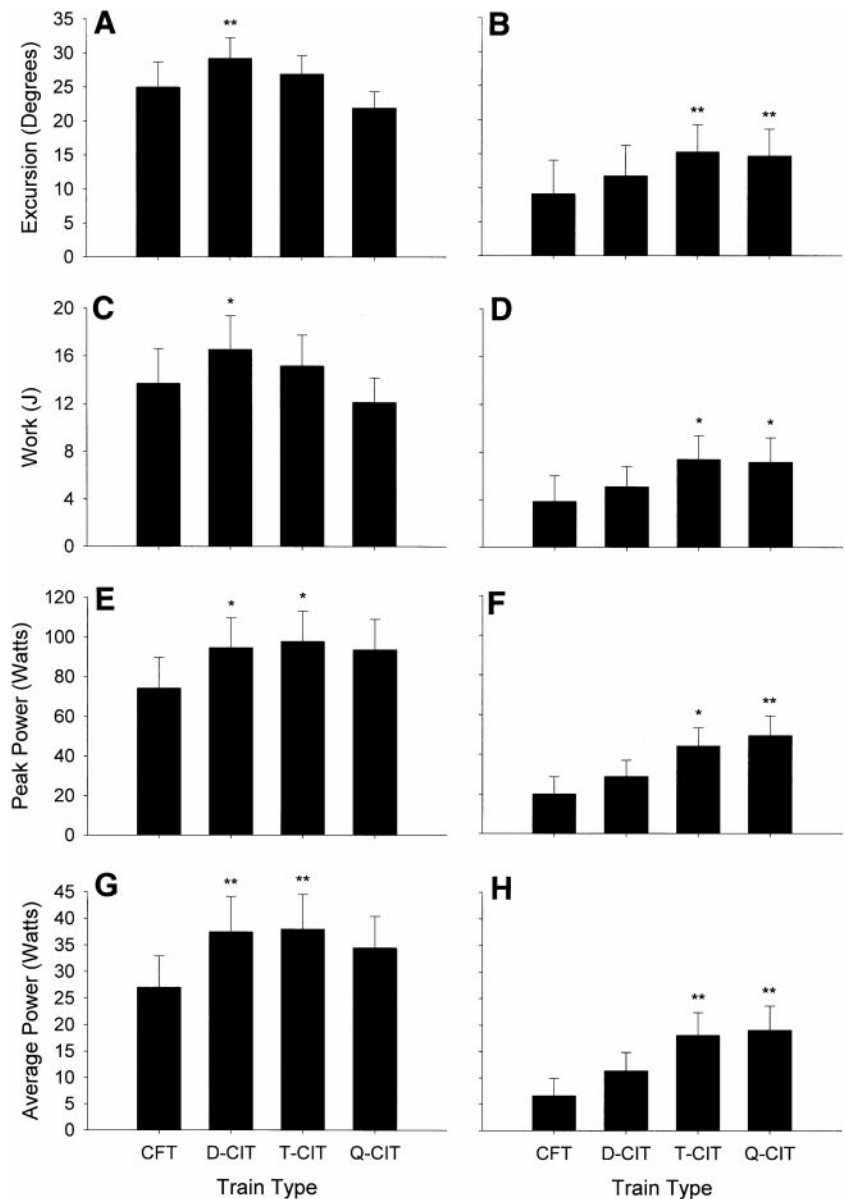


Fig. 6. Group prefatigue (*left*) and fatigued (*right*) excursion (A and B), work (C and D), peak power (E and F), and average power (G and H) in response to CFT and 5-ms IPI CIT. Values are means \pm SE; $n = 11$ subjects. CITs had 1, 2, or 3 brief IPIs (doublet, triplet, or quadruplet, respectively). Doublet, triplet, and quadruplet CITs are designated as D-CIT, T-CIT, or Q-CIT, respectively. Significant differences between each CIT and CFT: * $P \leq 0.05$; ** $P \leq 0.01$.

femoris muscle. Catchlike-inducing trains could augment muscle performance when the muscle was either fresh or fatigued. For fresh muscle, the optimal catchlike-inducing train was a doublet catchlike-inducing train with an initial interpulse interval equal to 5 ms. In fatigued muscle, the optimal catchlike-inducing train had an initial triplet of pulses, with the first two interpulse intervals equal to 5 ms. Both 5-ms interpulse interval triplet and quadruplet catchlike-inducing trains produced greater performance than did the constant-frequency train, but because no significant differences were noted between them for any measure, and because triplet catchlike-inducing train showed better performance than did the quadruplet catchlike-inducing train when the muscle was not fatigued, the triplet catchlike-inducing train was chosen as the optimal catchlike-inducing train. The relative augmentation was greater in the fatigued condition than when fresh.

As anticipated, the present study found that a catchlike-inducing train with one, two, or three initial interpulse intervals equal to 5 ms produced the greatest joint excursion, work, peak power, and average power. Previous investigations of the human quadriceps femoris muscle revealed that 5 ms was the best initial interpulse interval for catchlike-inducing trains during isometric contractions (3, 9, 29) and during concentric and eccentric isovelocity contractions (7). Thus it appears that burst-interpulse interval duration of 5 ms is a robust interval to use for catchlike-inducing train activation no matter what the mode of activation (i.e., isometric, concentric and eccentric isovelocity, and isotonic contractions) of the human quadriceps femoris muscle.

In animal models, initial catchlike-inducing train interpulse intervals of 5–10 ms were also optimal. In isometric contractions of cat medial gastrocnemius muscle, Zajac and Young (44) found that an initial

doublet of 5–10 ms produced the greatest force-time integrals. In cat single tibialis posterior motor units, Bevan and colleagues (1) used “optimized” variable-frequency trains with two short initial interpulse intervals equal to 10 ms. Hennig and Lomo (26) found that the optimal initial interpulse interval was 5 and 10 ms, respectively, in fast and slow motor units of rat extensor digitorum longus muscles. Binder-Macleod and Barrish (4) also have found catchlike-inducing trains with one or two initial interpulse intervals equal to 10 ms to be optimal for the rat soleus muscle. In frog sartorius muscle, Stevens (41) found that 5-ms interpulse-interval doublet and triplet initiated trains produced the greatest net work during isovelocity oscillatory length changes. A triplet train with 5-ms interpulse intervals and a total of 6 pulses could produce 80% of the net work that a 17-pulse constant frequency train could produce. Thus, although there are subtle differences in burst characteristics (i.e., 5- to 10-ms initial interpulse interval; one or two brief initial interpulse intervals) among species and muscle types, the presence of augmentation in performance when catchlike-inducing trains are used over constant-frequency trains is robust.

Previous studies examining the use of catchlike-inducing trains during nonisometric contractions have noted that the relative augmentation by catchlike-inducing trains tended to be less than the augmentations observed for isometric contractions (7, 16). Sandercock and Heckman (38) showed that force augmentation produced by catchlike-inducing activation decreases during isovelocity shortening movements compared with isometric contractions for cat soleus whole muscle and single motor units. Callister and colleagues (16) reported a slight decline in the force augmentation with catchlike-inducing train stimulation during shortening and lengthening isovelocity contractions compared with isometric contractions for the turtle external gastrocnemius muscle. In previous studies, we observed as much as 72% augmentation in peak force and 52% augmentation in force-time integrals during isometric contractions (9); however, we showed only ~5, 6, 14, and 35% greater force-time integral, peak force, average force, and rate of rise of force, respectively, during concentric isovelocity contractions when the muscle was fresh (7). Similar to isometric contractions, these enhancements were more pronounced during fatigue (~18, 30, 28, and 41%, respectively) but less than that observed isometrically (7). In contrast, catchlike-inducing trains are less effective in enhancing force production during eccentric isovelocity contractions but did produce a marked enhancement in the rate of rise of force (7). Augmentations by catchlike-inducing trains in the present study on isotonic contractions (see RESULTS) are relatively large, however, especially when the muscle is fatigued. The relative performance of catchlike-inducing trains vs. constant-frequency trains is related to the rate of rise of force in response to the stimulus trains.

Catchlike-inducing trains produce greater excursion, work, peak power, and average power than do constant-

frequency trains, because catchlike-inducing trains produce more rapid rates of rise of force. Faster rates of rise of force enable the preload on the muscle to be exceeded earlier during the stimulation train. This allows more of the train to contribute to muscle shortening. For example, when the muscle is fresh (Fig. 3), constant-frequency trains produce movement that started ~165 ms after onset of force production, whereas the optimal catchlike-inducing train produced movement ~75 ms after the onset of force. When the muscle is fatigued, constant-frequency trains and the optimal catchlike-inducing train produced movement at ~320 and ~85 ms after force onset, respectively. Thus, when the muscle is fatigued, catchlike-inducing trains retain their ability to produce rapid rates of rise of force and to cause muscle shortening, whereas constant frequency trains displayed slowing in the rate of rise of force. Slowing in the rate of rise of force caused the constant-frequency trains to become functionally ineffective because they could not exceed preload until near the end of the stimulus train and could not produce appreciable displacement. This functional impairment of the constant-frequency train resulted in augmentations by the catchlike-inducing trains that were of greater magnitude than that previously observed for isometric (9–11, 32) and isovelocity contractions (7). Stevens (41) also noted that catchlike-inducing trains augmented net work per cycle during oscillatory length changes in isolated frog sartorius muscles to a much greater extent than augmentations observed during isometric contractions.

Interestingly, catchlike-inducing trains could produce modest augmentations in isotonic performance when the muscle was fresh. Generally, for isometric contractions, no augmentation has been noted by catchlike-inducing trains over constant-frequency trains when the muscle was near optimum length and was not fatigued (9). For isometric contractions when the quadriceps femoris muscle was held in a shortened position, catchlike-inducing trains, comparable to those used in this study, elicited augmentations of 21% in peak force and 7% in force-time integral when the muscle was fresh (32). During concentric isovelocity movements (7), modest augmentations were noted when the muscle was fresh. Only a small augmentation of average force was noted during eccentric isovelocity movements for the fatigue state. The ability to produce greater augmentation in performance at short vs. near optimal length isometric contractions and for concentric vs. eccentric isovelocity movements when the muscle is fresh may be due to enhanced muscle stiffness and enhanced Ca^{2+} release produced by the initial burst of the catchlike-inducing train.

Parmigianni and Stein (35) proposed that enhanced muscle stiffness caused by catchlike-inducing train stimulation is due to greater efficiency in taking up the series elastic components of the muscle. They likened 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 train contribute primarily to increasing force (35). Wilson and colleagues (43) suggested that a stiff musculotendinous system helped to maximize isometric and concentric performance by improving contractile component length, rate of shortening, and transmission of force from the contractile component to the skeletal structures. The common factor in force augmentation observed for the present and previous studies when the muscle was fresh is that, in all cases, the effective series elastic component was greater when isometrically held in a shortened position (32) or continually increasing as the muscle was moved to a shorter position (7) than when held near optimal length. In contrast, during eccentric conditions (7) or when the muscle was held isometrically at a long length (10, 11), the muscle was either being passively stretched or placed in a stretched position so that there would be less of an advantage in taking up the series elastic component by the catchlike-inducing trains.

Changes in muscle stiffness may also explain the greater augmentation seen during fatigue. Curtin and Edman (20) noted a decrease in the stiffness of frog muscle fibers with fatigue and attributed the decrease in muscle stiffness to fewer attached cross bridges. Thus, if stiffness decreases with fatigue, then improving muscle stiffness with catchlike-inducing train activation may be more efficacious in augmenting force when the muscle is fatigued.

Duchateau and Hainaut (23) showed that another mechanism by which catchlike-inducing trains augment force is through increased Ca^{2+} release from the sarcoplasmic reticulum by the initial high-frequency burst. This present study and previous studies showing force augmentation in fresh muscle (7, 32) investigated muscle that was either shortening during the contraction or already in a shortened state. Ca^{2+} release per pulse (12, 42) and Ca^{2+} sensitivity of the myofibrils (18, 24, 25) have both been found to be diminished at short vs. long muscle lengths. Thus greater Ca^{2+} release by catchlike-inducing trains could partially compensate for the decreased Ca^{2+} release or sensitivity when the muscle is shortening or held at short lengths.

Recent work suggests that augmentation by catchlike-inducing trains parallels the development of low-frequency fatigue (37). In fresh muscle, catchlike-inducing trains may not produce augmentation over constant-frequency trains because of their shorter train duration unless Ca^{2+} release or sensitivity was reduced (i.e., when shortening or held at a short length). Because catchlike-inducing trains augment Ca^{2+} release from the sarcoplasmic reticulum, catchlike-inducing trains are less susceptible to impairments in excitation-contraction coupling associated with low-frequency fatigue (37) and can maintain their rates of rise of force when fatigued (9, 7, 10). Thus, although the catchlike-inducing trains in the present study have shorter train durations than do the constant-frequency trains, the ability to produce a more rapid rate of rise of force allows the catchlike-inducing trains to markedly enhance isotonic muscle performance.

Clinical implications. This study demonstrated the efficacy of 6-pulse catchlike-inducing trains in producing isotonic shortening contractions, which more closely mimic physiological movements than other conditions we have studied. Because catchlike-inducing trains produce greater joint excursion, work, peak power, and average power than do constant-frequency trains, regardless of fatigue condition, they may help to improve functional electrical stimulation applications that require stimulation to produce limb movements. One possible limitation is that the population of motor units activated with transcutaneous stimulation may vary because of shifting of the electrodes as the leg goes into extension. No gross discontinuities in the force trace were observed (e.g., see Fig. 2), which suggests that the motor unit population being recruited by the stimulation is consistent throughout the movement. Regardless, transcutaneous stimulation in which muscle shortening and limb movement occurs is often required in FES applications.

Conclusions. This study shows that, for the load condition tested, 6-pulse catchlike-inducing trains produced greater joint excursions, work, peak power, and average power than did 6-pulse constant-frequency trains, regardless of fatigue condition. When the muscle was fresh, a catchlike-inducing train with a single brief initial interpulse interval equal to 5 ms produced the greatest performance, whereas two initial interpulse intervals of 5 ms were optimal when the muscle was fatigued. Because catchlike-inducing trains were effective during shortening isotonic contractions, which closely mimic physiological movement, they may be of benefit during functional electrical stimulation applications. This study, however, only tested a single catchlike-inducing train base frequency, corresponding to an interpulse interval of 70 ms. Additionally, only one load condition was investigated. Future studies of catchlike-inducing trains to produce repetitive isotonic contractions are needed to explore the boundary conditions of base frequency and load on the efficacy of catchlike-inducing trains to produce isotonic contractions.

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Address for reprint requests and other correspondence: S. A. Binder-Macleod, Dept. of Physical Therapy, Univ. of Delaware, 303 McKinly Laboratory, Newark, DE 19716 (E-mail: sbinder@udel.edu).

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