Discharge patterns in human motor units during fatiguing arm movements

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Griffin, L., S. J. Garland, and T. Ivanova. Discharge patterns in human motor units during fatiguing arm movements. J. Appl. Physiol. 85(5): 1684–1692, 1998.—The purpose of this study was to determine whether short interspike intervals (ISIs of <20 ms) would occur naturally during voluntary movement and would increase in number with fatigue. Thirty-four triceps brachii motor units from nine subjects were assessed during a fatigue task consisting of fifty extension and fifty flexion elbow movements against a constant-load opposing extension. Nineteen motor units were recruited during the beginning of the fatigue task; the number of short ISIs was 7.1 ± 4.1% of the total number of ISIs in the first one-third of the task (unfatigued state). This value increased to 11.8 ± 5.9% for the last one-third of the task (fatigued state). Fifteen motor units were recruited during the fatigue task and discharged, with 16.4 ± 6.0% of short ISIs in the fatigued state. For all motor units, the number of short ISIs was positively correlated (r 2 = 0.85) with the recruitment threshold torque. Short ISIs occurred most frequently at movement initialization but also occurred throughout the movement. These results document the presence of short ISIs during voluntary movement and their increase in number during fatigue.

IN ISOMETRIC CONTRACTIONS, a short interspike interval (ISI) (10-ms duration) positioned at the onset of a stimulus train can increase peak force production (7, 27, 37) and can decrease the rate of fatigue (4, 7). Sandercoc and Heckman (32) tested, in anesthetized cats, the effect of eccentric and concentric contractions on the potentiation of force from stimulation trains incorporating short ISIs. They demonstrated that the initial force produced by a short ISI was large during movement, although the force did not remain as high throughout the movement as in an isometric contraction. The role of short ISIs during volitional movement in humans remains unknown.

During sustained submaximal isometric contractions of the elbow flexor muscles, Maton and Gamet (29) observed that newly recruited motor units started to fire in bursts and, within each burst, the first ISI was usually the shortest. The incidence of doublets during anisometric contractions has been rarely investigated, largely because of technical difficulties. We have overcome the technical limitations by using a subcutaneous fine-wire electrode that has been documented to remain stable during single-joint movements (16) and enables individual motor units to be followed during dynamic fatiguing contractions (30).

In our previous study on fatiguing arm movements, we found that the incidence of short ISIs was low during arm movements performed with a visually guided phase-plane tracking paradigm (30). A phase-plane tracking paradigm dictates the arm velocity as a function of arm position throughout the movement, thereby ensuring precision in the timing of the arm movement. Short ISIs may not have been utilized in the phase-plane tracking experiments because the subsequent increase in the rate of force development would have made it difficult for the subject to reproduce the phase-plane template accurately. We hypothesized that a step-tracking paradigm, in which only arm position is dictated, would result in an increased occurrence of short ISIs because it requires less skill and concentration than does the phase-plane tracking paradigm. It is possible that an easier tracking paradigm would incorporate different descending commands (and hence different synaptic inputs) that could enable the expression of short ISIs. Although this suggestion is highly speculative, there is some support for the notion. For example, H-reflex amplitude declined in human muscle with increases in task difficulty (25); thus decreasing the difficulty of the tracking paradigm may change the motoneuron output.

The purpose of this study was to investigate motor unit firing patterns of the lateral head of the triceps brachii muscle during submaximal dynamic fatiguing contractions. The primary objectives were to determine whether the discharge of motor units during movement would include short ISIs and whether the numbers of short ISIs would increase during muscle fatigue. An increase in the occurrence of short ISIs with fatigue would be consistent with the notion that they may be utilized to augment force production and decrease the rate of fatigue.

METHODS

Subjects. Three male and six female right-handed, healthy volunteers (age 21–40 yr) participated in the experiment. Subjects reported no history of metabolic or neuromuscular disorders. The experimental procedures were approved by the University Ethics Committee.

Experimental protocol. Subjects were seated with their right arm abducted 85° and were attached to a manipulandum at the elbow and wrist. The elbow was secured over the pivot point of the manipulandum handle. The wrist was placed in a neutral pronation/supination position by a cuff situated immediately proximal to the styloid processes of the ulna and radius. The subject’s hips and shoulders were stabilized with straps. Bipolar surface electromyographic (EMG) electrodes (2 cm in diameter) were placed longitudi—

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nally, 2 cm apart, over the muscle bellies of the biceps brachii and lateral head of the triceps brachii muscles. A bipolar subcutaneous fine-wire electrode was inserted with a hollow needle over the middle aspect of the lateral head of the triceps brachii to record motor unit potentials (15).

Subjects performed a fatigue task consisting of 50 extension and 50 flexion movements of the right elbow in the horizontal plane. The task was performed against a constant load that was set at 20% of the maximal voluntary contraction (MVC) of the elbow extensor muscles. The load that opposed elbow extension was placed on the handle of the manipulandum by a torque motor to induce fatigue of the triceps brachii muscle. Subjects were instructed to perform the movements “as fast and as accurately as possible” and hold the manipulandum against the load at the end points of the movement until the next target appeared on the screen. Flexion and extension movements were performed once every 4 s; thus each movement was separated by a sustained isometric contraction. Movement end points were displayed as vertical lines on a screen (step-tracking presentation). As subjects moved the manipulandum handle, they were provided with visual feedback of the angular displacement of the handle, displayed as a thin vertical line, which moved horizontally across the screen. Subjects matched the visual end-point targets, which were not bounded by any mechanical stops. Movements were performed from 70 to 110° of elbow flexion.

Measurements of elbow extension MVC and the recruitment threshold torque of motor units were taken before and after the fatigue task. Two MVCs were measured before and after the fatigue task with a dynamometer placed against the wrist cuff at an elbow angle of 90°. Subjects were instructed to increase the contraction force gradually to a maximum by the end of 5 s. The largest of the two MVC torque measurements was taken as the MVC of the subject. To determine the recruitment threshold torque of the motor units, visual feedback was provided on the screen while the subjects performed five ramp isometric contractions. Subjects were requested to hold their elbow at a 90° angle against a steadily increasing torque that pushed their elbow toward flexion. The computer-generated torque increased at a rate of 2 N·m·s⁻¹. Recruitment threshold torque was calculated this line to the end-point targets, which were not bounded by any mechanical stops. Movements were performed from 70 to 110° of elbow flexion.

Data recording and analysis. All data were recorded on VHS tape for off-line analysis. The angular position and velocity of the manipulandum handle (and hence the forearm) were recorded from a precision potentiometer and tachometer, respectively. These data were digitized off-line with a sampling rate of 1,000 Hz. Acceleration was determined by a two-point derivative of the velocity signal. The timing of movement onset, peak velocity, and movement end were obtained from the acceleration traces (16).

The surface EMG activity from the biceps brachii and triceps brachii muscles was filtered at 30–2,000 Hz, full-wave rectified, and subsequently digitized off-line at a sampling rate of 2,000 Hz. The EMGs for each movement were aligned to movement onset and averaged for the first one-third and the last one-third of the fatigue task. The average EMG data were integrated over 1.2 s starting 200 ms before movement onset.

The subcutaneous motor unit potentials of the lateral head of the triceps brachii muscle were filtered at 10–10,000 Hz and digitized off-line at a sampling rate of 10,000 Hz. Individual motor unit potentials were identified by computer using a template-matching algorithm (SPS-8701). This algorithm allows identification of individual waveform potentials on the basis of shape and amplitude. Unmatched potentials were analyzed further by using a waveform subtraction algorithm. Examples of motor unit waveforms are displayed in Fig. 1. All short ISIs (<20 ms) were analyzed twice to verify that any increase with fatigue was not due to an increase in false-positive errors. We considered intervals of <20 ms duration to be short ISIs [≥20 ms being consistent with the range of intervals that has been demonstrated to evoke the catch-like property in mammalian muscle (7, 9, 37)].

For each identified motor unit, the motor unit discharges over a 1.2-s interval (starting 200 ms before movement onset) were analyzed for each movement. The number of short ISIs was normalized to the total number of ISIs for each motor unit to ensure that any change in the number of short ISIs was not merely a function of a change in the probability of occurrence because of a change in overall discharge rate. In addition, short ISIs were placed into three 200-ms epochs surrounding movement onset, peak velocity, and movement end to determine the point in the movement at which short ISIs occurred most frequently.

Statistical analysis. The first 34 movements (first one-third) and the last 34 movements (last one-third) of the fatigue task were considered as unfatigued and fatigued states, respectively, as determined in a previous series of experiments (30). Movement kinematics (peak acceleration, peak deceleration, and duration) were contrasted between the first and last one-third of the fatigue task by using two-way repeated-measures ANOVA [factors: movement type (flexion or extension) and fatigue (first or last one-third)]. The same ANOVA method was used to contrast the surface integrated EMG from biceps and triceps in the unfatigued and fatigued states. Group means for MVC extensor torque and for motor unit recruitment threshold torque were compared with paired t-tests before and after the fatigue task.

Motor units were separated into two groups: motor units that were active from the beginning of the task and motor units that were newly recruited during the performance of the fatigue task. Statistical analysis was performed only for the first 10 movements because few motor units were newly recruited from the beginning of the fatigue task in the flexion movements. The distribution of ISIs was determined by using the Kolmogorov-Smirnov test with descriptive measures of skewness, kurtosis, and median ISI. Because the ISIs during fatiguing arm movements were not normally distributed (see results), a Mann-Whitney rank sum test was performed to compare the ISIs in the first and last one-third of the fatigue task for the motor units that were active from the beginning of the task. The mean number of normalized short ISIs was compared for the first and the last one-third of the fatigue task by using a paired t-test. Comparisons between the two groups of motor units (described above) were made for the number of normalized short ISIs and the median ISI by using independent t-tests in the last one-third of the task because the newly recruited motor units were not active throughout the first one-third of the task. An association between the number of short ISIs in the last one-third of the fatigue task and the recruitment threshold torque of the motor unit was examined by using linear-regression analysis. A one-way repeated-measures ANOVA with post hoc Student-Newman-Keuls test was used to determine whether there were any differences in the number of short ISIs at different phases of the movement (i.e., onset, peak velocity, end). All statistical analyses were performed with an α-level of significance of P = 0.05. Data in the text are presented as means ± SD.
RESULTS

Discharge patterns during movement. The subcutaneously recorded EMG from a single extension movement (number 43 of 50 extension movements) is displayed in Fig. 1. The potentials from four motor units are identified with different symbols, and their waveforms are displayed underneath. The waveforms are superimposed to demonstrate their consistent shape and the ability to discriminate accurately between motor units. Two of the motor units recorded during this movement discharged with short ISIs (underlined). The influence of fatigue is evident by the tremor at the end of the acceleration trace. Of the four motor units, one motor unit discharged with a short ISI as the first interval. Either the other units did not demonstrate short ISIs, or the short ISIs occurred later in the movement.

One type of short ISI evident in human voluntary contractions is called a “doublet.” A doublet is followed invariably by a long interval, compared with the regular discharge rate (3). Joint-interval histograms were utilized to determine the impact of a short ISI on the subsequent ISI. Figure 2A provides a representative example of one motor unit in which each ISI (denoted as i on the abscissa) is plotted against that of the next ISI (denoted as i + 1 on the ordinate) for the first and last one-thirds of the extension movements. The short ISIs form a vertical column (Fig. 2A, left), and the ISIs representing the regular discharge of the motor unit form a separate group (center). This figure demonstrates that the interval following the short ISI was not invariably longer than the regular discharge. The ISI histograms for the same motor unit are presented in Fig. 2B. This figure illustrates that the overall distribution of ISIs did not shift to lower values with fatigue; the median ISI was 80 ms in both the first and last one-third of the fatigue task. Thus the number of short ISIs increased as a separate distribution.

To quantify the overall distribution of ISIs, the Kolmogorov-Smirnov test revealed that only 2 of the 34 motor units had ISIs that were normally distributed. The skewness and kurtosis for all motor units were 0.88 ± 0.3 and 0.49 ± 1.26, respectively. For those motor units that were active from the beginning of the task, there was no difference in the ISIs between the first and last one-thirds of the fatigue task, as assessed by the Mann-Whitney rank sum test. The average values for the first and last one-thirds of the fatigue task were 75.7 ± 12.2 and 77.6 ± 11.9 ms for median ISI, 0.88 ±
Discharge patterns during fatigue. The presence of muscle fatigue was indicated by a decline in the MVC peak torque and an increase in the surface EMG during the performance of the task. The mean MVC peak torque decreased by $28.6 \pm 11.5\%$ ($12.6 \pm 6.6\ N\cdot m$) after the fatigue task. The mean integrated surface EMG increased by $22.1 \pm 23.9\%$ in the triceps brachii and $14.8 \pm 17.8\%$ in the biceps brachii muscles. However, the EMG activity in the biceps muscle during the performance of the task was so low (see Fig. 1) that the percent increase in biceps brachii was unlikely to be physiologically important.

A total of 34 motor units were recorded from the lateral head of triceps brachii muscle, 33 of which demonstrated short ISIs. Of these, 19 motor units were active from the beginning of the task, and 15 motor units were newly recruited during the performance of the fatigue task. During the extension movements, motor units that were active from the beginning of the fatigue task demonstrated a significant increase (from $7.1 \pm 4.1$ to $11.8 \pm 5.9\%$) in the number of short ISIs normalized to the total number of ISIs (Fig. 3, top). That is, ~7% of the total number of ISIs in the first one-third of the fatigue task were short ISIs compared with 12% in the last one-third of the fatigue task.

Fig. 2. A: joint-interval histogram from a single motor unit during first one-third (○) and last one-third (●) of extension movements. Each ISI (i) is plotted against the consecutive interval (i + 1). ISIs longer than 200 ms were excluded from analysis. Intervals following short ISIs are in vertical column near ordinate and can be contrasted to ISIs in regular discharge. B: ISI histograms for the same motor unit in first one-third (open bars) and last one-third (solid bars) of task. Total no. of ISIs in first and last one-thirds of task was 161 and 158, respectively. The increase in short ISIs was independent of any increase in overall discharge rate.

Fig. 3. No. of short ISIs expressed as %total no. of ISIs (top) and median ISIs (bottom) are plotted for all motor units. Data from last one-third (fatigue) of extension movements are plotted against first one-third (prefatigue). ●, Motor units that were active from beginning of task. Those motor units that were newly recruited during fatigue task (○) lie along ordinate because they were not active throughout entire first one-third of task.
However, the overall discharge rate for these 19 motor units (median ISI with the short ISIs excluded) did not change (Fig. 3, bottom). Thus the increase in the occurrence of short ISIs with fatigue was independent of any increase in motor unit firing rate or any increase in the total number of ISIs, because the number of short ISIs was normalized to the total number of ISIs for each motor unit.

Motor units that were newly recruited during the fatigue task demonstrated significantly more short ISIs (16.4 ± 6.0% of the total number of ISIs, Fig. 3, top) in the last one-third of the fatigue task than did motor units that were active from the beginning of the task (11.8 ± 5.9%). The average of the median ISIs for newly recruited motor units of 67.0 ± 11.9 ms was significantly lower than that for the motor units that were active from the beginning of the task. However, motor units that were newly recruited during the task discharged significantly fewer times per movement trial in the last one-third of the fatigue task than did motor units that were active from the beginning of the task (6.8 ± 3.6 and 8.9 ± 2.3 discharges/movement trial, respectively). Often newly recruited motor units discharged only during the acceleration phase of the movement, whereas motor units that were active from the beginning of the task discharged throughout the movement and into the holding phase between movements. Thus, in this fatiguing arm movement paradigm, the median ISI may not epitomize the overall level of activity of a motor unit.

The number of short ISIs in the last one-third of the fatigue task for all motor units combined was positively correlated with the recruitment threshold of the motor unit ($r^2 = 0.85$, Fig. 4). The majority of short ISIs occurred around movement onset, although short ISIs also occurred around peak velocity and movement termination; post hoc multiple comparisons revealed that significantly more short ISIs were situated at the onset of movement than during the course of the movement or movement end. The occurrence of short ISIs within the movement is depicted in Fig. 5. During the first one-third of the fatigue task, the percentage of short ISIs that occurred around movement onset was 3.2 ± 2.9% of total ISIs; however, 1.8 ± 2.5 and 2.0 ± 2.4% of total ISIs occurred around peak velocity and movement end, respectively. During the last one-third of the fatigue task, the percentage of short ISIs increased to 3.9 ± 3.0, 2.8 ± 3.3, and 3.4 ± 3.6% surrounding movement onset, peak velocity, and movement end, respectively. Newly recruited motor units demonstrated more short ISIs than did motor units that were active from the beginning of the task, particularly at movement onset; the percentage of short ISIs was 7.0 ± 5.3, 5.4 ± 6.5, and 2.6 ± 3.1% around movement onset, peak velocity, and movement end, respectively. The large SD arose from the variability among motor units; that is, one motor unit failed to demonstrate any short ISIs, whereas as many as 31% of total ISIs were short in one of the newly recruited motor units (see also Fig. 3, top).

During flexion movements, the majority of short ISIs occurred at peak velocity, i.e., at the onset of the triceps brachii EMG activity. However, only four motor units were recorded during the flexion movements from the beginning of the task. The number of normalized short

![Fig. 4. Relationship between no. of short ISIs in last one-third of fatigue task and prefatigue recruitment threshold of motor units. Short ISIs are expressed as %total no. of ISIs for each motor unit. Motor units that were active from beginning of task; o, newly recruited motor units. No. of short ISIs produced by motor unit is positively correlated with recruitment threshold of motor unit as represented by linear-regression line of best fit shown. MVC, maximal voluntary contraction.](image1)

![Fig. 5. No. of short ISIs for all recorded motor units expressed as %total no. of ISIs according to when they occurred in extension movements (i.e., at movement onset, peak velocity, or movement end). Motor units active from beginning of task for first one-third (open bars) and last one-third of task (solid bars) are shown. Hatched bars, newly recruited motor units for last one-third of fatigue task.](image2)
ISIs in these four units increased from $5.8 \pm 5.0\%$ in the first one-third to $11.3 \pm 3.1\%$ in the last one-third of the task. Nine motor units, previously active during extension movements, started to discharge during the last one-third of the flexion movements. The limited number of motor unit discharges, however, did not permit statistical analysis.

Movement kinematics. The mean duration of all extension and flexion movements for all nine subjects was $0.66 \pm 0.08$ s; this value did not change with fatigue. Because the rate of contraction can influence motor unit recruitment thresholds (8) and the discharge pattern of motor units (19), we wanted to ensure that an increase in the number of short ISIs during the task was attributable to muscle fatigue and not due to a change in movement acceleration. Thus the average acceleration in the first one-third of the task was compared with that of the last one-third by using repeated-measures ANOVA. There was no significant difference between the mean peak acceleration ($935.1 \pm 267.5$ vs. $914.6 \pm 293.5$ m/s$^2$) and deceleration ($753.8 \pm 185.6$ vs. $684.0 \pm 208.9$ m/s$^2$) during the first one-third and the last one-third of the fatigue task, respectively.

Motor unit recruitment thresholds. Motor unit recruitment threshold torques could be determined for 27 of the 34 motor units. Four motor units were not recruited during the ramps, and three motor units discharged too irregularly to determine an accurate recruitment threshold. The mean prefatigue recruitment threshold torque for motor units that were active from the beginning of the fatigue task was $5.5 \pm 3.8$ N·m (12.4 \% MVC) and was $10.1 \pm 2.9$ N·m (28.5 \% MVC) for newly recruited motor units. There was a significant decrease in the absolute torque for recruitment as seen in Fig. 6, top. Those motor units that demonstrated a modest increase in recruitment threshold following fatigue were low-threshold motor units from two subjects. When the recruitment threshold torque was expressed as a proportion of prefatigue and postfatigue MVCs (Fig. 6, bottom), there was no significant change with fatigue. The recruitment order of the motor units during the isometric ramp contractions was the same before and after the fatigue task.

DISCUSSION

The main finding of this study was that motor units discharged with short ISIs (<20 ms) during movements performed with a step-tracking paradigm. Furthermore, motor units discharged with more short ISIs during fatigue. The number of short ISIs present during fatigue was positively correlated with the recruitment threshold torque of the motor unit. Most short ISIs occurred at movement initiation, but short ISIs also occurred at movement termination and during the movement phase.

Discharge pattern during movement. Two types of short ISIs have been described in human voluntary contractions by Bawa and Calancie (3). One type of short ISI evident in human voluntary contractions was called a doublet. A doublet was followed invariably by a long interval, compared with the regular discharge rate, and occurred at low levels of force (3). Doublets have been observed during isometric contractions in a variety of muscles in humans, e.g., trapezius (12, 22), flexor carpi radialis (3), and tibialis anterior (1), particularly on initiation of motor unit activation (3). The short ISIs evident in the present experiment do not fit completely into the definition of a doublet because the interval following the short ISIs was not always longer than the ISI seen during regular discharge. However, it is important to reiterate that all of the previous studies were performed by using isometric contractions. The phenomenon of a long ISI always following a doublet may not be present during movement because the...
background excitation level of the motoneuron is not constant throughout the movement.

A second type of short ISI occurred at the onset of ballistic isometric contractions (13, 19). These short ISIs may be similar to those found in cat motoneurons with ramp intracellular injection of current (2). In the present study, the majority of short ISIs was found in the acceleration phase of movement, but the short ISIs were not always the first interval, and short ISIs were also found as the limb was decelerating (see Figs. 1 and 5). Thus the location of the short ISIs in the movement suggests that these short ISIs did not result solely from massive synaptic inputs to initiate ballistic movements. Furthermore, the time to peak force in these movements was twice as slow as that in the ballistic contractions studied by Desmedt and Godaux (13): 300 vs. 150 ms, respectively.

Discharge pattern during fatigue. Previous studies have found modulations in motor unit discharge rate during human voluntary fatiguing contractions. Isometric MVCs have been accompanied by a decrease in motor unit discharge rate (6, 28). Submaximal sustained isometric contractions have also resulted in decreased motor unit discharge rates (17); however, increased discharge rates have been demonstrated during intermittent submaximal isometric contractions (5) or during submaximal dynamic contractions (30). This study confirmed our previous accounts (30) that motor unit discharge rates do not decline during submaximal fatiguing arm movements. It is possible that feedback associated with the physical movement of the arm is implicated in the maintenance of motor unit discharge rates during fatiguing arm movements, but this notion awaits further investigation.

The increase in the occurrence of short ISIs during fatigue could not be attributed to altered movement kinematics during the task. We suggest that the increase in the occurrence of short ISIs could have resulted from increased excitation to the motoneuron pool or from intrinsic fatigue-related changes in the motoneuron. Although we have no direct evidence of changes to motoneuron properties in this study, other investigators have reported activity-dependent changes in intrinsic neuronal properties (20, 35). It is possible that fatigue is associated with altered ion-channel conductances in the motoneuron that may influence the probability of the motoneuron to discharge with short ISIs. The fact that, in the last one-third of the fatigue task, higher threshold motor units were more likely to discharge with short ISIs than were low-threshold motor units may support the hypothesis that intrinsic motoneuron properties contribute to the genesis of short ISIs.

Alternatively, high-threshold motor units may have been more likely to discharge with short ISIs because they were firing closer to their minimal firing frequencies than were the low-threshold motor units. Most doublets have been reported with weak contractions (and hence presumably slow-twitch motor units) performed at or near the minimum firing rate (3, 11, 31). In the last one-third of the present fatigue task, motor units that were newly recruited during the task displayed fewer motor unit discharges per movement trial. These motor units would have been closer to their recruitment threshold and, presumably, closer to their minimal firing frequency than were motor units that were active from the beginning of the task. In mammalian muscle, Spielmann et al. (33), using extracellular stimulation of cat motoneurons, found that type S motoneurons displayed more doublet firing than did type F motoneurons. However, Kirkwood and Munson (21) found that the occurrence of doublets was not related to the recruitment threshold of motoneurons in the anesthetized, paralyzed cat. This discrepancy surrounding the type of motor unit that was most likely to discharge with doublets may be related to the preparation, because Kudina (22) also found, similar to the present study, that high-threshold motor units were more likely to discharge with doublets in human muscle.

One explanation for the increase in the number of short ISIs during fatigue in the motor units that were active from the beginning of the task is that an increased level of excitation of the motoneuron pool is present. H-reflex amplitude has been found to increase during voluntary submaximal (30% MVC) fatiguing isometric contractions of the human triceps surae muscle (26). In the present study, the reduction in motor unit recruitment threshold torque, increase in surface integrated EMG activity, and recruitment of additional motor units are all suggestive of an increase in the excitatory drive to the motoneuron pool. For instance, approximately one-half of the recorded motor units were recruited during the course of the fatigue task. This recruitment could not be attributed to altered movement kinematics, because no subject demonstrated increased movement acceleration. We recognize, however, that a direct causal relationship between any increased excitation to the motoneuron and the incidence of short ISIs is not established in this study. Furthermore, Kirkwood and Munson (21) failed to demonstrate any increase in doublet firing with increasing excitatory drive, under nonfatiguing conditions, in inspiratory motoneurons of the cat. They suggested that doublet firing patterns could result from variations in synaptic inputs to the motoneurons. Clearly, fatiguing conditions would impart more variability in synaptic inputs to the motoneuron than would a nonfatiguing contraction.

Discharge pattern and force production. The majority of short ISIs occurred at movement initiation and occurred less often around peak velocity and movement termination. Other studies have shown that short ISIs frequently occur at the onset of motor unit recruitment (29). Double discharges have been observed at termination of motor unit firing (23) and less often during maintained contraction (1). These observations are consistent with our findings during dynamic fatiguing contractions.

The occurrence of short ISIs at the beginning of a contraction serves to increase the peak force and the rate of rise in force more than would be expected by the linear summation of the two pulses. In sustained
isometric contractions, this force can then be maintained by a lower firing frequency (10). Macefield et al. (27) used intraneural stimulation of motoneurons in human toe extensor muscles and found that the peak force was greater with an imposed double discharge at the onset of stimulation but the high force level was not maintained with a constant, slower discharge rate. During movement, the sustained increase in force from the short ISI was also less dramatic than in isometric contractions (32). In the present experiment, the additional short ISIs occurring throughout the movement may have served to maintain the force level (9) that otherwise would have dropped after the initial short ISI. Because we were unable to measure the force of individual motor units during the task, we can only speculate on a functional role of short ISIs in the augmentation of force production during fatigue.

There could be additional functions for short ISIs occurring throughout the movement. Short ISIs occurring at movement termination could have served to increase force production for joint stabilization against the preload at the movement end points. Short ISIs during the movement could take up the slack of the preload at the movement end points. Short ISIs during fatiguing movements.

In conclusion, dynamic muscle fatigue is associated with an increase in the occurrence of short ISIs. This finding is consistent with the suggestion that an increase in the number of short ISIs may serve to compensate for the loss of muscle force production during fatiguing arm movements.

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