Age-related enhancement of fatigue resistance is evident in men during both isometric and dynamic tasks

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Lanza, Ian R., David W. Russ, and Jane A. Kent-Braun. Age-related enhancement of fatigue resistance is evident in men during both isometric and dynamic tasks. J Appl Physiol 97: 967–975, 2004.—It has been suggested that the effects of old age on the ability to resist fatigue may be task dependent. To test one aspect of this hypothesis, we compared the neuromuscular responses of nine young (26 ± 4 yr, mean ± SD) and nine older (72 ± 4 yr) healthy, relatively sedentary men to intermittent isometric (3 min, 5 s contract/5 s rest) and dynamic (90°/s) maximum voluntary contractions (MVC) of the ankle dorsiflexor muscles. To assess the mechanisms of fatigue (defined as the ratio of postexercise MVC to preexercise MVC), we also measured isometric central activation ratios (CAR), tetanic torque, contractile properties, and compound muscle action potentials before and immediately after exercise. Because dynamic contractions are more neurally complex and metabolically demanding than isometric contractions, we expected an age-related fatigue resistance observed during isometric exercise to be absent during dynamic exercise. In contrast, older men (O) fatigued less than young (Y) during both isometric (O = 0.77 ± 0.07, Y = 0.66 ± 0.02, mean ± SE; P < 0.01) and dynamic (O = 0.45 ± 0.07, Y = 0.27 ± 0.02; P = 0.04) contractions (ratio of postexercise to preexercise MVC), with no evidence of peripheral activation failure in either group. We observed no obvious limitations in central activation in either group, as assessed using isometric CAR methods, after both isometric and dynamic contractions. Preexercise half-time of tetanic torque relaxation, which was longer in O compared with Y, was linearly associated with fatigue resistance during both protocols (r = 0.62 and 0.66, P ≤ 0.004, n = 18). These results suggest that relative fatigue resistance is enhanced in older adults during both isometric and isokinetic contractions and that age-related changes in fatigue may be due largely to differences within the muscle itself.

ankle dorsiflexors; compound muscle action potential; contractile properties; central activation

TWO MAJOR FUNCTIONAL CHALLENGES to the human neuromuscular system are the generation of force or power and the maintenance of force or power during sustained activity. In older adults, reduced force generation, or muscle weakness, occurs largely due to a loss of muscle mass (18, 35). It is generally accepted that this sarcopenia is likely to develop in most muscle groups after the sixth decade of life (35). In contrast, there is far less consensus as to the effect of old age on the ability to maintain force or power during activity and thereby to avoid fatigue (3). The results of some investigations suggest that older men and women fatigue more than young (12, 13, 34), which is consistent with studies in animal models (14). Other investigators, however, have demonstrated similar fatigability in young and old subjects (2, 33, 36), whereas still others have observed that older adults fatigue less than young (6, 17, 29). In these studies, fatigue is often quantified as a decrease in maximal force-generating capacity in response to exercise, although endurance time at a given force output is also used as a measure of fatigue.

Even less clear than the effect of old age on the magnitude of fatigue is its effect on the potential mechanisms that contribute to fatigue. Human aging is accompanied by a number of changes in the neuromuscular system that might affect fatigue, including motor unit remodeling (11), reduced maximal motor unit discharge rates (25), and a general shift toward a greater type I fiber composition (22). The extent of these age-related alterations appears to vary by muscle group and level of habitual physical activity (3, 21, 30). The impact of these various alterations may depend on the motor task used to evaluate fatigue (8). From a functional standpoint, maintaining successful independent living with increasing age requires the repeated use of both isometric and dynamic contractions, yet few data are available that provide a reasonably direct comparison of fatigue during these two types of contraction in older adults.

The purpose of the present study was to investigate the impact of old age on one aspect of the task specificity of muscle fatigue in humans. The particular design of this study allowed us to examine the effects of contraction type (isometric vs. dynamic) on fatigue while keeping muscle group and subject characteristics consistent. We hypothesized that older adults would fatigue less than young during intermittent maximal isometric contractions, consistent with existing data demonstrating enhanced fatigue resistance with age during intermittent maximal (6, 17) and submaximal isometric exercise (29). In this latter study, older subjects also demonstrated less intracellular acidosis and accumulation of Pcr, which was suggested as a mechanism for their lesser fatigue (29). We further hypothesized that older adults would fatigue more than young during intermittent, maximal dynamic contractions, due to greater central activation failure and impaired power production in the older subjects. Empirical support for this latter hypothesis is derived from our laboratory’s previous results suggesting that age-related impairments in dynamic tasks may exceed those of isometric tasks (27, 31), whereas theoretical support is provided by the potential impact of age-related alterations in central motor function (25) during tasks of greater neural complexity such as maximal dynamic contractions. Finally, one recent study showed greater central activation failure in the unfatigued muscles of older compared with young subjects that worsened with fatigue, suggesting an...
increased susceptibility of older adults to impaired voluntary activation (43).

In the present study, we compared fatigue in young and older men during two intermittent maximal voluntary contraction (MVC) protocols; one using isometric contractions (MVIC) and the other using dynamic contractions (MVDC). We recruited and studied young and older adults of similar physical activity levels to minimize the potentially confounding effect of habitual physical activity on muscle function. Potential mechanisms of fatigue were examined by measuring central and peripheral activation and muscle contractile properties, each of which may be altered by the aging process (12, 15, 43). The ankle dorsiflexor muscles were chosen for study because their function is highly relevant to locomotion and the prevention of falls in the elderly (32).

METHODS

Subjects

Nine young (26 ± 4 yr) and nine older (72 ± 4 yr) men were recruited from the University community and area Councils on Aging. In response to recent studies demonstrating an effect of sex on muscle fatigue (10, 42), we included only men in this study. All subjects provided informed consent in accordance with the procedures approved by the Human Subjects Review Board at the University of Massachusetts, Amherst. All subjects were in good health, free from disease or medication that might affect our measurements, and right leg dominant. Each subject’s ankle and brachial artery blood pressures were measured to confirm the absence of latent peripheral vascular disease in the study leg (38).

Volunteers were enrolled in the study only if they had exercised <20 min/day twice per week in the previous 2 mo. To quantify physical activity patterns, each subject wore a three-dimensional accelerometer (Tritrac Professional Products, www.stayhealthy.com) for 7 days. Accelerations were recorded in all three dimensions, and the vector magnitude was averaged over the 7-day period to obtain a daily average, as previously reported (28).

Experimental Setup

Subjects performed isometric and dynamic contractions of the left leg using a Biodex System 3 dynamometer (Biodex Medical, Shirley, NY). The subjects were positioned with −120° of hip extension (full hip extension = 180°) and −150° of knee extension (full knee extension = 180°). Straps mounted on the seat were tightened across the hips and thigh to prevent extraneous movement by the subjects. The leg was positioned such that the axis of rotation of the ankle joint was aligned with that of the dynamometer. The left foot was stabilized with a thermoplastic mold and secured to the footplate by using inelastic straps across the metatarsal-phalangeal joints. The dynamometer’s internal goniometer was calibrated by using a manual goniometer. Thereafter, all joint angle measurements were obtained from the dynamometer. The analog signals corresponding to torque, velocity, and joint angle were acquired and digitized by using customized Labview software (National Instruments, Austin, TX).

Surface electromyography (EMG) and electrical stimulation were applied as described elsewhere (26), and they were used to assess central activation, peripheral excitability, and the contractile properties of the ankle dorsiflexor muscles. All stimulating and surface EMG electrodes were 10-mm-diameter gold-plated disks. All stimulation pulses (200 μs) were delivered with a constant current stimulator (model DS7A, Digitimer, Hertfordshire, UK) at supramaximal intensity (115% of the intensity that produced a maximum-amplitude compound muscle action potential).

Central Activation

For the isometric protocol, we assessed voluntary activation of the ankle dorsiflexors by superimposing a train of supramaximal stimuli (50 Hz, 750 ms) on a MVIC. The resultant torque response was sampled at 500 Hz. The central activation ratio (CAR) was calculated as the peak MVIC divided by the peak total torque, where total torque was the sum of the MVIC and the superimposed tetanus (26). A CAR <1.0 indicates incomplete voluntary activation. The CAR measure was made before, at the end of, and during recovery from the isometric exercise. As a second measure of central activation, we compared the fall of MVIC with the fall of tetanic isometric torque, as described by Bigland-Ritchie and colleagues (7). Tetanic torque was obtained by stimulating (50 Hz, 750 ms) the relaxed muscle under isometric conditions. The CAR and tetanic torque measures were recorded during the final MVIC and immediately after the final MVIC, respectively.

Assessment of central activation during dynamic contractions is difficult for a variety of reasons (see DISCUSSION). For the dynamic fatigue protocol, we chose to address this issue by estimating central activation using the isometric CAR technique, with the understanding that this measure may not wholly reflect changes in central drive during dynamic contractions. The CAR was obtained before and immediately after exercise (<5 s after last dynamic contraction) and at intervals throughout the recovery period.

Peripheral Excitability

The compound muscle action potential (CMAP) was used to assess the excitability of the neuromuscular junction and sarcolemma before, immediately after, and throughout 10 min of recovery from exercise. The CMAP was obtained by delivering a single supramaximal stimulus of 0.2-ms duration and sampling the resultant EMG signal at 2,500 Hz. Changes in the peak-to-peak amplitude and duration of the CMAP served as indicators of changes in the excitability and propagation velocity of the neuromuscular junction and/or muscle membrane (26).

Contractile Properties

The maximal rate of torque development (RTD) and the half-time \( t_{1/2} \) of torque relaxation were determined from the electrically stimulated, isometric tetanic torque, as described previously (29). These measurements were performed before and immediately postexercise and at 5 and 10 min of recovery. The RTD provides an index of the muscle’s in vivo contractile speed and the \( t_{1/2} \) is an indirect indicator of several processes of torque relaxation, including calcium handling by the sarcoplasmic reticulum and/or dissociation of calcium from troponin (1, 9).

Habituation Sessions

Each subject reported to the laboratory for habituation on two occasions before the fatigue sessions. Subjects performed repeated maximal isometric and dynamic voluntary contractions until subsequent efforts were within 10% of the previous effort. Measures of central and peripheral activation and contractile properties were also obtained. After completion of the habituation sessions, the subjects returned to the laboratory on two additional days to perform the fatigue protocols. A minimum of 48 h elapsed between visits.

Experimental Sessions

This study was designed to compare muscle fatigue across age groups during isometric and concentric dorsiflexor muscle contractions. The exercise protocols were made to be as similar as possible, with the exception of the contraction mode. After completing two habituation sessions, subjects participated in two experimental sessions consisting of either the isometric or the dynamic fatigue test.
Each fatigue test was separated by at least 48 h, and the order of testing was randomized. We measured voluntary torque, electrically stimulated torque, central and peripheral activation, and contractile properties before and 0, 2, 5, and 10 min after each fatigue protocol.

**Preexercise measurements.** Before both the isometric and dynamic fatigue tests, supramaximal stimulus intensity was determined, and preexercise measurements of CMAP, MVIC, CAR, MVDC, and contractile properties were taken, in that order. Three CMAPs were recorded with 1 min of rest between successive measurements. Preexercise isometric strength was then determined by having subjects perform two to three MVICs (~5-s duration), with 30° of rest between contractions. Subjects repeated this measurement until the difference in peak torque from successive MVICs was 10% (typically 2–3 contractions). The highest value during these contractions was recorded as subject’s preexercise MVIC. Three MVDCs at 90°/s were then performed, and the highest peak power was recorded as the subject’s preexercise MVDC. After 2 min of rest, CAR was determined. After a further 2 min of rest, tetanic torque (50 Hz, 750 ms) and contractile properties were assessed. With the exception of the MVDC measurement, all preexercise measures were performed under isometric conditions.

**Isometric fatigue protocol.** After the preexercise measurements were completed, subjects performed 3 min of intermittent (5 s contractions/5 s relax) MVICs. Subjects were encouraged verbally and received visual torque feedback from a computer monitor. All isometric contractions were performed with the ankle plantar flexed to 30° from neutral, which has been shown to be the optimal angle for torque production in the dorsiflexors of young (37) and older (44) subjects. Fatigue was defined as the decline in peak isometric torque, expressed as the ratio of the peak torque produced during the last contraction to the peak torque produced during the preexercise MVIC. Central activation was measured during the final MVIC of the fatigue task; peripheral excitability and contractile function were measured immediately after exercise and at 2, 5, and 10 min of recovery. All recovery measures were performed under isometric conditions.

**Dynamic fatigue protocol.** On a separate day and again after completion of the preexercise measures, each subject performed 90 MVDCs at a nominal angular velocity of 90°/s (1.57 rad/s). This velocity was chosen on the basis of our recent work that showed an inability of some older subjects to successfully attain target velocities above 120°/s in an unfatigued state (31). The range of motion (ROM) about the ankle was mechanically limited to a total of 30° (15° on either side of the midpoint of the ROM for each subject), a range previously determined to be manageable for all older subjects (31). Torque, velocity, and angle data were acquired and digitized at 100 Hz. Peak muscle power (watts) was recorded as the product of peak torque (N·m) and angular velocity (rad/s), as described previously (31). Dynamic fatigue was defined as the fall in peak power production and expressed as the ratio of the average peak power of the last three contractions to the average peak power of the first three contractions. Because there were approximately three times as many dynamic contractions as isometric contractions, taking an average of three dynamic contractions most closely approximates the time frame of the isometric contractions. End-exercise and recovery measures were performed as described for the isometric fatigue protocol.

**Statistics**

Subject characteristics (height, mass, physical activity) were compared across age groups by using unpaired r-tests. To assess reliability of baseline measures across the two testing sessions, repeated-measures ANOVA was used to determine whether preexercise measures of MVIC, MVDC, and tetanic torque were similar across sessions (days) and intraclass correlation coefficients (ICC) were calculated for each of these measures.

Within each testing session, a mixed-model two-factor (age, time) repeated-measures ANOVA was used to assess changes in MVIC, MVDC, CAR, CMAP amplitude, MVIC duration, RTD, and t1/2 of tetanic torque relaxation during exercise. Where age × time interactions were found, post hoc comparisons were performed by using the Tukey-Kramer adjustment for multiple pairwise comparisons. A separate mixed-model repeated-measures ANOVA was used to assess recovery of these variables. For each protocol, we assessed the completeness of recovery within each age group by comparing the MVC after 10 min of recovery with the preexercise MVC by using ANOVA. As a secondary measure of central activation for the isometric protocol only, the fall of MVIC was compared with the fall of tetanic torque by using ANOVA. To compare the relative fatigue induced by the two protocols, two-factor (age, condition) ANOVA was used to compare the fall in isometric tetanic force after the isometric fatigue with the fall in isometric tetanic torque after the dynamic protocol in both age groups.

For each protocol, associations between fatigue and both strength (MVIC, MVDC) and contractile properties were determined by using linear regression analysis for all subjects combined. Descriptive data are presented as means ± SD; all other data are means ± SE.

**RESULTS**

**Subjects**

The average ages of the young and older groups were 26 ± 4 and 72 ± 4 yr, respectively. The young subjects were taller than the older subjects (181 ± 5 vs. 172 ± 4 cm; P < 0.001). There were no differences between groups in body mass (young = 72 ± 8, older = 75 ± 6 kg; P = 0.38) or physical activity level (young = 152 ± 35, older = 159 ± 59 arbitrary units; P = 0.77).

**Torque, Power, and Fatigue**

There were no differences in preexercise measures of MVIC, MVDC or tetanic torque across test days (ANOVA, P = 0.50–0.82 for the three variables; ICC r = 0.80–0.99). Before the isometric protocol, the older subjects produced ~14% less MVIC torque than the young, although this was not a statistically significant difference (Table 1). Before the dynamic protocol, the older men produced 25% less preexercise MVDC power compared with the young (P = 0.002; Table 2). Preexercise peak tetanic torque was 25.5% lower in older subjects at the isometric fatigue session (P = 0.03) and 17.3% lower at the dynamic fatigue session (P = 0.14; Tables 1 and 2).

Both young and older subjects had significant reductions in MVIC and tetanic torque after the isometric fatigue protocol (Table 1, Fig. 1A). The young group showed a greater decline in MVIC (P = 0.005) and tetanic torque (P = 0.006) than the older group (Fig. 1A, Table 1). During the 10-min recovery period, there was a main effect of age such that older men had relatively higher MVICs compared with young men (P < 0.001), presumably due to the difference in MVIC at fatigue (Fig. 1A). After 10 min of recovery, MVIC torque had returned to preexercise levels in the older men but not in the young men. However, there were no group × time interactions in the recovery of MVIC or tetanic torque, suggesting a similar overall pattern of torque recovery in the two groups and that age group differences in recovery were due to the differences present at the end of the exercise. Fatigue during the isometric protocol was only modestly associated with preexercise MVIC (r = 0.46, P = 0.06).
cant reductions in peak voluntary power during an MVIC, as reflected by the CAR measure (Tables 1 and 2). Immediately after the isometric fatigue protocol, there was no change in CAR in either age group (Table 1), nor was there a significant difference in the decline of MVIC compared with electrically stimulated tetanic torque (P = 0.08). Similarly, there was no change in either group in the isometric CAR immediately after the dynamic fatigue task (Table 2).

Peripheral Activation

The CMAP amplitude was greater in young compared with older adults before isometric (P = 0.05; Table 1) but not dynamic exercise (P = 0.09; Table 2) exercise. The CMAP duration was similar between young and older groups before

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Values are means ± SE for dorsiflexor muscle torque, central activation ratio (CAR), peripheral activation (CMAP), and contractile properties for 9 young and 9 older subjects. Preexercise values are shown for both age groups, with P values indicating differences across groups in baseline measures. Postexercise values are also given, and * indicate where these values differed from baseline within each group (P < 0.05). The right-most column shows the exercise-induced change relative to each group’s preexercise values. These changes are expressed at the ratios of postexercise to preexercise values for maximal isometric voluntary contraction (MVIC), tetanic torque, CMAP amplitude and duration, and half-time \( (t_{1/2}) \) of tetanic torque relaxation. Because the CAR and maximal RTD are ratios at baseline, the changes in these variables are expressed as postexercise minus preexercise values. P values indicate differences across groups in the change for each measure.

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Values are means ± SE for dorsiflexor muscle power, tetanic torque, CAR, CMAP, and contractile properties for 9 young and 9 older subjects. Preexercise values are shown for both age groups, with P values indicating differences across groups in baseline measures. Postexercise values are also given, and * indicate where these values differed from baseline within each group (P < 0.05). The right-most column shows the exercise-induced change relative to each group’s preexercise values. These changes are expressed at the ratios of postexercise to preexercise values for maximal dynamic voluntary contraction (MVIC), tetanic torque, CMAP amplitude and duration, and half-time \( (t_{1/2}) \) of tetanic torque relaxation. Because the CAR and maximal RTD are ratios at baseline, the changes in these variables are expressed as postexercise minus preexercise values. P values indicate differences across groups in the change for each measure.
exercise (Tables 1 and 2). Fatiguing isometric exercise elicited no significant change in the amplitude of the CMAP in either age group, although the duration of the CMAP increased similarly in both groups (Table 1).

As with isometric exercise, there was no change in CMAP amplitude in either group after dynamic exercise, but there was an increase in the duration of the CMAP that was similar in both groups (Table 2). There were no differences across age groups in CMAP amplitude or duration during recovery from either exercise protocol (data not shown).

**Contractile Properties**

Before exercise, the maximum RTDs were similar between groups (Tables 1 and 2). The $t_{1/2}$ of torque relaxation was longer in the unfatigued muscles of older compared with young subjects before the isometric exercise ($P = 0.02$; Table 1), although this difference was not significant before dynamic exercise ($P = 0.09$; Table 2). Interestingly, for all subjects combined, slower torque relaxation before exercise was associated with increased fatigue resistance during both the isometric ($r = 0.62, P = 0.005, n = 18$) and dynamic ($r = 0.66, P = 0.004, n = 18$) protocols, as shown in Fig. 2.

After isometric exercise, the RTD did not change in young subjects, but did increase in older subjects (Table 1), with a significant difference between the two groups in the magnitude of this response ($P = 0.02$). In contrast, isometric fatigue was accompanied by a slowing of the processes of force relaxation ($t_{1/2}$) in young but not older subjects, although the magnitude of this response was not significantly different between age groups (Table 1). Overall, the exercise-induced slowing of $t_{1/2}$ was not well correlated to fatigue during isometric exercise ($r = -0.41, P = 0.10, n = 18$; Fig. 3), presumably due in part to the lack of change in this variable in the older group.

Dynamic exercise resulted in decreases in the RTD in young but not older subjects, with the result that the magnitude of this response was greater in the young ($P = 0.04$; Table 2). Torque relaxation slowed markedly in both young and old groups in response to the dynamic contractions; the magnitude of this response was greater in young compared with older subjects (Table 2; $P = 0.02$). In contrast to isometric exercise, with dynamic exercise there was a significant association between torque relaxation and fatigue ($r = -0.75, P = 0.001, n = 18$; Fig. 3) such that those who slowed the most in response to exercise had the greatest fatigue. There were no differences

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**Fig. 1. Fatigue during the 2 protocols. A: isometric torque expressed relative to preexercise maximal voluntary isometric contraction (MVIC$_{pre}$), during 3 min (shaded bar) of intermittent MVICs and 10 min of recovery in 9 young and 9 older men. Values are means ± SE. Young men fatigued more than older men ($P = 0.005$), with no group × time interaction during recovery. B: peak power, expressed relative to the preexercise maximum voluntary dynamic contraction (MVDC$_{pre}$), during 90 dynamic contractions (shaded bar) in 9 young and 9 older men. Values are means ± SE. Young men fatigued more than older men ($P = 0.007$) with no group × time interaction during recovery. See text for details.**

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**Fig. 2. Relationships between fatigue (MVC$_{post}$/MVC$_{pre}$ ratio) and preexercise half-time ($t_{1/2}$) of tetanic torque relaxation after isometric (A) and dynamic (B) exercise in 9 young and 9 older men. Preexercise $t_{1/2}$ was associated with the ability to resist fatigue during both protocols.**
between the groups in the recovery of contractile properties (data not shown).

**Isometric vs. Dynamic Exercise**

To evaluate the task specificity of fatigue using a torque measure common to both protocols, we measured isometric tetanic torque before and immediately after each protocol. Both groups demonstrated a greater fall in tetanic torque after the dynamic protocol (Table 2) than after the isometric protocol (Table 1; \( P < 0.001 \) both groups), with no effect of age.

**DISCUSSION**

The main results of this study were that older men fatigued relatively less than young men of comparable habitual physical activity level during both isometric and dynamic exercise of the ankle dorsiflexors muscles and that the magnitude of fatigue was associated with in vivo muscle contractile properties. Our measures of central activation suggested that there were no age-related differences in the ability to fully activate the dorsiflexors muscles before or immediately after either type of exercise, although the measurement of central activation during dynamic contractions is somewhat problematic. Although fatigue resulted in prolonged CMAP durations, there was no overall decrease in peripheral excitability in young or older men during either fatiguing protocol. These results support our first hypothesis that older adults fatigue less than young adults during maximal isometric exercise. However, our second hypothesis was not supported, because older men showed no greater fatigue or central activation failure after repeated maximal dynamic contractions compared with young men. Overall, these results provide a unique observation that fatigue resistance in the ankle dorsiflexors is relatively enhanced in healthy older adults under both isometric and dynamic conditions.

**Torque, Power, and Fatigue**

Before exercise, older men generated \( \sim 14\% \) less voluntary isometric torque (not significant; Table 1), and \( \sim 25\% \) less peak muscle power (\( P = 0.002; \) Table 2) compared with the young men. The observation that the loss of power was somewhat greater than the loss of isometric torque in the unfatigued muscle is consistent with our laboratory’s recent work in this muscle group (31) and may be due, in part, to age-related differences in the time required to reach target velocity during dynamic contractions. Our laboratory previously found that older subjects require \( \sim 21\% \) more time than young subjects to reach a target velocity of 90°/s in the ankle dorsiflexors (31). Although all subjects in the present study achieved the target velocity of 90°/s during the preexercise dynamic contractions, the brevity of each contraction (1 s) may have resulted in the attainment of peak torque at a more extended position in the ROM in the older subjects, thus limiting their ability to develop maximal power. Furthermore, the relatively greater neural complexity of the dynamic task, discussed below in *Central Activation*, also may have contributed to the loss of power in the older group.

Our observation of increased fatigue resistance in older men during isometric exercise is consistent with other studies involving intermittent isometric contractions of the plantar flexors (6), adductor pollicis (17), and ankle dorsiflexors (29). However, some studies have shown no effect of age on muscle fatigue during isometric contractions of the knee extensors (6, 43), ankle dorsiflexors (6), and elbow flexors (2). A comparison across these studies reveals that protocols using duty cycles of 50% or less (i.e., work periods shorter than rest periods) have found increased fatigue resistance with age (6, 29), whereas those involving duty cycles >50% have found no effect of age on muscle fatigue (19, 43). A lower duty cycle may favor the relatively more oxidative nature of older muscle (29), as sufficient time would pass during the rest period for the adequate replenishment of oxygen to the working muscle. This, in turn, might be expected to enhance fatigue resistance in older adults under these conditions.

In the present study, older men also fatigued less than young men during repeated maximal dynamic contractions of the ankle dorsiflexors, a muscle group used primarily for posture, balance, and locomotion. The few previous studies that have examined the effects of age on muscle fatigue by using dynamic contractions have all studied the knee extensors muscles (30, 33, 36), and all reported no age-related change in fatigue resistance. The knee extensors are generally involved in more power-oriented activities than the dorsiflexors, many of which...
are unlikely to be maintained across the life span. Thus differences between the dorsiflexors and the knee extensors in their patterns of use may account for some of the discrepancies reported with regard to the effect of age on muscle fatigue. In addition, differences in the size and fiber type distribution of these two muscle groups, discussed below, may similarly contribute to the different results regarding age-related changes in fatigue.

To date, very limited data have been available regarding the task specificity of fatigue in young and older humans. Furthermore, the lack of control for subjects’ health and habitual physical activity level in previous studies complicates the interpretation of many results. A unique contribution of this study is the observation of an age-related enhancement in fatigue resistance that is apparent during both isometric and dynamic tasks performed by the same groups of healthy subjects who were matched for activity level. The fatigue tasks in the present study were designed to be as comparable as possible. Greater fatigue as a result of the dynamic task was observed in both older and young individuals, as indicated by the greater fall of voluntary (Fig. 1, B vs. A) and tetanic (Table 2 vs. Table 1) torque in response to the dynamic protocol. These data suggest that the age-related resistance to fatigue can be observed across a range of fatigue levels, as well as across different tasks.

Before exercise, electrically stimulated isometric tetanic torque was 17–25% lower in the older compared with the young group. In response to the isometric protocol, tetanic torque fell more in the young than the older group, consistent with the greater voluntary fatigue observed at that time in the young subjects. The dynamic protocol resulted in a marked decline in tetanic torque, with no significant effect of age on this change. The lack of an age effect may have been due in part to the fact that, whereas the fatiguing contractions were dynamic in nature, the tetanic torque measures were isometric. With both the isometric and dynamic protocols, the brief delay between the final voluntary contractions and the tetanic torque measure may have allowed some recovery of tetanic torque that followed. This possibility could account for the slight, although nonsignificant, difference in the fatigue of the voluntary vs. tetanic contractions after the isometric protocol.

Previous investigators have suggested that preexercise differences in muscular strength (and, by inference, muscle size) may explain enhanced fatigue resistance with age, presumably due to less occlusion of blood flow during contractions in smaller muscle (3, 8). However, we found that, during the isometric protocol, the relationship between preexercise muscular strength and fatigue could account for only 21% of the variability in fatigue. Similarly, preexercise dynamic torque or power could account at most for only 12–20% of the fatigue developed during the dynamic protocol. Thus, during the intermittent MVC protocols used in our study, it does not appear that muscle size, as reflected by MVC, was a major factor in the development of fatigue.

Central Activation

Before both exercise protocols, the young and older groups demonstrated full activation of the dorsiflexor muscles during MVICs (CAR, Tables 1 and 2), a result consistent with those from previous studies (11, 27, 29). For both study groups, no change in CAR was observed during the MVIC performed at the end of isometric exercise, nor were there differences in voluntary compared with electrically stimulated fatigue, suggesting that there was no central activation failure in either group as a result of this fatiguing protocol (7). Similarly, there was no change in CAR in either group at the end of the dynamic protocol. Overall, these results suggest that there were no apparent age-related differences in central fatigue that could explain the enhanced fatigue resistance found in the older men during both task conditions.

Although these results are consistent with several previous studies of fatigue during isometric exercise (20, 29), we had anticipated that the older men would demonstrate impaired central activation during the dynamic protocol. Maximal contractions require the ability to rapidly and repeatedly recruit all motor units at high discharge rates (16), the capacity for which may be diminished with age (25). It has been suggested that a more complex task such as dynamic exercise places a greater demand on the central nervous system than a simpler task such as isometric exercise (23, 40). Consistent with this concept, our laboratory has previously observed a marked slowing of rapid foot tap movements in older adults who showed no reductions in central activation or specific strength during isometric contractions (27). More recently, our laboratory reported a deficit in dynamic power production across a range of velocities in the ankle dorsiflexors of older adults that exceeded the decrease in isometric torque (31), a phenomenon also observed in the present study at 90°/s (Tables 1 and 2). Thus we had expected that the greater motor complexity of dynamic exercise would lead to fatigue due to central activation failure in the older men, a result we did not observe.

Although the present data suggest that central activation failure was not a major contributor to the development of fatigue, these results must be interpreted cautiously for the dynamic protocol. Our measures of central activation were limited to isometric contractions. We must infer by the absence of central activation failure during isometric contractions that none occurred during the dynamic contractions. Several investigators have attempted to assess voluntary activation under nonisometric conditions, but all of these methods have serious limitations. Babault et al. (4) used the interpolated twitch technique to assess central activation during concentric contractions of the knee extensor muscles, but others have shown superimposed stimulation to be unreliable during dynamic contractions (5). Newham et al. (40) assessed voluntary activation during concentric knee extensor contractions by superimposing brief trains of electrical stimulation during the voluntary contraction. Using this technique, the investigators were able to detect central activation failure at relatively low (20°/s), but not higher (120°/s), velocities. James et al. (23) assessed central fatigue during dynamic knee extension by supramaximal electrical stimulation during isokinetic releases. Unfortunately, this technique has limited application in human studies due to the discomfort associated with prolonged (>1,500 ms) supramaximal nerve stimulation, as well as the need to make the measurement during a release maneuver, which may prove difficult to perform quickly at the end of fatiguing exercise. More work in this area is necessary before we can fully clarify the role of central activation in the development of muscle fatigue during dynamic muscle contractions.
Peripheral Activation

Before exercise, the CMAP amplitude tended to be greater in young compared with older men, whereas there were no differences in CMAP duration. These results are consistent with some previous reports of CMAP in the dorsiflexor muscles (19, 29) and may reflect differences in surface electrode configuration, subcutaneous fat content, or preexercise muscle excitability. There were no changes from baseline in CMAP amplitude in either group after isometric or dynamic exercise, indicating that there were no fatigue-induced changes in neuromuscular junction or sarcolemmal excitability, a result consistent with a number of other studies (24, 29).

The duration of the CMAP increased comparably in both groups during isometric and dynamic exercise (Tables 1 and 2), suggesting that the net velocity of neuromuscular transmission or sarcolemmal action potential propagation was slowed as a result of exercise. Although the effect of slowed impulse propagation on muscle fatigue is unknown, the absence of age group differences in the present study suggests that this factor does not account for the greater fatigue shown by the young compared with older subjects. Overall, it appears that differences in peripheral activation do not explain the age-related enhancement in fatigue resistance observed in response to both isometric and dynamic exercise.

Contractile Properties

Before exercise, the maximum rate of tetanic torque development was similar in both age groups (Tables 1 and 2), consistent with the report of Van Schaik and colleagues (44). This result suggests that there were no obvious alterations in cross-bridge or sarcoplasmic reticulum calcium kinetics in the older subjects (44). In contrast, torque relaxation was somewhat prolonged in the unfatigued muscle of the older men (Tables 1 and 2). This age-related slowing of relaxation has been observed in previous studies (29, 41) and probably reflects the higher proportion of type I muscle fiber content of the tibialis anterior muscle in older adults (76% in young, 84% in old (22)). It is unlikely that slowed torque relaxation in the older group was due to deconditioning, because physical activity levels were similar between the groups. Interestingly, the preexercise $t_{1/2}$ was associated with the degree of fatigue that developed during both protocols (Fig. 2), illustrating that the slower muscle of the older group was also more fatigue resistant.

In response to isometric exercise, the maximum rate of tetanic torque development was unchanged in young men, but it increased significantly in older men (Table 1). This result suggests that calcium release from the sarcoplasmic reticulum, calcium sensitivity of the myofibrils, and the rate of cross-bridge cycling were not impaired (1) and, in fact, may have been potentiated in the older muscle during exercise. The isometric exercise protocol prolonged torque relaxation to a similar extent in both age groups (Table 1). Slowed force relaxation is often observed in fatigue and is thought to indicate impaired calcium uptake by the sarcoplasmic reticulum or slowed cross-bridge detachment resulting from the accumulation of ADP or P$_i$ in the myoplasm (1, 9).

In contrast to the isometric protocol, dynamic exercise resulted in a decrease in the maximum rate of tetanic torque development, with the young subjects exhibiting a greater reduction in RTD than the older subjects (Table 2). Exercise-induced slowing of RTD suggests that fatigue was accompanied by an impairment in the processes of excitation-contraction coupling or cross-bridge function, possibly due to the metabolic changes within the muscle that occur during fatigue (1). The greater slowing of RTD in young subjects suggests a greater impairment of intracellular processes in this group, which may partially explain why they fatigued more than the older subjects.

As with the isometric protocol, dynamic exercise also resulted in a prolonged $t_{1/2}$ for torque relaxation, although in this case the amount of slowing was greater in the young men (Table 2). It is reasonable to expect that the 90 dynamic contractions were more metabolically costly than the 18 isometric contractions (39) and likely resulted in greater accumulation of metabolic by-products such as P$_i$ and proton, which may explain the prolonged torque relaxation that we observed after the dynamic protocol. The relationship between fatigue and the slowing of torque relaxation observed during the dynamic protocol (Fig. 3) is consistent with the possibility that much of the fatigue may have been due to metabolic inhibition of contraction. In the present study, the older men had less of a slowing of torque relaxation and less fatigue than the young. The strong association between the slowing of relaxation and the degree of fatigue suggests that the greater fatigue in young compared with older individuals may have been the result of a greater accumulation of inhibitory metabolites in the young men. This hypothesis is supported by our laboratory’s recent observation that fatigue, as well as the accumulation of P$_i$ and proton, was less in older compared with young adults during incremental dorsiflexor contractions (29).

The results of this study show that older men fatigue less than young men during maximal isometric and dynamic intermittent exercise of the ankle dorsiflexor muscles. Thus, with muscle group and subject characteristics held constant, age-related enhancements in fatigue resistance appear to extend to multiple contraction modes. In both age groups, the dynamic condition elicited greater fatigue and perturbation of contractile properties than did the isometric condition. We found no evidence of age-related differences in central or peripheral activation failure that could explain the differences in fatigue, although the techniques available to assess central motor drive during dynamic contractions must be refined to fully clarify the role of central fatigue during repeated dynamic contractions. Overall, our results suggest that fatigue under both conditions developed due primarily to mechanisms distal to the sarclemma. Age-related differences in muscle metabolism, as suggested here by the associations between contractile properties and fatigue, could explain the relatively increased fatigue resistance observed in the older men.

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