Changes in motor unit discharge rate are not associated with the amount of twitch potentiation in old men

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Klein, C. S., C. L. Rice, T. D. Ivanova, and S. J. Garland. Changes in motor unit discharge rate are not associated with the amount of twitch potentiation in old men. J Appl Physiol 93: 1616–1621, 2002.—This study examined, in nine old men (82 ± 4 yr), whether there is an association between the magnitude of change in motor unit discharge rate and the amount of twitch potentiation after a conditioning contraction (CC). The evoked twitch force and motor unit discharge rate during isometric ramp-and-hold contractions (10–18 s) of the triceps brachii muscle at 10, 20, and 30% of the maximal voluntary contraction were determined before and 10 s, 2 min, 6 min, and 11 min after a 5-s CC at 75% maximal voluntary contraction. After the CC, there was a potentiation of twitch force (approximately twofold), and the discharge rate of the 47 sampled motor units declined (P < 0.05) an average of 1 Hz 10 s after the CC, compared with the control condition. The CC had no effect on the variability (coefficient of variation) of both force and discharge rate, as well as the electromyographic activity recorded over the triceps brachii and biceps brachii muscles. In contrast to our earlier study of young men (Klein CS, Ivanova TD, Rice CL, and Garland SJ, Neurosci Lett 316: 153–156, 2001), the magnitude of the reduction in discharge rate after the CC was not associated (r = 0.06) with the amount of twitch potentiation. These findings suggest an age-related alteration in the neural strategy for adjusting motor output to a muscle after a CC.

METHODS

Subjects. Nine healthy men, 76–86 yr (mean 82 ± 4 yr), participated in the study. Their mean weight and height were 74.9 ± 13.0 kg and 177.2 ± 5.9 cm, respectively. All subjects were ambulatory and were living independently in the community. They were free of medical conditions and medications that affect muscle performance. A few subjects participated in recreational activities such as golfing, bicycling, and walking, but none was highly trained. The local ethics review committee of the institution approved all procedures, and informed, written consent was obtained from each subject. Several aspects of the present data are compared with data obtained from young men who completed the same protocol (24).

Maximal voluntary contraction and twitch contractile properties. Subjects were seated with the nondominant (left) forearm resting in front of them on a platform in the horizontal plane (13). The shoulder and elbow were positioned securely in 80 and 90° of flexion, respectively. To measure dorsal interosseus and tibialis anterior muscles at 30–80% of maximal force. However, this contraction-induced reduction in discharge rate was blunted in the first dorsal interosseus muscle of older compared with younger subjects (12). The reason for this age-related difference in motor unit behavior is unclear.

One possible mechanism to explain this blunted reduction in discharge rate may relate to the diminished postactivation potentiation (PAP) of twitch force with advancing age (18, 34, 40). In other words, because of the lower PAP, a smaller reduction in discharge rate would be necessary to maintain a constant force output in old compared with young adults (1). The relationship between PAP and motor unit discharge rate has not been described in the older population. However, a significant negative correlation between the magnitude of the reduction in discharge rate and the amount of PAP was observed in the triceps brachii muscle of young men (24). In addition, age-related differences in PAP have not been determined in the muscles of the upper limb. Thus the purpose of the present study was to determine the relationship between the acute change in the discharge rate of motor units and PAP in old men.

The decrement in physical performance in adults over 65 yr of age can be ascribed, in part, to a loss of muscle mass and strength (23, 36). The impaired physical performance of older adults, such as reduced force steadiness, may also result from changes in the neural strategies used to control muscle force secondary to alterations in motor unit morphology and motor unit behavior (27, 37). An acute reduction in motor unit discharge rate has been observed in young adults during brief nonfatiguing (10 s) and fatiguing (several minutes) constant-force contractions (6, 13, 33). For example, De Luca and colleagues (6) reported a progressive decrease in the discharge rate of most motor units sampled during 8- to 15-s contractions of the first
elbow extensor force, the forearm was semipronated and the wrist was secured in a U-shaped brace that was mounted on a force transducer. The maximal voluntary contraction (MVC) of the elbow extensor muscles was recorded as the greatest force of three to five attempts, each held for 3 s, with a 2-min rest. Strong verbal encouragement and visual feedback were provided during the contractions.

Twitches were evoked by use of a constant voltage electrical stimulator. The cathode was an 8-mm disc electrode filled with conductive gel, which was placed over the motor point of the lateral head of the triceps brachii. The anode was a lead plate (8.5 × 5 cm) wrapped in gel-soaked gauze positioned lateral to the scapula over the teres minor muscle (to stimulate the radial nerve). Peak twitch force (Pt) at rest was determined by applying pulses (50–100 μs) of progressively greater voltage until the force plateaued. The voltage level used to determine Pt was maintained for the remainder of the protocol.

Motor unit and surface electromyography recording. Motor unit activity was recorded with branched bipolar fine-wire electrodes (stainless-steel with formvar insulation, 50 μm in diameter) inserted subcutaneously over the lateral head of the triceps brachii (11). Two electrodes were inserted, offset from each other by a distance of ~2 cm. The positions of the subcutaneous electrodes were adjusted so that one or more motor units were active during brief voluntary contractions at 10–30% MVC. Surface electromyography (EMG) was recorded with 8-mm electrodes placed in a bipolar configuration over the lateral head of triceps brachii and biceps brachii muscles. A ground strap was placed around the right wrist.

Experimental protocol. Subjects were tested on two occasions with the same protocol previously described for young subjects (24). On the first visit, the maximal isometric force (MVC) of the elbow extensor muscles was determined as described above, and the subjects practiced the entire protocol but without motor unit activity being recorded. During the second visit, which was held 3–7 days after the first, motor unit activity was recorded. To avoid PAP of twitch force before the conditioning contraction (CC), the MVC was not performed before the protocol on the second visit. Instead, the peak MVC determined during the first visit was used to set the target forces for the ramp-and-hold contractions. However, MVC force was measured at the end of the protocol during the second visit (see Data analysis).

A maximal twitch of the triceps brachii was recorded before any voluntary contractions (initial twitch; Fig. 1). For the control sequence of ramp-and-hold contractions, subjects traced force templates at 10, 20, and 30% MVC or 30, 20, and 10% MVC (balanced across the subjects), with twitches evoked 2 s after each contraction (control twitches). There was a 10- to 14-s rest period between each voluntary contraction. The rate of force increase and decrease during the ramp phase was 5% MVC/s, and the force plateau was maintained for 6 s. After the control sequence was recorded, PAP was induced by a 5-s CC at 75% of the MVC. The 75% MVC was chosen, rather than 100% MVC, to minimize movement of the subcutaneous electrodes during the contractions. The ramp-and-hold contractions were then repeated at 10 s, 2 min, 6 min, and 11 min after the CC. A maximal twitch was recorded before and after each ramp-and-hold contraction and 2 s after the CC, so that the recovery time course of PAP could be determined. Four subjects agreed to repeat the protocol after a 20-min rest but performed the contractions in reverse order to their first experiment, and different motor units were recorded. Therefore data are presented for nine subjects who completed a total of 13 tests.

Data analysis. Force, surface EMG, and motor unit activity were analyzed off-line by use of customized Spike 2 software. The surface EMG recordings were amplified, filtered at 10 Hz–1 kHz, and digitized at 2.5 kHz, and the force recordings were digitized at 0.5 kHz. The subcutaneous EMG signals were amplified, filtered with a 10 Hz–10 kHz band pass, and digitized at 20 kHz. Motor unit potentials were identified with a template-matching algorithm (Spike 2, Cambridge Electronics). The threshold forces of motor unit recruitment and derecruitment were determined as the force levels during the ramp phases at which a motor unit started or stopped discharging, respectively. The discharge rate (in Hz) of each motor unit was calculated as the average over the middle 2 s of the 6-s plateau. The coefficient of variation (CV) of discharge rate, CV of force, root mean square (RMS) of the surface EMG, and the average force were determined over the same 2-s period. The RMS of the EMG in the triceps brachii and biceps brachii muscles during the ramp-and-hold contractions were expressed as the percentage of the RMS EMG recorded during postprotocol MVCs of the elbow extensors and flexors, respectively. The contraction time (CT) of the twitch was determined as the time between the initial increase of force from baseline and peak force. One-half relaxation time (1/2 RT) was the time for peak force to fall to half its value.

Statistical analysis. A two-factor analysis of variance was used to compare the effects of force level (10, 20, and 30% MVC) and time on the absolute and relative changes in the variables as a result of the CC. A three-factor ANOVA (age group × force × time) was used to compare the present data to the results obtained in young subjects (24). Post hoc comparisons (Tukey’s test) were completed to separate any force level and time effects. The relationship between variables was determined with the Pearson’s product-moment correlation coefficient. Unless otherwise noted, data are presented as means ± SD, and the α level of significance was set at P < 0.05.

RESULTS

Contractile and motor unit properties before the CC. The MVC force and initial Pt, CT, and 1/2 RT (before the control ramp-and-hold contractions) were 171 ± 40 N, 7.8 ± 4.1 N, 93.3 ± 9.6 ms, and 79.2 ± 21.8 ms, respectively. After each ramp-and-hold contraction, a control twitch was evoked. The Pt increased (~20%) significantly (P < 0.05) after the 30% MVC but not
after the 10 or 20% MVC control contraction. Thus contraction intensity as low as 30% MVC was sufficient to evoke some potentiation of twitch force.

A total of 81 different motor units were sampled during the control ramp-and-hold contractions before the CC. The recruitment and derecruitment force thresholds of these motor units were 15.1 ± 6.5 and 14.3 ± 7.5% of the MVC, respectively. The mean motor unit discharge rate, CV of discharge rate, and CV of force during the control contractions are displayed in Table 1. The mean discharge rate, but not CV of discharge rate or CV of force, differed significantly (P < 0.001) between the three force levels.

**Contractile and motor unit properties after the CC.** The Pt significantly increased to 18.6 ± 9.3 N measured 2 s after the CC, an increase of 233 ± 29% relative to the initial twitch. The second series of ramp-and-hold contractions started 10 s after the CC. At this point, Pt was potentiated ~150–220%, CT was reduced by 12%, whereas 1/2 RT was unchanged, relative to the corresponding control twitch (Fig. 2). The changes in Pt and CT returned to control levels by 6 and 2 min, respectively. Of the 81 motor units sampled during the control contractions, 47 were recorded 10 s after the CC on the basis of an unchanged shape and amplitude of the motor unit waveform. The other units could not be followed reliably for analysis because of changes in the shape of the waveform after the CC. The discharge rate (Hz) of these 47 units before and after the CC at all force levels is summarized in Table 2, and the percent changes are displayed in Fig. 2. The discharge rate, 10 s after the CC, decreased by 0.5 Hz or more (range 0–3 Hz) in 90% of the motor units (P < 0.05) at all force levels and returned to control values by 6 min (Fig. 2). The average plateau force (N), CV of force, and CV of discharge rate did not change significantly from control values after the CC. Thus the reduction in discharge rate could not be attributed to the subjects failing to reach and maintain the target force.

The relative increase in Pt 10 s after the CC was not significantly correlated (r = 0.06, P > 0.05) with the relative decrease in discharge rate (Fig. 3). This figure also shows that the amount of PAP after the CC was not different between the twitches evoked after the first, second, and third ramp-and-hold contractions (P > 0.05). The RMS EMG of the triceps brachii was unchanged after the CC. Also, the level of coactivation (~1–3%) in the biceps brachii was not affected by the CC. The MVC force taken at the end of the protocol was not significantly different (paired t-test) from the MVC force recorded during the first visit, which suggests that minimal force fatigue occurred during the protocol.

**DISCUSSION**

Previous investigators demonstrated that the discharge rate of motor units decreased during constant-force contractions, and the magnitude of the reduction was greater at higher (i.e., 50–80% MVC) compared with lower intensities (i.e., 20% MVC) (6, 12, 13, 33). In

![Figure 2. Relative changes in twitch contractile properties and motor unit discharge rate of the triceps brachii muscle after the CC. Values are means ± SE presented as a percentage of the control response for all tests. Top: peak force (Pt), contraction time (CT), and one-half relaxation time (1/2 RT) of the twitch pooled for all contraction levels. Bottom: mean motor unit discharge rate during the 10, 20, and 30% MVCs. *Significant difference from control values on the basis of the analysis of the percentage change in discharge rate and contractile properties.](http://jap.physiology.org/)

Table 1. Mean and variability of motor unit discharge rate and variability of force during the control ramp-and-hold contractions

<table>
<thead>
<tr>
<th>Force Level</th>
<th>10% MVC</th>
<th>20% MVC</th>
<th>30% MVC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Discharge, Hz</td>
<td>12.4 ± 2.9</td>
<td>14.1 ± 2.4</td>
<td>15.6 ± 2.9</td>
</tr>
<tr>
<td>Discharge CV, %</td>
<td>10.7 ± 2.5</td>
<td>9.5 ± 3.2</td>
<td>12.7 ± 5.3</td>
</tr>
<tr>
<td>Force CV, %</td>
<td>1.7 ± 1.1</td>
<td>1.1 ± 0.9</td>
<td>1.5 ± 0.6</td>
</tr>
<tr>
<td>Number</td>
<td>21</td>
<td>38</td>
<td>41</td>
</tr>
</tbody>
</table>

The discharge rate (mean ± SD) of triceps brachii motor units (n = 81 units) during contractions at 10, 20, and 30% maximal voluntary contraction (CC) before the conditioning contraction (CT). Discharge CV (%) and force CV (%), variability of discharge rate and force, respectively, expressed as the coefficient of variation. The number of motor units sampled at each force level is indicated. Note that some motor units were sampled at 2 force levels. The discharge rates at all 3 force levels were significantly different from one another. Force level had no effect on CV of force or CV of discharge rate.

Table 2. Motor unit discharge rate of the triceps brachii before and after the CC

<table>
<thead>
<tr>
<th>Force Level</th>
<th>10% MVC</th>
<th>20% MVC</th>
<th>30% MVC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>13.0 ± 2.4(14)</td>
<td>14.4 ± 2.3(28)</td>
<td>16.8 ± 2.4(18)</td>
</tr>
<tr>
<td>10 s</td>
<td>11.9 ± 2.2(14)</td>
<td>13.3 ± 2.5(28)</td>
<td>15.9 ± 2.5(18)</td>
</tr>
<tr>
<td>2 min</td>
<td>12.5 ± 3.2(11)</td>
<td>13.4 ± 2.8(26)</td>
<td>16.4 ± 2.5(16)</td>
</tr>
<tr>
<td>6 min</td>
<td>11.9 ± 3.4(10)</td>
<td>14.1 ± 2.6(24)</td>
<td>16.3 ± 2.5(10)</td>
</tr>
<tr>
<td>11 min</td>
<td>11.1 ± 2.6(10)</td>
<td>14.3 ± 2.8(23)</td>
<td>16.8 ± 2.5(10)</td>
</tr>
</tbody>
</table>

Motor unit discharge rate in Hz (mean ± SD) of the triceps brachii during contractions at 10, 20, and 30% MVC before (control) and 10 s, 2 min, 6 min, and 11 min after a 5-s CC at 75% MVC in 9 subjects (13 tests). The total number of motor units sampled in all tests is indicated in parentheses. The number of motor units sampled was not constant because some units may not have been recruited or could not be identified reliably.
addition, the discharge rate of motor units declined less in older compared with younger adults during 20-s contractions at 50% of MVC, but not at 20% MVC (12). They proposed that the blunted response in discharge rate of the older subjects may be a consequence of less PAP, but contractile properties were not measured (12). The present study is the first to compare the acute changes of motor unit and contractile properties after PAP in old adults. The CC resulted in significant PAP as well as reduction in motor unit discharge rate. However, unlike our previous results in young men (24), the reduction in motor unit discharge rate was not significantly correlated with the magnitude of PAP. These findings indicate that the relationship between the acute changes in motor unit discharge rate and PAP is not well matched in older adults.

**Contractile properties and PAP.** The MVC was 41\% lower than the values previously recorded in the young men (24). Most of this strength difference probably reflects age-related muscle atrophy, rather than any major impairment in the ability to fully activate the elbow extensors (23). The initial Pt of the old men in the present study was 73\% lower, but CT and 1/2 RT were not significantly different, compared with young adults (24). Others have also reported minimal age-related difference in twitch duration of the elbow extensors or flexors (8, 21, 29). In contrast, a number of investigators found that the twitch duration is prolonged in distal muscles in older compared with younger subjects (3, 4, 7, 31, 32, 40).

The old men demonstrated significant PAP after the control 30\% MVC ramp-and-hold contraction (~20\%) and 2 s after the CC (233 ± 30\%). These values were similar to the level of PAP after the 30\% MVC (~20\%) and 2 s after the CC (212 ± 53\%) in young men (24). Moreover, a similar amount of PAP (~240\%) was reported in the triceps brachii of 65- to 78-yr-old men after a 5-s MVC, but no young subjects were studied (35). Thus it seems that age does not impair the capacity for PAP in the triceps brachii. In contrast to these findings, investigators previously reported that PAP was 25–75\% lower in the dorsiflexor and plantar flexor muscles in older compared with younger adults (18, 34, 40). The relative maintenance of PAP in the triceps brachii compared with the lower limb muscles with age may reflect differences in habitual activity, although this has not been tested experimentally. The maintenance of PAP in the triceps brachii with age may also be a reflection of inherent differences in the aging of upper vs. lower limb muscles. Others have shown that age-related differences of muscle size, strength, twitch...
duration, and number of motoneurons were less in the upper limb (or forelimb) than in the lower limb (or hindlimb) in humans and animals (15, 17, 25, 29). Thus the contractile properties and capacity for PAP (at least after a submaximal CC) in the arm muscles seem to be less affected by age than the lower limb muscles.

Ramp-and-hold contractions before the CC. Voluntary modulation of force depends primarily on the recruitment and denerervation of motor units and their pattern and frequency of discharge (6). The mean discharge rate during the 10 (~12 Hz), 20 (~14 Hz), and 30% (~16 Hz) MVCs before the CC are similar to the values recorded in the young men (24) and to values recorded by others who used intramuscular electrodes (28, 39). In addition, the variability (CV) of both discharge rate and force (i.e., steadiness) during the 2-s plateau were relatively low (<15%), and the relative EMG activity of the triceps brachii and biceps brachii during the contractions were similar to those of the young adults (24). Graves and co-workers (14) also reported no age-related difference in force steadiness (i.e., CV) or EMG activity of the agonist and antagonist muscles during isometric contractions of the elbow flexors at 5–65% of the MVC.

Consistent with our findings, Howard et al. (19) reported no age-related differences in motor unit discharge rate of the triceps brachii or biceps brachii during 10–30% MVCs of the elbow extensors and flexors, respectively, although only one subject was over 70 yr of age. Similarly, motor unit discharge rate of the vastus medialis muscle during submaximal and maximal (MVC) knee extensions was not different between old (80 yr) and young men (38). Conversely, an age-related reduction in motor unit discharge rate is apparent in the elbow extensor muscles during higher intensity (>50% MVC) contractions (21) and in more distal muscles at low and high force levels (4, 12, 19, 22, 30, 32). Considering the present and previous studies, it seems that age has minimal effect on motor unit properties and force steadiness of proximal compared with distal muscles, at least during moderate isometric contractions.

Ramp-and-hold contractions after the CC. Although there was a reduction in the discharge rate of motor units after the CC, the magnitude of the decrease (~1 Hz) was less than in the young (~2 Hz) adults (P < 0.001, ANOVA) (24). Additionally, few motor units demonstrated a reduction >2 Hz in the old men, but over one-half of the units in the young group declined by >2 Hz (Fig. 4). It was anticipated that the old men would demonstrate less reduction in motor unit discharge rate after the CC compared with the young men and that this difference might be explained by an age-related decline in PAP (12, 18, 34, 40). However, as described above, PAP of the triceps brachii was not affected by age. Moreover, there was no association between the magnitude of PAP and the reduction in discharge rate after the CC in the old group, although a significant negative correlation (r = −0.74) was demonstrated in the young group (24).

The lower discharge rate observed in the young and old after the CC may reflect a decrease in voluntary neural input to the motoneuron pool to maintain the target force when PAP is prominent. This line of reasoning is indirectly supported by the work of Hutton and colleagues (20), who found that young subjects, devoid of visual feedback of the target force, “overshoot” the target force after a CC, and the magnitude of the force error covaried with the intensity of the CC. A reduction in neural input to the motoneuron pool after the CC could also result in a decrease in the number of motor units recruited (i.e., denerervation). However, in the few instances that motor unit denerervation was clearly observed, recruitment of new motor units usually occurred. This suggests that there was some rotation among different motor units during recovery. Although we cannot rule out the possibility of denerervation of motor units, this may not be a significant compensatory strategy for PAP, at least under the current conditions.

In addition to possible changes in neural drive, the modulation of the decrease in discharge rate to changes in PAP likely requires a segmental feedback mechanism. For example, the smaller reduction in discharge rate after the CC in the old compared with the young men may also stem, in part, from reduced inhibitory influences of the motoneuron pool, secondary to age-related decreases in presynaptic inhibition (2, 9) and reflex sensitivity of muscle (5). Less reduction occurred in the amplitude of the soleus H-reflex during changes in body posture (26) and during vibration or electrical stimulation of the antagonist muscles in old compared with young subjects (2, 9). Also, the amplitude of the H-reflex, muscle stiffness, and stretch-induced afferent activity are all lower after an isometric CC in young subjects (10, 16), but comparable experiments on older adults have not been done.

In summary, the old men demonstrated significant PAP of the muscle twitch and a reduction in the discharge rate of motor units after the CC. However, the magnitude of the reduction in discharge rate was less than in young men (24), and there was no correlation between PAP and changes in discharge rate. These findings suggest that rate coding may be less important in older adults for adjusting the motor output subsequent to PAP.

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REFERENCES


