

Christopher A. Knight and Gary Kamen

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B. K. Barry, M. A. Pascoe, M. Jesunathadas and R. M. Enoka

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Modulation of motor unit firing rates during a complex sinusoidal force task in young and older adults

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Knight CA, Kamen G. Modulation of motor unit firing rates during a complex sinusoidal force task in young and older adults. *J Appl Physiol* 102: 122–129, 2007. First published September 7, 2006; doi:10.1152/jappphysiol.00455.2006.—This study compared motor unit rate coding and muscular force control in the first dorsal interosseous muscle of older ($n = 11$, mean 72.3 yr) and young ($n = 12$, mean 18.7 yr) adults. Rate coding during a sinusoidal isometric force-matching task was evaluated using spectral analysis of the time-varying changes in firing rate. The task required force modulations to match a trajectory comprising the sum of 0.15- and 0.45-Hz sine waves. Based on the amplitude of spectral peaks at 0.15 and 0.45 Hz, the amplitude of force modulation was similar in young and older adults at both frequencies ($F = 1.9$, $P = 0.17$). Force modulation gain (FMG) was computed as the ratio of the amplitude of force modulation to the amplitude of firing rate modulation. To account for rate coding differences related to the properties of the motoneuron, recruitment threshold force was used as a covariate in age-group comparisons. At both task frequencies, firing rate was modulated with less amplitude ($F = 0.14$, $P < 0.001$) and FMG was greater ($F = 0.27$, $P < 0.001$) in the older adults. In its transformation of neural input to mechanical output, muscle is known to act as a low-pass filter. Compared with modulation at 0.15 Hz, less change in force per change in firing rate at 0.45 Hz (lower FMG; $F = 0.67$, $P < 0.001$), independent of age group, is consistent with this filtering effect. Our conclusion is that there is a reduced amplitude of firing rate modulation in older adults.

motor control; muscle; rate coding; motoneuron

MUSCULAR FORCE IS GRADED BY the recruitment and derecruitment of motor units (18, 34) and by the modulation of their firing rates (13, 33). Within muscle, the transformation of neural input to mechanical output occurs with a low-pass filter effect that is due to the relatively slow time course of muscular contraction (38). The modulation of motor unit firing rate (rate coding) occurs at the same frequencies as those of the task (7, 8) and with an amplitude of modulation that is positively related to the frequency of force modulation (20, 25). During sinusoidal force modulation at constant peak-to-peak amplitude, an increase in the frequency of force modulation will require greater amplitude of firing rate modulation. This frequency-sensitive gain, which is more apparent at frequencies from >0.5 to 1-Hz, has been described as a necessity to overcome the low-pass filter characteristics of muscle (2, 38). Furthermore, cat preparations provided evidence of the optimal matching between a motoneuron's firing behavior and the contractile characteristics of the affiliated muscle unit (2). In young and older human adults, moderate-to-strong inverse

relationships between firing rates and motor unit contraction duration during constant-force conditions support the matching of firing behavior with contractile properties (6). However, compared with what is known about motor unit firing behavior during constant-force or ramp conditions, very little is known about age-related changes in the rate coding mechanism during tasks that require sinusoidal modulation of muscular force, especially in humans (39).

Normal aging is accompanied by reductions in strength, peak rates of force development, and power (5, 15, 17, 29); decreased force steadiness (14, 24, 26, 46); tremor (3); and poorer control during force-modulation tasks (39). Research on each of these topics has implicated age-related changes in motor unit morphology and firing behavior (11, 21, 42). Age-related changes in motor unit morphology (30, 32) and reductions in muscle fiber shortening velocity (27) result in motor units with greater size and twitch tension and slower contraction and relaxation speed (9). Assuming that motor units with greater twitch force and slower twitch relaxation times provide enhanced force summation, the aged motor unit may require less of an increase in firing rate for a given increase in force, compared with young adults.

This experiment was designed to compare the rate coding mechanism in young and older adults during a sum-of-sines force-matching task that required modulation at two different frequencies (0.15 and 0.45 Hz). This novel paradigm allowed us to quantify the amplitude of firing rate modulation in individual motor units at both of the two modulation frequencies. For individual motor units, the amplitude ratio of force modulation to firing rate modulation will be described here using a new variable term, force modulation gain (FMG). Considering the effects of age-related motor unit remodeling that results in large motor units with greater twitch forces and slower dynamics (9), and reductions in submaximal and peak motor unit firing rates (6, 22), it was hypothesized that there would be greater changes in force per change in firing rate in older adults (e.g., greater FMG).

METHODS

Participants. Thirty-one right-handed female adults were recruited from the local University community. To minimize variance in comparisons between groups, greater homogeneity was sought by recruiting only female subjects. The young subjects ($n = 16$) were from an undergraduate class in which they earned extra credit for their participation. Older adults ($n = 15$) were given remuneration for their participation. All subjects provided their written informed consent.

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The institutional review board for experimentation with human subjects approved all procedures.

With one exception, all subjects tolerated testing well. One older subject withdrew from the study because of discomfort of the needle electrode. Although they did not document any tremor or pathology on a medical history form, two subjects presented visible evidence of tremor in their force performance as well as atypical motor unit firing behavior in force recordings taken during a constant-force task (not presented here). The unusual firing behavior was a consistent short-long-short pattern in consecutive interspike intervals (ISIs). These two older subjects were excluded from the sample. In addition to these exclusions, adequate motor unit recordings for spectral analysis were not obtained from all subjects. Therefore, the final sample used in all analyses consisted of 12 young (mean 18.7 yr, range 18–20) and 11 older (mean 72.3 yr, range 62–88) adults. The average height and mass of the young group were 167.6 cm (SD 7.0) and 58.8 kg (SD 6.4). The average height and mass of the older group 162.8 cm (SD 7.1) and 69.8 kg (SD 11.3).

Protocol. The peak force from three maximal voluntary contractions (MVC) of the first dorsal interosseus muscle was taken as a measure of strength and used to scale the force-matching task. MVCs were measured again at the conclusion of testing for an assessment of fatigue. Following the initial MVCs, subjects practiced each of two force-matching conditions they would encounter during motor unit recordings (5 trials in 2 conditions). The second condition was a constant-force 20% MVC task for a separate aim not presented in this paper. Following the practice session, a quadrafil needle electrode was inserted in the first dorsal interosseus muscle (FDI) and positioned to obtain recordings in which distinct and consistent motor unit action potentials could be observed. The electrode was inserted in the distal region of the FDI with a shallow angle, allowing distal to proximal penetration. This orientation was intended to allow sampling from multiple motor units with deeper penetration of the electrode along the length of the muscle. Some subjects returned to the laboratory on a second occasion if motor unit recordings were not obtainable at the first visit.

The force-matching task began and ended with linear increases and decreases in force at 5% MVC/s. These linear regions were used for estimates of recruitment threshold forces. The plateau region of the task contained oscillations above and below the 20% MVC force

level. The oscillations consisted of the sum of a $\pm 3\%$ MVC 0.15-Hz sine wave and a $\pm 2.5\%$ MVC 0.45-Hz sine wave (Fig. 1, fifth panel). The resulting trajectory had a fundamental period of 6.66 s, and the peak oscillations were $\pm 4.14\%$ MVC. The 20% MVC force level was selected to favor continuous motor unit firing while minimizing fatigue during the 50-s trials. The 40-s duration of the plateau region was considered necessary to provide sufficiently long motor unit recordings for analyses in the frequency domain. Because full motor unit recruitment in FDI is achieved near 50% MVC, both recruitment and rate coding mechanisms contribute to the control of this task (7, 34).

Motor unit recordings. Using the same methodology as in a previous investigation (25), motor unit action potentials were recorded with a 25-gauge stainless steel needle electrode containing four 50- μm platinum-iridium wires epoxied in a side port 7.5 mm from the tip of the cannula. The exposed ends of the wires were arranged in a 200- μm square array. Differential amplification (Dantec Counterpoint, Dantec Elektronik Medicinsk, Skorlunde, Denmark; $10^{12}\text{-}\Omega$ input resistance, 25-pA bias current, band-pass filtered 1–10 kHz; -3 dB) of three pairs of wires provided three channels of motor unit recordings, each presenting the same motor unit action potential with different shape and amplitude due to the orientation of the bipolar recording surfaces relative to the propagation of the electrical potential. Together with a multichannel template-matching algorithm, this technique can successfully identify individual motor units even at maximal contraction intensities (23, 31). Motor unit signals were sampled at 51.2-kHz using a 12-bit analog-to-digital converter. During submaximal contractions (typically 5–10% MVC), and with the aid of audio feedback the needle electrode was manipulated within the FDI to find recording sites yielding multiple motor units. High-frequency, large-amplitude potentials were sought during needle manipulation. Once an adequate trial was obtained at a recording site, the electrode was repositioned to sample from other motor units. Using this approach, it is necessary to rely on the probability that this relocation, on the order of millimeters, provides sampling from different motor units. Fortunately, multiple motor units are typically sampled within a single site, which ensures that different motor units are being observed. Furthermore, motor unit data are usually taken from the single best recording site because greater signal quality facilitates the spike sorting process. The best site is determined during offline analysis after the subject has left. Subjects rested for 1 min

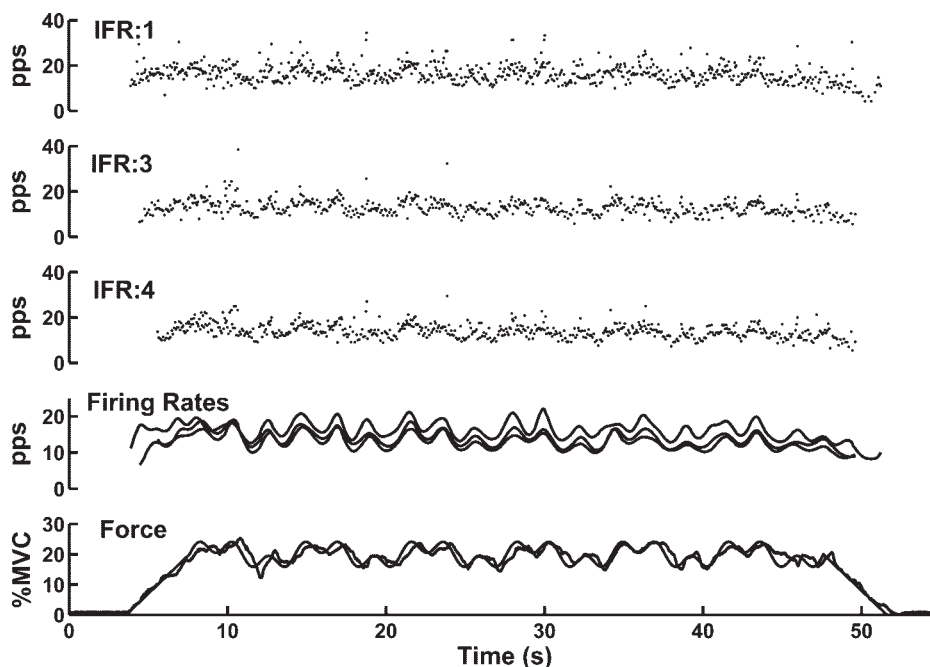


Fig. 1. The top 3 panels show the dot plots of instantaneous firing rates [(IFR) = (ISI^{-1}) , where ISI is interspike interval] for 3 motor units observed in a single trial. The fourth panel shows a smoothed (low-pass filtered at 5 Hz) representation of each motor unit's firing rate. This panel shows strong common drive among the three motor units and good correspondence with the modulation of muscular force (fifth panel). The smoothed firing rates are presented for graphical purposes only. Spectral analysis was conducted on unfiltered firing rates. MVC, maximal voluntary contraction; pps, pulses/s.

between consecutive trials, and none reported localized muscular fatigue in response to periodic inquiry.

Force recordings. Subjects applied isometric index finger abduction against a force transducer (model MB-10, Interface, Scottsdale, AZ; 0.013-N resolution) such that a real-time plot of their force matched the prescribed force trajectory on a computer monitor. Subjects were seated in a dental chair with the palmar surface of their left hand resting on a small wooden platform that positioned the force transducer perpendicular to the first finger at the distal phalangeal joint. A restraint positioned the thumb at 85° of abduction relative to the index finger. Force data were amplified using a custom-designed direct-current amplifier and sampled at a rate of 50 Hz. The computer monitor was positioned at eye level to the subject at a distance of 1.5 m. Over a dark blue background, subjects viewed a yellow line depicting the target force trajectory and a red line depicting their own force. The magnitude of force was presented along the y-axis as a percentage of maximal voluntary force, and time was presented along the x-axis. The 50-s trial was presented to the subject with the entire target trajectory visible and stationary throughout. The red line representing the subject's own force was presented from the left of the screen (0 s) to the right of the screen (50 s) as they attempted to match the vertical deviations of the trajectory. A computer monitor with a

15-in. viewing area (diagonal) was used to present the force-matching task to the subjects using DasyLab software (Dasytec USA, Amherst, NH). The screen resolution was set at 800×600 pixels. The amplitude resolution of the muscular force production was 4.55% MVC/cm. The temporal resolution was 2.37 s/cm.

Data analysis. For each trial, corresponding 19.8-s force and firing rate segments were extracted from the oscillatory region of the task. This specific duration was an integer multiple of the fundamental period of the task and therefore provides equal representation of high and low forces within the complex force-matching task. The mean, standard deviation and coefficient of variation of ISIs were computed from all available ISIs within these segments to provide general descriptors of firing rates and firing variability.

Frequency domain measures. To describe the amplitude of force and firing rate modulation, measures were derived from frequency spectra of the force and firing rate data. For any frequency domain analysis, only motor unit recordings that did not contain outlier ISIs were selected for analysis. Motor unit recordings were excluded from analysis if visual inspection of the ISI plot together with its ISI frequency histogram indicated transient derecruitment (Fig. 2). Motor units were included if the ISI histogram from the selected 19.8-s region of analysis did not contain ISIs that were separate from the

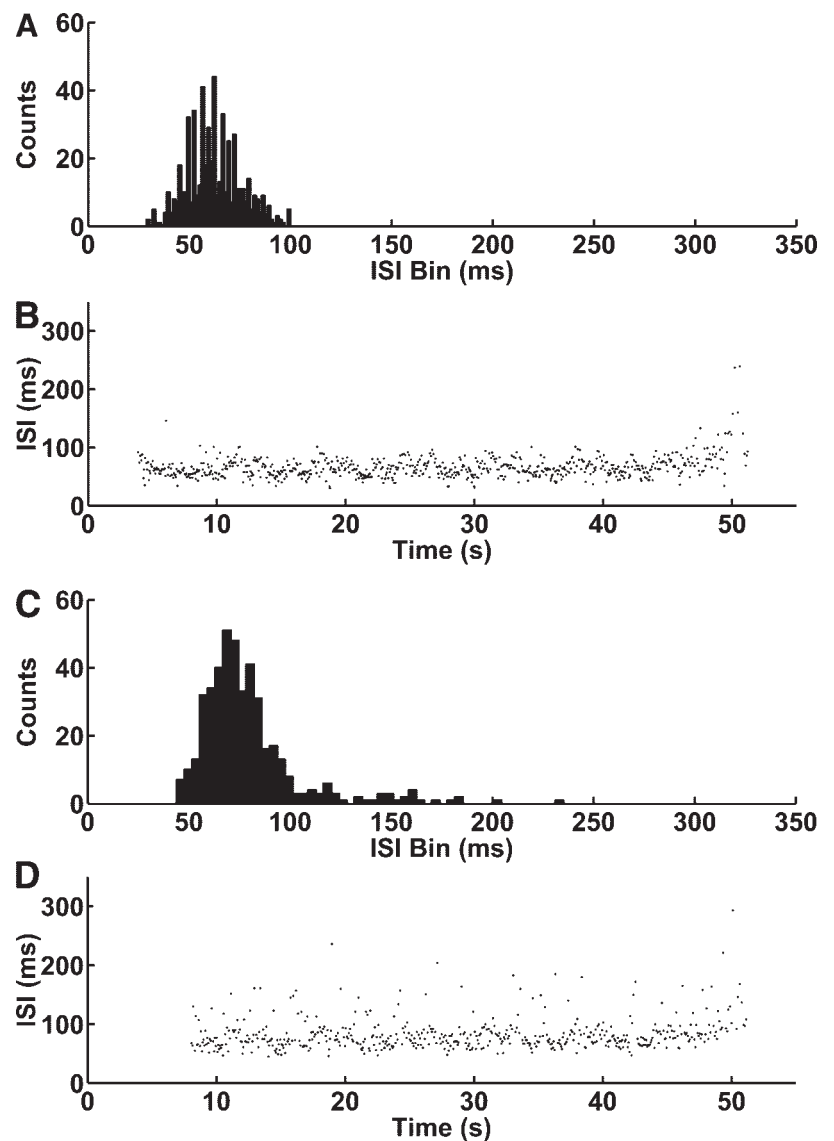


Fig. 2. ISI histograms (A and C) and raw ISIs (B and D) for 2 different motor units. The lower motor unit (C and D) was excluded from analysis because it had a recruitment threshold that was close to the required force during the contraction, evidenced by a broken ISI distribution and frequent occurrence of long ISIs, which are inconsistent with tonic firing.

overall distribution. Therefore, the resulting motor unit sample includes only motor units exhibiting continuous (tonic) firing. To account for any changes in mean firing rate throughout a trial, each firing rate time series was linearly detrended.

To quantify the amplitude of force and motor unit firing rate modulation at the two task-specific frequencies, the fast Fourier transform (FFT) was computed for each force and firing rate time series (1,024 point FFT, 005-Hz resolution, Fig. 3). For analysis of firing rate, a series of instantaneous firing rates was calculated as the inverse of the ISI series from each motor unit. This instantaneous firing rate series was then placed on a time base with the same sampling frequency as force (50 Hz) by linear interpolation (25). Others have applied the Fourier transform directly to firing data in the form of point processes (1). However, our application of the interpolation and the point process methods to simulated data with known periodicity supported the validity and greater resolution of the interpolation method with these data. A relevant factor in this decision was the relatively short (19.8 s) duration of our segments due to practical considerations noted above. Each segment of the force and firing rate data was linearly detrended. Within each of two 0.1-Hz bins centered at 0.15 and 0.45 Hz, the peak amplitude of the FFT was measured (Fig. 3, C and D). To quantify the amplitude of firing rate modulation per unit of force modulation while correcting for small differences in performance, the amplitude ratio of force modulation to firing rate modulation was computed as FMG [%MVC/pulses per s (pps)]. The area within these bins was also computed, but it is not reported here because the information was redundant with the peak amplitude data. When computed based on the area within the two frequency bins, the FMG measures were strongly correlated with those based on peak amplitudes (0.15 Hz: $r = 0.87$, 0.45 Hz: $r = 0.90$).

Statistical analysis. All statistical computations were conducted using SPSS software (version 13, SPSS, Chicago, IL). A two-factor ANOVA was used to evaluate differences between age groups (between subjects) and frequency (repeated: within subjects). Single-factor ANOVA was used to compare measures between groups when the frequency factor was irrelevant. Analysis of covariance (ANCOVA) was also conducted to control for the influence of motor unit recruitment threshold on the amplitude of firing rate modulation. Pearson correlation coefficients (r) were computed to describe rela-

tionships between selected variables, and a paired t -test comparing MVCs at the beginning and end of the test session was used to test for fatigue. All criterion measures are presented in text and figures as averages (SD).

RESULTS

The older and younger subjects possessed similar FDI MVC force [young: 14.2 N (SD 4.1), older: 14.6 N (SD 4.0), $F = 0.6$, $P = 0.45$]. There was no change in MVCs immediately following testing, indicating that the protocol was not fatiguing (paired $t = 1.5$, $P = 0.17$). Older adults exhibited poorer force matching performance with root mean square (RMS) error of force scores of 1.52% MVC (SD 0.29) and 2.08% MVC (SD 0.67) for the young and older groups, respectively ($F = 8.5$, $P = 0.008$).

Motor unit. A sample of 105 motor unit recordings was obtained (54 young, 51 older). Motor unit recruitment thresholds were derived from a subset of 100 motor units (force level at first firing). Motor units in the older adults had higher recruitment threshold forces [older: 9.9% MVC (SD 4.7), range 1.5- 18.4, young: 7.4% MVC (SD 4.1), range 0.1-18.25, $F = 8.3$, $P = 0.005$]. These thresholds were similar to those reported in prior reports from the FDI muscle in young and older adults, although one prior report utilized a ramp increase of 10% MVC/s compared with our rate of 5% MVC/s (12).

Based on computations from the oscillatory portion of the force-matching task (19.8-s segment), there were no age-related differences in mean ISIs [young: 65.5 ms (SD 11.0); older: 67.5 ms (SD 13.2); $F = 0.7$, $P = 0.4$], the standard deviation of ISIs [young: 18.9 ms (SD 8.0); older: 19.5 ms (SD 6.4); $F = 0.17$, $P = 0.7$], or the coefficient of variation of ISIs [young: 0.29 (SD 0.09); older: 0.29 (SD 0.08); $F = 0.11$, $P = 0.7$]. In this context, the standard deviation and coefficient of variation do not depict firing variability. Rather, they provide a gross indicator of the range of firing rate modulation.

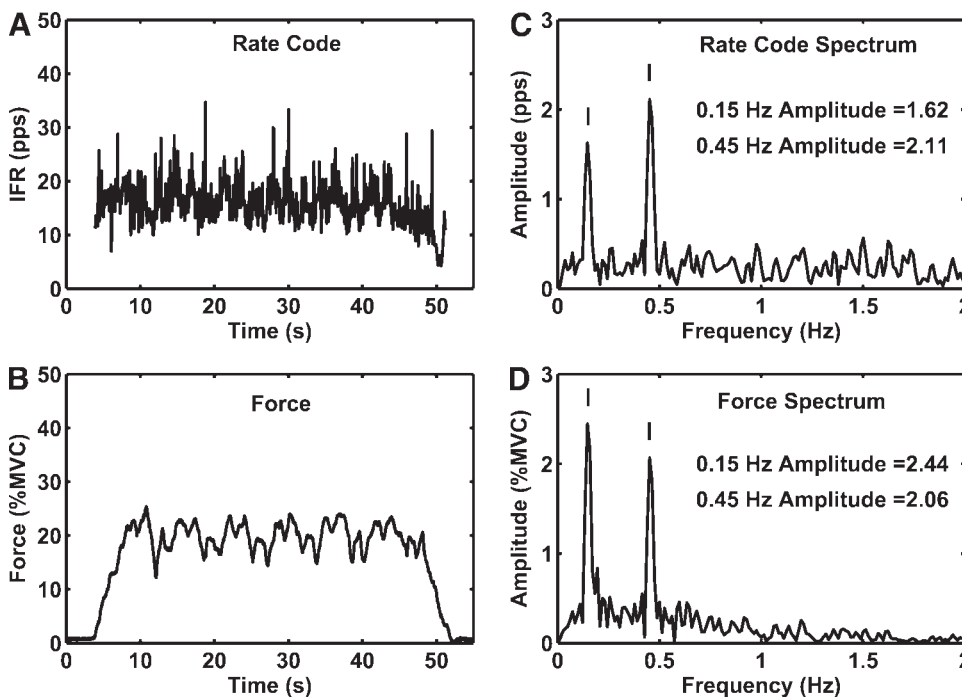


Fig. 3. IFR of a single motor unit (A) during the force-matching performance within 1 trial of the sum-of-sines task (B) are shown. Spectral estimates for firing rate modulation (C) and force modulation (D) show pronounced peaks at the 2 task frequencies (0.15 and 0.45 Hz). Peak amplitudes within 0.1-Hz bins surrounding the task frequencies were taken as the amplitude of modulation.

Force control and rate coding peak. Amplitudes from frequency spectra indicated that force modulation was similar in young and older adults within both the 0.15- and 0.45-Hz components (Fig. 4A; frequency \times group: $F = 2.3$, $P = 0.13$,

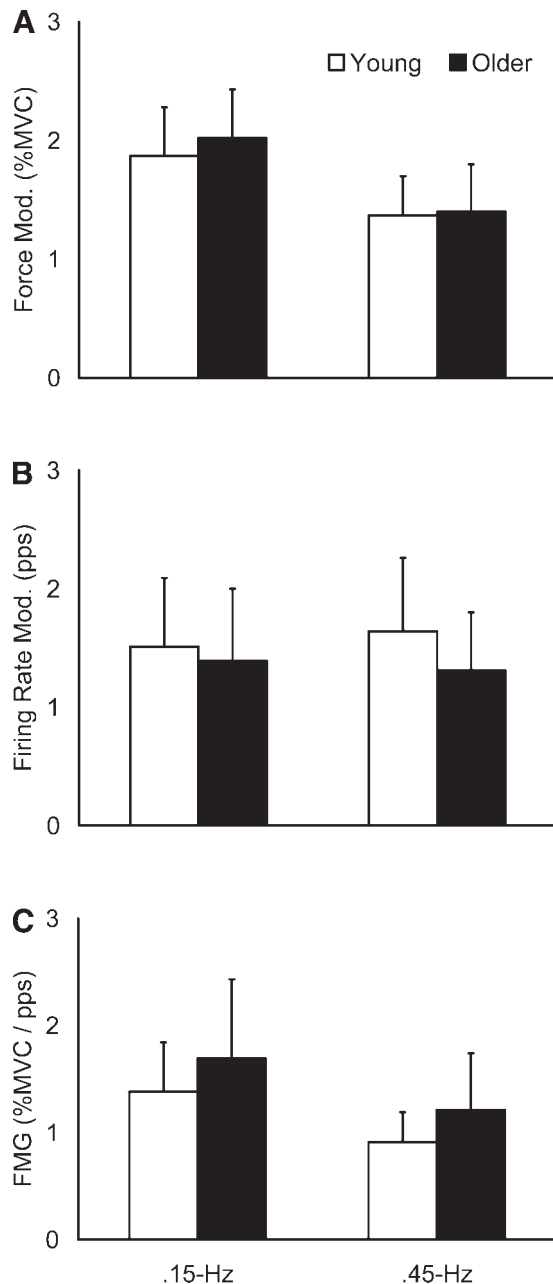


Fig. 4. A: average (SD) force modulation (Mod) amplitude. The amplitude of force modulation was significantly greater at 0.15 Hz compared with 0.45 Hz ($P < 0.001$), and this is consistent with the characteristics of the force-matching task. At both task frequencies, the amplitude of force modulation was similar in young and older adults ($P = 0.167$). B: average (SD) firing rate modulation amplitude. Within a significant group \times frequency interaction ($P = 0.01$), older adults had less amplitude of firing rate modulation compared with young adults at the higher task frequency ($P = 0.003$) but not at the lower task frequency ($P = 0.31$). C: average (SD) force modulation gain is the change in force per change in firing rate. Force modulation gain (FMG) was greater at the lower task frequency compared with the higher frequency ($P < 0.001$), and this is consistent with the low-pass filtering effects of muscle. Force modulation gain was greater in older adults than in young adults ($P = 0.001$), indicating that older adults imparted less change in firing rate to accomplish the same change in force.

group $F = 1.9$, $P = 0.167$). Thus, although RMS error scores indicated poorer force-matching performance in older adults, both groups modulated force throughout a similar range in each frequency component.

Even though the amplitude of force modulation was similar in both groups, a significant frequency \times group interaction in firing rate modulation ($F = 6.8$, $P = 0.01$) indicated that groups modulated firing rates differently within the higher (0.45 Hz) frequency component (Fig. 4B). The amplitude of firing rate modulation was similar at 0.15 Hz [young: 1.51 pps (SD 0.59); older: 1.39 pps (SD 0.61); $F = 1.0$, $P = 0.31$], but it was less in older adults at 0.45 Hz [young: 1.64 pps (SD 0.61); older: 1.31 pps (SD 0.49); $F = 9.3$, $P = 0.003$]. When interpreting the similar amplitude of firing rate modulation across frequencies, one must recall that the amplitude of force modulation was less at the higher frequency (Fig. 4A).

To account for differences in the amplitude of force modulation between frequencies and trials, the amplitude of force modulation was expressed relative to the corresponding amplitude of firing rate modulation. Therefore, FMG was calculated as the amplitude ratio of force rate modulation to firing rate modulation, within each task frequency (Fig. 4C). Consistent with the observations of Iyer et al. (20) and in agreement with the low-pass filter characteristics of muscle, FMG was less at 0.45 Hz [1.06% MVC/pps (SD 0.42)] than at 0.15 Hz [1.53% MVC/pps (SD 0.61)] for both groups ($F = 120$, $P < 0.001$). Thus, for a given change in firing rate, there was less change in muscular force at the higher frequency. FMG was greater in older adults [older: 1.45% MVC/pps (SD 0.48), young: 1.14% MVC/pps (SD 0.48), $F = 10.7$, $P = 0.001$] with no group \times frequency interaction ($F = 0.007$, $P = 0.9$). This age-related increase in FMG indicates that there was more change in force per change in firing rate in older adults.

Relationships among variables Pearson's correlation coefficients were computed to describe relationships between a motor unit's recruitment threshold and the amplitude of its firing rate modulation within each task frequency. Overall, significant (all $P < 0.01$) small-to-moderate correlations supported positive relationships between motor unit recruitment thresholds and the amplitude of firing rate modulation (0.15 Hz: $r = 0.49$, 0.45 Hz $r = 0.26$). In both age groups, these relationships were stronger at the 0.15-Hz frequency, which required greater force modulation. Within individual motor units, there was a strong relationship between the amplitude of firing rate modulation at the 0.15- and 0.45-Hz task frequencies (young: $r = 0.83$, older: $r = 0.63$, both $P < 0.001$). Thus motor units with a large amplitude of firing rate modulation at 0.15 Hz also exhibited a large amplitude of modulation at 0.45 Hz.

Analysis controlling for recruitment threshold (ANCOVA) A priori, it was expected that a motor unit's firing behavior during these oscillatory contractions would covary with its recruitment threshold (13). This was supported by the positive correlations between recruitment threshold forces and the amplitude of firing rate modulation. Considering this relationship, recruitment threshold was used as a covariate. For firing rate modulation and FMG measures at both frequencies, the assumption of parallel slopes between the covariate and the dependent variables was upheld based on tests of group by threshold interactions (all $P > 0.21$) (36). Controlling for recruitment threshold force strengthened the significance of the age-group differences that were observed in the original

ANOVA. While controlling the effects of recruitment threshold on the amplitude of firing rate modulation, the group \times frequency interaction was no longer significant ($P = 0.1$), and less firing rate modulation in older adults, at both frequencies, became significant ($F = 14$, $P < 0.001$). At 0.15 Hz, the adjusted amplitude of firing rate modulation was 1.59 pps (SD 0.52) in young adults and 1.29 pps (SD 0.52) in older adults. At 0.45 Hz, the adjusted amplitude of firing rate modulation was 1.68 pps (SD 0.53) in young adults and 1.24 pps (SD 0.53) in older adults. The absence of the group \times frequency interaction persisted for FMG ($P = 0.33$) and the greater FMG in older adults was significant at $F = 27$, $P < 0.001$. At 0.15 Hz, the adjusted amplitude of FMG was 1.31% MVC/pps (SD 0.54) in young adults and 1.80% MVC/pps (SD 0.54) in older adults. At 0.45 Hz, the adjusted amplitude of FMG was 0.88% MVC/pps (SD 0.39) in young adults and 1.28% MVC/pps (SD 0.40) in older adults. Figure 5 presents these averages and standard deviations after statistical adjustment for recruitment thresholds.

DISCUSSION

The main findings were as follows. 1) Firing rates were modulated less and the amount of change in force per change in firing rate was more in older adults than in young adults. 2) The amplitude of rate coding was positively related to the

motor unit's recruitment threshold force. 3) In both young and older adults, at the higher task frequency there was less change in force per change in firing rate, compared with the lower task frequency. The results support our hypothesized age-related reduction in the amplitude of firing rate modulation and are consistent with the need of the nervous system to overcome the low-pass filter characteristics of muscle. Multiple underlying mechanisms for these age-related differences in rate coding should be considered in the present interpretation and elucidated in future experiments.

Based on error measurements (RMS error), older adults exhibited poorer control of muscular force in this compound sinusoidal force-matching task. However, the more specific FFT measures indicated that the amplitude of force modulation was similar in young and older adults at both task frequencies. Therefore, young and older adults modulated force within the prescribed amplitude and frequency requirements similarly, and this supports our age-group comparisons of firing rate modulation. The difference in error scores likely reflects low-amplitude force corrections outside of the task frequencies or temporal deviations from the target force curve.

The spectral measures of firing rate modulation provided results that would be expected based on existing literature. For a given amplitude of force modulation, the amplitude of motor unit firing rate modulation is greater at higher modulation frequencies (20). In the present results, the amplitude of firing rate modulation was similar in the two frequencies (Fig. 4B) even though the amplitude of the force oscillations was less at 0.45 Hz than at 0.15 Hz (Fig. 4A). Therefore, the effects of oscillation frequency on the amplitude of firing rate modulation exist in these data as well. For direct comparisons between frequencies, the ratio of the amplitude of force modulation to the amplitude of firing rate modulation was computed as the variable termed FMG. This measure indicated that there was less gain at the higher task frequency (0.45 Hz), meaning that a given change in firing rate would result in less change in force, compared with the 0.15-Hz frequency (Fig. 4C). This is consistent with the low-pass filter characteristics of muscle (2). Based on experiments conducted in felines (2, 38), the effects of muscle filtering should become apparent above task frequencies of 0.5–1 Hz. The 0.45-Hz frequency component used here is near the beginning of this range, so small effects might be expected. Nevertheless, there were clear differences in FMG between 0.15 and 0.45 Hz, and there were similar age-group differences at both frequencies. We do recommend the extension of this protocol to higher frequencies where the filtering effects should be greater.

As hypothesized, firing rate was modulated less and there was greater FMG in older adults. Based on the comparison of ANOVA and ANCOVA results, these differences were greater when the influence of recruitment threshold was controlled statistically. The ANCOVA results provided stronger statistical support for group differences in firing rate modulation and FMG. This was expected considering that, with this 20% MVC task, each motor unit had a different proximity to its recruitment threshold force, thus influencing the relationship between changes in firing rate and changes in force (13).

The relationship between a motor unit's recruitment threshold force and the amplitude of firing rate modulation at the 20% MVC force level is an important consideration in the interpretation of these results. Some have observed a negative

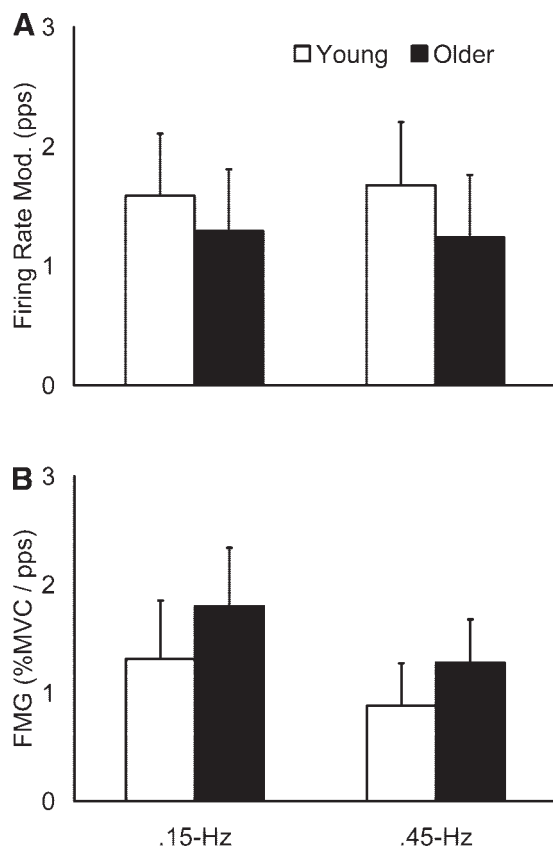


Fig. 5. A: average (SD) amplitude of firing rate modulation. When adjusted for motor unit recruitment threshold, the amplitude of firing rate modulation was less in older adults at both task frequencies ($P = 0.001$). B: similar results were obtained for force modulation gain, which was less in older adults at both task frequencies ($P < 0.001$) and less at the higher task frequency in both groups ($P < 0.001$). Both of these variables are adjusted means based on analysis of covariance using motor unit recruitment threshold as a covariate.

relationship between peak firing rates and recruitment threshold force for the same strength of submaximal contraction (7, 10, 41), whereas others have observed greater peak firing rates in higher threshold units (35, 45). Our observation that higher threshold motor units had greater amplitudes of firing rate modulation is different information compared with findings in these previous studies because we quantified the amount of firing rate modulation during submaximal conditions in which maximal firing rates were not likely to be observed. Importantly, in the 20% MVC condition, each observed motor unit was discharging with a different amount of excitation above its recruitment threshold (0.1–18.4% MVC). Considering this range, our positive relationship between the amplitude of firing rate modulation and recruitment threshold is best explained by a trilinear firing rate-to-force relationship that was observed by others (13). In this prior research, it was shown that the changes in firing rate per change in force are large at levels of excitation just above the motor unit's recruitment threshold. Within a midrange of force levels, motor units exhibited less of a change in firing rate per change in force. At the greatest forces, motor units again exhibited large changes in firing rate per change in force. This explains our finding that higher threshold motor units exhibited the greatest amplitude of firing rate modulation. The low-threshold motor units may have been operating within their midrange during the force oscillations (less change in firing rate per change in force). Meanwhile, our higher threshold motor units may have been operating within the range just above recruitment in which larger changes in firing rate are observed per change in force. Although logical, definitive evidence for this conclusion requires a complete force-firing rate profile for each motor unit that was observed.

Our explanation for less amplitude of firing rate modulation and the greater force output per change in firing rate in older adults is that larger motor unit twitch forces (4, 9, 14, 44) and prolonged contraction and half-relaxation times (9, 37) in aged muscle enhance the summation of motor unit force. Hypothetically, this altered contractility allows less of a change in firing rate to elicit the same change in muscular force, compared with young motor units. The matching of firing behavior to contractile properties is supported by animal research (2), and the altered contractility of aged muscle is well documented (4, 9, 14, 37, 44). Even so, one limitation of this experiment was the absence of contractile measures. Future research should include measures of whole muscle contractility or estimates of motor unit contractility via the technique of spike-triggered averaging. Indeed, this line of research would also benefit from parallel experiments based on animal preparations of aged muscle similar to those from young muscle (2).

An alternative explanation for less firing rate modulation in older adults is that a reduction in maximal firing rates in older adults (6, 22, 23, 40) limits the potential range of modulation. If this were true, greater recruitment of other motor units or less antagonist cocontraction would be necessary to achieve the same amplitude of force modulation. The present techniques did not allow us to test these alternative possibilities. The antagonist musculature [first palmar interosseous (FPI) (16)] was not recorded in this experiment. Some have demonstrated that age-related differences in antagonist cocontraction do exist (43), yet others present evidence of similar coactivation of FDI and FPI in older adults during position-holding and position-tracking tasks (28). Nevertheless, we reject the explanation of

a limited firing rate range. Whereas the amplitude of firing rate modulation was less in the older adults, the mean firing rates for both groups were the same. Therefore, a hypothetical limitation on maximal firing rate in older adults did not impinge on the mean firing rate required for oscillations around 20% MVC. This similarity of submaximal firing rates in young and older adults at 20% MVC is in agreement with the results of Kamen et al. (23), who observed no differences in firing rates at 50% MVC even though maximal firing rates were significantly less in older adults (young 50 pps, older 30 pps). Should a similar firing rate ceiling exist in the present sample, one might conjecture that a firing rate limit at 30 pps is not low enough to influence the amplitude of modulation around the mean rate of 14.8 pps that was observed in our sample of older adults. If it did, we would suspect that both the amplitude of firing rate modulation and the mean firing rates would also be less in our sample of older adults.

The new information provided by this experiment is that during the performance of the same force-oscillation task, older adults used less modulation of motor unit firing rates than young adults. Furthermore, the amount of change in firing rate during submaximal force oscillations is dependent on the motor unit's proximity to its recruitment threshold force, in both young and older adults. Motor units operating nearer to their thresholds exhibited greater firing rate modulation. The conclusions advanced in this paper should be further elucidated using tasks with single-frequency components in which effects of frequency and amplitude of force modulation are investigated separately. Future experiments should also incorporate measures of muscle contractility and antagonist muscle activity.

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GRANTS

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