The compensatory interaction between motor unit firing behavior and muscle force during fatigue

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Contessa P, De Luca CJ, Kline JC. The compensatory interaction between motor unit firing behavior and muscle force during fatigue. *J Neurophysiol* 116: 1579–1585, 2016. First published July 6, 2016; doi:10.1152/jn.00347.2016.—Throughout the literature, different observations of motor unit firing behavior during muscle fatigue have been reported and explained with varieties of conjectures. The disagreement amongst previous studies has resulted, in part, from the limited number of available motor units and from the misleading practice of grouping motor unit data across different subjects, contractions, and force levels. To establish a more clear understanding of motor unit control during fatigue, we investigated the firing behavior of motor units from the vastus lateralis muscle of individual subjects during a fatigue protocol of repeated voluntary constant force isometric contractions. Surface electromyographic decomposition technology provided the firings of 1,890 motor unit firing trains. These data revealed that to sustain the contraction force as the muscle fatigued, the following occurred: *1*) motor unit firing rates increased; *2*) new motor units were recruited; and *3*) motor unit recruitment thresholds decreased. Although the degree of these adaptations was subject specific, the behavior was consistent in all subjects. When we compared our empirical observations with those obtained from simulation, we found that the fatigue-induced changes in motor unit firing behavior can be explained by increasing excitation to the motoneuron pool that compensates for the fatigue-induced decrease in muscle force twitch reported in empirical studies. Yet, the fundamental motor unit control scheme remains invariant throughout the development of fatigue. These findings indicate that the central nervous system regulates motor unit firing behavior by adjusting the operating point of the excitation to the motoneuron pool to sustain the contraction force as the muscle fatigues.

muscle fatigue; motor units; firing rates; recruitment threshold; force twitch

NEW & NOTEWORTHY

This work provides a clear understanding of motor unit control during fatigue. It reveals that the excitation to the motoneuron pool adjusts motor unit firing behavior to compensate for the changing muscle force twitch. The degree of motor unit adaptation is subject specific. Yet, across all subjects, the fundamental control scheme governing motor unit firings remains unchanged.

MUSCLE FATIGUE IS ACCOMPANIED by adaptations in the firing rate and recruitment behavior of motor units. Studies by both us (Adam and De Luca 2005) and others [e.g., de Ruiter et al. (2005) and Mettler and Griffin (2016)] have reported that as a muscle fatigues during repeated or sustained submaximal volun-

tary contractions, active motor units increase their firing rates, and new motor units are recruited. Adam and De Luca (2003, 2005) and Contessa and De Luca (2013) have explained that these adaptations result from an increase in the excitation to the motoneuron pool to maintain muscle force at a constant level, despite the fatigue-induced reduction in muscle force twitch reported by Adam and De Luca (2005) and de Ruiter et al. (2005), among others.

Yet, this understanding of muscle fatigue remains disputed by some. Work by Enoka et al. (1989), Kelly et al. (2013), McManus et al. (2015), Mottram et al. (2005), and Vila-Chã et al. (2012), among others, report that during fatigue, the majority of motor units decreases their firing rates while new motor units are recruited. However, these opposing observations of firing behavior are confounded by the analysis of just a few motor units (typically 1–5 per contraction) obtained from intramuscular electromyographic (EMG) signals (Enoka et al. 1989; Kelly et al. 2013; Mottram et al. 2005) or by the practice of grouping motor unit data across different subjects, contractions, or force levels (McManus et al. 2015; Mottram et al. 2005; Vila-Chã et al. 2012). However, De Luca and Contessa (2012) and Hu et al. (2013) have warned that grouping motor unit data obscures the construct of motor unit firing behavior under normal conditions. During fatiguing contractions, where firing patterns vary over time and among subjects, this practice is likely to confuse the firing construct to an even greater degree.

To reconcile the differing reports in the literature, we set out to investigate motor unit firing behavior in individual subjects and contractions performed during a fatigue protocol of repeated voluntary submaximal isometric contractions of the vastus lateralis (VL) muscle. We applied a recently developed surface EMG (sEMG) decomposition technology, described by De Luca et al. (2006) and Nawab et al. (2010), to obtain the firings of dozens of concurrently active motor units during each contraction. As the VL fatigued, we observed the following: that *1*) motor unit firing rates increased; *2*) new motor units were recruited; and *3*) motor unit recruitment thresholds decreased. To understand the cause of these adaptations, we simulated the fatigue protocol with a mathematical model that replicates the decrease in muscle force twitch reported to occur with fatigue [e.g., Adam and De Luca (2005) and de Ruiter et al. (2005), among others]. The simulations reproduced all motor unit firing adaptations observed in our empirical data. The agreement of our simulated and empirical findings indicates that the operating point of the excitation to the motoneuron pool adjusts motor unit firing behavior to compensate for the changing muscle force twitch during fatigue.

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METHODS

Experimental protocol. Five healthy subjects, three men and two women between the ages of 24 and 33 yr old, participated. All subjects read, indicated they understood, and signed the informed consent form approved by the Western Institutional Review Board. Each subject was seated in an apparatus that measures isometric force during extension of the dominant lower limb while restraining hip movement and immobilizing the leg at a knee angle of 60° flexion. The force was filtered between 0 and 450 Hz, digitized at 20 kHz, and displayed for visual feedback. We recorded sEMG signals during voluntary isometric leg extension using a four-channel dEMG array sensor (Delsys, Natick, MA) placed on the skin over the VL. The sEMG signals were filtered between 20 and 450 Hz and sampled at 20 kHz using a Bagnoli EMG amplifier (Delsys, Natick, MA).

The subjects' MVC was measured as the greatest force of three repeated, 3 s maximal isometric leg-extension contractions. After at least ~10 min of rest, subjects were asked to perform a series of isometric contractions by tracking target force trajectories displayed on a monitor. The trajectories increased linearly at a rate of 10% MVC/s, up to 30% MVC, and remained at this force level for 48 s before decreasing linearly to a resting state at a rate of 10% MVC/s. After practicing the tracking task, subjects repeatedly performed the contraction until the average force decreased by >5% from the 30% MVC target. All contractions before this point were retained for the fatigue analysis. A 6-s rest interval was given between repetitions.

Motor unit analysis. The sEMG signals recorded during the contractions were decomposed into their constituent motor unit action potential (MUAP) trains (De Luca et al. 2006; Nawab et al. 2010). Validation of the extracted MUAP shapes and firing times was performed, as described by De Luca and Contessa (2012). Only firing trains obtained with >90% accuracy were considered for further analysis.

We characterized the firing behavior of each motor unit by measuring the following: *1*) the amplitude of the MUAP shape, calculated as the maximum amplitude of the positive and negative MUAP phases detected across the four channels of the sEMG signal; *2*) the motor unit recruitment threshold, calculated as the force level at which the motor unit started firing; and *3*) the motor unit average firing rate, calculated from the inverse of the interpulse intervals in a 10-s interval between 35 and 45 s during the constant force segment of each contraction.

RESULTS

As muscle fatigue developed during the repeated contractions, three adaptations in firing behavior were observed from the 1,890 motor unit firing trains studied across all subjects. The adaptations are depicted for a representative subject in Fig. 1, *A–C*.

1) The mean firing rates of motor units with similar-amplitude MUAPs (Fig. 1, *A–C*) increased throughout the mid- to late-fatigue contractions and across contractions, while the subject maintained the 30% MVC force level (Fig. 1, *A–C*). *2*) Additional higher-threshold, lower firing rate motor units were

During repeated fatiguing contractions the firing rates of individual motor units increase, their recruitment thresholds decrease and new motor units are recruited
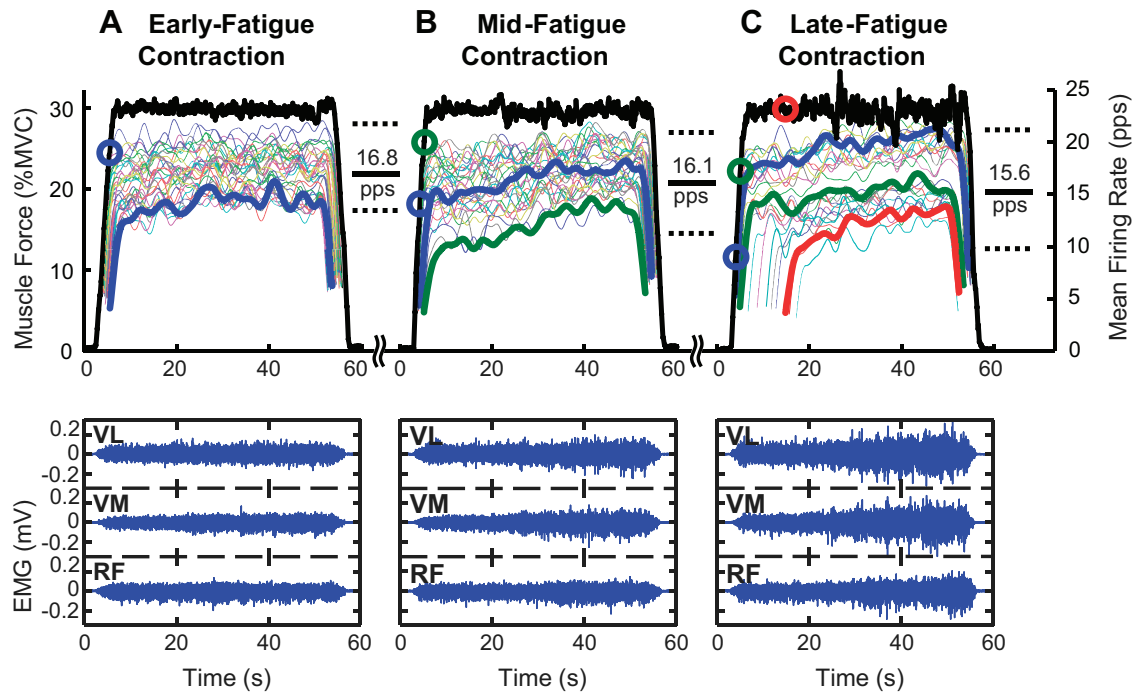

Fig. 1. *A–C*: three contractions performed by 1 subject at the beginning (*A*), middle (*B*), and end (*C*) of the fatigue protocol. *Top*: the solid black lines show the muscle force produced. The time-varying mean firing rates of 100 motor units obtained from the 3 contractions are calculated using a 4-s Hanning window and shown in faded colors. For clarity, 6 are emboldened. The same color across different contractions indicates motor units with similar MUAP amplitude. Note the recruitment of additional higher-threshold, lower-firing rate motor units during the increasing (green trace in *B*) and constant force (red trace in *C*) segments of subsequent contractions. Colored circles provide the force at which motor units are recruited. The decreasing force value of similarly colored circles in *A–C* indicates a decrease in the recruitment threshold of motor units with similar MUAP amplitude. On the *right* of each contraction, the dotted black lines indicate the range of firing rates for the detected motor units. The continuous black lines and numerical values indicate the average of all motor unit firing rates in each contraction. *Bottom*: sEMG signals recorded separately from the vastus lateralis (VL), vastus medialis (VM), and rectus femoris (RF) in the same subject during the fatigue protocol. The root-mean-square signal amplitude during the analysis interval increased from 0.033, 0.027, and 0.031 mV at the beginning to 0.060, 0.059, and 0.050 mV at the end of the fatigue protocol for the VL, VM, and RF muscles, respectively.

recruited during the increasing (see Fig. 1*B*) and constant force (see Fig. 1*C*) segments of subsequent contractions. *3*) Across each contraction, motor units with similar-amplitude MUAPs were recruited at progressively lower force thresholds (see Fig. 1, *A–C*).

These adaptations are apparent in the firing behavior of individual motor units. In contrast, when the firing rates are grouped across all motor units in each contraction, the average value (reported in Fig. 1) gives false indication of firing rate decrease with fatigue.

Note that the sEMG signals recorded from the VL, vastus medialis, and rectus femoris muscles of the quadriceps group similarly increased in amplitude during the fatigue protocol, as shown in Fig. 1, *A–C*. This indicates that the motor unit firing adaptations observed in the VL muscle are not a consequence of changes in the relative contribution of the knee extensor muscles to the exerted force.

The fatigue-induced increase in firing rates is further substantiated for all subjects in Fig. 2. Figure 2, *A–E*, shows the relation among average motor unit firing rate and MUAP amplitude for three contractions performed at the beginning, middle, and end of the fatigue protocol. The relation was characterized by an inverse exponential regression ($R^2 = 0.74 - 0.97$; Fig. 2*F*) in all contractions, indicating that motor units with higher-amplitude MUAPs maintained lower firing rates than those with lower-amplitude MUAPs (Fig. 2, *A–E*). The upward shift in the regression curves from early to mid to late fatigue demonstrates a progressive increase in motor unit firing rates. The presence of higher-amplitude MUAPs in the mid- and late-fatigue contractions
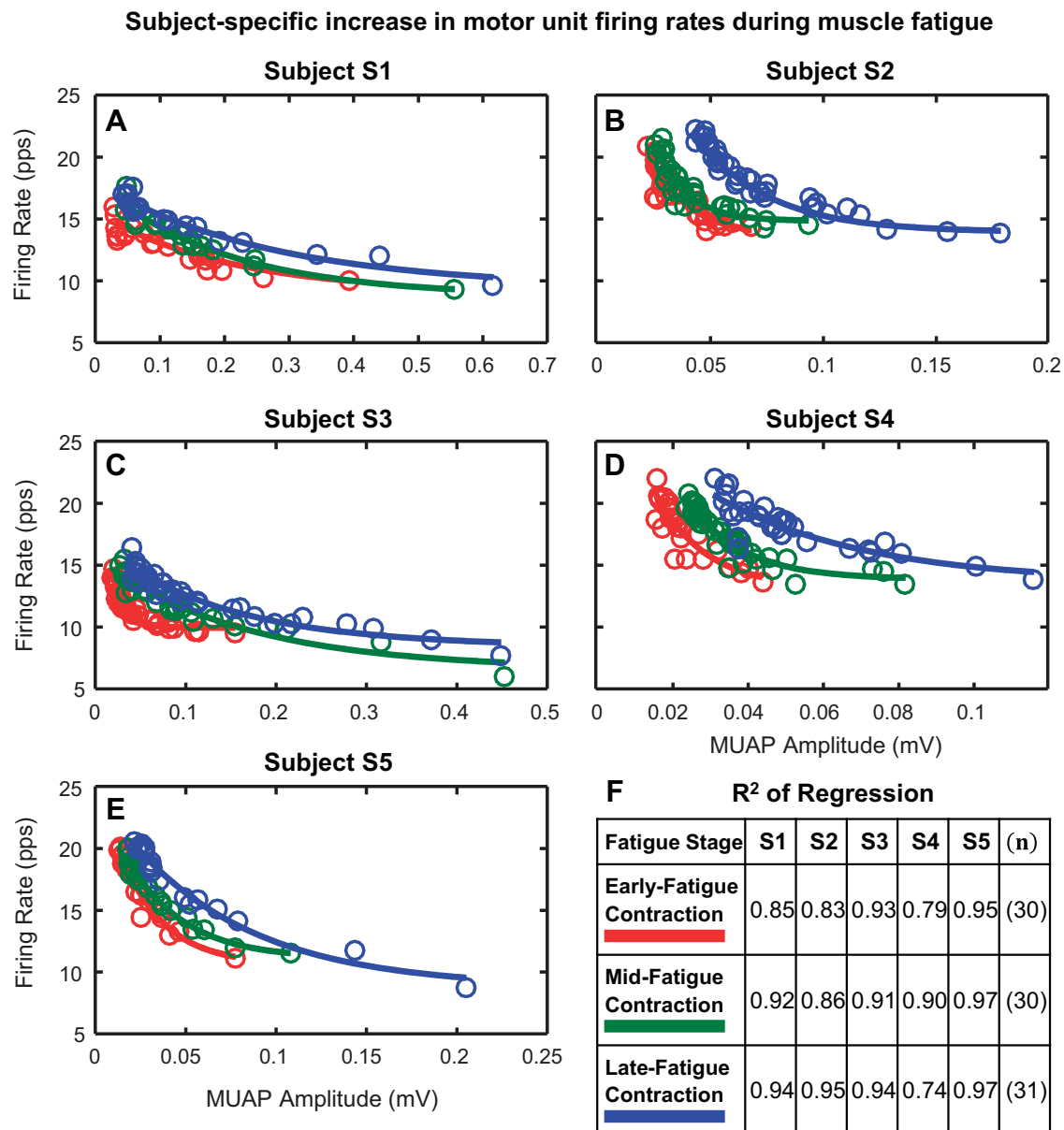
Subject-specific increase in motor unit firing rates during muscle fatigue

Fatigue Stage	S1	S2	S3	S4	S5	(n)
Early-Fatigue Contraction	0.85	0.83	0.93	0.79	0.95	(30)
Mid-Fatigue Contraction	0.92	0.86	0.91	0.90	0.97	(30)
Late-Fatigue Contraction	0.94	0.95	0.94	0.74	0.97	(31)

Fig. 2. *A–E*: subject-specific relation between average firing rate and MUAP amplitude for motor units obtained from 3 contractions at the beginning (red), middle (green), and end (blue) of the fatigue protocol. The data were fit with exponential functions of the form $y = A + Be^{(-Cx)}$. *F*: R^2 values and average number of motor units (*n*) of the regressions.

indicates that additional motor units were recruited as fatigue progressed.

Although consistent in trend, the degree of fatigue-induced changes in motor unit firing behavior was unique for each subject. For example, the firing rates of some motor units increased by 2–3 pulses/s (pps) in subject S1, whereas others increased by as much as 6–7 pps in subject S4 from the beginning to the end of the fatigue protocol.

The adaptations in motor unit recruitment threshold with fatigue are detailed in Fig. 3. Figure 3, *A–C*, shows the average recruitment threshold of motor units with similar-amplitude MUAPs in three contractions at the beginning (Fig. 3*A*), middle (Fig. 3*B*), and end (Fig. 3*C*) of the fatigue protocol for each subject. The average recruitment threshold decreased significantly from the beginning to the end of the contraction series ($P < 0.02$ for all subjects, Mann-Whitney-Wilcoxon test). The degree of the decrease was specific to each subject. Yet, the consistent decrease across subjects indicates that motor units with similar-amplitude MUAPs produce progressively less force as fatigue develops.

Figure 3, *D–H*, presents the relationship among MUAP amplitude, recruitment threshold, and contraction repetition for each subject. The different color bars represent the average MUAP amplitude in subsequent contraction repetitions from the first to the last contraction. Three groups of bars for each subject include motor units recruited within the 0–10%, 10–20%, and 20–30% MVC force range. Two trends can be seen from these data. Within each contraction, motor units with larger-amplitude MUAPs are recruited at progressively higher forces, as evidenced by the increasing height of similarly colored bars, from 0–10% to 10–20% and 20–30% MVC. This direct relationship between MUAP amplitude and recruitment threshold was maintained throughout the fatigue protocol. The second trend demonstrates that within each force range, motor units with higher-amplitude MUAPs are progressively recruited in subsequent contractions, as depicted by the positive slope of the linear regressions (see Fig. 3, *D–H*; $R^2 = 0.54$–0.96; Fig. 3*I*).

DISCUSSION

During fatigue, motor unit firing behavior adapts, but the control scheme remains unchanged. As submaximal contractions were repeated to fatigue the VL muscle, motor unit firing rates increased, new motor units were recruited, and the recruitment thresholds of all motor units decreased. These adaptations were observed by comparing the firing behavior of individual motor unit firing trains as a function of the MUAP amplitude across repeated contractions. Some studies have reported that MUAP amplitude may decrease with fatigue (Gydikov et al. 1976; Klein et al. 2006; Sandercock et al. 1985). However, even if a decrease in MUAP amplitude occurred in our study, the adaptations in motor unit firing behavior reported in Figs. 1–3 would still hold. In fact, a decrease in MUAP amplitude would accentuate the increase in firing rate, decrease in recruitment threshold, and recruitment of new motor units that occur as the VL muscle fatigues.

Our results are in agreement with those described by some studies, including those that tracked the same motor units across multiple contractions [e.g., Adam and De Luca (2003,

2005); de Ruiter et al. (2005); and Mettler and Griffin (2016), among others], but not all previous reports [such as Enoka et al. (1989); Kelly et al. (2013); McManus et al. (2015); Mottram et al. (2005); and Vila-Chã et al. (2012), among others]. Four advancements in our study support the validity of our work and explain why our results may differ from those of some previous reports.

1) We studied a comprehensive representation of firing behavior from a large data set of 1,890 motor units. The high yield was obtained using sEMG decomposition technology that provided, on average, 30 motor units per contraction. In contrast, most prior studies of muscle fatigue typically yielded only one to five motor units per contraction [e.g., Enoka et al. (1989); Kelly et al. (2013); and Mottram et al. (2005), among others].

2) We analyzed the firing behavior of individual motor units and observed a clear and consistent trend in firing adaptations. This is a critically important point. As demonstrated in Fig. 1, the averaging of all motor unit firing rates falsely indicates that firing rates decrease with fatigue, in part, because the recruitment of new motor units with lower firing rates distorts the group average. This likely contributes to confounding results in some previous fatigue studies [e.g., Enoka et al. (1989) and Vila-Chã et al. (2012), among others].

3) We analyzed motor unit firing behavior for individual subjects and found that the degree of fatigue-induced firing adaptation is subject dependent. Therefore, the indiscriminate grouping of motor unit data across subjects obscures the subject-specific progression of fatigue and firing adaptations in some previous studies [e.g., Mottram et al. (2005) and Vila-Chã et al. (2012), among others].

4) We analyzed motor unit firing behavior as a function of MUAP amplitude rather than recruitment threshold to avoid the bias that is introduced by decreasing recruitment thresholds during fatigue. This decrease is evidenced in our data and has previously been documented by Adam and De Luca (2003) and McManus et al. (2015), among others. It shifts the inverse relationship between motor unit firing rates and recruitment thresholds to lower recruitment threshold values, giving false indication of a firing rate decrease. Oversight of this bias could produce misleading results in fatigue studies.

Despite the adaptations in firing behavior that we observed, the fundamental motor unit control scheme did not change as a result of muscle fatigue. Specifically, the direct relationship between motor unit recruitment thresholds and MUAP amplitude, known as the "size principle," documented by Henneman (1957) and Hu et al. (2013), among others, was maintained in each contraction. We further observed that earlier recruited motor units displayed higher firing rates than later recruited ones in all contractions, indicating that the "onion-skin property" of motor unit firings previously described by De Luca and Erim (1994) was maintained during fatigue.

During fatigue, motor unit firing behavior compensates for changing mechanical properties of the muscle. It is well documented that the mechanical properties of motor units change during fatigue. Adam and De Luca (2005) and Vandervoort et al. (1983), among others, have empirically shown that the muscle force twitch increases after a brief contraction during the potentiation phase and later decreases as fatigue develops. Therefore, to maintain a contraction at a constant force level, Adam and De Luca (2005) and Contessa and De

Luca (2013) have proposed that the central nervous system changes the operating point of the excitation to the motoneuron pool to adjust the firing behavior of all motor units and to compensate for the changing muscle force twitch.

We tested the viability of this explanation for the firing adaptations observed in our study by simulating the empirical protocol using a mathematical model. The model simulates the motor unit firing behavior and the force output of the VL
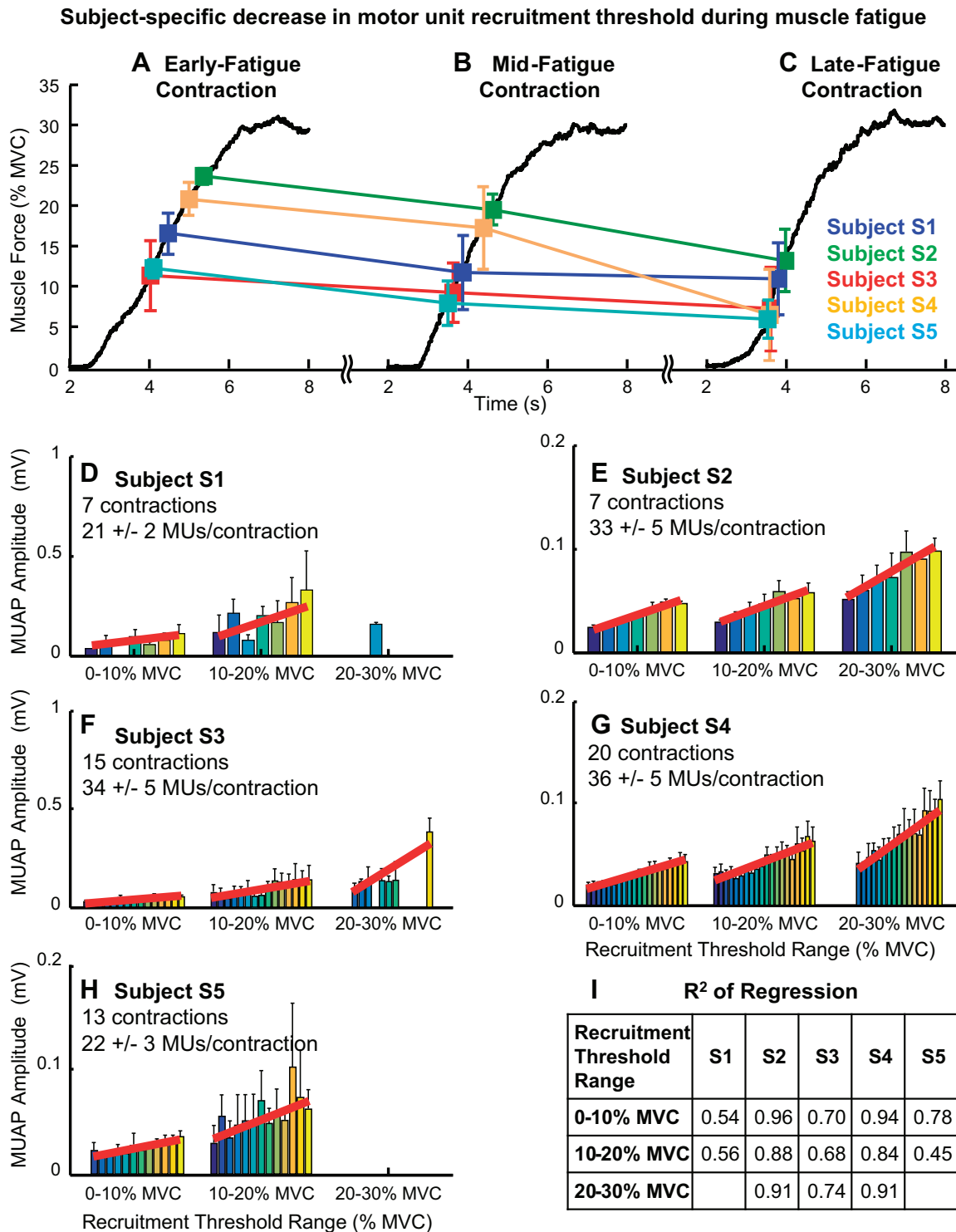

Fig. 3. *A–C*: decrease in the average recruitment threshold of motor units with similar MUAP amplitude in 3 contractions at the beginning (*A*), middle (*B*), and end (*C*) of the fatigue protocol. For clarity, data for each subject are superimposed on a representative subject's force (solid black lines). *D–H*: average MUAP amplitude for 3 groups of motor units recruited within the 0–10%, 10–20%, and 20–30% MVC force range. Each bar indicates the average MUAP amplitude in 1 contraction repetition, from the first (blue) to the last (yellow) contraction for each subject. The relation between average MUAP amplitude and contraction repetition was fit with linear regressions (red lines). *I*: R^2 values of the regressions.

muscle based on empirically documented force-twitch properties and the motor unit control scheme during isometric contractions, including the size-principle and onion-skin property of motor unit firings. For more details, refer to Contessa and De Luca (2013). Our intent was to determine the changes in the operating point of the excitation to the motoneuron pool and the resulting changes in motor unit firing behavior that occur when motor unit force twitches progressively change throughout simulated, repeated contractions, as documented by the empirical observations of Adam and De Luca (2005).

By changing the operating point at which the excitation drives motor units in the muscle, the model was able to reproduce all three adaptations in firing behavior that we observed in our empirical data (compare Fig. 4 with Fig. 1), while maintaining the size-principle and onion-skin property of motor unit firings. Throughout the first simulated contraction,

the force twitch of the active motor units gradually increases, as shown in Fig. 4D. Simultaneously, the excitation to the motoneuron pool decreases from the beginning to the end of the contraction (see Fig. 4G). The decrease in excitation is indicated as a leftward shift in the operating point in Fig. 4G and decreases motor unit firing rates.

It should be noted that our empirical data in Fig. 1A do not clearly show a systematic decrease in firing rate indicative of potentiation during the first contraction. This finding is not unexpected: although potentiation is documented throughout the literature [e.g., Adam and De Luca (2005) and Vandervoort et al. (1983), among others], its manifestation is not always visible and may have been affected by the practice contractions performed before the fatigue protocol. For instance, Adam and De Luca (2005) observed force-twitch potentiation in two out of three subjects during a fatigue protocol with the VL. Vandervoort et al. (1983) further showed that potentiation is
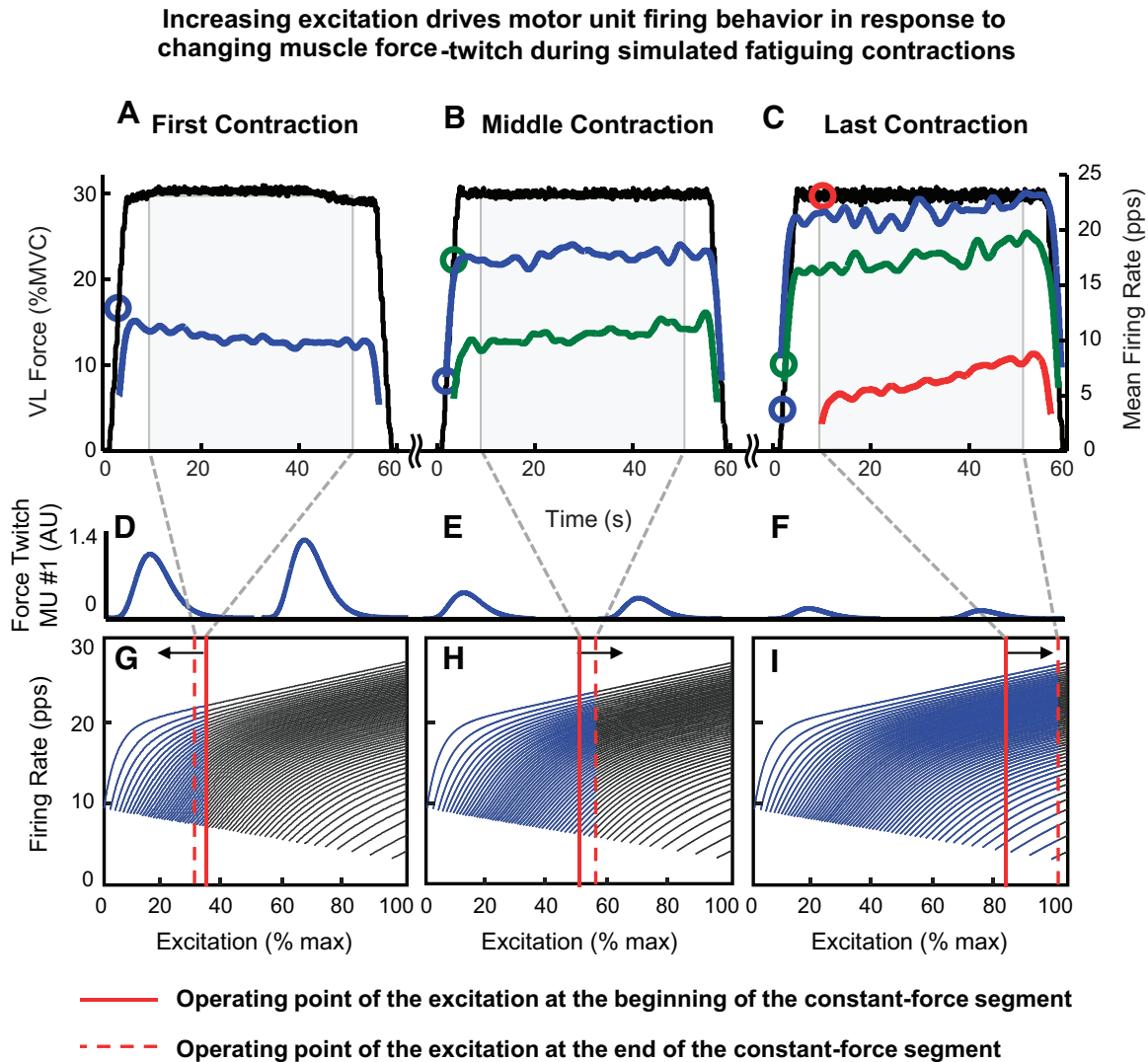
Increasing excitation drives motor unit firing behavior in response to changing muscle force-twitch during simulated fatiguing contractions

Fig. 4. *A–C*: colored traces indicate the time-varying mean firing rates of 3 selected motor units in 3 contractions at the beginning (*A*), middle (*B*), and end (*C*) of the simulated fatigue protocol. The black lines show the simulated force. Colored circles provide the force at which motor units are recruited. *D–F*: force twitch of a representative motor unit at the beginning and end of the constant force segment of each simulated contraction. *G–I*: blue and gray curves show the relation between excitation to the motoneuron pool and firing rate for 60 out of 600 simulated motor units of the VL muscle. Solid and dotted red lines indicate the operating point of the excitation to the motoneuron pool at the beginning and end, respectively, of the constant force segment of each simulated contraction. Blue curves indicate active motor units. The intersection of each firing rate curve with the excitation line indicates the firing rate value of motor units at the given excitation value.

influenced by factors such as the force level and duration of prior contractions.

As the simulated contractions progressed, motor unit force twitches begin to decrease (fatigue), as may be seen in Fig. 4*E*. To reach the 30% MVC target force, a higher excitation is required, because the summed force contribution of the previously active motor units can no longer produce the designated target force. Thus the operating point in the motoneuron pool shifts to the right (Fig. 4*H*). As a result, previously active motor units are recruited at lower force thresholds in subsequent contractions. According to the onion-skin control scheme, active motor units increase their firing rates, while simultaneously higher-threshold motor units are recruited (see Fig. 4*B*). By the end of the fatigue protocol, all three adaptations in firing behavior can be seen (Fig. 4*C*), as the force twitches are further reduced (Fig. 4*F*), and the operating point is further increased (Fig. 4*I*).

These data indicate that the firing rates and recruitment of motor units vary as a consequence of the changing muscle force twitch. This compensatory mechanism also explains why the degree of motor unit firing adaptations during fatigue varies among subjects, as the mechanical and biochemical characteristics of muscles may differ among individuals. Throughout these complementary adaptations, the onion-skin and size-principle properties that govern motor unit firing behavior remain invariant with muscle fatigue.

DISCLOSURES

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AUTHOR CONTRIBUTIONS

P.C., C.J.D., and J.C.K. conception and design of research; P.C. and J.C.K. performed experiments; P.C. and J.C.K. analyzed data; P.C., C.J.D., and J.C.K. interpreted results of experiments; P.C. and J.C.K. prepared figures; P.C., C.J.D., and J.C.K. drafted manuscript; P.C., C.J.D., and J.C.K. edited and revised manuscript; P.C., C.J.D., and J.C.K. approved final version of manuscript.

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