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**RESEARCH ARTICLE** | *Sensory Processing*

# The effects of vibration-induced altered stretch reflex sensitivity on maximal motor unit firing properties

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**Barrera-Curiel A, Colquhoun RJ, Hernandez-Sarabia JA, DeFreitas JM.** The effects of vibration-induced altered stretch reflex sensitivity on maximal motor unit firing properties. *J Neurophysiol* 121: 2215–2221, 2019. First published April 10, 2019; doi:10.1152/jn.00326.2018.—It is well known that muscle spindles have a monosynaptic, excitatory connection with $\alpha$-motoneurons. However, the influence of muscle spindles on human motor unit behavior during maximal efforts remains untested. It has also been shown that muscle spindle function, as assessed by peripheral reflexes, can be systematically manipulated with muscle vibration. Therefore, the purpose of this study was to analyze the effects of brief and prolonged vibration on maximal motor unit firing properties. A crossover design was used, in which each of the 24 participants performed one to three maximal knee extensions under three separate conditions: *1*) control, *2*) brief vibration that was applied during the contraction, and *3*) after prolonged vibration that was applied for ~20 min before the contraction. Multichannel EMG was recorded from the vastus lateralis during each contraction and was decomposed into its constituent motor unit action potential trains. Surprisingly, an approximate 9% reduction in maximal voluntary strength was observed not only after prolonged vibration but also during brief vibration. In addition, both vibration conditions had a large, significant effect on firing rates (a decrease in the rates) and a small to moderate, nonsignificant effect on recruitment thresholds (a small increase in the thresholds). Therefore, vibration had a detrimental influence on both maximal voluntary strength and motor unit firing properties, which we propose is due to altered function of the stretch reflex pathway.

**NEW & NOTEWORTHY** We used vibration to alter muscle spindle function and examined the vibration's influence on maximal motor unit properties. We discovered that vibration had a detrimental influence on motor unit behavior and motor output by decreasing motor unit firing rates, increasing recruitment thresholds, which led to decreased maximal strength. We believe that understanding the role of muscle spindles during maximal contractions provides a deeper insight into motor control and sensorimotor integration.

group Ia afferents; muscle spindle function; muscle vibration

## INTRODUCTION

Motor unit activation is controlled through the integration of descending, efferent drive and afferent feedback, which provides reflex assistance to supraspinal input (Macefield et al. 1993). Collectively, these two mechanisms provide excitation and inhibition, respectively, to motoneurons. Thus, changes in both central (i.e., descending drive) and/or peripheral (i.e., afferent feedback) mechanisms could result in altered excitability of the motoneuron pool.

Tendon or muscle vibration can alter the efficacy of the homonymous Ia afferent-$\alpha$-motoneuron pathway (Burke et al. 1976; Burke and Schiller 1976; Desmedt and Godaux 1978; Pope and DeFreitas 2015). Vibration has been shown to have both facilitatory and suppressive effects on muscle spindle activity, with either effect resulting in an altered motor output. It is believed that the effect of vibration on motor output depends on the duration of vibration. Prolonged vibration applied for 30 s or longer has been shown to significantly depress muscle spindle's activity, resulting in lower group Ia mean discharge rates (Ribot-Ciscar et al. 1998), reduced reflex magnitude, and increased (i.e., slower) reflex latency (Pope and DeFreitas 2015). As a result, decreased spindle function has been shown to lead to a significant decrease in maximal strength of 7–30% (Bongiovanni and Hagbarth 1990; Herda et al. 2009; Jackson and Turner 2003; Kouzaki et al. 2000; Macefield et al. 1993; Shinohara 2005; Ushiyama et al. 2005). On the other hand, brief vibration, defined here as 2 to 25 s of vibration, has resulted in additional excitation to the motoneuron pool and ultimately enhanced force production (Bongiovanni and Hagbarth 1990; Grande and Cafarelli 2003). However, the facilitatory effect of brief vibration has not been consistently shown. For example, Pope and DeFreitas (2015) showed that while brief vibration did increase the magnitude of the patellar tendon reflex (i.e., tendon taps), the increase was not statistically significant. Furthermore, the reflex latency actually became significantly slower. However, this study only shows the effects of vibration on an involuntary spinal reflex and may not be representative of the effects that altered spindle activity would have on voluntary motor control. In addition, the effects of spindle activity facilitation appear to be dependent on the intensity and duration of the voluntary contraction. For instance, an enhancement of force production after brief vibration has been apparent only during weak contractions (Grande and Cafarelli 2003), but this facilitatory effect disappeared as force level increased (Spiliopoulou et al. 2012). There is also an exception during fatiguing contractions, where brief vibration applied during a maximal contraction regained its facilitatory effect, seen by an increment in force level and

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electromyographic (EMG) activity (Bongiovanni and Hagbarth 1990).

Previous studies have also investigated the influence of vibration on motor unit (MU) firing rates (FR) during submaximal contractions, showing an initial increase in FR following brief vibration (Grande and Cafarelli 2003) and subsequent decrease after prolonged vibration (Bongiovanni et al. 1990). However, these studies were performed at a low, submaximal force levels (Grande and Cafarelli 2003; Mosier et al. 2017) or had long-lasting, fatiguing contractions (e.g., 1 min long in Bongiovanni and Hagbarth 1990). However, the effects of altered spindle function on MU behavior during maximal efforts remain unknown.

Because of technological limitations, analyzing firing behavior for more than a few MUs at a time was not possible in previous investigations. Nowadays, the surface electromyography (sEMG) decomposition technique developed by De Luca et al. (2006) allows the analysis of motor unit action potential trains during high-intensity contractions with greater motor unit yields when compared with indwelling recordings (De Luca and Hostage 2010). This technology could provide a deeper insight into maximal MU behavior following altered muscle spindle activity.

Considering these previous findings, the purpose of this study is to analyze the effects of brief and prolonged vibration on motor unit firing rates and recruitment thresholds during maximal contractions. We hypothesized that brief vibration, which stimulates the muscle spindles, would increase excitation to the motoneuron pool, thereby increasing motor unit firing rates. Conversely, we also hypothesized that prolonged vibration, which depresses the group Ia afferent pathway, would decrease the tonic excitation to the motoneuron pool, thereby decreasing motor unit firing rates.

## METHODS

*Participants.* Fourteen females and 10 males (age: 25 ± 6 yr) volunteered for this study. Prior to testing, each participant was informed about the experimental procedures, risks, and their ability to withdraw at any moment. Participants gave their written consent before any testing. To be included in this study, participants had to be completely free of any musculoskeletal injury or any diagnosed neurological disorder. This investigation was conducted in accordance with the Declaration of Helsinki and was approved by the Oklahoma State University's Institutional Review Board.

*Experimental design.* We examined the effects of altered stretch reflex sensitivity on maximal motor unit firing properties. The sensitivity of the quadriceps stretch reflex was systematically manipulated by applying vibration to the muscle. A crossover design was used, in which each subject performed each condition in the same order. Therefore, each participant performed one to three maximal ramp contractions of the knee extensors (the number of contractions depended on the participant's ability to follow the trajectory accurately) under three separate conditions: *1*) control, *2*) brief vibration that was applied during the contraction, and *3*) prolonged vibration that was applied for ~20 min before the contraction. Multichannel EMG was recorded from the vastus lateralis (VL) during each contraction and decomposed into its constituent motor unit action potential trains. A flow chart of the protocol is shown in Fig. 1. This study is part of a larger project, and the efficacy of this exact protocol in altering stretch reflex properties was shown in a previous publication from this project (Pope and DeFreitas 2015).

*Application of localized vibration.* As described previously (Pope and DeFreitas 2015), sinusoidal vibration was applied to the distal quadriceps group superior to the patella using a percussion hammer (Foredom Percussion Hammer, Bethel, CT) with an amplitude of 1.5 mm set at our hammer's maximal frequency (~66–70 Hz). A frequency between 70 and 100 Hz has been shown to preferentially activate Ia afferents (Roll et al. 1989). Additionally, an amplitude of 1.5 mm has shown to be effective for both types of vibration protocols, facilitation (Burke et al. 1976; Burke and Schiller 1976; Grande and Cafarelli 2003), and depression (Bongiovanni et al. 1990; Richardson et al. 2006). For the brief condition, the vibration of the quadriceps began at the onset of the ramp contraction. For the prolonged condition, the vibration was applied for ~20 min after completion of the brief condition's maximal voluntary contractions (MVCs) and reapplied for 1–3 min between each of the three postvibration ramp contractions to maintain depressed spindle activity (de Ruiter et al. 2003; Ribot-Ciscar et al. 1998). These brief and prolonged vibration protocols were designed with the intent of facilitating and depressing the sensitivity of the stretch reflex, respectively. However, it should be noted that our previous work showed that brief and prolonged vibration had similar effects on reflex latency, resulting in a significant increased reflex latency. (Pope and DeFreitas 2015). To avoid any carry-over effects, brief vibration was applied first and during the contraction, because its effects dissipate as soon as the stimulus is removed (Bongiovanni and Hagbarth 1990; Grande and Cafarelli 2003; Roll et al. 1989). On the other hand, the duration of prolonged vibration effects has not been clearly defined. Forty seconds (Ribot-Ciscar et al. 1998) to more than 180 min (de Ruiter et al. 2003) have been necessary for baseline measurements, such as Ia mean discharge rates and voluntary strength, to return to its resting values. Consequently, prolonged vibration was applied second and before the contraction (Herda et al. 2009; Kouzaki et al. 2000; Ribot-Ciscar et al. 1998; Richardson et al. 2006). In addition, it has been shown that prolonged sitting itself does not have any effect on knee extension MVC or EMG of the quadriceps (Kouzaki et al. 2000).

*Motor unit recordings.* Motor unit action potentials were recorded using a specialized five-pin surface array sensor (Delsys, Natick, MA), which was placed over the VL muscle and secured with hypoallergenic surgical tape at approximately two-thirds the distance between the center of the muscle belly toward the distal tendon (Zaheer et al. 2012). A reference electrode (Dermatrode; American Imex, Irvine, CA) was placed on the spinous process of the C7 vertebrae (Zaheer et al. 2012). This five-pin array sensor produces four separate EMG channels, and the motor unit action potential trains were extracted by applying the Precision Decomposition III algorithm

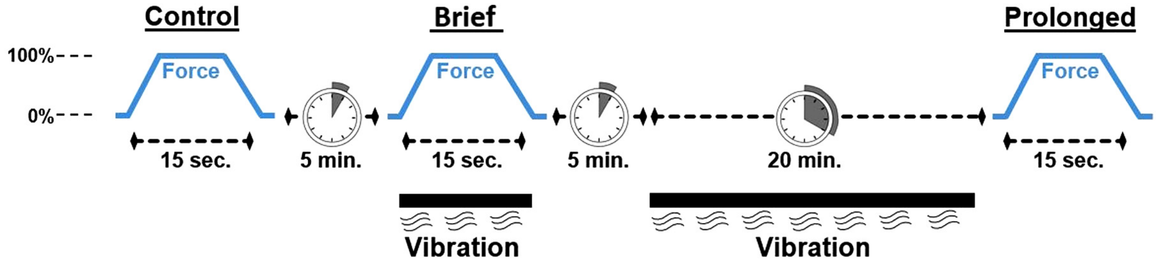

Fig. 1. Time line for experimental protocol. Three different conditions were control, brief vibration that was applied during the contraction, and prolonged vibration that was applied for ~20 min before the contraction.

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to the four channels, as described by De Luca et al. (2006) and improved upon by Nawab et al. (2010). Prior to the sensor placement, skin was properly prepared by shaving the area, gently abrading, and cleansing it with isopropyl alcohol. After electrode placement, subjects performed three unilateral isometric maximal knee extensions using the dominant leg, in which participants were seated in an upright position and restrained in a commercial dynamometer (Biodex System 4, Biodex Medical Systems, Shirley, NY), with a knee angle of 120° and a hip angle of ~110°. Participants were instructed to push as hard as possible for 3–4 s; the highest force value measured during a 1,000-ms epoch from the three extensions was designated as the subject's MVC. These MVCs were used to normalize the live torque feedback provided during the maximal ramp contractions, while motor units' instances of firings were recorded. Before testing, participants practiced tracing submaximal ramps to familiarize and assure proper adherence. This familiarization also served as a warm-up before the maximal contractions.

*Maximal ramp contractions.* Participants performed 1–3 maximal ramp contractions, which were normalized to each participant's MVC. The normalized template was displayed on a monitor overlaid with live torque feedback. These contractions lasted 15 s in total; the ramp increased and decreased at a rate of + 20 and −20% MVC/s, respectively, with a 5-s plateau at 100% MVC in between. The participants were instructed to trace the template line for the ramps up and down, but to contract as hard as possible during the maximal hold. An example of a tracing for each condition can be seen in Fig. 2. A 50-point moving average window (with a single datum point shift) was applied to smooth the signal, and the highest window of torque (Nm) was considered the maximal voluntary strength for that condition.

*MU exclusion criteria and analysis.* The accuracy of each individual's MU was assessed using the Decompose-Synthesize-Decompose-Compare test (De Luca and Contessa 2012). Only MUs that demonstrated at least 90.0% accuracy were used for further analysis. The firing characteristics of the accurate MUs were analyzed using custom-written software (LabVIEW; National Instruments, Austin, TX). This software was used to calculate the following properties for each identified MU: *1*) maximal firing rate ($FR_{MAX}$, pulses per second), which was assessed as the highest point on a smoothed mean firing rate curve (smoothing was performed with a 1-s Hanning window); *2*) recruitment threshold (RT), which was expressed as the absolute torque level (Nm) at which the MU began discharging; and *3*) MU $AP_{SIZE}$ (mV), which was measured as peak-to-peak amplitude of the action potential (AP) waveform templates (a template is the average shape of the AP across the contraction). To be able to compare within conditions, absolute recruitment thresholds were chosen due to the possible changes in maximal strength after brief (Bongiovanni and Hagbarth 1990; Grande and Cafarelli 2003) and prolonged vibration (Bongiovanni et al. 1990; Herda et al. 2009; Kouzaki et al. 2000; Richardson et al. 2006). Since four AP waveforms are provided from the four original EMG channels for each MU, the channel with the largest peak-to-peak amplitude was considered as the most representative of that motor unit's true shape and used for $AP_{SIZE}$ analysis. Under the presumption that vibration would have no effect on the amplitude of the action potentials, $AP_{SIZE}$ was used as an independent variable to examine potential changes in $FR_{MAX}$ and RT. To establish a sufficient relationship for MU RT vs. $AP_{SIZE}$, a RT range >15% of MVC was required (per contraction) for each participant to be included in any analysis.

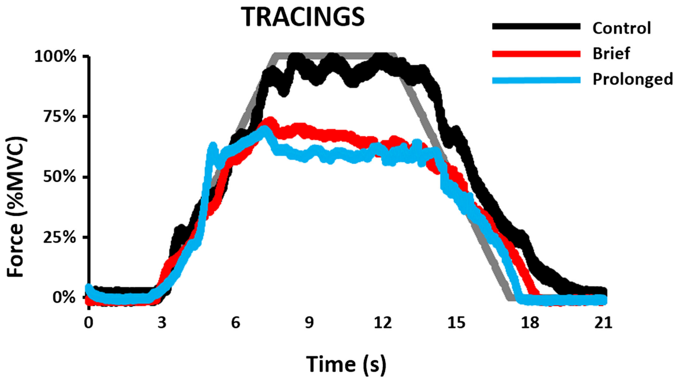

Fig. 2. Example of a representative torque tracing for each condition. A normalized template (gray line) was displayed on a monitor overlaid with live torque feedback. Participants were instructed to trace the template line for the ramps up and down, but to contract as hard as possible during the maximal hold. Black line denotes control condition, red line denotes brief vibration condition, and blue line denotes prolonged vibration condition.

*Statistical analysis.* RT versus $AP_{SIZE}$, $FR_{MAX}$ versus $AP_{SIZE}$ slope, and *y*-intercept values were calculated for each subject and each condition with linear regression. Outliers were removed when the standardized score was higher than ±2.5 SDs. Separate one-way, repeated-measures ANOVAs [control versus brief stimulation versus prolonged stimulation] were performed to assess the effects of vibration on the calculated regression coefficients for the aforementioned relationships. Two-way repeated-measures ANOVAs [condition (control versus brief versus prolonged) × gender (female versus male)] were used to test possible differences in voluntary maximal strength (Nm). When necessary, post hoc analyses with Bonferroni corrections were run. An $\alpha$-level of $P < 0.05$ was set a priori to determine statistical significance. Cohen's *d* effect sizes were performed for the brief and prolonged conditions to obtain the regression coefficients. All analyses were performed using SPSS software (version 21, IBM, Chicago, IL).

## RESULTS

*Effects of vibration on maximal voluntary strength.* There were no two-way interactions between condition and gender ($P = 0.47$) for maximal strength; however, there was a main effect for condition ($P < 0.001$) and gender ($P = 0.003$). Post hoc analyses indicated an approximate 9% reduction in maximal voluntary strength after both protocols (brief: −8.64%; prolonged: −9.08%; compared with control, $P < 0.001$) (see Fig. 3*A*). Figure 3*B* shows the individual responses to both vibration conditions.

*MU exclusion analysis.* Of the original 24 participants, 10 did not meet the established MU criteria (i.e., a RT range <15% of MVC for control, brief vibration, or prolonged vibration conditions) or were identified as outliers and were eliminated from all MU analyses. From the remaining 14 participants (8 women and 6 men), 1,318 MUs were detected (average per contraction = 34 MUs; total control = 422 MUs; brief = 447 MUs; prolonged = 449 MUs).

*Effects of vibration on maximal motor unit firing properties.* Vibration had a large effect on $FR_{MAX}$ slopes and *y*-intercepts after brief (Cohen's $d = -1.52$; 2.08, respectively) and prolonged vibration (−1.49; 1.31), as shown by a shift in the $FR_{MAX}$ versus $AP_{SIZE}$ relationships. One-way ANOVAs revealed a significant change in slopes ($P = 0.02$) and *y*-intercepts ($P = 0.042$). Post hoc analyses showed greater *y*-intercept values for the brief condition (32.89 ± 5.35) when compared with the control (29.42 ± 2.7) ($P = 0.039$). On the other hand, vibration had a small-to-moderate, nonsignificant ($P$ values >0.05) effect on RT slopes and *y*-intercepts after brief (Cohen's $d = 0.49$; −0.76) and prolonged (0.38; −0.77) vibration. Figure 4 shows the individual and group mean regression results to vibration.

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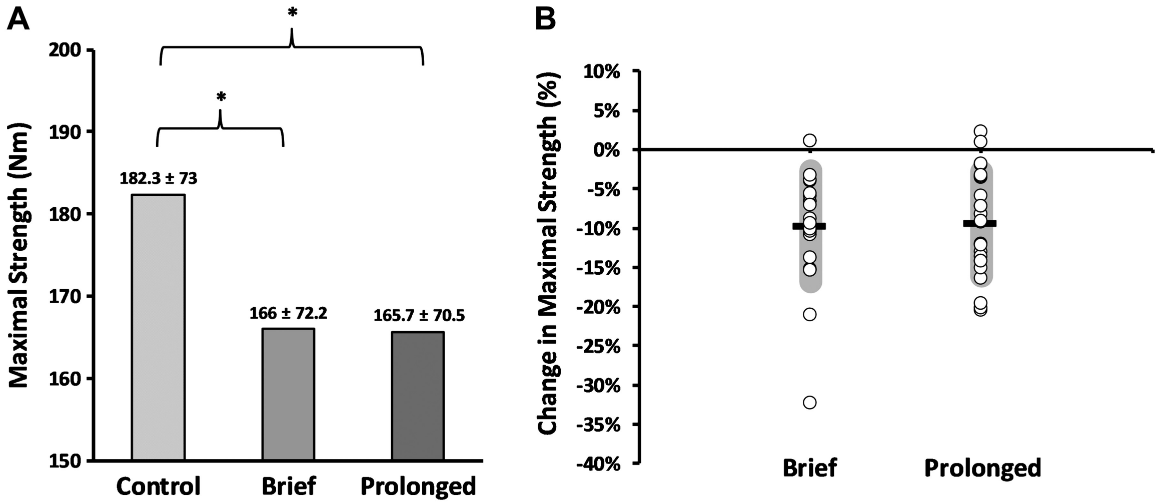

Fig. 3. *A*: group means in maximal voluntary knee extension strength (Nm) for each condition. *B*: changes in maximal voluntary strength for each individual subject for the two conditions (relative to the control condition) ($n = 24$). *Significant difference between conditions, $P < 0.01$.

## DISCUSSION

The primary finding from this study was that vibration had a detrimental effect on motor unit firing properties, independent of the vibration condition (brief or prolonged). This decrease in motor unit output was likely the cause behind an approximate 9% reduction in maximal voluntary strength.

*Effects of brief vibration during a maximal contraction.* On the basis of previous studies, we had hypothesized that 15 s of vibration would result in a facilitatory effect (Bosco et al. 1999). Surprisingly, we saw the opposite effect, where maximal strength was reduced and MU behavior results were similar to the prolonged vibration condition. There are two possible mechanisms that can explain this phenomenon: one relates to the Golgi tendon organs (GTO), while the other relates to the duration of our vibration protocol. Fallon and Macefield (2007) showed that when vibration is applied during a contraction, the discharge frequency of Group Ib afferents increases. Group Ib afferents synapse with inhibitory interneu-

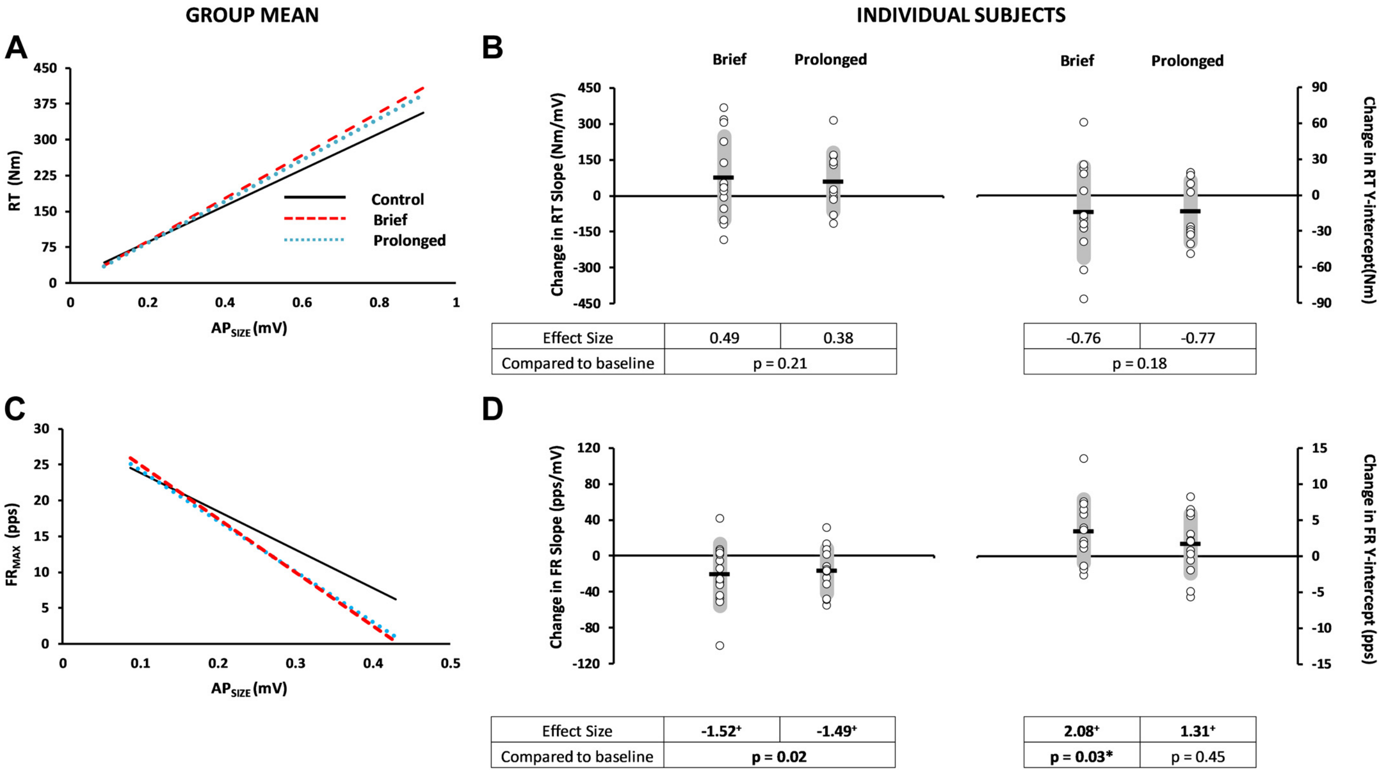

Fig. 4. Regression was performed on each individual subject's motor unit data. The two dependent variables were maximal motor unit firing rates ($FR_{MAX}$) and absolute recruitment thresholds (RT), and action potential size ($AP_{SIZE}$) was used as the independent variable. *A* and *C*: group means were calculated from the slopes and intercept coefficients of each individual subject's regressions. These regression lines are the group mean for each condition. *B* and *D*: changes in the individual subject regression coefficients from brief and prolonged vibration (relative to the control condition) ($n = 14$). *Significantly lower than the control condition, $P < 0.05$. $^+$Large effect size.

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rons, which could have resulted in increased inhibition to the homonymous motoneuron pool. The vibration applied in this protocol was during the contraction, which, therefore, could have activated GTO. On the other hand, regarding the duration of our vibration protocol, to our knowledge, the exact moment when muscle spindle facilitation starts to be depressed is unknown. The closest study we found is Bongiovanni and Hagbarth's study (1990), in which the authors observed a facilitatory effect at the beginning of a 20-s vibration protocol, but the initial increase was followed by a rapid decline. However, the exact duration for the facilitatory effect has not been reported. It appears that after only a few seconds, the facilitatory effect of vibration on motor output reverts. For instance, 2 s of vibration showed an increase in force (Grande and Cafarelli 2003), 3–4 s showed no difference (Bongiovanni and Hagbarth 1990), and our protocol, which lasted 15 s, showed a decrease in maximal strength. Consequently, it is also possible that our protocol was too long. Hence, these are two possible mechanisms that could explain the strength loss. However, further analyses are required to understand each one.

*Effects of vibration on maximal voluntary strength.* Our results showed a decrease in maximal strength of 8.64% after brief vibration and 9.08% after prolonged vibration. As previously mentioned, the results for the brief condition may be explained by changes in afferent feedback from muscle spindles and/or GTO. On the other hand, prolonged vibration has been shown to decrease Group Ia mean discharge rates (Ribot-Ciscar et al. 1998), reduced reflex magnitude, and increased (i.e., slower) reflex latency (Pope and DeFreitas 2015). The mechanisms behind the reduction in Group Ia afferent activity due to vibration can be presynaptic inhibition (PSI) (Hultborn et al. 1987) and/or transmitter depletion (Curtis and Eccles 1960) and/or increased threshold of Group Ia excitatory pathway to γ-loop (Hayward et al. 1986). The muscle spindle activity reduction has been shown to negatively affect maximal voluntary strength by 8–30% (Bongiovanni and Hagbarth 1990; Herda et al. 2009; Jackson and Turner 2003; Kouzaki et al. 2000; Macefield et al. 1993; Shinohara 2005; Ushiyama et al. 2005). Therefore, the results from our prolonged vibration condition are in agreement with previous studies.

*Effects of vibration on motor unit maximal properties.* Our rigorous MU inclusion criteria reduced our sample size of participants considerably. This loss of statistical power could explain why small to moderate increases in RT were not statistically significant. The changes seen in $y$-intercepts could be a product of the change in slopes. Pedhazur (1997) recommended that $y$-intercepts only be tested when no significant changes were seen in slopes. Therefore, because of the effect of vibration on the slopes, $y$-intercepts will not be further discussed. Figure 4 shows how changes to the slope coefficients of our primary two relationships ($FR_{MAX}$ versus $AP_{SIZE}$, and RT versus $AP_{SIZE}$) were consistent not only for the group means (between conditions), but also at the individual subject level.

There was a small increment in RT slopes and a steeper decline in $FR_{MAX}$ seen after vibration. These results could indicate that MUs were being recruited later and achieved lower FR, when vibration was applied. FR are a function of RTs and excitation level, where there exists a hierarchical inverse relationship of RTs and FR, meaning that MUs recruited later have lower FR than those that were recruited earlier (De Luca and Contessa 2012; De Luca and Hostage 2010). Therefore, it seems that when less net excitation is sent to the motoneuron pool, FR decrease (De Luca and Erim 1994). Contessa et al. (2016) showed that an increase in excitation can result in a decrease in RTs and an increase in FR. Our results follow the same principles of the hierarchal

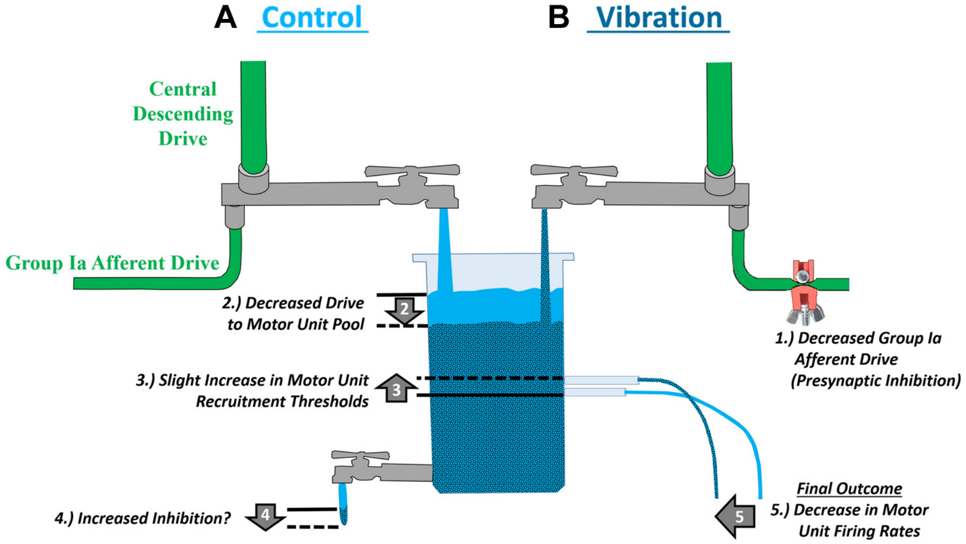

Fig. 5. Proposed model for the effects of vibration on motor unit outputs. This model is a revised and modified version of the Hydraulic Model of Common Drive, originally presented by De Luca and Erim (1994). The water pouring from the faucet into the beaker represents input excitation to the motor unit pool, while the faucet at the bottom left represents inhibition, and the level of water in the beaker represents the total net excitation. The spouts on the right side represent the recruitment threshold (i.e., the motor unit will not activate until the net excitation reaches the level of the spout), and the distance the water projects from the spout would be the firing rate. The light blue water and solid lines are the control condition, while the dark shaded water and dashed lines are during or after vibration. *1)* There is decreased drive from Group Ia afferents, possibly due to presynaptic inhibition, which would then cause *2)* a reduction in the net excitation to the motoneuron pool. *3)* There is a slight increase in motor unit recruitment thresholds (small-to-moderate effect size). *4)* An increase in inhibition due to activation of Golgi tendon organs may occur. *5)* Mechanisms 2–4 combined lead to a decrease in motor unit firing rates (large effect size). The decreased firing rate then leads to a decrease in maximal voluntary strength.

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inverse relationship between RTs and FRs, only evidenced by movement in the opposite direction.

The reduction in FRs during maximal contractions is consistent with previous studies using prolonged vibration (Bongiovanni et al. 1990) or muscle deafferentation (Macefield et al. 1993). It seems that because of the lack of muscle spindle support, MUs cannot achieve greater FR. Specifically, it appears that higher threshold MU are the most affected with a significant decrease in FR when Group Ia afferent feedback was removed (Macefield et al. 1993).

*Proposed model of the underlying mechanisms.* Figure 5 shows a plausible explanation that ties all of our findings together. We have revised and modified the Hydraulic Model of Common Drive (Fig. 4 in De Luca and Erim 1994) as a basis to explain the changes seen in this study. In short, the water pouring from the faucet into the beaker represents input excitation to the motor unit pool, the faucet at the bottom represents inhibition, and the level of water in the beaker represents the total net excitation. The spouts on the side represent the recruitment threshold (i.e., the MU will not activate until the net excitation reaches the level of the spout), and the distance the water projects from the spout would be the firing rate. Our primary modification to the model is the addition of multiple sources of excitation; the primary source would be descending drive, representing at least two-thirds of the total excitation. The secondary source would be excitation from Group Ia afferents, which may be as high as one-third of the excitation to the motoneuron pool (Macefield et al. 1993). We then include five observed or plausible changes due to the application of vibration. *1*) Vibration has been shown to decrease muscle spindle activity (Pope and DeFreitas 2015; Ribot-Ciscar et al. 1998), possibly through presynaptic inhibition (Hultborn et al. 1987). *2*) As a result, the net excitation to the motoneuron pool was likely reduced (Macefield et al. 1993). *3*) A small increment in RTs was seen, possibly meaning that the same MU was being recruited later. *4*) In the brief vibration condition, GTO could have been activated during vibration (Fallon and Macefield 2007), causing autogenic inhibition and, thus, decreasing the net excitation of the motoneuron pool. *5*) This later recruitment combined with the reduced excitation to the motoneuron pool would explain the reduction in $FR_{MAX}$. The firing rate of a motor unit is a function of how much additional excitation there is beyond the activation threshold of the neuron (until the motoneuron is saturated). Supporting the plausibility of this model is the fact that the slopes shown in Fig. 4*C* show that a motor unit's firing rate decreases with vibration as a function of its size. Therefore, the larger the MU is, the more susceptible its firing rate is to the effects of the vibration. Because the largest MU's firing rates are likely not saturated during maximal contractions, they are the units that would be susceptible to any changes in the net excitation to the pool. Therefore, it is probable that when there is less net excitation to the MU pool, caused by a decrease in muscle spindle activity and/or increased inhibition originating from GTO, the motor unit's RTs slightly increase and the firing rates decrease. This resultant decrease in $FR_{MAX}$ would also explain the ~9% reduction in maximal strength.

*Limitations.* First, while the short (5 s) ramp up to 100% effort was necessary to avoid fatigue, it may have made it difficult for the decomposition algorithm to precisely locate recruitment times; the 20% MVC/s represents the fastest ramp-up in the recommended range (Nawab et al. 2010). Second, the muscle spindles of the agonist muscle produce a reciprocal inhibition of the antagonist muscle (Corcos et al. 1989). Because of the significant increase in reflex latency after both brief and prolonged vibration, as previously reported (Pope and DeFreitas 2015), we have reason to believe that muscle spindle activity was diminished, so it is possible that antagonist coactivation might have increased (but was not measured), thus, also contributing to the decrease in agonist maximal voluntary strength. Third, we did not have any GTO discharge frequency data, so we proposed a role for GTO's potential based on previous studies. Lastly, vibration does not selectively or exclusively affect muscle spindles. While it has been shown that muscle vibration, indeed, affects muscle spindle function, it is a blunt tool that may affect many other, but smaller, sensory afferent feedback systems as well (e.g., cutaneous receptors, other mechanoreceptors).

*Recommendations for future studies.* Further research is needed to determine the precise moment when vibration-induced muscle spindle facilitation shifts to suppression during submaximal and maximal contractions, while controlling for vibration frequency. In addition, future studies examining muscle spindle function should account for potential changes in antagonist coactivation.

*Conclusions.* Applying muscle vibration influences maximal motor unit behavior and motor output. The motor unit behavior was altered by decreasing firing rates, slightly increasing recruitment thresholds, and ultimately reducing maximal strength. We suggest that these results indicate that the vibration led to a reduction in excitation to the motor unit pool due to reduced excitation from muscle spindles.

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## GRANTS

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

## AUTHOR CONTRIBUTIONS

J.M.D. conceived and designed research; A.B.-C. and R.J.C. performed experiments; A.B.-C. and J.A.H.-S. analyzed data; A.B.-C., R.J.C., J.A.H.-S., and J.M.D. interpreted results of experiments; A.B.-C. and J.M.D. prepared figures; A.B.-C. drafted manuscript; A.B.-C., R.J.C., J.A.H.-S., and J.M.D. edited and revised manuscript; A.B.-C., R.J.C., J.A.H.-S., and J.M.D. approved final version of manuscript.

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