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RESEARCH ARTICLE

Influence of stimulation frequency on early and late phase rate of torque and velocity development

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Abstract

The early (≤50 ms) rate of torque development (RTD) is dependent upon the speed of neuromuscular activation; however, few studies have evaluated the determinants of rate of velocity development (RVD), which may be load-dependent. The purpose here was to explore the relationship between stimulation frequency with the early and late (≥100 ms) phase isometric RTD and isotonic RVD. The knee extensors of 16 (five female) young recreationally active participants were stimulated using 14 frequencies from 1 to 100 Hz during isometric and isotonic ("unloaded" and 7.5% of the isometric maximal voluntary contraction [MVC]) contractions. Isometric RTD and isotonic RVD were evaluated for the early (0–50 ms) and late (0–100 ms) phases from torque and velocity onset, respectively. Sigmoid functions were fit and bilinear regressions were used to examine the slopes of the steep portion of the curve and the plateau frequency. RTD- and RVD-frequency relationships were well described by a sigmoid function (all $r^2 > 0.96$). Compared with the late phase, early isometric RTD, and unloaded RVD displayed lower slopes (all $P \leq 0.001$) and higher plateau frequencies (all $P < 0.001$). In contrast, early and late RVD of a moderately loaded isotonic contraction did not display different slopes ($P = 0.055$) or plateau frequencies ($P = 0.690$). Early isometric RTD and unloaded isotonic RVD are more dependent on changes in stimulation frequency compared with late phases. However, RVD for a moderately loaded isotonic contraction displayed similar responses for the early and late phases. Therefore, a high frequency of activation is critical for early torque and velocity generation but dependent upon the load for isotonic contractions.

NEW & NOTEWORTHY We show that during an "unloaded" isotonic contraction, the early phase rate of velocity development is more dependent upon a high electrical activation frequency compared with the late phase, similar to isometric torque. However, early and late phase rates of velocity development of moderately loaded isotonic contractions display similar responses. These results indicate that the determinants of isotonic shortening function are dependent on the externally applied load, highlighting the importance of task-specificity of contraction.

ballistic contraction; dynamic contraction; explosive contraction; force-frequency; neuromuscular electrical stimulation

INTRODUCTION

The ability to rapidly generate torque or angular rotation around a joint is critical for correcting perturbations that may occur during activities of daily living (1, 2), as well as during athletic events. The rapid generation of joint torque and angular displacement is often evaluated by the rate of force or torque development (RTD) during isometric contractions and the rate of velocity development (RVD, i.e., acceleration) during dynamic contractions, respectively. During both voluntary and electrically evoked isometric contractions, the maximum RTD (i.e., the peak of the first derivative of the torque-time signal) is often quantified, but this ignores aspects of the early (≤50 ms) and late (≥100 ms) phases of the contraction, which may be governed by different neuromuscular determinants such as rate of activation and absolute force capacity (1, 3). Indeed, the rate of neuromuscular activation derived from the integrated surface electromyogram has a greater influence on the early RTD in comparison to the late phase (4, 5). Despite the greater relevance to natural movements that involve joint rotation compared with isometric contractions, the influence of activation rate on RVD during shortening contractions has not been explored (6).

Using electrically evoked contractions, the force-frequency relationship provides a means to assess inherent characteristics of the muscle by controlling the activation input and recording the contractile output. The force-frequency relationship has been most often used to compare peak isometric torque output in relation to the frequency of stimulation, which displays a sigmoid relationship (7). However, the maximum RTD-frequency relationship also has been explored during isometric contractions in both human (8) and animal (9, 10) neuromuscular systems. In fast-twitch rat muscle, the frequency that elicits maximal tetanic torque (∼150 Hz) is lower than that which

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elicits the maximum RTD (~300 Hz) (10). In humans, although lower frequencies in general are required to achieve peak output, higher frequencies are still required to achieve peak RTD compared with peak torque (8); indicating that maximum RTD may be more dependent upon higher rates of neural activation compared with peak isometric torque. However, these RTD-frequency relationships have only been assessed with the maximal or peak RTD, and not evaluated with early and later phases of the contraction. This has limited our understanding of the determinants of RTD across the full spectrum of the contraction phase.

Although the activation rate is a critical aspect for both isometric RTD and dynamic RVD, and electrically evoked isometric contractions are often used to infer peripheral adaptations of dynamic contractile function (e.g., fatigue, potentiation, age-related adaptation), there are task-specific differences which may confound these relationships. Previous work has shown that both voluntary and electrically evoked isometric function is a poor index of dynamic contractile function at baseline and following fatiguing tasks (11–14). These findings indicate that isometric torque cannot be used as an index of dynamic contractile function. Because of these differences between isometric and dynamic contractile function, and the limited data to date investigating the early and late phase RVD, we have limited knowledge on the determinants of RVD during isotonic contractions. Thus, the purpose of this study was to compare the relationships between the frequency of electrical stimulation in the early and late phases of isometric RTD and isotonic RVD. We further tested the influence of isotonic load on the frequency-RVD. These relationships were assessed in human knee extensor muscles. We hypothesized that the early phases of isometric RTD and isotonic RVD would be modulated by a wider range of stimulation frequencies and require a higher activation rate to plateau compared with the later phases. Further, we hypothesized that early unloaded isotonic RVD would be more sensitive to changes in stimulation frequency compared with the loaded isotonic contractions.

METHODS

Participant Cohort and Ethical Statement

Young adult males ($n = 11$) and females ($n = 5$) were recruited from the local university population and were (±standard deviation [SD]) 24.7 ± 3.0 and 25.6 ± 4.3 yr old, 1.82 ± 0.06 and 1.61 ± 0.07 m in height with a body mass of 83.8 ± 8.3 and 59.5 ± 6.7 kg, respectively. Participants attended two data collection sessions (separated by a minimum of 72 h) and were instructed to avoid moderate to vigorous activity for 72 h before attending each data collection session. The same experimental sessions were completed on both days to average the results of the isometric and isotonic frequency curves. All participants were recreationally active and none were engaged in regular athletic training. This study was approved by the local University Human Research Ethics Board (No. 107505) and conformed to the declarations of Helsinki (except registration in a database) and informed written and verbal consents were obtained from all participants prior to testing.

Experimental Setup

Participants were seated on a multijoint dynamometer (HUMAN NORM, CSMi, Medical Solutions, Stoughton, MA) and the torque (Nm), angular velocity (°/s), and joint position (°) of the right knee extensors (dominant limb for all participants) were sampled at 1,000 Hz using a 12-bit analog to digital converter (Power 1401, CED). The lateral epicondyle of the femur was aligned with the axis of rotation and the leg was secured firmly to the knee extension attachment at the level of the lateral malleolus. The knee and hip joint angles were set to 90° and 110°, respectively. The right thigh, hips, and torso were secured to the dynamometer chair using nonelastic straps to minimize extraneous movements. The knee joint range of motion (ROM) was set from 90° (full extension referenced as 180°) to 150°. Real-time visual feedback was provided to participants on a monitor ~1 m away.

Electrical Stimulation

Two aluminum electrodes wrapped in gel-soaked cloth were secured to the distal and proximal anterior thigh. Muscle belly stimulation of the knee extensors was implemented over femoral nerve stimulation to overcome challenges in maintaining optimal electrode positioning over the femoral nerve during forceful, dynamic contractions (in which the shape and depth of the femoral canal are significantly modified). The electrodes varied in size from 20–26 cm × 7–11 cm for the distal electrode and 13–19 cm × 7–9 cm at the proximal electrode, to stimulate the largest proportion of the knee extensor muscles, while minimizing antagonist activation (though visual inspection and palpation). The proximal electrode was ~5–10 cm distal to the greater trochanter and the second electrode was placed ~5–15 cm distal of the proximal electrode. Square wave electrical pulses (1 ms at 400 V) were delivered through the electrodes using a constant current stimulator (DS7AH, Digitimer LTD, Welwyn Garden City, UK). A 1-ms pulse duration was utilized to minimize the current intensity used for stimulation (15).

Experimental Procedures

Both experimental sessions consisted of isometric MVC, isotonic MVC at three relative loads, and evaluation of one isometric and three isotonic (three loads) frequency curves. Participants performed two isometric MVCs at 90°, with the assessment of voluntary activation using the interpolated twitch technique (16), which has been shown previously to be a reliable and valid metric for voluntary activation (17). Participants were instructed to extend their knee as hard as possible for ~3 s, and immediately relax when instructed by the researcher (following the interpolated twitch). The current intensity for single pulse electrical stimulations was determined by incremental increases (25 mA) until a plateau in twitch torque occurred, which was then increased a further 20% (235 to 650 mA). A single pulse was delivered 2 s prior to the maximal voluntary effort, during the peak torque plateau, and 2 s following full relaxation. Participants were provided 5 min of rest between maximal contractions. The dynamometer was set to isotonic mode and the unloaded (minimum load to maintain 90° resting joint angle due to passive tension), 7.5% MVC, and 15% MVC torque loads were determined. Participants performed three maximal effort isotonic contractions at each load, until peak power varied by <10%, with 3 min of rest provided between loads. Participants were instructed to extend their knee as hard and as fast as possible, to achieve full range of motion in the shortest duration achievable.

Subsequently, the electrical current required to achieve ~50% of MVC torque during a 2 s 100 Hz tetanic stimulation was determined. Electrical current was increased in increments (5–10 mA) until torque plateaued at 50% MVC (32 to 140 mA). This current was maintained throughout the duration of the protocol for evaluating isometric and isotonic frequency relationships. Previous work has reported that submaximal stimulation provides results representative of whole muscle function (18). Following 5 min of rest, participants completed the stimulated isometric and three isotonic trials in a randomized order (see Fig. 1 in 14). However, given the lack of difference between the 7.5 and 15% loads, we only present the results for the 7.5% MVC. For each contraction mode, 1, 5, 7.5, 10, 12, 15, 17, 20, 25, 30, 40, 50, 75, and 100 Hz stimulations (20 s of rest between frequencies) were applied in ascending order each for 2 s or until end range of motion was achieved (or joint angle failed to reach the end range of motion). Current was automatically terminated for the isotonic stimulated contractions once the end range of motion was achieved using custom-made scripts. Following the final stimulated contraction set, 5 min of rest was provided, and isometric voluntary activation was retested.

Data Analysis

The isometric torque of voluntary and electrically evoked twitch and 50 Hz contractions were measured as the peak plateau torque for each contraction. Voluntary activation was evaluated as: 1 − (superimposed twitch torque ÷ potentiated resting twitch torque), as previously described (16). A single investigator manually determined the onset of torque and velocity as the last trough before the signal deflected away from the baseline noise, as previously described (19). A constant x-axis (time) scale of 500 ms and a y-axis scale of 1 Nm and 1°/s were used for manual onset determination. RTD and RVD were evaluated from isometric and isotonic contractions, respectively, and for each evoked contraction, early and late phases were determined for 0–50 ms and 0–100 ms, respectively. For each stimulation frequency, RTD and RVD were normalized to the maximal value obtained at 100 Hz of the same contraction mode and isotonic load. RTD and RVD were normalized to 100 Hz within a given contraction mode to compare the relative influence of stimulation frequency across the multiple contraction modes. All RTD and RVD calculations were measured on contractions elicited from electrical stimulation, thus no trials were excluded due to fluctuations in baseline signal (i.e., preactivation or voluntary antagonist activation). The time from the first pulse to velocity onset was evaluated at 100 Hz for the unloaded and moderately loaded isotonic contractions.

For each participant, isometric RTD and isotonic RVD at each frequency within a contraction mode were fit to a sigmoid function for evaluation of the relationship between frequency and contractile output (Fig. 1). The sigmoid function ($S \div (1 + e^{-k\times(x-x0)}) + C$) was fit to the data for each contraction mode using the Levenberg–Marquardt optimization function from the SciPy library (20). The sigmoid fitting (r^2)

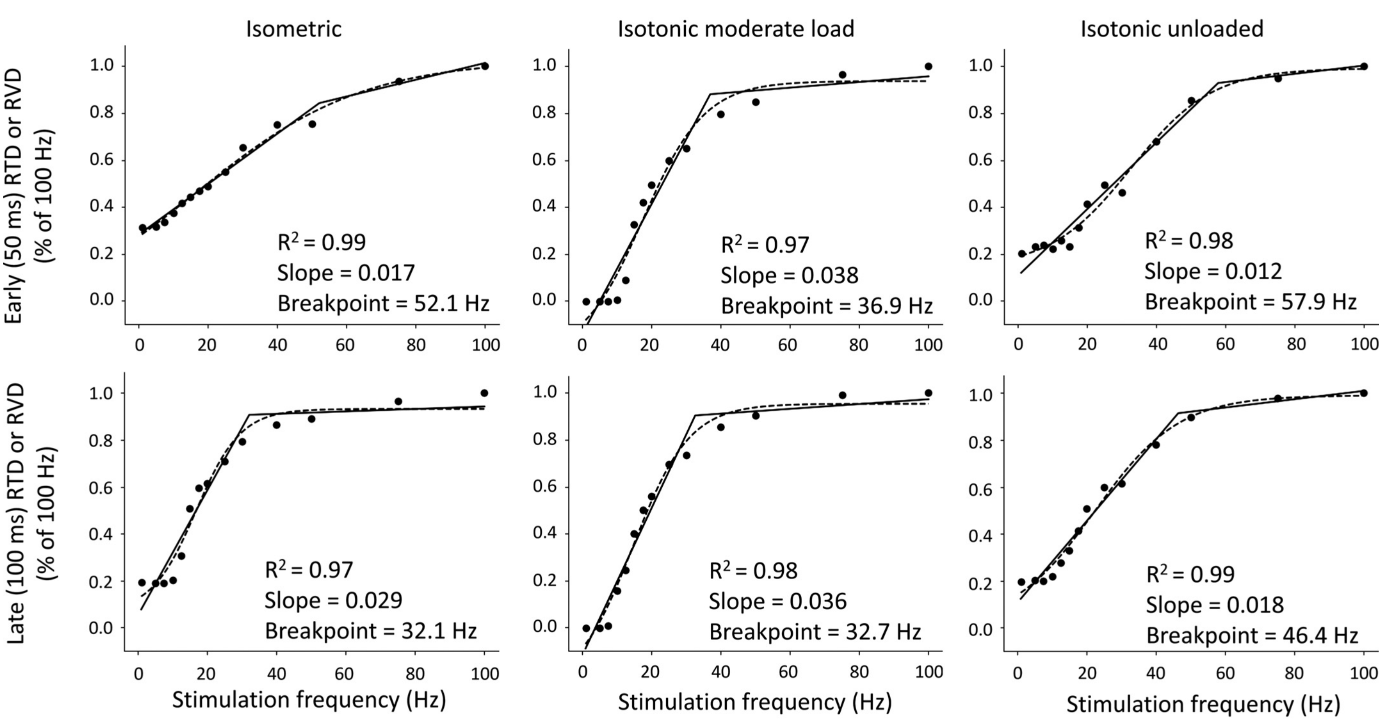

Figure 1. Example sigmoid fitting and segmental regression analysis from a single participant for early and late isometric RTD and isotonic RVD. All data are normalized to the 100 Hz output. Slope represents the steep portion of the segmental regression and breakpoint represents the frequency at which the sigmoid relationship flattens. R^2 represents the accuracy of sigmoid fitting. Dashed lines represent the sigmoid fitting and solid lines represent the segmental regression analysis. RTD, rate of torque development; RVD, rate of velocity development.

was evaluated as the ratio between the residual sum of squared error and the total sum of squared error. Fitted sigmoid data (100 data points evenly distributed from 1 to 100 Hz) were subsequently used in a linear segmental regression analysis to determine the slope of the steep portion of the sigmoid curve and the breakpoint at which the relationship plateaued. The mean squared error of the bilinear segmental regression was minimized using the SciPy library with the Nedler–Mead method (20). The slope of the first regression line was taken as the slope of the steep portion of the sigmoid relationship and the breakpoint frequency was taken as the frequency in which the two segmental regression lines intersected (Fig. 1).

Statistical Analysis

The normality of continuous variables was confirmed using the Shapiro–Wilk's test. Paired-sample *t* tests were used to examine differences in isometric MVC torque and voluntary activation between baseline and following the four stimulated frequency curves. Differences in time to velocity onset were also evaluated using a paired-sample *t* test. One-way ANOVAs were used to compare the slope of the steep portion of the curve and the breakpoint across the early (50 ms) and late (100 ms) isometric RTD and isotonic RVD (moderate and unloaded). A two-way ANOVA was used to evaluate the effects of frequency and phase of contraction (early vs. late) on isometric RTD, moderately loaded isotonic RVD, and unloaded isotonic RVD. A family-wise error rate of $\alpha = 0.05$ was maintained for post hoc comparisons using a Holm–Bonferroni correction factor (one-way ANOVA corrected for six comparisons and two-way ANOVAs corrected for 13 comparisons). All data are presented as mean ± SD and statistical significance was set as $\alpha \geq 0.05$. All statistical analyses were performed using JASP (Amsterdam, the Netherlands, version 0.17.2.1).

RESULTS

Mean isometric MVC torque and voluntary activation were 277.8 ± 101.4 Nm and 92.1 ± 3.8%, respectively. As targeted, baseline tetanic torque at 100 Hz stimulation achieved 50.5 ± 2.0% of MVC torque. Following the four electrically evoked torque-frequency curves, isometric MVC torque and voluntary activation were 277.4 ± 106.9 Nm and 92.1 ± 4.3%, respectively; indicating there were no differences with baseline contractile measures (MVC, $P = 0.948$; voluntary activation, $P = 0.964$). Across all participants, the average sigmoid fitting accuracy (R^2) was, early RTD: 0.98 ± 0.01, late RTD: 0.97 ± 0.01, moderate load early RVD: 0.97 ± 0.01, moderate load late RVD: 0.98 ± 0.01, unloaded early RVD: 0.96 ± 0.03, and unloaded late RVD: 0.97 ± 0.04. The time from the first pulse to velocity onset was shorter for unloaded (38 ± 8 ms) compared with moderately loaded (62 ± 13 ms, $P < 0.001$) isotonic contractions at 100 Hz stimulation frequency.

The slopes of the steep portion of the sigmoid relationships were significantly different between the early and late phases of isometric RTD and isotonic RVD (Fig. 2*A*, $P < 0.001$). Post hoc analysis demonstrated that the slope of the early isometric RTD (0.012 ± 0.003) was less steep than the late isometric RTD (0.025 ± 0.004, $P < 0.001$). However, slope steepness of the moderately loaded isotonic RVD was similar between the early (0.028 ± 0.005) and late phases (0.031 ± 0.005, $P = 0.055$). The slope of the early unloaded isotonic RVD (0.011 ± 0.003) was similar to the early isometric RTD (0.012 ± 0.003, $P = 0.653$), but less steep than that of the late unloaded isotonic RVD (0.016 ± 0.003, $P = 0.001$).

The breakpoint frequency was significantly different between the early and late phases of isometric RTD and isotonic RVD (Fig. 2*B*, $P < 0.001$). Post hoc analyses demonstrated that the early unloaded isotonic RVD (56.8 ± 7.0 Hz) was significantly higher than all other breakpoint frequencies (all $P < 0.001$). Early isometric RTD (47.7 ± 8.2 Hz) displayed a higher breakpoint frequency compared with late isometric RTD (33.0 ± 3.9 Hz, $P < 0.001$). No differences in breakpoint frequency were observed between early and late moderately loaded isotonic RVD (34.4 ± 4.9 vs. 32.1 ± 4.0 Hz, $P = 0.690$).

For isometric RTD (Fig. 3*A*), there was a main effect of frequency ($P < 0.001$) but not contraction phase ($P = 0.789$); however, an interaction was present ($P < 0.001$). The simple main effects revealed that early RTD was different than late RTD from 5 to 12.5 Hz and from 20 to 50 Hz (all adjusted $P < 0.001$). For moderately loaded isotonic RVD (Fig. 3*B*) there was a main effect of frequency ($P < 0.001$) and contraction phase ($P < 0.001$), but an interaction was present ($P < 0.001$). The simple main effects revealed differences between 17.5 to 50 Hz (all adjusted $P < 0.05$). For the unloaded isotonic RVD (Fig. 3*C*), there was a main effect of frequency ($P < 0.001$) but not contraction phase ($P = 0.239$); however, an interaction was present ($P < 0.001$). Simple main effects revealed differences between 1 to 12.5 Hz, between 17.5 to 30 Hz, and at 50 Hz (all adjusted $P < 0.05$). The differences in the early and late phases for RTD and RVD are shown in subplots 3*A*′–*C*′ (calculated as late phase − early phase), to graphically depict the magnitude of difference between these phases.

DISCUSSION

We report that the relationship between stimulation frequency and isometric RTD and isotonic RVD is dependent upon the contractile phase (early vs. late), and for isotonic contractions, the imposed load. Early RVD of an unloaded isotonic contraction was more responsive over a wider range of stimulation frequency (i.e., activation rate) compared with the late phase, indicating the rate of activation is more critical for the early phase of velocity generation for minimally loaded joints. However, early and late RVDs of a moderately loaded isotonic contraction were similarly responsive to the frequency of stimulation. We also observed that early isometric RTD is more modulated by stimulation frequency compared with late RTD, which is in agreement with previous results indicating that the rate of activation is more critical for the early compared with late phases of isometric torque production. These data provide a detailed understanding of the influence of neuromuscular activation frequency for shortening contractile function, across a range of isotonic loads.

The neuromuscular determinants of early and late phases of rapid RTD or RVD are often categorized as processes occurring within the central (e.g., motor unit firing rates)

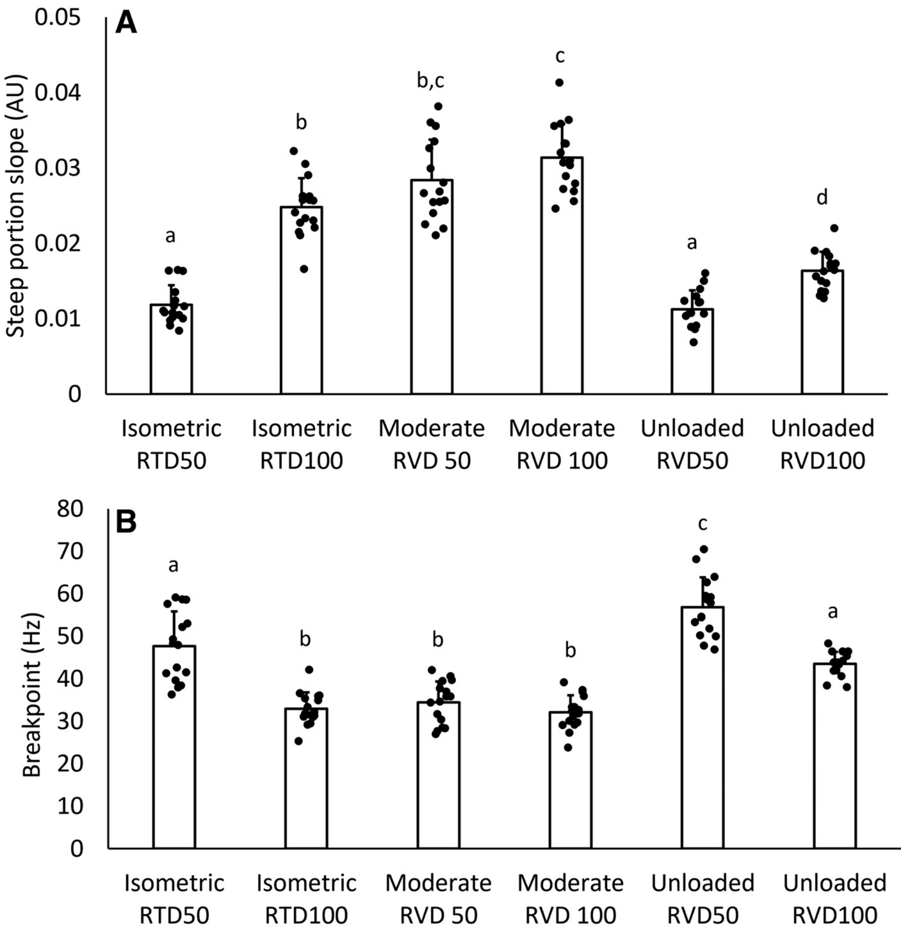

Figure 2. Mean slope of the steep portion (*A*) and breakpoint frequency (*B*) for isometric RTD and isotonic RVD. If two means share a letter, it indicates they are not statistically different from each other (adjusted $P > 0.05$). Data are presented as means ± SD. AU, arbitrary unit; RTD, rate of torque development; RVD, rate of velocity development.

and peripheral (e.g., muscle size, fiber composition, tendon stiffness) portions of the system (1, 3, 4, 21). Compared with slow isometric ramps, during rapid voluntary contractions, the motor unit recruitment range is compressed and the initial discharge rates are much higher; reaching rates of up to 200 pulses per second (22, 23). These features of compressed motor unit recruitment and high initial discharge rates are fundamental properties for achieving a high RTD, particularly during the early phase of the contraction (24). However, the majority of literature to date evaluating the determinants of explosive contractions has used isometric contractions, due to challenges in comparing torque during nonlinear changes in angle-torque-velocity relationships (25–27). We evaluated the dependence of muscle activation rate on RVD of unloaded and loaded isotonic contractions, which provides a more functionally relevant contraction paradigm in relation to natural movements. Similar to early isometric torque, we report that early RVD of an unloaded isotonic contraction displayed a less steep rise and higher breakpoint frequency compared with late RVD. The increased responsiveness of unloaded RVD to neuromuscular activation rate during the early phase of the contraction likely indicates that high motor unit discharge rates are critical for many natural movements involving fast rotation of an unloaded or minimally loaded limb (e.g., swing phase during brisk walking). However, the frequency-dependence of early and late RVDs is affected by the load, as moderately loaded (7.5 and 15% [data not shown] MVC) isotonic contractions displayed a similar responsiveness to input frequency between the early and late RVDs.

A key difference between unloaded and moderately loaded contractions is the time required to initiate movement from the onset of electrical stimulation, which was ~30% longer with moderately loaded compared with unloaded contractions at the 100 Hz stimulation frequency. Given the initial force augmentation that occurs with a brief high-frequency burst of two to four electrical pulses (e.g., catch-like property) (23), early isometric RTD, and unloaded isotonic RVD may be more sensitive to higher discharge rates due to increased sarcoplasmic Ca^{2+} release (28). For moderately loaded isotonic contractions, no movement will occur until a predefined torque is generated. Because the force augmentation for an initial high-frequency burst rapidly declines with time (29), the longer duration to movement onset with loaded isotonic contractions may attenuate the positive contractile output associated with catch-like properties. Thus, early RVD of moderately loaded isotonic contractions is less sensitive to higher stimulation frequencies. A similar time-dependent effect may be present for other factors that contribute to early RTD, but perhaps not RVD of loaded contractions. Indeed, previous studies have suggested that stiffer tendons are correlated with increased early RTD (30), although this may be attenuated when peak MVC is normalized (31, 32). However, we have shown recently that Achilles tendon stiffness is not correlated with early or late RVD of an isotonic contraction (loaded at 10 and 40% MVC

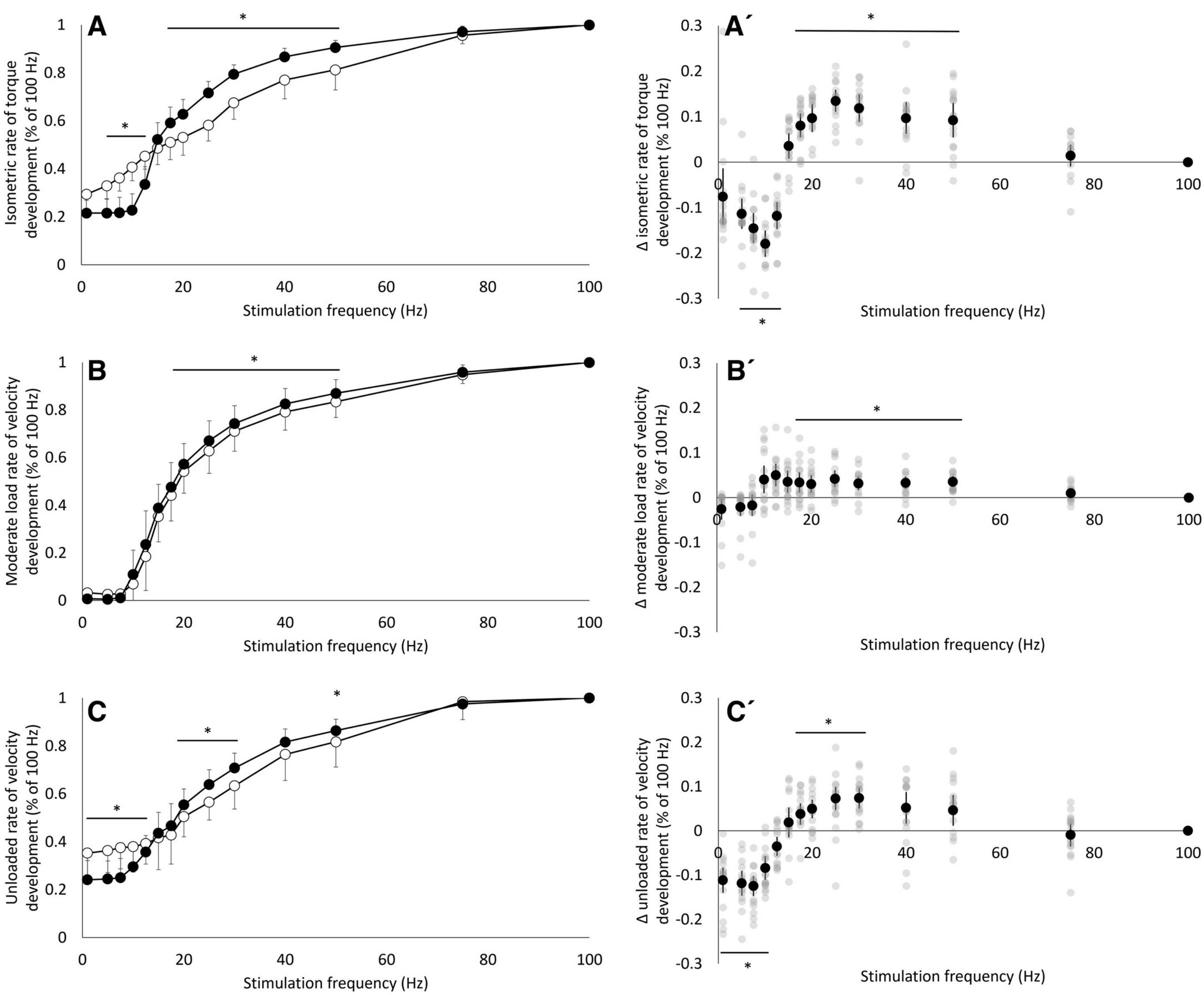

Figure 3. Frequency relationships for earlier and later isometric RTD (*A*), moderately loaded isotonic RVD (*B*), and unloaded isotonic RVD (*C*). Open and closed symbols represent early and late phases, respectively. Data are presented as means ± SD. The subplots (*A*′, *B*′, and *C*′) show the differences between the early and late phases for each graph (late–early phase). Black circles denote the mean difference (95% confidence interval indicated by vertical line) and gray points are individual data point differences. *Statistically different (adjusted $P < 0.05$) mean between frequencies for earlier and later RTD or RVD. RTD, rate of torque development; RVD, rate of velocity development.

torque) (33), likely due to using moderate-to-heavy loads, because the majority of the series-elastic compliance within the muscle-tendon complex would have been mitigated or removed prior to movement initiation.

Although they used a different dynamic contraction mode than was used here, Tillin et al. (6, 34, 35) evaluated dynamic RTD of iso-acceleration and iso-velocity contractions across both fast and slow concentric and eccentric contractions, while accounting for differences in angle-torque-velocity relationships. They reported that fast concentric contractions displayed higher normalized RTD in comparison to both isometric and eccentric contractions. Further, moderate to strong correlations (r = 0.50–0.85) were reported between RTD and normalized EMG (0–100 ms) for each contraction mode, highlighting the role of neural activation for these time-dependent contractile features (34). However, a higher RTD during electrically evoked fast concentric contractions was also reported, suggesting the increased ability to utilize a higher proportion of the maximal capacity during a fast shortening contraction may be an intrinsic component of skeletal muscle (6, 34). A further understanding of the key determinants between various contraction types (concentric, eccentric), modes (isokinetic, isotonic), and fundamental related parameters (angular velocity, loads) in both the early and late phases of the contraction provides a more comprehensive understanding of the interactions between neural and peripheral determinants during more naturalistic movements.

Compared with RVD, the determinants of RTD during the early and late phases of rapid isometric contractions are better characterized. Voluntary RTD from 0 to 40 ms (normalized to electrically evoked torque) is strongly correlated (r =

0.87) with the integrated surface electromyography that occurs before the onset of torque (5). Folland et al. (4) reported that the integrated surface electromyography was more strongly correlated with RTD at 50 ms (r = 0.71) in comparison with that at 150 ms (r = 0.48). Here, we demonstrated that early isometric RTD had a less steep rise and a higher breakpoint frequency in comparison to late isometric RTD, indicating early RTD requires a higher rate of input for maximal output. Although electrically evoked contractions cannot replicate natural neuromuscular activation patterns during voluntary control (36), these findings support previous reports (4, 5) demonstrating the rate of neuromuscular activation is more critical for the early phase of isometric torque generation in comparison to the later phases. Others have suggested that the rate of motor unit recruitment is more influential than the rate of discharge on RTD (37). Here, we controlled for the rate of recruitment (i.e., nearly complete synchronization of motor neuron activation), and showed that the frequency of stimulation, and thus the rate of motor unit discharge, was critical for modulating the early and late RTD. However, the direct application of these findings to voluntary contractions is unknown, because although the recruitment range is compressed during rapid contractions (37, 38), near synchronous recruitment of all motor units during a voluntary contraction is unlikely. Furthermore, it should be noted that we did not apply doublet forms of stimulation to potentially utilize the catch-like properties of the muscle, which may be present during voluntary recruitment of motor units (23).

We controlled the rate of activation to examine its influence on contractile output, but electrical stimulation does not mimic natural motor unit recruitment strategies during volitional contractions. Muscle belly electrical stimulation likely results in random recruitment order (36) and synchronously activates motor units. Furthermore, we used constant frequency trains of stimulation, which would not capture the inherent variability of motor unit firing rates (39) or take advantage of catch-like properties (23) of the muscle. Therefore, although our data support the importance of the rate of neural activation on RTD and RVD, it is limited to electrically evoked contractions. However, our findings with isometric contractions do align with previous literature indicating the importance of neuromuscular activation rate in the early and late phases of torque development. Similarly, but unlike natural voluntary contractions, all motor units are activated nearly synchronously with electrical stimulation, limiting our evaluations to frequency-dependent comparisons. Whereas others have shown both frequency and rate of motor unit recruitment are critical factors for determining isometric RTD (37). Although we observed a plateau in RTD and RVD for the early and late phases between ~75 and 100 Hz stimulation frequency, it has been shown previously that higher frequencies in humans are required to maximize isometric RTD (8). Therefore, our highest stimulation frequency may be considered submaximal to an extent, and thus it is unknown whether a very high-frequency burst (e.g., 300 Hz) would further increase either phase for RTD and RVD. However, because there were minimal differences between the early and late phases for frequencies above ~50 to 75 Hz for RTD and RVD, it is unlikely to alter our main conclusions. Finally, although targeting the stimulation current to achieve a sub-maximal torque output (e.g., 50% MVC) has been previously shown to be representative of whole-muscle torque output (18), it is unknown if the same principles apply to maximal current stimulation for early and late phase RTD and RVD.

In conclusion, we report that the early phase RTD of an isometric contraction is more dependent upon the rate of neuromuscular activation compared with the late phase. Similarly, the early RVD of an unloaded isotonic contraction is more sensitive to activation rate compared with the late phase. However, in a moderately loaded isotonic contraction, both the early and late phases were similarly modulated by the rate of activation. These findings indicate that the rate of neuromuscular activation may be a more critical determinant of the early isometric RTD and unloaded isotonic RVD when compared with the latter phase of the contraction, highlighting the importance of contraction mode (task) and externally applied load for understanding the contractile output during dynamic contractions.

DATA AVAILABILITY

Data will be made available upon reasonable request.

GRANTS

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

M.T.P., A.M.Z., and C.L.R. conceived and designed research; M.T.P. and A.M.Z. performed experiments; M.T.P. analyzed data; M.T.P., A.M.Z., and C.L.R. interpreted results of experiments; M.T.P. prepared figures; M.T.P. drafted manuscript; M.T.P., A.M.Z., and C.L.R. edited and revised manuscript; M.T.P., A.M.Z., and C.L.R. approved final version of manuscript.

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