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Contraction speed and type influences rapid utilisation of available muscle force: neural and contractile mechanisms

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Summary Statement

Time to maximum force in skeletal-muscle is shorter: at fast vs. slow contraction speeds, due to contractile mechanisms; and in concentric vs. isometric or eccentric contractions, due to neural mechanisms.

Abstract

This study investigated the influence of contraction speed and type on the human ability to rapidly increase torque and utilise the available maximum voluntary torque (MVT) as well as the neuromuscular mechanisms underpinning any effects. Fifteen young, healthy males completed explosive-voluntary knee-extensions in five conditions: isometric (ISO), and both concentric and eccentric at two constant accelerations of 500°.s^{-2} (CON_{SLOW} and ECC_{SLOW}) and 2000°.s^{-2} (CON_{FAST} and ECC_{FAST}). Explosive torque and quadriceps EMG were recorded every 25 ms up to 150 ms from their respective onsets and normalised to the available MVT and EMG at MVT, respectively, specific to that joint angle and velocity. Neural efficacy (explosive Voluntary:Evoked octet torque) was also measured, and torque data were entered into a Hill-type muscle model to estimate muscle performance. Explosive torques normalised to MVT (and normalised muscle forces) were greatest in the concentric, followed by isometric, and eccentric conditions; and in the fast compared with slow speeds within the same contraction type (CON_{FAST}>CON_{SLOW}>ISO, and ECC_{FAST}>ECC_{SLOW}). Normalised explosive-phase EMG and neural efficacy were greatest in concentric, followed by isometric and eccentric conditions, but were similar for fast and slow contractions of the same type. Thus, distinct neuromuscular activation appeared to explain the effect of contraction type but not speed on normalised explosive torque, suggesting the speed effect is an intrinsic contractile property. These results provide novel evidence that the ability to rapidly increase torque/force and utilise the available MVT is influenced by both contraction type and speed, due to neural and contractile mechanisms, respectively.

Introduction

The functional capacity of the musculoskeletal system is limited by maximum muscle strength, typically measured as the maximal voluntary torque (MVT) that can be generated around a joint. MVT is known to be dependent on the angle and angular velocity of the joint, in a manner well explained by the MVT-angle-velocity relationships (Anderson et al., 2007; Pain et al., 2013; Yeadon et al., 2006). When contracting from a low or resting state, it takes >100 ms to achieve the MVT available at a given joint angle and angular velocity (Tillin et al., 2012). Thus, explosive torque – the proportion of available MVT produced in a given contraction time (Maffiuletti et al., 2016) – is functionally important in some human movements where time for torque production is limited, such as during sprinting (Weyand et al., 2000) or balance recovery (Izquierdo et al., 1999; Palmer et al., 2015). However, little is known about the influence of joint angular velocity, including different types of contractions (concentric, eccentric and isometric) and different speeds within a contraction type, on explosive torque production.

Explosive torque production of human skeletal muscle in vivo is typically measured in isometric conditions, to avoid changes in joint angle, velocity, and acceleration that interact with torque in a non-linear manner to produce an inconsistent mechanical situation and confound measures of explosive torque (Maffiuletti et al., 2016). Thus, investigating the influence of joint angular velocity on explosive torque is problematic, and further complicated by the greater range of joint angles covered in a given contraction time during fast vs. slow speed contractions, and the opposite directions of concentric vs. eccentric contractions. We recently developed a novel approach to address these issues by assessing explosive torque in the mechanically consistent situation of constant acceleration from stationary, and by normalising explosive torque to the available torque (i.e., MVT) at each specific joint angle and velocity (Tillin et al., 2012). Results provided surprising evidence that explosive concentric contractions were able to express a considerably greater proportion (>1.6 fold) of available MVT than eccentric or isometric explosive contractions. However, concentric and eccentric contractions were only assessed at one constant joint angular acceleration of 2000°.s^{-2} eliciting fast speeds (i.e., explosive torques were measured between ~140-425°.s^{-1}). It is conceivable that the large effect of contraction type on explosive torque may be further delineated by contraction speed (e.g., slow vs. fast) within concentric and eccentric conditions.

The mechanisms for the effects of contraction speed and type (isometric, concentric, eccentric) on explosive torque production also requires investigation. Neuromuscular activation is known to be a key determinant of isometric explosive torque production (Folland et al., 2014) and thus may explain differences between contraction speed and type. We previously (Tillin et al., 2012) observed greater neuromuscular activation in the explosive phase of concentric compared with isometric or eccentric contractions via two independent measures – EMG amplitude normalised to maximal M-wave and neural efficacy (the ratio of Voluntary:Evoked octet torque) – that appeared to explain the faster utilisation of available MVT in the concentric condition. These two measures of neuromuscular activation were obtained through normalisation of voluntary explosive data (EMG and torque) to involuntary reference measures (M-wave and evoked octet, respectively). However, for explaining the capacity to rapidly utilise the available MVT (i.e., scaling of explosive torque to MVT) a better measure of neuromuscular activation may be to assess explosive-phase EMG scaled to EMG at MVT.

Series elastic components (SEC; e.g., tendons) uncouple joint (and muscle-tendon unit) from muscle fibre dynamics (Roberts, 2016), so it's possible that any effects of joint angular velocity (contraction type or speed) on explosive torque may be due to muscle-SEC interactions, and not indicative of the influence of muscle contractile velocity on explosive muscle force production. The effect of muscle contractile velocity on explosive force could be assessed by entering the torque data into a muscle model comprising contractile and SE components, to estimate muscle forces, lengths and velocities. This approach removes the influence of the SEC on the data and makes it possible to deduce that any effects of contractile speed on explosive muscle force, which could not be explained by neuromuscular activation, were an intrinsic property of the contracting muscle fibres.

The aim of this study was to investigate the effects of joint angular velocity on the ability to utilise the available MVT in explosive contractions, and assess the neuromuscular mechanisms contributing to any observed effects. We hypothesised that a greater proportion of available MVT would be expressed during: (i) fast compared with slow speeds within concentric and eccentric explosive contractions; and (ii) concentric compared to isometric or eccentric explosive contractions.

Materials and Methods

Participants

Fifteen healthy, male volunteers who were recreationally active, but not engaged in any systematic strength or endurance training, completed the study (age, 25 ± 3 years; height, 1.77 ± 0.04 m; mass, 77 ± 6 kg). Participants gave their informed consent before participation, which was approved by the Loughborough University ethical advisory committee, and conformed to the standards set by the Declaration of Helsinki. One participant was excluded from comparisons of the EMG data only (i.e., n = 14) due to spurious EMG recordings for one of the measurement sessions.

Overview

Participants visited the laboratory to complete two familiarisation sessions and two measurement sessions, each lasting ~90-120 min and separated by ~7 days. The familiarisation sessions involved all the activities completed in the two measurement sessions (Figure 1) but with no recordings, the exception being the involuntary explosive (electrically evoked octet) contractions, which were assessed entirely during the second familiarisation session. Specifically, following the warm-up, octet contractions were evoked and recorded in the same 5 contractile conditions as the explosive voluntary contractions (see below), in a random order after the isometric condition.

The overall design of the two measurement sessions involved participants performing explosive voluntary contractions of the knee extensors in 5 separate contractile conditions; isometric (ISO), concentric slow (CON_{SLOW}) and fast (CON_{FAST}), and eccentric slow (ECC_{SLOW}) and fast (ECC_{FAST}) (Table 1). For each measurement session to be manageable, explosive contractions were performed in only 3 conditions per session, with ISO common for both sessions (either ISO, CON_{SLOW}, and CON_{FAST} or ISO, ECC_{SLOW}, and ECC_{FAST}; Figure 1). The order of measurement sessions was randomised, and the order of slow and fast (concentric or eccentric) conditions within each session were also randomised and completed before ISO. Following the explosive contractions, maximum voluntary contractions (MVCs) were performed isometrically (at 5 angles) and dynamically at reciprocal (eccentric – concentric) isovelocities

(8 velocities) during both sessions. Explosive torque and electromyography (EMG) amplitude recorded during the explosive contractions were normalised to knee joint angle and angular velocity specific maximal voluntary torque (MVT) and EMG amplitude at MVT (EMG_{MVT}), respectively, determined from the isometric and isovelocity MVCs. Voluntary explosive torques were also assessed relative to involuntary explosive torques recorded in the same contractile conditions during evoked octet contractions.

Measurements

Dynamometer and EMG

Knee extensor contractions of the dominant leg only, were completed with an isokinetic dynamometer (Con-Trex; PHYSIOMED ELEKTROMEDIZEN AG, Schaittach, Germany) whilst the participant was seated with the hip at 80° flexion from the anatomical position, and restrained with tight shoulder and waist straps. The axis of rotation of the crank arm was aligned with the lateral knee joint space whilst participant produced a near MVC at a knee angle (~120°; 180° being the anatomical position) central to the active range in this study. Analogue torque and crank arm angle (representing knee angle) were sampled at 2000 Hz via an analogue to digital converter and PC using Spike2 software (CED micro 1401, CED, Cambridge, UK). Biofeedback was provided via a computer monitor in front of the participant. Torque and angle signals were digitally low-pass filtered using a zero-lag fourth order Butterworth filter with cut off frequency at 20 Hz (explosive voluntary and evoked contractions) or 8 Hz (isometric and isovelocity MVCs). The higher cut off frequency was required for the explosive contractions as some high frequency noise was necessary for time-aligning passive and active trials (see below), whilst a lower cut off frequency was necessary to accurately identify isovelocity periods during the MVCs. Measured torques in all isometric contractions and the explosive concentric and eccentric conditions were corrected for weight and acceleration of the shank by subtracting passive torques measured in the same contractile conditions, using methods previously described (Tillin et al., 2012). Measured torques in isovelocity conditions were corrected for the weight of the shank using a 6^{th}-order polynomial describing the passive torque – angle relationship, obtained from passively extending (from 70-170°) and flexing the knee at

10°.s^{-1}. Knee angular velocity was derived from the filtered knee angle signal by numerical differentiation with a 1-ms epoch.

Following preparation of the skin surface (shaving, lightly abrading and cleansing with 70% ethanol), two separate bipolar EMG electrode configurations were each placed over the belly of the rectus femoris (RF), vastus lateralis (VL), and vastus medialis (VM), parallel to the presumed orientation of the fibres (i.e., 6 single-differential EMG signals in total; Trigno, Delsys Inc., Boston, MA). Placements were at 65 and 55% (RF), 55 and 45% (VL), and 30 and 20% (VM) of the distance from the greater trochanter to the lateral knee-joint space. EMG signals (amplified x909) were sampled at 2000 Hz in synchronization with torque and angle via the same analogue to digital converter and PC, and band-passed filtered off-line between 6-500 Hz, with a zero-lag fourth order Butterworth filter.

Explosive Voluntary Contractions

Participants completed explosive voluntary contractions – in which they were instructed to extend their knee as "fast and hard" as possible for ~1 s with an emphasis on "fast"– in five separate conditions: isometric at a knee angle of 123° (ISO), and concentric and eccentric at constant accelerations of 500°.s^{-2} (CON_{SLOW} and ECC_{SLOW}) and 2000°.s^{-2} (CON_{FAST} and ECC_{FAST}). In the concentric and eccentric conditions, the crank arm moved slowly (10°.s^{-1}) through the range of motion (89-156°) to the start position for the acceleration phase (89° for concentric and 156° for eccentric conditions), from where it accelerated for 450 ms (CON_{SLOW} and ECC_{SLOW}) or 225 ms (CON_{FAST} and ECC_{FAST}), from 0°.s^{-1} to a peak velocity of 450°.s^{-1} (CON_{FAST}), -450°.s^{-1} (ECC_{FAST}), 225°.s^{-1} (CON_{SLOW}), or -225°.s^{-1} (ECC_{SLOW}), before decelerating to a stop at the opposite end of the range of motion. Knee angle at peak velocity was 140° (concentric conditions) or 105° (eccentric conditions). The ISO knee angle was selected as being in the centre of the range between the start of CON and ECC, and only one angle was tested as the effects of joint angle on the ability to rapidly utilise the available MVT during explosive contractions is only small (de Ruiter et al., 2004; Tillin et al., 2012). The kinematics of each condition are summarised in Table 1, and example collected data shown in Figure S1 of the supplementary files.

Participants were instructed to commence the explosive voluntary contractions from a resting state (i.e., zero active torque) and without prior countermovement (negative/flexor torque), at the start of the acceleration phase in the concentric and eccentric conditions, and in response to an audible signal in ISO. For the concentric and eccentric conditions, the knee angle signal was displayed on the computer monitor in front of participants with a horizontal cursor representing the start angle so that participants could anticipate the start of the acceleration phase. For each concentric and eccentric condition participants completed 15-20 explosive voluntary contractions (active trials, separated by ~30 s) and 3 passive trials (zero active torque; used to correct active trials for shank weight and acceleration; see Figure S1 of supplementary files). ISO involved 8-10 active trials (separated by ~30 s).

Off-line analysis was completed using custom-developed programs in MATLAB (The MathWorks inc., Natick, MA, USA). The concentric and eccentric active trials were excluded from further analysis if: corrected baseline torque exceeded ±2 Nm in the 2 s preceding active-torque onset; baseline torque in the 100-ms preceding active-torque changed by >2.5 Nm; and/or if active-torque onset occurred earlier than 20-ms (all conditions) or later than 75 ms (CON_{FAST} and ECC_{FAST} only) into the acceleration phase. Trials in ISO were excluded if baseline torque in the 100 ms preceding active-torque onset changed by >1 Nm. Torque onset in all conditions was defined as the point at which the first derivative of the active torque-time curve crossed zero for the last time (Tillin et al., 2012).

Of the valid active trials in each condition, the three with the highest normalised torque at 100 ms from torque onset were analysed further, which included recording absolute torque, knee angle, and angular velocity at 25-ms intervals from torque onset up to 150 ms. Absolute torque at each time point was therefore recorded at differing knee angle and angular velocity conditions for each contraction, and was consequently normalised to MVT at the same knee angle and angular velocity conditions, measured/interpolated in the same session. MVT for ISO was measured at 123°, whilst MVTs for the concentric and eccentric conditions were interpolated from a dynamic MVT function (i.e. torque-angle-velocity relationship; see below). Absolute torque, normalised torque, knee angle and angular velocity at each time point were averaged over the three active trials analysed in each condition. Explosive voluntary torque at 75 ms was also calculated as a percentage of evoked octet torque (see below) at 75 ms from torque onset recorded in the same condition (Voluntary:Evoked ratio), after normalising both separately to knee angle and angular velocity specific MVT. The Voluntary:Evoked torque ratio provided a measure of neural efficacy – the ability of the voluntary nervous system to utilise the available explosive torque capacity of the muscles (de Ruiter et al., 2004; Hannah et al., 2012).

The three explosive contractions in each condition selected for torque analysis were also analysed for EMG, which involved first identifying EMG onset (the instant an active EMG signal was first detected in any of the 6 EMG signals) using a visual, systematic inspection method (Tillin et al., 2010). Briefly, signals were viewed on a constant y-axis scale of 0.1 mV and x-axis scale of 500 ms, and EMG onset was defined as the last peak or trough before the signal deflected away from the baseline noise pattern. Visual inspection is considered by some researchers as the gold standard method for detecting signal onsets (Tillin et al., 2013). To assess neuromuscular activation during each condition, the RMS EMG amplitude of each EMG signal was measured over a 50-ms epoch (explosive-phase EMG) at 25-ms intervals from EMG onset up to 150 ms. Explosive-phase EMG at each time point was therefore recorded at differing knee angle and angular velocity conditions, and was consequently normalised to the RMS EMG at MVT (EMG_{MVT}) at the same knee angle and angular velocity conditions, in the same measurement session. For ISO, EMG_{MVT} was the measured value obtained at MVT during the MVCs at a 123° knee angle. For the concentric and eccentric conditions, EMG_{MVT} was linearly interpolated from the RMS EMG measured at the same knee angle (corresponding to the explosive-phase EMG knee angle) in the MVCs performed at the two measured isovelocities that the explosive-phase EMG velocity occurred between (e.g., if explosive-phase EMG was measured at 145°.s^{-1}, EMG_{MVT} was linearly interpolated from MVCs performed at 100°.s^{-1} and 250°.s^{-1}). Absolute and normalised explosive-phase EMG at each time point was averaged across the 6 EMG signals and across the three contractions at which it was measured, within each condition. Mean explosive-phase EMG (absolute and normalised) between 0-100 ms and 0-150 ms were also obtained by averaging explosive-phase EMG at 25 and 75 ms ($EMG_{0\text{-}100}$), and at 25, 75, and 125 ms ($EMG_{0\text{-}150}$).

Maximal Voluntary Contractions

Participants completed a total of 8 isometric MVCs (each separated by 3 min) across 5 different knee angles in a randomised order; 2 MVCs each at 91°, 123°, and 153°, and 1 MVC each at

107° and 138°. For each MVC, participants were instructed to extend their knee as hard as possible for 3-5 s. The greatest extensor torque (corrected for shank weight as above for ISO) recorded at each angle was defined as MVT for that angle. MVTs at all angles were used to establish a MVT – angle relationship (defined by a normal distribution curve; (Forrester et al., 2011)) that set the estimates and bounds of the dynamic MVT function, describing the MVT – angle – velocity relationship. To establish the dynamic MVT function, participants completed 2 sets of 4 reciprocal (continuous) eccentric-concentric isovelocity MVC cycles, at each of 4 different isovelocities; 50, 100, 250, and 400°.s^{-1}. Following a submaximal familiarisation at each velocity, sets were completed in a counterbalanced order: one maximal set of 4 cycles was completed at each velocity first in ascending order (slowest to fastest), and then one maximal set at each velocity in descending order, with sets separated by 3 min. For each set of 4 reciprocal MVC cycles, participants were instructed to extend their knee as hard as possible from ~0.5 s before the start of the set to the end of the set. This protocol pre-loads the muscles facilitating maximal voluntary neuromuscular activation, and therefore MVT, throughout the entire range of motion (King and Yeadon, 2002; Pain and Forrester, 2009; Yeadon et al., 2006), which was set between 70-170°, providing isovelocity ranges of approximately 77° (50°.s^{-1}), 75° (100°.s^{-1}), 62° (250°.s^{-1}), and 40° (400°.s^{-1}). A set was repeated if the greatest peak eccentric torque in that set was <90% of the greatest isometric MVT in that session. The best MVC at each separate concentric and eccentric velocity was defined as the one that produced the greatest sum of peak torque, mean torque, and work done, after scaling each of these parameters to the highest recorded value for that parameter at the same velocity. Data from the best MVC at each velocity were input into a 9-parameter mathematical model describing MVT as the product of joint angle and angular velocity (Forrester et al., 2011; Yeadon et al., 2006). A weighted RMS score function – which forced 85% of the measured values below the surface representing the dynamic MVT function to account for the largely one-sided errors caused by submaximal effort (Forrester et al., 2011) – optimised the 9 parameters of the dynamic MVT function, via a simulated annealing algorithm (Corana et al., 1987). Weighted RMS difference between interpolated and measured values was on average 6 ± 2 Nm (~1.3% of the greatest eccentric MVT). A separate dynamic MVT function was produced for each measurement session of each individual (see Figure S2 in supplementary files), and used for normalisation of measured explosive torques within the same session.

EMG signals in the isometric and isovelocity MVCs were smoothed with a 50-ms moving RMS time window to match the RMS epochs used for the explosive voluntary contractions. EMG_{MVT} was then calculated from the average RMS amplitude over a 10-ms epoch either at MVT for each isometric knee angle, or at any given knee angle for the best MVC at each isovelocity. The 10-ms epoch was selected for computational purposes because of the changing dynamics of the isovelocity contractions, which provided more than one data point, and thus more than one potential EMG_{MVT} value, per degree of movement. A 10-ms epoch provided a sufficiently small period to maximise angle resolution (which was 0.5, 1, 2.5, and 4° for 50, 100, 250, and 400°.s^{-1}, respectively) and minimise further smoothing of the data.

Hill-Type Muscle Model

Highly invasive methods are required to directly measure muscle dynamics *in vivo* (Biewener et al., 2014). Whilst estimates of muscle dynamics are possible using ultrasound video (Dick et al., 2017), for explosive contractions this requires high speed ultrasound and video capture, which were not available to the current study. Thus, we utilised a Hill-type muscle model comprising contractile and SE components to remove the influence of a SEC and estimate muscle dynamics. Torque and knee angle data from the three explosive contractions chosen for analysis in each condition were input into the muscle model, which estimated net muscle force, fibre length and contraction velocity for each knee extensor muscle (RF, VL, VM, and vastus intermedialis). The model was identical to that detailed in Appendix A of Pain and Forrester (2009). Briefly, measured torques were divided by derived patellar-tendon moment arm (Kellis and Baltzopoulos, 1999), multiplied by fractional PCSA for each knee extensor (Chow et al., 1999), and factored for pennation angle (Hoy et al., 1990), to estimate muscle fibre forces. Muscle-tendon unit (MTU) length was derived from hip and knee angles (Hawkins and Hull, 1990), whilst fibre length was the difference between MTU and SEC length factored for pennation angle. SEC length was the sum of SEC slack length (0.16 m for vasti and 0.36 m for RF; Jacobs et al., 1996) and SEC displacement, where SEC displacement was determined by dividing fibre force by SEC stiffness. SEC stiffness was a linear function between SEC slack length and maximum strain (6%; Karamanidis & Arampatzis, 2006) at maximum isometric force (5400 N for vasti and 930 N for RF; Jacobs et al., 1996). Muscle parameters obtained from the literature were scaled to the mass (forces) and height (lengths) of each participant, and contractile velocities were determined by differentiating the fibre length data. Data from the dynamic MVT function was also entered into the muscle model to estimate dynamic maximal voluntary force (MVF) as a function of the MVF – muscle fibre length – muscle velocity relationship. For each condition, the absolute explosive forces for each muscle recorded at 25-ms intervals from force onset were normalised to muscle fibre length and velocity specific MVF, averaged across the four muscles, and averaged across the 3 active trials that were analysed. Whilst there are likely to be some errors in the model's estimates of forces, lengths and velocities, it is assumed these would be similar for explosive and MVT phases of contraction and thus largely controlled for by normalising explosive forces to MVF.

Involuntary Explosive (Evoked Octet) Contractions

Supramaximal electrical stimulation of the femoral nerve with square-wave pulses (0.2-ms duration; DS7AH, Digitimer Ltd, UK) was used to evoke octet contractions (8 pulses at 300 Hz) whilst participants were voluntarily passive. The cathode (a 1-cm diameter custom adapted stimulation probe; Electro Medical Supplies, Wantage, UK) was taped down over the femoral triangle in a position that elicited the greatest twitch response to a single submaximal impulse, whilst the knee was at an isometric angle of 123°. The anode (carbon rubber, 7 × 5 cm; EMS Physio Ltd, Greenham, UK) was taped down over the greater trochanter. Remaining at a 123° knee angle, single impulses were evoked with increasing current intensity every 10-15 s until there was a plateau in peak twitch torque (maximal stimulation intensity). Participants were then familiarised with the octets by gradually increasing the current from an imperceptible level to 120% of maximal stimulation intensity. Thereafter, 3 supramaximal octet contractions were evoked in each condition: the ISO condition (separated by 15-20 s), and at 3-4° into the acceleration phase of CON_{FAST}, CON_{SLOW}, ECC_{FAST}, and ECC_{SLOW}, to approximately coincide with the onset of explosive voluntary torque during the dynamic conditions. Conditions were completed in a randomized order following ISO. Evoked octet torque at 75 ms from torque onset was measured and averaged across the three octets in each condition.

Statistical Analysis

Initially, normalised explosive torque in the ISO condition from both measurement sessions were compared across 6 contraction time points (two-way repeated measures ANOVA) and no main effect of session (P = 0.512) or interaction (P = 0.977) were found. Therefore, all dependent variables for ISO were averaged across the two measurement sessions before considering condition effects.

The effects of condition (CON_{SLOW} CON_{FAST}, ECC_{SLOW}, ECC_{FAST}, and ISO) and condition by time point (25, 50, 75, 100, 125, and 150 ms) on normalised explosive torque (and muscle force), absolute explosive-phase EMG, and normalised explosive-phase EMG were assessed via two-way repeated measures ANOVAs (5 conditions x 6 time points). One-way repeated measures ANOVAs were also used to assess the effects of condition on: normalised explosive torque (and muscle force) averaged across the 6 time points; explosive-phase $EMG_{0\text{-}150}$; and Voluntary:Evoked torque ratio at 75 ms. Paired differences in dependent variables were assessed via paired t-tests with Bonferroni corrections. Pearson product moment bivariate correlations assessed the relationships between normalised explosive torque at 100 ms and explosive-phase $EMG_{0\text{-}100}$, within each condition.

Results

Kinematics of the Explosive Contractions

Knee angle at torque onset in the explosive voluntary contractions was the same for CON_{SLOW} and CON_{FAST}, and the same for ECC_{SLOW} and ECC_{FAST} (Table 2, Figure 2A). CON_{SLOW} and ECC_{SLOW} displayed comparable changes in knee angle and angular velocity over the first 150 ms from torque onset, as did CON_{FAST} and ECC_{FAST} (Figure 2A and 2B). Torque onset occurred slightly earlier (i.e., at slower velocities) in the acceleration phase of voluntary compared to evoked contractions for all dynamic conditions (Table 2). Consequently, voluntary and evoked octet torques were first normalised to knee angle and angular velocity specific MVT before calculating the ratio of Voluntary:Evoked torque.

Estimated muscle fibre length at force onset in the explosive voluntary contractions was similar for CON_{SLOW} and CON_{FAST}, and identical for ECC_{SLOW} and ECC_{FAST} (Figure 3A), which is expected given the similar knee angles at torque onset within concentric and eccentric conditions. However, joint and muscle dynamics uncoupled during the first 150 ms from force onset, causing muscle-length changes per degree of knee-angle change to be different for each condition, and considerably greater in the concentric than corresponding eccentric conditions;

CON_{FAST}, (-0.90 ± 0.05 mm.°$^{-1}$) vs. ECC_{FAST} (-0.62 ± 0.05 mm.°$^{-1}$), and CON_{SLOW} (-1.23 ± 0.16 mm.°$^{-1}$) vs. ECC_{SLOW} (-0.50 ± 0.10 mm.°$^{-1}$). The greater length changes resulted in greater peak velocity changes from force onset in the concentric than corresponding eccentric conditions; CON_{FAST} (0.234 ± 0.018 m.s^{-1}) vs. ECC_{FAST} (0.135 ± 0.025 m.s^{-1}; P<0.001), and CON_{SLOW} (0.113 ± 0.013 m.s^{-1}) vs. ECC_{SLOW} (0.034 ± 0.014 m.s^{-1}; P<0.001; Figure 3A & 3B). There were changes in muscle fibre length in the ISO condition (Figure 3A), resulting in a shortening velocity profile which was similar in shape but with lower velocities than that of CON_{SLOW} (Figure 3B).

Voluntary Explosive Torque and Muscle Force

As expected, the absolute torque-time curves recorded over the first 150 ms from torque onset were affected by condition, and reflected the kinematics of each condition (Figure 2C). For example, the conditions exhibiting the higher torques at each time point were those characterised by more optimal situations: near optimal knee angle (~110-120°) and/or low or negative (eccentric) angular velocity (e.g., ISO throughout, CON_{SLOW} and CON_{FAST} up to 100-ms, and ECC_{FAST} after 100-ms). Likewise, the available MVT (measured, ISO; or interpolated, CON and ECC) during the different conditions also reflected joint kinematics: high throughout ISO which was performed near optimal knee angle; decreased throughout CON as shortening velocity increased; and increased throughout ECC as the knee accelerated to more optimal angles. The influence of knee angle and velocity on MVT in this study is displayed in Figure S2 of the supplementary files, but is beyond the scope and primary aims of this manuscript.

When explosive torque was normalised to available MVT at the same knee angle and angular velocity (Figure 2E) there was a main effect of condition (P<0.001) and a condition by time point interaction (P<0.001). Specific differences between conditions were found for all time points i.e. from 25 to 150 ms (Table 3) with normalised explosive torque always considerably greater in CON_{FAST}, followed by CON_{SLOW}, ISO, ECC_{FAST}, and ECC_{SLOW}. In fact, MVT was achieved after ~139 ms of explosive contraction in CON_{FAST} (by interpolating between the measured time points) and exceeded after 150 ms (108% MVT), but the % MVT achieved after 150 ms in the other conditions was only 73% (CON_{SLOW}), 61% (ISO), 59% (ECC_{FAST}), and

42% (ECC_{SLOW}; Figure 2D and Table 3). Normalised torque averaged across the 6 measured time points (Table 3) tended to show the same pattern with CON_{FAST} ~51% greater than CON_{SLOW} (P<0.001), CON_{SLOW} ~25% greater than ISO (P = 0.041), ISO similar to ECC_{FAST} (P = 0.472), and ECC_{FAST} ~33% greater than ECC_{SLOW} (P = 0.092; Figure 2E).

The effects of condition on estimated muscle forces (Figure 3C and D) were comparable to the effects on knee extensor torques. Absolute muscle forces at each time point (Figure 3C) were highest when muscle fibre length was closer to optimal length (e.g., ISO and CON_{SLOW} throughout), and muscle velocity was low (e.g., early phase of CON_{FAST}) or negative (e.g., late phase ECC_{FAST}). Estimated muscle forces normalised to muscle fibre length and velocity specific MVF (Figure 3D) were: greater in CON_{FAST} than all other conditions (all measured time points, P≤0.046); greater in CON_{SLOW} than ISO at 25 (P<0.001) and 50 ms (P = 0.045) but similar at later time points (P≥0.524); greater in both CON_{SLOW} and ISO than either eccentric condition (all measured time points after 25 ms, P≤0.012); and similar in ECC_{FAST} and ECC_{SLOW} except for at 150 ms when ECC_{FAST} was greater (P = 0.010). Normalised explosive force averaged across the 6 measured time points were greater in CON_{FAST} (60 ± 12 % MVF) than CON_{SLOW} (45 ± 8.2 % MVF; P = 0.003), similar in CON_{SLOW} compared with ISO (39 ± 4.4 % MVF; P = 0.340), greater in ISO than ECC_{FAST} (24 ± 8.7 % MVF; P<0.001) and similar in ECC_{FAST} than ECC_{SLOW} (18 ± 6.2 % MVF; P = 0.180).

Voluntary:Evoked Torque

There was a main effect of condition on the Voluntary:Evoked torque ratio at 75 ms from torque onset (P<0.001). The Voluntary:Evoked torque ratio in CON_{FAST} was similar to CON_{SLOW} (P = 0.619; Figure 4), but ~37% greater than ISO (P = 0.026; Figure 3), and ~175-190% greater than ECC_{FAST} and ECC_{SLOW} (p<0.001; Figure 4). The Voluntary:Evoked ratio in CON_{SLOW} was similar to ISO (P = 1.000; Figure 4) but ~102-139% greater in both of these conditions compared to either of the eccentric conditions (P≤0.005; Figure 4). There was no difference between ECC_{FAST} and ECC_{SLOW} for the Voluntary:Evoked ratio (P = 1.000; Figure 4).

Explosive-phase EMG

The effects of condition on explosive-phase EMG were similar for absolute (Figure 5A) and normalised (Figure 5B) EMG (normalised to knee angle and angular velocity specific EMG_{MVT}) data. For brevity, only the normalised EMG data are discussed. There was a main effect of condition ($P<0.001$) and a condition by time point interaction effect ($P<0.001$) on normalised explosive-phase EMG. Explosive-phase EMG_{0-150} was similar for CON_{FAST}, CON_{SLOW}, and ISO ($P = 1.000$; Figure 5B and Table 4), and more than twice as high in all three of these conditions (+120-141%; $P\leq0.001$) compared with ECC_{FAST} and ECC_{SLOW}, with no differences between ECC_{FAST} and ECC_{SLOW} ($P = 1.000$; Figure 4B, Table 4). In the concentric and isometric conditions, explosive-phase EMG exceeded EMG_{MVT} after <75 ms from EMG onset (Figure 5B, Table 4), continuing to rise in CON_{FAST} and CON_{SLOW} (to 127-129% EMG_{MVT}), but not ISO (Figure 5B, Table 4). As a result, explosive-phase EMG in CON_{FAST} tended to be greater than ISO at 125 ms ($P = 0.097$) and was significantly greater at 150 ms ($P = 0.008$; Figure 5B and Table 4). During the eccentric conditions, explosive-phase EMG increased more gradually reaching 77% (ECC_{FAST}) and 64% EMG_{MVT} (ECC_{SLOW}) at 150 ms from EMG onset (Figure 5B, Table 4).

Moderate to strong correlations between normalised torque at 100 ms and normalised explosive-phase EMG_{0-100} were observed in CON_{FAST} ($r = 0.50$, $P = 0.067$), CON_{SLOW} ($r = 0.85$, $P<0.001$), ISO ($r = 0.64$, $P = 0.010$), ECC_{FAST} ($r = 0.78$, $P = 0.001$), and ECC_{SLOW} ($r = 0.59$, $P = 0.026$).

The influence of knee angle and velocity on EMG_{MVT} in this study is displayed in Figure S2 of the supplementary files, but is beyond the scope and primary aims of this manuscript.

Discussion

These results provide novel evidence that the ability to rapidly utilise the available MVT in explosive muscle contractions is affected by both contraction type and speed. Specifically, the proportion of MVT expressed during the rising phase (first 150 ms) of explosive contraction was greatest in the concentric, followed by isometric and eccentric contraction conditions, and greater at the faster than slower conditions (throughout concentric and in the later phase of eccentric) within the same type of contraction. The effects of contraction type and speed on explosive torque appeared to be indicative of muscle performance and not due to SEC-muscle interactions, as estimated explosive muscle force (accounting for the behavior of the SEC) was influenced by condition in an almost identical manner to explosive joint torque. Normalised explosive-phase EMG and neural efficacy (Voluntary:Evoked torque) were greater in the concentric and isometric conditions compared to the eccentric conditions, suggesting that differences in neuromuscular activation were the primary explanation for the observed effects of contraction type on normalised explosive torque and muscle force. However, there were no differences in normalised explosive-phase EMG and neural efficacy between speeds for the same type of contraction (i.e. CON_{FAST} vs CON_{SLOW}, or ECC_{FAST} vs ECC_{SLOW}), suggesting that the effect of speed on normalised explosive torque was not due to neuromuscular activation and may be an intrinsic property of contracting myofibres.

The ability to explosively utilise the available torque (i.e. %MVT) showed a consistent pattern of CON>ISO>ECC. Considering the individual time points on the rising torque-time curve, ISO was considerably lower than CON_{FAST} (-44 to -79%) and CON_{SLOW} (-16 to -55%) at 6 and 3 time points, respectively, but higher than ECC_{SLOW} (+45-94%) and ECC_{FAST} (+40-50%) at 4 and 2 time points, respectively. Moreover, mean normalised explosive torque for 25-150 ms was different, or had a tendency to be different, between 4 of the 5 conditions in the order: CON_{FAST}>CON_{SLOW}>ISO & ECC_{FAST}>ECC_{SLOW}, the only exception being ISO vs ECC_{FAST} which, were similar. These results show an effect of contraction type on the ability to rapidly utilise available MVT in explosive contractions, and support the findings of our earlier work which first reported greater normalised explosive torque in concentric followed by isometric and eccentric contractions (Tillin et al., 2012). However, our previous study only measured explosive torque during fast concentric and eccentric accelerations (±2000°.s^{-2}) eliciting high speeds (~140-425°.s^{-1}), whilst the current study also considered slow concentric and eccentric accelerations (±500˚.s^{-1}) that reached slower speeds (~45-125°.s^{-1}), and showed the effects of contraction type were further delineated by contraction speed. When only considering the fast vs. slow conditions within each type of contraction, normalised explosive torque was greater in CON_{FAST} than CON_{SLOW} at all measured time points (+49-118%), and greater in ECC_{FAST} than ECC_{SLOW} at 150 ms (+40%). Thus, it appears that within either concentric or eccentric explosive contractions, the ability to rapidly utilise the available MVT increases with contraction speed, although these effects were considerably greater in concentric conditions and only became apparent in the later phase of the eccentric conditions. Interestingly, available MVT was achieved in <150 ms from torque onset in the CON_{FAST} condition, but the proportion of available MVT achieved in the other conditions after 150 ms was only 73% (CON_{SLOW}), 61% (ISO), 59% (ECC_{FAST}), and 42% (ECC_{SLOW}). Thus, it appears that the available MVT can be achieved in less than half the time (>300 ms) previously proposed based on isometric contractions (Aagaard et al., 2002; Thorstensson et al., 1976), but only in "fast concentric" contractions.

Neural efficacy (Voluntary:Evoked torque) in CON_{FAST}, CON_{SLOW}, and ISO were more than double that of the eccentric conditions, and CON_{FAST} was 40% greater than ISO. This provides evidence that voluntary neuromuscular activation in the explosive phase of contraction was influenced by the type of contraction, and was greatest in concentric, followed by isometric, and eccentric conditions, which supports the results of our earlier study showing similar effects (Tillin et al., 2012). Normalised explosive-phase EMG at each measured time point was also greater (+122-144% for EMG_{0-150}) in CON_{FAST}, CON_{SLOW}, and ISO compared with either ECC_{SLOW} or ECC_{FAST}, providing evidence consistent with the neural efficacy data, of lower neuromuscular activation during the rising torque-time curve of eccentric explosive contractions. These differences in neuromuscular activation shown by neural efficacy and explosive-phase EMG likely contribute to the improved ability to rapidly utilise MVT in concentric, followed by isometric and eccentric explosive contractions. Moreover, this is the first study to show a correlation between early phase neuromuscular activation (EMG_{0-100}) and explosive torque within different contractile conditions (r = 0.50-0.85), which had previously only been reported for isometric or isoinertial concentric conditions (de Ruiter et al., 2007; Del Balso and Cafarelli, 2007; Folland et al., 2014; Hernandez-Davo et al., 2015). Thus, neuromuscular activation appears to be an important determinant of both between and within contraction-type differences in normalised explosive torque.

Previous research suggests neuromuscular activation at MVT is influenced by contraction type in a similar way to what we have observed for the explosive phase of contraction (i.e., greater in both concentric and isometric than eccentric contractions (Aagaard, 2018; Aagaard et al., 2000; Duchateau and Enoka, 2008; Pain and Forrester, 2009; Westing et al., 1991). Despite these similar effects of contraction type on neuromuscular activation for both explosive and MVT (plateau) phases of contractions, the current study is the first to show that neuromuscular activation during the explosive phase of contraction does not scale to neuromuscular activation in the MVT phase, when comparing the different types of contraction. Specifically, explosive-phase EMG exceeded EMG_{MVT} (>100% EMG_{MVT}) <75 ms after EMG onset in CON_{FAST}, CON_{SLOW}, and ISO, but had only reached 77% and 64% of EMG_{MVT} after 150 ms in ECC_{FAST} and ECC_{SLOW}, respectively. High motor unit discharge rates (60-200 Hz) have been recorded for the first 2-6 discharges of explosive isometric contractions (Desmedt and Godaux, 1977; Van Cutsem and Duchateau, 2005), followed by a decline to a rate similar to that expected at MVT (~30-60 Hz (Kamen and Knight, 2004; Pucci et al., 2006; Van Cutsem et al., 1998)). Assuming this occurred in the isometric and concentric conditions of the present study, it might explain why explosive-phase EMG exceeded EMG_{MVT} within 75 ms, in those conditions. In contrast, the slower rate of rise in neuromuscular activation towards EMG_{MVT} in the eccentric conditions suggests an attenuated increase in motor unit recruitment and/or discharge rate compared with isometric and concentric conditions, possibly as a protective mechanism against high rates of eccentric loading that might cause injury. Explosive-phase EMG remained ~120-130% of EMG_{MVT} in the concentric contractions, but declined after 75-100 ms in ISO to plateau at 100% EMG_{MVT}, resulting in significant differences between CON_{FAST} and ISO after 150 ms. Thus, it appears that the high initial neuromuscular activation persists for longer (>150 ms) during the explosive phase of fast concentric contractions. The mechanism of this effect is unclear, but may be associated with lower absolute tension and thus reduced inhibitory feedback from mechano-sensory organs such as the Golgi-tendons, in the later phase of concentric compared to isometric explosive contractions (Figure 2C and 3C). Interestingly, MVT was exceeded after 150 ms in CON_{FAST} (i.e., 108% MVT), which may be due to explosive-phase EMG remaining >100% EMG_{MVT} after MVT was achieved at ~139 ms, and suggests fast explosive concentric contractions facilitate higher peak torques than the pre-loaded concentric MVCs completed at similar angular velocities. Whilst these mechanisms and their functional relevance require further investigation, the current study provides novel evidence of distinct neuromuscular activation patterns throughout the explosive phase of different types of contraction.

In contrast to the effect of contraction type, neuromuscular activation did not appear to explain the effects of contraction speed on explosive torque within concentric and eccentric contractions. No differences were observed in either neural efficacy or normalised explosive-phase EMG at any measured time point between CON_{FAST} and CON_{SLOW} despite 49-118% greater expression of available MVT throughout CON_{FAST}. Likewise, there were no differences in neural efficacy or normalised explosive-phase EMG at any time point between ECC_{FAST} and ECC_{SLOW}, despite a 40% greater utilisation of the available MVT after 150 ms in ECC_{FAST}. Therefore, mechanisms independent of neuromuscular activation (i.e., intrinsic to the muscle-SEC unit) may contribute to greater normalised explosive torques at fast vs slow speeds within the same type of contraction.

To investigate the influence of muscle-SEC interaction explanations for these effects, we entered our joint kinetic and kinematic data into a muscle model which estimated muscle forces, fibre lengths, and contraction velocities, and found clear evidence of uncoupling between joint and muscle dynamics that was variable between conditions. Specifically, the changes in muscle fibre length, and thus velocity, per degree of knee angle change was different for all conditions, but greater in the concentric than the corresponding eccentric conditions, likely due to longer starting muscle-tendon unit lengths and greater initial absolute muscle forces (Figure 3), bringing SEC closer to maximum strain in the concentric conditions. There was also muscle shortening throughout the ISO condition, causing a contractile velocity profile similar in shape though smaller in magnitude to CON_{SLOW}. Despite this uncoupling of joint and muscle dynamics, the effects of contraction type and speed on normalised explosive muscle force were virtually identical to the observed effects on normalised explosive torque, with the proportion of available MVF expressed during the different conditions generally in the order: CON_{FAST}>CON_{SLOW}>ISO>ECC_{FAST}>ECC_{SLOW}. It is of note that normalised explosive forces at 75-150 ms were similar for CON_{SLOW} and ISO, despite normalised explosive torques being greater in CON_{SLOW}. This might be expected when considering that contractile conditions on a muscle level in ISO are concentric, and the differences in shortening muscle velocity between ISO and CON_{SLOW} were small (Figure 3B). It is also of note that differences in normalised explosive force between ECC_{FAST} and ECC_{SLOW} were only observed after 150 ms, which is similar to normalised explosive torque. Given the almost identical results for joint-torque and muscle-force data, we can deduce that muscle-SEC interactions have not caused the observed effects of contraction type and speed.

The effects of contraction speed on normalised explosive torque/force within the different types of contraction could not be explained by either neuromuscular activation or muscle-SEC interactions (see above), and hence appear to reflect an intrinsic property of contracting muscle. In mixed whole muscle, fast twitch fibres provide an increasingly greater contribution to overall contractile force production as velocity increases (MacIntosh et al., 1993). Therefore, in the current study, the contribution of fast twitch fibres to net force output would have been greatest in CON_{FAST} followed by CON_{SLOW} and ISO, and greater in ECC_{FAST} than ECC_{SLOW}. In isometric conditions, fast twitch fibres have an 8-fold higher rate constant for tension development and thus a steeper RFD and faster time to peak tension than slow twitch fibres (Metzger and Moss, 1990). Assuming this translates to a faster time to available peak force in concentric and eccentric conditions, it may explain why a greater proportion of available MVF was expressed during the fast compared with slow conditions (i.e., CON_{FAST}>CON_{SLOW}>ISO, and ECC_{FAST}>ECC_{SLOW}), where fast twitch fibres provide a greater contribution to net force output. The effects of contraction speed on explosive torque/force were observable throughout the concentric contractions, but only in the later phase of the eccentric contractions. This may be due to a slower rate of rise in neuromuscular activation in the eccentric conditions (<80% EMG_{MVT} even after 150 ms), as the determinants of normalised explosive torque are predominantly neural, rather than contractile, in the early phase of contraction whilst neuromuscular activation is low (Folland et al., 2014).

There are some potential limitations of our methods. It is conceivable contractile history may have caused force depression and enhancement in the pre-loaded concentric and eccentric MVCs, respectively, which could have influenced the normalised explosive torques and may explain why MVT was exceeded in CON_{FAST}; however, we feel this is unlikely for the following reasons. (1) Force enhancements and depressions are considerably reduced/abolished when eccentric and concentric contractions are performed reciprocally (Fortuna et al., 2017;

Herzog and Leonard, 2000; Seiberl et al., 2015), as in our MVC protocols. (2) MVT was not exceeded in CON_{SLOW} where torques were normalised to low-velocity, high-torque MVCs expected to induce considerably greater force depression than the MVCs used for normalising CON_{FAST} (Herzog and Leonard, 1997). Another potential limitation of note, is that there are likely to be errors in the muscle fibre forces/lengths/velocities estimated by our muscle model, which relied on a number of assumptions based on literature data, and did not account for potential changes in gearing (Dick and Wakeling, 2017), SES stiffness (Raiteri et al., 2018), or pennation angle (Massey et al., 2015) throughout the contraction. However, many errors will be similar for estimated explosive and maximum voluntary forces and thus largely controlled for when normalising explosive to MVF. Furthermore, the purpose of the model was to isolate the influence of series elasticity on the effects of contraction speed and type on normalised explosive torque, and given the SEC in our model had no influence on these effects, it seems unlikely small adjustments in SEC characteristics will change this observation. Nevertheless, future research may want to consider whether changes in gearing, SES stiffness and pennation angle characteristics during contraction contribute to the effects of contraction speed and type on the ability to rapidly utilise the available MVT.

In conclusion, the present results provide novel evidence that the ability to rapidly utilise the available MVT in explosive contractions is not only influenced by contraction type (concentric>isometric>eccentric), but is greater at fast compared to slow contraction speeds within the same type of contraction. Using Hill-type force-velocity modeling similar effects were found for isolated muscle fiber performance, indicating limited influence of the SEC. The effects of contraction type on normalised explosive torque appeared largely due to distinct neuromuscular activation profiles during the explosive phase of contraction. In contrast, the effects of contraction speed within the same type of contraction may reflect an increasing reliance on fast-twitch fibres at high speeds.

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Competing Interests

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Figures

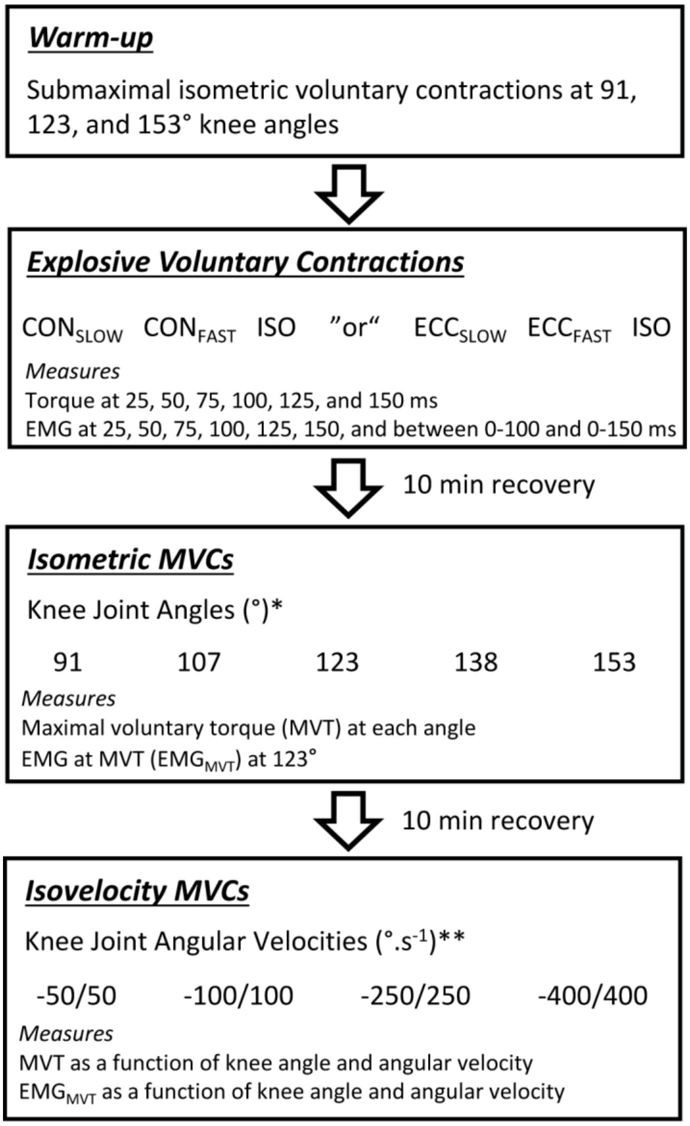


Figure 1. The protocol of explosive and maximal voluntary contractions (MVCs) completed in two separate measurement sessions, and the key measures obtained. The two measurement sessions were completed in a random order. Explosive voluntary contractions

were performed in five conditions across the two sessions; concentric slow (CON_{SLOW}) and fast (CON_{FAST}) in a random order, or eccentric slow (ECC_{SLOW}) and fast (ECC_{FAST}) in a random order, before isometric at a 123° knee angle (ISO). * randomised order. ** Reciprocal isovelocity MVCs (eccentric – concentric) were completed in the order of slowest to fastest before repeating in reverse order. All MVCs were performed in both measurement sessions.

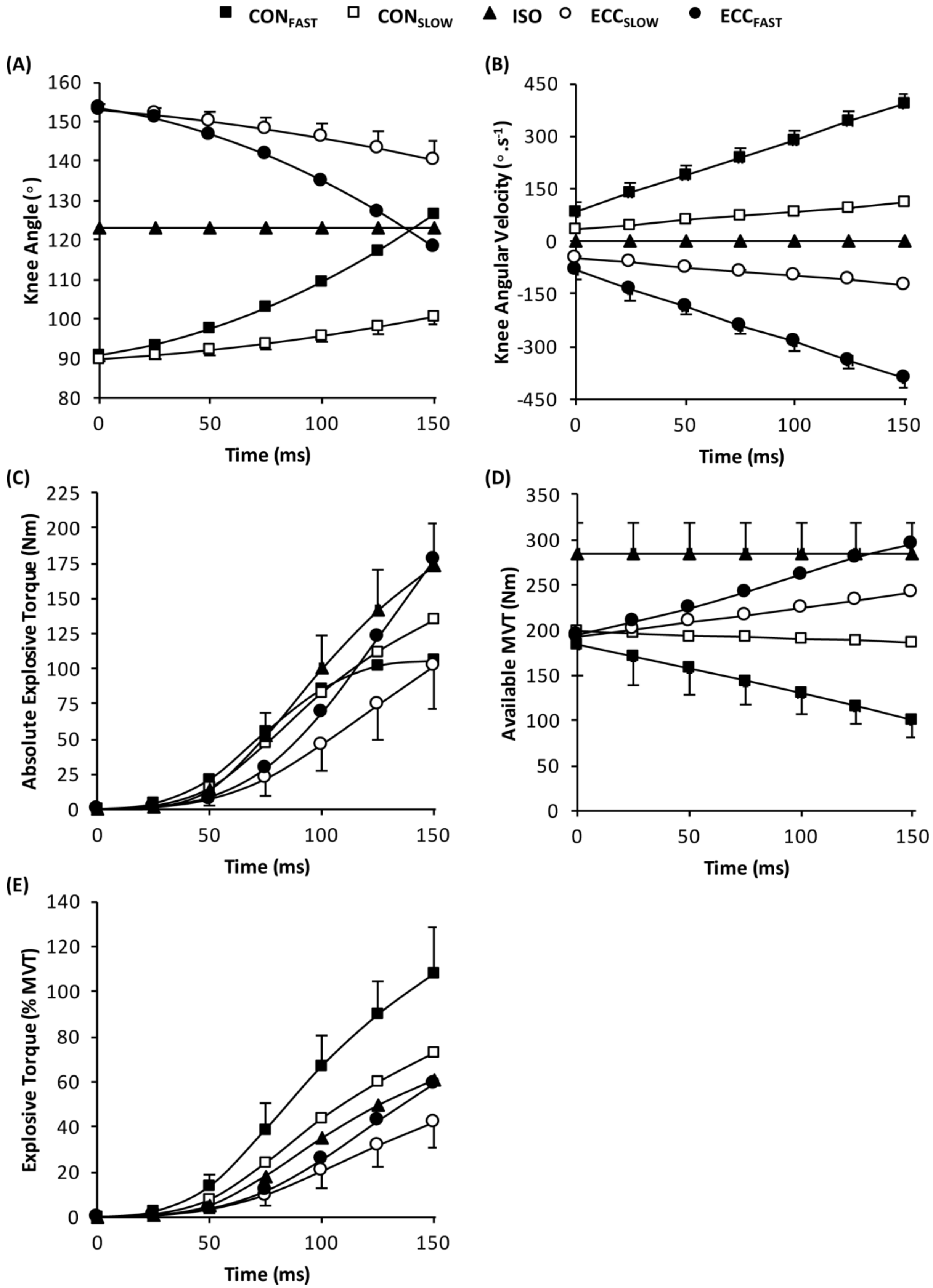

CON$_{FAST}$
CON$_{SLOW}$
ISO
ECC$_{SLOW}$
ECC$_{FAST}$
(A)
Knee Angle (°)
Time (ms)
(B)
Knee Angular Velocity (°.s^{-1})
Time (ms)
(C)
Absolute Explosive Torque (Nm)
Time (ms)
(D)
Available MVT (Nm)
Time (ms)
(E)
Explosive Torque (% MVT)
Time (ms)

Figure 2. Knee extension angle (A), angular velocity (B), absolute explosive torque (C), maximal voluntary torque (MVT) available at that knee angle and angular velocity (D), and explosive torque normalised to available MVT (E), during the first 150 ms of explosive voluntary contractions performed in five conditions; concentric or eccentric at a constant acceleration of 500°.s^{-2} (CON_{SLOW} or ECC_{SLOW}) or 2000°.s^{-2} (CON_{FAST} and ECC_{FAST}), and isometric (ISO) at a 123° knee angle. Data are mean (n = 15) with SD error bars on the highest and lowest conditions.

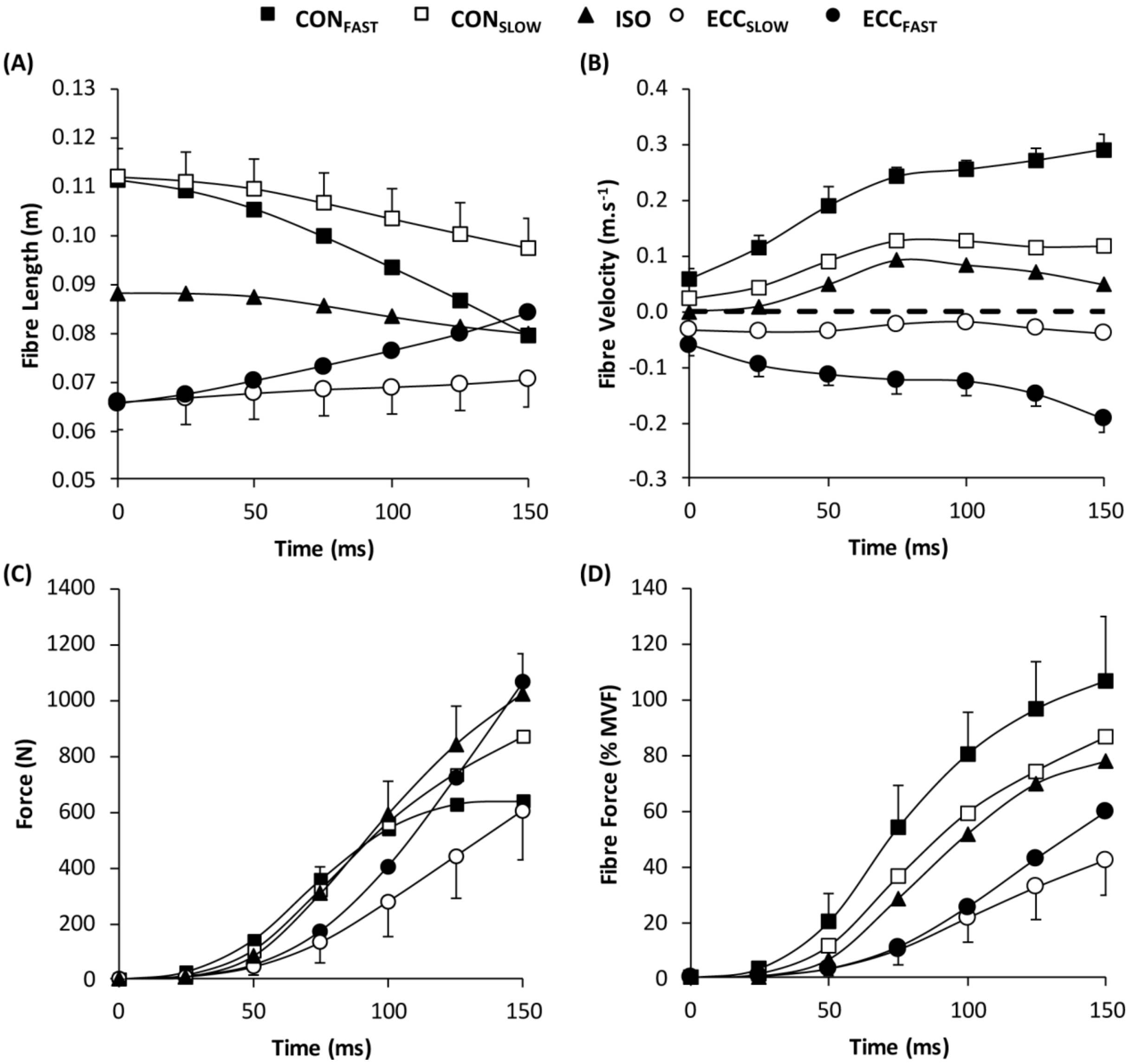


Figure 3. Estimated knee extensor muscle fibre length (A), velocity (B), absolute force (C), and force normalised (D) to muscle fibre length and velocity specific maximal voluntary force (MVF), during the first 150 ms of explosive voluntary contractions performed in five conditions: concentric or eccentric at a constant acceleration of 500°.s^{-2} (CON$_{SLOW}$ or ECC$_{SLOW}$) or 2000°.s^{-2} (CON$_{FAST}$ and ECC$_{FAST}$), and isometric (ISO) at a 123° knee angle. Data are mean (n = 15) with SD error bars on the highest and lowest conditions.

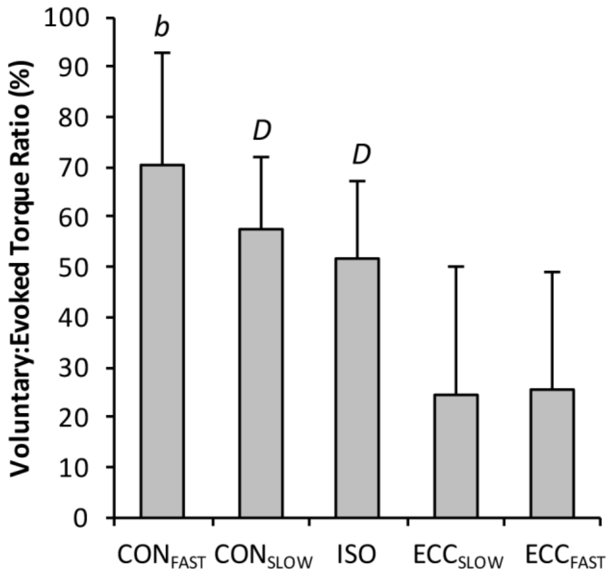


Figure 4. The ratio of explosive Voluntary:Evoked octet knee extensor torque recorded at 75 ms from torque onset during contractions performed in five conditions; concentric or eccentric at a constant acceleration of 500°.s^{-2} (CON_{SLOW} or ECC_{SLOW}) or 2000°.s^{-2} (CON_{FAST} and ECC_{FAST}), and isometric (ISO) at a 123° knee angle. Data are mean ± SD (n = 15). Paired differences are denoted by capital (P<0.01) or lowercase (P<0.05) letters; *B* (greater than ISO, ECC_{FAST}, and ECC_{SLOW}), and *D* (greater than ECC_{FAST}, and ECC_{SLOW}).

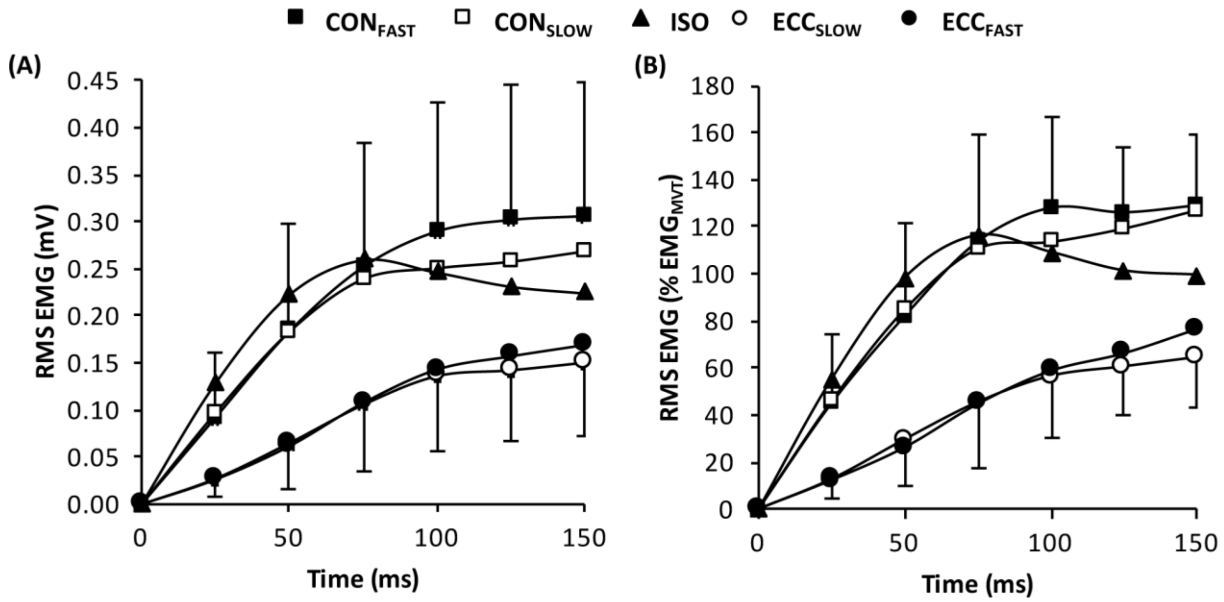


Figure 5. Quadriceps RMS EMG amplitude in absolute terms (A; pre-amplification) or normalised (B) to knee angle and angular velocity specific RMS EMG at MVT (EMGMVT), recorded at 25-ms intervals from EMG onset, during explosive contractions in five conditions; concentric or eccentric at a constant acceleration of 500°.s-2 (CON$_{SLOW}$ or ECC$_{SLOW}$) or 2000°.s-2 (CON$_{FAST}$ and ECC$_{FAST}$), and isometric (ISO) at a 123° knee angle. Data are mean (n = 14) with SD error bars on the highest and lowest conditions.

Tables

Table 1. The knee extension kinematics of five separate constant-acceleration conditions in which explosive voluntary contractions were performed.

	CON_{SLOW}	CON_{FAST}	ECC_{SLOW}	ECC_{FAST}	ISO
Acceleration ($°.s^{-2}$)	500	2000	-500	-2000	0
Start Angle (°)	89	89	156	156	123
Finish Angle (°)	140	140	105	105	123
Peak Velocity ($°.s^{-1}$)	225	450	-225	-450	0
Acceleration time (ms)	450	225	450	225	—

Table 2. Knee angle and angular velocity at voluntary EMG onset, voluntary torque onset, and evoked torque onset, during explosive voluntary or evoked knee extensions performed in four separate conditions; concentric or eccentric at a constant acceleration of $500°.s^{-2}$ (CON_{SLOW} or ECC_{SLOW}) or $2000°.s^{-2}$ (CON_{FAST} and ECC_{FAST}). Data are means ± SD (n = 15, torque onsets; n = 14, EMG onsets).

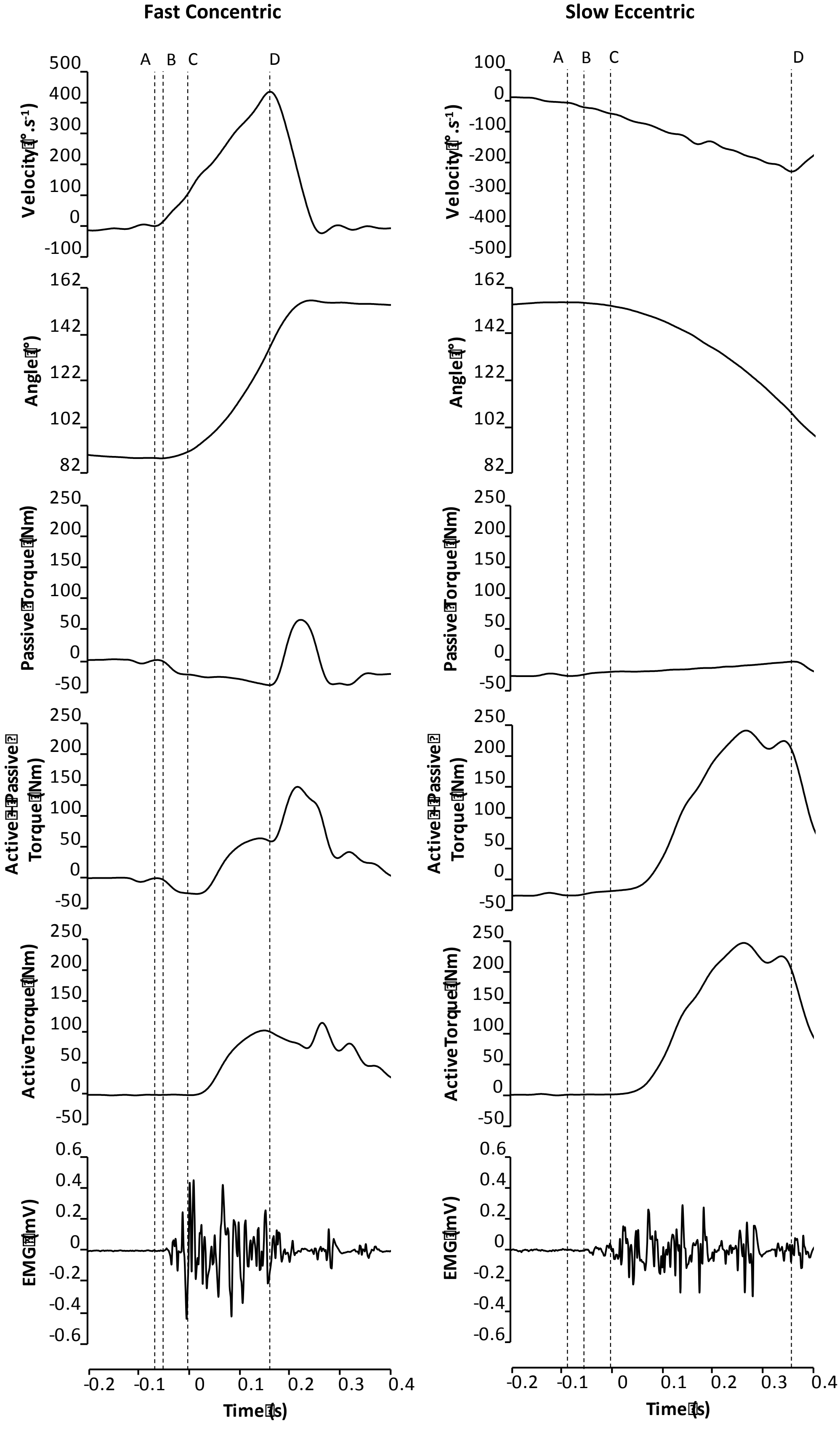
	Angle (°)			Velocity ($°.s^{-1}$)		
	Voluntary EMG onset	Voluntary torque onset	Evoked torque onset	Voluntary EMG onset	Voluntary torque onset	Evoked torque onset
CON_{SLOW}	88.9 ± 0.4	89.9 ± 0.8	92.3 ± 0.7	9.7 ± 11.1	33.5 ± 11.8	59.8 ± 10.9
CON_{FAST}	88.8 ± 0.2	90.7 ± 1.1	93.2 ± 1.3	3.4 ± 13.7	85.0 ± 25.5	133 ± 25.8
ECC_{SLOW}	155 ± 0.5	153 ± 1.4	152 ± 0.7	-11.9 ± 9.9	-46.3 ± 12.6	-60.3 ± 10.5
ECC_{FAST}	155 ± 0.3	154 ± 1.0	152 ± 1.4	-2.4 ± 14.0	-80.6 ± 25.8	-122 ± 28.9

Table 3. Normalised knee extensor torque at 25-ms intervals from torque onset (and the mean of these time points) during explosive voluntary contractions performed in five conditions; concentric or eccentric at a constant acceleration of 500°.s^{-2} (CON_{SLOW} or ECC_{SLOW}) or 2000°.s^{-2} (CON_{FAST} and ECC_{FAST}), and isometric (ISO) at a 123° knee angle. Data are presented as a percentage of the maximal voluntary capacity for torque production available at that angle and angular velocity i.e. knee angle and angular velocity specific maximal voluntary torque (MVT). Mean ± SD (n = 15). Paired differences are denoted by capital (P<0.01) or lowercase (P<0.05) letters; *A* (greater than all other conditions), *B* (greater than ISO, ECC_{FAST}, and ECC_{SLOW}), *C* (greater than ISO and ECC_{SLOW}), *D* (greater than ECC_{FAST}, and ECC_{SLOW}), and *E* (greater than ECC_{SLOW}).

Time (ms)	Torque (% MVT)				
	CON_{FAST}	CON_{SLOW}	ISO	ECC_{SLOW}	ECC_{FAST}
25z	2.4 ± 1.2[a]	1.1 ± 0.4[c]	0.5 ± 0.2z	0.7 ± 0.3z	1.0 ± 0.5z
50z	14 ± 6.5[a]	7.6 ± 2.7[b]	4.9 ± 1.4z	3.4 ± 2.1z	3.7 ± 2.1z
75 z	39 ± 11[A]	24 ± 7.4[D]	18 ± 4.4[D]	9.8 ± 4.8z	12 ± 5.9z
100z	67 ± 13[A]	44 ± 10[D]	35 ± 5.5[d]	20 ± 7.4z	25 ± 11z
125z	90 ± 15[A]	60 ± 10[d]	49 ± 6.1[E]	31 ± 9.1z	43 ± 15z
150z	108 ± 21[A]	73 ± 9.1[c]	61 ± 6.2[E]	42 ± 11z	59 ± 17[E]
Meanz	53 ± 10[A]	35 ± 6.3[b]	28 ± 3.8[E]	18 ± 5.3z	24 ± 8.2z

Table 4. Knee extensor RMS EMG amplitude as a percentage of knee angle and angular velocity specific RMS EMG at MVT (EMG_{MVT}), recorded at 25-ms intervals from EMG onset, and the mean between 0-150 ms (EMG_{0-150}), during explosive contractions performed in five conditions; concentric or eccentric at a constant acceleration of 500°.s^{-2} (CON_{SLOW} or ECC_{SLOW}) or 2000°.s^{-2} (CON_{FAST} and ECC_{FAST}), and isometric (ISO) at a 123° knee angle. Data are mean ± SD (n = 14). Paired differences are denoted by capital letters (P<0.01); *B* (greater than ISO, ECC_{FAST}, and ECC_{SLOW}), *D* (greater than ECC_{FAST}, and ECC_{SLOW}), and *E* (greater than ECC_{SLOW}).

Time (ms)	Explosive-Phase Knee Extensor EMG (% EMG_{MVT})				
	CON_{FAST}	CON_{SLOW}	ISO	ECC_{SLOW}	ECC_{FAST}
25z	45 ± 29^{D}	46 ± 25^{D}	55 ± 19^{D}	12 ± 10	13 ± 7.7z
50z	82 ± 40^{D}	85 ± 38^{D}	98 ± 27^{D}	26 ± 18z	29 ± 20z
75 z	114 ± 45^{D}	111 ± 39^{D}	116 ± 26^{D}	45 ± 31z	45 ± 28z
100z	128 ± 39^{D}	114 ± 30^{D}	109 ± 23^{D}	59 ± 31z	56 ± 26z
125z	126 ± 27^{D}	120 ± 23^{D}	101 ± 21^{D}	67 ± 25z	60 ± 20z
150z	129 ± 30^{B}	127 ± 35^{D}	99 ± 20^{E}	77 ± 25z	64 ± 21z
EMG_{0-150z}	95 ± 29 ^{D}	92 ± 27^{D}	91 ± 19^{D}	41 ± 19z	39 ± 17z



Fast Concentric
Slow Eccentric
A
B
C
D
Velocity (°.s-1)
Angle (°)
Passive Torque (Nm)
Active + Passive Torque (Nm)
Active Torque (Nm)
EMG (mV)
Time (s)

Figure S1. Knee angular velocity, angle, extension torque, and vastus lateralis EMG data, collected during explosive voluntary contractions performed in an isokinetic dynamometer in two conditions; fast concentric (left column) and slow eccentric (right column). In each condition the crank arm accelerated at a constant 2000º.s^{-2} (fast) or -500º.s^{-2} (slow) from a stationary angle (dashed line A) of 89º (concentric) or 156º (eccentric) to peak velocities (dashed line D) of 450º.s^{-1} (fast) or -225º.s^{-1} (slow), before decelerating to stop at the opposite end of the range of motion. Concentric slow and eccentric fast conditions were also completed, though data are not presented here. Participants were instructed to push as "fast and hard" as possible at the start of the acceleration phase. Note, EMG onset (dashed line B) typically occurred soon after the start of the acceleration phase, and active torque onset (dashed line C) after ~50 ms (concentric) or ~70 ms (eccentric) from EMG onset. Active torque was determined by subtracting passive torque measured whilst the participant remained voluntarily passive, from the torques (active + passive) measured during the explosive voluntary contraction. Trials were only considered valid where active torque onset occurred after 20 ms of acceleration (concentric and eccentric conditions), and before 75 ms of acceleration (for fast conditions only). The 20-ms threshold was an attempt to align active onsets with those occurring during evoked involuntary contractions completed during the same conditions to assess neural efficacy. The 75-ms cut-off ensured there was a minimum of 150 ms of explosive contraction before peak velocity in the fast conditions where acceleration lasted for 225 ms. The 20 to 75-ms cut-offs also ensured similar angles but distinct velocities at active torque onset for fast and slow conditions within the same contraction type (See Table 2 in the manuscript). Data are post signal filtering and examples from only one contraction by the same participant in each condition.

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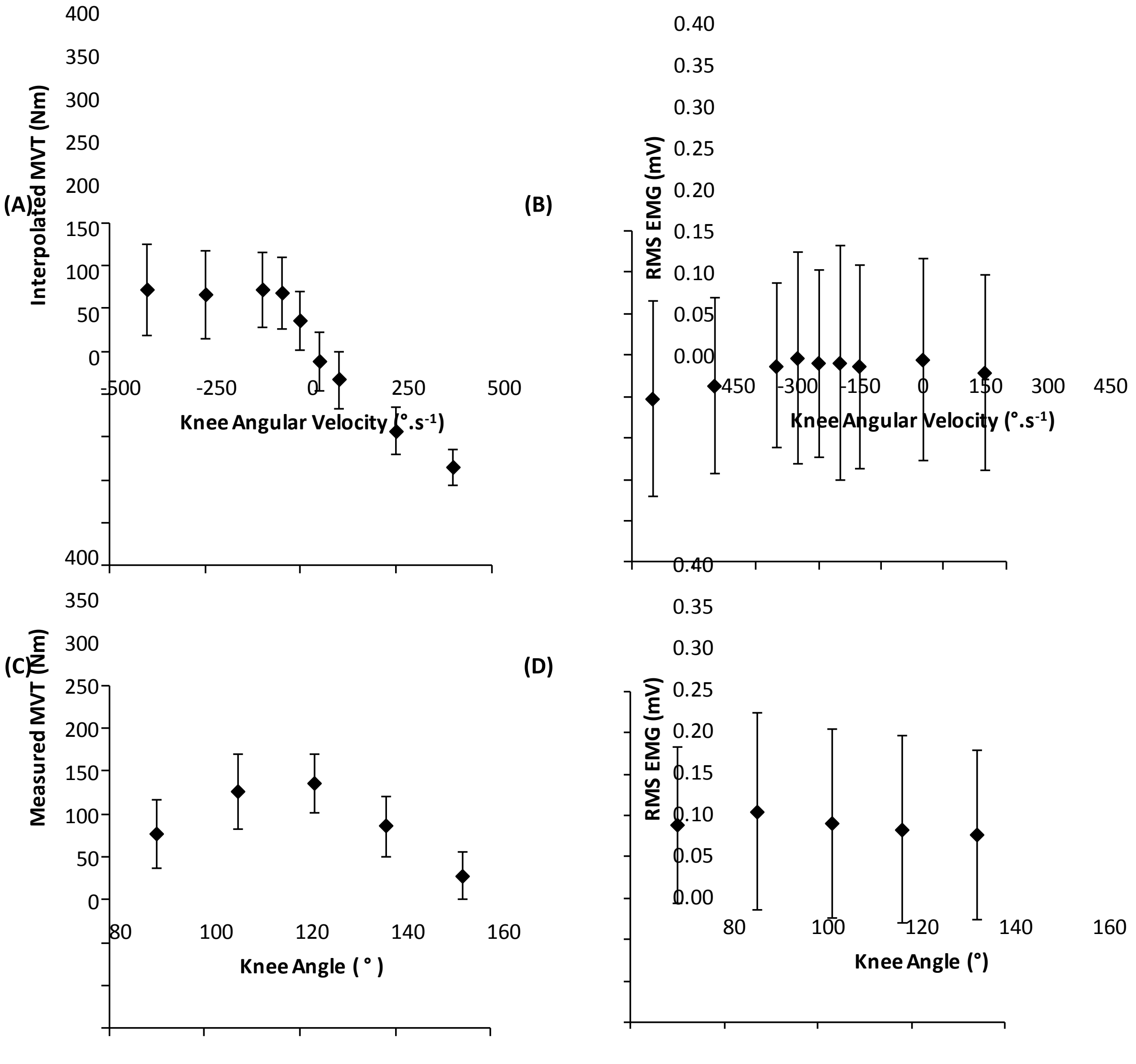

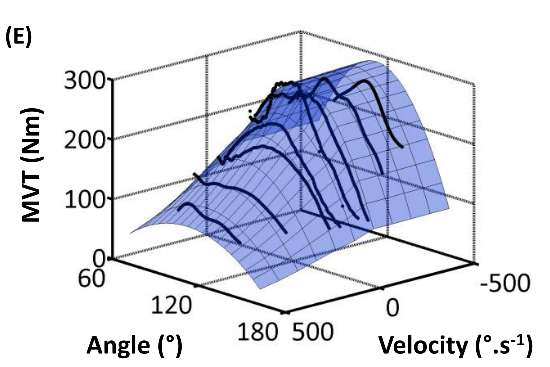

Figure S2. The influence of knee angular velocity and angle on knee extensor maximal voluntary torque (MVT) and EMG amplitude at MVT: (A) MVT at 123° for different velocities, interpolated from a 9-parameter dynamic MVT function (Yeadon *et al.*, 2006, Forrester *et al.*, 2011); (B) EMG recorded at 123° during the isovelocity maximal voluntary contractions (MVCs) used to establish the dynamic MVT function; (C) MVT and (D) EMG at MVT, measured during isometric MVCs at different angles; (E) the dynamic MVT function (3D surface) and the measured values used to establish the function (dark dots), for one participant. Data in A-D are averaged across two separate measurement sessions before calculating the mean ± SD for n = 15 (MVT) or n = 14 (EMG). EMG amplitudes are pre-amplification and averaged across the three superficial quadriceps muscles.

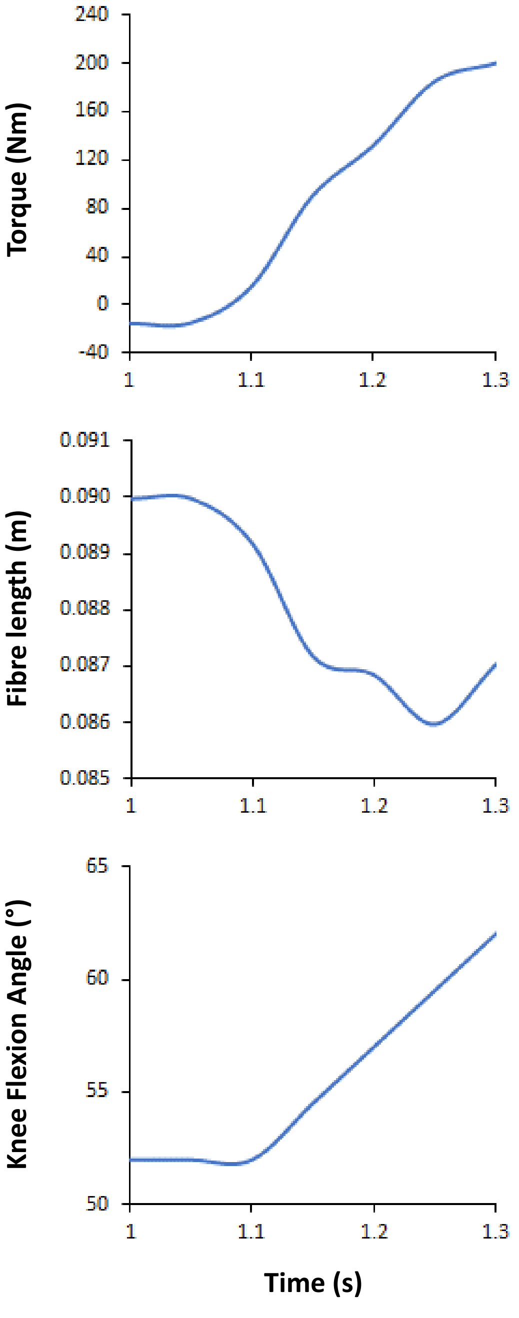

Figure S3: Hill-Type muscle model response with different initial mechanical conditions during eccentric-type contractions. Our muscle model did not detect fibre shortening during either of the eccentric conditions in our study (Figure 3 in the manuscript), which were performed without pre-load. However, previous studies have observed muscle fibre shortening during the early phase of eccentric knee extensor contractions performed with minimal pre-load (e.g., Hahn, 2018, Journal of Sport and Health Science, 7:275-281). Here we show the fibre length predicted from our Hill-type muscle model using knee joint torque and angle data similar to that of Hahn (2018). We used the average of subject-specific parameters from our study (e.g., mass, height, leg length, etc). The results provide good evidence that with similar mechanical conditions to Hahn (2018), our muscle model detects fibre shortening during the early phase of an eccentric-type contraction, consistent with Hahn's measurements. Further, the results suggest specific mechanical conditions (not present in our study) are required to elicit fibre shortening during eccentric-type contractions (see Figure 4S for suggestions).

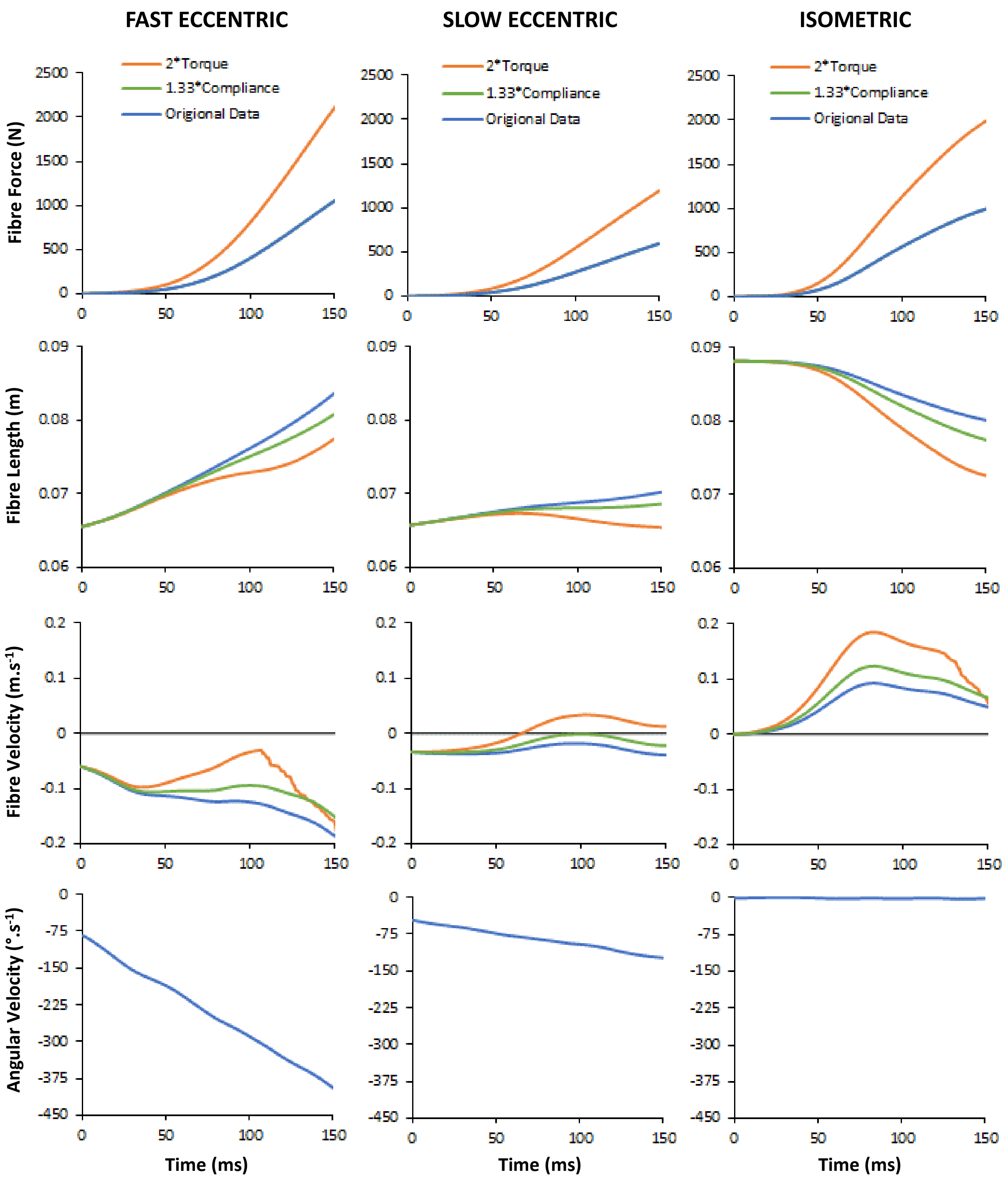

Figure S4: The influence of joint torque production, SEC compliance, and joint angular velocity on fibre behaviour estimated by our hill type muscle model. Here we show how doubling input torques shifted fibre velocity upwards in all conditions, causing a shortening velocity after 75 ms in the eccentric slow condition. Increasing series compliance by 33% (top end of normal variability of a similar cohort; Massey et al., 2017, Exp. Physiol, 102:448-461) also shifted fibre velocity upwards in all conditions. Angular velocity, and thus the rate of MTU strain was considerably greater in the eccentric fast than eccentric slow condition, which would explain why fibre lengthening velocity in the eccentric fast condition did not get close to positive (unlike the eccentric slow condition) when torque or compliance were increased. These results show that increasing torque input or SEC compliance had similar effects on all conditions (including the concentrics, though not presented). Furthermore, fibre shortening can occur during eccentric-type contractions but only when torque and/or SEC compliance are sufficiently high, and/or when MTU strain rate is sufficiently low. Data are mean of the four quadriceps heads for n = 15.

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