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RESEARCH ARTICLE

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

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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 deg s^{-2} (CON_{SLOW} and ECC_{SLOW}) and 2000 deg 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 the 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 conditions, 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, owing to neural and contractile mechanisms, respectively.

KEY WORDS: Concentric and eccentric contractions, Force–velocity relationship, Intrinsic contractile properties, Muscle strength, Neural activation, Rate of force development

INTRODUCTION

The functional capacity of the musculoskeletal system is limited by maximum muscle strength, typically measured as the maximum 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 versus slow speed contractions, and the opposite directions of concentric versus 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 a stationary position, 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 deg s^{-2}, eliciting fast speeds (i.e. explosive torques were measured between ∼140 and 425 deg 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 versus 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 – electromyography (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

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List of abbreviations

$\mathrm{CON_{FAST}}$	concentric fast
$\mathrm{CON_{SLOW}}$	concentric slow
$\mathrm{ECC_{FAST}}$	eccentric fast
$\mathrm{ECC_{SLOW}}$	eccentric slow
EMG	electromyography
$\mathrm{EMG_{0–100}}$	mean explosive-phase EMG between 0 and 100 ms
$\mathrm{EMG_{0–150}}$	mean explosive-phase EMG between 0 and 150 ms
$\mathrm{EMG_{MVT}}$	EMG amplitude at MVT
ISO	isometric
MVC	maximum voluntary contraction
MVF	maximum voluntary force
MVT	maximum voluntary torque
RF	rectus femoris
RMS	root mean square
SEC	series elastic component
VL	vastus lateralis
VM	vastus medialis

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 is 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 that could not be explained by neuromuscular activation were an intrinsic property of the contracting muscle fibres.

The aim of the prsesnt 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 with 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 written 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) owing to spurious EMG recordings for one of the measurement sessions.

Overview

Participants visited the laboratory at Loughborough University and gave their written informed consent 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 (Fig. 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 five contractile conditions as the explosive voluntary contractions (see below), in a random order after the isometric condition.

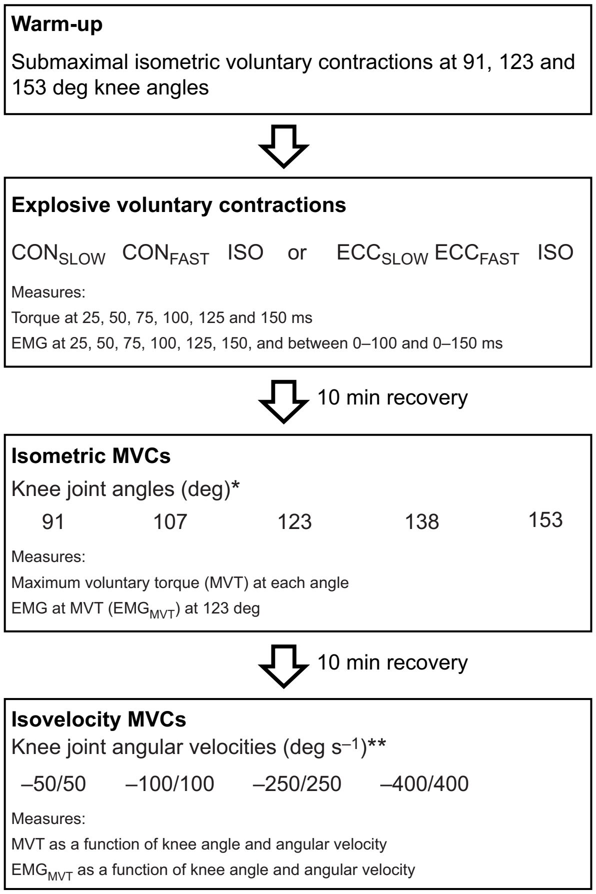

Fig. 1. The protocol of explosive and maximum voluntary contractions (MVCs) completed in two separate measurement sessions, and the key measures obtained. The two measurement sessions were completed in a random order. Explosive voluntary contractions were performed in five conditions across the two sessions: concentric slow ($\mathrm{CON_{SLOW}}$) and fast ($\mathrm{CON_{FAST}}$) in a random order, or eccentric slow ($\mathrm{ECC_{SLOW}}$) and fast ($\mathrm{ECC_{FAST}}$) in a random order, before isometric at a 123 deg 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.

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

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

	$\mathrm{CON_{SLOW}}$	$\mathrm{CON_{FAST}}$	$\mathrm{ECC_{SLOW}}$	$\mathrm{ECC_{FAST}}$	ISO
Acceleration (deg s^{-2})	500	2000	−500	−2000	0
Start angle (deg)	89	89	156	156	123
Finish angle (deg)	140	140	105	105	123
Peak velocity (deg s^{-1})	225	450	−225	−450	0
Acceleration time (ms)	450	225	450	225	–

isovelocities (eight velocities) during both sessions. Explosive torque and EMG amplitude recorded during the explosive contractions were normalised to knee joint angle- and angular velocity-specific maximum voluntary torque (MVT) and EMG amplitude at MVT ($\mathrm{EMG_{MVT}}$), 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 deg 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 the participant produced a near MVC at a knee angle (∼120 deg; 180 deg 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 a 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 sixth-order polynomial describing the passive torque–angle relationship, obtained from passively extending (from 70 to 170 deg) and flexing the knee at 10 deg 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. six single-differential EMG signals in total; Trigno, Delsys Inc., Boston, MA, USA). 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 ×909) 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 and 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 as hard’ as possible for ∼1 s with an emphasis on ‘fast’ – in five separate conditions: isometric at a knee angle of 123 deg (ISO), and concentric and eccentric at constant accelerations of 500 deg s^{-2} ($\mathrm{CON_{SLOW}}$ and $\mathrm{ECC_{SLOW}}$) and 2000 deg s^{-2} ($\mathrm{CON_{FAST}}$ and $\mathrm{ECC_{FAST}}$). In the concentric and eccentric conditions, the crank arm moved slowly (10 deg s^{-1}) through the range of motion (89–156 deg) to the start position for the acceleration phase (89 deg for concentric and 156 deg for eccentric conditions), from where it accelerated for 450 ms ($\mathrm{CON_{SLOW}}$ and $\mathrm{ECC_{SLOW}}$) or 225 ms ($\mathrm{CON_{FAST}}$ and $\mathrm{ECC_{FAST}}$), from 0 deg s^{-1} to a peak velocity of 450 deg s^{-1} ($\mathrm{CON_{FAST}}$), −450 deg s^{-1} ($\mathrm{ECC_{FAST}}$), 225 deg s^{-1} ($\mathrm{CON_{SLOW}}$) or −225 deg s^{-1} ($\mathrm{ECC_{SLOW}}$), before decelerating to a stop at the opposite end of the range of motion. Knee angle at peak velocity was 140 deg (concentric conditions) or 105 deg (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 are 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 are shown in Fig. S1.

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 the 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 three passive trials (zero active torque; used to correct active trials for shank weight and acceleration; see Fig. S1). ISO involved eight to 10 active trials (separated by ∼30 s).

Off-line analysis was completed using custom-developed programs in MATLAB (The MathWorks, Natick, MA, USA). The concentric and eccentric active trials were excluded from further analysis if: corrected baseline torque exceeded ±2 N m in the 2 s preceding active-torque onset; baseline torque in the 100 ms preceding active torque changed by >2.5 N m; and/or active-torque onset occurred earlier than 20 ms (all conditions) or later than 75 ms ($\mathrm{CON_{FAST}}$ and $\mathrm{ECC_{FAST}}$ only) into the acceleration phase. Trials in ISO were excluded if baseline torque in the 100 ms preceding active-torque onset changed by >1 N m. 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 deg, 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 six 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 root mean square (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 ($\mathrm{EMG_{MVT}}$) at the same knee angle and angular velocity conditions, in the same measurement session. For ISO, $\mathrm{EMG_{MVT}}$ was the measured value obtained at MVT during the MVCs at a 123 deg knee angle. For the concentric and eccentric conditions, $\mathrm{EMG_{MVT}}$ 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 deg $\mathrm{s^{-1}}$, $\mathrm{EMG_{MVT}}$ was linearly interpolated from MVCs performed at 100 and 250 deg $\mathrm{s^{-1}}$). Absolute and normalised explosive-phase EMG at each time point was averaged across the six EMG signals and across the three contractions at which it was measured, within each condition. Mean explosive-phase EMGs (absolute and normalised) between 0 and 100 ms, and between 0 and 150 ms were also obtained by averaging explosive-phase EMG at 25 and 75 ms ($\mathrm{EMG_{0-100}}$), and at 25, 75 and 125 ms ($\mathrm{EMG_{0-150}}$).

Maximum voluntary contractions

Participants completed a total of eight isometric MVCs (each separated by 3 min) across five different knee angles in a randomised order: two MVCs each at 91, 123 and 153 deg, and one MVC each at 107 and 138 deg. 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 an 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 two sets of four reciprocal (continuous) eccentric–concentric isovelocity MVC cycles, at each of four different isovelocities: 50, 100, 250 and 400 deg $\mathrm{s^{-1}}$. Following a submaximal familiarisation at each velocity, sets were completed in a counterbalanced order: one maximal set of four 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 four 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 and 170 deg, providing isovelocity ranges of approximately 77 deg (50 deg $\mathrm{s^{-1}}$), 75 deg (100 deg $\mathrm{s^{-1}}$), 62 deg (250 deg $\mathrm{s^{-1}}$) and 40 deg (400 deg $\mathrm{s^{-1}}$). 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 nine-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 nine parameters of the dynamic MVT function, via a simulated annealing algorithm (Corana et al., 1987). The weighted RMS difference between interpolated and measured values was on average 6±2 N m (∼1.3% of the greatest eccentric MVT). A separate dynamic MVT function was produced for each measurement session of each individual (see Fig. S2), 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. $\mathrm{EMG_{MVT}}$ 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 $\mathrm{EMG_{MVT}}$ 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 deg for 50, 100, 250 and 400 deg $\mathrm{s^{-1}}$, 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 for the present study. Thus, we utilised a Hill-type muscle model comprising contractile and SE components to remove the influence of an 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 and Arampatzis, 2006) at maximum isometric force (5400 N for vasti and 930 N for RF; Jacobs et al., 1996). Muscle model 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 were also entered into the muscle model to estimate dynamic maximum 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 three 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 (eight 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 deg. The anode (carbon rubber, 7×5 cm; EMS Physio Ltd, Greenham, UK) was taped down over the greater trochanter. Remaining at a 123 deg 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, three supramaximal octet contractions were evoked in each condition: the ISO condition (separated by 15–20 s), and at 3–4 deg into the acceleration phase of $\mathrm{CON_{FAST}}$, $\mathrm{CON_{SLOW}}$, $\mathrm{ECC_{FAST}}$ and $\mathrm{ECC_{SLOW}}$, 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 was compared across six 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 ($\mathrm{CON_{SLOW}}$, $\mathrm{CON_{FAST}}$, $\mathrm{ECC_{SLOW}}$, $\mathrm{ECC_{FAST}}$ 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 (five conditions×six 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 six time points; explosive-phase $\mathrm{EMG_{0-150}}$; 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 $\mathrm{EMG_{0-100}}$ within each condition.

RESULTS

Kinematics of the explosive contractions

Knee angle at torque onset in the explosive voluntary contractions was the same for $\mathrm{CON_{SLOW}}$ and $\mathrm{CON_{FAST}}$, and the same for $\mathrm{ECC_{SLOW}}$ and $\mathrm{ECC_{FAST}}$ (Table 2, Fig. 2A). $\mathrm{CON_{SLOW}}$ and $\mathrm{ECC_{SLOW}}$ displayed comparable changes in knee angle and angular velocity over the first 150 ms from torque onset, as did $\mathrm{CON_{FAST}}$ and $\mathrm{ECC_{FAST}}$ (Fig. 2A,B). Torque onset occurred slightly earlier (i.e. at slower velocities) in the acceleration phase of voluntary compared with 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 $\mathrm{CON_{SLOW}}$ and $\mathrm{CON_{FAST}}$, and identical for $\mathrm{ECC_{SLOW}}$ and $\mathrm{ECC_{FAST}}$ (Fig. 3A), which was 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

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 deg s^{-2} ($\mathrm{CON_{SLOW}}$ or $\mathrm{ECC_{SLOW}}$) or 2000 deg s^{-2} ($\mathrm{CON_{FAST}}$ and $\mathrm{ECC_{FAST}}$)

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

Data are means±s.d. (n=15, torque onsets; n=14, EMG onsets).

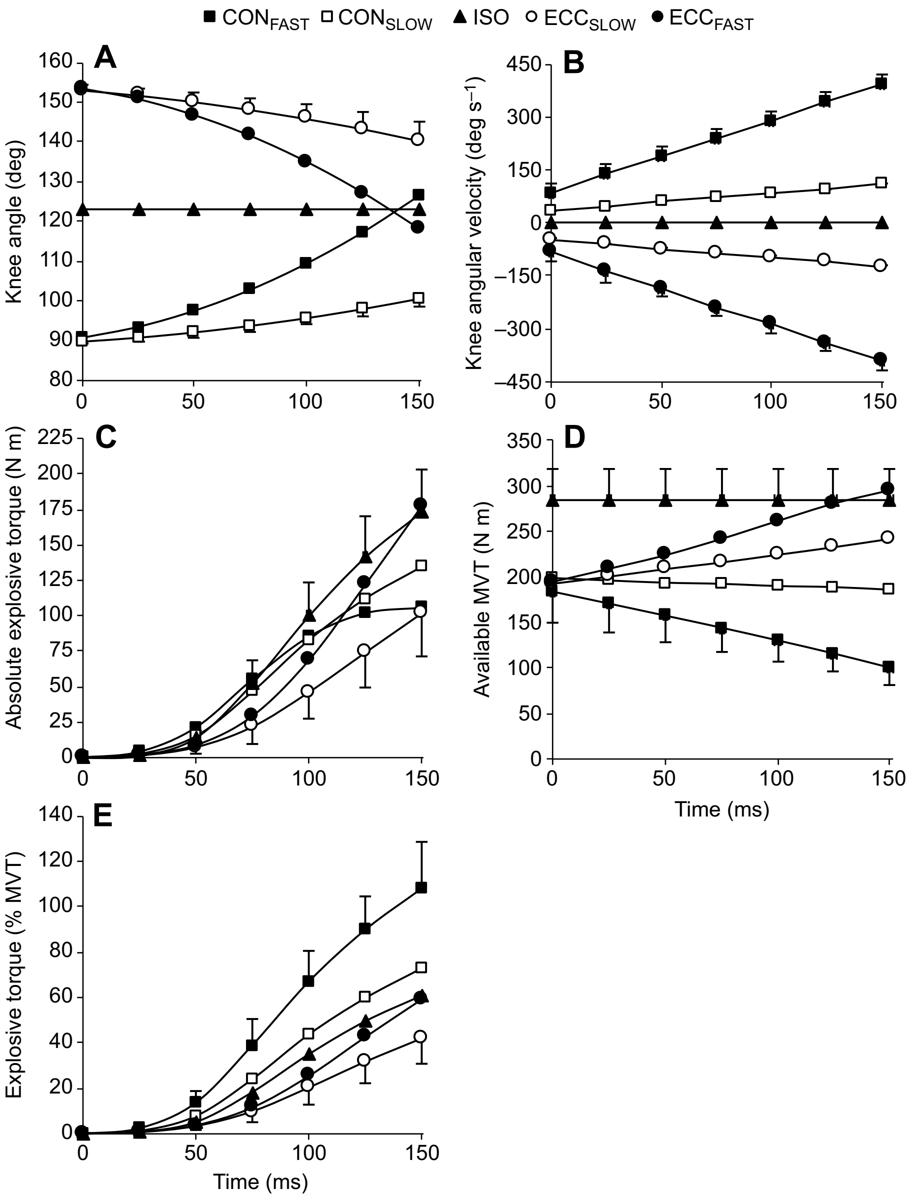

Fig. 2. Knee extension dynamics recorded during the first 150 ms of explosive voluntary contractions performed in five conditions: concentric or eccentric at a constant acceleration of 500 deg s^{-2} (CON$_{SLOW}$ or ECC$_{SLOW}$) or 2000 deg s^{-2} (CON$_{FAST}$ and ECC$_{FAST}$), and isometric (ISO) at a 123 deg knee angle. Knee extension angle (A), angular velocity (B), absolute explosive torque (C), maximum voluntary torque (MVT) available at that knee angle and angular velocity (D), and explosive torque normalised to available MVT (E). Data are means (*n*=15) with s.d. error bars on the highest and lowest conditions.

condition, and considerably greater in the concentric than in the corresponding eccentric conditions [CON$_{FAST}$ (−0.90±0.05 mm deg^{-1}) versus ECC$_{FAST}$ (−0.62±0.05 mm deg^{-1}), and CON$_{SLOW}$ (−1.23±0.16 mm deg^{-1}) versus ECC$_{SLOW}$ (−0.50±0.10 mm deg^{-1})]. The greater length changes resulted in greater peak velocity changes from force onset in the concentric than in the corresponding eccentric conditions [CON$_{FAST}$ (0.234±0.018 m s^{-1}) versus ECC$_{FAST}$ (0.135±0.025 m s^{-1}; $P<0.001$), and CON$_{SLOW}$ (0.113±0.013 m s^{-1}) versus ECC$_{SLOW}$ (0.034±0.014 m s^{-1}; $P<0.001$; Fig. 3A,B)]. There were changes in muscle fibre length in the ISO condition (Fig. 3A), resulting in a shortening velocity profile which was similar in shape but with lower velocities than that of CON$_{SLOW}$ (Fig. 3B). Examples of how varying the initial mechanical conditions and muscle model input characteristics influenced estimations of muscle fibre dynamics are presented in Figs S3 and S4.

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 (Fig. 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 deg) 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: MVT was high throughout ISO, which was performed near optimal knee angle; it decreased throughout CON as shortening velocity increased; and it 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 Fig. S2, but is beyond the scope and primary aims of this study.

When explosive torque was normalised to available MVT at the same knee angle and angular velocity (Fig. 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$_{SLOW}$.

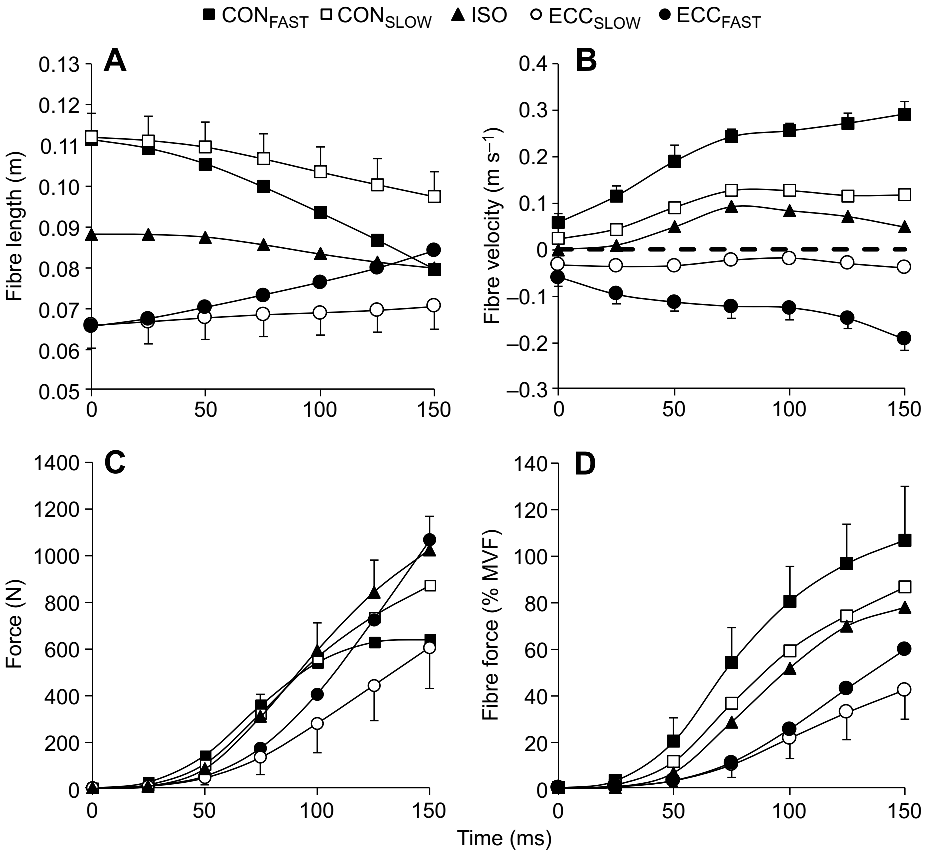

Fig. 3. Knee extensor muscle fibre dynamics estimated during the first 150 ms of explosive voluntary contractions performed in five conditions: concentric or eccentric at a constant acceleration of 500 deg s^{-2} (CON_{SLOW} or ECC_{SLOW}) or 2000 deg s^{-2} (CON_{FAST} and ECC_{FAST}), and isometric (ISO) at a 123 deg knee angle. Estimated muscle fibre length (A), velocity (B), absolute force (C) and force normalised (D) to muscle fibre length- and velocity-specific maximum voluntary force (MVF). Data are means (*n*=15) with s.d. error bars on the highest and lowest conditions.

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 percentage MVT achieved after 150 ms in the other conditions was only 73% (CON_{SLOW}), 61% (ISO), 59% (ECC_{FAST}) and 42% (ECC_{SLOW}; Fig. 2D, Table 3). Normalised torque averaged across the six 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; Fig. 2E).

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 deg s^{-2} (CON_{SLOW} or ECC_{SLOW}) or 2000 deg s^{-2} (CON_{FAST} and ECC_{FAST}), and isometric (ISO) at a 123 deg knee angle

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

Data are presented as a mean±s.d. (*n*=15) percentage of the maximum voluntary capacity for torque production available at that angle and angular velocity, i.e. knee angle- and angular velocity-specific maximum voluntary torque (MVT). Paired differences are denoted by uppercase (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}].

The effects of condition on estimated muscle forces (Fig. 3C,D) were comparable to the effects on knee extensor torques. Absolute muscle forces at each time point (Fig. 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 (Fig. 3D) were: greater in CON_{FAST} than in all other conditions (all measured time points, P≤0.046); greater in CON_{SLOW} than ISO at 25 ms (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 in 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 six measured time points was greater in CON_{FAST} (60±12% MVF) than in CON_{SLOW} (45±8.2% MVF; P=0.003), similar in CON_{SLOW} and ISO (39±4.4% MVF; P=0.340), greater in ISO than in ECC_{FAST} (24±8.7% MVF; P<0.001) and similar in ECC_{FAST} and ECC_{SLOW} (18±6.2% MVF; P=0.180).

Voluntary:evoked torque ratio

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 that in CON_{SLOW} (P=0.619), but ∼37% greater than that in ISO (P=0.026) and ∼175–190% greater than that in ECC_{FAST} and ECC_{SLOW} (P<0.001; Fig. 4). The voluntary:evoked ratio in CON_{SLOW} was similar to that in ISO (P=1.000) but ∼102–139% greater in both of these conditions

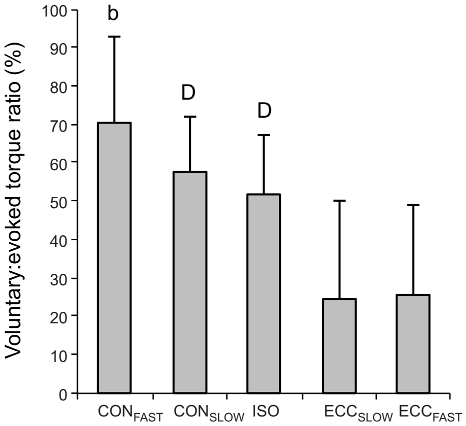

Fig. 4. The ratio of explosive voluntary:evoked octet knee extensor torque recorded at 75 ms from torque onset during contractions performed in five conditions: concentric or eccentric at a constant acceleration of 500 deg s^{-2} (CON$_{SLOW}$ or ECC$_{SLOW}$) or 2000 deg s^{-2} (CON$_{FAST}$ and ECC$_{FAST}$), and isometric (ISO) at a 123 deg knee angle. Data are means ±s.d. (*n*=15). Paired differences are denoted by uppercase ($P<0.01$) or lowercase ($P<0.05$) letters [b, greater than ISO, ECC$_{FAST}$ and ECC$_{SLOW}$; D, greater than ECC$_{FAST}$ and ECC$_{SLOW}$].

compared with either of the eccentric conditions ($P\leq0.005$; Fig. 4). There was no difference between ECC$_{FAST}$ and ECC$_{SLOW}$ for the voluntary:evoked ratio (P=1.000; Fig. 4).

Explosive-phase EMG

The effects of condition on explosive-phase EMG were similar for absolute (Fig. 5A) and normalised (normalised to knee angle- and angular velocity-specific EMG$_{MVT}$) EMG data (Fig. 5B). 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; Fig. 5B, Table 4), and more than twice as high in all three of these conditions (+120–141%; $P\leq0.001$) compared with for ECC$_{FAST}$ and ECC$_{SLOW}$, with no differences between ECC$_{FAST}$ and ECC$_{SLOW}$ (P=1.000; Fig. 4B, Table 4). In the concentric and isometric conditions, explosive-phase EMG exceeded EMG$_{MVT}$ after <75 ms from EMG onset (Fig. 5B, Table 4), continuing to rise in CON$_{FAST}$ and CON$_{SLOW}$ (to 127–129% EMG$_{MVT}$), but not ISO (Fig. 5B, Table 4). As a result, explosive-phase EMG in CON$_{FAST}$ tended to be greater than that in ISO at 125 ms (P=0.097) and was significantly greater at 150 ms (P=0.008; Fig. 5B, 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 (Fig. 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 Fig. S2, but is beyond the scope and primary aims of this study.

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 conditions, followed by the isometric and eccentric contraction conditions, and greater in the faster than in 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 muscle–SEC 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 with 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$_{FAST}$ versus CON$_{SLOW}$, or ECC$_{FAST}$ versus 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 six and three time points,

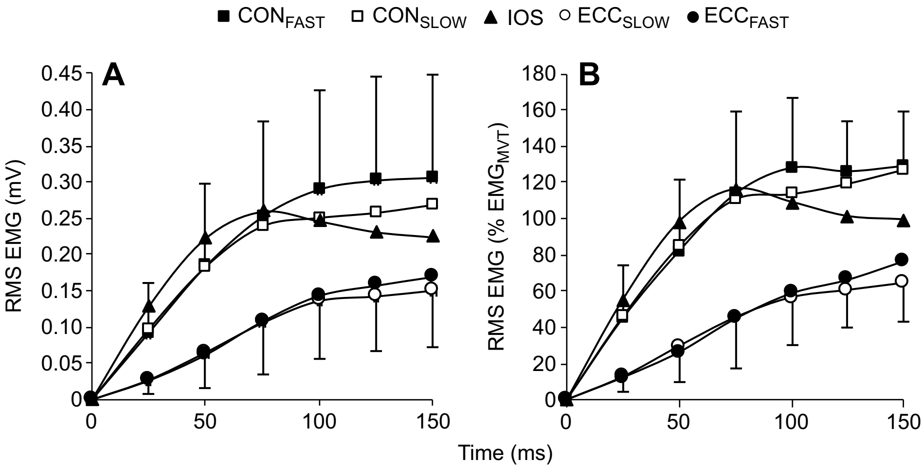

Fig. 5. Quadriceps RMS EMG amplitude recorded during explosive contractions in five conditions: concentric or eccentric at a constant acceleration of 500 deg s^{-2} (CON$_{SLOW}$ or ECC$_{SLOW}$) or 2000 deg s^{-2} (CON$_{FAST}$ and ECC$_{FAST}$), and isometric (ISO) at a 123 deg knee angle. EMG amplitudes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

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 and 150 ms ($EMG_{0–150}$) during explosive contractions performed in five conditions: concentric or eccentric at a constant acceleration of 500 deg s^{-2} (CON_{SLOW} or ECC_{SLOW}) or 2000 deg s^{-2} (CON_{FAST} and ECC_{FAST}), and isometric (ISO) at a 123 deg knee angle

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

Data are means±s.d. (n=14). Paired differences are denoted by uppercase 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}].

respectively, but higher than ECC_{SLOW} (+45–94%) and ECC_{FAST} (+40–50%) at four and two time points, respectively. Moreover, mean normalised explosive torque for 25–150 ms was different, or had a tendency to be different, between four of the five conditions in the order: CON_{FAST}>CON_{SLOW}>ISO, and ECC_{FAST}>ECC_{SLOW}, the only exception being ISO and 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 deg s^{-2}) eliciting high speeds (~140–425 deg s^{-1}), whilst the present study also considered slow concentric and eccentric accelerations (±500 deg s^{-2}) that reached slower speeds (~45–125 deg s^{-1}), and showed that the effects of contraction type were further delineated by contraction speed. When only considering the fast versus slow conditions within each type of contraction, normalised explosive torque was greater in CON_{FAST} than in CON_{SLOW} at all measured time points (+49–118%), and greater in ECC_{FAST} than in 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 was more than double that of the eccentric conditions, and was 40% greater in CON_{FAST} than in 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 explosive contractions, 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-Davó 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 present 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 two to six 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 at ~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 with isometric explosive contractions (Figs 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 that 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 present 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 the 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 versus 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 that 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 in the corresponding eccentric conditions, likely owing to longer starting muscle–tendon unit lengths and greater initial absolute muscle forces (Fig. 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 fibre level in ISO are concentric, and the differences in shortening muscle velocity between ISO and CON_{SLOW} were small (Fig. 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 present 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 in ECC_{SLOW}. In isometric conditions, fast-twitch fibres have an 8-fold higher rate constant for tension development and thus a steeper rate of force development 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 the 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 that 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. First, 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. Second, 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 data from the literature, and did not account for potential changes in gearing (Dick and Wakeling, 2017), SEC 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 force 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 that small adjustments in SEC characteristics will change this observation. Nevertheless, future research may want to consider whether changes in gearing, SEC 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 also greater at fast compared with slow contraction speeds within the same type of contraction. Using Hill-type force–velocity modelling, similar effects were found for isolated muscle fibre performance, indicating a limited influence of the SEC. The effects of contraction type on normalised explosive torque appeared to be 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

The authors declare no competing or financial interests.

Author contributions

Conceptualization: N.A.T., M.T.P., J.P.F.; Methodology: N.A.T., M.T.P., J.P.F.; Software: N.A.T., M.T.P.; Validation: N.A.T., M.T.P., J.P.F.; Formal analysis: N.A.T.; Investigation: N.A.T.; Resources: N.A.T., M.T.P., J.P.F.; Data curation: N.A.T.; Writing - original draft: N.A.T., M.T.P., J.P.F.; Writing - review & editing: N.A.T., M.T.P., J.P.F.; Visualization: N.A.T., M.T.P., J.P.F.; Supervision: N.A.T., M.T.P., J.P.F.; Project administration: N.A.T., M.T.P., J.P.F.; Funding acquisition: N.A.T., J.P.F.

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Supplementary information

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