Webber, Sandra, and Dean Kriellaars. Neuromuscular factors contributing to in vivo eccentric moment generation. J. Appl. Physiol. 83(1): 40-45, 1997.—Muscle series elasticity and its contribution to eccentric moment generation was examined in humans. While subjects [male, n = 30; age 26.3 ± 4.8 (SD) yr; body mass 78.8 ± 13.1 kg] performed an isometric contraction of the knee extensors at 60° of knee flexion, a quick stretch was imposed with a 12°-step displacement at 100%. The test was performed at 10 isometric activation levels ranging from 1.7 to 95.2% of maximal voluntary contraction (MVC). A strong linear relationship was observed between the peak imposed eccentric moment derived from quick stretch and the isometric activation level (y = 1.44x + 7.08; r = 0.99). This increase in the eccentric moment is consistent with an actomyosin-dependent elasticity located in series with the contractile element of muscle. By extrapolating the linear relationship to 100% MVC, the predicted maximum eccentric moment was found to be 151% MVC, consistent with in vitro data. A maximal voluntary, knee extensor strength test was also performed (5-95°, 3 repetitions, ±50, 100, 150, 200, and 250%). The predicted maximum eccentric moment was 206% of the angle- and velocity-matched, maximal voluntary eccentric moments. This was attributed to a potent neural regulatory mechanism that limits the recruitment and/or discharge of motor units during maximal voluntary eccentric contractions.

According to the in vitro force-velocity relationship depicted for maximally activated muscle, force generated during muscle lengthening substantially exceeds maximum isometric force, which in turn exceeds force produced during muscle shortening (7-9, 12, 14, 24). Moment-angular velocity relationships derived from human studies demonstrate that the isometric, maximal voluntary contraction (MVC) exceeds peak and angle-specific concentric moments that decrease with increasing velocity of shortening (6, 17, 32, 33). However, the ratio of eccentric to isometric moments is not consistent with that observed for in vitro force-velocity data. Peak forces generated during muscle lengthening in vitro have been shown to reach 1.5-1.9 maximum isometric force (8, 11, 12, 24), whereas human studies have generally found that maximal voluntary eccentric moments are not statistically greater than MVC (6, 23, 25, 32-34). Studies have employed electrical stimulation (6, 34) and quick stretch (10, 28) in attempts to achieve eccentric magnitudes similar to in vitro data (2, 4, 18, 35). The eccentric-to-isometric ratios achieved in these studies have not reached the lower range of that observed in vitro.

The neuromuscular factors that contribute to the generation of resultant joint moment during eccentric muscle activity are not well understood. Investigators have postulated that differences in actomyosin cross-bridge cycling and engagement processes might allow for greater moment production during eccentric contractions compared with concentric or isometric contractions (10, 12, 24). The presence of a series elastic component related to cross-bridge engagement may be the most significant factor responsible for the enhanced moment generation observed during lengthening contractions (2, 9, 10, 15, 18, 35).

Understanding the neuromuscular factors that contribute to the ability to control segmental rotation (or strength) is important. This study was designed to examine the relationship between maximal voluntary eccentric moments and eccentric moments generated by a quick stretch imposed during different levels of isometric contraction.

Materials and Methods

Subjects. Physically active men [n = 30, age 26.3 ± 4.8 (SD) yr; height 177.3 ± 7.5 cm; mass 78.8 ± 13.1 kg] with no known knee joint pathology served as subjects for the study after providing informed consent. Ethical approval for this study was granted by the Faculty Committee on the Use of Human Subjects in Research of the Faculty of Medicine, University of Manitoba (Canada).

Dynamometry. Three tests were performed on each subject in the following order: isometric test, step test, and isovelocity strength test. Subjects were provided with strong verbal encouragement to elicit maximal effort during the isometric and isovelocity strength tests. All tests were performed on a Kin-Com 500H dynamometer (Chattecx, Hixon, TN) after each subject warmed up on a Monark 818E cycle ergometer at 35 W for 5 min. Each subject's dominant leg (one used to kick a ball) was tested (25 right and 5 left legs). Subjects were seated on the dynamometer with the backrest reclined 15° from the vertical position. Straps were secured around the chest, waist, and thigh for stabilization. The axis of rotation of the dynamometer was visually aligned with the lateral femoral condyle when the knee was flexed 90° (full knee extension = 0°). The pad on the dynamometer actuator arm was then securely fastened about the subject's leg at a comfortable position ~5 cm proximal to the medial malleolus.

The angle, angular velocity, and moment data were exported from the dynamometer and analyzed by using Isomap dynamometry software (Isodeye, Winnipeg, Manitoba). Angular acceleration was derived through numerical differentiation of the unfiltered angular velocity waveform. The moment about the knee (Mk) represents the net rotational tendency of all tissue forces spanning the knee including the muscle, ligament, and bone-on-bone forces. Mk was derived by correcting the recorded dynamometer moment for the moment of the weight of the leg, foot, and resistance pad. Moments (Mk) generated in the knee extension direction were designated as positive.

Isovelocity test. Each subject performed a maximal voluntary isometric contraction of the knee extensors at a knee joint angle of 70° for 5 s. The Mk data derived from the
isometric test were averaged over a 1-s duration encompassing the peak value and was termed the maximal isometric moment (i.e., MVC).

Step test. A quick stretch of the knee extensors was imposed by applying a 12°-step angular displacement in the flexion direction at 100°/s while the subject was instructed to maintain a constant level of isometric contraction at 60° of knee flexion. The total duration of the quick stretch perturbation including the acceleration phases was 200 ms (Fig. 1). The high acceleration setting was used on the dynamometer with peak angular acceleration near 3,000°/s². After each perturbation, the leg was returned to the starting position at 30°/s. A 4-s pause was provided after each perturbation.

Each subject was required to perform the step test with 10 levels of isometric activation ranging from 5 to 95% of MVC. The 10 perturbations were performed in 2 sets of 5 repetitions (interleaved levels), with a 2-min rest between sets and a 4-s pause between perturbations. The subjects were instructed to produce a constant isometric contraction near the target level. The subject viewed the dynamometer monitor, which displayed the force transducer values numerically and provided a real-time continuous graphical display of the force values. This feedback was used to assist subjects in attaining relatively constant isometric Mₖ near the specified target levels. The subjects were instructed to relax after the perturbation was completed and while the actuator arm returned the leg to the starting position. With these instructions, the subjects produced isometric contractions that were steady but that were systematically lower than the specified target levels.

The Mₖ data for each imposed eccentric contraction consisted of two peaks (Fig. 1). The first peak occurred consistently 40 ms after onset of the perturbation. This is an acceleration-dependent inertial moment equal to the product of the angular acceleration and the moment of inertia of the leg, foot, and resistance pad (13). The peak imposed eccentric Mₖ (second peak) was determined for each of the 10 initial isometric levels during the constant angular velocity or isovelocity phase (Fig. 1). The magnitude of the initial isometric Mₖ was determined by averaging the moment data in a 220-ms window just before onset of the perturbation. Linear regression was performed between the initial isometric Mₖ (independent) and the peak imposed eccentric Mₖ (dependent).

The musculotendinous tissues about the knee contribute a passive component to Mₖ. The contribution of the passive component was estimated by applying the step test perturbation (5 repetitions) while the subject was relaxed. The mean passive component was then subtracted from the Mₖ to partially account for differences in the passive resistance of tissues among subjects. In this range of motion, the magnitude of the passive component was small [2.76 ± 2.71 (SD) N·m].

Very good test-retest reliability (n = 5) was observed for the step test by using the slope parameter derived from linear regression with an intraclass correlation coefficient of 0.91.

Stretch-evoked reflex contribution. The contribution of a stretch-evoked reflex contribution from the quadriceps to Mₖ was assessed in 10 additional subjects. Passive dispacements (3 repetitions, 0–90° flexion, 135°/s) were imposed with differential electromyographic (EMG) recording of the quadriceps muscle group [Adult Medtronic Cleantrace electrodes, 2- to 4-cm spacing between active electrodes located midthigh, 44 MΩ at 60-Hz preamplifier input impedance, >90-db common mode rejection ratio, 10–1,000 Hz (±3-db band-pass filtered)]. The band-pass-filtered EMG, angle, angular velocity, and dynamometer moment were digitized (12 bit) at 2,000 Hz. A stretch-evoked increase in the quadriceps EMG was not observed. In two additional subjects, quadriceps EMG was recorded during the step test with 10 isometric activation levels. A stretch-evoked response was not observed in the EMG at any of the isometric levels.

Strength test. Subjects performed three maximal voluntary concentric and eccentric knee extensor contractions at five speeds (50, 100, 150, 200 and 250°/s) through a 90° range of motion (5–95° knee flexion). A 4-s pause was provided between successive concentric and eccentric contractions at each velocity. A 2-min rest was given between test speeds. Order of testing was blocked (50, 100, 150, 200, and 250 or 150, 200, 250, 50, and 100°/s). A familiarization bout was provided, consisting of three low-level, submaximal repetitions of concentric and eccentric contractions at each test speed.

Analysis of data obtained from the strength test was restricted to isovelocity regions. Under normal operation, the dynamometer actuator arm’s speed fluctuates about the preset value throughout the range of motion. The isovelocity region of each repetition recorded in this study was determined by using an angular acceleration threshold of ±300°/ s². At constant angular velocity, the sum of all moments acting about the dynamometer axis of rotation equals zero. When the dynamometer actuator arm is undergoing acceleration, the moments sum to the product of the angular accelera-
tion and the moment of inertia of the attached segments (13).

In this study, the maximum error in determining the magnitude of $M_k$ associated with a $\pm 300^\circ/s^2$ angular acceleration threshold corresponded to $\pm 3.0\,\text{N} \cdot \text{m}$.

Absolute peak $M_k$ (largest of the peak moments from 3 repetitions), mean peak $M_k$ (average of the peak moments from 3 repetitions), and mean angle-specific $M_k$ (average of moments recorded at $70^\circ$ over 3 repetitions) were determined for eccentric and concentric contractions for all speeds. The angle of occurrence of peak $M_k$ was also recorded. Acceptable test-retest reliability ($n = 5$) was obtained, with intraclass correlation coefficients ranging from 0.7 to 0.92 for the strength parameters.

RESULTS

The peak imposed eccentric $M_k$ and the initial isometric $M_k$ derived from the step test were normalized to MVC and expressed as a percentage (%MVC). A strong linear relationship (Fig. 2) was observed between the normalized magnitudes of the peak imposed eccentric $M_k$ and magnitudes of the initial isometric $M_k$ ($y = 1.44x + 7.08; r = 0.99, P < 0.001$). The linear equation was used to predict the maximum imposed eccentric moment ($y$) corresponding to 100% MVC ($x = 100$). The predicted maximum imposed eccentric $M_k$ was equal to 151% MVC. A strong linear relationship with similar coefficients (slope and intercept) was observed for all subjects (Table 1). Because the peak imposed eccentric $M_k$ occurred at $69.3^\circ \pm 1.3\,\text{SD}$, $70^\circ$ was specified as the angle for the angle-specific $M_k$.

The $M_k$-angular velocity relationship is shown in Fig. 3. The isometric MVC was significantly greater ($P < 0.05$, paired t-test) than absolute peak eccentric $M_k$ at 50%. MVC was significantly greater than the mean ($P < 0.001$, paired t-test) and angle-specific $M_k$ ($P < 0.001$, paired t-test) at 50%. Examination of the eccentric $M_k$ data for each subject revealed that 12 of the 30 subjects generated peak eccentric moments for one or more eccentric contractions that were greater than MVC (on average 9.96% greater than MVC).

The predicted maximum imposed eccentric $M_k$ (481.7 N·m or 151% MVC) was dramatically greater than MVC (318.86 ± 12.84 N·m) at the same joint angle ($70^\circ$). At the same angular velocity ($\pm 100^\circ/s$), the

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Minimum and maximum initial isometric values are shown as a percentage of maximal voluntary contraction (MVC).

Fig. 2. Relationship between peak imposed eccentric moments and initial isometric moments from step test. A strong linear relationship was observed ($y = 1.44x + 7.08; r^2 = 0.98$). For each subject ($n = 30$), 10 initial isometric contractions were performed (range 1.7–95.2% MVC for group).

Fig. 3. Moment-angular velocity relationship for knee extensors is plotted by using absolute peak moments (●), mean peak moments (□), and mean angle-specific moments at $70^\circ$ (○) and ■. Mean MVC and maximum imposed eccentric moment predicted from linear equation obtained from step test (Fig. 2), respectively. SE bars are shown when they exceed symbol size.
DISCUSSION

In this study, a strong linear relationship was demonstrated between the initial isometric activation level and the peak eccentric moment resulting from a quick stretch imposed during different levels of isometric contraction. The increase in moment observed during the imposed stretch was attributed to the development of short-range stiffness arising from an elastic component (16, 19, 21, 22, 29, 30) of the activated sarcomeres consistent with that observed in vitro. With the use of the linear equation derived from the step test, the eccentric moment corresponding to 100% MVC was determined. The predicted maximum eccentric moment was substantially greater than the maximal voluntary eccentric moment at the same joint angle and velocity. This was attributed to a restricted activation of the knee extensors during maximal voluntary eccentric contractions.

If muscles were maximally activated during an isovelocity strength test, one would expect that the eccentric-to-isometric ratio would be similar to that observed in isolated muscle. Previous studies have demonstrated eccentric-to-isometric ratios near 1 (range 0.76–1.11), which are lower than in vitro data (range 1.5–1.9) (6, 23, 25, 32–34). Using the step test, we have demonstrated the maximum imposed eccentric moment was 151% MVC predicted from the linear equation, which is consistent with the force-velocity relationship established for maximally activated muscle in vitro (8, 11, 12, 24). The magnitude of increase in force elicited with stretch has been shown to be related to the velocity of stretch in isolated muscle preparations (8, 9). For one subject, the step test was performed at two additional velocities. The maximum imposed eccentric moments were observed to increase in a linear fashion with increasing velocity of the step test, reaching 167% MVC at 150°/s and 183% MVC at 200°/s.

Compared with other studies (10, 28) that have applied stretch to voluntarily activated muscle, our findings reveal substantially greater imposed eccentric moments. Gulch et al. (10) studied eccentric force behavior in intact human skeletal muscle by imposing constant angular velocity eccentric motion on maximal effort isometric elbow flexion contractions at different velocities and over different ranges of motion. Although Gulch et al. demonstrated that forced lengthening of activated muscle induced a double-peaked increment in force, they did not interpret or quantify this phenomenon. Thomson and Chapman (28) also studied imposed eccentric moment generation, demonstrating that peak imposed eccentric forearm supination supination moments ranged from ~108 to 126% MVC. However, Thomson and Chapman used the peak eccentric moment generated at the end of a large imposed range of motion to represent imposed eccentric moment. Given the large ranges of motion (80 and 160°) and the total time associated with this motion, voluntary control of muscle activation may have influenced the magnitudes of these moments. In this study, the likelihood of voluntary activation of the knee extensors during the step test is minimal, given that the subjects were concentrating on maintaining a constant isometric contraction; the duration of the interstimulus period reduced the possibility for anticipation; and the time to the peak imposed eccentric moment was less than normal reaction times.

In 1990, Westing et al. (34) demonstrated that angle-specific eccentric moments increased by 21–24% above the maximal voluntary isometric level when maximally tolerated electrical stimulation was superimposed during maximal voluntary eccentric contraction. Dudley et al. (6) performed a similar experiment to that of Westing et al. (34) by using high-intensity, superficial electrical stimulation of the quadriceps and reported induced eccentric values that were 1.4 times MVC. Compared with our predicted values of a 51% increase, this smaller increase may have resulted from a level of electrical stimulation limited by pain, which did not allow complete activation of nerves supplying the underlying musculature.

Cocontraction of the knee flexors is known to occur during isovelocity strength tests of the knee extensors (27). Increased knee flexor activity would result in a decreased extensor M<sub>E</sub>. However, it is difficult to envision that increased knee flexor activity during voluntary knee extensor eccentric contractions could solely account for the substantial difference observed between the imposed and the voluntary eccentric moments.

In this study, we performed two control experiments in which quadriceps EMG was recorded during the step test to examine the contribution of stretch-evoked reflex activation of quadriceps motor units to the imposed eccentric moment. We demonstrated that the step test stimulus velocity was below the threshold for stretch reflex activation under passive conditions, similar to the findings of Burke et al. (5). Furthermore, we did not observe a stretch reflex response with any isometric level employed in the step test.

Investigators have speculated that a neural regulatory mechanism may limit the level of muscular activation during voluntary eccentric contractions to protect the musculoskeletal system from injury (17, 31, 33). Westing et al. (31) demonstrated that quadriceps EMG levels were lower (10–30%) for maximal effort eccentric contractions compared with concentric contractions at identical velocities, which is consistent with restricted neuromuscular activation (26) and decreased energy cost (1, 3, 20) during voluntary eccentric activity. In this study, the difference between maximal voluntary and predicted maximum imposed eccentric moments was substantial (206% of angle- and velocity-matched, maximal voluntary moments), which is consistent with a potent neural regulatory mechanism that would limit motor unit activation (recruitment and/or discharge frequency) during maximal voluntary eccentric contractions. The generalizability of this finding from isovelo-
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ity strength tests for the knee extensors to other behaviors or tasks is unknown.

Subjects were requested to produce a constant isometric moment to achieve a relatively constant level of muscle activation before the step perturbation. When instructed to maintain a constant isometric contraction, subjects produced isometric contractions that were systematically lower than the target levels, especially when target levels exceeded 80% MVC, resulting in a decreased number of data points in the upper portion of this relationship. The data points in a decreased number of data points in the upper

cial when target levels exceeded 80% MVC, resulting in a decreased number of data points in the upper portion of this relationship. The data points >80% MVC were generally slightly below the regression line (Fig. 2), which might indicate that the imposed eccentric moments were no longer linearly related to the amount of actomyosin engaged. However, examination of individual regression results for subjects who achieved levels >80% MVC (Table 1) revealed that strong linear relationships were maintained throughout the entire range of MVC levels produced up to 95% MVC. Given the strong linear relationship observed to that level, it is difficult to envision a mechanism through which further activation of muscle fibres would not result in a further increase in the imposed eccentric moment.

In summary, we demonstrated that the magnitude of eccentric moments induced through quick stretch was linearly proportional to the level of isometric activation. The magnitude of the predicted maximum eccentric moment was shown to be 151% MVC, which is within the range reported for isolated muscle (1.5–1.9 maximum isometric force). The finding that maximal voluntary eccentric moments were substantially lower than the predicted maximum imposed eccentric moments was attributed to a neural regulatory mechanism that significantly limits motor unit activation (recruitment or discharge frequency) during voluntary eccentric contraction.

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