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ORIGINAL ARTICLE

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Contraction history affects the in vivo quadriceps torque-velocity relationship in humans

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Abstract We hypothesized that the history of contraction would affect the in vivo quadriceps torque-velocity relationship. We examined the quadriceps torque-velocity relationship of the human knee extensors at the descending and ascending limb of the torque-position relationship by initiating the knee extension at a knee angle position of 1.39 rad (80°) or 0.87 rad (50°) over a 0.52 rad (30°) range of motion under conditions of constant or linearly increasing velocity. Maximal voluntary isometric knee extension torque (M_0) was measured at 1.87 rad, 0.87 rad, and 0.35 rad, and concentric torque was measured. The subjects carried out ten maximal knee extensions at ten distinct velocities, each velocity ranging between 0.52 rad·s^{-1} to 5.24 rad·s^{-1} in steps of 0.52 rad·s^{-1}. Peak concentric torque was measured and mean torque calculated from the respective torque-time curves. Peak or mean torque, computed from the individual torque-time curves, and velocity data were fitted to the Hill equation under the four experimental conditions and the curve parameters computed. The M_0 was similar at 0.87 rad and 1.39 rad, but it was significantly lower at 0.35 rad. In the low-velocity domain of the torque-velocity curve where a plateau normally occurs, peak torque was always lower than M_0. Peak and mean torque were significantly greater under linearly increasing velocity conditions and the 1.39 rad starting knee position. Mean torque but not peak torque data could be well fitted to the Hill equation and the two computations resulted in significantly different Hill curve parameters including the concavity ratio, peak power, and maximal angular velocity. We concluded that the history of contraction significantly modifies the in vivo torque-velocity relationship of the human quadriceps muscle. Muscle mechanics and not neural factors may have accounted for the inconsistencies in the human torque-velocity relationships reported previously.

Keywords Muscle mechanics · Knee extensors · Constant speed · Constant acceleration · Hill equation

Introduction

The knee extensor torque-joint angle relationship is of an ascending-descending type because the highest isometric torque is produced at 0.87–1.04 rad of knee flexion, and the torque production is significantly lower at smaller or greater joint angles (Smidt 1973; Hoy et al. 1990). In most of the cases researchers have used a 1.56 rad range of motion to study the torque-velocity relationship in knee extensors. During isokinetic knee extension, peak torque (M_p) normally occurs at around 1.04 rad on average (Thorstensson et al. 1976; Froese and Houston 1985; Taylor et al. 1991). Taylor et al. (1991) found that the knee angle at M_p had a linear inverse relationship with the knee extension velocity. Angular displacements of 20° and 40° were needed to develop M_p at the lowest (0.52 rad s^{-1}) and the highest (5.2 rad·s^{-1}) constant velocities, respectively. Therefore, the location of M_p on the torque-position curve varies during isokinetic contractions, for slow-speed contractions most likely on the ascending limb and for fast contractions at the joint position where the maximal voluntary isometric knee extension torque (M_0) occurs. Hence it is conceivable that the history of contraction would affect M_p and the shape of the torque-velocity relationship. We thus hypothesized that performing knee extension on the ascending or descending portions

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of the torque-position curve would affect the parameters of Hill's torque-velocity relationship (1938), including the dynamic constants a and b, the concavity index (a/M_0), maximal angular velocity (ω_0), peak power (P_0), the optimal torque (M_{P0}) and optimal angular velocity (ω_{P0}).

We specifically propose that the history of contraction on the descending compared to the ascending segment of the torque-position curve would shift the torque-velocity curve and reduce the mechanical power of knee extensors. Numerous researchers have reported on force (torque)-velocity relationship of voluntary muscle contraction under conditions of constant load (Wilkie 1950; Kaneko 1970; Kaneko et al. 1983), constant torque spring (De Koning et al. 1982, 1985), and inertial loads (Tihanyi et al. 1982). In most of the cases the researchers have found that the force-velocity relationship is non-linear and similar in both in situ and in vitro studies and have been able to fit the force (torque) and velocity data to the hyperbolic curve and to calculate the characteristics of the curve using the equation of Hill (1938).

When, instead of load, the velocity was controlled, most researchers did not attempt, or were unable, to fit the torque and velocity data to Hill's equation (Thorstensson et al. 1976; Perrine and Edgerton 1978; Gregor et al. 1979; Wickiewicz et al. 1984; Froese and Houston 1985; Westing and Seger 1989; Hortobágyi and Katch 1990; Taylor et al. 1991) with a few exceptions (Parker et al. 1983; MacIntosh et al. 1993; Martin et al. 1995). Several authors also observed that the torque-velocity relationship departed from the hyperbolic curve at low angular velocities (Perrine and Edgerton 1978; Caiozzo et al. 1981; Wickiewicz et al. 1984; Froese and Houston 1985; Taylor et al. 1991). Presumably, the reaching of a plateau in the torque-velocity relationship at low velocities occurred because the torque-velocity relationship was constructed from constant angle torque instead of M_p. Ostering et al. (1982) tested this prediction and indeed found that the torque-velocity curves flattened if constant angle torque were used, whereas using M_p, the curve became hyperbolic. In contrast, Yates and Kamon (1983), and Hortobágyi and Katch (1990) could find no substantial difference between the two methods.

These inconsistencies in the literature suggest that there may be a conceptual flaw in the use of peak or constant-angle torques in constructing the torque-velocity relationships in human muscle. However, it is still not clear why M_p or constant-angle torque and velocity data cannot be fitted to Hill's equation. We suspect that neither M_p nor constant angle torque represents adequately the working capacity of the muscle during shortening. When the load is controlled, the gravitational force of the load (weight) variable entered in Hill equation is constant. Because, under these conditions, the peak force is always greater than the gravitational force due to the weight moved in the controlled load condition, the use of peak force in the Hill equation would shift the force-velocity relationship to the right, deviating from the expected rectangular hyperbolic curve. The same principle applies to a situation where the output measurement is not linear force but torque, and the situation can be similar in a rotational system when torque is measured and the angular velocity is controlled. We hypothesized that if the mean torque (M_m) is calculated from the torque-time data at each applied constant velocity and used as input data to the Hill equation, the M_m values would represent the working capacity of the muscle and would yield a better fit to the Hill equation than M_p. The rationale for this hypothesis comes from the observation that the $b(F_0–F)$ term in the Hill equation indicates the rate of doing work by the muscle.

There is another significant difference between constant load and constant velocity conditions. Namely, in the constant load condition the contraction velocity, controlled voluntarily, increases steadily and the ω_0 is normally measured at the end of the contraction (Tihanyi et al.1982). Because the velocity is very high at the very beginning of the movement, the muscle is unable to develop the expected tension that would otherwise be possible if the acceleration were low. Therefore, under isokinetic conditions it can be assumed that due to this fact the peak and the calculated M_m would both be depressed, resulting in a non-characteristic torque-velocity relationship, especially at high constant velocities. Under constant inertial load conditions Tihanyi et al. (1982) found that the velocity increased linearly from the start of the knee extension and that torque data could be meaningfully fitted to the Hill equation. Therefore, if the controlled velocity was linearly increased, resulting in constant acceleration, there should be enough time for the knee extensors to develop the highest possible tension. Hence, the peak as well as M_m would be greater than the torques under constant velocity conditions. We also assumed that M_m data acquired at linearly increasing velocities, could be better fitted to the Hill equation and that the characteristic parameters of the rectangular hyperbolic curve would also be different, but similar to those reported by Tihanyi et al. (1982).

The purpose of the study was threefold:

1. To assess the influence of M_p and M_m on the torque-velocity relationship
2. To attempt to fit torque and velocity data to Hill's equation
3. To compare the force-velocity characteristics obtained over the descending and ascending limbs of the torque-joint angle relationship under the conditions of constant or linearly increasing velocity.

Methods

Subjects

Randomly selected from a pool of 50 athletes, 10 healthy male physical education university students, with a background in gymnastics and track and field events, participated in the study. None of the subjects had a history of knee injury and at the time of the study all of them were free of orthopaedic abnormalities. Their mean (SD) age, body mass and body height were 23.2 (2.1) years, 78.1 (5.7) kg and 1.83 (0.05) m, respectively. Each subject signed an informed consent form that had been approved by the University's Ethics Committee.

Instrumentation

A custom-built computer-controlled dynamometer (Multicont II, Mediagnost, Budapest and Mechatronic Kft, Szeged, Hungary) was used to collect torque-time, joint position-time, and angular velocity-time data during knee extension. An electric servo-motor (Mavilors AC Servo-motor, M10, Spain) controlled the stainless steel lever arm (600×50×10 mm) of the dynamometer. The measuring unit of the dynamometer comprised three main components:

1. The servo motor was an AC flat sinusoidal brushless motor (type MA-10, Mavilor Motors, Spain; maximal speed 6,000 rpm, maximal continuous torque 5.8 N·m, short term M_p 40.7 N·m)
2. The gear drive was a backlash free compact cyclo drive (type: FAD 25, Lorenz Braren Gmbh, Germany; reduction ratio 59, rated output torque 460 N·m, maximal short-term output torque 971 N·m)
3. The load cell was a unit designed and manufactured specifically for this application. It resembled two disks connected to each other by eight radially positioned thin ribs. It was made of high tensile-strength steel and due to its unique shape it was sensitive only to torque loads. There were four strain gauges glued to the flexible ribs of the load cell (sensitivity 0.5 N·m, maximal torque 500 N·m).

The joint position was measured using a built-in potentiometer from the driver having a resolution of 0.01 rad. Velocity was computed by differentiating the position-time data. The pre-programmed electrical servomotor controlled velocity. During concentric contractions the velocity varied less than 0.05 rad·s^{-1}. The torque, angular displacement and velocity were recorded using a personal computer, following analogue to digital conversion at 0.5 kHz, and were stored for later analysis.

Procedure

Each subject participated in four test sessions. The sessions were separated by 2 days of rest. Each session started with a 10 min warm-up that included 5 min of jogging in an indoor track and field facility, stretching, and submaximal unilateral isometric and concentric practice knee extension efforts on the dynamometer. Subjects were positioned on the dynamometer which had its seat back reclined so that the hip joint was at 1.9 rad. Crossover shoulder straps, a lap belt, and a wide strap across the thighs stabilised the torso and prevented hip extension. The dominant leg was attached through an ankle cuff to the lever arm of the dynamometer. The apparent centre of rotation of the knee joint was aligned with the centre of rotation of the lever arm.

The four experimental conditions were administered randomly, one condition per test. The four conditions were a combination of two different knee joint positions to start a concentric knee extension effort [0.87 rad (50°) and 1.39 rad (80°)] and two different knee extension velocities [constant (C), or linearly (L) increasing], i.e. C_{50}, C_{80}, L_{50}, L_{80} (Figs. 1 and 2).

First, M_0 was determined at 0.35 rad (20°), 0.87 rad (50°), and 1.39 rad (80°) of knee flexion (full knee extension corresponded to a 0 rad joint angle). Subjects performed five maximal unilateral efforts with 2 min of rest between each. Normally the subjects produced their personal greatest torque within three trials. The maximal torque for the previous effort was displayed on a monitor to motivate subjects.

Next, subjects performed ten consecutive knee extensions, at 0.52, 1.05, 1.57, 2.09, 3.5, 3,84, 4.19, 4.54, 4.89 and 5.24 rad·s^{-1} under the four experimental conditions (C_{50}, C_{80}, L_{50}, L_{80}). These knee extensions started at either 0.87 rad (50°) or 1.39 rad (80°) knee joint position and the range of motion was 0.52 rad (30°). After each knee extension effort, the leg was allowed passively to return to the starting position. Representative examples of torque-time, position-time, and velocity-time curves are illustrated in Figs. 1 and 2.

Computer software controlled the lever arm at constant (C_{50}, C_{80}) or linearly increasing (L_{50}, L_{80}) velocities. The linearly increasing velocity was programmed so that the target velocity was reached at the end of the knee extension with constant angular acceleration. Subjects were instructed to initiate the knee extension rapidly. When the 25 N·m torque threshold was reached, the dynamometer driver released the lever arm from its static position, allowing the subject to execute instantaneously the knee extension movement. Based on preliminary experiments, we chose the 25 N·m torque threshold to reduce the delay caused by the subject-dynamometer interface and to load the series-elastic elements. Depending on the specific velocity condition, the lever arm reached constant velocity in 10–22 ms (Fig. 1). To eliminate fatigue, the knee extensions were separated by 30 s of rest. In addition, there was a 2 min rest between each velocity condition.

Data analysis

All data analysis was performed offline. The knee extension torque values were adjusted for the effect of gravity associated with the mass of the leg. Of the isometric efforts, the highest torque was used in the statistical analysis. For the dynamic knee extensions, the peak concentric torque (M_p) was defined as the highest torque of the specific torque-time curve (Fig. 2). The M_m was also calculated from the respective torque-time curves as follows:

$$M_m = \frac{\sum_{i=1}^{N} M_{(i)}}{N}$$

where n is the number of measured samples during the total movement time and $M_{(i)}$ is the measured moment in the *ith* sample derived from the respective torque-time curve. The torque was determined at each 2 ms.

Of the total efforts, M_p and M_m values of the five best trials were averaged and used to determine the torque-angular velocity (M-ω) relationship plotted for each subject. A least squares fit of the Hill characteristic equation $[(M+a)(\omega+b)=(M_0+a)b]$ was made by applying a special curve fitting program (Tihanyi et al. 1982). The characteristics of the Hill hyperbolic curve were calculated for each subject, and averaged for all subjects. Using Hill equation, the algorithm computed the following parameters for each subject: constants a and b, concavity of the M-ω curve (a/M_0), ω_0, P_0, M_{P0}, percentage of maximal torque at maximal power ($\%M_{P0}$), and angular velocity at maximal power (ω_{P0}).

Statistical analysis

Means and standard deviations (SD) were computed for the measured and calculated values. The curve parameters obtained under the four experimental conditions were compared using a repeated measures analysis of variance followed by Tukey's post-hoc contrast. The probability level for statistical significance was set at $P<0.05$.

Results

Comparison of M_0, M_p and M_m

As shown in Fig. 3 the M_0 measured at 0.87 rad or at 1.39 rad were almost numerically identical. However, subjects produced 2.8 times less M_0 at 0.35 rad than at 0.87 rad or 1.39 rad.

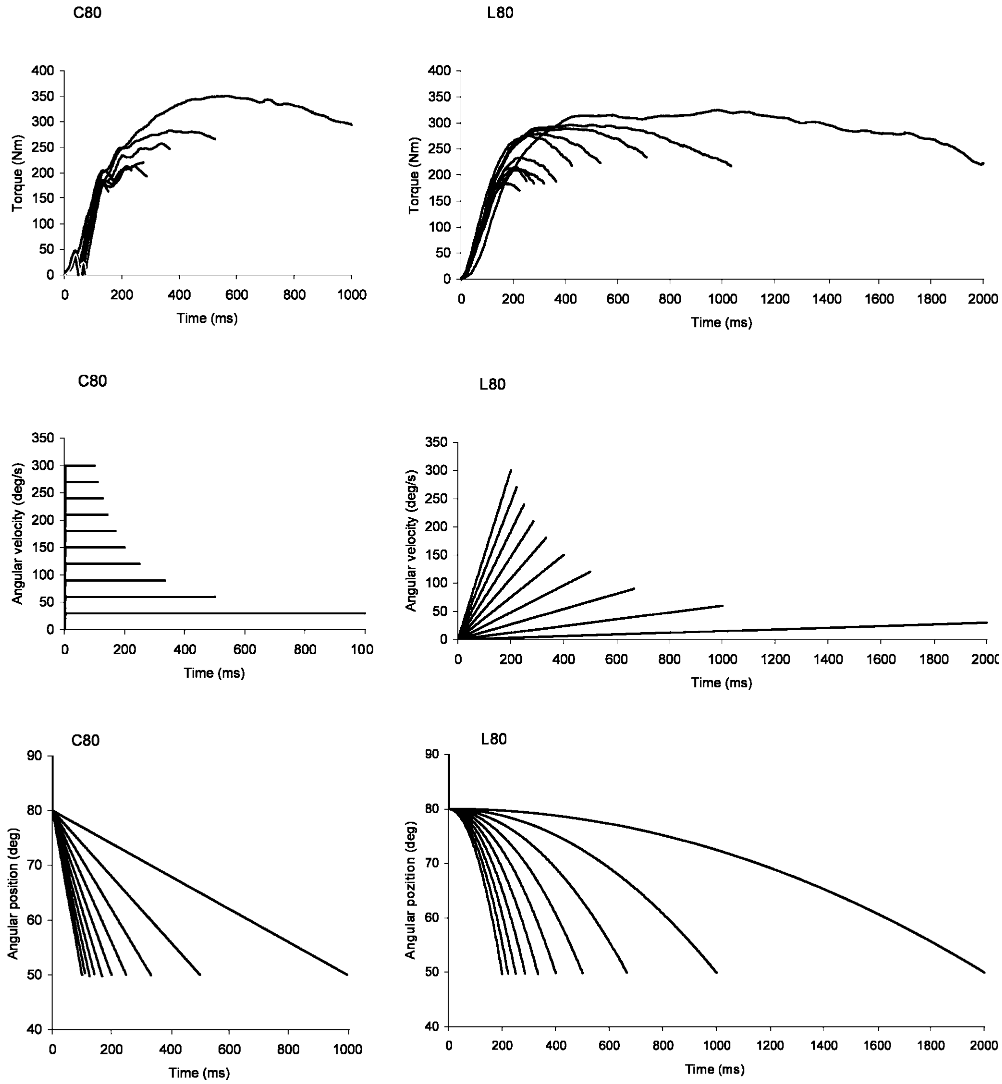


Fig. 1. Representative torque-time, position-time and velocity-time curves for knee extension performed at constant (C_{80}) and linearly increasing (L_{80}) velocity in one subject. Knee extension started at 1.39 rad (80°). Note that the subject reached maximal velocities at the very beginning of the knee extension in the constant velocity condition. In contrast, the subject reached maximal velocity at the end of the knee extension in the condition of linearly increasing velocity. The time to complete the knee extension movement in the linearly increasing velocity condition was twice as long as that in the constant velocity condition

Also shown in Fig. 3 is that the highest M_p values at 0.52 rad·s^{-1} were significantly lower compared to M_0 at 0.87 rad or at 1.39 rad. The M_p values at C_{80} and L_{80} occurred at 1.12 (0.07) rad and 1.38 (0.12) rad, respectively. These M_p were 16% and 11% lower than M_0 at 1.39 rad. When the knee extension started at 0.86 rad, M_p occurred at 0.83 (0.09) rad (C_{50}) and 0.75 (0.08) rad (L_{50}), which were 25.3% and 13.8%, respectively, lower than M_0 at 0.87 rad (Fig. 3). In all comparisons, the differences between M_0 and M_p at 0.52 rad·s^{-1} were significant.

As shown in Fig. 4 M_m values were significantly lower than the M_p values at any velocity except at the lowest velocity under L_{80} and C_{80}. The differences between M_p and M_m increased as a function of velocity, with the smallest difference observed under L_{80}.

The M-ω relationship

Also shown in Fig. 4 is that the M and ω data derived under the four experimental conditions fit the hyperbolic curve only when the M_m values were used. When M_p was plotted against the ω the M-ω relationship was curvilinear at C_{80} and C_{50}, but the data did not fit the Hill equation. As for L_{80} and L_{50} conditions, the relationship seemed to be linear rather than curvilinear, and the data did not fit the hyperbolic curve (unfilled symbols in Fig. 4).

Also indicated in Fig. 4 is that the concavity of the four curves is different. Indeed, Table 1 shows that the a/M_0 values were significantly different between the four conditions. The a/M_0 for C_{80} was 2.6 times and for L_{80} was 2.3 times greater than the a/M_0 values for the C_{50} and L_{50} conditions, respectively. The a/M_0 for L_{80} was 1.3 times and for L_{50} was 1.5 times greater than the a/M_0 values for C_{80} and C_{50}, respectively. These differences among a/M_0 values under the four experimental conditions were significant ($P<0.05$). Also shown in Table 1 is that the estimated ω_0 values derived from Hill's equation with the velocity at L_{80} were significantly greater ($P<0.05$) than the velocities at C_{80}, L_{50} and C_{50}. There was no significant difference in estimated ω_0 between L_{50} and C_{50}.

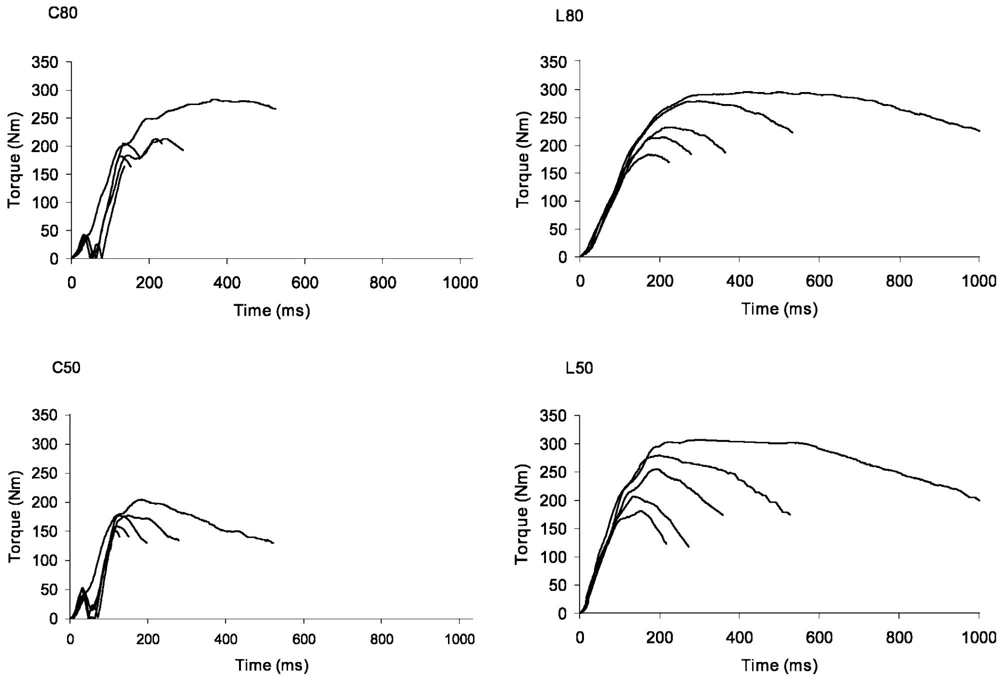


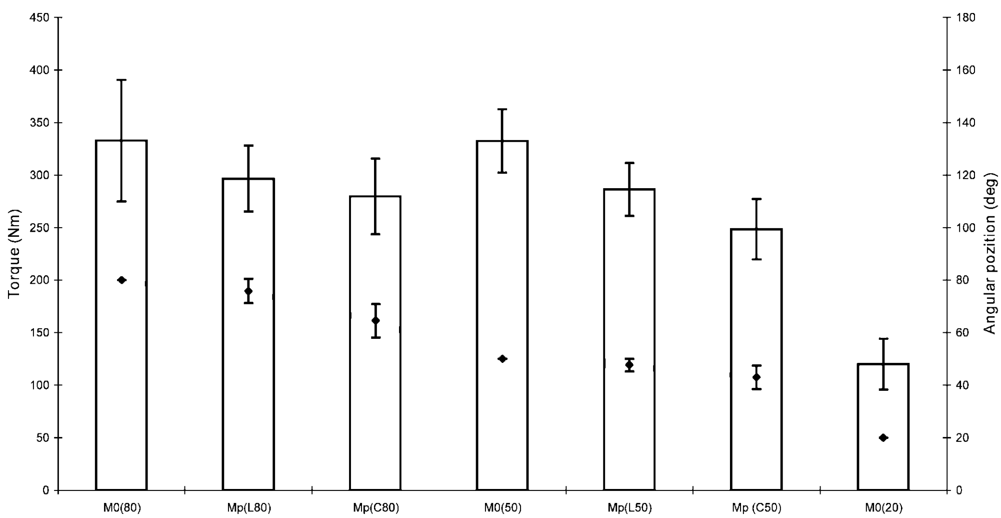
Fig. 2. Representative torque-time curves recorded at 1.05, 2.09, 3.84, 4.54, and 5.24 rad s^{-1} in four experimental conditions (C_{80}, L_{80}, C_{50}, L_{50}, where C indicates constant and L linearly increasing velocity, and 50 and 80 indicate the starting knee-joint angles in degrees). Note the large and rapid decline in torque after the peak when subject started the knee extension at 0.87 rad (C_{50} and L_{50}). In contrast, peak torque was maintained over a much longer period when the subject started the knee extension at 1.39 rad (C_{80} and L_{80})

Power-velocity relationship

Shown in Fig. 4 is the mean power-velocity curves calculated for the four experimental conditions and in Table 2 the group mean data. The P_0 was the highest at L_{80} and the lowest at C_{50} corresponding to the highest and lowest a/M_0 values, respectively. The P_0 was greater ($P < 0.05$) under conditions of linearly increasing velocity compared to constant velocity. Table 2 also shows that P_0 was less when the knee extension started at 0.87 rad, compared to 1.39 rad (L_{80}, C_{80}).

The M_{P0} and ω_{P0} varied under the four experimental conditions. The highest M_{P0} occurred at L_{80} where it represented 33.0% of M_0. The lowest M_{P0} occurred at C_{50} where it represented 23.2% of M_0. In addition, subjects produced higher ($P < 0.05$) M_{P0} and ω_{P0} when they performed knee extension with linearly increasing compared to constant velocity.

Fig. 3. Group mean (SD) of maximal isometric torque (*M_0*), peak torque (*M_p*) (*columns*), and joint position (*diamonds*) estimated for the different experimental conditions. The $M_0(80)$, $M_0(50)$, and $M_0(20)$ reflect the M_0 at 1.39 rad (80°), 0.87 rad (50°), and 0.35 rad (20°) of knee flexion, respectively. The $M_p(L_{80})$, $M_p(C_{80})$, $M_p(L_{50})$ and $M_p(C_{50})$ denote M_p measured at the slowest angular velocity (0.52 rad s^{-1}) for L_{80}, C_{80}, L_{50}, C_{50}, where C indicates constant and L linearly increasing velocity and 50 and 80 indicate the starting knee-joint angles in degrees. The joint position represents the average of the positions at which the M_p was determined during the slowest velocity. Note that M_p was always less than M_0 measured at a starting position of knee extension, i.e. at 1.39 rad (80°) or at 0.87 rad (50°). The M_0 was significantly greater at 1.39 rad (80°) or at 0.87 rad (50°) than M_0 at 0.35 rad (20°). $M_0(80)$ was significantly greater than $M_p(L_{80})$ and $M_p(C_{80})$. The $M_p(L_{80})$ was significantly greater than $M_p(C_{80})$. The $M_0(50)$ was significantly greater than $M_p(L_{50})$ and $M_p(C_{50})$. The $M_p(L_{50})$ was significantly greater than $M_p(C_{50})$



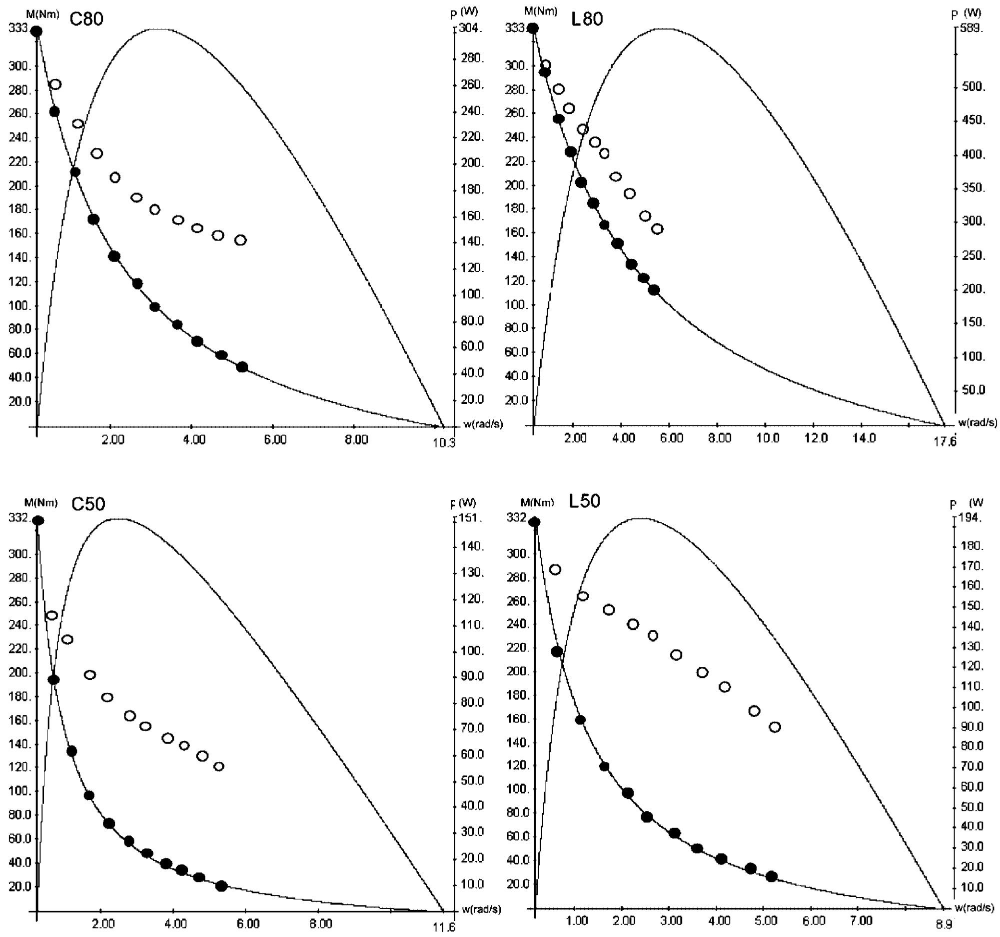


Fig. 4. Angular velocity (ω)-torque (M) and angular velocity-power (P) relationships for C_{80}, L_{80}, C_{50} and L_{50} (where C indicates constant and L indicates linearly increasing velocities, and 80 and 50 indicate the starting position of knee extension in degrees). *Unfilled symbols* indicate the peak M-ω relationships and the *filled symbols* indicate the mean M-ω relationships. Note that the unfilled symbols deviate from the hyperbolic curve, which was drawn by mean M data fitting to the Hill equation (1938)

Discussion

The main finding was that the history of contraction affected the in vivo quadriceps M-ω relationship. Specifically, we found that:

1. The M_0 was greater than M_p at the lowest test velocity (0.52 rad s^{-1})
2. M_p increased as knee extension velocity decreased without a plateau at low velocities
3. The M_p-ω relationship was linear under conditions of linearly increasing velocity but curvilinear under conditions of constant velocity
4. Whereas the M_m values fitted the Hill-equation under each experimental condition, the M_p values did not
5. The characteristics of the Hill hyperbolic curve varied as a function of the experimental conditions.

M_0 and angle relationship

As has been reported previously (Smidt 1973; Hoy et al. 1990), we found that M_0 was significantly greater at 0.87 rad than at 0.35 rad, so we were able to test the hypothesis that the M-ω curve would be affected whether it was measured on the descending or ascending limbs of the torque-position curve. Because M_0 was similar at 0.87 rad and 1.39 rad. we were able to examine the M-ω relationship without the confounding influence of the initial torque values being different under the four experimental conditions.

M_m compared to M_p

A considerable amount of attention has been devoted to the shape of the M-ω relationship in human muscle. In several cases a plateau in the low-velocity domain has been reported (Thorstensson et al. 1977; Perrine and Edgerton 1978; Caiozzo et al. 1981; Wickiewicz et al. 1984; Froese and Houston 1985; Vanderwoort et al. 1987; Taylor et al. 1991) whereas in an equally high number of reports the M-ω relationship has had the pattern originally reported by Hill (1938) for isolated mammalian muscle (Coyle et al. 1981; Ivy et al. 1981; Yates and Kamon 1983; Parker et al. 1983; Westing and Seger 1989; Hortobágyi and Katch 1990; MacIntosh et al. 1993; Martin et al. 1995). In some cases the use of constant-angle torque produced the desired curvilinear M-ω relationship without a plateau, but in other cases the M-ω relationship still had a plateau despite

Table 1. Mean (SD) of maximal isometric torque (M_0), maximal calculated angular velocity (ω_0) and concavity index (a/M_0). *C, L* Constant and linearly increasing velocities; 80, 50, starting position of knee extension in degrees

	M_0 (N·m)	ω_0 (rad·s^{1-})	a/M_0
C_{80}	332.9 (57.9)	10.2 (1.2)[b]	0.26 (0.07)[b]
L_{80}	332.9 (57.9)	16.4 (0.9)[a]	0.35 (0.11)[a]
C_{50}	332.4 (30.3)	8.9 (2.2)	0.10 (0.07)
L_{50}	332.4 (30.3)	8.5 (0.9)	0.15 (0.04)[c]

[a]Significant difference between L_{80} and C_{80}, L_{80} and C_{50}, L_{80} and L_{50}
[b]Significant difference between C_{80} and C_{50}, C_{80} and L_{50}
[c]Significant difference between L_{50} and C_{50}

Table 2. Mean (SD) of peak power (P_0), torque at P_0 (M_{P0}), percentile torque at P_0 ($\%M_{P0}$) and angular velocity at P_0 (ω_{P0})

	P_0 (W)	ω_{P0} (rad·s^{1-})	M_{P0} (N·m)	$\%M_{P0}$ (%)
C_{80}	306.2 (45.9)[d]	3.1 (0.02)[b]	99.4 (10.4)[b]	30.1 (0.03)[b]
L_{80}	591.3 (61.8)[a]	5.4 (0.04)[a]	109.4 (12.3)[a]	33.0 (0.04)[a]
C_{50}	161.0 (85.3)	4.5 (0.05)	75.0 (15.9)	23.2 (0.03)
L_{50}	332.4 (30.3)[c]	3.8 (0.03)[c]	88.2 (12.7)[c]	26.2 (0.02)[c]

[a]Significant difference between L_{80} and C_{80}, L_{80} and C_{50}, L_{80} and L_{50}
[b]Significant difference between C_{80} and C_{50}, C_{80} and L_{50}
[c]Significant difference between L_{50} and C_{50}
[d] Significant difference between C_{80} and L_{50}

using constant-angle torque (Yates and Kamon 1983; Hortobágyi and Katch 1990). We suggest that the results of the present study may resolve this issue. We propose that the reported inconsistencies in the shape of the M-ω relationship are due to the conceptually incorrect use of the M_p data. In the present study, M_p (measured during concentric contraction) was significantly lower than M_0 and our data did not exhibit a plateau in the M-ω relationship. Even though our M_P data did not show a plateau, it could not be fitted to the Hill equation. If we consider that mechanical work is linearly related to the area under the torque-angle curve, it is apparent that M_m is the appropriate input variable to the Hill equation. Indeed, the M_m values, as calculated from the torque-time curves in the present study, could be successfully fitted to a rectangular hyperbolic curve. This is because M_m represents the mechanical work that is done by the knee extensors on the lever arm during muscle contraction. Indeed, the bF_0–bF (or more accurately in our case, bM_0–bM_m) term derived from the Hill equation indicates the rate of work. From this approach M_m in the Hill equation represents the M_m that can be calculated from the respective torque-time curves. Because M_m is always lower than the M_p, it may very well explain why researchers, with one exception (MacIntosh et al. 1993), have been unable to fit their data to the Hill equation under isokinetic conditions.

Several alternative hypotheses could potentially account for the plateau phenomenon and the inability to fit M_p data to the Hill equation. One possibility is that the plateau is the result of some neural inhibition. However, Gandevia et al. (1998) reported that during maximal effort interpolation of concentric contraction twitches revealed maximal or near maximal activation, at least in the elbow flexors. Hortobágyi and Katch (1990) also demonstrated that trained subjects, similar to the subjects in the present study, produced a M-ω relationship without a plateau, indicating the absence of neural inhibition. Another possibility is that increasing co-activation of knee flexors may reduce the net extension torque, producing a plateau in the M-ω curve. Thomas et al. (1987) reported a curvilinear M-ω relationship without a plateau in plantar flexors using electrically stimulation-evoked torque data. Because antagonist co-activation under electrical stimulation cannot be expected, the co-activation of knee flexors may cause the plateau phenomenon under voluntary contraction especially at low contraction velocities.

Finally, it is reasonable to assume that regular strength training may decrease the magnitude of antagonistic muscle coactivation and reduce neural inhibition associated with this antagonistic activation (Carolan and Cafarelli 1992). The subjects in the present study had been exposed to high torque generation during training and were probably able to activate fully the knee extensors at low velocities without a large amount of hamstring coactivation, as were the trained subjects in the studies by MacIntosh et al. (1993) and Hortobágyi and Katch (1990).

According to expectations, M_p exceeded M_m and the difference increased with increasing velocity (Fig. 4). This increasing difference can be attributed to a shortening of contraction time with increasing knee extension velocity (Fig. 2). The M_p at each velocity was significantly lower under constant velocity conditions compared to the linear velocity conditions and this difference affected the M-ω relationship. When M_p was produced under conditions of linearly increasing velocity the M-ω relationship was linear. In contrast, when M_p was produced under conditions of constant velocity, the relationship was curvilinear. Yet the M-ω data could not be fitted by hyperbolic functions. The reason for the difference in the M-ω relationship between conditions of constant and linearly increasing velocities is that the target velocity is reached in 4–22 ms, a time interval that is substantially shorter than the 60–100 ms necessary for the muscle to develop M_p over a 0.52 rad range of motion or to reach maximal contraction velocity (Tihanyi et al. 1982). In contrast, under conditions of linearly increasing velocity the respective maximal target velocity is reached at the end of the knee extension with sufficient time for the muscle to develop tension that is proportional to the applied knee extension velocity.

The M-ω characteristics

Because the M_m values at each velocity were significantly greater under conditions of linearly increasing velocity compared to constant velocity, and also in the ascending compared to the descending torque-position relationship, the parameters of the rectangular hyperbolic curve showed characteristic differences. Maximal estimated velocity based on a prediction from the Hill curve, was significantly higher on the ascending limb of the torque-position relationship than the descending limb under both constant or linearly increasing conditions. This difference could have been the result of a reduced working capacity of the muscle on the descending limb of the torque-position relationship. The somewhat paradoxical question as to how torque can affect maximal estimated velocity if at ω_0 no torque is produced, can be resolved by examining the details of the Hill equation. Because the maximal estimated velocity is calculated from the Hill equation [$(\omega_0 = b(M_0 \cdot a^{-1})$], the ω_0 is under the combined influence of the M_0, M_m and ω_0 as the constants a and b are computed by plotting M_m (at the respective velocity) against $M_0-(M_m \cdot \omega^{-1})$. Since the M_0 was similar in both ascending and descending limbs of the torque-position relationship and the preset velocity was the same for L_{80} and L_{50} but the M_m values at the same velocity were different, one can assume that M_m, especially at high velocities, influenced the ω_0 predominantly. Because the M_m values were greater on the ascending than on the descending limb of the torque-position curve, it is apparent that the estimated ω_0 would be greater for the ascending torque-position condition. Because the four heads of the knee extensors are pinnated (Wickiewicz et al. 1983; Yamaguchi et al. 1990) and the pinnation angles range between 0.05 and 0.13 rad, knee joint position may also influence the architecture of the quadriceps and such changes in pinnation may also be the reason for the greater torque production at joint positions exceeding 0.87 rad. Smidt (1973) reported that the calculated force-position curve of the knee extensors did not follow the torque-position curve beyond 0.87 rad, i.e. the isometric force increased beyond 0.87 rad, and levelled out at 1.56 rad. This observation can be attributed to at least two factors. Probably the muscle fibres contract over a shorter than optimal length at smaller joint angles on the descending limb of the torque-position curve, when the pennation angle of the fibres would also be greater. If the pennation angle is greater then the force generation of the whole muscle would be lower in the same muscle. Greater pennation angle would also result in a lower contraction velocity of the whole muscle because the difference between the directions of the force vector representing the muscle fibres and the whole muscle becomes greater (Baratta et al. 1995). These architectural considerations suggest that maximal estimated velocity under L_{50} (C_{50}) is lower than that under L_{80} (C_{80}) experimental conditions.

Maximal estimated velocity at C_{50} is significantly greater than at C_{80}, but the difference is considerably less than under conditions of linearly increasing velocity. Probably the pennation angle had less of an influence on maximal estimated velocity under conditions of constant compared to linearly increasing velocity. The main influencing factor was not the pennation angle, but the rate of velocity development. In other words, the peak velocity was reached in a very short time under conditions of constant velocity, so short that the quadriceps could not extend the knee as fast as the driver rotated the shaft. Because the rate of velocity development of the knee extensors was lower at high constant velocities (0.52 rad, 1.02 rad) than it was for the driver, the quadriceps could not develop their maximal tension during the acceleration phase – at least not at the fastest applied constant velocities.

For example, if the preset constant velocity, acceleration and range of motion were 10 rad s^{-1}, 260 rad s^{-2} and 0.52 rad, respectively, then the knee extension would have been completed in 52 ms. However, the knee extension time under conditions of constant velocity would have been even less because 20 ms was needed to reach the final target velocity. Because the acceleration of the lever arm rotated by the driver was greater than the acceleration of the shank, it can be imagined that the shank would have lagged behind the accelerating lever arm. Subsequently, the muscle would have become fully activated, but the remaining 32 ms would not have been long enough for the muscle to develop tension and produce torque. We therefore applied 25 N·m pre-tension in this study to avoid the delay in developing tension. Apparently, this threshold torque was not high enough and at the highest applied velocities the torque dropped to 0 at the beginning of the contraction, indicating the inability of the knee extensors to follow the motion of the lever arm.

The concavity of the M-ω curve

The a/M_0 value characterizes the concavity of the M-ω curve and it ranged between 0.10 and 0.35. The a/M_0 value was significantly greater on the ascending (1.39 rad–0.87 rad) than on the descending (0.87 rad–0.35 rad) limb of the torque-position curve. That the a/M_0 varied according to the location on the torque-position curve can be explained by the fact that the M_m at each applied velocity was significantly lower on the descending than on the ascending limb of the torque-position curve, indicating the lower working capacity. From the rearranged Hill equation ($M_m\omega + a\omega = bM_0 - bM_m$), it is clear that if the M_m is low then the rate of doing work becomes low. The lower a/M_0 value on the descending limb of the torque-position curve indicates a decreased working capacity of the knee extensors, i.e. the bM_0–bM is lower because less and less torque is generated due to the decreasing moment-arm of the knee extensors and the greater pinnation angle. It is also possible that the knee extensors work in a length range that is shorter than the optimal. Because the working capacity in this joint angle range is reduced by the limited torque generation, the rate of change of energy ($M_m\omega + a\omega$), i.e. power, is also depressed. From the Hill equation it is apparent that if the a/M_0 value increases then P_0 also increases. In other words, if the torque-velocity curve becomes less concave then the P_0 is greater. Indeed, we calculated the greatest a/M_0 and P_0 at L_{80} and the lowest at C_{50}. The magnitudes of a/M_0 and $\%M_{P0}$ were similar to those reported by Hill (1970), Wilkie (1950), Kaneko (1970), Kawahatsu and Ikai (1972), Kaneko et al. (1983), Tihanyi et al. (1982), and MacIntosh et al. (1993). Because power is the product of torque and velocity, the a/M_0 value also influences the M_{P0} and ω_{P0}, which is greater at L_{80} and C_{80} than at L_{50} and C_{50}, and M_{P0} and ω_{P0} is greater under conditions of linearly increasing, than of constant, velocities in accordance with our prior reasoning.

We conclude that M_m is the appropriate input variable for the Hill equation in contrast to M_p because M_m represents the working capacity of the muscle. The plateau phenomenon can be avoided if peak concentric torque is measured independently of joint angle position or M_m is calculated. Also, the training status of the subjects may decrease the neural inhibition and coactivation of the antagonist muscle at low velocities. On the ascending limb of the torque-position curve muscle can produce greater power than on the descending limb because the torque producing capacity is greater due to the greater moment arm and probably the smaller pinnation angle. The linearly increasing controlled velocity provides similar conditions for the contracting muscle than does the constant load condition. The results of the present study thus suggest that the history of contraction affects the in vivo M-ω relationship of the human quadriceps.

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