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Initial phase of maximal voluntary and electrically stimulated knee extension torque development at different knee angles

C. J. de Ruiter,[1] R. D. Kooistra,[1] M. I. Paalman,[1] and A. de Haan[1,2]

[1]*Institute for Fundamental and Clinical Human Movement Sciences, Vrije University, 1081 BT Amsterdam, The Netherlands; and* [2]*Institute for Biophysical and Clinical Research into Human Movement, Manchester Metropolitan University, Cheshire 5 T7 2HL, United Kingdom*

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De Ruiter, C. J., R. D. Kooistra, M. I. Paalman, and A. de Haan. Initial phase of maximal voluntary and electrically stimulated knee extension torque development at different knee angles. *J Appl Physiol* 97: 1693–1701, 2004. First published June 4, 2004; doi:10.1152/japplphysiol.00230.2004.—We investigated the capacity for torque development and muscle activation at the onset of fast voluntary isometric knee extensions at 30, 60, and 90° knee angle. Experiments were performed in subjects ($n = 7$) who had high levels (>90%) of activation at the plateau of maximal voluntary contractions. During maximal electrical nerve stimulation (8 pulses at 300 Hz), the maximal rate of torque development (MRTD) and torque time integral over the first 40 ms (TTI40) changed in proportion with torque at the different knee angles (highest values at 60°). At each knee angle, voluntary MRTD and stimulated MRTD were similar ($P < 0.05$), but time to voluntary MRTD was significantly longer. Voluntary TTI40 was independent ($P > 0.05$) of knee angle and on average (all subjects and angles) only 40% of stimulated TTI40. However, among subjects, the averaged (across knee angles) values ranged from 10.3 ± 3.1 to 83.3 ± 3.2% and were positively related ($r^2 = 0.75$, $P < 0.05$) to the knee-extensor surface EMG at the start of torque development. It was concluded that, although all subjects had high levels of voluntary activation at the plateau of maximal voluntary contraction, among subjects and independent of knee angle, the capacity for fast muscle activation varied substantially. Moreover, in all subjects, torque developed considerably faster during maximal electrical stimulation than during maximal voluntary effort. At different knee angles, stimulated MRTD and TTI40 changed in proportion with stimulated torque, but voluntary MRTD and TTI40 changed less than maximal voluntary torque.

voluntary activation; electromyography; rapid muscle strength; maximal rate of force development

THE RATE AT WHICH MUSCLE FORCE DEVELOPS at the onset of muscle contraction is reflected by the rate of rise of joint torque, which is an important determinant of performance in various (sports) activities. Duration of many movements, such as postural balance corrections in everyday life, cycling, boxing, sprinting, and jumping, requires contraction times in the order of 50–250 ms (e.g., Refs. 21, 23), which is considerably shorter than the time needed to reach maximal isometric torque levels (~500 ms). Indeed, as would be expected, performance during fast ballistic and/or power-demanding tasks has been found to benefit from high rates of force development (24, 29).

There are several factors, such as muscle fiber-type composition (7), tendon stiffness (32), and temperature (11), that affect the rate of torque and muscle force development. However, probably the most important factor is muscle activation. First, the rate of torque rise strongly depends on muscle activation, and it has been shown that maximal rates of force development can only be obtained at high pulse rates during electrical stimulation (7), pulse rates that are, in both animal (8) and human muscle (11, 13), about double that needed for maximal isometric force production. Second, Van Cutsem et al. (37) showed that, also in vivo, the rate of torque development depends on the discharge rate (muscle activation) of the activated motor units. Third, the rate of torque development can be improved by a training-induced increase of muscle activation, as was shown by increases in surface electromyography (EMG) (1, 18) and motor unit firing rates (37) at the start of torque development.

It is a common finding that, at the plateau of a maximal voluntary isometric contraction, healthy subjects can make use of ~95% of the maximal torque capacity (MTC) of their muscles (6, 13, 14, 36), although lower percentages (85–90%) have also been reported (2, 5). Nevertheless, to date, it is still unknown to which extent subjects are able to make use of the muscles' maximal capacity for isometric torque development during fast voluntary muscle contractions. Therefore, the primary goal of the present study was to investigate this in the knee extensors, which in many sports are involved in rapid torque generation.

Given the high [300 Hz (11, 13)] pulse frequencies needed to obtain the muscles' maximal capacity of torque development during maximal electrical stimulation and the high discharge rates of activated motor units after specific training during fast torque development (37), the first hypothesis was that the maximal voluntary rate of torque development would be slower than the electrically induced rate of torque development because initial muscle activation at the start of torque rise was expected to be lower during voluntary contractions. Moreover, subjects with various training backgrounds were included in the study, and our second hypothesis was that the intersubject variation in initial muscle activation and consequently rate of torque development would be greater than the intersubject variation in muscle activation at the plateau of a maximal isometric contraction.

For relatively small muscle groups, voluntary activation (VA) during static effort seems to be close to maximal and independent of muscle length (6, 14). However, for the knee extensors, it has been reported that maximal VA at the plateau phase of an isometric contraction is knee angle dependent (3,

Address for reprint requests and other correspondence: C. J. de Ruiter, Institute for Fundamental and Clinical Human Movement Sciences, Vrije Universiteit, Van der Boechorststraat 9, 1081 BT Amsterdam, The Netherlands (E-mail: C_J_de_Ruiter@FBW.VU.NL).

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4). Moreover, the effects of knee angle on torque rise during maximal electrical activation and VA are, to the best of our knowledge, unknown. From work on isolated preparations, it could be deduced that isometric contractile speed changes approximately in proportion with force when muscle (fiber) length is varied (10, 15, 31, 35). However, in vivo, muscles are connected to other muscles and structures (e.g., bone) via connective tissue, and the contractile part of the muscle interacts with substantially more elastic structures in series than in most in vitro and in situ studies. These factors may affect the length dependency of torque rise. Moreover, muscle activation in the aforementioned studies probably was not high enough to obtain maximal rates of isometric force development (7, 10). Nevertheless, based on these earlier studies (10, 15, 31, 35), our third hypothesis was that the rates of maximal voluntarily and electrically induced isometric torque development would change in proportion to the maximal isometric torque at different knee angles.

METHODS

Subjects. Seven healthy male subjects (age: 19–40 yr; weight: 79–85 kg; height: 1.72–1.94 m) with different training backgrounds signed informed consents, and the local ethics committee approved the study. The subjects came to our laboratory three times with at least 2 days between visits. On the first day, subjects were familiarized with the procedures and the electrical stimulation and practiced to perform maximally fast isometric knee extensions starting from full relaxation, thus without exerting any preflexion or preextension torque. Subjects with VA (see *Isometric torque measurement*) lower than 90% at the plateau of a maximal voluntary contraction (MVC) at 90° knee angle were excluded from further participation. On the other 2 days, subjects were tested in random order at 30 and 60°, and at 90 and 60° knee angles (see *Protocol*). We chose not to investigate three angles in a single session, because in that case the duration of a session would have been over 1.5 h, which might have led to some form of unwanted fatigue or decreased motivation. However, we did want to have information about test-retest variability, and therefore we performed the measurements at 60° on both experimental days.

Isometric torque measurement. Contractile properties of the knee extensors of the dominant leg were investigated using a custom-made dynamometer. Subjects sat in a backward-inclined (15°) chair with a 100° hip angle. Subjects were firmly secured with straps fastening hips and shoulders. The lower leg was tightly strapped to a strain gauge transducer (KAP, E/200 Hz, Bienfait BV Haarlem, The Netherlands) placed ~25 cm distal from the knee joint, which measured the force exerted at the shin. The real-time force applied to the force transducer was displayed online on a computer monitor and digitally stored (1 kHz). At each angle, force signals were automatically corrected for gravity: the average force applied by the weight of the limb at the transducer during the first 50 ms after the start of a measurement, with the subject sitting relaxed in the dynamometer, was set at zero force by the computer program. Extension torque was calculated by multiplication of force with the individual lever arm.

To minimize the dampening effect that exists in any interface between shin and aluminum transducer, but to simultaneously avoid pain, this interface only consisted of a standard hard shin protector as used during soccer. Before every muscle contraction, the upper leg was firmly strapped down to the seat just above the knee; this strap was released between contractions. The axis of rotation of the knee was aligned with the axis of rotation of the dynamometer. Measurements were made at 30, 60, and 90° knee flexion angles (0° indicated a straight leg). The compliance of the dynamometer at the position of the transducer was 1.4×10^{-4} deg/Nm. The dynamometer was constructed to minimize the changes in knee angles during force development, which nevertheless always occurred when the knee extensors went from the passive to active state during an isometric contraction. The dynamometer arm was set in a position that the indicated knee angles were angles in the active state when subjects exerted torque at ~50% of maximal torque. During pilot experiments using an electrogoniometer attached to the lateral side of the knee, the changes (passive-active angle) in knee angle were found to be 3–7° and independent of the knee angle. Before the experiments, the knee angles were set manually using a goniometer and the greater trochantor of the femur, the lateral epicondyle, and the lateral malleolus as anatomic landmarks.

Electrical stimulation. Constant current electrical stimulation (100-μs pulses) was applied using a computer-controlled stimulator (model DS7H, Digitimer, Welwyn Garden City, UK) and a pair of self-adhesive surface electrodes (Schwa-medico). After shaving of the skin, the cathode (5 × 5 cm) was placed in the femoral triangle above the femoral nerve, and the anode was placed transversely over the gluteal fold. At the start of each session, stimulation current was increased until force in response to a burst of eight pulses applied at 300 Hz (octet) leveled off. The latter always occurred between 300 and 500 mA, and it was assumed that, at that point, all of the knee extensor muscle fibers were activated. Pilot experiments ($n = 8$) showed that the same current level provided maximal activation at different knee angles. Moreover, in addition to the leveling off of torque with any further increase in stimulation current, action potential size in response to twitch stimulation also leveled off. From previous experiments (13), we knew that the maximal rate of torque development (MRTD) could only be obtained during stimulation at 300 Hz. Additional pilot experiments showed that a minimum of six pulses was required to reach the MRTD in every subject. Therefore, in the present study, eight pulses (at 300 Hz) were applied to ensure that MRTD was always attained.

Surface EMG. EMG activity of the vastus lateralis, rectus femoris, and long head of the biceps femoris muscle was recorded using surface Ag-AgCl electrodes (diameter = 17 mm, F-454AE, Medeq, Gnosis GmbH, Austria). After shaving, roughening, and cleaning of the skin with 70% ethanol, electrodes were placed in a bipolar configuration, parallel to muscle-fiber direction, with an interelectrode distance of 40 mm at the distal one-third of the muscles. Reference electrodes were placed on the left and right patella and on the right tibia. Surface EMG signals were amplified (×1,000), digitized (1 kHz), and stored with the force signal on computer disc. The custom-built amplifiers (INPHO Sense Medical Electronics, Kortenhoef, The Netherlands) had a frequency response of 10 (6 dB) to 10,000 Hz (12 dB) with an isolation rejection ratio exceeding 156 dB. Electrode sites were marked to ensure identical placement of electrodes during the next session.

Protocol. To make a straight-forward comparison between maximal voluntary and electrically induced torque rise, isometric knee extensions were performed without any pretension and/or counter movement, since we anticipated that measurements with pretension and/or prestretch would have been more difficult to standardize.

At each of the two knee angles investigated during a session (either 30 and 60° or 90 and 60°), the following procedure was followed. First, there were approximately five isometric contractions at ~50% MVC, which were needed to set the lever arm such that the correct active knee angle was obtained. Thereafter, the stimulation current was increased in five to seven steps until maximal activation was reached, i.e., until no further increase of torque in response to octet-stimulation occurred. Together, the foregoing contractions served also as warm-up. The actual measurements started with two maximal voluntary extension and flexion contractions, which were made under strong verbal encouragement and with online visual feedback. The flexion contractions were made to obtain maximal surface EMG values of the biceps femoris muscle at the three knee angles, which were used to normalize flexor EMG during isometric knee extensions. Only if the last attempt was >10% higher than the first was an extra attempt made. In this way, the total number of contractions was limited to prevent fatigue. In addition, 3 min of rest were held between contractions.

Subsequently, one octet-stimulation was applied on the relaxed muscle; from this contraction, torque development under conditions of maximal activation was determined. This was followed by three to six voluntary attempts to increase knee extension torque from a fully relaxed state as fast (and hard) as possible. The emphasis of instruction was on fast (33), but peak torque had to reach at least 70% of MVC values. Attempts during which torque deviated from baseline values before the onset of the maximal attempt were discarded. Subjects were encouraged to improve on the time it took to develop torque from 2 to 30% MVC value. In addition, they were told what their 2–30% MVC time during octet stimulation was, and they were encouraged to try to improve on that time. If the last attempt was >1 ms faster than the previous attempt, an extra attempt was made, with a minimum of three and a maximum of six attempts. Finally, to calculate VA at the plateau of an MVC, octet stimulation on the relaxed knee extensor muscles followed by octet stimulation superimposed at the plateau of an MVC was performed twice, where VA = 1 − [octet amplitude at MVC·(octet amplitude at resting muscle)$^{-1}$]·100% (4, 9, 36, 38).

If force had changed >1% during the 100 ms before the superimposition of the octet, the attempt was discarded and one additional attempt was made. If necessary, the timing of the superimposed octet, which was set at an individually adjusted time (usually 1.5–3 s after torque onset) before each attempt, was adjusted. From the attempt with the highest value of VA, the MTC of the knee extensors was calculated using the equation MTC = (maximal voluntary torque)·VA^{-1}·(100%)$^{-1}$ (12). MTC is an estimate of the maximal isometric torque under conditions of maximal muscle activation.

Data analysis. As a measure of the rate of torque development, we used the torque time integral over the first 40 ms (TTI40) after the onset of torque development. TTI40 reflects the entire time history of the start of muscle contraction. Onset of torque development (start of the contraction) was defined as the point at which the force curve exceeded average baseline force by more than three standard deviations (~1 N measured at the shin transducer). TTI40 obtained with electrical octet stimulation was assumed to denote the maximal capacity of force development of the knee extensor muscles under conditions of maximal activation.

We chose to integrate torque over the first 40 ms because, after octet stimulation, there was still a steep rise of torque without signs of relaxation during the first 40 ms (e.g., see Fig. 5*A*), indicating that the muscle was still maximally activated.

Some measure of MRTD has often been used as an indicator of the maximal contractile rate (1, 7, 10, 11, 13, 24, 29, 32, 33, 38). Therefore, in the present study, besides TTI40, peak MRTD during electrically stimulated and fast voluntary contractions was calculated and taken as the maximum of the filtered (fourth-order, 50-Hz, low-pass filter), differentiated torque signals of the fastest contractions. This filter was found not to affect the course of torque development; it only removed high-frequency noise from the signal. To correct for differences in maximal torque among the subjects and because we expected MRTD to change in proportion to the maximal torque produced at each angle, MRTDs were normalized to maximal torque at each angle. If torque during MVC was higher than MTC (see DISCUSSION), MVC torque was taken as the maximal torque. In addition, the time to MRTD was defined as the time from the start of the contraction to the moment at which MRTD was reached.

As an indication of VA at the very start of muscle contraction, rectified surface EMG (rsEMG) signals obtained during fast voluntary contractions were averaged over 40 ms before the onset of torque development. This was done because the very first EMG changes in some of the voluntary contractions were seen up to 40 ms before torque onset, indicating that electromechanical delay (EMD) was shorter than 40 ms in all contractions. During octet stimulation, there was a steep onset of torque, and the start of muscle activation was computer controlled, and consequently more reliable EMD values could be obtained with electrical stimulation. EMD was defined as the time lag between the stimulation artifact in the EMG signal caused by the first pulse of the octet and onset of torque development (as defined above).

EMG signals were low-pass filtered at 500 Hz (fourth-order Butterworth) before they were rectified. rsEMG was expressed as a percentage of rsEMG values obtained at the plateau of the highest MVC at the same knee angle: for each muscle, rsEMG was averaged over 100 ms before the moment the highest torque at the plateau was produced, and this value was taken as 100%. No significant differences were found between rsEMG of rectus and vastus during torque development, and therefore the average values of both muscles will be presented.

Statistics. The results are presented as means ± SD. Knee-angle effects (means ± SD) were tested for significance ($P < 0.05$) with repeated-measures ANOVA followed by Bonferroni post hoc tests. Pearsons's correlation coefficient was calculated to establish significance of correlation. The test-retest reliability between the two measurements at 60° made on different days was analyzed using the intraclass correlation coefficient (ICC). Unless indicated otherwise, for each subject, the mean value of the two measurements at the 60° knee angle was used for calculation of group mean values at 60°, and statistical analysis related to the effects of knee angle.

RESULTS

Maximal torque. Average torque of the two measurements at the 60° knee angle during maximal voluntary knee extension was 315.1 ± 64.4 Nm; MVC torque at 30° and 90° was significantly lower (Fig. 1, Table 1). Relative to the maximum torques obtained at 60° (Fig. 1), at the 30° knee angle, voluntary knee extension torque was low (56.2 ± 7.09%) compared with peak torque obtained during octet stimulation (82.7 ± 10.5%). ICCs for the above parameters were high (Table 1).

VA. VA (Table 1) at 30, 60, and 90° knee angle was 89.9 ± 11.0, 88.9 ± 7.0, and 96.5 ± 2.9%, respectively, with a tendency ($P = 0.07$) for better activation at 90°. With these values for VA, the MTCs (Table 1) were calculated. At each knee angle, MTC, as calculated from MVCs with superimposed stimulation, was found to be similar ($P < 0.05$) to the MVC found in contractions without superimposed electrical stimulation. This indicates that VA at torque plateau of an

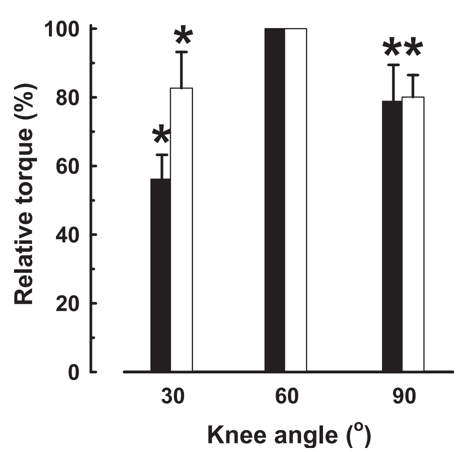

Fig. 1. Normalized torque-angle relations for maximal voluntary knee extension (solid bars) and electrical stimulation with 8 pulses applied at 300 Hz (open bars). Values are means ± SD ($n = 7$); torque at 60° knee flexion = 100%. *Significantly different from value at 60° ($P < 0.05$).

Table 1. *Maximal torque production and voluntary activation*

	30°	60° (1st)	60° (2nd)	90°	ICC
MVC, Nm	182.7±40.7*	305.8±57.8	319.8±64.8	242.2±34.1*	0.95†
MTC, Nm	183.5±43.3*	302.8±53.5	305.2±64.0	231.4±30.8*	0.97†
VA, %	89.9±10.9	88.8±7.7	89.0±9.2	96.5±2.9	0.91†
Octet, Nm	110.1±25.5*	131.4±23.7	134.7±27.7	107.4±24.6*	0.97†

Values (means ± SD, n = 7) for maximal voluntary isometric knee extensions (MVC), maximal knee extension torque capacity (MTC), voluntary activation (VA), and peak torque after electrical stimulation with 8 pulses applied on the resting knee extensors (Octet) at 30, 60, and 90° knee angle. For the 2 measurements made at 60° on different days, the intraclass correlation coefficient (ICC) was calculated and presented in the last column. *Significantly different from value at 60°. †Significant ICC.

MVC was high in all subjects. Moreover, ICC for VA was acceptable (Table 1).

MRTD. The highest values for MRTD were obtained at 60° knee angle (Table 2). After normalization to the maximal torque obtained at each angle, there was a significant main effect of knee angle for the voluntary contractions (post hoc tests were not significant). After normalization, stimulated MRTD was significantly higher at 30° (Fig. 2). However, when stimulated MRTD was normalized to the peak torque reached during the same electrically induced contraction, the knee angle effect disappeared. After this way of normalization, MRTD values at 30, 60, and 90° became 2.15 ± 0.38, 2.08 ± 0.45, and 1.85 ± 0.26 %peak stimulated torque/ms, respectively ($P > 0.05$).

Surprisingly, at each knee angle, voluntary and electrically induced MRTD were similar (P = 0.86; Table 2, Fig. 2). However, the time to MRTD was, on average, almost twice as long ($P < 0.05$) during voluntary compared with electrically induced contractions (Table 2). During fast voluntary contractions, time to MRTD tended to decrease with an increase of knee angle. However, the value at 30° was not significantly different (P = 0.06) from that at 60° (Table 2).

Initial phase of torque development. EMD during octet stimulation was not significantly different among knee angles (Table 2).

TTI40 was significantly higher for the electrically induced compared with the voluntary fast contractions (Table 2). There was no significant relation (r^2 = 0.08) between the latter and the former among the subjects, indicating that differences in contractile speed of the muscle tendon complex as expressed in the electrically stimulated TTI40 did not determine voluntary TTI40. The only angle effect found was for electrically induced TTI40, which was significantly lower at 90° than at 60° knee angle (Table 2). To correct for the absolute torque differences among the subjects and among knee angles, voluntary TTI40 was normalized in two different ways. Voluntary TTI40 was expressed as a percentage of the electrically induced TTI40 at each knee angle (Fig. 3*A*) and relative to the maximal isometric torque (either MTC or MVC) obtained at each knee angle (Fig. 3*B*).

Figure 3*A* shows that, during voluntary fast contractions, TTI40 was, on average, only ~40% of the TTI40 that the muscle was capable of during maximal electrical activation. There was a significant (P = 0.02) main effect of knee angle, but pairwise comparisons were not significant. There was no significant knee-angle effect when voluntary TTI40 was normalized to maximal isometric torque at each angle (Fig. 3*B*). The highest values for TTI40 induced by electrical stimulation were obtained at 60° (Table 2). After normalization to maximal isometric torque at each angle, stimulated TTI40 was significantly higher at 30° (Fig. 3*B*). However, and similar to what

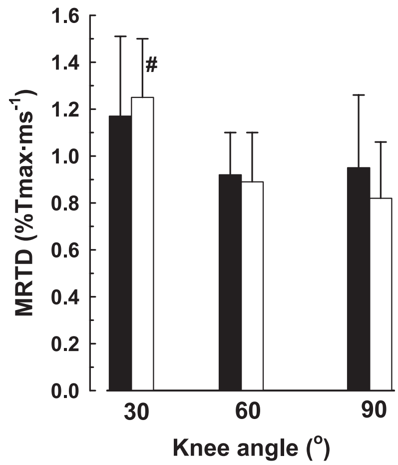

Fig. 2. Maximal rate of torque development (MRTD) normalized to the maximal torque (Tmax) obtained at each knee angle during isometric knee extensions at different knee angles with voluntary attempts (filled bars) and with electrical nerve stimulation (open bars). Values are means ± SD of n = 7 subjects. MRTD was similar with electrical and voluntary activation ($P > 0.05$). During voluntary activation, there was a significant main effect of knee angle without post hoc differences. #Significantly different from 60 and 90° ($P < 0.05$).

Table 2. *Parameters related to torque development*

	30°	60° (1st)	60° (2nd)	90°	ICC
stimTTI40, N·m^{-}·s^{-}	0.85±0.27	0.91±0.20	0.95±0.15	0.73±0.21*	0.92†
volTTI40, N·m^{-1}·s^{-1}	0.32±0.27	0.33±0.24	0.36±0.23	0.35±0.21	0.98†
stimMRTD, N·m^{-1}·s^{-1}	2,396±806	2,856±1,092	2,804±912	1,997±597*	0.96†
volMRTD, N·m^{-1}·s^{-1}	2,202±890*	2,996±902	2,801±944	2,297±716	0.76†
stimTimetoMRTD, ms	36±8	38±2	34±7	30±9	0.11
volTimetoMRTD, ms	67±20	58±10	56±11	52±10*	0.98†
rsEMG$_{-40\text{-}0}$, %	27.3±14.2	22.1±12.6	25.2±18.4	24.5±10.1	0.82†
EMD, ms	21.6±3.2	20.0±1.0	21.3±1.7	20.1±3.1	0.29

Values (means ± SD, n = 7) for torque time integral during the first 40 ms of torque development (TTI40), maximal rates of torque development (MRTD), and time to MRTD of electrically stimulated (stim) and maximal voluntary (vol) fast knee extensions are presented in *rows 1–6.* Average rectified surface EMG during 40 ms before fast voluntary torque onset (rsEMG$_{-40\text{-}0}$) and electromechanical delay (EMD) are presented in *rows 7* and *8.* For the 2 measurements made at 60° on different days, the ICC was calculated and presented in the last column. *Significantly different from value at 60°. †Significant ICC.

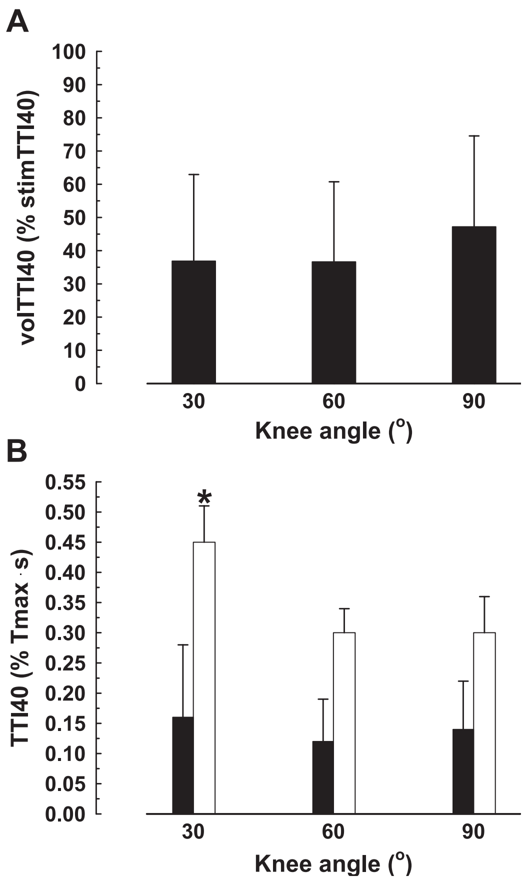

Fig. 3. Torque time integral over the first 40 ms (TTI40) of fast voluntary torque development (volTTI40) as a function of knee angle, as a percentage of the electrically induced TTI40 (stimTTI40) at each angle (*A*), and normalized to the maximal isometric torque (filled bars in *B*) obtained at each angle (Tmax). Normalized stimTTI40 is indicated by the open bars in *B*. Values are means ± SD of $n = 7$ subjects. There was a significant main effect of knee angle without post hoc differences (*A*). *Significantly different from 60° ($P < 0.05$).

occurred with MRTD, when stimulated TTI40 was normalized to the peak torque reached during the same electrically induced contraction, there was no significant effect of knee angle. After this way of normalization, stimulated TTI40 values at 30, 60, and 90°became 0.76 ± 0.10, 0.71 ± 0.13 and 0.70 ± 0.15 %peak stimulated torque/s, respectively ($P < 0.05$).

Figure 4 shows that the ability to make use of the muscles' capacity for fast torque development during the first 40 ms varied substantially among subjects (from 10.3 ± 3.1% in *subject 7* to 83.3 ± 3.2% in *subject 1*) and that this ability was relatively stable across knee angles and experimental days (the 2 measurements at 60°).

To visualize the different abilities for initial fast torque development among our subjects, torque time traces (at the 60° knee angle) of the best (*subject 1*) and worst performer (*subject 6*), who had comparable values for TTI40 when induced by octet stimulation, are presented in Fig. 5. Note that the rate of torque development on electrical octet stimulation was very similar in both of these subjects (Fig. 5*A*), indicating that there were only small differences in the maximal contractile rate of muscle force development between these subjects. However, there was a noticeable difference with respect to torque rise during the voluntary fast contractions (Fig. 5*B*). The steepest parts of the torque traces (MRTD) in Fig. 5*B* are comparable for both subjects. However, note that MRTD was reached 33 ms later after the start of torque development in *subject 6* than in *subject 1*. The different capacities for fast voluntary torque rise become even more evident when voluntary and electrically induced torque rises are plotted together for both subjects (Fig. 5, *C* and *D*); only the best performer (*subject 1*) approached the electrically induced torque rise (dashed line) during a fast voluntary attempt (Fig. 5*D*). Note that the subjects had different capacities for fast voluntary torque development despite the fact that they all had very high VA at the plateau of MVC. Given the small variation in VA at torque plateau among subjects, it is not surprising that there were no significant correlations between VA and TTI40 at any of the knee angles: r^2 values at 30, 60, and 90° knee angle were 0.26, 0.14 and 0.46% stimulated TTI40, respectively.

Agonist surface EMG. During 40 ms before the start of fast voluntary isometric knee extension torque development, average rsEMG of the knee extensors expressed relative to rsEMG at the plateau of the highest MVC at each knee angle (100%) was ~25% and independent of knee angle (Table 2). Among subjects, rsEMG of the knee extensors ranged from 5.8 ± 1.3% (average value of four measurements at three knee angles) in the subject with the lowest voluntary TTI40 (*subject 7*) to 40.3 ± 5.2% in the subject with the highest TTI40 (*subject 1*). The different EMG patterns among subjects during fast torque development are clearly illustrated in Fig. 5, *E* and *F*. Note the early and high EMG burst for *subject 1* (Fig. 5*F*).

There were significantly positive linear relations (mean average data points) between rsEMG of the knee extensors before the start of torque development on the one hand and voluntary TTI40 ($r^2 = 0.75$) on the other hand; voluntary TTI40 normalized to maximal torque production at 60° ($r^2 = 0.74$), and voluntary TTI40 normalized to TTI40 obtained with octet stimulation ($r^2 = 0.76$, Fig. 6). Significant relations were also obtained when the values were analyzed separately for each knee angle. For example, the relations between initial rsEMG and voluntary TTI40 at 30°, 60° (first day), 60° (second day), and 90° were all significant, and the r^2 values were 0.62, 0.59,

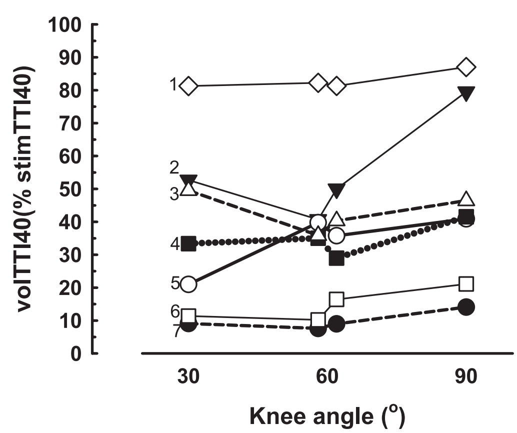

Fig. 4. Individual values of torque time integral over volTTI40 as a function of knee angle and as a percentage of stimTTI40 at each angle and numbered. Values of 4 measurements obtained at 3 different knee angles on 2 different days (there were 2 measurements at 60°) are shown. Different symbols represent values for different subjects.

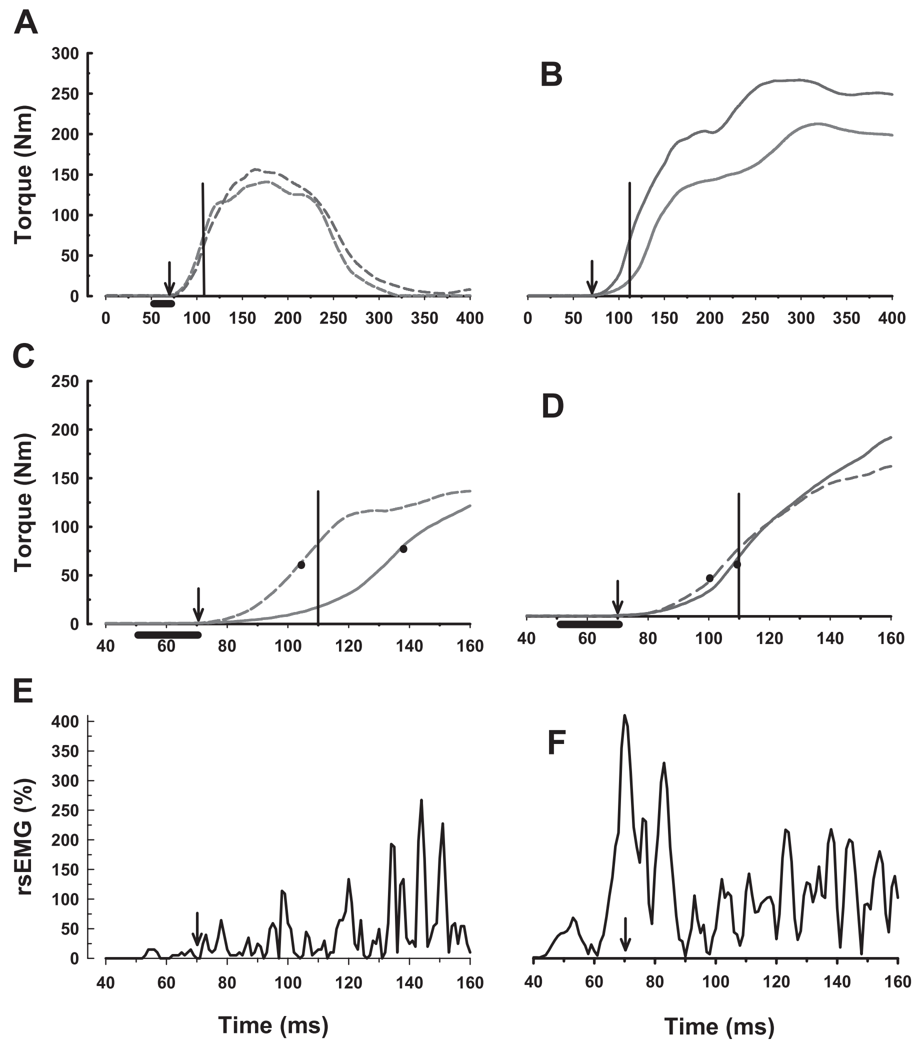

Fig. 5. Torque time traces of 2 subjects (bold line *subject 1*, thin line *subject 6*) with similar responses after electrical nerve stimulation (8 pulses at 300 Hz indicated by the black bars under the time-axis) at 60° knee angle (*A*) but of which the voluntary attempts were considerably different (*B*). The voluntary and electrically induced torque responses are plotted together on a different time scale for subject 6 (*C*) and for *subject 1* (*D*). Note that only *subject 1* (*D*) was able to approach the electrically induced torque rise (broken line) during a voluntary attempt (solid line). Arrows at time = 70 ms indicate the start of torque development, and the vertical lines in *A–D* are plotted to visualize the border of the areas under the curves (TTI40) that were used as an index of initial force development. Dots on the torque traces in *C* and *D* indicate the point of maximal rate of torque development. Rectified surface EMG (rsEMG) of the vastis lateralis muscle is shown as a percentage of average EMG at torque plateau of the highest MVC attempt (100%) for *subject 6* (*E*) and *1* (*F*).

0.83, and 0.59% stimulated TTI40, respectively. In addition, there was a significant negative linear relation (mean average data points) between initial rsEMG and time to voluntary MRTD ($r^2 = 0.78$).

Antagonist surface EMG. During the plateau phase of maximal voluntary isometric knee extensions, rsEMG of the long head of the biceps femoris muscle was 8.3 ± 2.9, 9.1 ± 5.2, and 8.5 ± 4.7% of maximum values obtained at the 30, 60, and 90° knee angle, respectively ($P > 0.05$). Biceps femoris EMG activity during the 40 ms before the start of fast torque development ranged (all measurements) from 0.44 to 2.91% of maximum values, also without a significant knee angle effect.

DISCUSSION

Voluntary TTI40 was, on average, only 40% of electrically stimulated TTI40, but there was a considerable range (10.3–83.3%) among our subjects. Moreover, voluntary TTI40 was positively related to the surface EMG of the knee extensors before the start of torque development, whereas it was not related to the TTI40 induced with electrical stimulation. Therefore, the ability for fast torque development seemed to predominantly depend on the increase of muscle activation at the beginning of the contraction and not so much on the muscles' maximal contractile rate. Across knee angles, there were proportional differences of torque, MRTD, and TTI40 during electrical stimulation, which was in line with the third hypothesis. However, compared with stimulated torque, MVC torque at 30° was relatively low. Consequently, after normalization to the MVC at each angle, MRTD and TTI40 were relatively high at the 30° knee angle.

At the plateau of isometric contractions. Both the maximal torque values and the shape of the torque angle relation of maximal voluntary knee extensions are within the range reported by others (4, 16, 25, 27, 28). In the present study, VA tended to be somewhat lower ($P = 0.08$) at the shorter muscle lengths (Table 1), which is similar to the results of Becker and Awiszus (4) but in contrast to work of Babault et al. (3) and also not in line with recent findings of Newman et al. (27) who did not find an effect of knee angle on VA. However, it has to be noted that, in the present study, knee extension torque during MVCs that were performed without superimposed stimulation was often higher than the torque levels reached during attempts with superimposed electrical stimulation, during which subjects apparently anticipated on the (unpleasant) burst stimulation. Therefore, at each of the knee angles, average MVC and MTC were similar (Table 1; $P < 0.05$), indicating

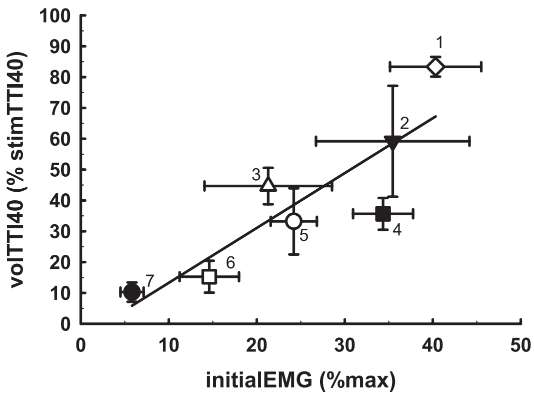

Fig. 6. The volTTI40 expressed as % stimTTI40 as a function of voluntary activation (initialEMG). Individual data (means ± SD of 4 attempts at 3 different knee angles) are plotted (see also Fig. 4). The initialEMG is the mean value of the rsEMG obtained during 40 ms before the start of torque development, expressed as a percentage of the values obtained at the plateau of the highest MVC at each angle (100%). When for each subject the average values for both parameters were taken, there was a significant positive linear relation (r^2 = 0.76) between both parameters: $y = 1.78x - 4.53$.

that VA was high in all subjects. This is not surprising, because subjects with poor activation were not included in the present study (see METHODS). Obviously, subjects with poor activation at plateau MVC would have had poor activation at the start of fast torque development.

Initial phase of fast torque development. An unexpected finding was that there were no differences between MRTD during fast voluntary contractions and during electrical stimulation. However, the time to MRTD was significantly longer during fast MVCs (Table. 2). The most likely explanation is that, during voluntary effort, it takes longer before maximal saturating intracellular calcium concentrations are reached than during electrical-burst stimulation with 300 Hz. These findings also show that the time to MRTD has to be taken into account and that MRTD in itself cannot straight-forwardly be used to quantify voluntary rate of torque development. We have no satisfactory explanation for the tendency of voluntary time to MRTD to decrease with increasing knee angle. However, because this knee angle effect was absent with electrical stimulation, a (subtle) knee angle dependent difference in muscle activation, rather than a biomechanical factor, may account for this tendency.

A prominent finding of the present study was that voluntary TTI40 was, on average, only 40% of the electrically induced TTI40 (Fig. 3*A*), but, as anticipated, voluntary TTI40 varied considerably among subjects and ranged from 10.3 to 83.3% stimulated TTI40.

In principle, voluntary torque development may have been affected by antagonist activity (coactivation). However, in the present study, coactivation could be ignored, because at all knee angles, very low levels (~1%) of antagonist EMG were found at the start of torque development. Even at the plateau of a MVC, antagonist activity was relatively low (~9%) and similar at all knee angles. The latter finding is in accordance with the results of others (27, 30).

rsEMG before the start of torque development was ~25% of maximum values at all knee angles. There was a significant positive linear (r^2 = 0.76) relation between initial rsEMG and voluntary TTI40 (Fig. 6). Moreover, there was no relation (r^2 = 0.08) between voluntary and electrically induced TTI40. These findings strongly suggest that activation of the knee extensors was the most prominent determinant of initial torque development.

Knee-angle effect. There was no significant effect of joint angle on EMD, which is in contrast to what was recently shown for human medial gastrocnemius muscle (26). Apparently, within the present range of knee angles, the potential differences in internal slack to be taken up by the contractile elements were not large enough to lead to detectable differences in EMD. The EMD of ~20 ms found in the present study is considerably shorter than the 40 ms (32) and 100 ms (39) reported for knee extensors but similar to recent values obtained for gastrocnemius muscle (26). The low ICC for EMD was predominantly due to the very similar EMDs among subjects; consequently, even modest variation (range: 0–4 ms) between the two measurements within the subjects will lead to a relatively low ICC (see also stimulated time to MRTD; Table 2).

Voluntary TTI40 (Fig. 3*B*) was similar at different knee angles after normalization to maximal isometric torque at each angle. However, the absolute values of voluntary TTI40 were also very similar across knee angles. It may have been that, although the within-subject variation in TTI40 was low relative to the between-subject variation (ICC = 0.98), it was too high to detect relatively small potential effects of knee angle on this parameter.

After normalization to the maximal voluntary isometric torque, MRTD was significantly higher at 30° (shortest muscle length) during electrical stimulation, and it tended to be higher at 30° during voluntary effort (Fig. 2*A*). Moreover, normalized TTI40 during electrical stimulation was also significantly higher at 30° (Fig. 3*B*). This is not in accordance with earlier in vitro/in situ studies, which showed that contractile speed and force changed approximately in proportion with muscle length (15, 31, 35). Recently, De Haan et al. (10) showed that, in maximally activated rat medial gastrocnemius muscle, the maximal rate of force development decreased in proportion to the maximal isometric force at lengths up to optimum length. Above optimum length, tetanic force development becomes slower (19), but this may occur predominantly during the later phase of force rise when a redistribution of sarcomere lengths may have developed (19) and not necessarily at the initiation of force development, which was investigated in the present study.

Note, however, that at the 30° knee angle the knee extensors muscles operate on the steep part of the ascending limb of their length-tension relation (20). Therefore, and as suggested before (34), after activation at 30°, shortening of the contractile elements, at the expense of lengthening of the series elastic structures, may bring the contractile elements further down the ascending limb of their length-tension relation. Consequently, in the early phase of a contraction at the 30° knee angle, when TTI40 and MRTD were obtained, more cross bridges may have contributed to torque production than at the plateau of MVC. Moreover, the unavoidable 3° to 7° knee extension, which always occurred during an isometric contraction (see METHODS), probably also contributed to a decrease of the number of force-producing cross bridges in the course of a single contraction at 30°. This would also explain why at 30° peak stimulated torque was ~60% of MVC torque, whereas at 60 and 90°, when the contractile elements function more on the plateau of their length-force relation, it was only 40–45% (Table 2). Thus, on the ascending limb of the torque-angle relation (30°), it may be misleading to normalize parameters obtained during the early phase of torque production to MVC torque. Indeed, the angle effects for MRTD and TTI40 during electrical stimulation disappeared after normalization to the peak torque reached in the same contraction instead of MVC torque. Thus, during electrical stimulation at different knee angles, MRTD, TTI40, and torque did change in proportion. During voluntary contractions, this was also found for MRTD (although with different times to MRTD across knee angles) but not for TTI40.

Functional significance. The rate at which torque develops probably is an important determinant of performance in various (sports) activities (1, 22, 24, 29). In the present study, torque development was investigated without pretension and/or countermovement, similar to what occurs during getting out of the blocks at the start of a sprint in track and field and with kicking or punching during karate and boxing. Moreover, power production during short concentric contractions benefits from high levels of instantaneous muscle activation (8). Nevertheless, although increased rates of force development after resistance training have been found and related to increases of the neural drive (1, 17, 37), the exact extent to which the present results are of functional significance for in vivo movements, with or without pretension and/or prestretch, remains to be established. In addition, it is unknown whether specific training can bring fast voluntary torque development to the levels that the muscles are capable of during maximal high-frequency electrical activation, and it remains to be investigated how specific this kind of training must be in relation to the test used.

In conclusion, the capacity for fast voluntary torque development at different knee angles varied considerably among subjects. This occurred despite the fact that all subjects were able to activate their muscles close to maximal at the plateau of an MVC. The present findings strongly suggest that the ability for fast torque development depends on the specific ability for fast muscle activation at contraction onset.

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