



# Knee and ankle joint torque–angle relationships of multi-joint leg extension

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## ABSTRACT

The force–length–relation ( $F$ – $l$ – $r$ ) is an important property of skeletal muscle to characterise its function, whereas for *in vivo* human muscles, torque–angle relationships ( $T$ – $a$ – $r$ ) represent the maximum muscular capacity as a function of joint angle. However, since *in vivo* force/torque–length data is only available for rotational single-joint movements the purpose of the present study was to identify torque–angle–relationships for multi-joint leg extension. Therefore, inverse dynamics served for calculation of ankle and knee joint torques of 18 male subjects when performing maximum voluntary isometric contractions in a seated leg press. Measurements in increments of 10° knee angle from 30° to 100° knee flexion resulted in eight discrete angle configurations of hip, knee and ankle joints. For the knee joint we found an ascending–descending  $T$ – $a$ – $r$  with a maximum torque of  $289.5 \pm 43.3$  N m, which closely matches literature data from rotational knee extension. In comparison to literature we observed a shift of optimum knee angle towards knee extension. In contrast, the  $T$ – $a$ – $r$  of the ankle joint vastly differed from relationships obtained for isolated plantar flexion. For the ankle  $T$ – $a$ – $r$  derived from multi-joint leg extension subjects operated over different sections of the force–length curve, but the ankle  $T$ – $a$ – $r$  derived from isolated joint efforts was over the ascending limb for all subjects. Moreover, mean maximum torque of  $234.7 \pm 56.6$  N m exceeded maximal strength of isolated plantar flexion ( $185.7 \pm 27.8$  N m). From these findings we conclude that muscle function between isolated and more physiological multi-joint tasks differs. This should be considered for ergonomic and sports optimisation as well as for modelling and simulation of human movement.

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## 1. Introduction

Skeletal muscle force production depends upon its length and shows a parabolic function. This so called force–length relationship ( $F$ – $l$ – $r$ ) has been established for isolated muscle preparations (Edman and Reggiani, 1987) and is explained by myofilament overlap and the cross-bridge theory of contraction (Huxley, 1957). For *in vivo* muscles, the  $F$ – $l$ – $r$  is converted at the joint into the relationship between torque and joint angle. Therefore, several difficulties arise: first, the force exerted by muscles is influenced by anatomical constraints like muscle architecture (Kawakami et al., 1998; Chow et al., 2000; Maganaris, 2001), elasticity of musculo-tendinous tissues (Maganaris and Paul, 2000; Muramatsu et al., 2002; De Monte and Arampatzis, 2008) and joint geometry (Maganaris et al., 2000; Krevolin et al., 2004; Maganaris et al., 2006). Second, voluntary muscle activation is not constant as a function of muscle length (Kennedy and Cresswell, 2001; Babault et al., 2003; Miyamoto and Oda, 2003; Pasquet et al., 2006). Finally, joint torques as measured by dynamometers can differ from real joint torques (Herzog, 1988) and the resultant joint torque is the sum of torques generated by all muscles crossing the joint.

According to this, there is lot of research (e.g. Herzog and ter Keurs, 1988; Chow et al., 1999; Ichinose et al., 2000; Maganaris, 2004; Winter and Challis, 2008a) concerning *in vivo*  $F$ – $l$ – $r$ . For the ankle joint the main findings of these investigations are that mm. soleus and gastrocnemii do not work over the total range of the  $F$ – $l$ – $r$ , but on the ascending limb and the plateau region of the  $F$ – $l$ – $r$  (Herzog et al., 1991b). However, variations have been observed indicating the possibility of m. gastrocnemius to operate on the plateau region and the descending limb of the  $F$ – $l$ – $r$  (Winter and Challis, 2008b). The amount of maximum ankle joint torques ranges from 120 up to 200 N m (Kawakami et al., 2000; Maganaris, 2003; Winter and Challis, 2008b). Regarding quadriceps femoris, literature reports from an ascending–descending  $F$ – $l$ – $r$  with an optimum joint angle around 60° knee flexion (Kuhlig et al., 1984). For males, maximum torques reach approximately 300 N m (Pincivero et al., 2004; Hahn et al., 2007). However, optimum joint angle as well as the portion of the  $F$ – $l$ – $r$  used for force production can vary due to gender or specific training (Herzog et al., 1991a; Pincivero et al., 2004).

Concerning *in vivo* force–length properties, experimentally observed ankle and knee  $T$ – $a$ – $r$  show good agreement to the findings of modelling approaches. Thus, they seem to be good estimates to investigate *in vivo* muscle function (Herzog and Ait-Haddou, 2003). However, all results of both, torque–angle data and modelling approaches are based on experiments using

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isolated single-joint contractions but there is no data on  $T$ - $a$ - $r$  of ankle and knee joint obtained from multi-joint leg extensions. Since multi-joint leg extension involves hip, knee and ankle joints, muscle activation as well as force production are not only influenced by muscle length but also by intermuscular coordination. Moreover, theoretically, the biarticular muscles of the leg simultaneously shorten at one joint while they are lengthened at the other joint. Finally, during leg extension absence of co-contraction as assumed frequently for single-joint movements (Ichinose et al., 1997) is no longer valid (Hahn, 2011).

Therefore, the purpose of this study was to identify knee and ankle joints  $T$ - $a$ - $r$  resulting from multi-joint leg extensions. Assuming that the simultaneous contraction of hip, knee and ankle joint muscles would be the sum of isolated single-joint contractions, according to literature one would expect an ascending  $T$ - $a$ - $r$  for the ankle and an ascending–descending  $T$ - $a$ - $r$  for the knee joint during multi-joint leg extension as well. However, due to the different shape of the ankle  $T$ - $a$ - $r$  as well as higher maximal ankle torque found during multi-joint leg extension, a follow-up on isolated plantar flexion was carried out with the same subjects to check if the observed differences are of systematic nature or just due to subjects.

## 2. Methods

### 2.1. Subjects

Male subjects ( $n=18$ ;  $30 \pm 6.3$  yr,  $1.81 \pm 0.08$  m,  $77.9 \pm 5.2$  kg) without neuromuscular disorders or injuries participated in this study. For the follow-up nine of the original subjects ( $35.0 \pm 8.3$  yr,  $1.79 \pm 0.06$  m,  $77.7 \pm 4.2$  kg) performed isolated plantar flexions. Free, written informed consent was obtained and the study was conducted according to the Declaration of Helsinki and approved by the institutional review board for human research.

### 2.2. Experimental settings and determination of joint angle positions

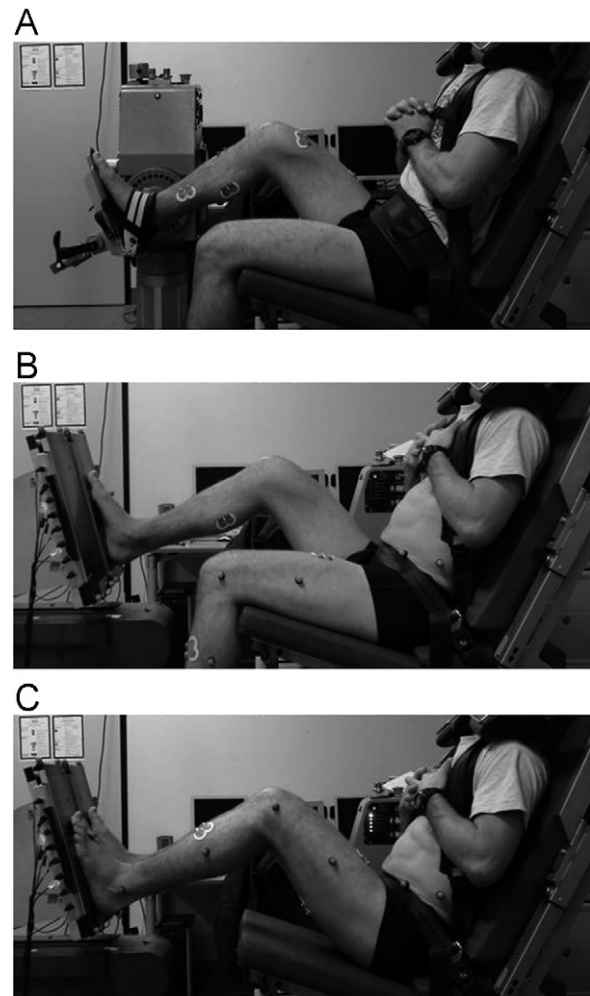
For both, multi-joint leg extension as well as isolated plantar flexion identical joint angle configurations of hip, knee and ankle joints were investigated in a motor driven dynamometer (IsoMed2000, D&R Ferstl GmbH, Germany). The only differences between the two approaches was the replacement of the force plate used for multi-joint contractions by a foot adaptor for direct measurement of ankle joint torques and importantly the instruction to subjects to solely activate their plantar flexor muscles during the isolated ankle joint measurements. Thus, identical mechanical conditions were investigated when activating the muscles of the whole limb compared to an isolated activation of the plantar flexor muscles (see also Section 2.4 and Fig. 1).

Subjects were placed on the dynamometer with the horizontal seat always reclined to  $5^\circ$  and the backrest reclined to  $50^\circ$ . The pelvis was secured by a safety belt and upper body by two safety belts and two shoulder pads. The footrest with the force plate (multi-joint) as well as the foot adaptor (ankle joint) was rotated by  $15^\circ$  from vertical towards plantar flexion and fixed. Foot placement was always at 0.1 m above the seat. Therefore this is a closed system and joint angle configuration can only be varied by changing the distance between the footrest and the backrest. This was done by horizontal moving of the footrest or the backrest. In this study, ROM was  $30$ – $100^\circ$  knee flexion ( $0^\circ$  refers to the straight leg) and measurements were done in increments of  $10^\circ$  knee angle. After determination of the positions for the smallest and biggest predefined knee joint angles manually, knowing the change of distance  $\Delta s$  and the positioning of the foot, footrest and

backrest described above, a two segment model of the lower limb with identical segment lengths allowed for the calculation of individual leg positions in the dynamometer that resulted in the desired knee angles (Hahn et al., 2005). The ankle, knee and hip joint angles resulting from this positioning were measured by a motion analysis system (2.4) and are presented in Table 1.

### 2.3. Experimental protocol

Subjects attended three sessions on 3 different days, with at least 1 rest day between sessions. In two preparation sessions, subjects were familiarised and



**Fig. 1.** Replicated experimental settings and markerset. (A) (top) shows the setup for the isolated plantar flexion measurements (follow-up) with identical joint angle configurations as for the multi-joint setup shown in (B) (middle). The foot adaptor used for ankle joint contractions (A) allowed for direct measurement of ankle joint torque, while the forces measured at the feet by the force plate (B) served as input for inverse dynamics. (C) (bottom) shows the Plug-In-Gait markerset with a marker placed on the iliac crest instead of the usual location on the back of the pelvis.

**Table 1**

Hip, knee and ankle joint angle configurations, resulting from the positioning at predefined knee joint angles as described in the methods section ( $n=18$ ). Hip and knee joint angles are flexion angles, negative ankle angles refer to plantar flexion, positive ankle angles to dorsal extension.

Angle (deg.)	Positioning (desired knee joint flexion angle (deg.))							
	30	40	50	60	70	80	90	100
Hip joint	$70.2 \pm 9.7^*$	$75.6 \pm 7.7^*$	$79.7 \pm 8.9^*$	$87.6 \pm 8.3$	$92.8 \pm 8.8^*$	$100.6 \pm 9.9^*$	$105.7 \pm 9.5$	$109.4 \pm 6.8$
Knee joint	$31.0 \pm 2.6^*$	$39.5 \pm 2.7^*$	$50.7 \pm 2.6^*$	$59.6 \pm 1.5^*$	$69.3 \pm 1.6^*$	$79.4 \pm 1.5^*$	$89.1 \pm 1.9^*$	$98.2 \pm 1.9$
Ankle joint	$-8.3 \pm 2.6^*$	$-4.3 \pm 2.5^*$	$0.9 \pm 2.6^*$	$5.0 \pm 2.3^*$	$9.4 \pm 2.3^*$	$14.4 \pm 2.7^*$	$19.9 \pm 3.0^*$	$23.1 \pm 2.4$

Values are means  $\pm$  SD. \* Indicate a significant difference between two adjacent data sets of joint angle from left to right ( $p < 0.05$ ). Reading example: ankle joint angle  $-8.3 \pm 2.6^*$  at position  $30^\circ$  indicates a significant difference to ankle joint angle at the position of  $40^\circ$ .

trained to perform maximal voluntary isometric contractions. Subjects were instructed to develop their maximum force and then to maintain this force for the duration of the test. Start and end of each contraction were clearly announced and verbal encouragement was given during contractions. In the third test session, subjects performed the test protocol, which was split up into three sets. All sets consisted of 8 isometric contractions each at a different angle configuration of hip, knee and ankle joints (Table 1). For each angle configuration, subjects had to make 3 repetitions, resulting in a total of 24 contractions. The same procedure was repeated for the ankle joint measurements during the follow-up study. Besides training to perform maximal voluntary plantar flexions, subjects also practised to solely activate their plantar flexor muscles during contractions.

To avoid learning or sequence effects, isometric contractions at different knee angles were presented in a random order in any set. In addition a minimum rest of 3 and 5 min was enforced at all times between contractions and sets, respectively.

#### 2.4. Data collection and analysis

During multi-joint contractions external reaction forces were measured for each leg by force plates with 3-component force sensors (KISTLER, Switzerland). A VICON MX-3 Motion-System (Vicon Motion Systems, UK) served for measuring lower extremity kinematics. Due to the sedentary position in the leg press, the Plug-In-Gait-marker set (Davis et al. 1991) was slightly modified and markers were placed on the left and right iliac crest. Four additional markers were placed on each force plate to assess their position for the kinetic calculation model. Capturing frequency was 240 Hz and kinematic measurements were synchronised with force measurements by software. Joint torques in knee and ankle joints were calculated by methods of inverse dynamics. To account for inertial properties the anthropometrical model was scaled to individual weight and height by linear regression (Zatsiorsky et al., 1984) and segment inertia parameters were adjusted according to de Leva (1996). Since errors of calculations based on simple models are known to increase for transversal and frontal plane torques (McGinley et al., 2009) only sagittal plane torques are reported.

Ankle joint torque (follow-up) was measured directly by the dynamometer. Subjects were tightly strapped to the foot adaptor. Ankle joint axis and the rotation axis of the dynamometer were aligned carefully when subjects performed a maximal voluntary contraction. Data sampling frequency was 200 Hz.

Joint torques were smoothed using a recursive 4th order Butterworth low pass filter with a cut-off frequency of 6 Hz. For the analysis of multi-joint leg extension, peak resultant external reaction force was determined from smoothed force-time histories for each knee flexion angle. Subsequently, corresponding joint torques in knee and ankle joints ( $M_K$  and  $M_A$ ) were taken at the same instant of time.  $T$ - $a$ - $r$  for isolated plantar flexion was derived from maximum angle specific torque measurements. For both, multi-joint and ankle joint tests, corresponding passive joint torques ( $M_{K,passive}$  and/or  $M_{A,passive}$ ) were obtained 2 s after termination of muscle activation.

#### 2.5. Assessment of muscle activation

Muscle activation of mm. rectus femoris (RF), vastus medialis (VM), biceps femoris (BF), gastrocnemius medialis (GM) and tibialis anterior (TA) was obtained using surface electromyography (EMG). Bipolar electrodes (Ambu Blue Sensor N-Electrodes, Denmark) were placed with an inter-electrode distance of 20 mm, while a single reference electrode was attached to the patella. Skin preparation and electrode placement were done according to SENIAM (Hermens et al., 1999). Due to a change in EMG-system (myon RFTD, myon AG, Baar, Switzerland) additional recordings of mm. vastus lateralis (VL), gastrocnemius lateralis (GL) and soleus (SOL) were obtained during the follow-up study.

#### 2.6. Statistics

After determining the best trials of each subject (i.e. the trial with the greatest leg extension force/plantar flexion torque), mean values  $\pm$  SD were calculated and served for statistical analysis. After checking normality, repeated measures ANOVA and Bonferroni–Holm post hoc comparisons served for statistical analysis of joint torques from the multi-joint tasks. Two-way repeated measures ANOVA and Bonferroni–Holm post hoc tests served for comparisons between multi-joint and isolated ankle joint contractions (task (multi- vs. ankle joint), joint angle) as well as for comparisons between the original group and the sub-group of the follow-up. Alpha level was set to  $p \leq 0.05$ .

### 3. Results

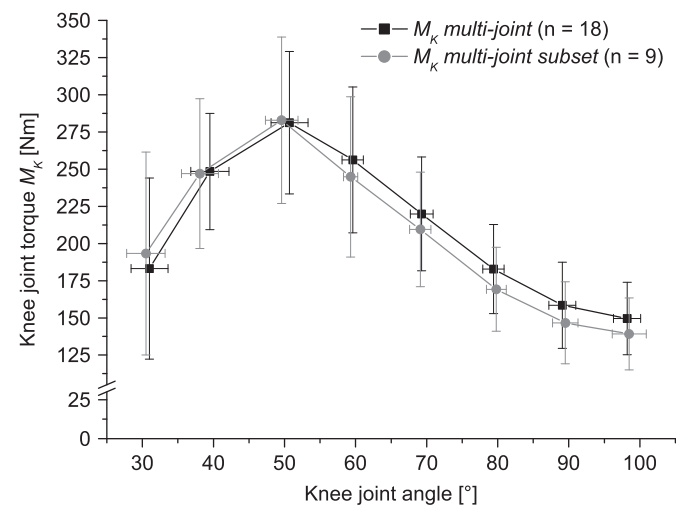
For knee and ankle joints, results from the multi-joint experiments are presented for the original group and the sub-group. Results on ankle joint torque from isolated plantar flexion are reported for the sub-group only.

#### 3.1. Knee joint torque ( $M_K$ )

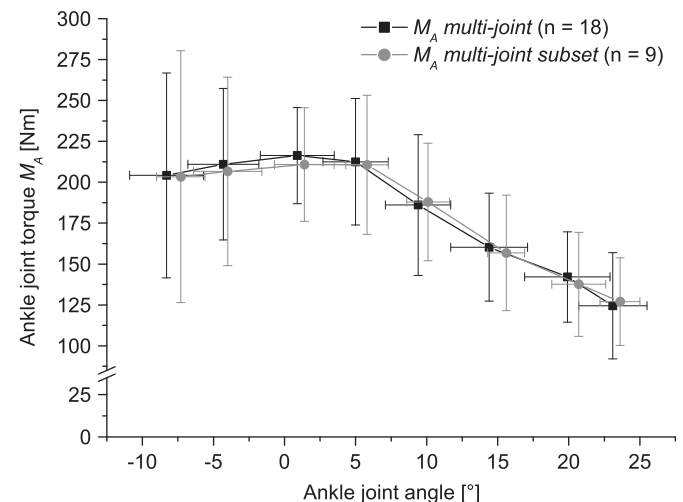
For the knee joint we found an ascending–descending  $T$ - $a$ - $r$  with a maximum  $M_K$  of  $289.5 \pm 43.3$  N m at an optimum knee angle of  $50.4 \pm 8.9^\circ$ . However, individual maximum  $M_K$  from 193 to 346 N m occurred between  $28.1^\circ$  and  $62.2^\circ$ . Mean  $M_{K,passive}$  only reached  $-2.4 \pm 6.1$  to  $4.9 \pm 6.7$  N m. Within the multi-joint data, no significant differences were found between groups (Fig. 2).

#### 3.2. Ankle joint torque ( $M_A$ )

For multi-joint leg extension, the  $T$ - $a$ - $r$  showed a plateau region from  $-8.3 \pm 2.6^\circ$  plantar flexion to  $5.0 \pm 2.3^\circ$  dorsal extension with a maximum  $M_A$  of  $234.5 \pm 44.0$  N m at  $-0.8 \pm 4.9^\circ$ . For ankle angles  $> 5.0^\circ$  dorsal extension, there was a descending limb with decreasing  $M_A$  to  $130.3 \pm 25.5$  N m at  $23.1 \pm 2.4^\circ$  dorsal extension (Fig. 3). Although all individual  $T$ - $a$ - $r$  ended in the



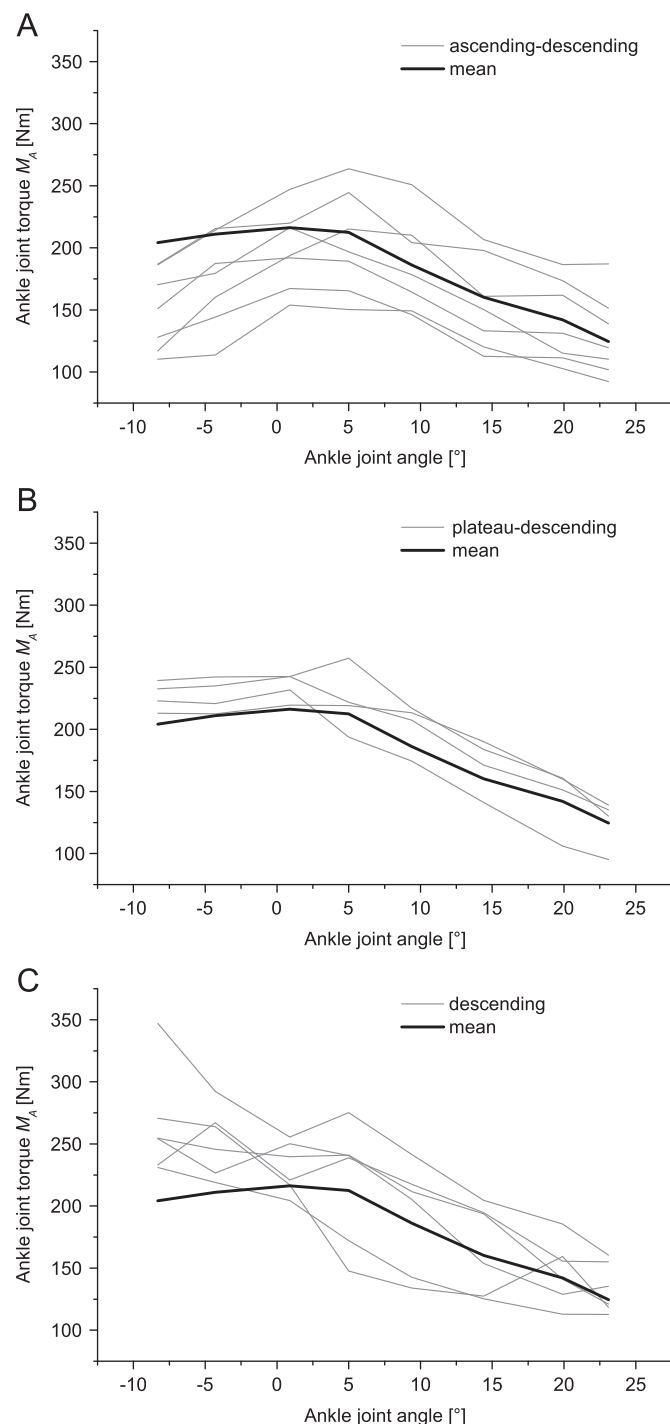
**Fig. 2.**  $T$ - $a$ - $r$  of the knee joint for multi-joint leg extension. For both, all subjects from the original study (black squares) as well as the sub-group of subjects from the follow-up study (grey circles) we found ascending–descending  $T$ - $a$  curves and no significant differences between groups. Figure shows angle specific mean values  $\pm$  SD.



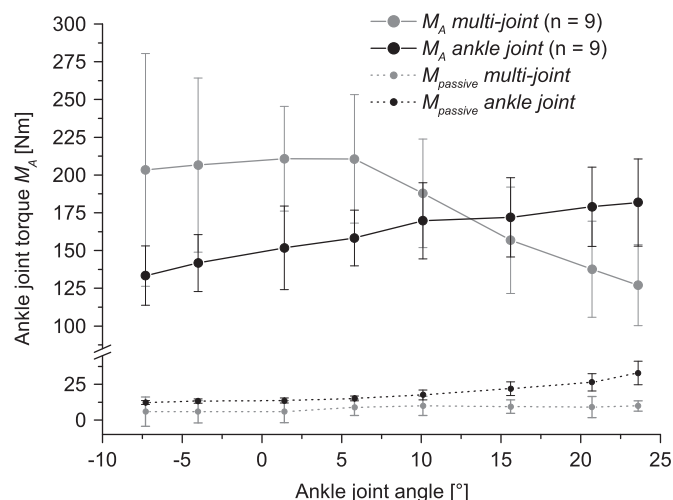
**Fig. 3.**  $T$ - $a$ - $r$  of the ankle joint for multi-joint leg extension. Negative ankle angles refer to plantar flexion, positive ankle angles to dorsal extension. For both, all subjects from the original study (black squares) as well as the sub-group of subjects from the follow-up study (grey circles)  $T$ - $a$  curves started on a plateau and passed into a descending limb. No significant differences between groups were found. Figure shows angle specific mean values  $\pm$  SD.

descending limb described above, the shape of individual  $T$ - $a$ - $r$  and occurrence of individual maxima varied strongly (Fig. 4). Maxima were found over the whole plateau region of the average  $T$ - $a$ - $r$ , ranging from 154 to 347 N m. Independent of joint angle  $M_{A\_passive}$  reached  $6.8 \pm 7.9$  to  $10.7 \pm 8.4$  N m. No significant differences were found between the original and the sub-group.

For isolated plantar flexion we observed an ascending  $T$ - $a$ - $r$  with a plateau region for ankle joint angles  $\geq 15.6 \pm 3.1^\circ$  dorsal



**Fig. 4.** Individual  $T$ - $a$ - $r$  for the ankle joint during multi-joint leg extension. Negative ankle angles refer to plantar flexion, positive ankle angles to dorsal extension. Subjects showed three different shapes of  $T$ - $a$ - $r$ , ascending–descending (A), plateau–descending (B) similar to mean (bold black) and descending (C). This variability was not found for isolated plantar flexion. One subject was excluded from this figure, because of an unclassifiable shape of the  $T$ - $a$ - $r$ .



**Fig. 5.** Comparison of active (solid lines) as well as passive (dotted lines) ankle  $T$ - $a$ - $r$  for multi-joint and ankle joint contractions. Negative ankle angles refer to plantar flexion, positive ankle angles to dorsal extension. Grey circles represent multi-joint data, whereas black circles show the ascending  $T$ - $a$ - $r$  found for isolated plantar flexion. For both, active and passive data, ANOVA revealed distinct curve shapes for multi-joint and ankle joint contractions. Figure shows angle specific mean values  $\pm$  SD.

extension. Angle specific  $M_A$  increased from  $133.4 \pm 19.6$  to  $181.8 \pm 28.9$  N m, whereas maximum  $M_A$  was  $185.7 \pm 27.8$  N m, ranging from 160 to 237 N m. Moreover, ANOVA revealed a significant influence of joint angle on  $M_{A\_passive}$ , which increased with joint angle from  $12.3 \pm 1.3$  to  $32.9 \pm 8.2$  N m.

Comparing  $M_A$  from multi-joint and isolated ankle joint contractions, two-way repeated ANOVA showed no significance for task but for joint angle and the interaction of task  $\times$  joint angle. That means  $M_A$  varies with joint angle and the  $T$ - $a$ - $r$  of multi- and isolated ankle joint contractions show different curve shapes (Fig. 5). Moreover, as expected from the instruction to subjects to solely activate their plantar flexors during ankle joint contractions, EMG showed different activation patterns for the multi-joint compared to the ankle joint approach (Fig. 6). Concerning  $M_{A\_passive}$  task, joint angle and task\*joint angle showed significance.

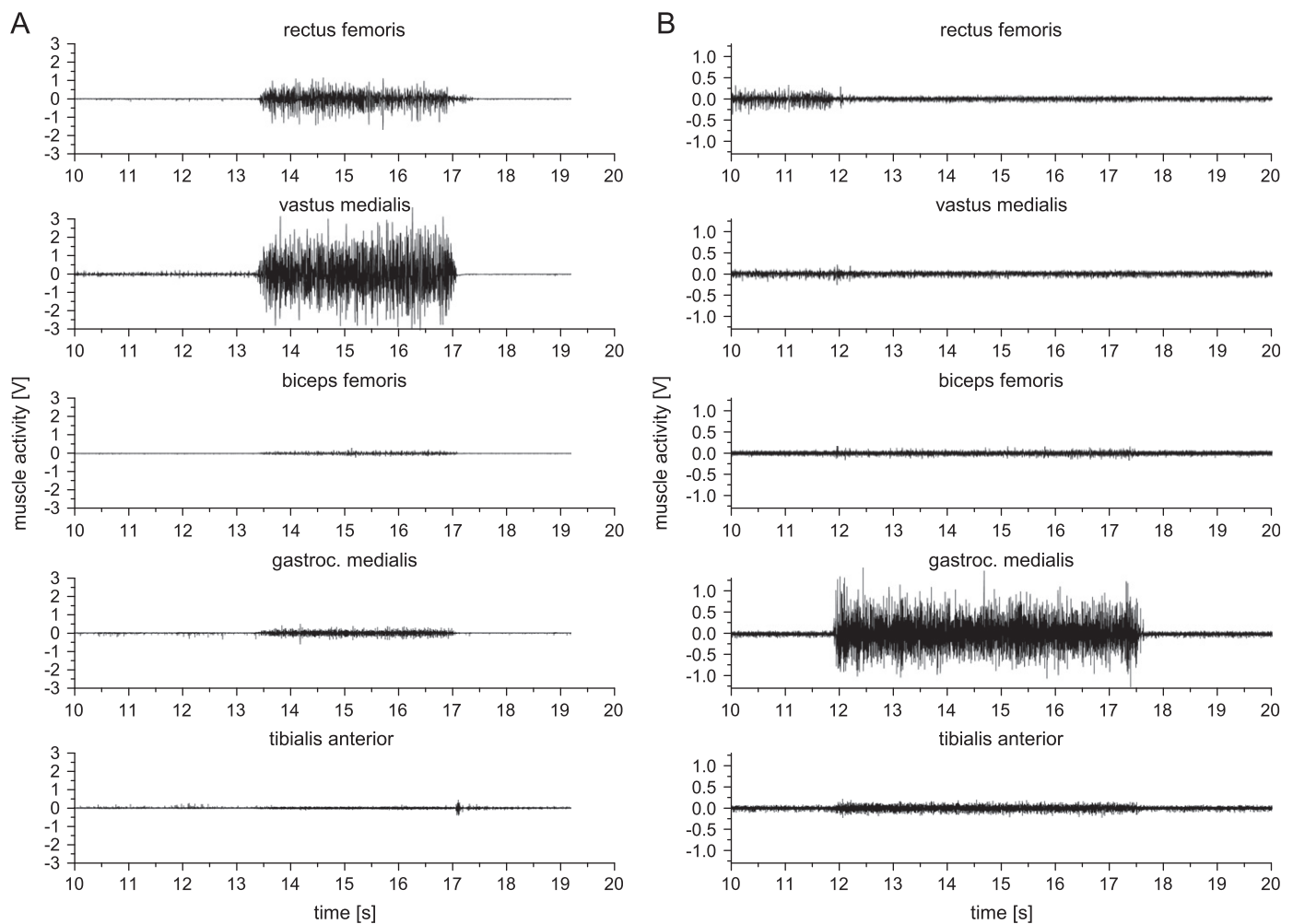
## 4. Discussion

### 4.1. $T$ - $a$ - $r$ for the knee joint

In agreement with former investigations on knee extension (Pincivero et al., 2004; Hahn et al., 2007), we found an ascending–descending  $T$ - $a$ - $r$  with a maximum  $M_K$  similar to former reports. Thus, knee extensor muscles seem to act with maximum effort.

In contrast to literature, maximum  $M_K$  occurred at  $50.4 \pm 8.9^\circ$  knee flexion. Compared to findings on single-joint knee extension (see Table 3 in Pincivero et al., 2004) this corresponds to a shift of optimum joint angle of approximately  $10^\circ$ . Although occurrence of  $M_K$  and the shape of  $T$ - $a$ - $r$  have been reported to vary individually (Herzog et al., 1991a), this seems not to apply to our nonspecific trained subjects. It is rather assumed that this difference may result from biarticular RF and interactions between the quadriceps muscles (Huijing, 2003). Due to the combined hip and knee extension during multi-joint leg extension, RF simultaneously shortens at the knee while it is lengthened at the hip joint. According to model calculations (Delp et al., 2007), this results in a reduced change of normalised RF fibre length of  $0.23\Delta l_0$  compared to  $0.43\Delta l_0$  for single-joint knee





**Fig. 6.** Exemplar muscle activity of RF, VM, BF, GM and TA muscles during multi-joint leg extension (A) and isolated plantar flexion (B). The figures clearly indicate different activation patterns during multi-joint and isolated ankle joint contractions. While during leg extension highest activity was found for knee extensor muscles RF and VM, these muscles were silent during ankle joint contraction, which showed highest activation for GM muscle. Note the different scaling of the y-axis, indicating that a direct comparison of activation levels between contraction types was not possible due a change in EMG systems.

extension. Thus, for given joint configurations  $\leq 60^\circ$  knee flexion, RF operated closer to its optimum length, which should have contributed to greater force and torque output and the observed shift of optimum joint angle. Moreover, in comparison to a single-joint knee extension, the lengthening of RF at the hip joint is likely to have resulted in an altered relative position of RF to its neighbouring muscles. At least for animal studies, this is known to result in different force output and optimum length of the interacting muscles caused by myofascial force transmission (Huijing and Baan, 2003; Maas et al., 2004). However, such effects have not yet been investigated for a multi-joint movement of the whole human limb and considered to be small or absent in physiological conditions (Herbert et al., 2008; Bojsen-Moller et al., 2010; Maas and Sandercock, 2010).

#### 4.2. $T$ - $a$ - $r$ for the ankle joint

The  $T$ - $a$ - $r$  for isolated plantar flexion coincides well with literature on single-joint experiments (Herzog et al., 1991b; Maganaris, 2001) and m. triceps surae was observed to act on the ascending limb. The slightly reduced maximum  $M_A$  ( $186 \pm 28$  vs.  $201 \pm 17$  in Maganaris, 2003) probably results from flexed knee joint, which leads to reduced force capacity of GM and GL.

In contrast to that,  $T$ - $a$ - $r$  obtained during multi-joint leg extension started on a plateau and passed into a descending limb. Additionally, maximum  $M_A$  ( $235 \pm 44$  N m) was higher than that of isolated plantar flexion. Apart from Winter and Challis (2008b) this finding does not agree with common knowledge on  $T$ - $a$ - $r$  of single-joint plantar flexion (e.g. Kawakami et al., 2000). Although it was shown (Winter and Challis, 2008a) that a modelled gastrocnemius muscle with physiologically realistic parameters (Out et al., 1996) can act on the descending limb, muscle diversity is not a factor in this study since within-subject comparisons were done. However, two different methods were used to determine  $T$ - $a$ - $r$  for ankle and multi-joint contractions. Arampatzis et al. (2005) found that ankle joint torques as measured by a dynamometer differed from those calculated by inverse dynamics. However, major parts of the differences observed in their study probably originate from the axis of rotation of the ankle and the dynamometer drifting away from each other during contractions. This drift is assumed to be caused by the alignment of rotation axis, which was done at rest, whereas in the present study this was done when subjects performed a maximal contraction. Moreover, Arampatzis et al. (2005) observed a systematic error, which would affect torques at each joint angle equally, but not leading to distinct curve shapes as observed in this study.

Likewise, due to identical joint angle configurations, muscle lengths as well as the position of muscles in relation to each other should not have differed much between single- and multi-joint contractions and therefore cannot explain the observed differences between  $T$ - $a$ - $r$  of the ankle. However, different plantar flexor activation may have influenced the results (Higham and Biewener, 2011) and during multi-joint leg extension there was strong activity of the knee extensor muscles that was not present during isolated plantar flexion (Fig. 6). While antagonistic activity is often thought to be prejudicial to torque production, for gastrocnemius muscles this might have led to a counter bearing at the knee joint. That means that GM and GL are able to produce more force contributing to plantar flexion when the knee joint is fixed by the antagonistic knee extensor muscles. Similarly, it was suggested that force of QF can be transferred by the biarticular muscles GM and GL to be used for plantar flexion during functional multi-joint tasks (van Ingen Schenau et al., 1987). Hence, for both theories, it would be expected that  $T$ - $a$ - $r$  of the knee and the ankle joints are highly correlated, which was true for average  $T$ - $a$  curves ( $r=0.91$ ). In contrast, correlations for single subjects were highly variable, ranging from  $r=-0.17$  to  $0.92$ . Another mechanism in terms of intermuscular force transmission, possibly contributing to the different  $T$ - $a$ - $r$  of multi-joint and isolated ankle joint contractions, may be the linkage between gastrocnemius and hamstring muscles that was shown for passive joint movement (Huijing, 2009). For multi-joint leg extension EMG-joint-angle-relations for GM and BF showed the same characteristic, similar to the shape of the ankle  $T$ - $a$ - $r$  (Hahn, 2011), whereas during isolated plantar flexion BF was almost silent independent of joint angles (Fig. 6). However, this needs further investigation and due to the change in EMG systems, a comparison of EMG-results from the original and the follow-up study remains tentative.

## 5. Conclusion

This study demonstrated that  $T$ - $a$ - $r$  of knee extensor and plantar flexor muscles differ between multi-joint leg extension and corresponding single-joint contractions. While the differences to literature observed for quadriceps femoris are thought to be mainly caused by distinct length changes of RF and myofascial force transmission, the results for the ankle joint are more complex. Curve characteristics dramatically changed from an ascending  $T$ - $a$ - $r$  for the ankle joint to a descending  $T$ - $a$ - $r$  during the multi-joint task, although the amount of shift varied between subjects. With a counter bearing effect and/or redistribution of force by biarticular muscles as well as a potential intermuscular force transmission of gastrocnemius and hamstring muscles, possible explanations have been suggested, but further research is needed to confirm these ideas.

Nevertheless, the results of this investigation are considered to be of importance for analysis, modelling and simulation of human movement because multi-joint contractions represent natural movements much better than isolated single-joint contractions. Moreover, force-length or  $T$ - $a$  properties are essential input or validation parameters for Hill-type muscle models and should be based on relevant contraction conditions.

## Conflict of interest statement

None of the authors has any conflict of interest.

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