

成長および加齢に伴う柔軟性の変化とその改善方法に関する研究

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はしがき

身体が十分にその機能を発揮するためには、関節可動域の大きい、しなやかな動きが必要であり、この点で柔軟性は行動体力の基本的要素であるといえる。柔軟性の大小に基づく関節可動性は、日常生活やスポーツパフォーマンスのできばえに大きな影響を及ぼすばかりではなく、関節障害や転倒の頻度にも影響を及ぼすことが指摘されている。このことは、発育途上にある子どものスポーツ障害・外傷を未然に防いだり、高齢者のQOLを高め、寝たきりにならない自立支援を進めるうえで特に重要である。しかし、他の体力要素に比べて、柔軟性のメカニズムは不明な点が多く、柔軟性の評価方法や改善方法に関する明確な指針が存在しないのが現状である。

柔軟性（関節可動域）には関節運動に関わる骨格筋の量的・機能的特性が関係することが予想される。すなわち、骨格筋量や筋腱複合体の力学的特性に存在する個人差は、各人の柔軟性に少なからず影響を及ぼすものと考えられる。なぜならば、筋腱複合体は関節運動に伴って変形し、その長さを変化させるが、その過程で外部の関節の可動性に影響するからである。筋腱特性に性差が存在したり、成長、加齢に伴って筋腱特性が変化したりすると、柔軟性もこれに対応した変動を示すことになるだろう。さらに、トレーニングによる筋腱特性の一過的、慢性的な変化は、柔軟性と深く関わってくるものと思われる。本研究は、これらの点を明らかにすることを目的とした。

研究結果の詳細は以下の研究報告に示す通りである。柔軟性と筋腱特性の関連性について、加齢、性差の観点から検討した横断的研究から始まり、筋腱複合体の受動伸長時・力発揮時の変形と関節トルクとの関連性などに関する研究を通して、受動伸長や力発揮が筋腱複合体の特性を一過的に変化させることが明らかになり、柔軟性のトレーニングへの方向性が示された。

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特集

● 中高年者の生活機能を表す新しい体力・健康スケール ●

中高齢者の筋特性

川上 泰雄¹⁾・金久 博昭²⁾・福永 哲夫³⁾

一般に、日常生活における身体活動量は加齢に伴って減少する傾向にあり、身体の各器官や組織は加齢とともに運動不足の影響が加わり、加速度的にその機能が低下する。身体諸機能の低下は腰痛や骨粗鬆症などの疾患を誘発し、「寝たきり老人」などの現象を引き起こす¹⁾。加齢とともに身体の機能がある程度減弱することはやむを得ないとはいえ、機能低下の程度を最小限に食い止め、日常動作を不自由なく行なうことができる状態を保っておくことは必要不可欠なことである。このことは、超高齢化社会を迎えた現代において緊急なテーマであるといえよう。

福永ら¹⁾は、日常生活を遂行するために必要な身体適正を「生活フィットネス」と定義し、その主因子として身体組成、関節トルク、動作パワー、走パワーをあげている。これらの因子は骨格筋の形態的・機能的特性（ここでは筋特性と呼ぶことにする）がその背景になっていると考えられる。本稿では、われわれがこれまでに計測してきた一般人の生活フィットネスのデータを通じて、中高齢者の筋特性や筋特性の加齢変化についてまとめてみる。なお、データの多くは文部科学省科学技術振興調整費〔代表 村上和雄；平成11～16年〕により実施された研究成果（日本体力医学会の学

表1 対象となった被験者

| | 被験者数 | | 年齢 | |
|-----|------|-----|------------|------------|
| | 男性 | 女性 | 男性 | 女性 |
| 20代 | 227 | 91 | 20.7 ± 3.1 | 21.2 ± 3.2 |
| 30代 | 74 | 31 | 34.1 ± 3.0 | 35.4 ± 2.8 |
| 40代 | 47 | 18 | 44.1 ± 3.1 | 47.4 ± 1.3 |
| 50代 | 47 | 101 | 53.9 ± 3.2 | 55.0 ± 2.7 |
| 60代 | 108 | 273 | 65.6 ± 2.7 | 64.5 ± 2.7 |
| 70代 | 92 | 120 | 73.0 ± 2.4 | 73.5 ± 3.3 |

会誌「体力科学」において報告；文献参照）であることをあらかじめおことわりしておく。

1. 筋力

まず、首都圏在住の20～80歳までの男女1,229名（男性595名、女性634名）を対象にわれわれが行なった生活フィットネス測定筋力データ¹⁾を紹介しよう。表1に被験者の概要を示す。年齢群によって被験者数にばらつきがあるが、現在も計測を継続中である。

筋力として関節トルクを計測した。肘関節、膝関節について、数回の練習の後、等尺性伸展、屈曲トルクを被験者の最大努力で発揮してもらい、

筆者：1) かわかみ やすお（早稲田大学スポーツ科学部）
 2) かねひさ ひろあき（東京大学大学院総合文化研究科）
 3) ふくなが てつお（早稲田大学スポーツ科学部）

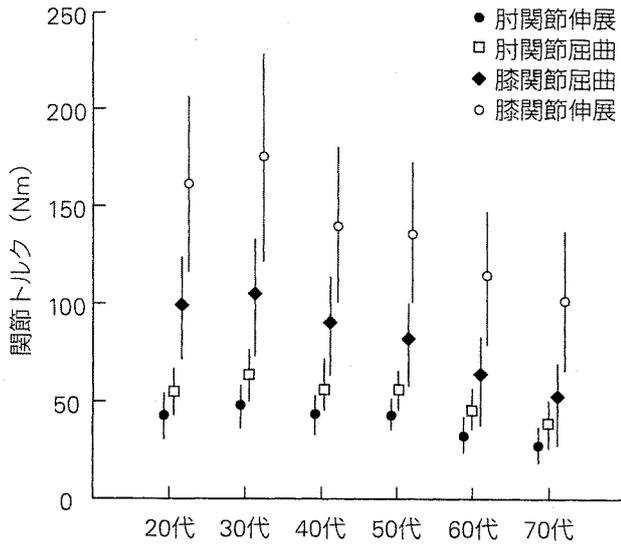


図1-1 関節トルクの年代ごとの平均値および標準偏差：男性（文献1より筆者作図）

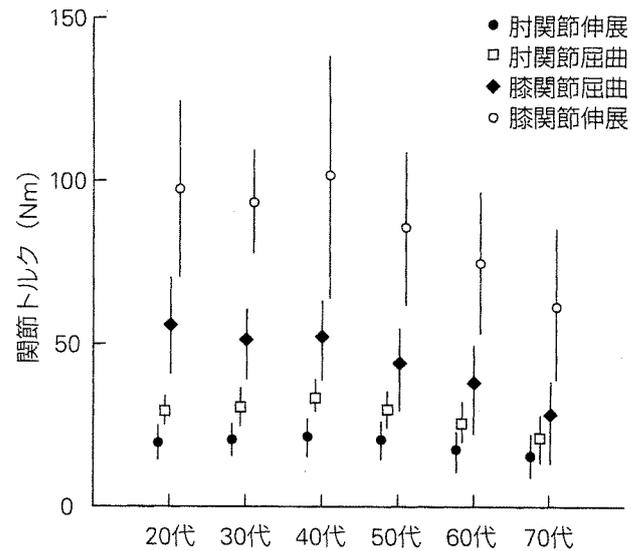


図1-2 関節トルクの年代ごとの平均値および標準偏差：女性（文献1より筆者作図）

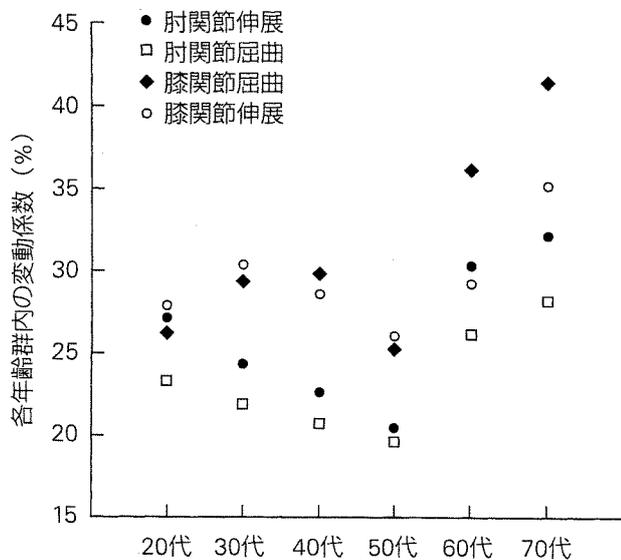


図2-1 関節トルクの変動係数：男性

(各年代の平均値と標準偏差から算出：文献1より筆者作図)

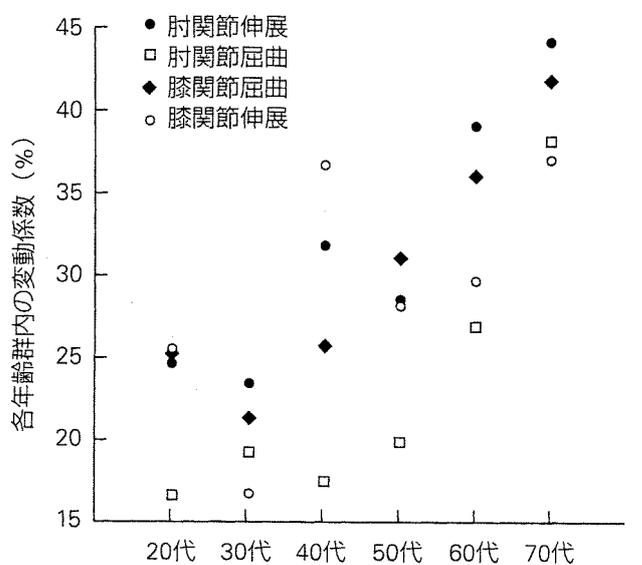


図2-2 関節トルクの変動係数：女性

(各年代の平均値と標準偏差から算出：文献1より筆者作図)

最大値を計測した。関節角度はどちらの関節も90°に設定した。

得られた関節トルクの各年代の平均値を図1-1, 2に示す。若年齢群に比べて、中高年齢群で筋力が低い傾向にあることがわかる。男女とも、低下傾向は肘関節に比べて膝関節で顕著である。肘関節トルクの場合、40歳代や50歳代は20・30歳代と同レベルであるが、60・70歳代で低下傾向となっ

ていく。一方、膝関節トルクは屈曲、伸展ともに30歳代をピークとしてそれ以上の年齢群で直線的な低下傾向が観察される。70歳代では、20歳代に比べて、肘関節伸展トルクで男性が64%、女性が80%、肘関節屈曲トルクで男女とも70%、膝関節伸展トルクで男性が62%、女性が64%、膝関節屈曲トルクで男性が49%、女性が47%であった。ただし、後述するように、このことから「70歳

代は20歳代に比べて下肢の筋力がおよそ半分に低下する」と結論するのは早計である。というのも、各群ともに筋力にかなりのばらつきが認められるからである。各群の平均値と標準偏差から変動係数を計算したものを図2-1, 2に示すが、50歳代までは横ばいもしくは若干の低下傾向が認められるのに対して、60歳代以降では変動係数が急激に増加する。70歳代では分布の標準偏差は平均値の40%以上に達する場合がある。被験者による筋力の変動幅が高齢者では非常に大きいことがわかる。70歳代男女では膝関節伸展トルクは10Nmから165Nmにわたる（これらの最大値、最小値がどちらも男性のものであることも注目すべき点である）。こうした筋力の差異は何によって生じているのだろうか。

図3は、高齢者男女6名（65～75歳，男女各3名，定期的に身体運動を実施）および大学生男女11名（19～25歳，男性5名女性6名）を対象として、足関節底屈筋群の機能的特性について検討した結果である²⁾。筋力計を用いて、最大努力で等尺性足関節底屈動作を行なったときのトルクを測定するとともに、動作中に脛骨神経に経皮電気刺激を行ない、最大随意筋活動時の神経系の興奮水準を定量化した（twitch-interpolation法）。随意最大トルクと神経系の興奮水準はともに高齢者群が青年群よりも有意に低い値であり、高齢者群のトルクは青年群のおよそ70%，興奮水準は青年群が平均98%なのに対して高齢者群は平均90%であった。高齢者群の特徴として、大きな個人差がみられた。被験者によっては、青年よりも高いトルクを発揮した高齢者もいる一方で、青年の半分にも満たないトルクしか発揮できない高齢者も存在した。また、「全力」を出しているつもりであっても、本来の能力の65%しか発揮できない者（測定を複数回行なっても同じ結果であった）や、100%の全力発揮が可能な者もいる、というのが高齢者群の特徴である。結果として、高齢者群の場合、トルクの最大値は最小値の5倍にも及び、図2, 3と同様の結果となった。なお、この研究においては腓腹筋の筋厚も計測したが、青年群と

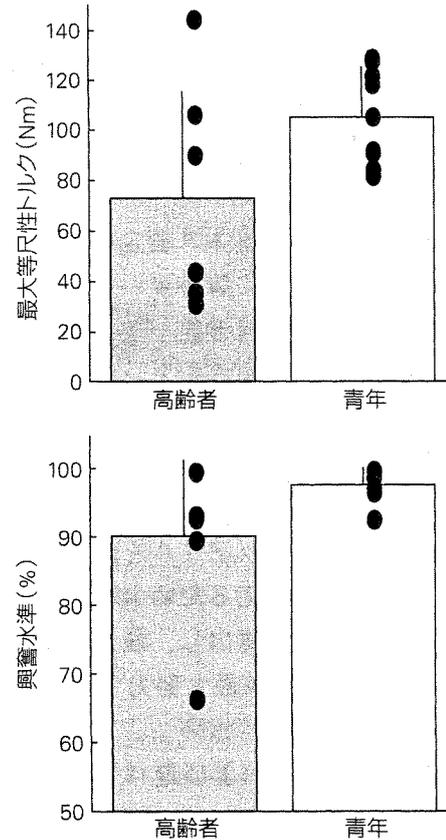


図3 高齢者男女 (n=6) および青年男女 (n=11) における最大等尺性足底屈トルク (上) および神経系の興奮水準 (下) (文献2より筆者作図)
棒グラフは各群の平均値および標準偏差、点は個々の被験者のデータを示す。

高齢者群に有意差は認められなかった。下腿の場合、筋量よりも筋力に加齢の影響が色濃く現れるようである。高齢者群にみられる筋力低下は、主として神経系（大脳レベル）の興奮水準の低下に起因していることが示唆される。なお脊髄運動神経細胞の興奮性も高齢者群で低値を示した²⁾。

青年（20歳代）と高齢者（70歳代）の比較を通じて筋量（筋厚）の加齢変化について検討した報告³⁾によると、筋厚の加齢変化には身体内部位差が存在し、下肢筋群の中では大腿前部に位置する筋群は男女ともに加齢による低下がもっとも大きく現れる。筋力発揮能力の低下にはこうした筋萎縮も大きな影響を及ぼすことになる。筋力、筋量に生じるマイナス方向の変化とその個人差は、日常の身体活動のレベルの違いの影響が高齢者に

なるにしたがって、筋特性の差として蓄積していく結果であると考えられる。

2. 動作パワー・走パワー

一般人の生活フィットネス測定においてわれわれは、動作パワーとして脚伸展パワーおよび走パワーを計測している。脚伸展パワーは、脚伸展パワー測定装置を用い、座位をとった状態で股関節角度 45° 、膝関節角度 90° の状態から水平方向に全力で脚伸展を行ない、最大パワーを計測するものである。負荷は体重相当のものとしている。走パワーは自走式トレッドミルを改造し、ベルトの回転速度と身体を支えるためのハンドルにかかる力の積からパワーを算出し、最大値を計測するものであり⁴⁾、被験者は最大努力で走運動を行なう。

図4は脚伸展パワーおよび走パワー（体重当たり）を年齢群別に男女についてみたものである。各年代において女性は男性よりもパワーが低値を示すが、その差は脚伸展の方が大きく、およそ55～60%である（走パワーは女性が男性の約60～80%）。動作によって男女差が異なることが興味深い。この男女差は年齢群間で一貫した傾向はなく、加齢による影響は少ないようである。ただし、パワーそのものは高年齢群ほど低くなる傾向であり、とくに60歳代、70歳代で低下が顕著である。低下が大きいのは走パワーで、20歳代に比較して70歳代は男性が36%、女性が31%であり、関節トルクよりも低下率が高い。また、40歳代、50歳代にすでに平均値が20・30歳代を下回っているのも走パワーの特徴である。日常で頻繁に行なわれる動作の加齢変化がもっとも大きいのは皮肉なことであるが、これは日常生活における身体運動の減少を如実に反映したものだともいえる。

関節トルクと同様に、脚伸展パワー、走パワーともに個人間変動が大きい。高年齢群ほど変動が大きくなる、という傾向が脚伸展パワーでより顕著である（変動係数は男性が20歳代で23%、70

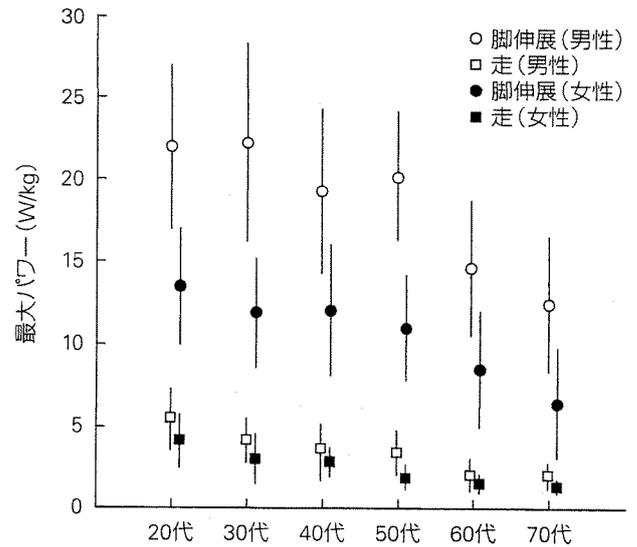


図4 脚伸展パワーおよび走パワー（それぞれ体重当たり）の年代ごとの平均値および標準偏差（文献1より筆者作図）

歳代が32%、女性が20歳代で27%、70歳代で52%）。脚伸展パワーや走パワーと大腿四頭筋の筋量との間には高い相関関係がみられる¹⁾ことから、大腿前面に生じやすい筋萎縮がパワー低下に大きく影響していると考えられる。走パワーはまた歩幅と高い相関関係を有しており、加齢に伴う歩幅の低下も走パワー低下の一因となる¹⁾。脚伸展パワーにおける年齢の影響は膝関節伸展トルクよりも大きく、加齢に伴うパワー低下は筋量低下だけでは説明できない⁵⁾。これは、神経系の興奮水準の低下や、複数の関節や筋群を協調させる能力の低下も影響している可能性がある。筋力・筋パワーの評価においては日常生活に即した動作を用いる必要がある。

3. 筋特性と関節機能—柔軟性の観点から

筋特性の加齢変化は、筋力や動作パワーといった、いわゆる「力強さ」だけに影響を及ぼすものではない。関節機能と筋量や筋力のかかわりやそれらの加齢変化について、柔軟性を例にあげて説明する。

大きな関節可動域でしなやかに動くことのできる能力、すなわち関節の柔軟性は特に中高齢者の

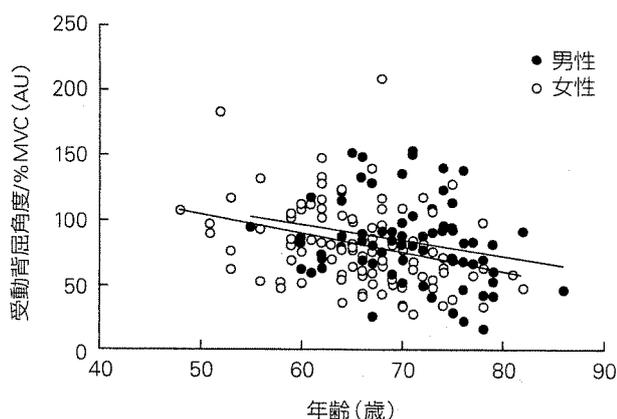


図5 中高齢者における年齢と受動背屈角度との関係 (文献6より筆者作図)

受動背屈角度は負荷トルクの最大等尺性足底屈トルクに対する割合で正規化した。図中の直線は回帰直線を示す。

日常生活の遂行能力と深い関係をもっていると考えられる。筆者らは、柔軟性を関節可動域と定義し、中・高年齢者を対象に、関節可動域の規定因子について検討を行なった⁶⁾。被験者は185名の健常な中高齢者（女性116名，男性69名；48～86歳）であった。モータを使って足関節を一定のトルクで背屈方向に回転したときの背屈角度を計測した。同じトルクを付加しても，それによって受動的に生じる足背屈の角度変化は被験者によって異なり，足関節の「柔らかい」人や「堅い」人が存在した。

男女とも，受動背屈角度と下腿後部の筋厚との間には有意な負の相関関係が認められ，背屈時に伸長される下腿後部の筋群が多いことによる伸長抵抗性が柔軟性と関係していることが明らかになった。受動背屈角度は高齢の被験者ほど小さくなる傾向であり（図5），これは腓腹筋やアキレス腱の伸長性の違いと関係していた。これらの結果から，柔軟性を左右する因子として，筋量（多いほど柔軟性が低い），筋力（大きいほど柔軟性が高い），筋腱複合体の材質特性（堅いほど柔軟性が低い）をあげることができる。高齢者の場合は，筋萎縮によって受動伸長組織が減少するが，組織そのものの伸長性が低下することにより，受動背

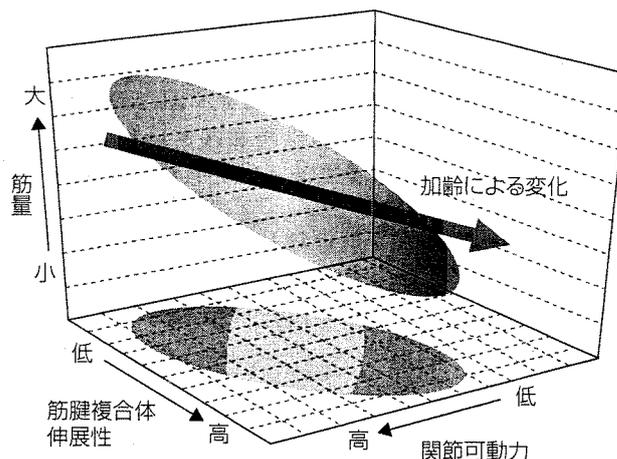


図6 中高齢者における筋量，筋腱複合体伸長性，関節可動性の相互関係の模式図（文献6より筆者作図）

加齢による変化は図中の分布（楕円）を斜め方向に横切るかたちで生じると考えられる。

屈角度が減少する。高齢者に顕著な筋力低下が自力で動かせる可動域の幅をさらに狭める可能性がある（図6）。高齢者においては，しなやかな動きのためにも筋力トレーニングが必要であろう。

おわりに

中高年の筋特性をひとことで表現すると，「個人差が大きい」ことである。子どものときからの日常生活における生活パターンが蓄積されていく中で個人差が拡大していく。プラス方向，マイナス方向ともに適応性の高い骨格筋に個人差があらわれやすいこと，そしてその影響は日常生活に直接的な影響を及ぼすことに注意する必要がある。中高年者に対して，「あなたは何歳ですから平均的にいってこのくらいの筋力が必要です」ということはできても，そのために必要な運動プログラムは千差万別である。人生を通じて蓄積された筋量変化と筋力変化のパターンがそれぞれ異なり，しかも個人差が大きく，その結果として，実際に運動を行なうための体力（身体組成などの「器」や多関節動作のパフォーマンス，柔軟性などの要素を含めて）がさまざまであることがその理由である。精度の高い生活フィットネス評価を行なう意義はこの点にあると考えられる。

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Musculotendinous Factors Influencing Difference in Ankle Joint Flexibility between Women and Men

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Flexibility is often evaluated from the joint range of motion (ROM), but the mechanisms underlying gender differences in joint ROM have not been elucidated. The purpose of this study was to investigate the factors influencing the difference in ankle joint ROM between men and women with respect to the extensibility of muscle-tendon complex. Eighteen men (21-26 yr, 66.4±6.0kg, 173.7±7.4cm mean±SD) and 12 women (19-27yr, 52.9±4.8kg, 163.4±4.3cm) participated in this study. Each subject was seated with the knee extended, and the ankle joint was attached to a foot plate, by which the ankle joint was passively dorsiflexed with torque gradually increasing from zero to a value at which the passive loading to the ankle joint was just tolerable for each subject. During the passive loading, real-time ultrasonogram was taken to track the movement of MTJ (muscle-tendon junction of the gastrocnemius medialis and Achilles tendon) as the elongation of muscle belly (dMus). The change of MTC (muscle-tendon complex) length (dMTC) during the passive dorsiflexion was estimated from changes in ankle joint angle. Tendon elongation (dTen) was calculated by subtracting dMus from dMTC. There was no significant difference in normalized passive torque during passive dorsiflexion between men and women. Women were more flexible, i.e., they demonstrated greater dMTC, which was accompanied by greater dTen at lower torque levels. However, dMus was not different between men and women. It was concluded that gender difference in the joint ROM at the ankle reflects more compliant Achilles tendon in women than in men.

Keywords: flexibility, gender difference, ankle joint, muscle-tendon complex

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1. Introduction

Flexibility is a physical fitness and is often evaluated from the joint range of motion (ROM). It is defined as "performance of smooth and extensive movement of body joints" (Takata, 1990). Reports on the significance of flexibility have focused on contribution of preventing injuries and improving sports performance (Alter, 1996; Kuriyama, et al., 1986; Yamamoto, 1996). For example, in the hurdles an extensive joint ROM is required in the hip joint while, in swimming, a wide range of motion in the shoulder joint is more advantageous for strokes in

free style (Yamamoto, 1996). Factors to define ROM include skeletal constitution, extensibility of muscle and tendon tissues, influence of the nervous system, and tolerance to pain (Noris, 1999). Another study reports that MTC elongation is one factor to regulate the joint ROM (Alter, 1996) because the joint ROM is affected by direct crossing of the muscle-tendon complex (MTC) through the joint.

Women are thought to have better flexibility than men. Actually, there are many reports than women have larger joint range of motion (ROM) than men (Grimston, 1993; Riemann, 2001).

Kawakami, et al., (2003) have referred to the

Table 1 Physical characteristics of the subjects. Data are means (SD)

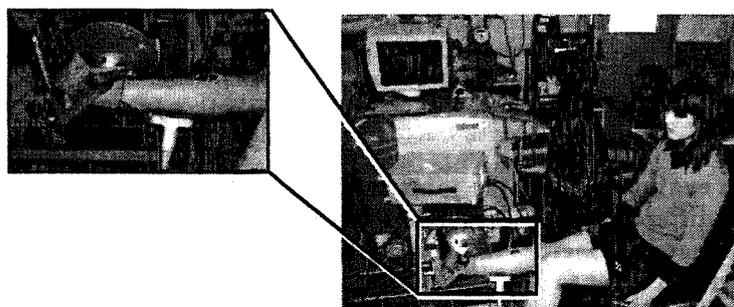
| | Age (yrs) | Weight (kg) | Height (cm) | SL (cm) | Circum. (cm) | TL (cm) |
|-----------------|------------|-------------|--------------|-------------|--------------|-------------|
| Men (n=18) | 22.4 (1.7) | 66.4 (6.0) | 173.3 (7.4) | 40.3 (2.9) | 37.5 (3.0) | 21.7 (2.7) |
| Women (n=12) | 21.8 (2.0) | 52.9 (4.8)* | 163.4 (4.3)* | 37.7 (1.4)* | 35.5 (2.2)* | 19.4 (1.7)* |

SL: Shank Length

*: Significantly different from men, $p < 0.05$

Circum.: Circumference of calf

TL: Achilles Tendon Length (distal to the gastrocnemius muscle belly)

**Figure 1** Experimental Setting

regulatory factors of ankle joint ROM in their study on the middle-aged and the elderly, saying that the passive dorsiflexion angle is affected by elongation resistance of the muscle group elongated and that women have greater passive dorsiflexion angle than men because of the difference in muscle volume. They also reported that the dynamic property of tendon tissues affects gender difference of passive dorsiflexion angle. Kubo, et al., (2003) explain that, by comparing characteristics of the tendon tissues of the gastrocnemius medialis between men and women, stiffness and hysteresis of the Achilles tendon of women are significantly lower than those of men.

One factor influential on the joint ROM may be the difference of extensibility of muscle and tendon tissues. From the above-mentioned studies of gender difference on tendon tissue, we hypothesized that tendon elongation especially may affect gender difference of the joint ROM. Based on this hypothesis, the purpose of this study is to examine gender difference on extensibility and joint ROM of the triceps surae muscles and tendon when the ankle joint is passively dorsiflexed.

2. Method

2.1. Subjects

We conducted the experiment with 18 men and 12 women who were healthy and had never had medical problems in their legs and feet, (**Table 1**: Physical characteristics of the subjects). Prior to the experiment, the subjects were sufficiently informed of the purpose and method of the experiment before providing written consent. The experiment was approved by the Ethics Committee of the Faculty of Sport Sciences at Waseda University.

2.2. Measurement

As the subjects' physical characteristics measurement, we measured the shank length, the circumference of calf, and the Achilles tendon length. The shank length was from the knee absconsio to the lateral malleous of the tibia, the circumference was measured, at the position proximal 30% of the shank length. Using an ultrasonic with its probe mounted with a water bag (ALOKA, Japan), we visually checked the distance between bone-tendon transition part of the Achilles tendon and the distal end of gastrocnemius medialis and made it the Achilles tendon length. The muscle length of the

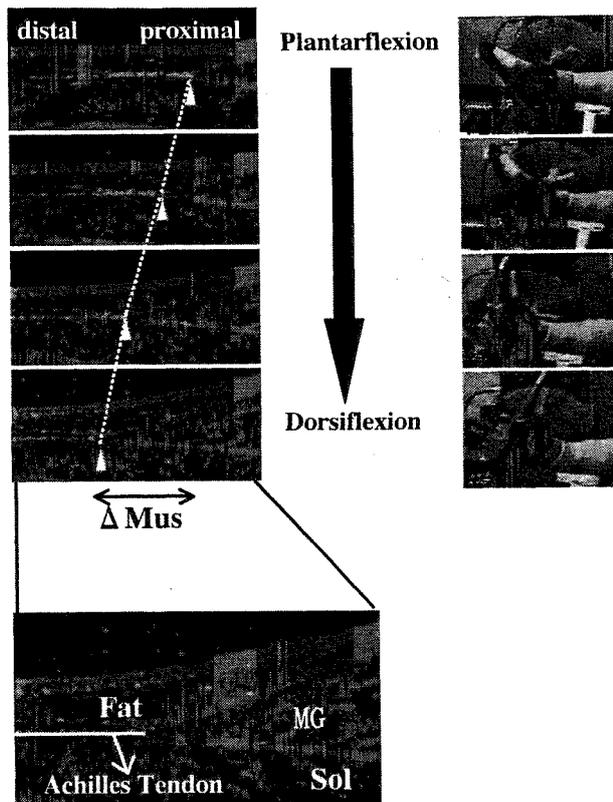


Figure 2 The movement of MTJ when the ankle joint was passively dorsiflexed

gastrocnemius was calculated by subtracting the Achilles tendon length from the shank length.

The subjects were seated with the knee joint fully extended while their ankle joint was fixed onto the foot plate of the dynamometer (VINE, Japan). The measurement was made by rotating the foot plate to the ankle joint dorsiflexion direction with the start point at 30 degrees plantar flexion. The examiner gradually increased loading to the ankle dorsiflexion direction by operating the torque output of the dynamometer. We instructed the subjects to relax the plantar flexion muscle group and not to make movements against passive dorsiflexion during measurement. Final loading was decided from a preliminary measurement to a degree in which the subjects subjectively felt stretching to elongation of the crural triceps surae muscles as "moderate stretch feeling" to "a little strained". Following Warren, et al., (1992), we obtained this indicator by the visual analog scale method. This load was different for each subject, and the torque to this load and the passive ankle joint dorsiflexion angle that occurred by motor rotation were used for analysis. Surface

electromyogram was obtained from the gastrocnemius medialis, lateralis, soleus, tibialis anterior, biceps femoris (long head) muscle, and we confirmed no muscle discharge by passive muscle elongation.

Using a specially-prepared angle meter (VINE, Japan), we measured the joint angle (active plantar-dorsi-flexion angle) when the subjects performed ankle plantar-dorsi-flexion movement with a maximum effort. The angle meter fixed at the shank and foot part had been designed to permit free ankle joint plantar-dorsi-flexion movement. Correlation taken from the passive dorsiflexion angle measured by the dynamometer and joint ROM measured by the angle meter was $r=0.735$, which was significant at a 0.1% level. From this, we considered that the decision of loading obtained by the visual analog scale method could sufficiently reflect the subjects' joint ROM.

By fixing the probe of the ultrasonic device (SSD-6500, ALOKA, Japan) on the skin over the muscle-tendon junction (MTJ) of the gastrocnemius medialis and Achilles tendon, we took an image of the movement of MTJ (Figure 2) accompanied by ankle joint dorsiflexion, and measured this movement as muscle elongation. The moment arm lengths as a function of joint angles were estimated from Rugg, et al. (1990), and the elongation of muscle-tendon complex of triceps surae muscles was estimated from the change of moment arm length (Figure 3). The tendon elongation was defined as the difference between the estimated value of MTC's total elongation and the actual measured value of muscle elongation. Change of the ankle joint angle during dorsiflexion was measured by attaching a goniometer (Biometrics, UK) to the ankle joint's medial malleolus. We also measured the passive torque generated by plantar flexor muscle group by dorsiflexing the foot plate of the dynamometer. During the measurement, changes of the ankle joint angle and passive torque were recorded through an A/D converter (Power Lab: AD Instruments, Australia) into a computer at 1kHz.

Also, as an indicator of muscle strength of the triceps surae muscles, we measured the ankle joint MVC torque when isometric plantar flexion was made in a maximum voluntary effort. At the time of MVC measurement, the ankle joint angle was fixed to the foot plate of the dynamometer at 0 degree anatomically neutral position. The torque was measured twice, with a sufficient resting between two

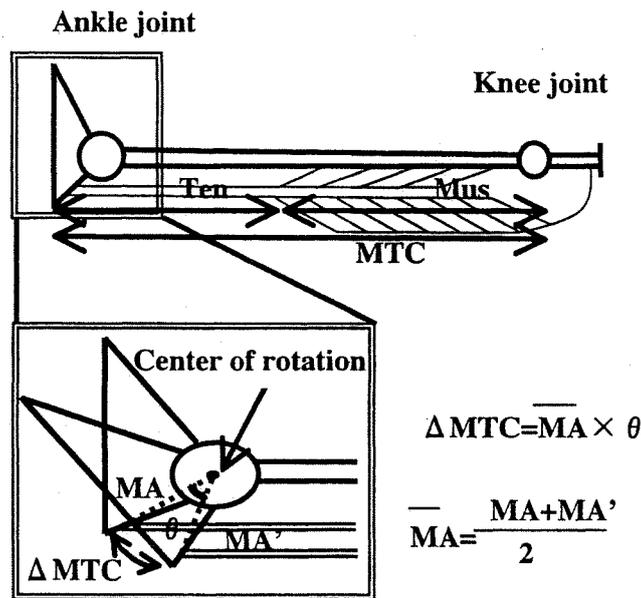


Figure 3 The change of MTC (Muscle-tendon Complex) length (ΔMTC) during passive dorsiflexion was estimated from changes in ankle joint angle (θ) and moment arm lengths (MA)

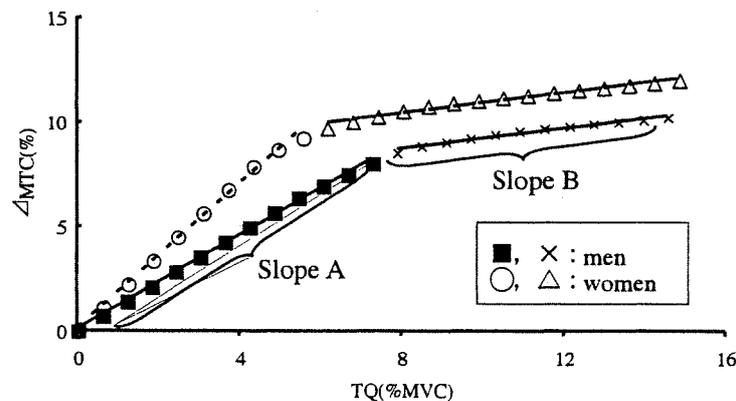


Figure 4 Typical example of passive TQ(%MVC) and ΔMTC (%) during the test

measurements. When there was a difference of more than 10% between two measurements, we made the third measurement.

2.3. Analyse

MTC elongation, muscle elongation, and tendon elongation were increased to the increase of the passive torque, and two phases were clearly observed in all subjects (**Figure 4**). Therefore, we call hereafter the first phase Phase A and the second Phase B.

Each elongation to the passive torque was linearly regressed in each subject, and was divided at a point where the residual of two regression lines became least. The slope of regression of the subjects were averaged in every group and compared between men and women.

In consideration of difference in physique and muscle strength by gender, MTC elongation, muscle elongation, and tendon elongation were normalized by the shank length, the muscle length of the gastrocnemius, and the Achilles tendon length,

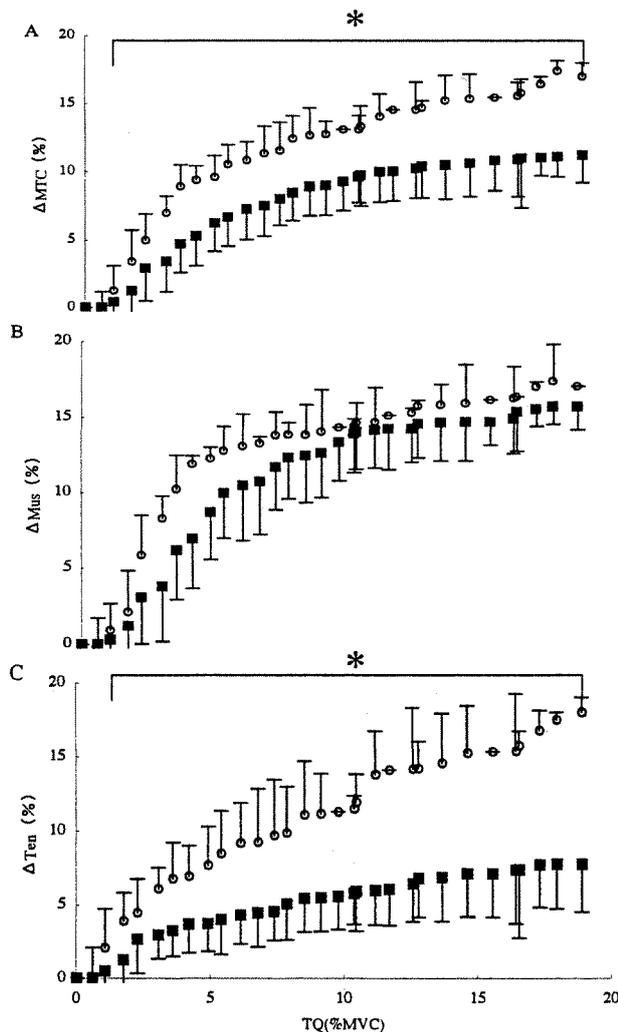


Figure 5 The relationship between relative torque and Δ MTC (A), Δ Mus (B), Δ Ten (C), relative to the initial length ■: Men, ○: Women

respectively, and the passive torque was normalized by plantar flexion MVC torque.

To verify the reproducibility of the method used in this experiment, we performed passive dorsiflexion of ankle joint twice in the same procedure on another day more than one week after the initial experiment. For the second passive dorsiflexion, the subjects had a twenty minute rest after the first one. There was no significant difference between the first and the second ankle joint dorsiflexion angle to a constant passive torque and the MTJ displacement in each subject, nor in the foot plantar flexion torque. Therefore, we judged that there was no difference in each indicator obtained from the two measurements.

2.4. Statistics

We used an unpaired T-test for comparison of gender difference with judgment criteria of statistical significance of $p < 0.05$.

3. Results

Figure 5A shows MTC elongation to the increase of the passive torque; **Figure 5B**, muscle elongation; **Figure 5C**, tendon elongation. Both Phase A and Phase B with greater slope show greater elongation to the constant passive torque. The slope of Phase A in women, when compared with men, was greater in MTC elongation (women: 8.3 > men: 5.2, $p = 0.0027$), and difference was observed at the point of the first small passive torque during the measurement but no difference was observed in Phase B ($p = 0.1250$). Similarly, in muscle elongation and tendon elongation, women had bigger values in Phase A than men (muscle elongation, women: 4.6 > men: 3.1, $p = 0.0063$, tendon elongation, women: 3.7 > men: 2.3, $p = 0.0239$). In Phase B, although there was no difference in tendon elongation ($p = 0.3868$), men showed significantly bigger values in the muscle elongation (men: 0.7, women: 0.3, $p = 0.0007$).

Table 2 shows the final values during the passive dorsiflexion. Women showed significantly bigger values than men in the ankle joint dorsiflexion angle, and also in the MTC elongation per shank length.

In muscle elongation and tendon elongation, women were significantly greater in tendon elongation. However, in muscle elongation, men and women did not show any difference. From the fact that the passive torque normalized in MVC showed no significant difference between men and women, we thought that there was no gender difference in the relative loading of passive dorsiflexion.

Also, when we saw correlation between relative MTC elongation and relative values of each index by sex, both men and women showed a significant positive correlation between MTC elongation and tendon elongation (men: $r = 0.89$, $p < 0.001$, women: $r = 0.79$, $p < 0.01$, **Table 3**, **Figure 6B**). However, no significant correlation was observed between MTC elongation and muscle elongation in either sex (**Table 3**, **Figure 6A**).

Table 2 The normalized final values during passive dorsiflexion. Data are means (SD)

| | AJA (deg) | Δ MTC (%) | Δ Mus (%) | Δ Ten (%) | TQ (%) |
|--------------|----------------|------------------|------------------|------------------|------------|
| Men (n=18) | 16.7 (6.5) | 12.1 (1.7) | 15.9 (1.7) | 9.3 (1.9) | 17.4 (5.1) |
| Women (n=12) | 26.0 (7.6) *** | 15.3 (1.7)*** | 15.2 (2.5) | 15.1 (3.3)*** | 19.8 (4.3) |

AJA: Ankle Joint Angle during passive dorsiflexion ***: Significantly different from men, $p < 0.001$

Table 3 Correlation coefficients between Δ MTC and Δ Mus and Δ Ten.

| | Δ Mus (%) | Δ Ten (%) |
|--------------|------------------|-----------------------|
| Men (n=18) | 0.362 (n.s.) | 0.886 ($p < 0.001$) |
| Women (n=12) | 0.365 (n.s.) | 0.787 ($p < 0.01$) |

4. Discussion

The result of this study showed that women have more compliant Achilles tendons than men. It also suggested that tendon elongation may contribute to the greatness of the joint ROM.

Although Oda, et al., (2002) did not examine gender difference in MTC of the triceps surae muscles, muscle architecture and functional characteristics such as they shared maximum dorsiflexion angle, joint stiffness, plantar flexion muscles strength, calf circumference, triceps surae muscle thickness, and muscle belly length were more strongly related to passive maximum dorsiflexion ROM than to tendon characteristics such as tendon cross-sectional area and tendon length. The result is different from these of the present study in which we found that MTC elongation (= maximum dorsiflexion angle) was more strongly affected by tendon elongation than by muscle elongation.

There is a report that only the "Toe-Region" of tendon's 'force-length relationship is used under MVC (Ito, et al., 1998; Maganaris, et al., 1999). Phase A and B observed in the present study might fall within this "Toe-Region". Yet, greater MTC elongation, muscle elongation, and tendon elongation of women were notable in Phase A and a clear gender difference was observed in the slope of Phase A. Phase A of the present study is thought to correspond to the region with low stress in the "Toe-Region". Ker (1992), and Jozsa, et al., (1997) have reported that the toe-region occupies the region with "low stress" (2% of extremely low strain) in stress-strain relations and that collagenous tendons and ligaments are mainly extended. Also, in constitution, crimp constitution preceding elongation of waviness as well

as elongation of waviness held by collagen fiber of tendon tissue are transformed. Therefore, in relation to gender difference seen in Phase A of tendon elongation, gender difference of joint ROM may be affected by the difference between waviness of collagen fiber and crimp before waviness is extended. The present study examined gender difference of joint ROM in view of muscle elongation and tendon elongation. There is also a report that joint laxity due to the ligament and skeleton may also affect gender difference of joint ROM (Wilkerson, et al., 2000; Brown, et al., 2000). These points need further detailed study.

Kawakami, et al., (2003) performed a similar experiment with middle-aged and elderly men and women and observed, from the fact that a negative correlation was seen between passive dorsiflexion angle and thickness of plantar flexor muscles, that the amount of muscle may affect passive elongation and that the higher flexibility of women than men owes to the difference in the volume of muscle. This is what Oda, et al., (2002) asserted. The result of the present study, however, did not show significant correlation between MTC elongation and calf circumference: correlation between the absolute values and the calf circumference in the MTC elongation was, men: $r = -0.239$ (n.s.), and women: $r = -0.569$ (n.s.), and correlation between the relative values and the calf circumference in the MTC elongation was, men: $r = -0.410$ (n.s.), women: $r = 0.282$ (n.s.). From these results, influence of the muscle volume of the triceps surae muscles on the ankle joint dorsiflexion angle and MTC elongation could not be corroborated in this study.

From the correlation between MTC elongation and muscle elongation, and the correlation between

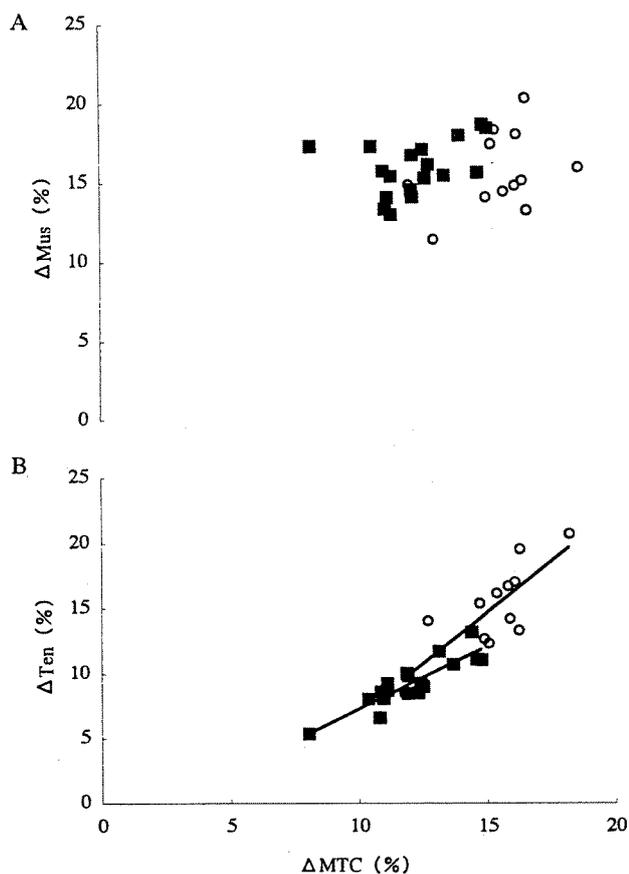


Figure 6 A: The relationship between Δ MTC and Δ Mus
 ■: Men ($r=0.362$, n.s.), ○: Women ($r=0.365$, n.s.)
 B: The relationship between Δ MTC and Δ Ten
 ■: Men ($r=0.886$, $p<0.001$), ○: Women ($r=0.787$, $p<0.01$)

MTC elongation and tendon elongation, a positive significant correlation was observed in tendon elongation in both sexes (men: $r=0.89$, $p<0.001$, women: $r=0.79$, $p<0.01$) but not in muscle elongation in both sexes. Although significant correlation was not observed in relative MTC elongation and muscle elongation that was done without discriminating the subjects' sex as a trial ($r=0.228$, n.s.), a significant positive correlation was observed in relative MTC elongation and tendon elongation ($r=0.901$, $p<0.001$). These results showed that individual difference of tendon elongation may affect individual difference of MTC elongation.

In the latter half of two phases of muscle elongation to the passive torque (Phase B), men slope was significantly greater than women. It demonstrates that women muscle elongation

notably increases with the increase of the passive torque in Phase A while in Phase B little increase was observed. Meanwhile, although men muscle elongation with the increase of the passive torque is significantly lower than women in Phase A, it continues increasing in the Phase B.

From the above results, it may be concluded that men's tendons have more difficulty in extending than women's tendons with the same loading. At the "Toe-Region", men compensate difficulty extending the tendon by muscle elongation in Phase B. On the contrary, women might use tendon elongation for Phase B of MTC elongation and do not show much muscle elongation. If muscle elongation has its limit, the women muscle belly may be extended close to this limit in Phase A of the "Toe-Region" and further elongation might have been restricted. However, this point is only our speculation.

Kubo, et al., (2003), in their report, showed the relationship between muscle strength and tendon elongation when adult men and women gradually exerted plantar flexion torque from rest to MVC. Kubo, et al., (2003) presented the result that in the relationship of Fm (muscle force)-L (tendon elongation), men, when compared with women, had a significantly smaller value of L in muscle force of more than 50N. The present study demonstrated gender difference in plantar flexor muscle strength of less than 50N, in which Kubo, et al., (2003) concluded to the contrary. The difference in the result between the present study and that of Kubo, et al., (2003) might be gender difference in tendon elongation by muscle contraction in the study of Kubo, et al., (2003) vs. gender difference in tendon elongation by passive tendon elongation in this study. This report explains gender difference in the tendon properties just as in the shape of muscle. In the function, women have significantly lower stiffness and hysteresis than men, which means women have compliant tendons. From the result verified in this study like the study by Kubo, et al., (2003), the women's tendon is more compliant than that of men's, which might exhibit gender difference in the joint range of motion.

Gender difference observed in MTC elongation with a swell loading in the Toe-Region of the tendon suggests that, even in a movement generating a small torque that frequently occurs in daily life, gender difference of the joint range of motion may affect gender difference of the performance of the

movement. Gender difference in the indices of flexibility such as standing anteflexion and prone leaning flexibility might relate to this finding. Its physiological meaning should require further study.

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The Effects of Strength Training on Muscle Architecture in Humans

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The present paper reviews previous studies on changes in muscle architecture in humans as a result of strength training. Muscle architecture here refers to 1) muscle size, 2) pennation angle, and 3) muscle fiber length. Training-induced changes are summarized respectively. A typical outcome of strength training is muscle hypertrophy, which is manifested as an increase in muscle size evaluated by cross-sectional area and muscle volume. However, changes also occur in pennation angles and, possibly, in muscle fiber lengths. Increased pennation angles after training have the detrimental effect of producing a reduced force transmission from muscle fibers to tendon, which might lead to a decrease in specific tension or muscle force per physiological cross-sectional area. Recent *in vivo* studies on human muscles have revealed that changes in pennation angles resulting from training and contraction are much greater than previously thought.

Keywords: muscle cross-sectional area, pennation angle, fiber length, specific tension

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1. Introduction

The effects of strength training on muscle size and function have been the focus of exercise science for more than a century. Numerous studies have been undertaken, and even today, novel findings are being reported. In this review, rather than providing an extensive review of these studies, we focus instead on a recently emerging idea concerning the strength training effects on muscle architecture and its functional significance. There is increasing evidence of the importance of muscle architecture in muscle force production, and it has been shown that muscle architecture changes as a result of strength training. There are several aspects of muscle architecture, and the time course of strength gain as a result of training is not a simple function of muscle size. Strength training refers to resistance training in which skeletal muscle is encumbered by a resistive load for the enhancement of muscle strength and power, and the increase in size (hypertrophy). Other types of training such as endurance (either cardiopulmonary or muscular) are beyond the scope of the present article.

Muscle architecture is a widely applicable concept

for the arrangement of muscle components within the framework of the musculoskeletal system. The following levels have been defined (Gans and de Free 1987), i.e., 1) the organization of the sarcomeres and their placement within fibers; 2) the placement of fibers within muscle; and 3) the placement of muscle within the skeleton. The term placement can be regarded as the way in which sarcomeres, fibers, and muscles are arranged in space relative to surrounding structures, as well as the magnitude of their quantity (i.e., size) (Kawakami, et al., 2000a). For instance, with respect to the second level, human skeletal muscle has a wide variety of fascicle (or muscle fiber) arrangements typically classified into pennate and parallel-fibered muscle (Gans and de Free 1987). Also, fiber and muscle cross-sectional areas (CSA) are the parameters of muscle architecture at the second and third levels, respectively. Training-induced morphological changes in human skeletal muscle typically manifest at these levels of muscle architecture, which are addressed in the present article.

2. Training-induced changes in muscle architecture

2.1. Muscle size

As a result of strength training, there occurs an enlargement of muscle fibers and, hence, an increase in muscle size (MacDougall, et al., 1980). In human studies, muscle size is assessed from partial information such as the thickness of the muscle belly or CSA of a muscle or muscle groups. Although there is a highly significant correlation ($r = 0.9$) between the thickness and CSA of a muscle (Martinson and Stokes, 1991), the latter is frequently used in training studies, since the former is only a partial, one-dimensional measure of muscle. To measure muscle CSA in humans, imaging techniques such as ultrasonography (US, Dons, et al., 1979; Ikai and Fukunaga, 1970; Ichinose, et al., 1998), computed tomography (CT, Alway, et al., 1990; Davies, et al., 1988; Jones and Rutherford, 1987; Luthi, et al., 1986), and magnetic resonance imaging have been used (MRI, Akima, et al., 2003; Cureton, et al., 1988; Housh, et al., 1992; Kawakami, et al., 1995). It has been shown in these studies that muscle CSA increases by 5 – 20% as a result of strength training lasting 5 – 12 weeks.

In reality, muscle presents three-dimensionally, and a training-induced enlargement takes place throughout the muscle. Therefore, it is more appropriate to evaluate muscle size over the entire muscle belly. Recently, taking CSAs serially from the proximal to the distal end of the muscle has been possible by MRI. This method was initially introduced by Mungiole and Martin (1990), and later developed by Fukunaga, et al., (1992). It was shown by this method that muscle hypertrophy by strength training resulted in inhomogeneous increases in CSAs over the muscle length (Narici, et al., 1989). Roman, et al., (1993) found after 12 weeks of elbow flexor muscle strength training in elderly subjects an increase in a single slice CSA by 23%, while the muscle volume increased by only 14%. From this result, they negated the single-slice-based evaluation of muscle size. A similar finding was reported by Aagaard, et al., (2000) for quadriceps muscles. Kawakami, et al., (1995), however, did not find significant differences in changes in CSAs over the lengths of the triceps surae muscles after 16-weeks strength training (Figure 1). No decisive

conclusion has yet made regarding the intra-muscle inhomogeneity of muscle hypertrophy. However, it has been shown that muscle volume is related more to joint torque than to CSA (Fukunaga, et al., 2001). Thus, when evaluating joint performance from muscle size, the muscle volume rather than CSA should be measured. Recent studies have adopted muscle volume as a measure of muscle size (e.g., Kanehisa, et al., 2002; Tracy, et al., 1999; Tesch, et al., 2003); however, other studies exist that evaluate muscle size from a single, anatomical CSA (e.g., Ahtiainen, et al., 2005; Gondin, et al., 2005; Hubal, et al., 2005).

2.2. Pennation angle

Skeletal muscles are roughly divided into two types with respect to the arrangement of fascicles or muscle fibers, i.e., parallel-fibered muscles in which fibers with length close to that of the whole muscle lie almost parallel to the muscle line of action, and pennate muscles, in which short fibers insert into tendons at an angle to the muscle line of action (Gans and de Free 1987). The angulation of muscle fibers relative to the line of action of muscle in pennate muscles is known as pennation angle.

Fiber pennation is considered to be a packing strategy by which more fibers can be contained in a muscle compared with parallel-fibered muscles (Gans and Gaunt, 1991). The gastrocnemius, a typical unipennate muscle, has more than 1 million fibers while the parallel sartorius muscle has approximately 100,000 fibers (McComas, 1996). Thus, the physiological CSA (total CSAs of fibers in a muscle) of pennate muscles is larger than parallel-fibered muscles (Yamaguchi, et al., 1990). From this fact, it has been thought that pennate muscles are designed for force production while parallel-fibered muscles are designed for excursion and speed (Huijing and Woittiez, 1984; Lieber and Blevins, 1989). Recently, however, pennate muscles have been shown to possess prominent power (force x speed) potential owing to muscle-tendon interaction (Kawakami, et al., 2002).

Kawakami, et al. (1993, 2000a) measured pennation angles of the triceps brachii muscle *in vivo* using ultrasonography for subjects including normal individuals and highly-trained bodybuilders. The pennation angles were within the range of 5° and 55°, which were smaller and much greater than the

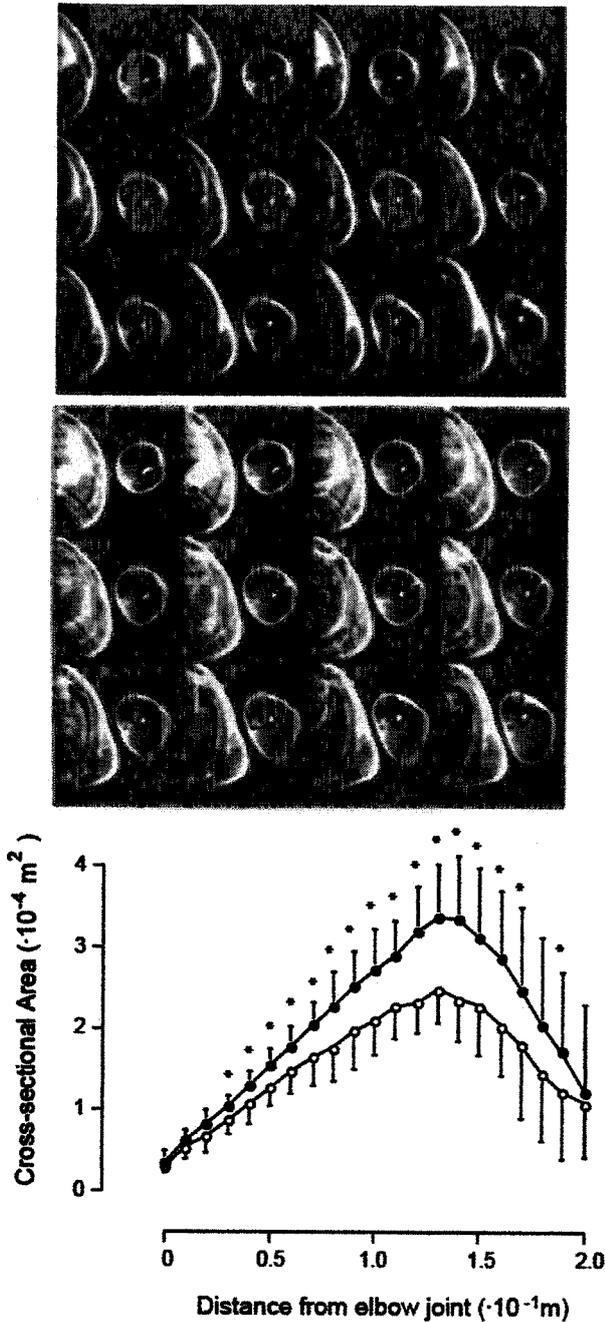


Figure 1 Series cross-sectional MRI images of the upper arm (from top left to bottom right; distal to proximal) before (upper panel) and after (lower panel) strength training of elbow flexor muscle for 16 weeks. The series anatomical cross-sectional areas before (○) and after (●) training are also shown (bottom trace) (Kawakami et al., 1995). In each image, triceps brachii muscles are seen in the lower half of the upper arm.

published data on human cadavers (Yamaguchi, et al., 1990). They further investigated the relationship between pennation angles and muscle thickness, and

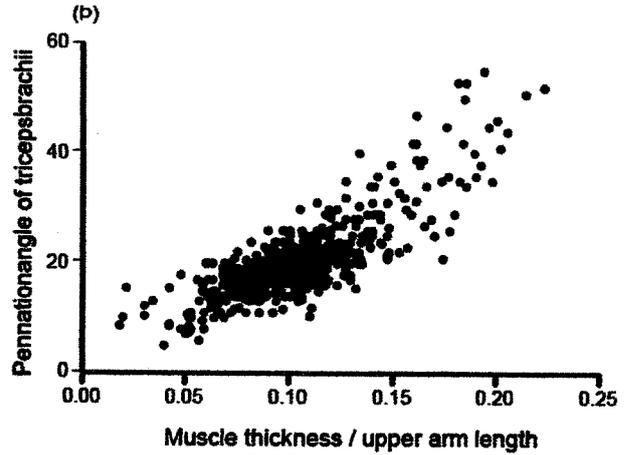


Figure 2 The relationship between pennation angles and muscle thickness (normalized by the upper arm length) (Kawakami et al., 2000a). The subjects were 637 women and men including (normal individuals OR non athletes?) and highly-trained bodybuilders.

found a significant correlation (Figure 2), which provided experimental evidence of the contention in previous studies that muscle hypertrophy accompanies an increase in pennation angles (Jones and Rutherford, 1987; Maxwell, et al., 1974; Narici, et al., 1989). It was further confirmed, through a longitudinal study, that hypertrophy by strength training was actually accompanied by an average increase in pennation angles in the triceps brachii muscles that increased their total volume by 32% and physiological CSA by 33% (Kawakami, et al., 1995). Henriksson-Larsen, et al., (1992) failed to find a significant correlation between pennation angles and muscle fiber CSA in the human vastus lateralis muscle. Rutherford and Jones (1992) found a correlation between pennation angles and muscle CSA of the vastus lateralis; however, they reported no changes in pennation angles after strength training that induced an increase in muscle CSA by 5%. These studies suggest inter-muscle differences in training-induced responses in fiber architecture. However, later Aagaard, et al., (2001) found both a correlation between pennation angles and muscle volume and an increase in pennation angle after a strength training of the vastus lateralis muscle that increased muscle CSA and volume by 10%. It appears, therefore, that the differences in the tendency between the studies are simply due to the magnitude of the muscle hypertrophy resulting from training, and that the increase in pennation angles is a general outcome of hypertrophied pennate muscles

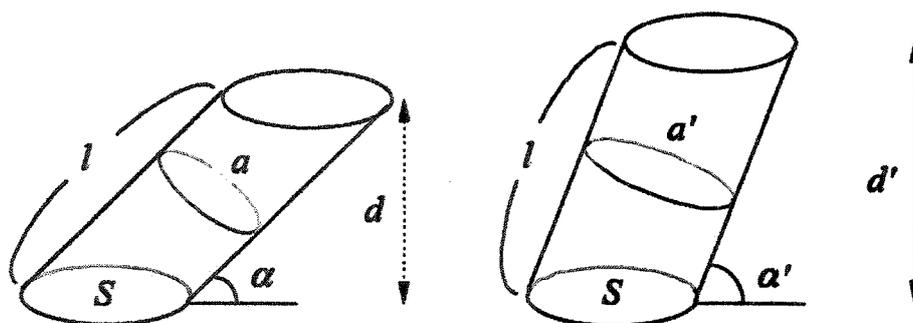


Figure 3 A model of muscle fiber architectural change as a result of hypertrophy (Kawakami, 2002). Left, pre-training, right, post-training. a : cross-sectional area of a muscle fiber, α : pennation angle, l : muscle fiber length, S : the area of aponeuroses occupied by the muscle fiber, d : distance between aponeuroses

(Figure 3) (Kawakami, et al., 2002). This change appears to be independent of gender difference (Ichinose, et al., 1998). Clearly, such a change might cause a different time-course of changes in anatomical and physiological CSA's (Klein, et al., 2001).

2.3. Muscle fiber length

Among architectural parameters of the skeletal muscle, fiber length are particularly important because the force exerted by muscle fiber is determined by its length (force-length relationship) (Gans, 1982). Long fibers can shorten at faster speed than short fibers, so that fiber length affects the force-velocity relationship as well (Kawakami and Fukunaga, in press). In the present study, we regard fiber and fascicle lengths as identical, which has been shown in pennate muscles with short fibers such as the triceps surae (Kawakami, et al., 2000b).

There is some evidence from animal studies concerning the plasticity of muscle fiber length. Immobilization of quail muscle in a stretched and loaded condition increased both CSA and the length of muscle fibers (Alway, et al., 1989), unlike normal atrophic responses of immobilized muscles (Herbert and Balnave, 1993). The increase in muscle fiber length is due to the newly formed series of sarcomeres at both ends of the fiber (Garrett, et al., 1988). Similarly, running training in rats with eccentric loads to the thigh muscle resulted in an increase in the number of serial sarcomeres (Lynn and Morgan, 1994). They attributed this result to an inherent protection mechanism against popping (breakage) of sarcomeres that is known to occur

by repeated eccentric contractions. A shift in the force-length relationship to longer lengths has been observed in humans as an acute response to eccentric loading (Brockett, et al., 2001; Jones, et al., 1997). These findings suggest the possibility of muscle fiber length changes by human strength training, though no clear data have yet been presented.

In humans, muscle fiber length has been determined from a dissection of cadaver specimens (Alexander and Vernon, 1975; An, et al., 1989; Friedrich and Brand, 1990; Huijing, 1985; McComas, 1996; Wickiewicz, et al., 1983; Yamaguchi, et al., 1990). Recently, fiber length measurement has been carried out *in vivo* through imaging techniques such as MRI (Scott, et al., 1993) and ultrasonography (Kawakami, et al., 1995, 1998, 2000a, 2000b, 2002; Kumagai, et al., 2000; Rutherford and Jones 1992). By this technique, it has been possible to study the inter- and intra-individual differences in fiber length. The fiber lengths of the triceps surae muscles exhibit a large variability among individuals, and they are not correlated with lower leg lengths (Chow, et al., 2000). Cadaver observations have also provided variable muscle fiber lengths among individuals (Murray, et al., 2000). These findings suggest the question of whether muscle fiber lengths are genetically determined or altered after birth. Abe, et al. (2000) found longer fascicle lengths in sprinters than in long distance runners. Long fascicle lengths correlated with sprint performance both in women and men (Abe, et al., 2001; Kumagai, et al., 2000). These findings confirm the inter-individual variability in fascicle or muscle fiber length, suggesting once again the possibility that fiber length is altered by specific training, which warrants further longitudinal studies.

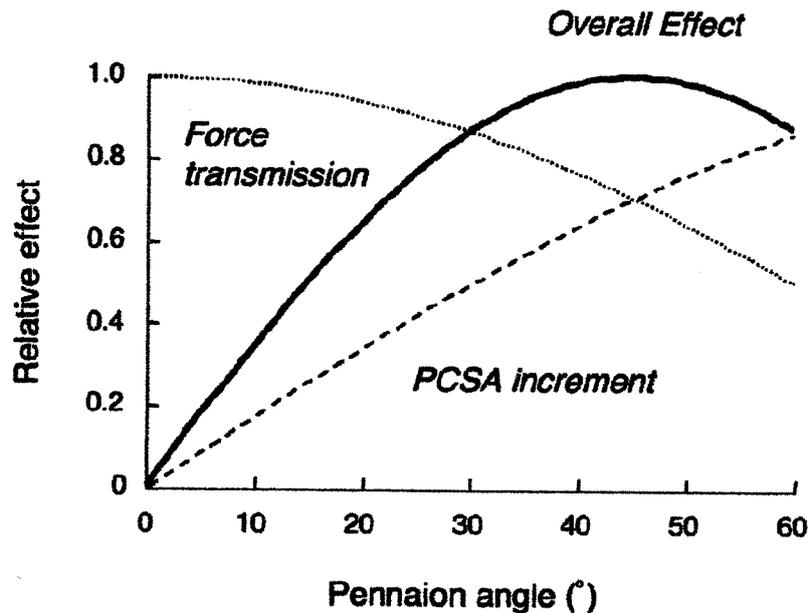


Figure 4 Positive and negative effects of pennation angles (based on Alexander & Vernon, 1975). As the pennation angle increases, the physiological cross-sectional area (PCSA) increases, but force transmission from muscle fibers to tendon decreases. These two factors result in an overall effect.

3. Functional consequences of architectural changes in skeletal muscle by strength training

3.1. Force transmission from muscle fibers to tendon

The pennation angle determines the transmission of muscle fiber force to tendon (Gans and de Vree, 1987; Wickiewicz, et al., 1983). Alexander and Vernon (1975) predicted from a simple planimetric model of a pennate muscle that an increase in pennation angle results in muscle force enhancement by virtue of an increment in physiological CSA, though pennation angles above 45° cause a detrimental effect for a decrease in muscle force (Figure 4). Previously, it was believed that changes in fiber pennation, if any, would not be a major determinant of changes in force generation as a result of strength training (Jones, et al., 1989). One of the rationales for this belief was a relatively small (~20°) pennation angle in human cadavers (Alexander and Vernon, 1975). However, as described above, it is now widely accepted that muscle hypertrophy accompanies an increase in pennation angles reaching as much as 55° (Kawakami, et al., 1993, 2000a). Therefore, the influence of pennation

angle increase on muscle fiber force transmission might be substantial. Hypertrophied muscles with large pennation angles, therefore, might have disadvantageous force-producing capacities, as evidenced by a decrease in specific tension.

3.2. Specific tension

Muscle strength is known to be a linear function of size (e.g. CSA) (Gadeberg, et al., 1999; Ikai and Fukunaga, 1968; Maughan, et al., 1983; Roy and Edgerton 1992; Sale, et al., 1987). This is because muscle fiber force is closely related with CSA (Close, 1972). The specific tension, i.e., muscle force relative to physiological CSA, is fairly constant, regardless of its fiber type compositions (Nygaard, et al., 1983; Spector, et al., 1980). Although there are some studies reporting fiber-type dependence of specific tension (e.g., Powell, et al., 1984), it has been pointed out that the variation in the specific tension between different fiber types is due to methodological errors in assessing fiber CSA (Eldred, et al., 1993).

The predictability of muscle force generating capability from muscle size, however, is questioned since it has been shown both in animals and in humans that there are training-induced changes in specific tension. Apart from possible changes in

neural activation or drive to muscle force generation (Aagaard, et al. 2000; Jones and Rutherford, 1987; Ploutz, et al 1994; Sale, 1988; Kitai and Sale, 1989; Sale and MacDougall 1981) and biochemical malfunction in hypertrophied muscles (Kandarian and Williams, 1993), recent studies have shown that strength training alters muscle architecture as described above, which could affect the linearity in the relationship between muscle size and strength. As described above, an increase in pennation angles can lead to a muscle force deficit due to a reduced muscle fiber force being transmitted to tendon. In other words, the disadvantageous effect of pennation (less efficient force transmission from muscle fibers to tendon) may be further amplified after strength training. This might explain the large deviation of reported specific tensions in human muscles (An, et al., 1989; Ikai and Fukunaga, 1968; Kawakami, et al., 1994; Narici, et al., 1989). Maughan, et al. (1983) demonstrated an inverse relationship between muscle CSA and the ratio of muscle strength to muscle CSA and suggested that in larger muscles pennation angles might be greater, resulting in a smaller strength-to-CSA ratio. Ikegawa, et al. (1994) and Kawakami, et al. (1995) have shown that this can actually be the case.

4. Future perspectives

It is now clear that muscle architecture changes through strength training, with the changes being sometimes well beyond previous expectations. The importance of muscle architecture in muscle functions, therefore, cannot be overemphasized, and studies on training (and detraining) responses should thus take into consideration architectural changes in the muscles involved. Before concluding the present review, I will summarize recently emerging ideas that should also be taken into account in discussions of muscle architecture in humans and some future perspectives.

4.1. Intra-muscle differences in muscle architecture

Muscle fiber length, pennation angles and other architectural parameters are often studied at a certain position within a muscle (e.g., at muscle belly) (Aagaard, et al., 2001; Abe, et al., 2000; Fukunaga, et al., 1997; Kawakami, et al., 1993). However, there

might be architectural variability within a muscle. In this regard, previous studies are not in agreement, with some studies on human cadaver specimens showing fiber length variability (Huijing, 1985; Scott, et al., 1993) and others reporting identical muscle fiber length throughout muscle (Friedrich and Brand, 1990; Scott, et al., 1993; Wickiewicz, et al., 1983). Kawakami, et al., (2000a) studied intramuscular variation in fascicle arrangement of the human gastrocnemius muscle in vivo. They reported fairly uniform muscle fiber lengths both at rest and during isometric contraction at 50% of the maximal level. The magnitude of shortening of fibers upon contraction (30 - 34 %) was identical. On the other hand, pennation angles differed significantly at different positions.

Muscle fibers are arranged in a three-dimensional space (Lam, et al., 1991; Otten, 1988; Scott, et al., 1993). Because of this, the possibility of misevaluation of muscle fiber length and pennation angles exists. A recent study revealed a potential source of error in determining pennation angles and muscle fiber lengths (Kurihara, et al., 2005). If there is deviation between the plane of the ultrasound image and that of fibers, fiber lengths are underestimated and pennation angles are overestimated (Kurihara, et al., 2005). This error can be avoided by assuring a proper plane that is parallel to fibers and perpendicular to the aponeuroses onto which fibers are attached, but it is not always possible with the conventional two-dimensional ultrasonography. Thus, for accurate evaluation of architectural parameters, the three-dimensional imaging technique (e.g., 3D-ultrasonography) should be used. In addition, a recent study has shown inhomogenous activity within a muscle (Kinugasa, et al., 2005), which may also alter internal fiber architecture if such activity persists throughout training. Future training studies will reveal changes in three-dimensional fiber architecture as a result of strength training.

4.2. Changes in muscle architecture upon contraction

Because pennate muscles have long tendinous tissues, there is a large amount of muscle-tendon interaction, and muscle fibers shorten even during isometric contractions. This internal fiber shortening results in an increase in pennation angles which

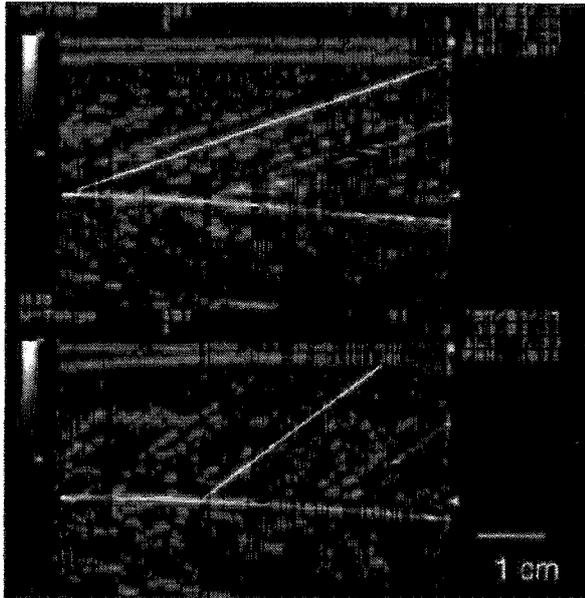


Figure 5 Ultrasonic image of the gastrocnemius muscle at rest (top) and during maximal isometric contraction (bottom). One fascicle is highlighted by a straight line. Left, distal, right, proximal.

reaches up to 70° in the medial gastrocnemius during maximal contraction even in non athletes (Kawakami, et al., 1998, Figure 5). Thus, the effect of pennation angles on muscle force production, and the functional impact of their increase, may be much greater than previously thought. The magnitude of muscle-tendon interaction varies among individuals (Kawakami and Fukunaga, in press), and it changes as a result of strength training (Kubo, et al., 2002). Therefore, even if there is no apparent architectural change after training in a resting muscle, there is high probability for altered pennation angles and muscle fiber lengths during contraction, which should be tested in future studies.

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Effects of Passive Ankle and Knee Joint Motions on the Length of Fascicle and Tendon of the Medial Gastrocnemius Muscle

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The purpose of this study was to investigate the effects of passive ankle and knee joint motions on the length of fascicle and tendon of the gastrocnemius muscle. The ankle joint was passively moved from maximal dorsiflexed position to maximal plantar flexed position, while the knee joint was fixed at 0° (fully extended position). Also, the knee joint was passively extended from 90° to 0°, while the ankle joint was fixed at 0° (neutral position). In each test condition, lengths of fascicle and external tendon of the medial gastrocnemius were measured by ultrasonography. The length of external tendon was significantly changed by the ankle joint motion, but not by the knee joint motion. This demonstrates that the length of the external tendon distal to the muscle belly is influenced only by the angle changes of the joint distal to the gastrocnemius muscle. The change in fascicle length during the knee joint motion was significantly larger than during the ankle joint motion in spite of a similar length change of total muscle-tendon complex between the two motions. This demonstrates that fascicles located proximally to the external tendon are more influenced by the angle changes of the joint proximal to the gastrocnemius muscle. These results reveal that angle changes of each joint located in the proximal and distal parts of a biarticular muscle have different effects on the length of fascicle and external tendon.

Keywords: fascicle, external tendon, knee joint, ankle joint, medial gastrocnemius muscle

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1. Introduction

The length of muscle is a determinant of its force producing potential (Gordon, et al., 1966). Furthermore, the changes in the tendon length affect the latency of stretch reflex (Fellows & Thilmann 1989) and the contractile capability of muscle (Hof, et al., 1983, Herbert, et al., 2002). Therefore, it is quite important to focus on the length changes of both muscle and tendon for considering the function of the muscle-tendon complex (MTC) in human movements.

Passive joint motions without muscle contraction change the length of MTC (Stolov & Weilepp 1966, Grieve, et al., 1978). Indeed, previous studies have

quantified the length changes of each tissue within MTC such as muscle fascicles (Herbert, et al., 2002) or external tendon (Muraoka, et al., 2002) in the medial gastrocnemius muscle (MG), and examined how the change in joint angle affects the tissue lengths. In the case of a biarticular muscle, however, the morphological characteristics of tendon differ between proximal and distal parts, i.e. the tendon of the biarticular muscle may attach to the tendon of an adjacent monoarticular muscle. For example, the distal external tendon of the MG attaches to the tendon of the soleus muscle (Bojsen-Moller, et al., 2004). In such a case, it is speculated that the effects of joint motions on the length of fascicle or external tendon differ between the proximal

and distal joints.

Previous studies, which used animals (Ettema 1997, Huijing & Baan 2003) or human cadavers (Grieve, et al., 1978, Visser, et al., 1990, Spoor, et al., 1990), have tried to investigate the length change in MTC when each of proximal and distal joint angles is passively changed. However, these studies have examined only the change of MTC and have not determined the change in such tissues as muscle or tendon. In contrast, Mai & Lieber (1990) has shown the relationship between joint angle and sarcomere length in respect to each proximal and distal joint in frogs. In addition, Kawakami et al. (1998) and Herbert et al. (2002) have measured fascicle length by changing each proximal and distal joint angle on humans *in vivo*. However, the moment arm of the joint located proximal to biarticular muscle is not always equal to the one located distal to it. Therefore, it is necessary to determine the length changes of each tissue relative to a given MTC length in order to compare the influence of both proximal and distal joint motions on the tissues. Such comparison has never been tried so far. The investigation on the length changes of fascicle and external tendon during each of proximal and distal joint motions will clarify the difference in the influence of each joint motion on the function of MTC, and give further knowledge concerning the characteristics of biarticular muscles. The present study aimed to compare the effects of passive ankle and knee joint motions on the length of the fascicle and external tendon in human MG.

2. Methods

2.1. Subjects

Seven healthy men voluntarily participated in the present study. The means \pm standard deviations (SDs) of their age, height and weight were 24.4 ± 2.0 years, 170.3 ± 4.5 cm and 66.7 ± 6.0 kg, respectively. All subjects had no disability in their right leg. The purpose and method of this study and the risk involved in implementing experiments were explained in detail to all the participants. Written informed consent was obtained from each subject before the experiments.

2.2. Experiment protocol

The subjects lay prone on a test bench and performed maximal voluntary contraction (MVC) of each of the plantar flexion and dorsiflexion. The right foot of the subject was strapped at the attachment of a dynamometer (Model VEL-016, VINE, Japan) with the ankle joint angle at 0° (neutral position: the sole of the foot and the tibia at an angle of 90° , negative values for dorsiflexion and positive values for plantar flexion). The rotation axis of the ankle joint was aligned with that of the dynamometer. Knee joint angle was at 0° (fully extended position). After a warm-up exercise with submaximal contractions, the subjects were encouraged to exert MVC in isometric plantar flexion and dorsiflexion. They performed two maximal trials for each action with a rest of more than one minute between each trial. The trial with the larger torque was used for further analysis.

The subjects also lay in a prone position during passive ankle joint motion (AJ) (Figure 1A). The ankle joint of the subject was passively changed by the dynamometer from maximally dorsiflexed to plantar flexed position. Angular velocity was set to keep below $5^\circ/\text{s}$, because it has been verified that stretch reflex is not provoked when the angular velocity is below $5^\circ/\text{s}$ (Hufschmidt & Mauritz 1985, Nicol & Komi 1999). Each subject was instructed to relax the leg muscles completely during the measurement.

In the measurements of passive knee joint motion (KJ), the subject was asked to take a kneeling position on the test bench (Figure 1B). The ankle was fixed to the attachment of the dynamometer at 0° . The subject was instructed to extend the knee joints slowly from the

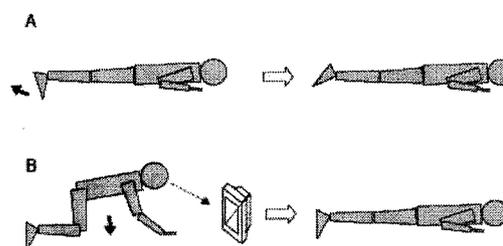


Figure 1 Schematic drawings of the passive ankle joint motion (A) and the passive knee joint motion (B). A: The ankle joint was passively moved from maximal dorsiflexed position (left) to maximal plantar flexed position (right). B: The subjects slowly extended their knee joints from 90° (left) to 0° (right). The knee joint angle measured by a goniometer was visually fed back to the subjects using a monitor which was placed in front of them.

knees at more than 90° to 0° . In KJ, the knee joint angles measured with a goniometer (SG150, Biometrics, UK) were fed back visually to the subject by a monitor set in front of him (Figure 1B). With this feedback, each subject could extend his knee joints so as not to exceed the angular velocity of more than $5^\circ/\text{s}$. Moreover, the subjects were instructed to extend the knee joints using the hip joint and arms, with leg muscles completely relaxed. In our preliminary experiment, we ascertained that fixing the probe of an ultrasound apparatus was difficult in the sitting posture. To avoid sliding of the probe during KJ, therefore, the present study employed the posture as shown in Figure 1B.

2.3. Data acquisition

Displacement of the muscle tendon junction (MTJ), fascicle length and pennation angle of MG in AJ and KJ were measured using a B-mode ultrasonic apparatus (SSD-6500, Aloka, Japan). An electronic linear array probe (UST-5712, 10 MHz wave frequency, Aloka, Japan) was placed on the muscle belly and MTJ along the longitudinal direction of the MG. Echo jelly was applied on the surface of the probe. When the probe was attached on MTJ, a water bag (MP-2463, Aloka, Japan) was placed under the probe in consideration of the irregularity of the skin. In addition, a marker was placed between the water bag and the skin and fixed on the skin. The probe was fixed on the skin using surgical tape until both AJ and KJ were finished. Ultrasonic images were recorded on videotape (S-VHS) at 30 Hz via a video timer (VTG-55, FOR-A, Japan) for synchronizing.

The Ultrasonic images were digitally converted using a media converter (ADVC-500, Canopus, Japan) and scanned in a computer. An image processing program (Image J, National Institute of Health, USA) was used for measuring MTJ excursion, fascicle length and pennation angle. The analysis was conducted at every 1° of the angle change in the ankle and knee joints in AJ and KJ, respectively. The MTJ was determined as the intersection point of the most distal fascicle and deep aponeurosis (Figure 2A). The MTJ excursion was defined as the horizontal displacement of MTJ relative to the marker. The fascicle length was measured as the distance from the intersection points of fascicle and two aponeuroses (Figure 2B). The pennation angle was determined as the angle between fascicle and deep aponeurosis (Figure 2B).

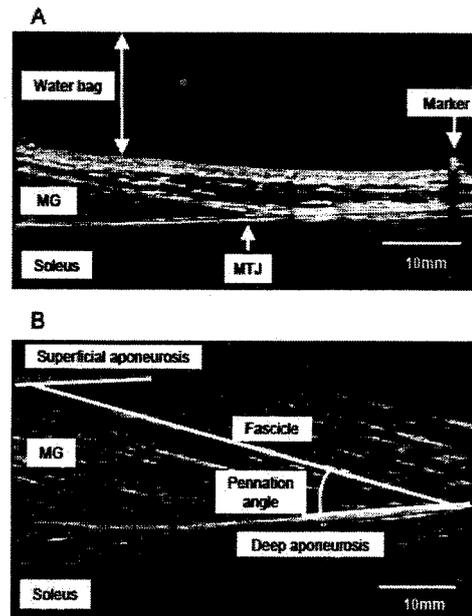


Figure 2 Ultrasonographic images of the MTJ (A) and the muscle belly (B). A: The coordinate of MTJ was determined as the intersection of the most distal fascicle and the deep aponeurosis. B: Fascicle length was determined as the length between the cross-points of fascicle and aponeuroses. Pennation angle was defined as the angle between the line of fascicle and deep aponeurosis.

The accuracy of each measurement on MTJ excursion, the fascicle length and the pennation angle using ultrasonic images has been verified by Muramatsu et al. (2001) and Fukunaga et al. (1997).

Bipolar surface EMGs were recorded from MG, lateral gastrocnemius, soleus and tibialis anterior muscles. Disposable electrodes (Blue Sensor, Ambu A/S, Denmark, sensor: Ag/AgCl, sensor area: 13.2 mm^2) were placed at the belly of each muscle with an inter-electrode distance of 20 mm after the skin's resistance was alleviated. The reference electrode was placed at the medial malleolus of the left foot. The EMG signals were amplified (input impedance $>10 \text{ M}\Omega$, common mode rejection ratio $>54 \text{ dB}$, signal to noise ratio $<6 \mu \text{ Vrms}$, time constant: 0.03 s, hi-cut filter: off) with a multi telemeter system (WEB-5000, NIHON KOHDEN, Japan).

Goniometers were used to measure the angles of ankle (SG110/A, Biometrics, UK) and knee (SG150, Biometrics, UK) joints. The joint angles and EMG signals were digitally converted using an A/D converter (PowerLab/16SP, AD Instruments, Australia), and

transferred to a computer at 1 kHz sampling frequency.

2.4. Data processing

The MTC length change (ΔL_{MTC}) of MG was calculated from the ankle and knee joint angles and leg length (the knee joint center-the ankle joint center) of each subject (Grieve, et al., 1978). The joint angles were processed with a Butterworth-type low-pass filter of fourth order (cutoff frequency: 20 Hz).

In the present study, the distal external tendon of MG was defined as the part from MTJ to the end of the Achilles' tendon. The length change of the distal external tendon (ΔL_{ET}) during AJ was calculated as the difference between the excursion of the end of Achilles' tendon and MTJ excursion measured with the ultrasonography (Muraoka, et al., 2002). The excursion of the end of Achilles' tendon was regarded as identical to ΔL_{MTC} in AJ. In KJ, the end of Achilles' tendon excursion was rarely observed (the change in ankle joint: $0.1 \pm 1.2^\circ$, the excursion of end of Achilles' tendon: 0.1 ± 1.0 mm), because the ankle joint was fixed. Therefore, ΔL_{ET} during KJ was determined by defining the proximal excursion of MTJ as lengthening and the distal excursion of MTJ as shortening. In consideration of the change in pennation angle, fascicle length change (ΔL_F) was calculated by the formula shown below.

$$\Delta L_F = L_F \cdot \cos\alpha - L_{F0} \cdot \cos\alpha_0$$

L_F : fascicle length, α : pennation angle, L_{F0} : fascicle length with ankle and knee joints at 0° , α_0 : pennation angle with ankle and knee joints at 0°

ΔL_{ET} and ΔL_F were calculated every 5 mm of ΔL_{MTC} on the basis of ankle and knee joint angles at 0° .

EMG data were full wave rectified. In MVC test, the mean amplitude of EMG was calculated during 500 ms when the exerted torque reached a steady state. In AJ and KJ, the mean amplitude was calculated every 500 ms and standardized by the value in MVC test.

2.5. Statistical analysis

Descriptive data are presented as the means \pm SDs. A two-way analysis of variance (ANOVA) with repeated measures [2×6 , test condition (AJ, KJ) $\times \Delta L_{MTC}$ (-25, -20, -15, -10, -5, 0 mm)] was used to test the effects of the test condition and ΔL_{MTC} . When the interaction between the two factors was significant, a one-way

ANOVA was conducted on every group categorized by the two factors. When F value was significant as a result of one-way ANOVA, a multiple comparison test (Bonferroni) was used to test the significance of difference between average values. Statistical analysis software (SPSS 12.0J, SPSS Japan, Japan) was used for all analyses mentioned above. Statistical significance was set at $p < 0.05$.

3. Results

The angles of the ankle joint in AJ ranged from -9° to 35° . The angular velocity of the knee joint in KJ ranged between $1.6^\circ/s$ and $4.2^\circ/s$. The EMG activities of MG in AJ and KJ were $0.4 \pm 0.6\%$ and $1.7 \pm 1.7\%$ at most, respectively.

In AJ, MTJ moved to distal (4.1 ± 1.1 mm) during the dorsiflexion and moved to proximal (-17.5 ± 1.9 mm) during the plantar flexion, compared to the basic position with both ankle and knee joint angles at 0° (Figure 3, left). In contrast, MTJ excursion in KJ was negligible (-0.2 ± 1.3 mm) (Figure 3, right). The plantar flexion from -9° to 35° shortened the fascicle from 66.5 ± 5.9 mm to 44.6 ± 4.7 mm, and increased the pennation angle from $18.6 \pm 1.7^\circ$ to $26.1 \pm 1.5^\circ$. The knee extension from 90° to 0° lengthened the fascicle from 39.4 ± 4.5 mm to 61.7 ± 4.6 mm and decreased the pennation angle from $24.0 \pm 2.3^\circ$ to $20.2 \pm 2.0^\circ$.

Figure 4 shows the relationship between ΔL_{ET} and ΔL_{MTC} . Two-way ANOVA indicated that the two main factors, test condition and ΔL_{MTC} , were statistically significant. In addition, since significant interaction ($p < 0.01$) was also observed between the two factors, one-way ANOVA was performed on every group and a multi comparison test was conducted. As a result, ΔL_{ET} in AJ was significantly lower when ΔL_{MTC} ranged from -25 to -5 mm compared to the value when ΔL_{MTC} was 0 mm. However, ΔL_{ET} at every ΔL_{MTC} in KJ did not significantly differ from the value when ΔL_{MTC} was 0 mm. Significant differences in ΔL_{ET} were found between AJ and KJ when ΔL_{MTC} was -25, -20, -15 and -10 mm.

Figure 5 shows the relationship between ΔL_F and ΔL_{MTC} . As a result of the two-way ANOVA, the effects of the test condition and ΔL_{MTC} were significant ($p < 0.01$). Since significant interaction ($p < 0.01$) was also observed between the two factors, one-way ANOVA was performed on every group and a multi comparison test

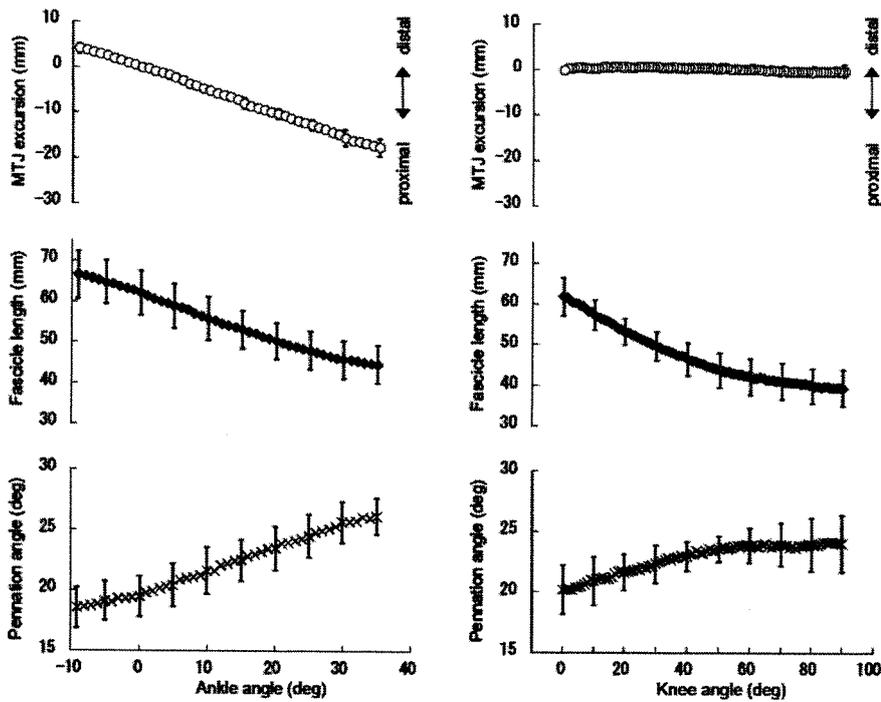


Figure 3 Changes in MTJ excursion, fascicle length and pennation angle at various ankle (left) and knee (right) angles. In the MTJ excursion, positive values indicate the displacement to the distal end, while negative values indicate the displacement to the proximal end.

was conducted. The result showed that ΔL_F values during both AJ and KJ when ΔL_{MTC} ranged from -25 to -5 mm were significantly lower than that when ΔL_{MTC} was 0 mm. The differences in ΔL_F between AJ and KJ were significant when ΔL_{MTC} were -25, -20, -15 and -10 mm.

4. Discussion

The main findings of this study were 1) the external tendon length of MG changed in AJ, but not in KJ (Figure 4), and 2) ΔL_F at a given ΔL_{MTC} differed

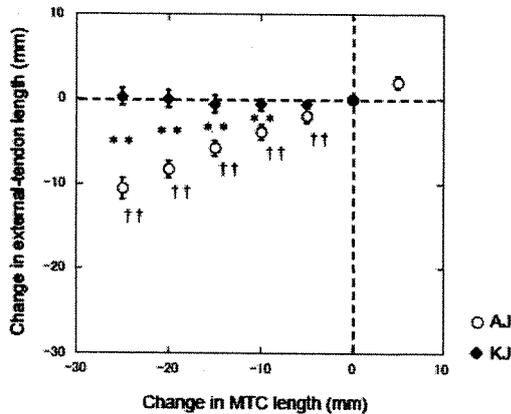


Figure 4 Relationship between length change of MTC and that of external tendon. The length of external tendon was significantly changed by the ankle joint motion, but not by the knee joint motion. *Significant differences between AJ and KJ. *: $P < 0.05$, **: $P < 0.01$. †Significantly different from the value at ΔL_{MTC} 0 mm. †: $P < 0.05$, ††: $P < 0.01$.

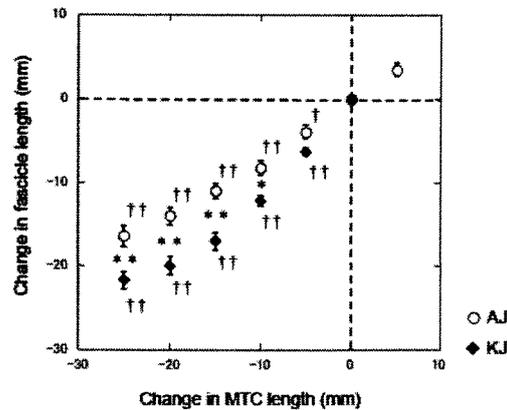


Figure 5 Relationship between length change of MTC and that of fascicle. Length change of fascicle during KJ was significantly greater than during AJ. *Significant differences between AJ and KJ. *: $P < 0.05$, **: $P < 0.01$. †Significantly different from the value at ΔL_{MTC} 0 mm. †: $P < 0.05$, ††: $P < 0.01$.

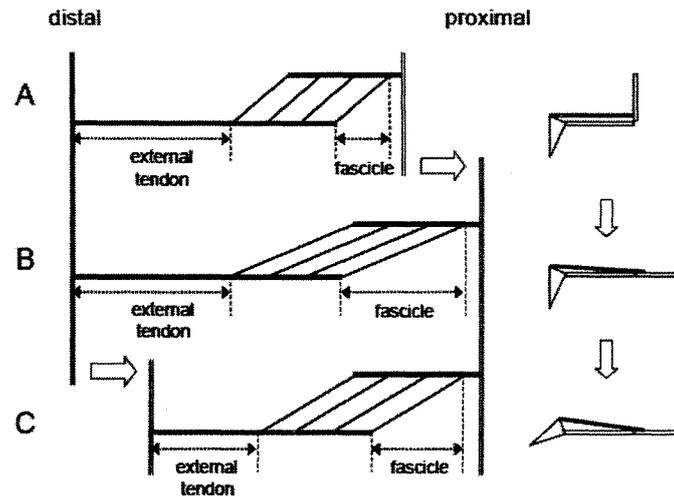


Figure 6 Planimetric models of the muscle-tendon complex in knee flexed position (A), ankle and knee angle at 0°(B), and in the plantar flexed position (C). Length of the external tendon located distally to the fascicles is influenced only by the angle change of the joint distal to the gastrocnemius muscle. Length of the fascicles located proximally to the external tendon is more influenced by the angle change of the joint proximal to the gastrocnemius muscle.

between AJ and KJ (Figure 5).

The present study aimed to investigate the behavior of MTC during passive joint motions. Before interpreting the results obtained here, we should comment on whether the measurement during KJ was actually taken under passive condition, because the subjects extended the knee joint by themselves using the trunk and thigh. While the subjects performed KJ, they were informed about the knee joint angle by visual feedback and instructed to maintain the change below 5°/s. As a result, they could extend the knee joint slowly without EMG activity of MG. Therefore, the KJ procedure employed in this study could successfully change the MTC length of MG passively.

MTC can be expressed in a planimetric model (Huijing & Woittiez 1984, 1985). However, MG becomes a biased model because fascicle is located at proximal within the MTC, and the longer external tendon at distal. Using this model, a schematic view of the present result (Figure 4, 5) is shown as Figure 6. In Figure 6, external tendon and aponeurosis are expressed serially parallel, because other muscles and bones adjoin to them *in vivo* (Kawakami, et al., 1998). 'A' stands for the MTC at the knee flexed position, 'B' for the MTC with ankle and knee joint angles at 0° and 'C' for the MTC at the ankle plantar flexed position. As shown in this figure, although

the length change of MTC induced by the changes in proximal (knee) joint angle (A-B) is identical with that induced by the changes in distal (ankle) joint angle (B-C), the lengths of the external tendon and fascicle are different between A and C. This means that the fascicle at proximal is strongly affected by the changes in proximal joint angles, whereas the external tendon at distal is greatly influenced by the changes in distal joint ones. It was reported that the length change is more apparent in fascicle than in tendon when the MTC length is passively changed (Stolov & Weillepp 1966, Hawkins & Bey 1997). However, the present results indicate that, at least in MG, not only the difference in the magnitude of passive extension between muscle and tendon, but also the difference in the joint to move, i.e. proximal or distal, is an important factor affecting the length changes in the fascicle and external tendon.

The difference in ΔL_{ET} and ΔL_F between AJ and KJ can be explained by the fact that the distal external tendon of MG attaches to the tendinous tissue (external tendon and aponeurosis) of the soleus muscle (Bojsen-Moller, et al., 2004). The soleus muscle is monoarticular muscle which crosses only the ankle joint and its architecture is not changed by the rotation of the knee joint (Kawakami, et al., 1998). Hence, it is reasonable to assume that the tendinous tissue length of

the soleus did not change in KJ, and therefore the length of distal external tendon of MG was not altered by KJ, because it depends on the rigidity of the tendinous tissue of the soleus muscle in passive joint motions. On the other hand, the fascicle, whose passive extension level was greater than that of the tendon (external tendon), was mainly lengthened in KJ.

Furthermore, the viscosity of MTC may also affect the length changes in external tendon and fascicle. In the present study, we analyzed the shortening phase of MTC in AJ and the lengthening phase in KJ (Figure 1). However, there is a possibility that the changes in MTC would not always be the same between the shortening and lengthening phases, because MTC is characteristically viscous (Lieber, et al., 2000). If so, this might be a reason for the difference in ΔL_{ET} and ΔL_F between AJ and KJ (Figure 4 and 5). Moreover, since the moment arm of ankle is different from that of knee in MG (Grieve, et al., 1978), the velocity of the MTC would not be identical between AJ and KJ even when the angular velocity was almost the same "below 5°/s". Hence, it seems that the difference in the velocity of MTC also affected the present results (Figure 4 and 5), because the influence of viscosity depends on the velocity of the length change. However, the velocity of MTC was extremely low, 0.9 ± 0.1 %/s in AJ and 0.2 ± 0.1 %/s in KJ. It has been shown that the velocity of MTC (Heerkens, et al., 1987, Syme 1990) and tendon (Herrick, et al., 1978, Ker 1981) in the locomotion have a small influence on their viscosity. Therefore, the influences of differences in analyzed phases and in the velocities of MTC on ΔL_{ET} and ΔL_F would be negligible.

The gastrocnemius muscle has a role to transfer the power exerted by the knee extensor muscles to the plantar flexion of ankle joint during the multi-joint movements of the lower extremity (Gregoire, et al., 1984, van Ingen Schenau, et al., 1987). In this case, it is essential for gastrocnemius MTC to be taut, not slack (van Ingen Schenau, et al., 1990). In the present result, the length of distal external tendon of MG less changed when the knee joint angle was changed with the ankle joint at 0° (Figure 4). Given that the external tendon of MG is taut with both ankle and knee joints at 0° (Muraoka, et al., 2004), it would maintain the taut state with ankle joint at 0° regardless of the changes in the knee joint angles. Furthermore it is likely that the whole tendinous tissue of MG, including the proximal tendinous tissue,

never changed in the length and was taut during KJ, because ΔL_F was almost identical with ΔL_{MTC} (Figure 5). The reasons why the length of tendinous tissue other than the distal external tendon did not change are unknown, but may be attributed to the following two factors: 1) the absolute length change would be small in the proximal external tendon because of its shortness compared to the distal external tendon, and 2) the length change in aponeurosis is smaller than that in external tendon during passive joint motions (Muraoka, et al., 2002). In either case, we can say that MG tendinous tissue maintains the taut state regardless of the knee joint angles and effectively transfers the power of the knee extension to the plantar flexion.

In summary, the present findings showed that the length changes in external tendon and fascicle relative to a given MTC length differed between the ankle and knee joint motions. This difference may be caused by the fact that the external tendon of MG attaches to the tendinous tissue of soleus muscle. The length changes in external tendon and fascicle induced by joint angle changes may be suitable for the function of MG as biarticular muscle to transfer the power of the knee extension to the plantar flexion.

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Use of Three-Dimensional Ultrasonography for the Analysis of the Fascicle Length of Human Gastrocnemius Muscle During Contractions

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The fascicle lengths of the human gastrocnemius muscle during isometric plantar flexions were analyzed using a three-dimensional ultrasound system (3D-US). Prior to measurements *in vivo*, the accuracy and reproducibility of the 3D-US were examined by taking images of a phantom. The horizontal errors were 0.3 - 1.0%, and the vertical errors were 1.2 - 1.6%. In addition, the coefficients of variance for the repeated measurements were 3.3% and 1.7% for horizontal and vertical directions, respectively. Second, both at rest and each of five intensities {20,40,60,80,100% of maximum voluntary contraction (MVC)}, at a fixed ankle joint angle of 90deg, the 3D-US images of gastrocnemius muscles were obtained and used to determine fascicle length. The fascicle length was also measured using two-dimensional ultrasound system (2D-US), and the values obtained by 2D-US were used to make comparisons with those by 3D-US. From rest to MVC, the fascicle length decreased as a function of relative torque levels from 6.0 (± 0.5) cm to 3.1 (± 0.4) cm with 3D-US, and, in a similar manner, from 5.6 (± 0.5) cm to 3.0 (± 0.4) cm with 2D-US. Thus the present study indicated the accuracy and reproducibility of the 3D-US measurements and its usefulness for determining the fascicle lengths of human muscles in three-dimensional space. The fascicle length measurements determined by 3D-US were, however, significantly longer than those of 2D-US.

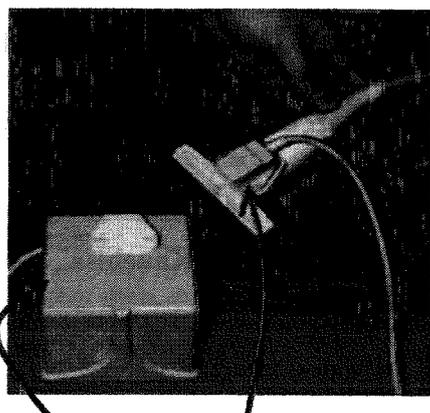
Keywords: ultrasonography, fascicle length, contraction-induced changes, isometric contractions

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1. Introduction

Muscle architecture is a primary determinant of muscle function [Lieber and Friden (2000)]. It has been shown in humans as well as in animals that muscle architecture changes during contractions even in isometric actions [Fukunaga, et al., (1997); Huijing, et al., (1989); Zuurbier and Huijing (1993)]. According to the previous findings on this subject, the length of fascicles of muscle fibers (fascicle length) shortens and the angle of fascicles (pennation angle) increases as contraction intensity increases [Fukunaga, et al., (1997); Kawakami, et al., (1998, 2000); Maganaris, et al., (1998); Narici, et al., (1996)].

In human skeletal muscles, the measurements of architecture have been conducted by magnetic resonance imaging (MRI) or two-dimensional ultrasonography (2D-US). These methods are non-invasive, and useful for observing muscles both at rest and during contractions. However, these methods have a disadvantage when understanding the three-dimensional muscle architecture, because in principle they are based on planar imaging technique. Within a muscle, fibers are arranged in a three-dimensional space [Agur, et al., (2003); Lam, et al., (1991); Muramatsu, et al., (2002); Otten (1988); Savelberg, et al., (2001); Van Leeuwen and Spoor (1992)]. Agur et al. (2003) showed that most of the muscle fibers within a human cadaver soleus muscle



Electromagnetic position sensor
(Static reference and attached sensor)

Figure 1 An ultrasonic probe with an electromagnetic position sensor attached and an electromagnetic static reference sensor.

were curved and arranged obliquely. As for the curvature, Muramatsu et al. (2002) reported that the fascicle curvature existed in human gastrocnemius muscle and changed by both contraction levels and fascicle length. While, Savelberg et al. (2001) indicated that, for the rat plantaris muscle, contraction induced an asymmetrical displacement of the fibers in a direction perpendicular to their longitudinal axis, resulting in a helical deformation of the whole muscle. It is reasonable to suppose that those three-dimensional internal arrangements and curvatures of muscle fascicles exist and contraction-induced spatial movements occur off a simple planer image in human skeletal muscles as well.

A few attempts have been carried out to measure three-dimensional muscle architecture using MRI [Scott, et al., (1993)] or 2D-US [Kawakami, et al., (2000)]. However, these approaches were only applied to relaxed muscle, not to contracted muscle. Three-dimensional ultrasound system (3D-US) employs multiple images of two-dimensional brightness mode (B-mode) ultrasonography together with the three-dimensional coordinates of each image to reconstruct the three-dimensional shape of an object [Fry, et al., (2003); Hiblar, et al., (2003)]. This method enables to measure three-dimensional muscle architecture both at rest and during contractions. By the use of the 3D-US, Fry et al. (2003) succeeded in three-dimensional reconstructions of human skeletal muscle, and suggested that the architecture

and morphology of the muscles are visible within these images. However, they measured only the muscle belly length of gastrocnemius in a relaxed situation. Hiblar et al. (2003) used 3D-US to measure the fascicle orientation (i.e. pennation angle) of human tibialis anterior muscle. It was the first case for determining muscle architecture during contraction using 3D-US. In their results, however, there were considerable variations in the measurements (coefficients of variation are 30-40%). Hence, whether 3D-US is useful for determining contraction-induced changes in muscle architecture remains a question.

The present study aimed to ascertain the usefulness of 3D-US in order to measure the three-dimensional muscle architecture. For this purpose, we first constructed the images of an object with a known shape by using 3D-US and confirmed the reliability of the measurements by estimating the errors and the coefficients of variation of the measurements. Then, we determined the fascicle length of human medial gastrocnemius muscle, as indices of muscle architecture, during relaxed and contracted conditions at various intensities, and compared them with the values obtained by 2D-US.

2. Materials and Methods

2.1. Confirming the accuracy and reproducibility of 3D-US

In the present study, we employed a 3D-US (USE-1200, Nihon-Kohden, Japan) with an electromagnetic position sensor attached to the ultrasonic transducer (Figure 1). This system included a B-mode ultrasonic machine (SSD-5500, Aloka, Japan; with a 7.5MHz linear array probe) that provided real-time, two-dimensional images at a rate of 30 images/s. During the scanning, the probe was moved by a well-trained tester in an appropriate direction. The velocity of the probe movement is associated with the quality of the image. Therefore, the tester gave full attention to maintain the continuity and constant speed of the movement. Transverse serial images were retrieved as composite video signals from the ultrasonic machine and stored in a computer simultaneously with the positional information provided by the electromagnetic position sensor (also recorded at 30 Hz). From them, three-dimensional ultrasound images were

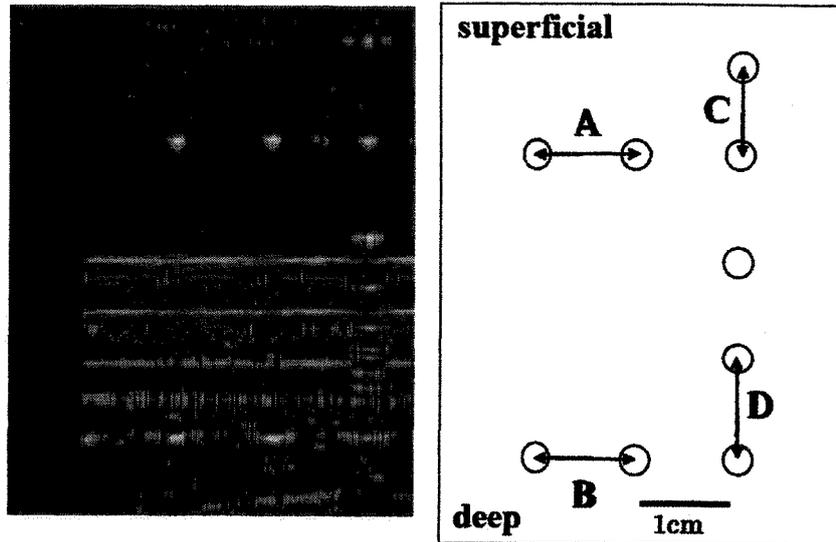


Figure 2 Left, An ultrasound image of the echoes of thin piano strings in an acrylic water tank. Right, Schematic diagram of the image, circle: echoes of thin piano strings. A: horizontal measurements, superficial level (closer to the ultrasound probe), B: horizontal measure, deep level (further from the probe), C: vertical measurements, superficial level, D: vertical measurements, deep level.

reconstructed using a software (Tomtec3D, Tomtec, Germany).

The accuracy and reproducibility of the 3D-US measurements were confirmed by imaging a phantom, an acrylic water tank ($37 \times 15 \times 25$ D cm) with tensed thin piano strings at a known interval (1cm). The horizontal and vertical distances measured by choosing two echoes of piano strings in the reconstructed images as shown in Figure 2. Horizontal distances were measured both at the superficial level (A) and the deep level (B). The superficial level was closer to the ultrasound probe, and the deep level was further from the probe by 3 cm below the superficial level. The vertical measurements were both at the superficial level (C) and at the deep level (D). The errors of the distance measurement in the reconstructed image were calculated with the following equation,

$$\text{Error (\%)} = \frac{|\text{measured value} - \text{actual value}|}{\text{actual value}} \times 100.$$

The reconstructed three-dimensional ultrasound images of 20 trials were used for horizontal and vertical distance measurements. These measurements were repeated at least 2 times for each reconstructed image.

2.2. In vivo measurements

Four healthy men (27.8 ± 2.2 yrs, mean \pm S.D.) volunteered for the measurements. Their means and standard deviations (S.D.s) of height and body mass were 174.5 ± 5.5 cm and 66.0 ± 8.2 kg, respectively. The study took approval of the ethics committee of the University of Tokyo. Informed consent was obtained from each subject before the study began.

The subject lay prone on the examining table and his right foot was firmly attached to an electric dynamometer (Myolet, Asics, Japan). The subject's posterior leg was coated with transmission gel to obtain acoustic coupling. The ankle joint was fixed at 90 deg, and the knee joint was positioned at 0 deg (full extension). During the ultrasound data acquisition, the subjects were asked to relax (relaxed condition) or to maintain isometric plantar flexions (active conditions) at different contraction intensities, and the probe was moved by the tester along the longitudinal axis of the muscle belly from the calcaneus to the knee cleft just proximal to the femoral condyles. Transverse serial images of the muscle were retrieved from the ultrasonic machine and stored in a computer simultaneously with the positional information. From them, three-dimensional ultrasound images were reconstructed (Figure 3a).

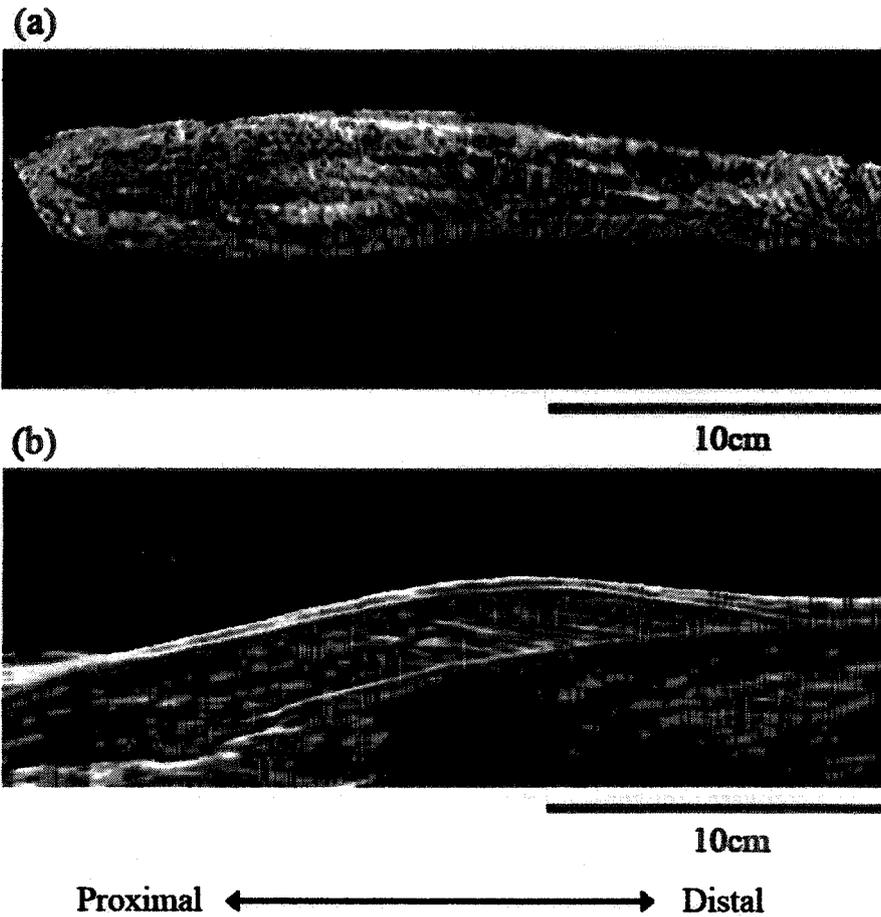


Figure 3 (a) A typical example of a three-dimensional ultrasound image of gastrocnemius muscle. (b) A typical example of an ultrasound image of gastrocnemius muscle. This planar image including the longitudinal axis of the fascicle was cut from the reconstructed three-dimensional ultrasound image.

Prior to the ultrasonographic measurements under the active conditions, the subjects were asked to perform maximum voluntary contraction (MVC) of plantar flexion for 5 s. Two trials were made for each subject, with at least 2 min intervals between contractions. Confirming the steadiness of MVC and the values of MVC torque, the test procedure proceeded to the next step. After the completion of MVC trials and a rest period of two minutes, the subjects were instructed to perform isometric plantar flexion up to the levels of five contraction intensities (20, 40, 60, 80, 100 % of MVC) with a visual feedback of the developed torque on an oscilloscope. The duration of contraction depended on each subject's ability to steadily maintain the contraction (about 5-30 s). The subjects maintained 20-30 s at 20

or 40 %MVC, and 5-10 s at 60, 80 or 100 %MVC. At least 2 min of rest was allowed between contractions.

The echoes from interspaces of the fascicles were visible in the 3D-US images, as observed in conventional 2D-US images (Figure 3b). At a position proximal 30 % of the length between the popliteal crease and the center of the lateral malleolus, clearly visible fascicles were identified on each images. In the 3D-US images of this study, we identified this position using the markers placed on the skin that changed the brightness of echoes. We analyzed fascicle length at this level, because this level is where the anatomical cross-sectional area of the gastrocnemius muscle is maximal [Fukunaga, et al., (1992)]. In addition, it has been shown that there was no significant difference between architectural

Table 1 The errors and coefficients of variation of horizontal and vertical length measurements by 3D-US confirmed by imaging a phantom.

| | A | B | C | D |
|-------|------|------|------|------|
| Error | 0.3% | 1.0% | 1.6% | 1.2% |
| CV | 3.2% | 3.3% | 1.7% | 1.7% |

A: horizontal measurements, superficial level (closer to the ultrasound probe), B: horizontal measure, deep level (further from the probe), C: vertical measurements, superficial level, D: vertical measurements, deep level, all the nominations were depicted in Figure 2.

parameters of different regions and sections within a human gastrocnemius muscle *in vivo* [Maganaris, et al., (1998)].

By the use of the software (Tomtec3D, Tomtec, Germany), the gastrocnemius muscle could be cut at any oblique planes by rotating the 3D-US images. For the measurement of fascicle length, 3D-US images were rotated around the three orthogonal axes in order to select a proper plane including the longitudinal axis of the fascicle. The criterion of judgment was the fascicle was clearly visible from one end to the other. After determining the proper plane, the fascicle length was measured along the fascicle as the distance between its aponeurotic attachments [Kawakami, et al., (1998); Maganaris, et al., (1998)]. The 3D-US measurements for fascicle length were repeated three times for each subject/condition. We repeated the above procedures three times to choose three fascicles near the position of described above and mean values were used as the representing values.

The fascicle length was also measured using 2D-US for the same subjects and same conditions as the 3D-US measurements. The values obtained by 2D-US were used to make comparisons with those by 3D-US. In the 2D-US measurements, the probe of the ultrasonic apparatus was placed as the previous studies [Kawakami, et al., (1998); Maganaris, et al., (1998)]. In short, the center of the probe placed the proximal levels 30 % of the distance between the popliteal crease and the center of the lateral malleolus, and its direction was parallel to the long head of the muscle belly of the medial gastrocnemius muscle. We analyzed fascicle length in printed images as previously reported in Kawakami et

al. (1998). In the 2D-US measurements, only one printed image for each subject/condition was obtained, then, we repeated the measurement three times in each printed image and mean values were used for comparison with those in the 3D-US measurements.

2.3. Statistics

Descriptive data were presented as means and standard deviations (S.D.s). A two-way analysis of variance (ANOVA) with repeated measures was used to examine the significances of the F ratios for the main effects and interactions of torque levels and two methods on measured variables. Significant differences among means at $p < 0.05$ were detected using a TukeyHSD post hoc test. The probability level for statistical significance was set at $p < 0.05$.

3. Results

3.1. Accuracy and reproducibility of 3D-US

The mean values of errors in horizontal direction observed in the superficial and deep areas of the image were 0.3 % and 1.0 %, respectively (Table 1). The mean values of errors in vertical direction observed in the upper and lower regions of the images were 1.6 % and 1.2%, respectively. The coefficients of variance (CV) for the repeated distance measurements were 1.7 - 3.3 %.

3.2. Contraction induced changes in fascicle length

The fascicle lengths as a function of plantar flexion torques are shown in Figure 4. As the plantar flexion torque increased, fascicle length decreased. The mean values (\pm S.D.s) of the fascicle length in the 3D-US measurement decreased from 6.0 (\pm 0.5) cm in the relaxed condition to 3.1 (\pm 0.4) cm at MVC, in a similar manner, those of the 2D-US measurement decreased from 5.6 (\pm 0.5) cm in the relaxed condition to 3.0 (\pm 0.4) cm at MVC. The fascicle length at intensities of 40% and above was shorter than that in the relaxed condition both for 3D-US and 2D-US measurements.

The fascicle length determined by 3D-US, however, tended to be longer than that determined by 2D-US. The two-way ANOVA indicated that the effect of not only the intensity but also the method

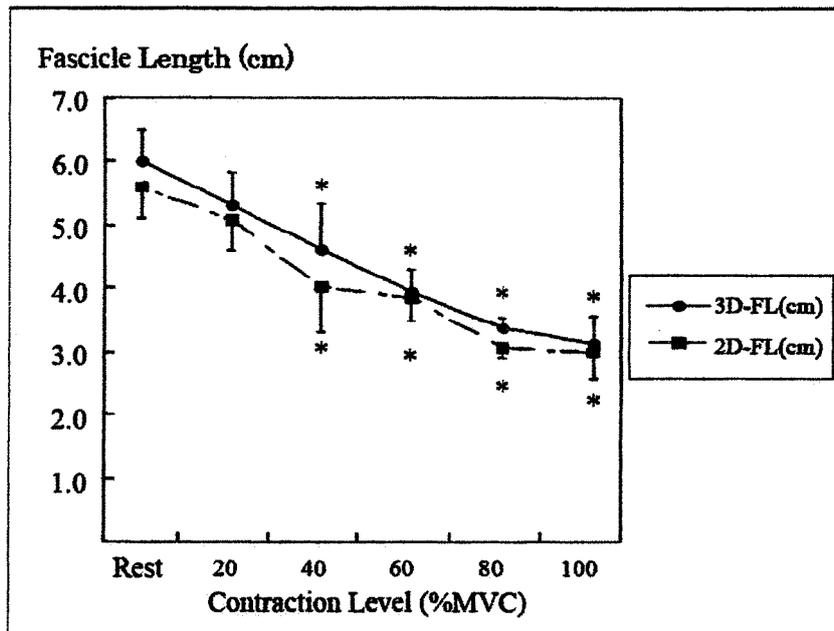


Figure 4 Fascicle lengths of human medial gastrocnemius muscle during isometric plantar flexion at submaximal and maximal intensities. The relationship of fascicle length to the relative torque was curvilinear in both methods.
 3D-FL: fascicle length measurements with 3D-US. 2D-FL: fascicle length measurements with 2D-US.
 * Significant changes compared with the relaxed condition ($p<0.05$).

on the measured fascicle length was significant ($p<0.0001$ for intensity and $p=0.016$ for method) without a significant interaction (intensity \times method).

4. Discussion

This study confirmed the accuracy and reproducibility of 3D-US for measuring the length of the objects in the three-dimensional space. The horizontal and vertical errors in 3D-US distance measurements 0.3 - 1.0 % and 1.2 - 1.6 %, respectively, were comparable to those reported by Kawakami et al. (1993), 1.3 % with 2D-US. In addition to the high accuracy of the length measurements, the CVs for the repeated distance measurements were 3.3 % and 1.7 % for horizontal and vertical directions, respectively. These values were considerably lower than those reported by Hiblar et al. (2003) who used 3D-US measurements, 30-40%. Although the criteria of the selection of ultrasound images were similar in the two studies, the procedure of the measurements were different in the two studies. Hiblar et al. (2003) firstly selected an image and then determined each fascicle involved in the selected image. On the other hand, we repeated

the selection of the appropriate ultrasound image for determining the length of a single fascicle. The difference in the procedure used for the fascicle length determination might be assumed to be a reason for the difference between the observed CV values in the present and Hiblar et al. (2003)'s studies. The observed CV values of ours were within the range of those reported previously for fascicle length measurement (0-8%)[Fukunaga, et al., (1997); Kawakami, et al., (1998); Maganaris, et al., (1998)]. Judging from these results, therefore, we may conclude that the 3D-US system used in this study has sufficient accuracy and reproducibility to measure the length of the objects in ultrasound images.

After the confirmation of the accuracy and reproducibility of 3D-US, we determined the fascicle length of the gastrocnemius muscle at relaxed condition and during isometric plantar flexions with various force production levels. Most of previous sonographic studies on the contraction-induced changes in the architecture of the human gastrocnemius muscle have used conventional 2D-US [Kawakami, et al., (1998, 2000); Maganaris, et al., (1998); Narici, et al., (1996)]. The architectural parameters analyzed in these studies

Table 2 Fascicle lengths measurement of medial gastrocnemius muscle in the relaxed condition and during maximal voluntary contraction (MVC) of plantar flexion of the present results and as reported in the literature.

| Reference | Fascicle Length (cm) | | Joint angle(deg) | | Subjects physical constitutions | | | |
|-------------------------|----------------------|-------------|------------------|------|---------------------------------|-------------------------|-------------|------------|
| | Relaxed | MVC | Ankle | Knee | Age(yrs) | Height(cm) | Weight(kg) | |
| This study (3D-US) | 6.0 (0.5) | 3.1 (0.4) | 90 | 0 | 4Men | 27.8 (2.2) | 174.5 (5.5) | 66.0 (8.2) |
| Previous method (2D-US) | 5.6 (0.5) | 3.0 (0.4) | | | | | | |
| Kawakami et al. (2000) | 5.4 - 5.7 | 3.6 - 3.9 * | 90 | 0 | 6Men | No mention in the paper | | |
| Kawakami et al. (1998) | 5.2 (0.7) | 3.1 (0.5) | 90 | 0 | 6Men | 21-53 | 175 (5) | 71 (7) |
| Maganaris et al. (1998) | 4.5 (0.2) | 2.34 (0.19) | 90 | 90 | 6Men | 28 (3) | 175 (8) | 75 (5) |
| Narici et al. (1996) | 5.08 (0.36) | 3.29 (0.36) | 110 | 0 | 6Men | 38 (8) | 176 (5) | 67.8 (6.5) |

Values are means (S.D.s). The mean age, height, and body mass of the subjects in each report are also shown.

* at a level of 50% MVC.

differ for the relaxed and active conditions (Table 2). The fascicle length of the gastrocnemius muscle changes with respect to both the ankle and the knee joint angles [Kawakami, et al., (1998); Narici, et al., (1996)]. The present study employed the same joint angle conditions as those used by Kawakami et al. (1998, 2000), but not by others [Maganaris, et al., (1998); Narici, et al., (1996)]. A comparison of the present study on 2D-US measurements and Kawakami et al. (1998) revealed the measured fascicle length for the gastrocnemius muscle to be similar in two studies. Comparing with the fascicle length measurements of 3D-US to that of 2D-US, the curvilinear relationship between fascicle length and plantar flexion torque was similar (Figure 4), and the ratios of fascicle shortening from rest to MVC were similar, i.e., 52% with 3D-US and 53% with 2D-US. In the present results, however, the average fascicle lengths determined by 3D-US were longer by 2.4 – 14.0 % than those by 2D-US measurements. This difference was far beyond the range of errors of length measurements in 3D-US, and the two-way ANOVA indicates that the measured fascicle length determined by 3D-US was significantly longer than that by 2D-US. Hence, the present result indicates that in vivo observations on the contraction-induced changes in fascicle length vary by the use of each of 3D-US or 2D-US, even if the shape of the changes in fascicle length over torque development is similar in the two measurements.

The observed difference between the fascicle length measurements of 3D-US and 2D-US could be due to our proviso that the fascicle was clearly visible

from one end to the other, which made it possible to select the proper plane along to the longitudinal axis of muscle fascicle. We measured the fascicle length by changing the sectional planes of 3D-US images in the medio-lateral and proximo-distal directions, and found that the fascicle length in the proper plane was the longest (Figure 5). In the 2D-US measurements, we determined that the ultrasound probe was oriented along the mid-sagittal axis of muscle belly. The orientation of the fascicle, however, was not always along the longitudinal axis of muscle belly.

In the present study, the fascicle length was determined at the proximal levels 30 % of the distance between the popliteal crease and the center of the lateral malleolus. If there is a position related difference in the architecture of muscle, it can be one of the reasons for the difference between the fascicle length measurements of 3D-US and 2D-US, because in 3D-US measurements we picked up three different fascicles near the proximal 30%. However, this possibility is unlikely, since it has been shown that there is marked uniform architecture throughout a muscle [Friederich and Brand (1990); Wickiewicz, et al., (1983)], especially in the fascicle length of the medial gastrocnemius muscle [Kawakami, et al., (2000); Maganaris, et al., (1998); Narici, et al., (1996)]. Whether there is difference in architectural parameters within a muscle should be clarified, in case we analyze the muscle architecture of the other muscles. The present 3D-US can be a useful tool for them because it can be imaging the whole muscle.

We considered the fascicle as straight, and the fascicle length was measured as the distance between

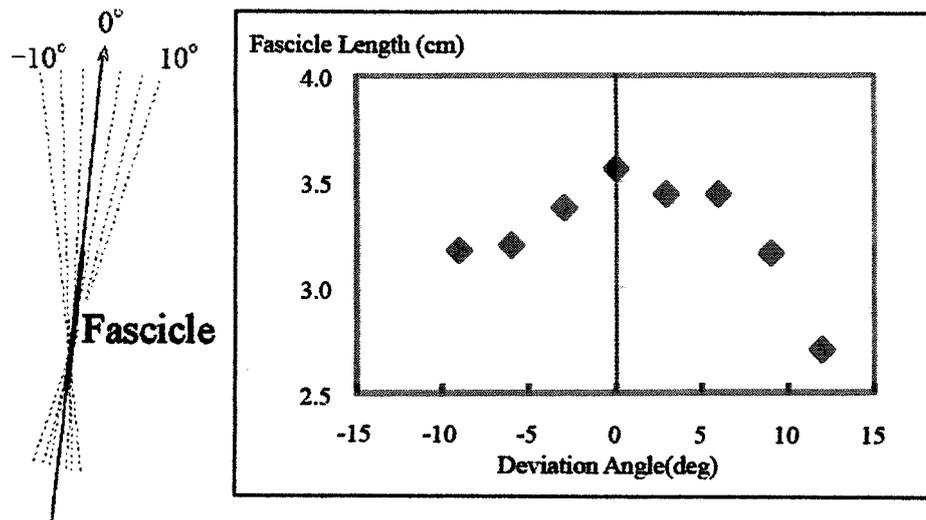


Figure 5 A typical example of length measurements of a single fascicle of medial gastrocnemius muscle during 40 % MVC isometric plantar flexion. The measurements were taken at various planes in medio-lateral and proximo-distal directions. The illustration of the deviation angles are shown in the left diagram.

its aponeurotic attachments in this paper. We ignored the curvature of the fascicle, if it could be seen in the images, since Muramatsu et al. (2002) showed that the average underestimation by ignoring the curvature was ~ 6%, which might not seem to be critically large in gastrocnemius muscle. However, the error would be substantially large in muscle with longer fascicles such as vastus lateralis or tibialis anterior [Wickiewicz, et al., (1983)]. For example, Finni et al. (2003) estimated the fascicle length of vastus lateralis muscle from the architectural values within a visible area of the ultrasound image, and Ito et al. (1998) measured fascicle length of tibialis anterior muscle with a digital curvimeter. For analyzing fascicle length of these muscles, the further investigation with considering the curvature is needed, which is possible in 3D-US.

The data obtained in this paper can be also acquired with manipulation of the probe orientation simply by using 2D-US. However, we may say that 3D-US has potential advantages for analyzing the three-dimensional architecture of human skeletal muscle, such as the spatial orientation of fascicles or the curvature of each fascicle. Additionally, the present 3D-US can be a useful tool for imaging the whole muscle.

In conclusion, the present study showed that the 3D-US method was capable of reliably measuring the

values of fascicle length of human skeletal muscle. As compared with conventional measurements, 3D-US has potential advantages for analyzing the three-dimensional architecture of human skeletal muscle.

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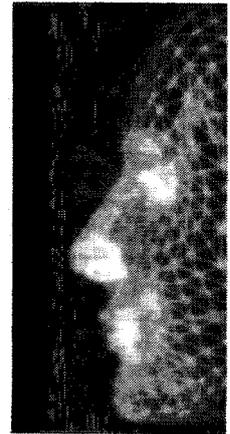
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Virtual Humans and Social Agents

Modeling and simulating the deformation of human skeletal muscle based on anatomy and physiology

By Robson R. Lemos*, Jon Rokne, Gladimir V. G. Baranoski, Yasuo Kawakami and Toshiyuki Kurihara



This paper describes the modeling and simulation of the deformation of human skeletal muscle at different structural levels based on sound scientific principles, experimental evidence, and state-of-art muscle anatomy and physiology. The equations of a continuum model of a muscle with realistic architecture, including internal arrangement of muscle fibers and passive structures, and deformation, including activation relations, was developed and solved with the finite element method. The continuum model is used as the basis of a strategy for controlling muscle deformation using activation relations. In order to demonstrate the functionality of the model, it was used to investigate force production and structural changes during contraction of the human tibialis anterior for maximally and submaximally activated muscle behavior. From a comparison with experimental data obtained from ultrasound imaging, we concluded that the modeling and simulation of the continuum based on physiologically meaningful parameters as described in the paper is both an excellent predictor of force production observations and of changes in internal geometry under various test conditions. It is therefore a valuable tool for controlling muscle deformation during movement. Copyright © 2005 John Wiley & Sons, Ltd.

KEY WORDS: physically-based muscle modeling; medical three-dimensional simulation

Introduction

Two major constituents of mammals are the skeleton and the skeletal muscles. In most mammals the skeletal muscle accounts for at least 40% of whole body mass;¹ thus, it is an important feature. Additionally, whereas the skeleton is a rigid framework, the skeletal muscles deform in response to contractions of muscle fibers. These deformations are visible when mammals move. In computer animation of virtual mammals, in particular, humans, the deformations of muscles therefore have to be taken into account. However, the models currently

available typically do not allow for muscle deformation. This means that the increasing demand for realism and predictability in computer graphics² and bioengineering applications³ cannot be met. The model described in this paper is a step towards the automatic modeling of the deformation in virtual humans in a predictive manner through the interrelationships of the muscle anatomy and function with applications in computer graphics. Similarly, the model can simulate a complex muscle structure so that muscle function can be investigated in bioengineering.

A three-dimensional structural continuum model of whole muscle was developed.⁴ The model was applied to simulate contraction and the associated deformations of a skeletal animal muscle for maximally activated muscle behavior.⁵ The model was used to investigate force production and structural changes during contraction of the human tibialis anterior (TA) for maximally and submaximally activated muscle behavior using

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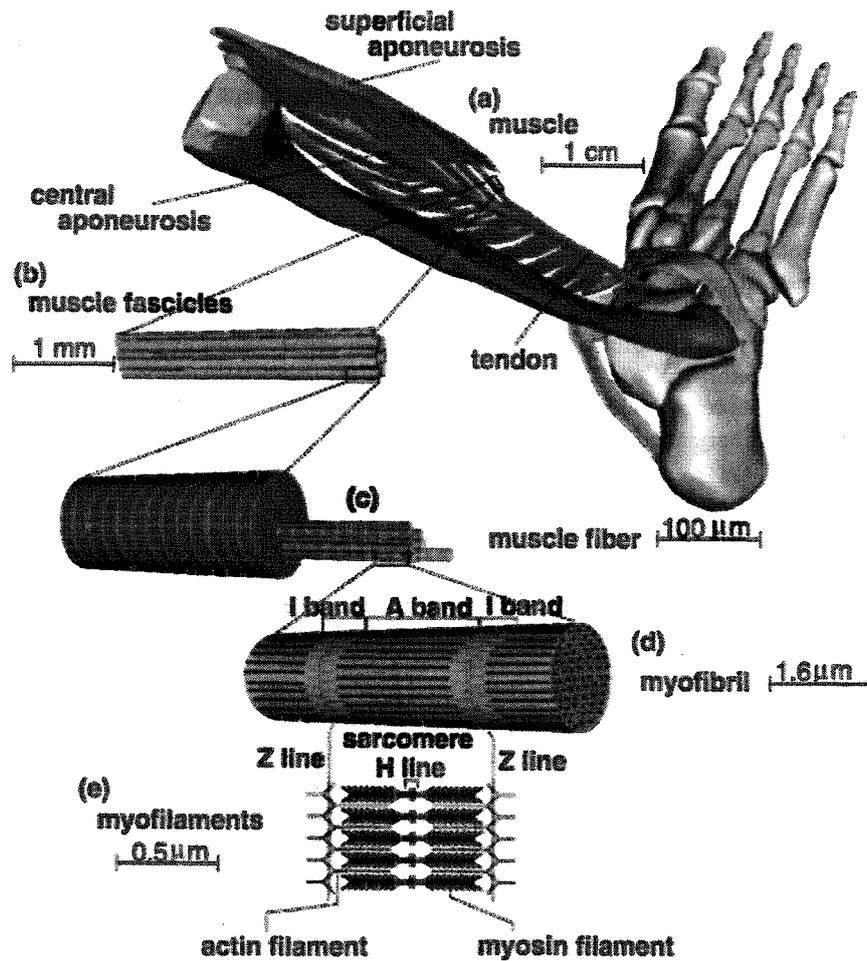


Figure 1. Structural levels. (a) muscle (fiber-aponeurosis-tendon complex); (b) fiber bundle or fascicle; (c) fiber (cell); (d) myofibril; (e) sarcomere (contractile unit).

activation relations based on physiologically meaningful parameters. The novel feature of the approach is that it incorporates several structural levels of representation to predict force relationship, taking into account activation relations for controlling muscle deformation, starting from the muscle fiber level (Figure 1).

The aim of this study is, therefore, to present the modeling and simulation of the deformation of human skeletal muscles at different structural levels for maximally and submaximally activated muscle behavior. In the next section, relevant literature is presented and biological considerations regarding muscle modeling are provided. In the third section continuum model of muscle, the three-dimensional continuum model of muscle is presented. In the fourth section modeling the human Tibialis Anterior muscle, the modeling of the human TA muscle is described. In the fifth section,

muscle deformation simulation and evaluation are shown. Finally, a discussion and some conclusions are presented in the eighth and ninth sections, respectively.

Related Work and Biological Considerations

Computer graphics researchers have proposed models in which individual muscles are represented in an anatomically appropriate manner.^{6,7} In the models proposed by Chen and Zeltzer⁸ and Ng-Thow-Hing and Fiume,⁹ muscle deformation is obtained based on mechanical principles. Non-linear properties of muscles were neglected, however.

The principal elements of the muscle structure, which form the skeletal muscle architecture, are known as the fiber-aponeurosis-tendon complex (Figure 1), a highly non-linear constrained system. In computer graphics, previous work by Teran *et al.*¹⁰ included non-linear properties of muscle. The muscle geometry was extracted from the segmented visible human dataset.¹¹ This dataset does not contain detailed information about the fiber-aponeurosis-tendon complex. Simplifying assumptions for the aponeurosis properties and structure (a thin layer of connective tissue within a muscle to which fiber attach) were therefore made in the modeling of the muscle behavior (and its corresponding anatomy). The aponeurosis plays an important role in the internal and external muscle deformation.¹² According to Reference [10] the tendon/aponeurosis and fiber information could be improved with the aid of scanning technologies or anatomy experts. In biomechanics, Gielen *et al.*¹³ described a planar model representing the mid-sagittal plane of the muscle belly. Oomens *et al.*¹⁴ extended the mid-sagittal plane continuum model of Gielen *et al.*¹³ to a model with a more realistic three-dimensional geometry. According to these authors,¹⁴ further improvements of the model are needed in the transverse plane geometry in order to obtain the actual three-dimensional representation of the muscle. Fernandez *et al.*¹⁵ presented an anatomically based finite element geometric model to match human specific musculo-skeletal system. Blemker *et al.*¹⁶ used a non-linear finite element analysis to simulate a three-dimensional skeletal muscle, simplified by axial symmetry. In cardiac and skeletal muscles models, it has been pointed out that the orientation of muscle fibers and activation, has a large influence on stresses and strains.³ Because of this, a model of skeletal muscle should have a detailed description of the three-dimensional architecture and deformations so as to have predictive value. The model should also include a mechanism to automatically produce muscle deformation during movement.

Based on spatial distribution analysis¹⁷ it has been shown that some muscles are compartmentalized. Assuming that parts of the muscle corresponding to neuromuscular compartments are activated separately during contraction as a result of some type of different functional or task-specific roles during movement, an interesting force production related property can be investigated. This force production related property, which is difficult to determine in human muscles, is known as the non-linear summation of force¹⁸ in which *submaximally activated muscle behavior* during contractions can be investigated. Studies in animal muscles¹⁸

indicate that the non-linear summation of force has functional implications for controlling skeletal muscle during movement.

Continuum Model of Muscle

A non-linear dynamic finite element model (FEM) that allows for designing and simulating a general, variable muscle fiber architecture was developed. A full explanation of the continuum model can be found in Reference [4]. For completeness the general features of the model are also included here.

One possible way to formulate the non-linear equations of motion is by means of the principle of virtual work (PVW). The PVW states that the equations of motion of a deformable body are equivalent to the satisfaction of the following simple scalar equation:

$$IVW - EVW \equiv 0 \quad (1)$$

identically for all virtual displacement fields. In the equation above, IVW is the total internal virtual work and EVW is the total external virtual work performed during the deformation of the body. The PVW can be modified to take into account geometric constraints by the addition of new variables ('Lagrange multipliers').

One of the advantages of the formulation in terms of the PVW is that it is amenable to direct numerical implementation. The system of non-linear equations derived from the PVW were solved using the full Newton's method and the secant method¹⁹ so that execution speeds and accuracies of solutions could be compared. In order to include time-dependent effects, such as viscosity and inertia, the Houbolt implicit time integration technique²⁰ was adopted.

As the tissue matrix deforms, it performs external and internal virtual work. The applied external forces, as well as the forces of inertia, will perform a small amount of work on the virtual displacements. This work is the external virtual work (EVW). As an example, if concentrated forces \mathbf{f} are applied at given points of the body, the external virtual work can be obtained as:

$$EVW = \sum \mathbf{f} \cdot \delta \mathbf{u} - \int_V \rho \ddot{\mathbf{u}} \cdot \delta \mathbf{u} dV \quad (2)$$

Here, the summation extends over the number of external forces. A dot represents the ordinary inner ('dot') product of vectors. The mass density in the reference configuration is denoted by ρ , the reference volume by V , and the acceleration vector by $\ddot{\mathbf{u}}$.

At the same time, a deformable body will sustain an IVW representing the work done by the internal distributed forces (stresses) on the small changes of deformation. The formulation for the IVW for passive and active muscle soft tissues is described below. Moreover, for the active muscle fibers a strategy for controlling muscle deformation using activation relations is described.

Passive Soft Tissue Modeling

In the large deformation regime, we first need to describe the kinematics of the deformation. For that, we use the deformation gradient tensor F which is a mapping from the undeformed reference configuration to the deformed spatial configuration.² From the deformation gradient we can extract all the information needed about the state of strain by eliminating the rotational component. One way to do this is by calculating the right Cauchy–Green tensor² as $C = F^T F$.

A material whose constitutive behavior is characterized by specifying its internal energy stored per unit volume is called a hyperelastic material. We can define specific functional forms of its internal energy. Using the functional form known as the Mooney–Rivlin relation² the first Piola–Kirchhoff stress tensor, a convenient measure of stress, can be obtained as:

$$T = 2aF + 2b(F\text{tr}(C) - FC) - pI \quad (3)$$

where a and b are material parameters which obey the scalar equation, $a + b = \frac{1}{2}\mu$, μ is a material parameter known as ground-state shear modulus,² and p is a Lagrange multiplier representing a hydrostatic pressure associated with the incompressibility constraint.

In this context, the internal virtual work within a referential volume v is the work of the internal forces, or stresses, and is given by:

$$IVW_{\text{tissue}} = \int_V \text{tr}(T^T \delta F) dV \quad (4)$$

where tr represents the trace of a tensor.

In order to represent the wrinkling observed in tendons, a constitutive passive equation with pseudo-wrinkling of the fibrous tissue of the tendon is included. The pseudo-wrinkling of the fibrous tissue is assumed to obey an exponential constitutive law

$$Nt = \sigma t \cdot At \quad (5)$$

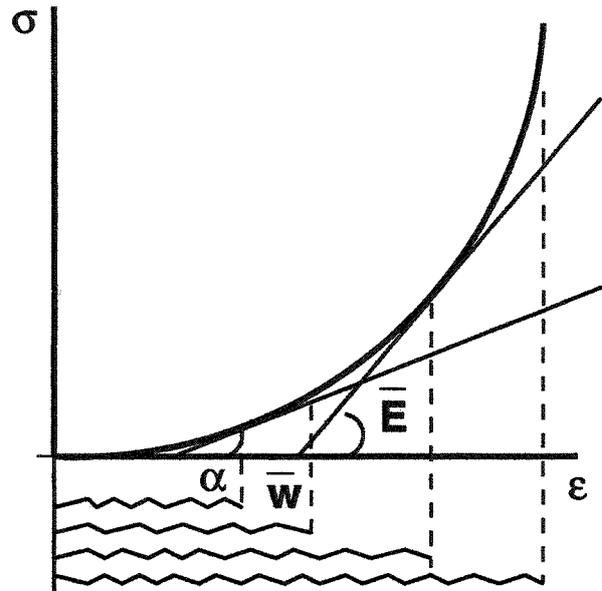


Figure 2. Tendon fibrous tissue behavior.

where At is the cross-sectional area of the tendon and σt is the stress (N/mm^2) given by the following equation

$$\sigma t = \begin{cases} \bar{E} \left[\varepsilon - \bar{w} \left(1 - e^{-\left(\frac{1-\alpha}{\bar{w}} \right) \varepsilon} \right) \right] & \text{for } \varepsilon \geq 0 \\ \alpha \bar{E} \varepsilon & \text{for } \varepsilon < 0 \end{cases} \quad (6)$$

α and \bar{w} are parameters to control the toe region of the constitutive equation and ε is the strain, that is, the elongation of the tendon member divided by the length of the original force-free configuration (Figure 2).

The internal virtual work of the tendon is given by

$$IVW_{\text{tendon}} = Nt \delta e \quad (7)$$

where δe is the small variation in the elongation produced by the virtual displacements of the endpoints of the tendon element.

Active Soft Tissue Modeling

In order to represent the active soft tissues, the active elements are distributed unidirectionally within the muscle tissue. The force–length relation in fully activated isolated fibers or fiber bundles is well known (Figure 3). Each point on the graph representing the force–length relation of a muscle fiber is obtained by means of a separate experiment, whereby the muscle is first passively brought to a desired length, and only then activated to the maximum at constant length (namely,

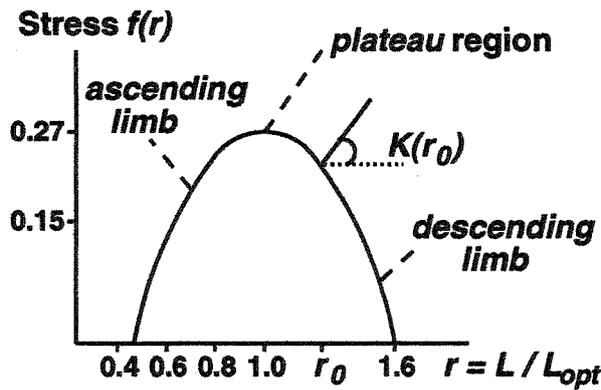


Figure 3. Muscle fiber behavior.

under isometric conditions). Studies have shown that, after arriving at a point in the force-length relation, if the length of the muscle is further increased or decreased without reducing the activation, the force will not follow the graph of the basic force-length relation. Instead, it will tend to follow approximately a straight line with a positive slope.²¹ Otherwise, the behavior would be unstable whenever the starting point lies in the descending limb of the force-length relation. In the present model, the ability of specifying the value of that positive stiffness associated with extra lengthening at full activation is included in the force-length relation.

In this context, the force-length relation is represented by the parabola:²²

$$f(r) = -0.772r^2 + 1.544r - 0.494 \quad (8)$$

expressing the normal stress (N/mm²) as a function of the ratio $r = L/L_{opt}$ between current fiber length, L , and optimal fiber length, L_{opt} . The optimal length corresponds to the vertex of the parabola. We assume, somewhat arbitrarily, that the stress corresponds to the presence of 10 000 individual fibers per mm². The number of fibers n_f running through a given element can be specified, so that the total force for the active fibers within that element is given (in Newtons) by:

$$F_{act} = a [f(r_0) + k(r_0)(r - r_0)] \frac{n_f}{10\,000} \quad (9)$$

where a is an activation parameter ($0 \leq a \leq 1$), and r_0 is the value of r upon first activation. The positive stiffness $K(r_0)$ represents the behavior for active elongations beyond the initial length. In other words, the enforcement of stability through positive stiffness introduces a memory effect at the fiber level. The muscle fiber remembers the current length when it was first activated

until the activation disappears. When the activation disappears, the current length is forgotten and a new current length will take place upon the reappearance of any level of activation. This activation relation is amenable to direct implementation of a strategy for controlling muscle deformation during movement.

The contribution to the IVW of a given active element when the velocity dependence is neglected is given by:

$$IVW_{fiber} = \sum F_{act} \delta e \quad (10)$$

where δe is the small variation in the elongation produced by the virtual displacements of the endpoints of the active element.

The contribution for the IVW of a given active element when the FEM is time-dependent is given by:

$$IVW_{fiber} = \sum f(v) F_{act} \delta e \quad (11)$$

where $f(v) = 1 - \tanh(v/v_0)$ is the force-velocity dependence, v is speed in mm/second, and v_0 is the maximal velocity of shortening of a given muscle. It corresponds to a multiplicative factor into the constitutive law (Equation 9) due to the inclusion of a viscous component in the muscle fibers.

Strategy for Controlling Muscle Deformation Using Activation Relations

In the continuum model a simple strategy for controlling muscle deformation and muscle force using activation relations is introduced. For that the following quantities have to be defined: the attachment sites of the muscle within the skeletal system; the kinematics of skeletal system for a given target movement; the amount of activation of each muscle during the target movement; and, the spatial location of anatomical compartments in the muscle, if applicable.

The muscle-tendon length (and muscle fiber length) in the passive state can be obtained from the attachment sites of the muscle within the skeletal system. The speed that the muscle-tendon length was shortened or stretched during movement can be obtained from the kinematics of the skeletal system. In the continuum muscle model the muscle force and muscle deformation will be obtained as a function of muscle-tendon length, the contractile speed of the muscle-tendon length, and amount of activation.

In the model we assume that all muscle fibers are recruited at the same time (i.e., uniformly) to reach a given amount of activation. A possible choice of

non-uniform recruitment of muscle fibers would be to consider the fiber type distribution of a given muscle and recruit groups of muscle fibers (motor units) non-uniformly according to some type of principle (e.g., some motor units recruited first and other motor units recruited progressively). However, the force control mechanism in skeletal muscle is also influenced by other factors and a comprehensive force control paradigm is not yet available.

In the proposed activation–recruitment relation, the muscle fiber non-uniformities are included in the muscle structure. The initial internal muscle structure for each hexahedra element (Figure 7) in the passive state is used to calculate the initial ratio of fiber length r and optimal fiber length L_{opt} for each fiber (Equation 9). This ratio turns out to be non-uniform, and it is used to predict muscle force over the entire range of motion. Therefore, in the activation relation all the muscle fibers will be recruited at the same time but each muscle fiber will be at a different position in the force–length relationship (Figure 3).

In the case of compartmentalized muscles which contain anatomical compartments each having a separate innervation branch we adopt the activation relation in separate parts of the muscle. This control strategy might be used for a group of individual muscles. In this way submaximally activated muscle behavior during contraction of compartmentalized muscles can be investigated as well as the implications in muscle deformation and force production.

Modeling the Human Tibialis Anterior Muscle

A current trend in computer graphics is to compare theoretical results (results provided by the model) with experimental results (in our case, results obtained by ultrasound medical imaging assessment) so that their accuracy can be directly examined and the models can be used in a predictive manner. This section details various aspects of our method.

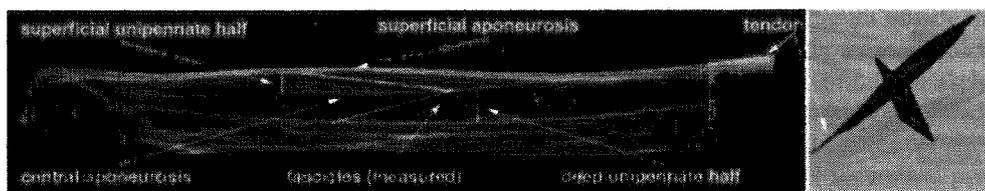


Figure 4. Longitudinal ultrasound image and polygonal boundary of the human TA.

Experimental Muscle Deformation Measurement

A detailed description of the experimental protocol and muscle deformation measurement performed for the model can be found elsewhere.²³

In order to investigate structural changes and force production in the human TA during contraction, relaxed and activated fascicle lengths (or fiber bundles), angle of pennation (i.e., angle between the muscle's line-of-action and the direction of the muscle fibers), and external forces were measured.

For the fascicle lengths and angles of pennation measurement, longitudinal sectional images of the human TA were obtained using a real-time ultrasound apparatus. For passive deformations, measurements of the muscle deformation geometry were taken at ankle angles of -10° (dorsiflexion direction), 0° (the foot at right angle to the shank), $+10^\circ$, $+20^\circ$, and $+30^\circ$ (plantarflexion direction) (Figure 5). Isometric contractions (muscle at constant length) during maximum voluntary contraction (MVC) were obtained, as well. For isometric contractions, during different force levels (20%, 40%, 60%, 80%, and 100% MVC), measurements of the muscle deformation geometry were taken at the ankle angle of $+30^\circ$.

The tendon force was estimated 281.42 N at an ankle angle of $+30^\circ$ during MVC using a similar technique described in Ito *et al.*²³

External and Internal Muscle Geometry Reconstruction

The external geometry was found from cross-sectional images obtained by magnetic resonance imaging. The actual internal geometry was found from longitudinal images obtained by ultrasonography. The hexahedral mesh was obtained from polygonal boundaries for TA (Figure 4) using the software *Truegrid*. The position and orientation the fascicle for the measurements were approximated in the internal geometry.

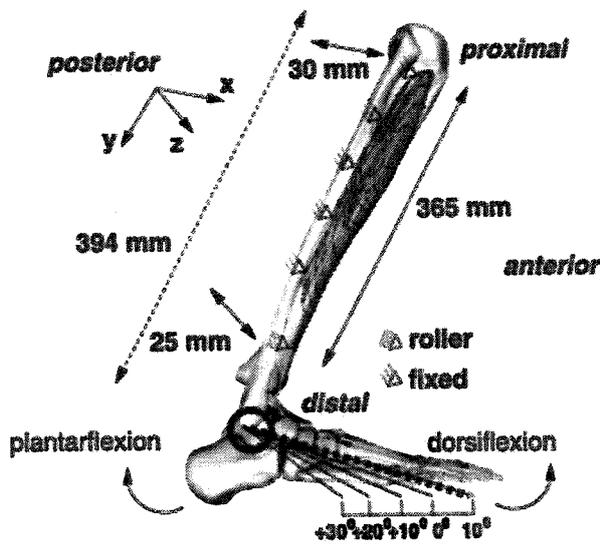


Figure 5. Human TA hexahedral mesh.

The resultant hexahedral mesh had 390 elements (i.e., eight-node brick-like element) including elements for muscle tissue, aponeurosis, and tendon (Figure 5). The visualization at the whole muscle level and the fiber level are shown in Figures 6 and 7, respectively.

Activation of Anatomical Muscle Compartments

Wolf and Kim¹⁷ found that the human TA has three distinct neuromuscular compartments (Figure 7). The anterior aspect of the muscle has one partition (A head, Figure 7). The posterior aspect of the muscle has two partitions (B head and C head, Figure 7). Studies in animal muscles¹⁸ have been performed in non-linear summation of force. In these studies parts of the muscle corresponding to neuromuscular compartments

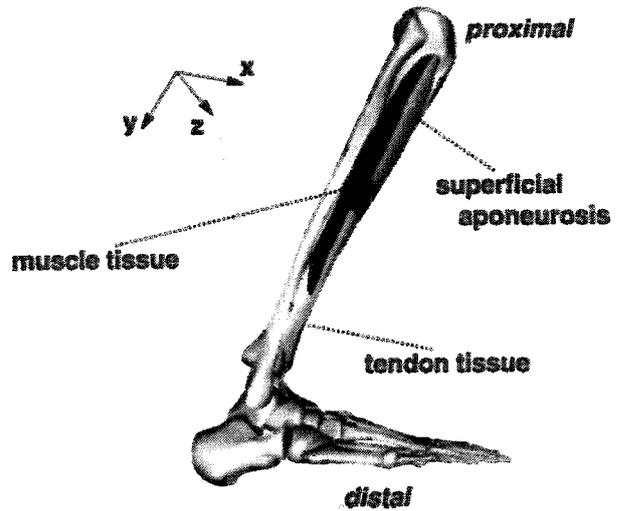


Figure 6. Human TA at the whole muscle level.

are activated separately. Sandercok¹⁸ introduced the non-linear summation of force as

$$F_n(t) = F_{AB}(t) - F_A(t) - F_B(t) \quad (12)$$

where $F_{AB}(t)$ was described as the force measured when both parts A and B of the muscle are activated together. $F_A(t)$ and $F_B(t)$ were described when force of part A and part B, respectively, were stimulated alone.

For the investigation of non-linear summation of muscle force on human TA, a simple theoretical formulation can be adopted. For example, $F_{AB}(t)$ can be described as the force measured when both the deep and the superficial unipennate half of TA are activated together. $F_A(t)$ and $F_B(t)$ can be described when the deep unipennate half of TA and the superficial unipennate half of TA were activated alone.

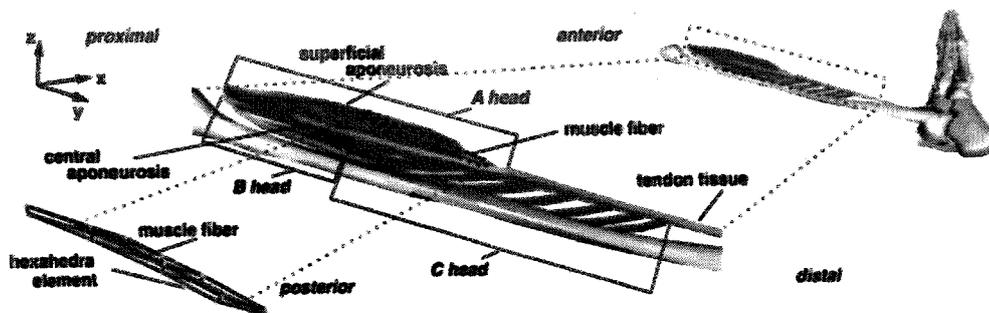


Figure 7. Human TA at the fiber bundle level and muscle compartments.

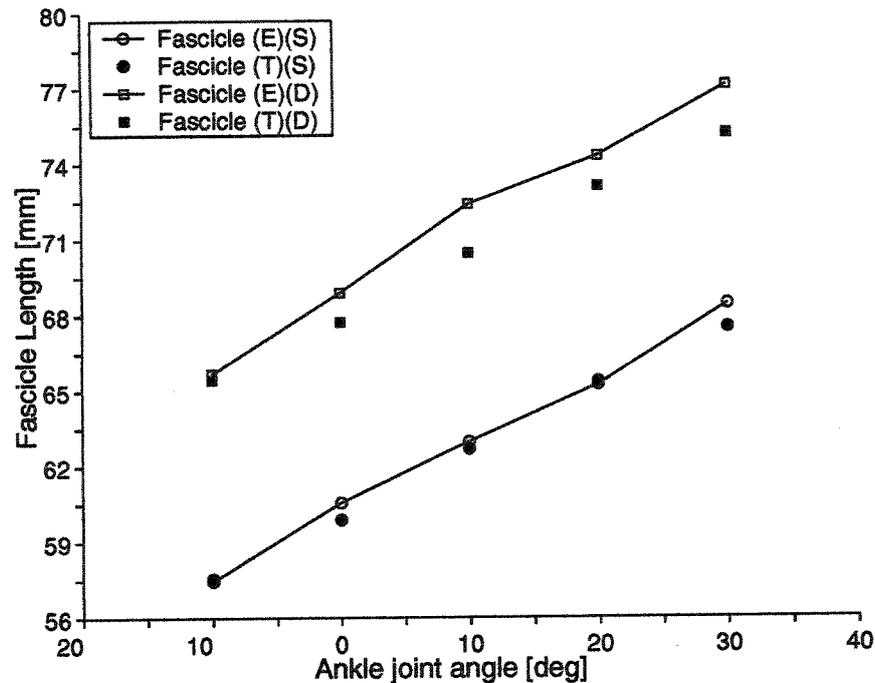


Figure 8. Passive deformations for the experimental (E) and theoretical fascicle lengths (T), for superficial (S) and deep (D) unipennate half.

Muscle Deformation Simulation and Evaluation

For the simulation, parameters such as boundary conditions and material parameters for the passive structures had to be specified (Figure 5).

In the simulation of the passive deformations, the distal insertion (tendon) is moved passively from the ankle joint of -10° to $+30^\circ$ (Figure 8). Shear modulus (μ) for the superficial aponeurosis, central aponeurosis, and muscle tissue were $\mu = 15$ MPa, $\mu = 2$ MPa, and $\mu = 0.015$ MPa, respectively (Mooney–Rivlin relation). For the tendon, the shear modulus (μ) for the tissue matrix was $\mu = 10$ MPa (Mooney–Rivlin relation) and the Young's modulus (\bar{E}) and parameters α and \bar{w} for the tendon (Equation 5) were $\bar{E} = 2000$ MPa, $\alpha = 0.015$ (1.5% of \bar{E}) and $\bar{w} = 0.15$ (15.0% of \bar{E}), respectively.

In the isometric contraction simulations, the distal insertion (tendon) is moved passively from the ankle joint of -10° to $+30^\circ$. The muscle is held at the ankle joint of $+30^\circ$ and it is activated to the maximum. In Figure 9, comparisons of fascicle lengths and angle of pennation between simulated and experimental results for different levels of MVC are shown. The

undeformed and deformed geometry at the muscle fiber level at the ankle joint of $+30^\circ$ for maximally and submaximally activated muscle behavior is shown (Figure 10). The simulated muscle force was 270.16 N. When only the deep unipennate half was maximally activated, the force was 175.70 N. And, when only the superficial unipennate half was fully activated, the force was 170.98 N.

For the CPU time statistics, the simulation on a 3.2 GHz Intel Pentium 4 CPU using the full Newton method required approximately 11 hours. Under the same conditions using the Secant method required approximately 5 hours.

Discussion

It was shown that the continuum muscle model can be used to predict conceptually force production properties and structural changes in human skeletal muscles for maximally and submaximally activated muscle behavior. Regarding the simulation of the internal geometry during deformation, the theoretical predictions for the relaxed fascicle lengths at different ankle joint angles (Figure 8) agreed well with the observed experimental

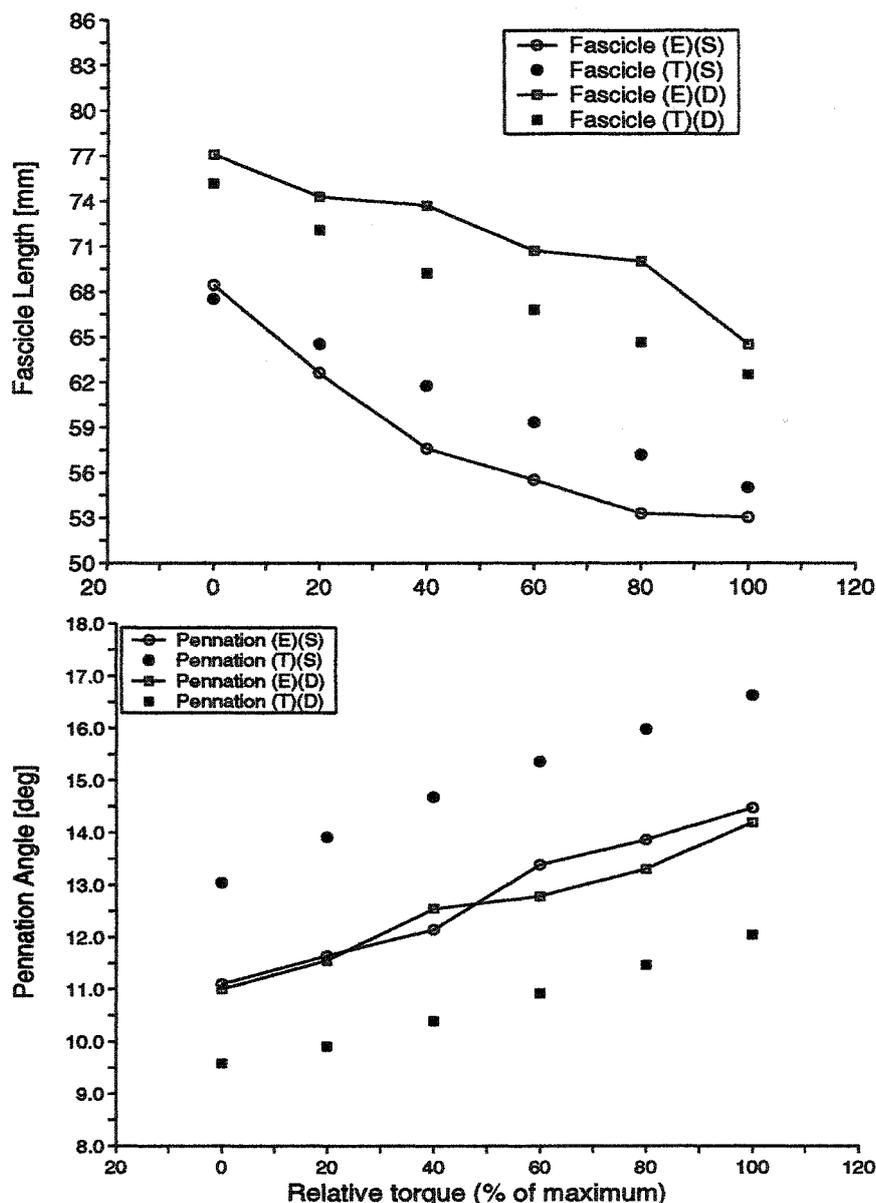


Figure 9. Fascicle lengths and angles of pennation for experimental (E) and theoretical (T) results, for superficial (S) and deep (D) unipennate half.

data. The theoretical predictions for the fascicle lengths and pennation angles at the ankle joint angle of $+30^\circ$ during different levels of maximum activation state show good quantitative and qualitative agreement with the measured experimental data (Figure 9).

Regarding the simulation of the force production properties, the force-length production of the muscle in maximum activation state at ankle joint angle of $+30^\circ$ agreed well with experimental data for maximum vo-

luntary contraction. The following non-linear summation of force was observed during the interaction of the compartments adopted for the human TA: $(F_{AB}(t) < F_A(t) + F_B(t))$. The explanation of this observed simulated result is related to the series elasticity of the muscle. This explanation is based on the idea that when more neuromuscular compartments are activated, more muscle fibers will contract. As a result, the increased fibers shortening causes decreasing forces.

The dynamics of muscle contraction is obtained at different structural levels for maximally and submaximally activated muscle behavior which allows for meaningful insight into deformation and contractile process of whole muscle contraction (Figure 10).

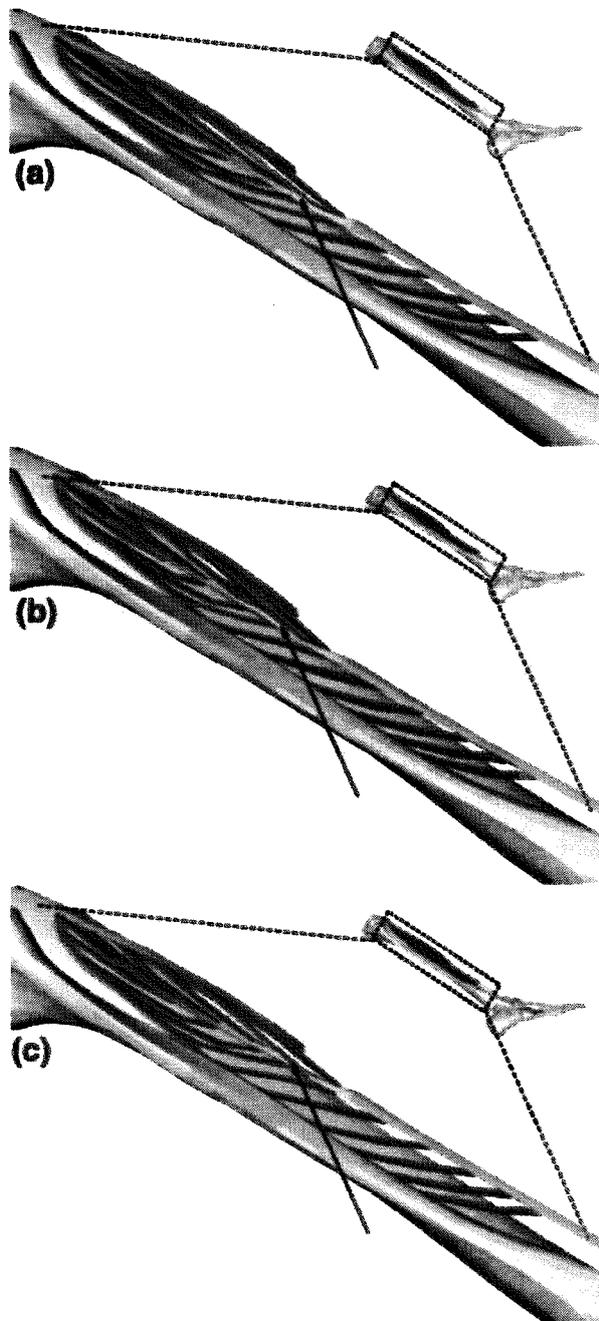


Figure 10. Human TA deformation (a) relaxed state (blue fiber always relaxed) (b) 100% of activation for whole muscle (c) 100% of activation only for the superficial unipennate half.

Conclusions and Future Work

The proposed model represents a step toward the use of physiologically-based muscle representations in rendering and animation frameworks.

In order to produce the animation of realistic skeletal muscle deformation, and to study muscle function during contraction, models incorporating actual three-dimensional geometries are needed.

Regarding the CPU time statistics, the full Newton's method is more computationally expensive than the secant method of Broyden.¹⁹ This is due the fact that the function evaluation is expensive to calculate.

For the modeling and simulation of the human skeletal muscle structure a next step might include the modeling of the three main ankle extensor muscles of the human lower limb (e.g., tibialis anterior muscle, gastrocnemius muscle, and soleus muscle) and the simulation of the human movement during specific tasks (e.g., walking, running, and jumping) exploring the muscle control strategies introduced in this paper for a group of muscles.

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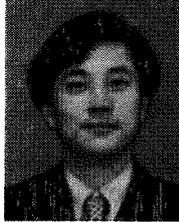


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Short Report

Human Skeletal Muscle Size and Architecture: Variability and Interdependence

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ABSTRACT Seven hundred and eleven women and men (aged 3–94 years, including normal individuals and highly trained bodybuilders) were tested for the thickness and pennation angles of their triceps brachii (TB), vastus lateralis (VL), and gastrocnemius medialis (GM) muscles. The variations of muscle thickness and pennation angles were largest in TB (6–66 mm and 5–55°), followed by VL (8–45 mm and 7–33°) and GM (11–36 mm and 12–33°), and women showed smaller variations than men. These results suggest the existence of muscle- and gender-specificity in the variability of muscle dimensions. Significant positive correlations were observed between muscle thickness and pennation angles ($r = 0.81, 0.61, \text{ and } 0.56$; for TB, VL, and GM, respectively), indicating that the size-dependence of the pennation angle is a general feature of pennate muscles. *Am. J. Hum. Biol.* 18:845–848, 2006. © 2006 Wiley-Liss, Inc.

Skeletal muscle force production is influenced by a muscle's size and architecture (arrangement of muscle fibers). It is known that human skeletal muscle size has considerable plasticity, and it was shown that muscle architecture shows interindividual variations (Chow et al., 2000; Henriksson-Larsen et al., 1992; Kawakami et al., 1993). Little is known, however, of whether the amount of plasticity in muscle size and architecture is muscle- or gender-specific.

Kawakami et al. (1993) found for the triceps brachii muscle that the pennation angle (Pa) was positively correlated with muscle thickness (Mt), and pointed out the dependence of muscle force kinetics on size. However, studies on other muscles failed to find such a relationship (Abe et al., 1999; Henriksson-Larsen et al., 1992). The question remains as to whether the muscle-size dependence of Pa is a general property of pennate muscles or a unique feature of specific muscles.

In order to clarify the intermuscle variability of muscle size and architecture and their interdependence, we carried out measurements of Mt and Pa for different muscles in the upper and lower limbs from a large number of populations with widely varying muscle size.

METHODS

Subjects

Females ($n = 284$) and males ($n = 427$) (aged 3–94 years; mean height, 160.7 ± 14.1

SD (91.0–193.0) cm; mean mass, 60.4 ± 18.3 SD (12.9–181.9) kg) participated in this study. Subjects were sedentary, normal, and moderately to highly active individuals, highly trained bodybuilders at national and international levels for both sexes, and male sumo wrestlers. Children and elderly individuals were included to examine the lower limit of muscle size in humans. Informed consent to participate in this study was obtained from subjects, and from their parents when the subjects were children. This study carried approval of the Ethics Committee of the Department of Life Sciences, University of Tokyo.

Muscles tested

Three muscles (triceps brachii, TB; vastus lateralis, VL; and gastrocnemius medialis, GM) were tested. The measurement sites were at levels 60% of the upper arm length distal to the acromion process for TB, 50% of the thigh length for VL, and 30% of the leg length distal to the popliteal crease for GM. Each level is where the anatomical cross-sectional area of

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the respective muscle is maximal (Fukunaga et al., 1992; Kawakami et al., 1994; Narici et al., 1992). The subject stood on a level surface during measurement. The subject relaxed tested muscles as much as possible. Right limbs were tested.

Measurement of Mt and Pa

A real-time ultrasonic apparatus (SSD-2000, Aloka, Japan) was used. A transducer with a 7.5-MHz scanning head coated with transmission gel was placed onto the skin without depressing the skin surface. At the level described above, the medio-lateral center was determined for each muscle from ultrasonography. At this position, the subcutaneous adipose tissue-muscle interface and muscle-muscle (VL and GM) or muscle-bone (TB) interface were identified from the cross-sectional ultrasonic image, and the distance between adjacent interfaces was measured to the nearest 0.5 mm as Mt (Kawakami et al., 1993). We regarded Mt as a measure of muscle size, based on highly significant correlations (coefficient of correlation ~ 0.90) between Mt and cross-sectional area of muscle (Martinson and Stokes, 1991; Abe et al., 1997).

At the same position, a longitudinal ultrasonic image was obtained so that the fascicles were visualized along their whole lengths from the superficial to the deep aponeuroses. The angle at which the fascicles arose from the deep aponeurosis was measured to the nearest 0.5° as Pa (Kawakami et al., 1993). Pa was determined for three fascicles within the image, and averaged. Figure 1 shows typical ultrasonic images of the three muscles. The measurement variability in Mt and Pa was confirmed to be <1 mm and 1° , respectively, with intraclass correlation coefficients of $r > 0.98$ (Kawakami et al., 1993).

Statistical analysis

Mt and Pa were tested for intermuscle and gender differences in variability in terms of coefficients of variation (CV). The relationship between Mt and Pa was tested for statistical significance using the Pearson correlation (r). The slopes of linear regression were also compared for significant differences between muscles and between genders. A $P < 0.05$ level of confidence was used in all tests. Unless otherwise stated, mean values \pm SD are given.

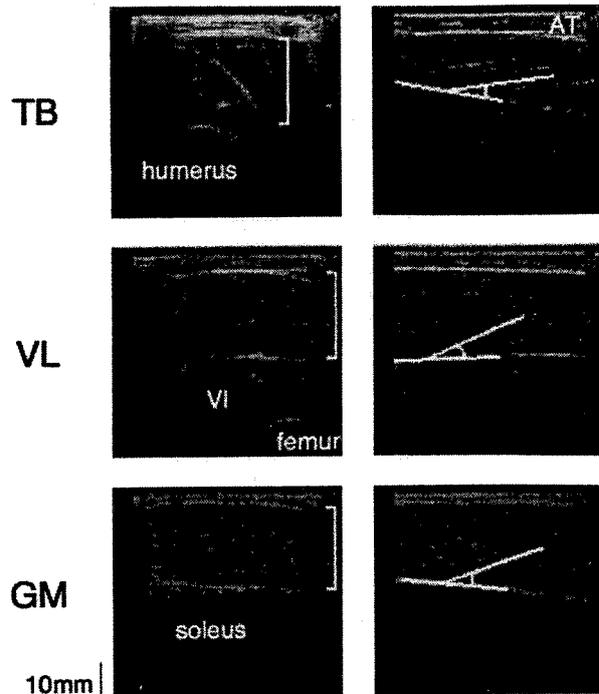


Fig. 1. Ultrasonic images (cross-sectional, left row; longitudinal, right row) of triceps brachii (TB), vastus lateralis (VL), and gastrocnemius medialis (GM) muscles. Muscle thickness (left row) and pennation angles (right row) were measured as distance between adipose tissue/muscle and muscle/muscle (VL and GM) or muscle/bone (TB) interfaces, and angles made by fascicles and deep aponeurosis, respectively. AT, adipose tissue; VI, vastus intermedius.

RESULTS

The Mt of TB, VL, and GM were 31 ± 10 (women, 6–42; men, 11–66), 23 ± 6 (8–33 and 12–45), and 21 ± 4 (10–27 and 11–36) mm, respectively. The Pa of the three corresponding muscles were 20 ± 7 (6–27 and 5–55), 19 ± 4 (7–24 and 9–33), and 21 ± 3 (12–26 and 13–33) $^\circ$, respectively. There were significant differences in CVs of Mt and Pa between muscles, in the decreasing order of TB, VL, and GM. Women showed CVs both for Mt and Pa than men.

Figure 2 shows the relationships between Mt and Pa for TB, VL, and GM. Each Mt was normalized to the limb length (upper arm for TB, thigh for VL, and leg for GM) to correct for intersubject differences in stature. Significant positive correlations were observed, with coefficients $r = 0.81, 0.61,$ and 0.56 for TB, VL, and GM, respectively. Those correlations were also significant for both women ($r = 0.65, 0.59,$ and 0.48) and men ($r = 0.81, 0.56,$ and 0.59). The slope of regression was significantly higher for GM compared with VL except for

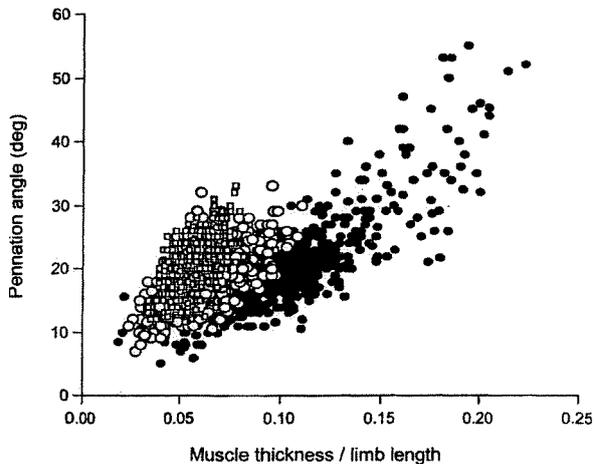


Fig. 2. Relationships between pennation angles and muscle thickness of TB (solid circle), VL (open circles), and GM (squares) ($n = 711$).

women. The slope of TB was significantly lower in women than in men.

DISCUSSION

The present ranges of Pa are much wider than in the published data on cadavers (Yamaguchi et al., 1990) and in vivo humans (Chow et al., 2000; Kawakami et al., 1993; Rutherford and Jones, 1992). Our result shows differences in the range of variability in Mt and Pa between muscles, with decreasing magnitude in the order of TB, VL, and GM. Since the present data include those of highly-trained athletes, this result is unlikely due to the difference in the amount of training between muscles; rather, it could be due to intermuscle differences in hypertrophic response to training and/or growth. The order of variations in Mt and Pa corresponds to that of the index of muscle architecture, i.e., muscle fiber length/muscle length (Lieber and Brown, 1992; Yamaguchi et al., 1990). This coincidence hints at the notion that there are some architectural factors, possibly including muscle fiber length, that limit the magnitude of muscle hypertrophy. This factor might be related to the higher slope of regression between Mt and Pa in GM than in VL. The architectural limitation might also be able to explain the lower trainability of the lower compared with the upper limb muscles (Abe et al., 2000). However, these arguments are purely speculative, and await further experimental verification.

A lack of significant difference in regression slopes between GM and VL in women might be due to smaller variations of Mt and Pa compared with men. A higher regression slope of

male TB could be attributable to a previous finding for this muscle (Kawakami et al., 1993), that Pa increased more than Mt in extremely hypertrophied muscles.

Significant positive correlations between Mt and Pa in all muscles give experimental evidence to the contention that muscle hypertrophy accompanies an increase in Pa. Significant correlations were found even when women and men were separately analyzed. Failure to find such correlations for the same muscles (Abe et al., 1999; Henriksson-Larsen et al., 1992) would be due to a limited sample size and/or variations in muscle dimensions.

The force applied to the tendon by the contraction of muscle fibers is reduced by a factor of $\cos(Pa)$ from the sum of the forces of individual fibers (Kawakami et al., 1993). In this study, we found variations in Pa from 5–55° in TB, corresponding to force-reduction factors of 0.996 and 0.574. GM has a much smaller variability in this factor (0.978–0.839). These differences might be able to partly explain the inconsistency in specific tension (muscle force per physiological cross-sectional area) reported for these muscles (Fukunaga et al., 1996; Kawakami et al., 1994; Narici et al., 1992).

In conclusion, intermuscle and gender differences in the variability of muscle size and architecture suggest a divergence in inherent plasticity in muscle dimensions. We also conclude that the size-dependence of pennation angles is a general feature of pennate muscles. These arguments should be taken into consideration when assessing human muscle functions.

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ベッドレストによる足関節可動域および筋腱複合体の受動伸長性の変化

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柔軟性, 関節可動域, 不活動, 下腿三頭筋, アキレス腱

【目的】

人間の身体に不活動が及ぼす影響は、神経・筋特性を中心にこれまで数多くの検討がなされているが、柔軟性の変化については不明な点が多い。本研究では、柔軟性を関節可動域と定義し、安静臥床（ベッドレスト）による関節運動の激減が関節可動域の変化に及ぼす影響について調べた。また、関節可動域の規定因子²⁾と考えられる筋腱複合体の伸長性の変化についても検討を行った。

【方法】

被検者は事前に実験参加に同意した 5 名の健常学生 (21-24 歳, 175±10cm; 平均±標準偏差) であった。被検者は頭部を 6° 低くした姿勢で 3 週間のベッドレストを行った。検者が 24 時間体制で常駐し、トイレとシャワー以外は臥床状態を維持するように配慮した。期間中、被検者の体重は維持された (65±5→65±6kg)。

ベッドレスト前後に以下の測定²⁾を行った。被検者は筋力計 (VINE 社製) のシート上で座位 (左膝関節は完全伸展位) をとり、非利き足である左足部を筋力計のフットプレートに固定した。フットプレートは等速で底屈 40° の位置を始点として足背屈方向に回転した。一定の受動トルクが生じてフットプレートが回転を停止した時点の足関節角度 (受動背屈角度) を計測した。アナログスケール法による被検者の主観的なストレッチ感が「ややつばる感じ」を覚える程度の負荷を最大値とし、それよりも低い負荷から 10 秒毎のステップで負荷を増加させた。被検者には、底屈筋群を緊張させず、受動背屈に抗する動きを行わないように指示した。負荷トルクはベッドレスト前後で同一であった。

Bモード超音波装置 (SSD-5500, Aloka 社製) を用いて、腓腹筋内側頭の遠位筋腱移行部の足背屈に伴う移動量 (腓腹筋筋腹伸長) を、底屈 40° の位置からの変位として各ステップの 10 秒目に計測した。次に、関節角度を変化させたときの筋腱複合体全長の変化を推定¹⁾し、次式によって腱 (アキレス腱, 腓腹筋の外部腱) の伸長を推定した。

腱伸長 = 筋腱複合体長変化 - 筋腹長変化

上記に加えて、特別に作製した角度計 (VINE 社製) を用いて、被検者が最大努力で背屈動作を行ったときの足関節角度 (能動背屈角度) を計測した。

【結果と考察】

負荷トルクが増すにつれて受動背屈角度は増加し、増加の程度はベッドレスト後に有意に大きくなった (図 1)。能動背屈角度も 5 名中 4 名 (1 名は変化なし) に

おいてベッドレスト後に増加した (-18±5° → -24±5° ; 5 名の平均)。受動背屈中に筋腹・腱ともに伸長されたが、双方ともベッドレスト後に増加幅が拡大する傾向にあったものの有意差は認められなかった (図 2)。これは筋腹伸長と腱伸長の程度が被検者によって一定の傾向を示さなかったためである。本研究の結果から、ベッドレストによって足関節可動域が拡大する、すなわち、足部の柔軟性が高くなることが示された。

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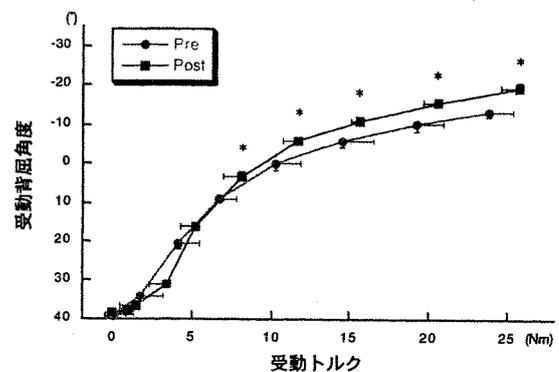


図 1: 負荷トルクと受動背屈角度の関係 (5 名の平均±標準偏差) 背屈角度はプラスが底屈方向, マイナスが背屈方向を示す

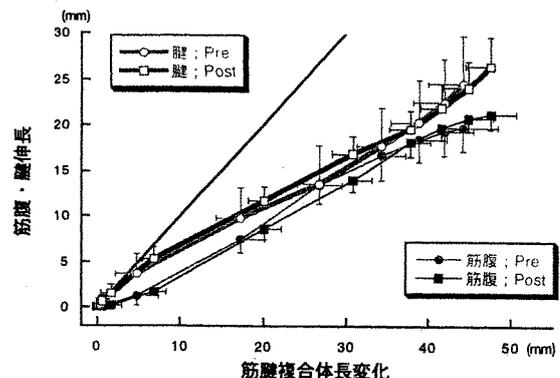


図 2: 受動背屈中の筋腱複合体長変化と筋腹・腱伸長の関係 (5 名の平均±標準偏差; 細線: 筋腹伸長; 太線: 腱伸長); 直線は identical line を示す

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バレエダンサーの足関節の特徴 —足関節可動域と下腿三頭筋・腱の伸長に着目して—

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関節可動域の性差について, また関節可動域が大きいと考えられるバレエダンサーの特徴を筋・腱の伸長の計測を通じて検討した. 成人男女 (女性バレエダンサーを含む) の足関節を対象とし, 以下の実験を行なった. 膝関節完全伸展の座位をとった被検者の足関節を, 筋力計のフットプレートに底屈 40° で固定した. フットプレートは等速 (100° / 秒) で受動的に被検者の足関節を背屈方向に回転し, 一定の受動トルクが生じたところで停止するように設計されていた. 足関節の角度変化およびその際の受動トルクと最終的な足関節背屈角度を計測した. また, 超音波装置の探触子を腓腹筋の遠位の筋腱移行部 (MTJ) に固定した. B モード超音波法により足関節背屈にともなう遠位への MTJ の移動量を計測し, この移動量を筋線維の伸長とした. 被検者の下腿長を用いて, 関節の角度変化による MTC 全長変化を先行研究の推定式より算出し, 腱組織 (アキレス腱, 腓腹筋の外部腱) の伸長を [MTC 全長変化 - MTJ の移動量] をもとに推定した. これらのパラメータについての性差, およびバレエダンサーの特徴を報告する.

長時間の静的ストレッチングが下腿三頭筋の伸長に及ぼす急性効果

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柔軟性, 筋腱複合体, 足関節

長時間の静的な足関節背屈ストレッチングが下腿三頭筋の伸長に及ぼす急性効果を検討した。ストレッチングの前後に以下の計測を行なった。被検者 (n=6) は膝関節完全伸展の仰臥位で、足関節をフットプレートに固定された。モーターの回転によって底屈 30° から受動トルクを漸増させ、足関節を背屈させた。その際、超音波Bモード法を用いて、腓腹筋内側頭の遠位筋腱移行部 (MTJ) の移動量を計測し、その移動量を筋の伸長とした。ストレッチングでは、被検者の足関節を一定の受動トルク (計測時の最大受動トルクの90%) で、20分間背屈させた。ストレッチング後の計測で、一定の受動トルクに対する足関節背屈角度は増加した (最大背屈角度: $18.5 \pm 5.8 \rightarrow 22.8 \pm 8.5$; 平均 \pm SD) にも関わらず、MTJの移動量は変化しなかった。足関節角度変化が下腿三頭筋の筋腱複合体の全長変化を表すとすると、足関節背屈角度の増加は腱伸長による可能性が考えられる。本研究の結果から、20分間の静的なストレッチングでは、筋よりも腱が伸長されやすくなることが示唆された。

高齢者にみられる足関節可動域の性差

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柔軟性, 関節可動域, 加齢, 下腿三頭筋, アキレス腱

【目的】

柔軟性は関節可動域の大小を通じて評価される。大きな関節可動域でしなやかに動く能力が日常生活の遂行能力と深い関係をもっていると考えられる高齢者にとって、柔軟性は重要な体力因子である。本研究では、高年齢者を対象に、関節可動域の性差およびその規定因子について検討を行った。

【方法】

被検者は事前に実験参加に同意した 140 名の健常な高齢者 (65-83 歳; 女性 86 名, 男性 54 名; 平均年齢に男女差なし) であった。被験者は定期的な身体運動を実施していた。被検者は筋力計 (VINE 社製) のシート上で座位 (右膝関節は完全伸展位) をとり、筋力計のフットプレートに固定された右足部をリラックスさせた。フットプレートは等速で底屈 40° を始点として足背屈方向に回転した。受動背屈によって足関節に受動トルクが生じ、フットプレートの設定トルクと等しくなるとプレートの回転が停止するように設計されていた。設定トルクをステップ状に増加させることで、受動背屈量を増加させた。

Bモード超音波装置 (SSD-900, Aloka 社製) を用いて、腓腹筋内側頭の遠位筋腱移行部の足背屈に伴う移動 (腓腹筋筋腹伸長) を、底屈 40° の位置からの変位として各ステップ毎に計測した。次に、関節角度を変化させたときの筋腱複合体全長の変化を推定し、次式によって腱 (アキレス腱, 腓腹筋の外部腱) の伸長を推定した。

腱伸長 = 筋腱複合体全長変化 - 筋腹長変化

上記に加えて、特別に作製した角度計 (VINE 社製) を用いて、被検者自身が最大努力で背屈動作を行ったときの足関節角度 (能動背屈角度) を計測した。

【結果と考察】

設定トルクが増すにつれて受動足背屈が進行し、関節角度変化は男性よりも女性が大きかった (図 1)。このときの筋腹の伸長率 (安静時の推定筋腹長に対する増加率) は、女性が男性を上回っていた (図 2)。一方、能動背屈角度には男女差はみられなかった。

以上の結果は、足関節の受動背屈角度が伸長される組織 (下腿三頭筋を中心とした足底屈筋群) の多寡に依存し、一方、能動背屈角度は背屈筋群の筋量や筋力の影響も受けることを示唆する。これは中高年者を対象とした先行研究²⁾を支持する結果であるが、腱伸長率 (安静時

のアキレス腱長に対する増加率) に性差がみられない (図 2) など、高齢者に特有の傾向も認められた。

謝辞 本研究を行うにあたりご協力をいただいた早稲田大学大学院加藤えみか氏および東京大学大学院 千野謙太郎氏、栗原俊之氏に感謝いたします。

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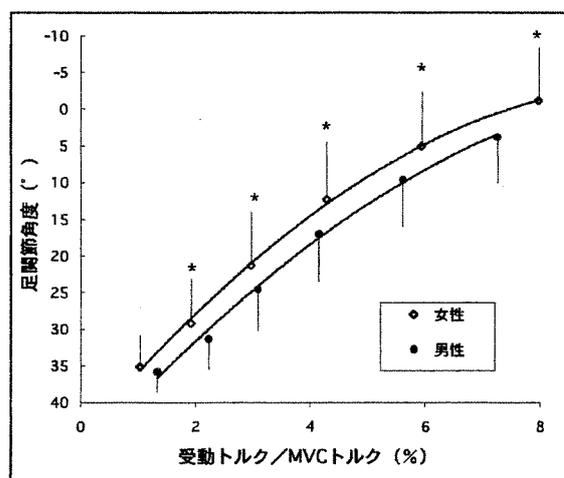


図 1: 負荷トルク (最大随意筋力で正規化) と受動背屈角度の関係 (平均値 ± 標準偏差) 背屈角度はプラスが底屈方向, マイナスが背屈方向を示す。*男女差あり (P<0.05)

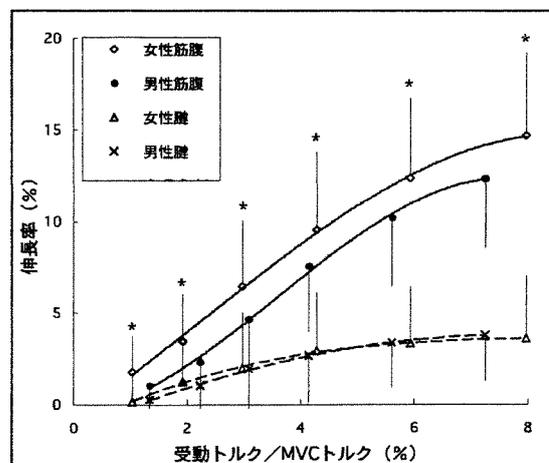


図 2: 受動背屈中の筋腹・腱伸長 (平均値 ± 標準偏差; 実線: 筋腹伸長; 破線: 腱伸長)。*男女差あり (P<0.05)

足関節の静的ストレッチング中にアキレス腱が伸長する

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本研究では、長時間の足関節背屈方向への静的ストレッチングが下腿三頭筋・腱に及ぼす影響を検討することを目的とした。

被検者は 6 名の健常な男性であった。膝関節完全伸展の仰臥位で、足関節を筋力計のフットプレートに固定し、静的な背屈方向のストレッチングを 20 分間行ない、その際の足関節角度、受動トルク、筋線維伸長を記録した。筋線維伸長は、超音波装置の探触子を腓腹筋内側頭の遠位筋腱移行部の皮膚上に固定し、B モード超音波法により計測した足関節の背屈にともなう、遠位筋腱移行部の移動量として計測した。

また、先行研究より算出した筋腱複合体の全長変化の推定値と筋線維伸長の実測値の差を求め、これを腱伸長とした。

ストレッチング中に、一定の受動トルクに対する足関節背屈角度は $18.8 \pm 6.9 \text{deg}$ → $22.3 \pm 7.9 \text{deg}$ へ増加し ($p < 0.05$)、筋腱複合体の全長も $2.8 \pm 1.1 \text{mm}$ 伸長した ($p < 0.05$)。

筋線維はストレッチング開始時に伸長した ($27.6 \pm 2.5 \text{mm}$) が、伸長の度合いはストレッチングの前後で変化がみられなかった ($0.08 \pm 0.002 \text{mm}$)。このことは、ストレッチングの継続による筋腱複合体長の増加は腓腹筋の外部腱の伸長によるものであることを示している。20 分間のストレッチングによってアキレス腱を中心とする腓腹筋の外部腱が伸長することが明らかになった。

REPETITIVE MUSCLE CONTRACTIONS INDUCE MECHANICAL CHANGES OF ACHILLES TENDON.

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INTRODUCTION

Muscle contraction induces tendon elongation¹). Repetitive muscle contractions are known to induce tendon creep²), but the presence of concurrent changes in mechanical properties of the tendon has not been elucidated. The purpose of this study was to investigate changes in the muscle-tendon complex mechanical properties during and after repetitive muscle contractions.

METHODS

Six men (mean ± SD for the age, body mass and height was 23.5 ± 1.2 years, 68.3 ± 7.1 kg, 172.7 ± 5.6 cm) performed 15 repetitive isometric ramp contractions. The subject was seated with the knee extended, and the ankle joint was attached to the foot plate at the right angles to the tibial axis. Preceding the experiment, MVC torque was measured, and the target torque was determined based on MVC. Before and after repetitive contractions, the following flexibility test was performed. The subject was seated with the knee extended, and the ankle joint was attached to the foot plate at an angle of 30° plantarflexion. The foot plate was connected to a dynamometer (VINE, Japan), by which the ankle joint was passively dorsiflexed with torque gradually increasing from zero to a value at which the passive loading to the ankle joint was just tolerable for each subject. The dorsiflexion angle and passive torque generated by plantar flexor muscles were measured during the test. During the passive loading, real-time ultrasonogram (SSD-6500, Aloka, Japan) was taken to track the movement MTJ (muscle-tendon junction of the gastrocnemius medialis and Achilles tendon). The movement of MTJ with dorsiflexion was assumed to be equal to the elongation of muscle belly (dMus). According to the estimated Achilles tendon moment arm¹). The change of MTC (muscle-tendon complex) length (dMTC) during the passive dorsiflexion was estimated from changes in ankle joint angle. Tendon elongation (dTEn) was calculated by subtracting dMus from dMTC. Tendon force (TF) was estimated from the torque and moment arm length³).

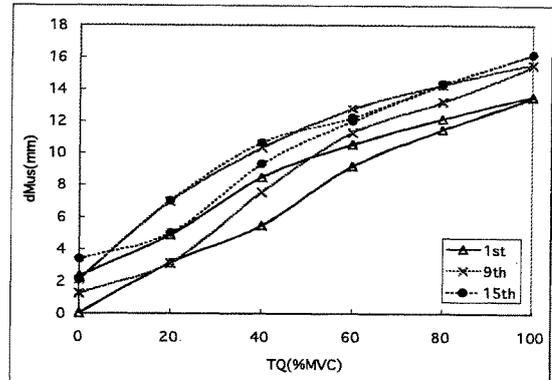


Figure 1: The relation between tendon force and dMus during 15 repetitive contractions, just only the 1st, 9th and 15th contractions are shown.

RESULTS AND DISCUSSION

The changes in dMus during 15 repetitive contractions are shown in Figure 1. The first contraction showed a different pattern compared with other contractions (p<0.05), dMus shifted proximally during repetitive contractions. This result indicates that repetitive contractions induced tendon creep. The flexibility test showed dMTC which involved an increase in dTen (p<0.05), but dMus did not change significantly. The elongated tendon changed its passive length-force curve, especially at the toe-region. Altered toe-region of the tendon length-force curve suggests structural changes of tendon as a result of repetitive contractions.

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Table 1: Elongation of MTC, Muscle and tendon during flexibility test. (): post test, *: p<0.05

| Tendon Force (N) | 100 | 200 | 300 | 400 | 500 |
|------------------|--------------------------|--------------------------|---------------------------|--------------------------|--------------------------|
| Elongation (mm) | | | | | |
| MTC | 16.0 ± 3.0 (21.9 ± 7.4*) | 23.8 ± 7.5 (29.3 ± 5.9*) | 28.4 ± 10.3 (32.6 ± 5.2*) | 33.1 ± 10.7 (34.9 ± 5.1) | 35.0 ± 14.1 (37.0 ± 5.2) |
| Muscle | 11.5 ± 6.0 (13.8 ± 5.4) | 18.4 ± 7.4 (20.0 ± 4.8) | 20.8 ± 7.1 (22.6 ± 4.6) | 23.0 ± 7.3 (23.8 ± 4.4) | 24.4 ± 7.1 (25.7 ± 4.5) |
| Tendon | 4.5 ± 3.5 (8.1 ± 2.7*) | 5.5 ± 3.1 (9.3 ± 2.3*) | 7.6 ± 4.2 (10.0 ± 3.2) | 10.1 ± 4.6 (11.1 ± 3.3) | 10.7 ± 4.2 (11.4 ± 3.4) |

1-B-3 アキレス腱のどこが伸びるのか？

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アキレス腱は、伸長し弾性エネルギーを貯蔵することでスプリント動作やジャンプパフォーマンスにおいて重要なはたらきをしていると考えられている。本研究では、アキレス腱（腓腹筋内側頭の遠位端から踵骨隆起まで；腱膜および外部腱からなる）、腱膜（腓腹筋遠位端からヒラメ筋遠位端まで）および外部腱（ヒラメ筋遠位端から踵骨隆起まで）の伸長率、さらにはアキレス腱のヤング率を求め、アキレス腱の各部位における伸びおよび材質について検討を行った。被検者には足関節角度0度のうつ伏せの姿勢で、最大（MVC）および最大下（20, 40, 60, 80%MVC）のレベルで等尺性足底屈筋力発揮を行なわせ、その時のアキレス腱長を3D超音波法にて計測し、分析をおこなった。その結果、アキレス腱における外部腱の伸長率は腱膜よりも大きい傾向がみられ、アキレス腱全体の伸長率にはこの外部腱の貢献が大きいことが示唆された。さらに詳細な報告は当日の発表において行う。

キーワード：アキレス腱 伸長率 外部腱 腱膜

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2C-08

異なる強度の等尺性底屈トルク発揮が下腿三頭筋・腱の伸長性に及ぼす影響

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等尺性筋活動後、筋・腱の力学的特性が一過性に变化することが明らかにされている。このことは等尺性筋活動であっても筋は短縮し、腱は伸長することと関連づけられる。本研究では強度の異なる等尺性筋活動が筋・腱の力学的特性に及ぼす影響について検討した。健康な成人男性 10 名を対象に膝関節完全伸展の座位、足関節角度 0 度で等尺性底屈動作を最大筋力に対する 30、50、80% で 15 回行った。各試行の前後で受動背屈を行い、足関節角度変化から腓腹筋の筋腱複合体伸長を算出した。超音波装置で腓腹筋内側頭とアキレス腱の筋腱移行部を撮像し、背屈にともなう遠位への移動を計測した。この移動を筋伸長とし、筋腱複合体伸長と筋伸長の差から腱伸長を推定した。受動背屈中に得られた受動トルクと筋腱複合体伸長、筋伸長、腱伸長を回帰して、各々の傾き（伸長／トルク比）を強度ごとに求めた。いずれの強度でも筋腱複合体伸長／トルク比は試行の前後で変化しなかったが、筋伸長／トルク比は有意に減少し、腱伸長／トルク比は有意に増加した。さらに、筋・腱伸長／トルク比の変化から高強度の試行ほど筋は伸長しにくく、腱は伸長しやすくなることが示唆された。等尺性筋活動で筋・腱の力学的特性は変化し、その変化は強度による影響を受けることが示された。

足関節可動域の性差および年齢差とアキレス腱の伸長性の関係

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足関節の関節可動域には、性差や年代差が存在することがこれまでに報告されている (Nigg, et al., 1992)。本研究では、足関節の関節可動域の性差および年代差に影響を及ぼす因子について検討した。対象としたのは、成長期 (13.4 ± 0.6 歳)、成人 (22.2 ± 1.8 歳)、高齢者 (71.3 ± 4.8 歳) の男女であった。膝関節完全伸展、足関節角度 30 度の状態から被検者の足関節を受動的に背屈し、足関節角度変化から下腿三頭筋の筋腱複合体伸長、超音波装置を用いて筋伸長を計測し、両者から腱伸長を推定した。足関節背屈角度、筋腱複合体伸長、腱伸長は成長期の男女・成人女性・高齢女性の方が成人男性・高齢男性よりも有意に大きかったが、筋伸長には差がみられなかった。このことから、関節可動域には腱伸長が大きな影響を及ぼすことが示された。また、成長期には関節可動域の性差はみられないが、男性は加齢にともない腱が伸長しにくくなることで関節可動域が減少することが示唆された。

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Changes in mechanical properties of Achilles tendon resulting from muscle contraction and stretching.

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Muscle contraction and stretching are known to induce tendon elongation. We defined tendon elongation induced by muscle contraction as “active tendon elongation”, and by stretching as “passive tendon elongation”. The purpose of this study was to investigate the difference in mechanical properties between the two types of tendon elongation.

Methods. Experiment 1: The subject (n=8 men) was seated with the knee extended, and the ankle joint was attached to the foot plate at the right angles to the tibial axis, and performed 15 repetitive isometric ramp plantar flexions (up to 80% maximal voluntary contraction: MVC). During the experiment, we measured plantar flexion torque and the travel of muscle-tendon junction of the gastrocnemius medialis and Achilles tendon (MTJ) by ultrasonogram. Experiment 2: The subject (n=6 men) had his ankle dorsiflexed passively for 20 minutes in a supine position with the hip and knee extended. During the experiment, we measured passive plantar flexion torque, ankle joint angle, and the travel of MTJ.

Before and after experiment 1 and 2, the subject had his ankle dorsiflexed passively, to determine length changes in muscle-tendon complex (MTC), muscle and tendon. The travel of MTJ was assumed to be equal to the muscle elongation (dMus). The change of MTC length (dMTC) was estimated from changes in ankle joint angle. Tendon elongation (dTEN) was calculated by subtracting dMus from dMTC.

Results and discussion. Experiment 1: Contraction resulted in a shift of MTJ proximally during repetitive contractions. This result indicates that repetitive contractions induced tendon creep. Passive dorsiflexion showed no change in dMTC before and after contraction, but dMus decreased and dTEN increased.

Experiment 2: After passive dorsiflexion for 20 minutes, dMTC and dTEN increased, but dMus did not change. These results suggest that both active and passive tendon elongation resulted in changes in tendon mechanical properties, but that active tendon elongation decreased extensibility of muscle belly.