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Taija Finni

Muscle Mechanics During Human Movement Revealed by *In Vivo* Measurements of Tendon Force and Muscle Length

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Academic Dissertation

Neuromuscular Research Center,
Department of Biology of Physical Activity,
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Mammalle ja Papalle

Blessed in the man who finds wisdom,
the man who gains understanding.
Proverbs 3:13

ABSTRACT

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The present series of experiments utilized *in vivo* tendon force and fascicle length measurements for studying muscle mechanics during human locomotion. The behavior of quadriceps femoris and triceps surae muscle groups was examined in several different jumping exercises as well as during isokinetic knee and ankle extensions. In order to know how the muscle functions in natural locomotion as compared to its output during maximal constant velocity conditions, interaction between muscle and tendon lengths was studied. Special emphasis was given for understanding the benefits of pre-stretch in stretch-shortening cycle (SSC) of muscle function. The results suggest that there may be several interactive, task specific mechanisms that contribute to the enhanced performance in SSC exercises. Together with external loading conditions, the varying neural activity pattern sets the conditions for elastic energy storage and recoil by controlling the relative changes in muscle and tendon lengths. Greater activity level and force in a drop jump, for example, emphasize the role of elastic recoil from tendons as compared to a counter movement jump where also other mechanisms need to be acknowledged. Results from both submaximal jumps and maximal knee extensions suggest that enhancement may be related to length dependent behavior of muscle force. In addition to these mechanisms, contractile potentiation can have a role in SSC but may not be responsible for the major enhancement occurring in late concentric phase at high shortening velocities. Results from hopping with small knee-joint angular displacement suggest that there may be a particular frequency and jumping height at which the elastic bouncing is best utilized and at the same time the concentric phase is most economical. Results also support earlier observations that the economy of the shortening phase must be compromised at some point in order to produce more power and improve the jumping height.

Key words: *In vivo* tendon force, fascicle length, force-velocity, neuromuscular function, force enhancement, stretch-shortening cycle, locomotion

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not always taken the easy way. I have rode the roller coaster and made mistakes – but hopefully learned from them. You know that I am wise beyond my tears. I am ever grateful for your tireless efforts to aid my well-being.

LIST OF ORIGINAL ARTICLES

The present thesis is mainly based on the following papers, which will be referred to by their roman numerals. In addition, some data not presented in the papers are also included.

I Finni T, Komi PV and Lepola V 2000. In vivo triceps surae and quadriceps femoris muscle function in a squat jump and counter movement jump. Eur J Appl Physiol 83: 416-426.

II Finni T, Komi PV and Lepola V 2001. In vivo muscle mechanics during normal locomotion is dependent on movement amplitude and contraction intensity. Eur J Appl Physiol 85: 170-176.

III Finni T, Ikegawa S, Lepola V and Komi PV 2001. In vivo behavior of vastus lateralis muscle during dynamic performances. Eur J Sport Sci [Online]1,1. Human Kinetics and European College of Sport Science. http://www.humankinetics.com/ejss.

IV Finni T and Komi PV. Two methods to estimate tendinous tissue elongation during human movement. Submitted for publication.

V Finni T, Ikegawa S and Komi PV 2001. Concentric force enhancement during human movement. Acta Physiol Scand. In press.

VI Finni T, Ikegawa S, Lepola V and Komi PV. Comparison of force-velocity relationships of vastus lateralis muscle in isokinetic and in stretch-shortening cycle exercises. Submitted for publication.

CONTENTS

1 INTRODUCTION

Natural movement is an outcome from highly organized neuromuscular system that has a complex control mechanism. The control system behind the easy-looking locomotion requires information about the properties and the behavior of movement generating and transmitting tissues, that is, muscles, tendons and skeleton. Muscles are motors that produce force to propel our locomotion. They are controlled by the nervous system both by voluntary and by reflex commands. Besides neural activation, the generated force varies also with muscle length and velocity. Isolated animal experiments have provided fundamental knowledge of the relationships between force, length and velocity. Although these relationships are well established in conditions where the muscle is maximally activated, the submaximal and variable activity level makes it difficult to estimate the behavior of the muscle during our most natural locomotion, such as walking, running or jumping.

A counter movement that normally precedes fast and powerful movements in sports and normal locomotion was first called the "wind-up" movement by Asmussen and Sorensen (1971). Later, the phenomenon where the muscle undergoes stretching prior to shortening has been called stretch-shortening cycle (SSC) of muscle function (Norman & Komi 1979). Stretch-shortening cycle of muscle function has been studied extensively since the early work of Cavagna et al. (1965, 1968) who showed that shortening work is enhanced after stretch. The true nature of SSC is, however, not revealed in isolated conditions neither in animal nor in human studies. Gregor et al. (1988) showed, by comparing maximal isotonic loading and submaximal running in cats, that during natural locomotion the neuromuscular system could produce a higher force and power output than in maximal isometric or constant velocity conditions. The enhanced muscle output in SSC could be attributed to elastic mechanisms or contractile machinery itself, or it may result from varying neural activity with interaction of muscle and tendon compartments. In any case, there are several factors that interplay in SSC to achieve the economical, yet effective movements that are used every day. The SSC of muscle function in its beauty is purposeful and suited for the task at hand. The present thesis takes a step to comprehend the mechanisms acting in our bodies to serve this appropriate muscle function. This work is continuation to the earlier reviews and thesis work done at the Department of Biology of Physical Activity that deal with SSC muscle function (Aura 1985, Avela 1998, Bosco 1982, Horita 2000, Komi 1984, 1990, 2000, Kyröläinen 1995, Nicol 1992).

2 REVIEW OF THE LITERATURE

2.1 Muscle-tendon unit

The muscle is connected in series with tendon(s) that attach the entire muscle-tendon unit to the skeletal system. The term “muscle” often refers not only to the muscle fibers but is also used for the entire muscle-tendon unit (MTU). Here, the word “muscle” signifies a compartment that extends from a distal muscle-tendon junction to a proximal one. Capacity of a muscle to produce force or shorten at given velocity is dependent on muscle’s basic properties. Effectiveness of the produced force also depends on muscle architecture and joint design. Muscles create torque around the joints with interaction of tendons. Although tendon and aponeurosis are passive components, they cannot be considered purely rigid links between the skeleton and muscle because of their non-linear properties.

2.1.1 Skeletal muscle architecture

The filaments of the contractile system, actin and myosin, reside in a sarcomere overlapping each other. Interaction of these filaments generates force that is transmitted to tendons through serial and lateral force transmission (Huijing 1999, Monti et al. 1999, Patel and Lieber 1997, Young et al. 2000). Sarcomeres are arranged in series to form a single muscle fiber. Several muscle fibers in parallel form fiber bundles, or fascicles. However, not all the fibers within a fascicle have the same length and they may begin and end within the muscle fascicle itself (Ounjian et al. 1991, Young et al. 2000). Thus, fascicle length does not necessarily correspond to fiber length.

Arrangement of muscle fibers within a muscle into a parallel alignment or into a certain angle (i.e. pennation) in respect to the muscle’s force-generating axis has been well described in the literature (e.g. Gans 1982, Gans and DeVree 1987, Herbert and Gandevia 1995, Kawakami et al. 1993, Sacks and Roy 1982, Scott et al. 1993, Woittiez et al. 1985). The muscles in focus in the present study are the extensor muscles of the human lower limb. Muscles in both the quadriceps femoris (QF) and in the triceps surae (TS) muscle groups have pennate arrangements. Table 1 summarizes architectural features of these muscles. In a pennate arrangement, geometrically thinking, all the force produced by a muscle fiber is not transmitted to the tendon: the force in line with force-generating axis is the force produced by the fiber multiplied by cosine of it's pennation angle. The advantage of pennation is that the physiological cross-sectional area (PSCA) can be great. As a consequence, the force that the pennate muscle can produce is greater than that of paralleled muscles because PSCA and maximum force are proportional (Powell et al. 1984).

TABLE 1 Architectural features of soleus (SOL), gastrocnemius medialis (GM), gastrocnemius lateralis (GL), vastus lateralis (VL), vastus medialis (VM), vastus intermedius (VI) and rectus femoris (RF) muscles. The index number indicates reference: 1) Woittiez et al. 1985, 2) Wickiewicz et al. 1983, 3) Hoy et al. 1990 (vasti and gastrocnemius muscles are lumped). Note that these cadaver pennation angles can differ considerably from those found *in vivo.* E.g. Fukunaga et al. (1997a) reported VL pennation angles between 14 and 21°. For GM Kawakami et al. (1998) demonstrated angles up to 67° during maximal voluntary contraction.

	SOL	GM	GL	VL	VM	VI	RF
Muscle length (cm)	24.0_1	20.2_1	17.6_1	32.4_2	33.5_2	32.9_2	31.6_2
Fiber length (cm)	3.8_1	4.8_1	5.6_1	6.6_2	7.0_2	6.8_2	6.6_2
	2.4_3	4.8_3		8.4_3			8.2_3
Tendon length (cm)	27.0_3	42.5_3		22.5_3			41.0_3
Pennation angle (°)	25_1	20_1	20_1	5_2	5_2	5_2	5_2
	25_3	15_3		5_3			5_3
Tendon L / Fiber L ratio	11.3_3	8.9_3		2.7_3			5_3

Shortening velocity of a pennate muscle, on the one hand, is less than that of a paralleled muscle. In the pennate muscles, fiber rotation, i.e. increase in pennation angle, occurs simultaneously with shortening. This results in lower shortening velocity in the fiber level as compared to the whole muscle velocity. On the other hand, a pennate muscle that is designed for force production can produce high joint angular velocity if it has a small moment arm in the joint it acts on (Lieber 1992, Lieber and Fridén 2000). Energetically, for given fractional shortening, a paralleled fibered muscle consumes more energy but also performs more work than a pennate muscle (Roberts et al. 1998).

Fascicle length and orientation show rather large inter-individual variation. This variation may stem from differences in training background (Kawakami et al. 1993, Kearns et al 1998, Kumagai et al 2000) or from gender variability (Chow et al. 2000). Furthermore, pennation angle may not be the same along the length of a muscle (Scott et al. 1993). Therefore, the muscle fibers may not function uniformly. Similarly, non-uniform behavior of fiber segments or sarcomeres within a muscle fiber has been described (Edman and Reggeani 1984, Julian and Morgan 1979).

2.1.2 Series elastic component

Series elastic compliance is a property of multi-component system that includes muscle, tendon and aponeurosis (i.e. internal tendon) elasticity. Each of these components acts differently in relation with muscle force. Muscle’s compliance resides in the cross-bridges (Huxley and Simmons 1971), in filament lattice (Horowitz et al. 1986) and in connective tissue (Kovanen et al. 1984). Although a passive muscle can be strained more than a tendon or aponeurosis (Trestik and Lieber 1993), the tendinous tissue is responsible for majority of the elongation of MTU in active condition (Alexander and Bennet-Clark 1977, Herbert and Crosbie 1997, Morgan et al. 1978). Furthermore, in pennate muscles, angulation of muscle fibers with line of force-generating axis introduces an extra compliance in the MTU.

Tendon consists of collagen and elastin embedded in a proteoglycan-water matrix. Tropocollagen molecule cross-linking and complex collagen fibril arrangement form a buffer medium against high forces the tendons are exposed to during movements (Józsa & Kannus 1997). Unloaded, the collagen fibers have a wavy configuration that gives rise to the toe region of the stress-strain relation of tendons. In this concave toe region, little force is needed to elongate the tissue. Continued stretch requires more force as the tendon becomes stiffer. Stiffness increases with tendon cross-sectional area and with decreasing tendon length (Butler et al. 1978). Tendons have been suggested to bear strains as high as 20 and 50% (Józsa & Kannus 1997) although usually strain levels below 10% are reported (Benedict et al. 1968, Hawkins and Bey 1997, Trestik and Lieber 1993). In physiological levels of loading tendons are reported to strain less than 3 % (Simonsen et al. 1988).

Tendons are strong with tensile strength up to 11 $kN\cdot cm^{-2}$, a value that has been measured during running (Komi et al. 1992). The tendons of the extensor muscles are considered stronger than the flexor tendons (Benedict et al. 1968). For major extensors in the human lower limb, the patellar tendon is straight originating from distal tip of patella and inserting to tuberositas tibia. The Achilles tendon twists up to 90° in medio-posterior direction as it decends towards insertion site in the calcaneus. Pattern of fusion of gastrocnemius and soleus tendons can vary dramatically between individuals (Jozsa & Kannus 1997). These factors together with differential muscle contributions may be sources for non-uniform stress distribution that has been implied in Achilles tendon injury etiology (Arndt et al. 1998).

Tendinous tissues are viscoelastic with hysteresis, creep and force-relaxation properties (Butler et al. 1978). Tendon alone is mostly elastic as velocity of length change is predominantly determined by the rate of force development (Huijing 1992). In MTUs that have majority of connective tissue in internal tendon, the effects of viscosity on muscle fiber length change can be marked (Lieber et al. 2000). Aponeurosis has been reported to strain similar amount than the thick tendon (Trestik & Lieber 1993) or to strain more than the tendon (Lieber et al. 2000). Lieber et al. (2000) demonstrated that both the tendon and aponeurosis experience different amount of strain if loaded passively or actively. Furthermore, aponeurosis can experience different amount of strain along the MTU (Maganaris & Paul 2000, Magnusson et al. 2001, Zuurbier et al. 1994) although opposite results have also been published (Muramatsu et al. 2001).

Magnitude of series elasticity in MTU can be evaluated using tendon length-to-muscle fiber length ratio (Zajac 1989). In the triceps surae muscle the muscle fibers are relatively short in relation to their tendons. Thus, soleus and gastrocnemius MTUs having large ratios can be considered compliant whereas the knee extensor MTUs are stiffer (Table 1). These ratios reflect muscle function, for example the triceps surae MTU acts as effective energy storage during running and jumping (Alexander and Bennet-Clark 1977, Fukashiro et al. 1995b). It has been shown that the amount of series elastic compliance can affect the internal energetics of muscle contraction (Ettema 1996b). Furthermore, tendons can have different dimensions, Young's modulus and moment arms that influence movement efficiency (Voigt et al. 1995a). Compliance of MTU is affected by immobilization (Kubo et al. 2000), fatigue (Kubo et al. 2001a), exercise (Pousson et al. 1990, Cornu et al. 1997), stretching (Kubo et al. 2001b), and can have effects on spindle function (Rack et al. 1983).

Elastic elements can store substantial amounts of energy. Although many researchers using *in situ* muscle preparations have emphasized elasticity in active cross-bridges (Cavagna 1977, Goubel 1987, Huxley and Simmons 1971, Rack and Westbury 1974), studies have shown that tendinous tissue is responsible for majority of the elongation of MTU (Herbert and Crosbie 1997, Morgan et al. 1978, Roberts et al. 1997). Alexander and Bennet-Clark (1977) reported that tendons can store 5-10 times more elastic strain energy than muscles in human running. The amount of stored energy depends on the magnitude of force and amplitude of stretch in the tendon. When cross-bridge elasticity is considered, amplitude and velocity of the stretch affect the attained force (Edman et al. 1978). In addition, different animal fiber types (slow or fast twitch fibers) have different elastic properties, slow fibered muscles being stiffer (Goubel & Marini 1987). When the force is released and the muscle is allowed to shorten, the energy is recoiled. In natural locomotion, utilization of the recoil energy depends on the magnitude of force prior to shortening, time delay between lengthening and shortening, and timing of activation and relaxation of the contractile apparatus (Aura & Komi 1987, Bosco et al. 1981, 1982a, 1982b, Ettema 1996b, Lou et al. 1999). Besides elastic energy storage, tendons have important effect on muscle fiber length and velocity. Compliant tendons act as a buffer decreasing strain in the muscle and allow muscles to work in high force and low velocity region of the force-velocity relationship (2.2.4) (Lieber et al. 1992).

2.2 Muscle function

2.2.1 Neural input to muscle

A volley of nervous impulses that reaches a muscle is created in the central motor system and is modified by sensory information. Voluntary activity is supplemented with feedback information from muscles, tendons and joints through proprioceptive reflex system. This information is required for adjusting the motor program to fit to the task at hand and to associate environmental factors. Pre-programmed neural activity that is delivered to muscle before the actual movement, and motor control strategy are important for purposeful locomotion with SSC of muscle function (Melvill Jones & Watt 1971, Moritani et al. 1991). In hopping, for example, α-motoneurone pool excitability is enhanced just before touch down and in the early phase of the contact (e.g. Dyhre-Poulsen et al. 1991). Consequently, incoming commands through voluntary and reflex pathways are efficiently delivered to the muscle to enhance the system stiffness to compensate upcoming yielding upon ground contact (Cordo & Rymer 1982, Dyhre-Poulsen et al. 1991, Moritani et al. 1990, Voigt et al. 1998). The stretch reflex response activated via muscle spindle afferent discharge has important role in stiffness regulation (Nichols & Houk 1976) that has consequences on force and elastic mechanisms during SSC (Morgan et al. 1978). The reflex response has been shown to be sensitive to loading conditions (Komi & Gollhofer 1997) and training background (Kyröläinen & Komi 1995). Electromyographic activity (Dietz et al. 1979), muscle stiffness (Hoffer and Andreassen 1981) and the entire SSC performance are dramatically reduced without an active reflex system (Kilani et al. 1989).

When the action potential reaches the muscle and causes excitation-contraction coupling, there is a delay before force is developed. This electromechanical delay has been reported to be around 40 or 14 ms when the force is measured from external device or using tendon force transducers (Norman & Komi 1979, Nicol and Komi 1998, respectively). The delay includes activation process with calcium dynamics and cross-bridge function, and time spent for internal organization of muscle and tendon lengths (Zajac 1989). There is also a delay between the neural excitation ceasing and the force falling to zero. Activation and relaxation times are related to fiber types; fast twitch fibers have shorter rise time and shorter half-relaxation time than slow fibers (Gydikov et al. 1976). In several studies, activation and deactivation dynamics have been discussed as determining factors for optimal power and work production (Askew & March 1998, Curtin & Woledge 1996, Ettema 1996b, Lou et al. 1999).

2.2.2 Types of muscle actions

Once the muscle is activated, it produces force through cross-bridge function (for reviews see HE Huxley 1969 and AF Huxley 2000). The type of muscle action that results from the developed tension depends on the external forces. When the ends of the muscle are prevented from drawing closer together, the action is isometric. In many human studies, however, the term isometric is used when there is no information about the change in muscle fiber length, but the muscle-tendon unit length or the related joint angles remain unchanged. If the “isometric” action is tested by keeping the joint angles constant, the muscle does, in fact, shorten because the developed tension lengthens the tendinous tissues. During free movements, the tendon interaction and varying activity level may cause the muscle action to be isometric although the joint angles do change (Hof et al. 1983).

Dynamic actions involve changes in muscle length. In concentric action, the muscle shortens and in eccentric action the muscle lengthens. In human studies concentric and eccentric muscle actions are often examined in constant velocity or “isokinetic” movements (e.g. Komi 1973). It must be noted, however, that in common isokinetic exercises the shortening or lengthening velocity of the muscle is not constant, although the joint angular movement is (Ichinose et al. 1997).

Natural locomotion rarely involves pure forms of isometric, concentric or eccentric actions but is combination of these. An eccentric action that is immediately followed by a concentric one is called stretch-shortening cycle (SSC). Initially, it was used when MTU was observed to stretch and shorten without information about changes in muscle fiber length (Norman & Komi 1979, Komi 1984). The term SSC is commonly used in both of these levels. However, it is important to notice that force enhancement and contractile potentiation phenomena related to SSC require that the muscle is active during the lengthening phase. In the following concentric phase the output may be more powerful than the outcome from pure concentric action. This stretch-induced performance enhancement has been studied extensively after Cavagna et al. (1965, 1968) suggested potential mechanisms for work enhancement in isolated muscles and in intact human elbow flexors (see 2.3.2).

2.2.3 Length dependence of force

Tension developed by a muscle varies with its length. The isometric force-length relationship, obtained during maximal activation at variety of muscle lengths, shows that the greatest forces can be produced at lengths in the middle of the range, where the overlap between actin and myosin filaments allows maximum number of cross-bridges (Fig. 1A). The original study of force-length relationships by Gordon et al. (1966) was performed with isolated segments along single muscle fibers and the curve was made up of four linear segments. Later, the relationship has been shown to be more bell-shaped than polygonal (Edman & Reggeani 1987) and the shape is similar if measured in the level of sarcomere, fiber bundle or entire muscle-tendon unit (Cavagna et al. 1968, Ettema 1996a, Meijer et al 1997). Increased compliance within the muscle shifts the relationship to longer lengths (Lieber et al. 1992, Kawakami & Lieber 2000). For MTU an additional compliance has the same effect. The shift is present also after damaging eccentric exercise both in animal and human MTUs (Whitehead et al. 1998, 2001). In compliant units it is hypothesized that the muscle fibers work at ascending (shorter end) limb of the MTU force-length relationship (Zajac 1989). Also, if the force-length relationship is derived using submaximal activation, the optimum length at which the greatest force can be produced locates at longer muscle lengths (Ichinose et al. 1997, Rack & Westbury 1969, Stephenson & Wendt 1984).

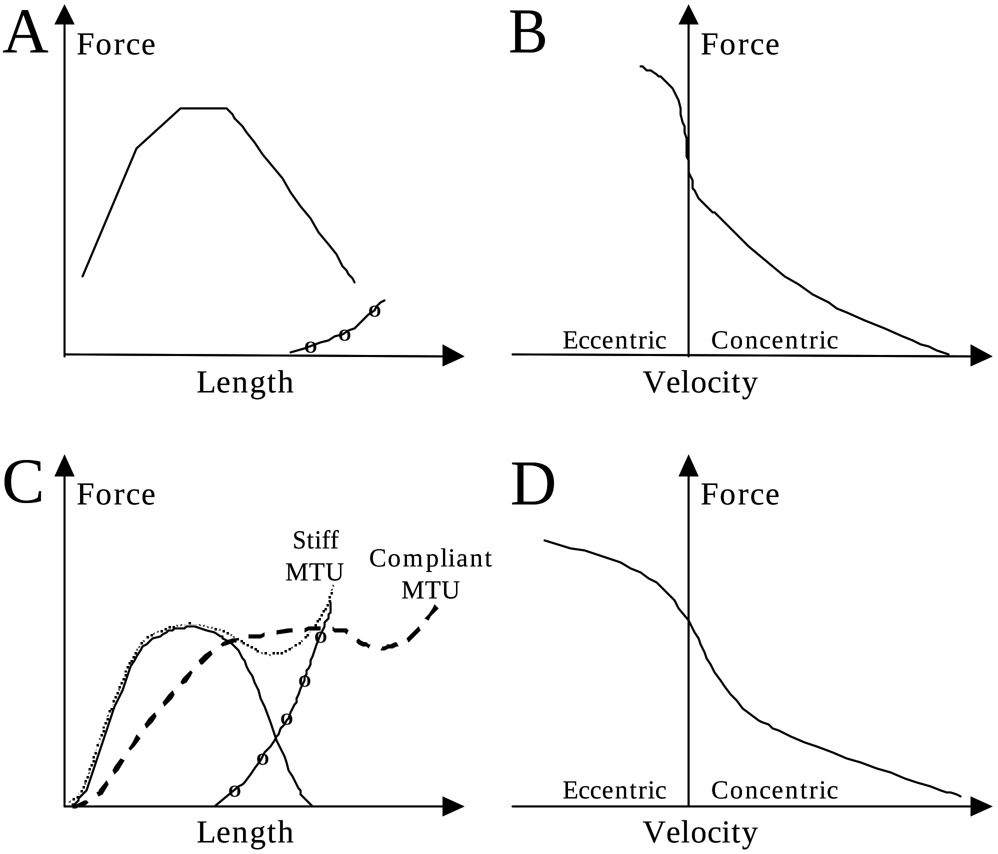

FIGURE 1 Force-length (left) and force-velocity relationships (right) of isolated muscle fibers (top) and of intact human muscles (bottom). A) Maximum tetanic tension (solid line) and resting tension (line with circles) as a function of sarcomere lengths of an isolated skeletal muscle fiber (drawn after Edman 1979). B) Classic force-velocity relationship in a single frog muscle fiber expresses a double hyperbolic shape during shortening. Near maximum isometric force the shortening velocity is very low and provides stability within the contractile system (drawn after Edman 1988). C) Force-length curve of an intact, active muscle (solid line) and passive muscle-tendon unit (line with circles). Total force-length curve of a muscle-tendon unit is shown (dotted line). In a compliant MTU (dashed line) the curve is distorted to the right as compared to a stiff MTU (drawn after Zajac 1989). D) In intact human muscles the classical force-velocity relationship is normally obtained by allowing lengthening the muscle or allowing it to shorten at constant velocity (Abbot et al. 1952, Hill 1938). Then, the force value is taken at a given muscle length in each condition. In intact muscle the curve differs slightly from the shape recorded from single fiber (drawn after Komi 1973).

Passive tension of muscle has reported to comprise the sum of tensions from passive elements within and between muscle fibers, from a viscous resistance to filament sliding, and from cycling cross-bridges (Bartoo et al. 1997, Proske & Morgan 1999). In the entire MTU the passive tension comprises also tendon and aponeurosis, although the muscle compartment strains the most when MTU is being lengthened (Trestik and Lieber 1993) (Fig. 1).

Muscle fiber length at macroscopic level reflects the number of sarcomeres in series along the fiber. Thus, long fibers have more sarcomeres in series. The number of sarcomeres adapts to inactivity (Williams & Goldspink 1978) or eccentric training (Lynn & Morgan 1994); consequently, the operating range in the force-length curve may be relatively constant. Recently, Burkholder and Lieber (2001) have reviewed ranges of lengths of sarcomere in different species and muscles. They concluded that there is no typical length range at which the sarcomeres function. For human muscles, the wrist extensors have been reported to operate at short lengths (Lieber et al. 1994) and VL sarcomeres have been suggested to operate in the ascending limb and in the plateau region of the relationship (Cutts 1989).

In a muscle-joint system, the relative fiber length-to-moment arm ratio is the major determinant of the shape of the isometric torque-angle curve (Lieber & Shoemaker 1992). In the human triceps surae muscle, the most important determinants have been shown to be slack length of the series elastic elements, mean moment arm, maximum force, and fiber length (Out et al. 1995). A muscle with large moment arm length (i.e. length of a vector from the axis of joint rotation to a point in the line of action of the muscle where a straight angle forms) can produce greater moment with smaller excursion than an identical muscle with a small moment arm (Lieber & Friden 2000). The moment arm length changes during joint rotation and it may not be the greatest at optimum muscle length. Consequently, the muscle force-length and joint moment-angle relations do not coincide (Gillard et al. 2000, Hoy et al. 1990, Lieber et al. 1997). In a system where several muscles act as synergists, the interrelationships between the highly specialized muscles reveal the advantage of having variable fiber lengths, moment arms and architectures between the muscles; from a mass point of view it is more efficient to have several muscles than one large muscle for production of force and excursion (Lieber et al. 1997, Lieber & Friden 2000).

2.2.4 Velocity dependence of force

The force that a muscle can produce is dependent on the velocity of its length change. The relationship between muscle force and shortening velocity was first studied by Lewin and Wyman (1927) and is generally expressed with rectangular hyperbola formulated by Hill (1938). In eccentric actions the force that a muscle can generate is greater than in concentric or isometric actions. The classical relationship shown in figure 1 has been obtained by allowing fully activated muscles to change their length at constant speed. The shape of the relationship is similar if single muscle fiber (Edman et al. 1978, Julian & Morgan

1979), isolated muscle (Hill 1938) or intact muscle groups have been examined (Komi 1973, Tihanyi et al. 1982, Wilkie 1950).

The energetic cost of shortening (positive work) has been found to be greater than that of lengthening (negative work) by measuring oxygen consumption (Abbot et al. 1952, Asmussen 1952, Bigland & Lippold 1954) or ATP synthesis (Ryschon et al. 1997). It has been suggested that an active cross-bridge, when lengthened, may be able to perform multiple cycles without splitting more than one ATP molecule for energy (Lombardi et al. 1992). Another reason for high efficiency of eccentric work may be attributed to the stretch-induced force enhancement phenomenon (see 2.2.5).

The classical force-velocity curve when measured with constant tetanic stimulation (animal studies) or maximal voluntary activation (human studies) is a good measure of the maximum sustainable power output of a muscle. However, it does not give a realistic measure of the instantaneous power of a muscle nor the work available through a full contraction-relaxation cycle under natural conditions the muscles normally operate (Josephson 1993). Both the force-length (2.2.4) and force-velocity relationships have very different shapes during natural locomotion. This is because during movements, muscles act with constantly varying length and velocity. Furthermore, as the force changes continuously, also the length of series elastic element varies and interacts with shortening or lengthening of the muscle (see 2.3).

2.2.5 History dependence of force

Previous shortening and lengthening have an effect on muscle’s force generating capacity. An active stretch increases isometric force generating capacity (Edman et al. 1978). Force enhancement during and after the stretch has been studied extensively (see Morgan 1994, Noble 1992, Brown & Loeb 2000). The enhancement, being pronounced at long muscle lengths, has been attributed to altered cross-bridge function or sarcomere inhomogenieties (Edman et al. 1978, Edman 1999, Julian and Morgan 1979, Morgan 1990, Sugi & Tsuchiya 1988). However, the intrinsic mechanisms underlying the force-enhancement phenomenon are not known.

Actively shortening muscle loses temporarily part of its contractile strength (Herzog & Leonard 1997a, Meijer et al. 1997). The magnitude of force depression increases with shortening distance, the phenomenon being greatest at short muscle lengths (Edman 1980). In intact muscles, the initial rapid fall of force at the beginning of shortening is generally believed to result from unloading of the series elastic component while the basic mechanism of force depression has been attributed to several factors including sarcomere non-uniformities (Edman et al. 1993, Herzog & Leonard 2000).

In force enhancement and depression phenomena, both short- (transient) and long-lasting (residual) components have been described. The significance of these components to locomotion *in vivo* is controversial. While the transient force-enhancement may be too short to play a role *in vivo*, some believe that residual component may enhance the SSC performance (Edman 1997) although others suggest this mechanism to have negligible effects (Brown & Loeb 2000). Usefulness of the phenomenon described by Cavagna and Citterio (1974) with increase in muscle compliance and consequent release of potential energy after stretch, has also been questioned as a potential mechanism to be operative in whole body system *in vivo* (Lensel & Goubel 1987, Goubel 1987). In any case, literature suggests that a small and rapid stretch of muscle fibers may be most effective in natural movement with SSC of muscle function (Bosco et al. 1981, Ettema et al. 1990, Komi & Gollhofer 1997).

Passive muscle tissue has also history dependent behavior, called thixotropy (Cambell & Lakie 1998, Proske et al. 1993, Proske and Morgan 1999). Thixotropy refers to the dependence of stretch responses on the immediate history of contraction and length changes. Especially, at intermediate muscle lengths a resting muscle can be either slack or taut depending on the previous history of contraction and length changes. The presence or absence of slack (i.e. looseness) can have dramatic effect on the following tension development in subsequent phase of movement. For example, slack may be introduced by contracting a muscle at a long length, and then letting a relaxed muscle to shorten to a test length. Effects of slack can be removed by activating the muscle after the test length has been reached (Proske et al. 1993, Whitehead et al. 2001).

2.3 *In vivo* muscle mechanics during locomotion

2.3.1 *In vivo* muscle function

Direct measurement of muscle forces during locomotion was made possible after Salmons (1969) first introduced the buckle-type force transducer. Later, the method has been applied to both animal (e.g. Gregor et al. 1988, Walmsley et al. 1978, Whiting et al. 1984) and human experiments (e.g. Fukashiro et al. 1993, Gregor et al. 1991, Komi et al. 1984, Komi et al. 1987, Komi et al. 1992, Nicol & Komi 1999). Studies using direct recordings of tendomuscular forces have provided important insights into function of a particular muscle, functional adaptation to variable conditions (Biewener & Gills 1999, Komi et al. 1992), load sharing between muscles (Herzog et al. 1994), role of elastic energy (Gregor et al. 1988, Roberts et al. 1997) and neural control of locomotion (Walmsley et al. 1978). However, accurate assessment of mechanical power output of a muscle requires also direct measurement of muscle length during movement. Sonomicrometry technique developed by Griffiths (1987) has been adopted for animal studies for muscle fiber length measurements, while B-mode ultrasonography has been applied in human studies (e.g. Fukunaga et al. 1997a, 1997b). Simultaneous *in vivo* force and length measurements have been performed e.g. in running turkeys (Roberts et al. 1997) and in flying pigeons (Biewener et al. 1998). The detailed animal studies have contributed to the current knowledge that the muscles are not only motors but also can act as brakes, springs and struts (Dickinson et al. 2000).

In situ and *in vitro* studies using cyclic length changes and variable stimulation cycle have revealed important aspects on efficiency (Barclay 1994, Josephson 1993, Curtin & Woledge 1996) and pre-stretch potentiation (Ettema et al. 1992, Takarada et al. 1997b). In these studies, it has been possible to vary systematically the input and work output of a muscle and use combinations that are close to function *in vivo.* A study on mouse muscles has shown that a soleus muscle yields a higher power output but consumes less energy than does an extensor digitorum longus that is a fast twitch muscle (Barclay 1994). This is because the energetic cost is relatively insensitive to the muscle’s mechanical performance and because each cross-bridge cycle consumes one ATP (adenosine triphosphate). Therefore, efficiency of the muscles having slow twitch fibers may be high in cyclic movements due to the fact that their cross-bridges perform fewer cycles than do those in fast twitch muscles. Curtin and Woledge (1996) have shown that the briefest stimulation (twitch) gave the highest efficiency in sinusoidal movement. Maximum power, however, required longer duty cycles. These results give support to the notion that optimizing conditions for power production compromises efficiency. Lou et al. (1999) showed that a substantial fraction of external work is done by the series elastic component in the late push-off phase when the shortening of a muscle occurs during relaxation. Indeed, in natural locomotion, the muscular activity often decays before the end of push-off phase (Fukashiro et al. 1995b, Kyröläinen et al. 1999). As pointed out by Hof et al. (1983), a natural submaximal activation pattern is probably crucial for optimal muscle-tendon performance where elastic energy is effectively utilized. The effective use of elastic recoil energy requires, however, that the relaxation and force decrease must occur in such way that the contractile element remains strong enough to maintain its length or even shorten (Ettema 1996b) as shown in running turkeys (Roberts et al. 1997).

During walking in cats, medial gastrocnemius muscle fibers have been reported to shorten despite stretch of the MTU (Griffiths 1991). In human high load hopping spindle shortening during MTU lengthening has been modeled in gastrocnemius but not in soleus muscle that behaved similarly as the entire MTU (Voigt et al. 1998). These results have raised questions about muscle spindle function. Because muscle stretch is a major stimulus for spindle activation, how the reflexes could be operative if the muscles do not lengthen *in vivo*? Herzog and Leonard (2000b) have suggested that while the muscle fibers may be shortening in cat gastrocnemius muscle, the soleus muscle may be a better indicator for muscle spindle length changes. As the soleus is a postural muscle, the suggestion put forward by the authors that the ankle extensor reflex responses may be dominated by signals from soleus the GA responses having a secondary role (Herzog & Leonard 2000b), seems reasonable. On the contrary to the result from the cat study (Griffiths 1991), a recent report on human walking where gastrocnemius muscle lengths were measured with ultrasonography showed that changes in fascicle length were in the same direction as in MTU, but showed a little time shift and a considerable difference in the magnitude of length change (Fukunaga et al. 2001). These observations remind that there may be several different behaviors that may be species, muscle or task dependent; function of one muscle may not be generalized to cover other muscles even if they are agonists.

2.3.2 Human movement studies

In majority of human experiments, direct measurement of muscle force or length is not possible. Consequently, forces have been estimated using EMG-to-force processing, optimization or inverse dynamics with anatomical measurements (e.g. Hof et al. 1983, Prilutsky & Zatsiorsky 1994, Spägele et al. 1999, Voigt et al. 1998, Winters & Stark 1988). Muscle lengths have been obtained from kinematic recordings with application of models to predict tendomuscular length changes (e.g. Grieve et al. 1978, Hawkins & Hull 1990). Models are valuable but their utility depends on accuracy of their various components. Considering the properties of muscle, limited data of *in vitro* or cadaver studies is often applied in the models. Only in few studies comparisons between estimated and measured tendomuscular forces have been made (Fukashiro et al. 1993, Gregor et al. 1991). These studies have pointed out the possibility for overestimation of Achilles tendon forces using joint moment calculations during cycling and vertical jumping. Thus, direct measurement of tendomuscular loading provides a greater understanding of muscle function during natural movement. In addition, combination of tendomuscular force recordings simultaneously with fascicle length measurements by ultrasonography (e.g. Fukunaga et al. 1997b) provides tools to examine also output of a muscle during human locomotion. The following discussion focuses on different aspects of jumping exercises that were also used in the series of experiments in this thesis.

Standing jumps with and without a counter movement have been widely explored both experimentally (e.g. Asmussen & Bonde-Petersen 1974, Komi & Bosco 1978, Gollhofer et al. 1992, Fukashiro et al. 1995) and by computer simulations (e.g. Pandy & Zajac 1991, Bobbert et al. 1996). These studies have shown that a counter movement with SSC of muscle function enhances performance. The enhancement has been attributed to increased myoelectrical activity with reflex action (Bosco et al. 1982a), recoil of elastic energy (Komi & Bosco 1978, Fukashiro et al. 1995), the time available for force development (Bobbert et al. 1996), a high force at the end of the stretching phase (Zajac 1993) and contractile element potentiation (Walshe et al. 1998). Although counter movement jump produces higher jumping height than squatting jump, it cannot be considered as an efficient SSC exercise. This is because the impact load and activity levels during the downward phase are quite low, and because the transition between stretching and shortening takes relatively long time (Komi & Gollhofer 1997). The possibility of storing and utilizing mechanical energy by muscles exists in exercises where the contracted muscles are forcibly stretched immediately before shortening. Consequently, the storage and release of mechanical energy depends greatly on the type of movement (Gavagna

1977). Therefore, drop jump and repetitive hopping performances, for example, are very different as compared to counter movement jump for the purpose of studying potentiation mechanisms in SSC type exercise.

Neuromuscular behavior in bouncing jumps has been extensively studied in search for mechanisms of movement control (Moritani et al. 1991, Voigt et al. 1998), role of elasticity in locomotion (Fukashiro et al. 1995b, Komi & Bosco 1978, Voigt et al. 1995b), and neuromuscular adaptation to variable conditions (Avela et al. 1994, Gollhofer and Kyröläinen 1991, Farley et al. 1998). In hopping, the impact loads and tendomuscular forces are higher than in counter movement jump enabling greater amount of elastic energy to be stored (Fukashiro et al. 1995b). Use of elastic energy may be related to sex (Komi & Bosco 1978), fiber type in the predominantly used muscles (Bosco et al. 1982) or movement amplitude (Thys et al. 1975). The smaller the movement amplitude during the ground contact, the better the elastic energy may be utilized in order to improve the efficiency of positive work (Thys et al. 1975). Furthermore, an effective multi-joint movement requires well-timed pre-activation and precise timing between agonist and antagonist muscles (Gollhofer & Kyröläinen 1991). High activity bursts via reflex system after a stretch of an activated muscle can enhance muscle stiffness, and consequently, affect elastic mechanisms (Gollhofer et al. 1984, Horita et al. 1996, Kyröläinen et al. 1990). Possibly, a stiff muscle in series with a compliant tendon would be most beneficial for utilization of elastic energy (Hof et al. 1983). Hopping frequency can also affect the use of elastic energy. Farley et al. (1991) observed that when subjects hopped with high or preferred frequency, the body behaved in a springlike manner. At low frequency of hopping the utilization of elastic energy was reduced because of longer contact time. Farley et al. (1991, 1998) have further shown that changes in hopping frequency are attained by altering leg stiffness, and especially the ankle joint stiffness. It must be noted that frequency in hopping experiments has been calculated in two ways. Farley et al. (1991) have used resonant period determined from contact time while Melvill Jones and Watt (1971), for example, have reported frequency as hops per second.

During locomotion, a special feature of biarticular muscles is that they may function as a transfer system for energy rather than as work generators. Winters and Stark (1988) showed with their model that gastrocnemius could both start fast movements and store elastic energy, and demonstrated task dependent function of synergistic plantarflexor muscles. Human gastrocnemius has been reported to function as energy transfer between the knee and ankle in jumping although the direction of power delivery has been debated (Bobbert & Ingen Schenau 1988, Pandy & Zajac 1991, Prilutsky & Zatsiorsky 1994). Furthermore, Pandy and Zajac (1991) concluded that an important contribution from gastrocnemius muscle to the jumping performance did not come through unique biarticular function of the muscle while Soest et al. (1993) challenged this point of view. These controversies have resulted from differences in modeling methods, which further stresses the importance for more direct measurements of musculotendinous mechanics during locomotion.

3 PURPOSE OF THE STUDY

In vivo muscle function has been studied both in isolation and during locomotion. Animal studies have provided fundamental information about basic dependencies and behavior of the muscle (e.g. Gordon et al. 1966, Hill 1938). Most of these experiments are done using constant or maximal activation that rarely occur during natural locomotion. Human studies with *in vivo* tendon force measurements have benefited from advances in measuring techniques. An invasive buckle-type tendon force transducer (Komi et al. 1984, Komi et al. 1987, Komi 1990) has recently been replaced by less invasive optic fiber force transducer that provides an instrument for routine experiments (Komi et al. 1996, Arndt et al. 1998, Finni et al. 1998). By combining the novel optic fiber method for tendon force measurements and ultrasonographic imaging for fascicle length determination the conventional force, electromyographic and kinematic recordings together with modeling provide unique combination of tools to study muscle function in human movement. The purposes of the present study can therefore be outlined as follows:

1) Usually, forces produced by individual muscles or muscle groups, and length changes in muscle-tendon unit have been estimated in human movement studies (Hof et al. 1983, Bobbert et al. 1986, Gollhofer et al. 1992). Combination of direct measurement of tendomuscular forces and fascicle lengths can provide unique information about muscle function in humans. Therefore, the general aim was to describe tendomuscular loading patterns and to examine how the basic force-length and force-velocity relationships occur in natural locomotion (I, II, III, V, VI).

2) The second purpose was to examine how the muscle function differs between different jumping types and how the neuromuscular function is modified when the performance is altered (I, III). More specifically, effects of contraction intensity and magnitude of MTU

length change on relative loading and muscle input-output ratio in the triceps surae and quadriceps femoris muscles were studied (II).

3) Tendons do not act as simple force transmitters, but they interact with the muscles they are attached to. Compliance of tendinous tissue can modify the operating length and velocity of the muscle and, consequently, affect force production. Therefore, it is of interest to study changes in tendinous tissue length during human movement. The purpose was to utilize tendomuscular force and fascicle length measurements for estimating length changes in different compartments of MTU. Two different approaches were tested for estimating the tendinous tissue length change (I, IV).

4) Muscle fascicle length may be assumed to reflect changes in the muscle fiber level. It has been shown in animals that change in muscle fiber length may not correspond to those in the MTU (Griffiths 1991, Roberts et al. 1997). Therefore, muscle fascicle behavior during natural human movement was examined and compared to changes in MTU length (III, IV, VI). Furthermore, changes in fascicle length in vastus lateralis muscle were studied in controlled eccentric and concentric knee extension movements. It was hypothesized that the changes in fascicle and MTU lengths would be in the same direction although the magnitude of velocities would be different (V, VI).

5) Enhanced concentric performance after stretch has been attributed to the use of elastic energy, myoelectrical potentiation with reflex contribution (Bosco et al. 1981 1982), to the enhanced force after stretching phase (Bobbert et al. 1996, Edman 1997, Takarada et al. 1997a), and to time-dependent activation mechanics (Bobbert et al. 1996). Although many of these mechanisms have been studied in detail in animal models, their role in locomotion *in vivo* remains unresolved. Therefore, the final aim was to investigate pure concentric and stretch-shortening cycle exercises for understanding the possible mechanisms contributing to the enhanced concentric performance in SSC (I, V, VI).

4 RESEARCH METHODS

4.1 Subjects

Total of 18 volunteers (7 women, 11 men) participated in this study and additional 6 subjects were involved in the pilot studies. Table 2 presents the physical characteristics of the subjects in each experiment that are reported in the original papers. The subjects had a heterogeneous background in physical activities, some being sedentary while few were national level top athletes. They were informed of the risks and benefits associated with the experiments and gave their written consent. The recommendations contained in the Declaration of Helsinki were followed. The use of the optic fiber force transducer in these studies was approved by the ethics committee of the Central Hospital of Central Finland.

TABLE 2 Mean (SD) of the physical characteristics of the subjects.

Experiment	1	2	3
Age (yrs)	26 (10)	28 (8)	27 (4)
Height (cm)	171 (7)	177 (10)	180 (7)
Body mass (kg)	70 (14)	70 (12)	75 (8)
Original paper	I, II	II	III-VI

4.2 Experimental design

4.2.1 Experiment 1 (I, II)

Four subjects performed squat jumps (SJ), counter movement jumps (CMJ) and hopping (HOP) on a force plate as normal bilateral performances. The same jumps were repeated unilaterally on a sledge ergometer (Kaneko et al. 1984) having an angle of 20.3° in respect to horizontal position (Fig. 2). In SJ and CMJ the jumping height was moderately increased after each effort but even the last performances were quite submaximal. The subjects practiced the jumps a day prior to actual measurements during which they were given feedback of the knee joint angular displacement. Purpose was to keep the minimum knee joint angle the same (120°; 180° being full extension) in SJ and CMJ. During HOP, amplitude of the knee joint angular displacement was 56°, and the subjects were free to choose their hopping height and frequency.

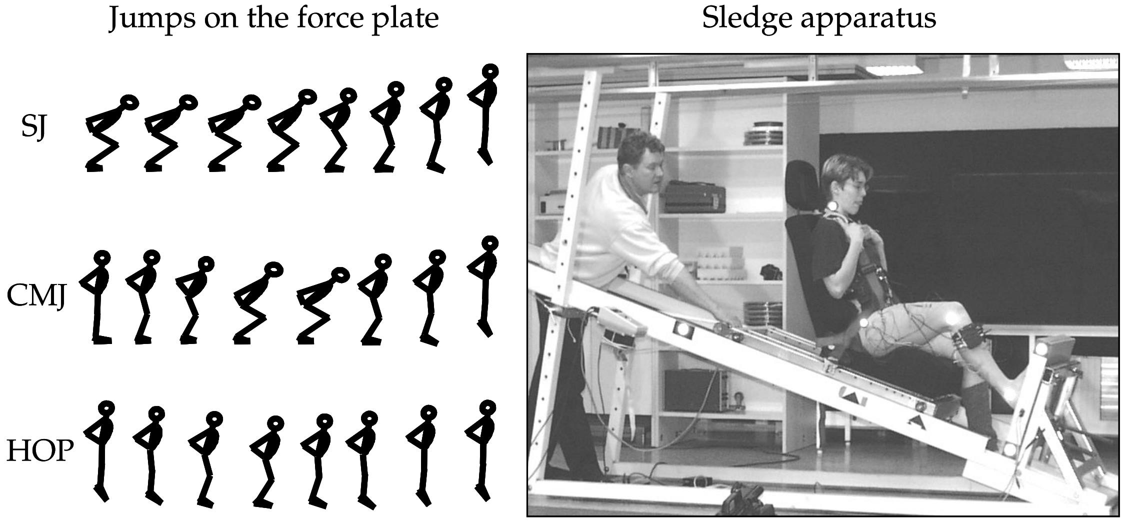

FIGURE 2 Schematic figure of the squat jump (SJ), counter movement jump (CMJ) and hopping (HOP) that were performed bilaterally on the force plate (left). On the right, a subject in the sledge apparatus during the actual measurements. The sledge-jumps were done unilaterally. A black box attached to the subject's shank is the optic fiber transmitter-receiver unit.

During the performances both Achilles (ATF) and patellar tendon forces (PTF) were measured *in vivo* with the optic fiber method (Komi et al. 1996, Arndt et al. 1998, Finni et al. 1998) (Fig 3). In addition, electromyographic activities (EMG), reaction forces and joint angular changes were recorded. Muscle-tendon lengths were calculated and Achilles tendon length changes were estimated with the method of Voigt et al. (1995a). Both Achilles and patellar tendon cross-sectional areas were measured using ultrasonography (Aloka SSD 280LS with 7.5 MHz linear array transducer). Thickness and width were measured from the images and the measures were used to calculate the cross-sectional area assuming the transverse section of the tendon is a regular ellipse (Kallinen & Suominen 1994).

Prior to the jumping maneuvers, maximal isometric plantarflexions were performed on an ankle ergometer (Avela et al. 1999, Nicol et al. 1996). Maximal knee extensions were measured with a knee extension device (Komi et al. 2000) (Fig. 3). In both cases, the performances were done with three different ankle and knee joint angles, respectively. Also, maximal concentric actions with constant joint angular velocity (i.e. isokinetic actions) were done in order to construct force-velocity curves for triceps surae (TS) and quadriceps femoris muscles (QF). The velocities used were 15, 20, 45 and 60°· s^{-1} (ankle) and 60, 120, 180 and 230°· s^{-1} (knee). During the movement with maximal voluntary contraction, a double twitch stimulus was delivered to tibial or femoral nerve approximately 60 ms prior to the angle of 90° or 120° at which the force value was taken for analysis, respectively. In a double twitch, two consecutive supramaximal stimuli were delivered to nerve with cathode (∅ 1.5 cm) over the tibial or femoral nerve, and the anode (5 × 8 cm) placed superior to the patella or over the hip, respectively (McKenzie & Gandevia 1991, Strojnik & Komi 1998).

4.2.2 Experiment 2 (II)

One subject performed repetitive bilateral hopping with large (56°) and small (23°) knee joint angular displacement on a force plate. In the small amplitude hopping the jumping height was gradually increased. In addition, four other subjects performed the small amplitude hopping protocol also. The subjects were free to choose their hopping frequency, contact time and target height. For the purpose of control the subjects were provided with visual feedback of their knee angular displacement. ATF, PTF, reaction force, EMG activities and kinematics were recorded during the performances similarly as in experiment 1.

4.2.3 Experiment 3 (III-VI)

Nine subjects were involved in experiment 3 that included isokinetic knee extensions and unilateral sledge jumps. First, the entire length of the vastus lateralis muscle was imaged using ultrasonography from all subjects. The purpose was to construct a picture of the whole muscle and evaluate accuracy of the estimation method used for fascicle length determination. Then, maximum isometric knee extension with five different knee angles (90, 120, 140, 160 and 175°) was measured in a knee extension device (Fig. 3). Maximal concentric and eccentric actions at three different velocities (60, 120 and 180°$\cdot$ s^{-1}) were performed in a random order. Also, passive and maximal eccentric-concentric actions at each velocity were recorded. Then, the subjects moved to the sledge apparatus where submaximal SJ, CMJ, repetitive CMJ and drop jumps (DJ) were performed (Fig. 2). The subjects were able to control their performance with visual feedback of the predetermined target height and lowest position.

In addition, four of the subjects had an optic fiber inserted into the patellar tendon on a separate day. They repeated the sledge performances after calibration procedure of the optic fiber force transducer in the knee extension device (Fig. 3).

In all performances, vastus lateralis fascicle lengths were imaged by ultrasonography, and EMG activities, forces and kinematics were recorded. Patellar tendon cross-sectional area was also determined by ultrasonography (Aloka SSD 2000) as done in experiment 1 for calculation of stress in the tendon.

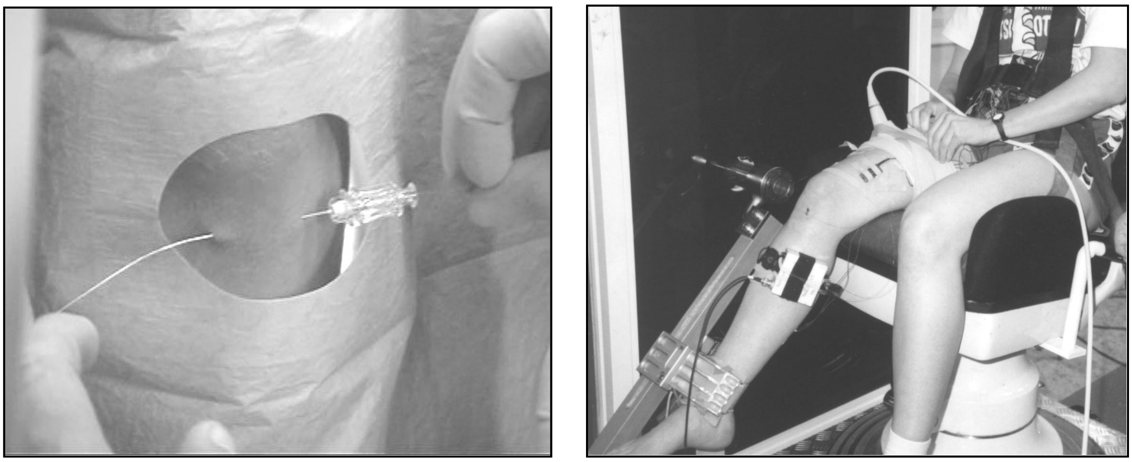

FIGURE 3 An optic fiber force transducer has been passed through patellar tendon with a help of a hollow needle (left). After the needle has been removed the fiber remains in situ. On the right, a subject is sitting in the knee extension device during calibration of the tendon force transducer. A little amount of blood is coming out of the insertion site near the patellar tendon. The tips of the fiber have been attached to the light transmitter-receiver unit that is fixed to the subject's shank. An ultrasound probe has been secured to the subject's thigh for fascicle length measurements. Knee extension force was measured with a strain gauge in the lever arm of the ergometer.

4.3 Recording procedures and analysis

4.3.1 *In vivo* force measurements

4.3.1.1 Optic fiber force transducer

Direct tendon forces from Achilles (I, II) and patellar tendons (I, II, III, IV, VI) were measured with an optic fiber technique (Komi et al. 1996). This method requires a light transmitter and a receiver, and a piece of an optical fiber that can be sterilized and used *in vivo*. In the present study, a light emitting diode (GaAlAs semiconductor, HFBR-1414, Hewlett Packard, USA) was used as a transmitter. The created light signal having wavelength of 820 nm was sent through the core of a two-layer optic fiber. In the other end of the fiber, the light signal was detected by a photodiode receiver (pin-type, HFBR-2414, Hewlett Packard, USA), converted into an analogue signal and sent further to a recording computer. Small size of the transmitter-receiver unit and the use of telemetry enabled the subjects to perform unrestricted movements with the force transducer in situ.

The use of the optic fiber as a transducer for tendomuscular forces is based on light intensity modulation occurring in a micro-deformable optical fiber (Bocquet & Noel 1987). When the two-layer fiber is compressed, the amount of light traveling through is reduced. Figure 4 illustrates how the light rays can leak out of the fiber core when it is not straight. The magnitude of reduction depends on fiber characteristics such as fiber diameter and minimum bending radii (Hecht 1993). During tendomuscular loading, tensile stress develops within the tendon fibers (Butler et al. 1978). This stress then compresses the plastic optic fiber inside the tendon and reduces the transmitted light. A linear relationship has been reported between an increasing loading of the tendon and the intensity of light passing through the optic fiber (Komi et al. 1996, Arndt et al. 1998) even in maximal voluntary contractions (Finni et al. 1998).

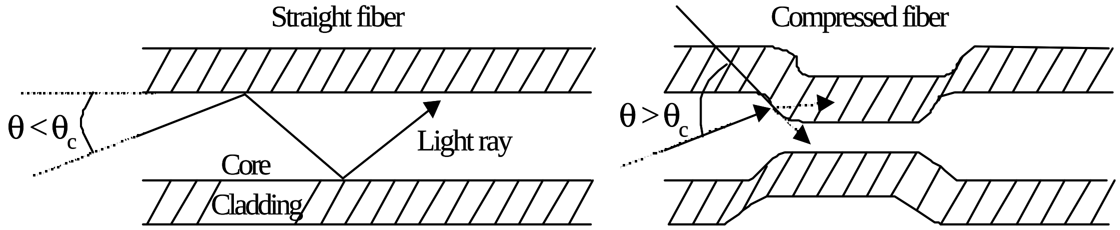

FIGURE 4 In a straight step index multimode fiber a light ray is trapped by total internal reflection within the fiber core provided that the angle θ is smaller than the critical angle θ_c. In a compressed or bent fiber the ray incidents on the interface at angle greater than θ_c and part of the light leaks out.

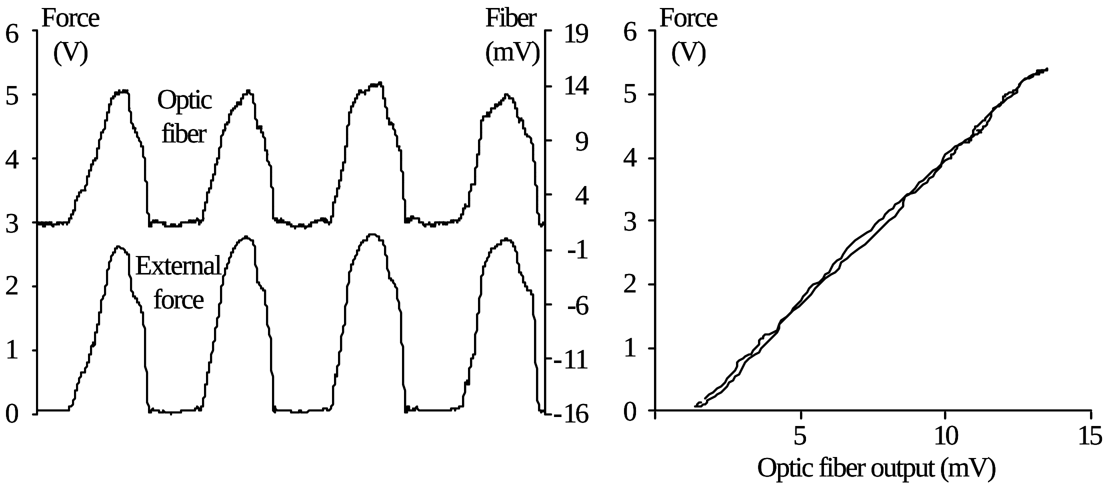

FIGURE 5 Responses of the optic fiber to dynamic loading was tested by compressing the fiber between calibration scissors. Hysteresis loop (right) obtained from dynamic loading-unloading cycles (left).

The optic fiber method has been tested both in animal preparations (Komi et al. 1996) and in human experiments (Arndt et al. 1998, Finni et al. 1998, Komi et al. 1995). Furthermore, the optic fiber behavior has been tested mechanically. Recordings during dynamic loading-unloading cycles are shown in figure 5. Hysteresis of the fiber output was found negligible.

In intact human tendon, movement of the skin during locomotion may cause artifact to the signal. By pulling the skin along the tendon near to the site of insertion of the optic fiber the magnitude of artifact was evaluated (I). During full ankle plantarflexion the potential artifact could be the greatest if the skin is folded around the Achilles tendon. This problem was not present in the patellar tendon.

The optic fiber used in this study had a polymethyl methachrylate core and a fluorinated polymer cladding with a diameter of 0.5 mm. Prior to use, the ends of the fiber were cut straight and smoothed carefully with sandpapers having surface roughness of 12, 3, and 0.3 microns. The fiber was then sterilized with ethylene oxide, aired for 24 hours and sealed to a sterile bag to be opened just before the insertion.

4.3.1.2 Insertion procedure

A pad covered with anesthetic cream containing lidocain-prilocain was kept over the insertion site at least one hour before the insertion of the optic fiber took place. In the Achilles tendon, the insertion site was approximately 3 cm proximal to the calcaneus. In the patellar tendon the site was in the middle of the tendon. During the insertion procedure, the subjects were either sitting or lying on their back depending on the most suitable condition for the protocol used. In spite of the different posture, ankle and knee joint angles were always secured to 90° and 120°, respectively.

Aseptic conditions were ensured during the insertion procedure. After removal of the anesthetic cream, the insertion site and the surrounding skin were cleaned carefully with antiseptic liquid. Then, a 19-gauge needle was passed through the tendon on a sagittal plane after which the optic fiber was threaded through the needle. By removing the needle, the fiber remained *in situ*. Then, tips of the fiber were carefully cleaned and attached to the transmitter-receiver unit (Fig. 3).

4.3.1.3 Calibration

Calibration of the optic fiber was performed with subjects at the same position as during the insertion procedure. The optic fiber outputs from Achilles and patellar tendons were related to externally measured plantarflexor and knee extension forces, respectively. In a normal calibration setting, the subjects were asked to maintain steady submaximal force levels for few seconds. The magnitude of forces used in calibration was normally 10, 20, 30 and 40% of maximal voluntary contraction (MVC). In some cases also 100% MVC was used (see below).

The plantarflexor force was measured with a strain gauge force transducer under the ball of the foot with the same equipment as described earlier (II) (Arndt et al. 1998), or using an ankle ergometer device (I, II) (Avela et al. 1999, Nicol et al. 1996). Knee extension forces were measured with a custom built machine (I, II, III, IV, VI) (Komi et al. 2000) or using the same device as Arndt et al. (1998) that was modified to knee extension (II) (see also 4.3.3). External force was calculated to represent the tendon force using balance of moments around the joints (Fig. 6). The assumptions required for this calculation include: 1) knee and ankle are frictionless joints, 2) there is no movement of joint angles during contractions, 3) moment arms are constant at different activity levels, 4) the moment arms were determined correctly for given joint angle (see 4.3.1.4) and 5) external force is produced only by the triceps surae (in case of ATF calibration) or quadriceps femoris muscle groups (in case of PTF calibration). The movement of the joint angles was minimized by careful attachment of the subject to the required position. The stability of the position was evaluated by asking the subject to contract muscles and examining if there was joint displacement. Modifications were done if necessary.

EMG recordings showed that there was no activity in the hamstring muscles during calibration of the patellar tendon force. Furthermore, as the force produced by the knee extensor muscles is transmitted to the skeletal system through patellar tendon, the external force measured from the lever arm of the knee extension apparatus was produced purely by the quadriceps femoris muscles. This was not the case for plantarflexor force. In addition to the triceps surae muscle group, flexor digitorum longus, flexor hallucis longus, peroneus and tibialis posterior muscles assist the plantarflexing movement. Therefore, an electrical stimulation procedure was used to confirm that only the soleus and gastrocnemius muscles contributed to the plantarflexor force. This was done by applying stimulation (30 Hz, 0.2 ms square wave pulse, Neuropack Four mini, Nihon Kohden, Japan) to the relaxed plantarflexor muscles via self-adhering stimulation electrodes (5 × 5 cm, StimTrode, Axelgaard Manufacturing, USA). Anodes were placed over proximal part of the medial and lateral gastrocnemius muscle bellies and a common cathode was placed distally on the muscle-tendon region. The difference between the gradients of the regression lines in voluntary and stimulation procedure can be attributed to force contribution from deeper plantarflexor muscles (Fig. 6). When necessary, the calibration protocol was repeated during and/or after the measurements to ensure stability of the optic fiber transducer output. In some cases the fiber in Achilles tendon lost it’s property due to permanent deformation. This was probably caused by high forces during intensive jumps. These performances were not included in the analysis (Fig. 6D). It must be emphasized that after the calibration procedure has been performed the changes in moment arms during actual movements do not need to be taken into consideration in the force calculations.

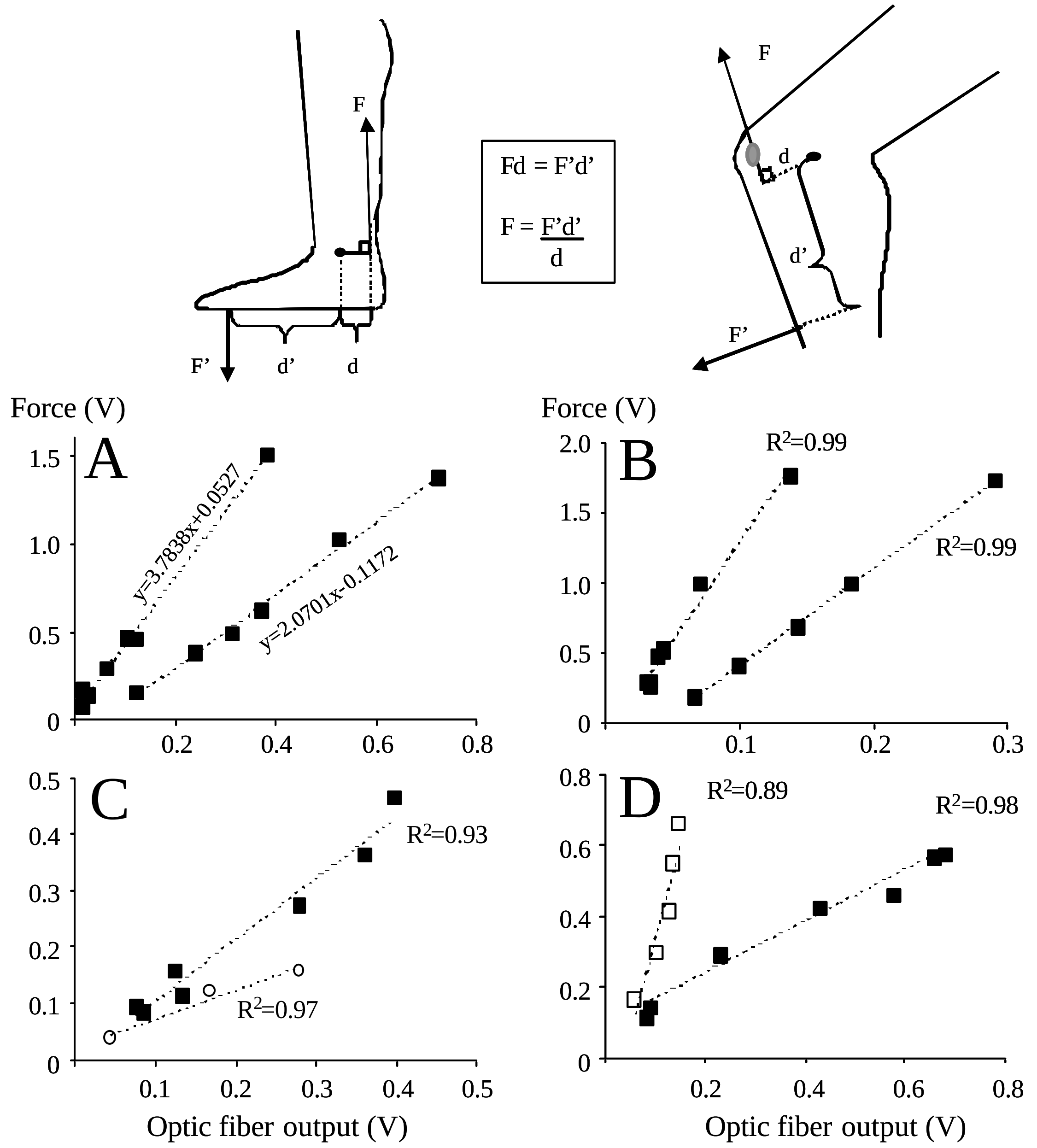

FIGURE 6 Calibration of the tendon force transducer. External force (F') was related to the optic fiber signal using a linear model and equation of balance of moments in the corresponding joints. A) Achilles tendon force calibration up to maximum effort. Equations of linearity were used in converting the fiber output to force values. Curves from two subjects. B) Patellar tendon force calibration up to maximum effort. Curves from two subjects. C) For some subjects, calibration curves using voluntary (filled squares) and stimulation (open circles) protocol were not identical showing the possibility for overestimation of the Achilles tendon force if contribution from other plantarflexor muscles was not considered. D) In a few exceptional cases, the optic fiber signal recorded from Achilles tendon was saturated after performing high intensity hopping (open squares) as compared to measurements done prior to the performances (black squares). d; moment arm of the tendon, d'; moment arm of the foot.

4.3.1.4 Moment arm determination

Two methods were used to determine tendon moment arms and axis of rotation in the knee and ankle joints. In the first method (I, II), they were obtained by using external landmarks and by rotating the distal segment of the corresponding joint on a marker table. With subjects contracting their muscles isometrically at joint angles specific to the calibration, the outlines of the leg and foot were projected on to the marker table. The proximal segment was held firmly in place while the distal segment, with markers attached along, was rotated. Lines drawn by the distal segment markers were used to determine a center of rotation at the joint angle corresponding to the calibration angle. The moment arms were then measured from the marker table and compared to those measured using anatomical landmarks.

In the second method (III-VI), moment arms were determined from radiographs taken at three different knee joint angles with contracted muscles. Images at angles of approximately 180°, 120° and 60° were superimposed to a transparency in order to determine the axis of rotation and moment arm of the patellar tendon (Spoor & van Leeuwen 1992). External forces measured in maximal eccentric and concentric knee extensions were converted into muscle force using individually calculated formula for angle dependent moment arms (V, VI).

4.3.1.5 Vastus lateralis fascicle force (III, IV, VI)

Vastus lateralis force (F_{VL}) in the direction of the muscle fibers (fascicles) was deduced from patellar tendon force similarly to Ichinose et al. (2000): $F_{VL} = PTF \cdot 34\%(\cos\alpha)^{-1}$, where α is the angle between deeper aponeurosis and the fascicle, and 34 % is considered as a relative physiological cross-sectional area (PSCA) of VL to the total PCSA of quadriceps femoris muscle (Akima et al. 1995).

4.3.2 Muscle and tendon length measurements

Model of Hawkins and Hull (1990) was used to estimate the length changes in the muscle-tendon unit (MTU_{length}). The model requires information about joint angles that were obtained using potentiometer of the knee ergometer (V, VI) or from high-speed video analysis (I, II, III, IV, VI). The jumping maneuvers were filmed at 200 Hz in the sagittal plane. Reflective markers on the neck, trochanter major, center of rotation of the knee, lateral malleolus, heel and fifth metatarsal head were digitized from the video using Motus software (Peak Performance Technologies, USA). Soleus and gastrocnemius MTU lengths were averaged to represent length changes in the TS muscle and the QF muscle lengths correspond to averaged length changes in the vasti muscles. This averaging procedure simplified the presentation of the length changes together with the forces measured from the tendons of corresponding muscle groups. The pattern of muscle length behavior was similar between the muscles within the muscle group in the conditions used, and therefore the averaging procedure was considered justified.

Length of the vastus lateralis fascicle was calculated on the basis of ultrasonographic measurements (III-VI). Ultrasound technique has been widely applied to study muscle function and tendinous tissue behavior in isometric and in isokinetic movements (e.g. Fukunaga et al. 1996 1997, Herbert & Gandevia 1995, Ichinose et al. 1997, Fukashiro et al. 1995a). Several authors have reported great individual differences in fascicle lengths, pennation angles and in their elongation when joint angular changes were equal (e.g. Kawakami et al. 1993, Kearns et al. 1988, Yamamoto 2000). Aloka SSD-2000 ultrasonographic device with a 7.5 MHz linear array probe and a scanning frequency of 42 Hz was used to image the fascicles. The probe was secured to the subject's mid-thigh after clear visibility of the echoes from fascicle interface during contraction and movement was confirmed by the researcher. Fascicle interfaces appear as light stripes in the ultrasound image. One of these stripes was chosen for analysis and was traced throughout the movement. The images were recorded to a videotape with sampling frequency of 50 Hz. A parallelogram model (Fig. 7) was used when the images were digitized with Motus software (Peak Performance Technologies, USA). During locomotion the fascicle moves in relation to skin where the probe was attached. Therefore, the entire fascicle was not always fully visible within the image area. Thus, estimation of the full length was necessary. Another reason for estimation was that some subjects had notably longer fascicle than could be visualized at a time. The total fascicle length l_{fasc} was calculated as follows: $l_{fasc} = l_{meas} + h(\sin\alpha)^{-1}$, where l_{meas} is actually measured length, h is the distance of fascicle end point from the superficial aponeurosis and α is the angle between fascicle and deeper aponeurosis. When the aponeuroses were not in parallel, the angle between them was subtracted from α to make the calculation possible (Fig. 7). The error for estimating the entire length of the fascicle was 2-7% as measured from constructed images of the whole vastus lateralis muscle. This error was caused by the curvature of the aponeurosis and fascicles. In addition, small but possible angulation (1-10°) of the superficial aponeurosis from the horizontal position introduces an error that is less than 0.5%. The changes in fascicle length in the direction of line of pull was calculated as $l_x = l_{fasc} \cdot \cos\alpha$.

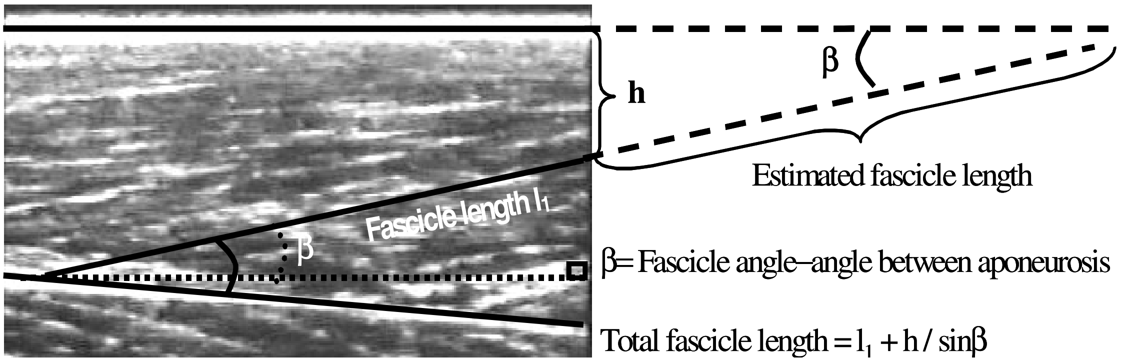

FIGURE 7 A parallelogram model used in fascicle length determination.

Length changes in the tendinous tissue, i.e. tendon and aponeurosis, were calculated as $l_{tendinous} = MTU_{length} - l_x$ (IV, VI). Length changes in the thick tendon were estimated using model of Voigt et al. (1995a). This model, utilizing quadratic tendon force function $F_{tendon} = k(\Delta l_{tendon})^2$, was used to calculate length changes in Achilles tendon (I) and in QF tendon (IV). Constant k in the formula was calculated as follows: $k = [Y \cdot T_{\varnothing} (\varepsilon_{max} - \varepsilon_{toe}) 10^2] (\varepsilon_{max} \cdot l_o)^{-2}$, where Y is Young's modulus (1.2 GPa used), $T_{\varnothing}$ is tendon cross-sectional area (individually measured), ε is strain (values as Voigt et al. 1995a) and l_o is tendon resting length (from Yamaguchi et al. 1990). Instantaneous velocities of the obtained lengths were calculated by dividing infinitesimal change in length with the corresponding time.

4.3.3 Conventional force measurements

Plantarflexor forces in isokinetic and isometric conditions were measured with the ankle ergometer (Avela et al. 1999, Nicol et al. 1996). In this device, movement of a pedal, where the foot was mounted, was controlled by a digital feedback system. Rotation axes of the pedal and ankle joint were coincided. Torque around the rotation axis of the pedal was measured by a piezoelectric crystal transducer (Kistler, Winterhur, Switzerland). Conversion of torque to force was made possible by using 1 cm elevation under the point of force application in the ball of the foot. Thus, the moment arm was easily determined. In maximal concentric isokinetic movements the initial ankle joint angle was 90° (180° being full extension) from where the pedal was driven the first 12.5° to a dorsiflexed position. At this position the subjects had one second to produce as high force as possible before the concentric movement with pedal rotation of 30° started. The subjects were instructed to sustain the maximum effort throughout the motion.

Knee extension forces in isokinetic and isometric conditions were measured by a strain gauge attached to a lever arm of the ergometer (Komi et al. 2000). The lower leg of the subject was fixed to the lever arm, length of which could be read from an inbuilt ruler. The parallel alignment of the rotation axis of the lever arm and knee joint were tested with passive and active extension-flexion movements. Maximal eccentric (ECC) and concentric actions (CON) were performed with angular displacements from 160° to 90° and from 90 to 160°, respectively. In addition, eccentric-concentric knee extension (SSC) was performed at knee angular velocity of $120\ ^\circ \cdot s^{-1}$. Maximum preactivation was used in each condition. In both ankle and knee ergometers the inertial effects were compensated by subtracting the signal recorded in passive condition from that obtained in the active effort.

Reaction forces were measured with a force plate (Raute Oy, Lahti and University of Jyväskylä, Finland) both in vertical jumping (I, II) and in sledge jumping performances (I, III, IV, VI).

4.3.4 Muscular activity

Bipolar surface electrodes (Beckmann miniature skin electrodes, USA) with interelectrode distance of 20 mm were used to record electromyographic activities from tibialis anterior, soleus, gastrocnemius medialis, vastus lateralis and rectus femoris muscles (experiment 1 and 2) and from tibialis anterior, soleus, vastus lateralis, vastus medialis, rectus femoris and biceps femoris muscles (experiment 3). The electrode positions were chosen according to the recommendations of SENIAM (Hermens & Freriks 1997). The EMG signals were amplified and sent telemetrically to the recording computer. The signals were high pass filtered (20 Hz before sampling) and full wave rectified. Then, they were integrated and averaged to obtain average EMG (aEMG) for different phases of movements. The jumping performances were divided into braking and push-off phases and the isokinetic movements were divided into 50 ms periods (V) or averaged over 80 ms using symmetrical moving average procedure (VI).

4.3.5 Data collection and processing

Analog signals were collected to a PC with a frequency of 1 kHz. An electronic pulse was used to synchronize the analog and video data. As the analog and video data were recorded at different frequencies, they were later resampled at 200 Hz to for multiple calculations and data presentation. The jumping height (h) was determined either from the net impulse (NI) or from the take-off velocity (v_o) of the center of mass in the following ways:

$h = v_o^2 (2g)^{-1}$ or $h = (NI \cdot m)^2 (2g)^{-1}$

$NI = \int [F_z(t) - mg]dt$, where F_z is vertical reaction force, t is time and m is mass

The movement of center of mass was determined from kinematic analysis using mass segment parameters from Dempster (1955). In the sledge jumps, the displacement of the sledge seat was measured with a pulse meter. The movement of the sledge seat together with knee joint angular signal from electrical goniometer was used as a feedback for subjects for the purpose to control their performances during the jumping performances.

Hopping frequency (II) was calculated from consecutive touchdowns divided by the corresponding time ($\text{hops} \cdot s^{-1}$). Stiffness of the leg spring was determined from the ratio of the peak vertical ground reaction force to the vertical displacement of the center of the mass during contact phase (Farley et al. 1991, McMahon & Cheng 1990).

Isokinetic force-velocity relationships were constructed utilizing Hill's parabolic equation $(F+a)(V+b)=b(F_o+a)$, where F is muscle force, F_o is maximal isometric muscle force, V is velocity of muscle at given F, and *a* and *b* are constants. First, constants *a* and *b* were determined by plotting F against $(F_o-F) \cdot V^{-1}$ as done by Tihanyi et al. (1982). Fitting the line by least squares did not always produce satisfactory correlation. Thus, a solver function (Microsoft Excel) was used to find values of *a* and *b* in the equation $F= b(F_o+a)/(V+b)-a$ so, that the values F, F_o and V would correspond to experimentally measured values. Because terms $(a/P_o) = (b/V_o)$ are constants, the calculations contained constrains to ensure the validity of this equation, and that the maximum velocity (V_o) would have values within reasonable physiological range. This solving process was repeated for each experimentally derived force (F) and velocity (V) value pairs, and average values of the calculated *a*'s and *b*'s were used.

Power produced by the muscle-tendon unit was calculated by multiplying tendon force with MTU velocity. Both instantaneous and average power outputs over eccentric and concentric phases were calculated (I).

4.4 Statistical methods

Means and standard deviations (SD) or standard errors (SE) were calculated for each subject group. Pearson's correlation coefficients were calculated to find out significant relationships between selected parameters. The data was tested for normality because low number of subjects, and often non-parametric tests were chosen. Friedman's two-way Anova was used to reveal differences in parameters during different velocity or jumping conditions. Student's two-tailed t-test, Wilcoxon signed rank-test or Mann-Whitney U-test was used to determine differences between two parameters such as differences in eccentric and concentric phases or between two jumping conditions. Level of significance in all tests was set to $p<0.05$.

5 RESULTS

This chapter gives an overview of the results of the experiments. Original papers (I-VI) should be consulted for additional details.

5.1 Muscle mechanics during jumping

5.1.1 Neuromuscular behavior

Typical patterns of reaction force and patellar tendon loading during unilateral sledge performances and bilateral jumps on the force plate are shown in figure 8. Due to the inclination of the sledge, the reaction forces in unilateral sledge jumps were only 20 % of those recorded during normal bilateral jumps on a force plate (I). In general, the tendon loading patterns were similar, the major difference between the two conditions being in contact times and movement amplitudes. Comparison of reaction forces and EMG activity patterns showed no differences when subjects performed the jumps with or without the optic fiber force transducers intact (Fig. 9).

The loading patterns remained quite constant but the peak forces increased together with jumping height (I, II). A change in the amplitude of knee joint angular displacement during hopping altered the relative loading of the TS and QF muscles. During large amplitude jumps the patellar tendon was primarily loaded whereas during jumping with small amplitude the Achilles tendon forces were greater (Fig 10). The effect of movement amplitude is further illustrated in figures 16 and 17.

The force in the end of eccentric phase correlated positively with peak power in the concentric phase both in TS ($r^2 = 0.63$, $p < 0.01$) and QF muscles ($r^2 = 0.85$, $p < 0.01$) (I). Comparison of muscle input (i.e. EMG activity) and mean power output of the TS and QF muscles showed that using the same input, more power could be produced in the concentric phase of CMJ as compared to SJ (I). In hopping, the input-output ratio of TS muscle showed an optimum when the jumping height was low and it was performed close to a natural hopping frequency of 2.1 Hz (Melvill Jones and Watt 1971). Preferential preactivation of gastrocnemius muscle was evident in both small and large amplitude hopping but major EMG activity of triceps surae muscle occurred in the eccentric phase of small amplitude hopping (II).

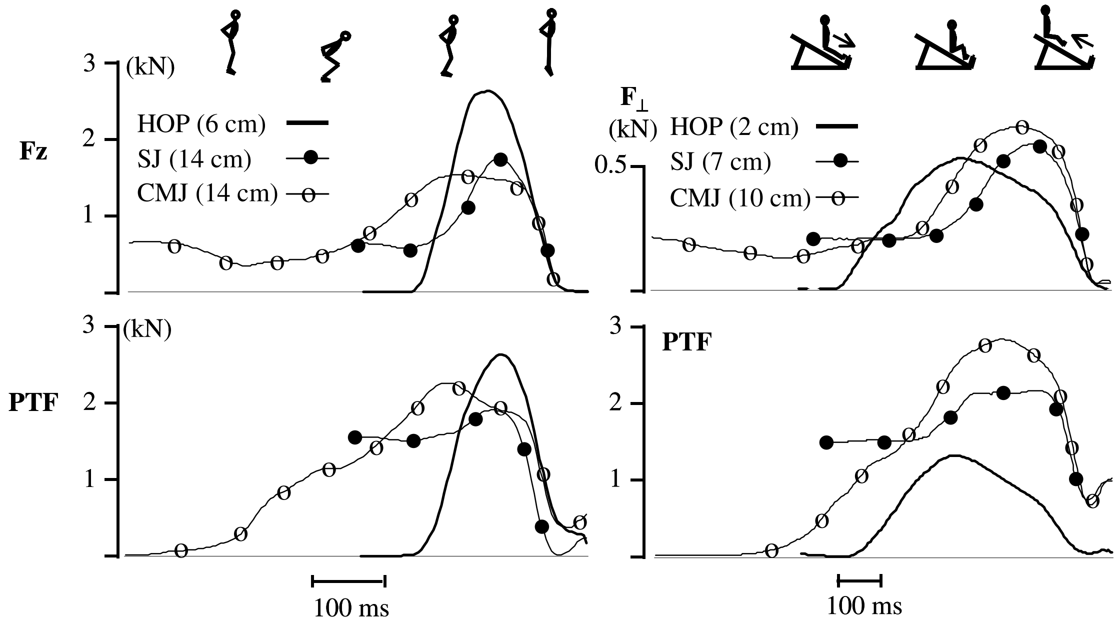

FIGURE 8 Reaction forces (top) and patellar tendon forces (below) during squat jump (SJ), counter movement jump (CMJ) and hopping (HOP) on the force plate (left) and on the sledge (right). Jumping heights are given from these particular jumps from one subject. Note: the reaction force and time scales are different between the bilateral force plate and unilateral sledge conditions. See paper I for average curves.

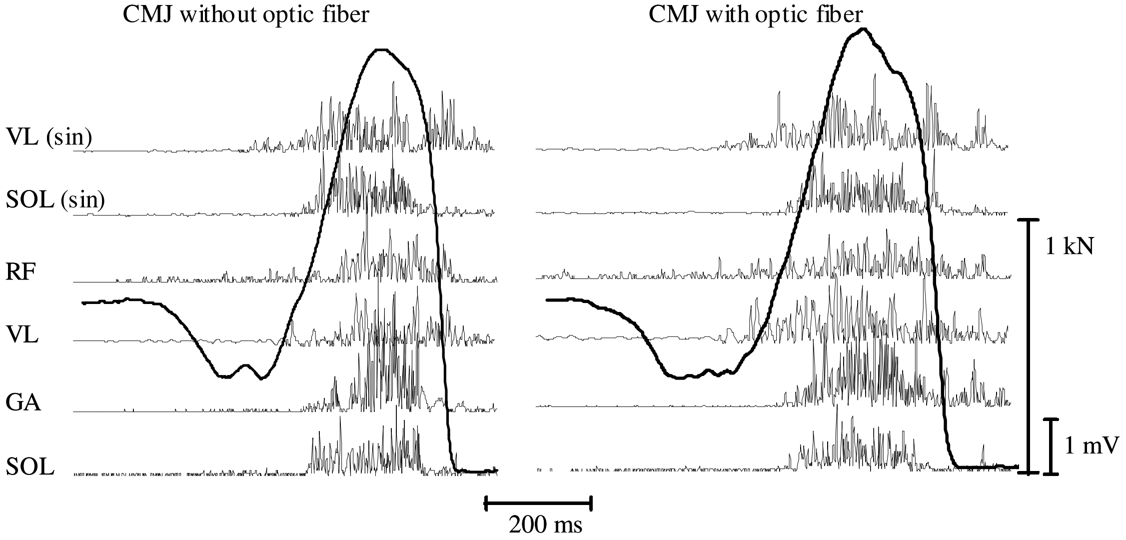

FIGURE 9 Comparison of vertical ground reaction forces (Fz), and EMG patterns during counter movement jump (CMJ) with (right) and without (left) the optic fibers in the tendons.

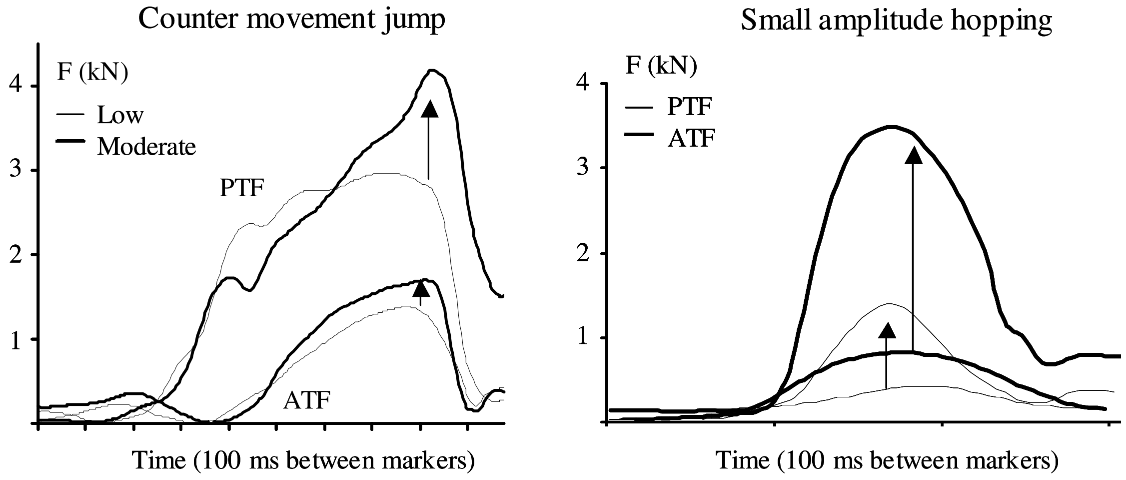

FIGURE 10 Effect of intensity on tendon loading. During large amplitude movements such as CMJ (left) or hopping with 56° knee joint displacement the patellar tendon was primarily loaded. In small amplitude hopping with knee flexion of 23° during the ground contact phase the Achilles tendon produced greatest forces (right). Increase in jumping height (upward arrows) did not alter the loading patterns but the peak forces were increased. Representative examples from two individuals.

During hopping with different amplitudes, the peak stretching velocities (0.33 vs. 0.36 m· s^{-1} for small- and large-amplitude, respectively) and activity patterns remained quite similar in QF muscle in spite of different magnitudes of stretch in the muscle. The aEMG of VL muscle was greater ($p<0.05$) in the eccentric than in concentric phase in both hopping conditions (II).

In large amplitude jumps the QF did greater work and produced more power than the TS muscle (Fig 11). In large amplitude hopping, however, the relative contribution of TS increased but did not exceed the contribution of QF. Figure 12 shows that the peak powers were reached almost simultaneously for QF and TS muscles in submaximal, large amplitude hopping.

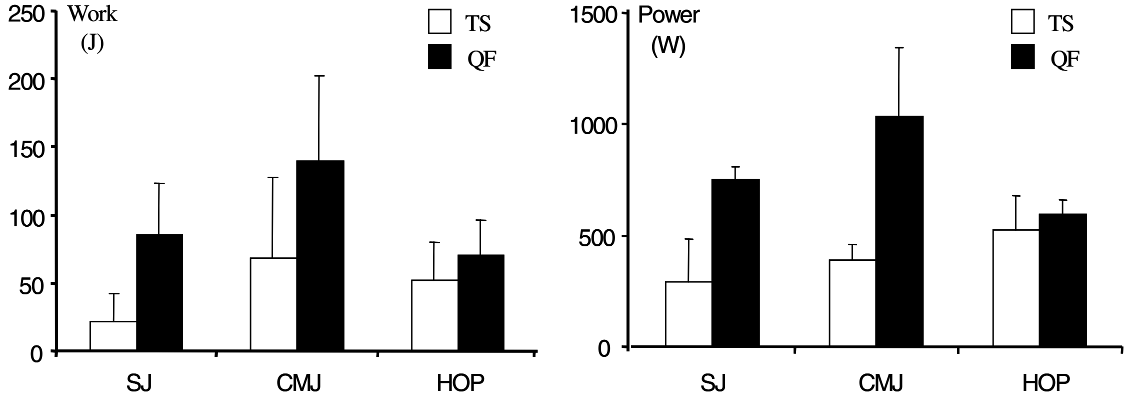

FIGURE 11 Positive work (left) and peak power (right) produced by triceps surae (TS) and quadriceps femoris (QF) muscles in squat jump (SJ), counter movement jump (CMJ) and hopping with large amplitude (HOP).

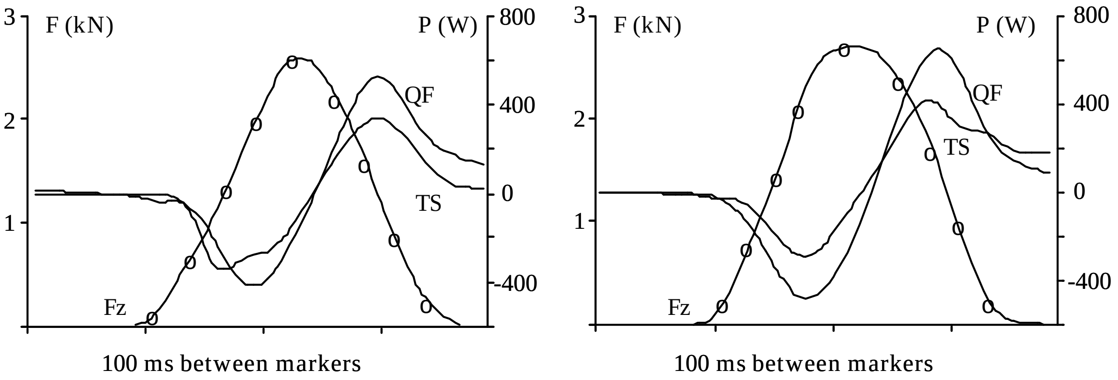

FIGURE 12 Two representative examples of power-time curves during large amplitude hopping on the force plate. Peak powers in quadriceps femoris (QF) and triceps surae (TS) muscles were reached almost simultaneously in these submaximal performances.

5.1.2 Muscle-tendon behavior

Changes in MTU, muscle and tendon compartments were estimated for the purpose of examining muscle function in greater detail during different locomotion conditions. Soleus muscle compartment length during jumping was modeled in paper I and vastus lateralis muscle fascicle length was determined from ultrasonographic images in papers III, V and VI.

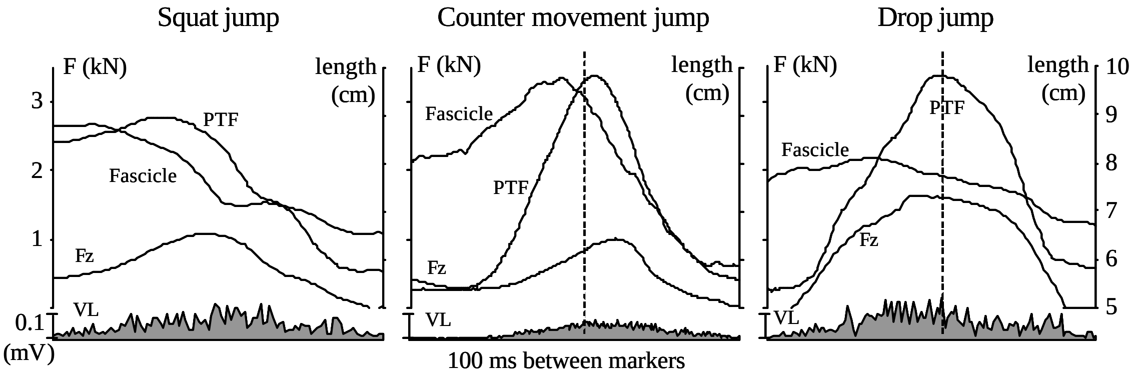

FIGURE 13 Fascicle lengths, patellar tendon forces, reaction forces and vastus lateralis EMGs during unilateral SJ, CMJ and DJ on the sledge apparatus. Dashed vertical lines indicate time at which the muscle-tendon unit started to shorten.

In all the measured SSC exercises where the MTU was stretched prior to shortening, the muscle compartments behaved similarly (Figs. 13 and 14). The magnitude of length change was, however, different depending on the movement amplitude, contraction intensity and examined muscle (I, III). For example, during drop jumps the change in VL fascicle length was smaller than in CMJ although the MTU length change was same in both conditions (Fig. 13) (III). This was because the greater EMG activity in DJ reduced both the magnitude and velocity of the fascicle length change as compared to the CMJ. During the downward movement in CMJ, the initial lengthening of both TS and

QF MTUs occurred with little activity. This is illustrated in the level of muscle compartment in figures 13 and 14. When the activity in the end of lengthening phase and in early shortening phase increased, there was possibility for the force to continue the increase during muscle shortening also (I, III). During SJ, the muscle compartment, as modeled for soleus and measured for VL, shortened throughout the performance.

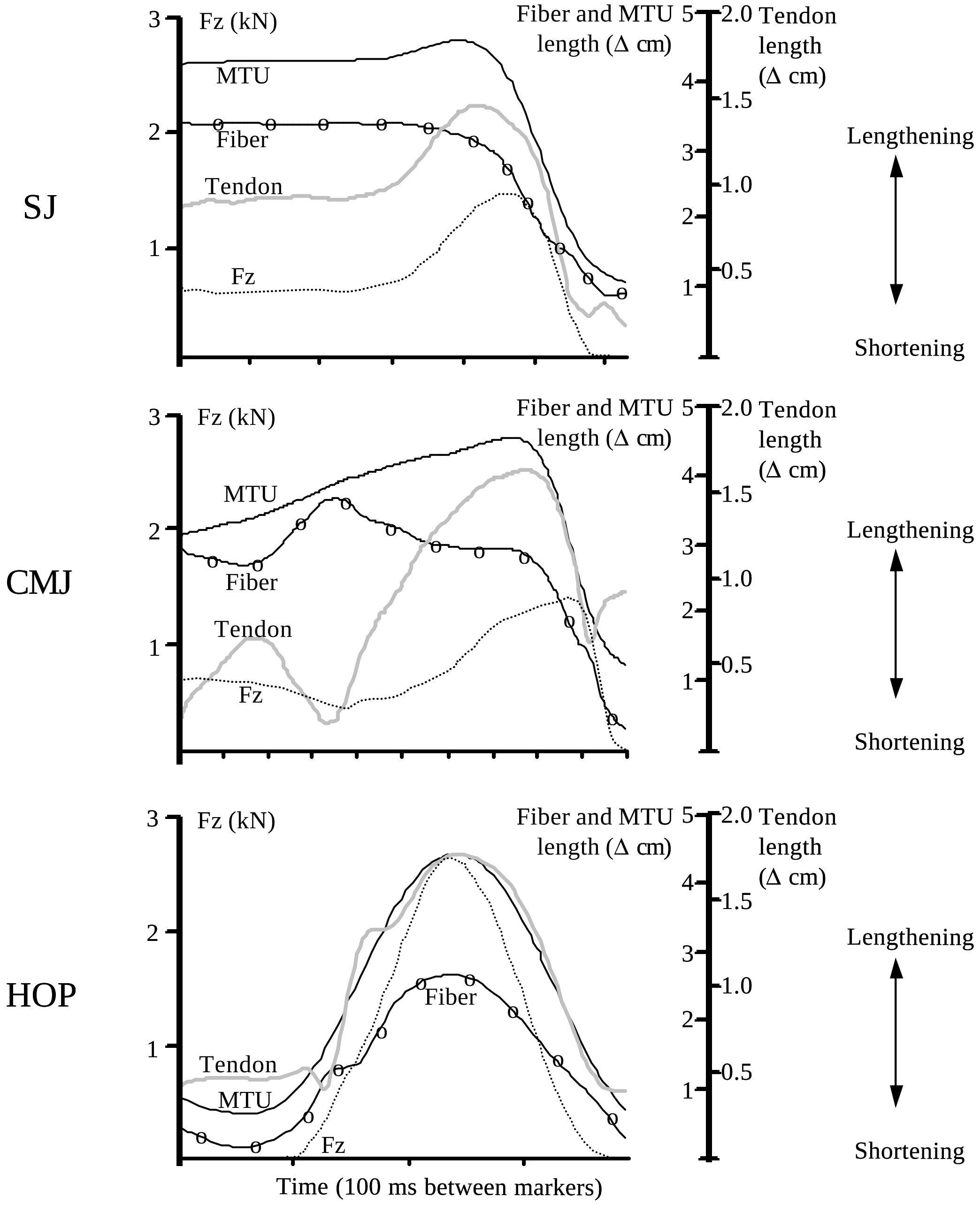

FIGURE 14 An example of muscle-tendon interaction in the triceps surae muscle during squat jump (top), counter movement jump (middle) and hopping (below). Fz; vertical ground reaction force, MTU; muscle-tendon unit length, tendon; tendon length calculated with the force method, fiber; estimated muscle fiber length change. For average curves see paper I.

Tendinous tissue length changes were estimated by two methods. The method of Voigt (Voigt et al. 1995a) in combination with direct tendon force measurements (force method) was used to calculate Achilles tendon length changes during jumping (I). This method predicted that the Achilles tendon stretches prior to shortening in SJ, CMJ and HOP (Fig. 14). Furthermore, the force method was compared to the results obtained from direct measure of *in vivo* fascicle length change and MTU length estimation (kinematic method). Both the force and kinematic approaches predicted the same pattern of behavior during different jumping types for tendinous tissue of the vastus lateralis muscle (Fig. 15). The magnitude of length change, however, differed considerably between the methods. The absolute length changes and strain were greater using kinematic method (IV).

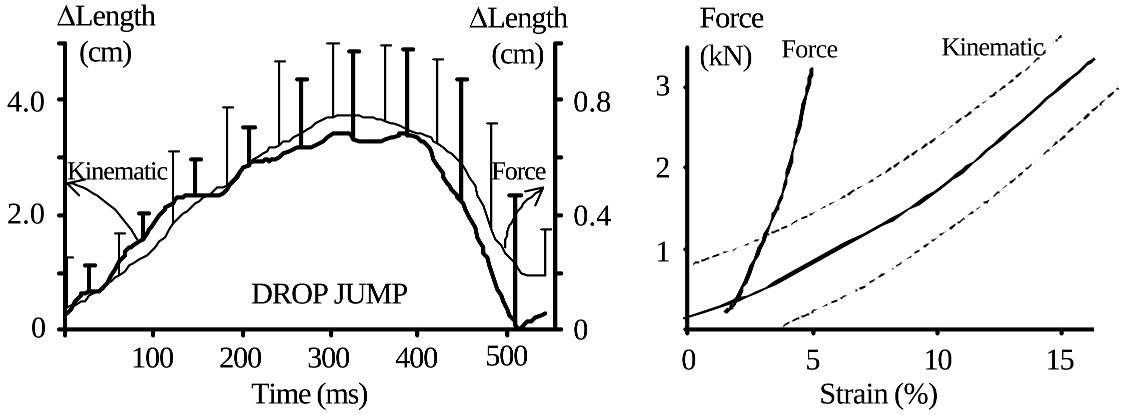

FIGURE 15 Tendinous tissue behavior estimated using kinematic and force method gave the same patterns of length change but the magnitude differed considerably (left). Comparison of tendon force -strain relationships with the two methods (right). Individual 95% confidence interval (CI) for kinematic regression line is shown as dotted lines. For force method CI is marginal. Error bars represent SD.

5.1.3 Force-length-velocity relationships

The instantaneous force-length and force-velocity curves during natural locomotion differ considerably from the isometric and isokinetic relationships obtained using maximal activation. In the following, instantaneous force-length and force-velocity relationships are first presented in the level of muscle-tendon unit with examples of CMJ and hopping on a force plate (Fig. 16 and 17). In every condition, the force-length curves traveled counterclockwise direction for both TS and QF muscles (I, III).

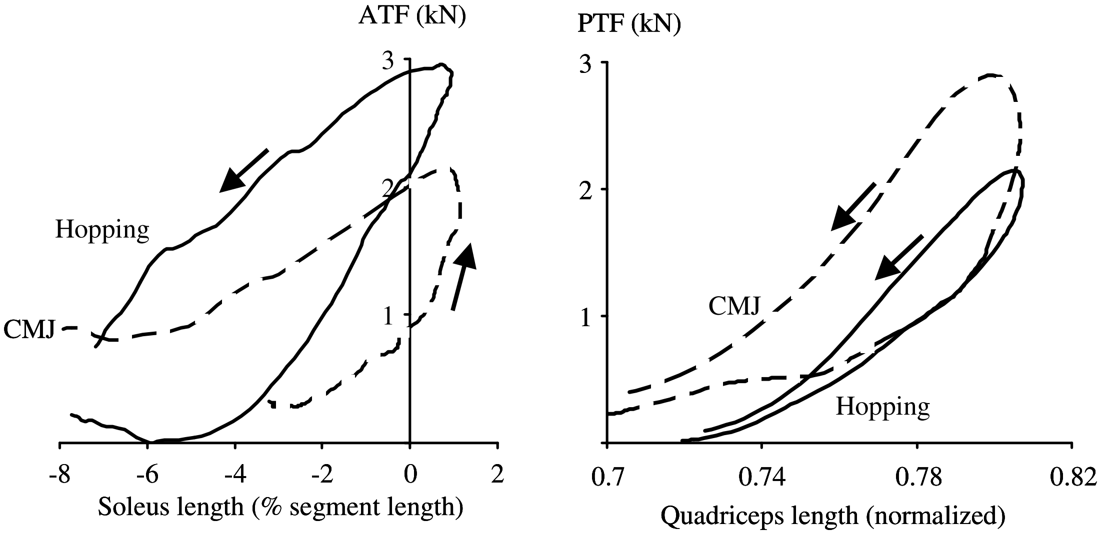

FIGURE 16 Force-length relationship during hopping (solid line) and counter movement jump (CMJ, dashed line) in the triceps surae (left) and quadriceps femoris muscle-tendon units (right). First, MTUs lengthened and force increased. During shortening further increases in force could be seen. During CMJ the patellar tendon was primarily loaded whereas the Achilles tendon forces were greater during hopping.

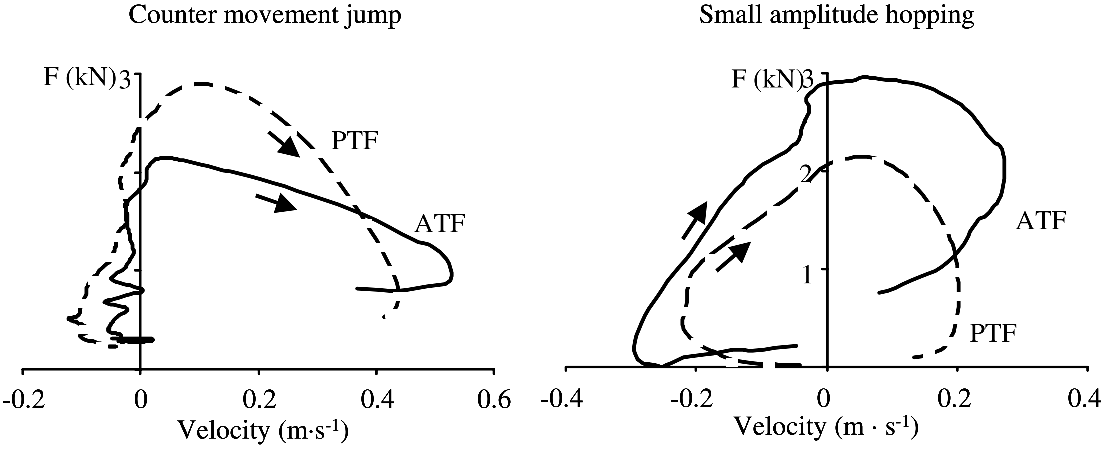

FIGURE 17 Force-velocity relationships in counter movement jump (left) and hopping (right). In hopping the stretching velocities were greater both in TS and QF muscle-tendon units as compared to CMJ. Negative velocity denotes stretching and positive shortening of the MTU, respectively. ATF; Achilles tendon force (solid line), PTF; patellar tendon force (dashed line).

Force-velocity curves measured in maximal isokinetic conditions could exceed those measured during submaximal locomotion. Figure 18 shows both the instantaneous and isokinetic force-velocity curves. SJ, CMJ and HOP were submaximal bilateral jumps on the force plate and the isokinetic "classical" curve was measured with the ankle ergometer and fitted to the Hill's equation. The two classical curves show the magnitude of overestimation of ATF if contribution of other plantarflexor muscles is neglected. In figure 19 the magnitude of enhancement is further illustrated in hopping where the examples are taken from small and large amplitude performances.

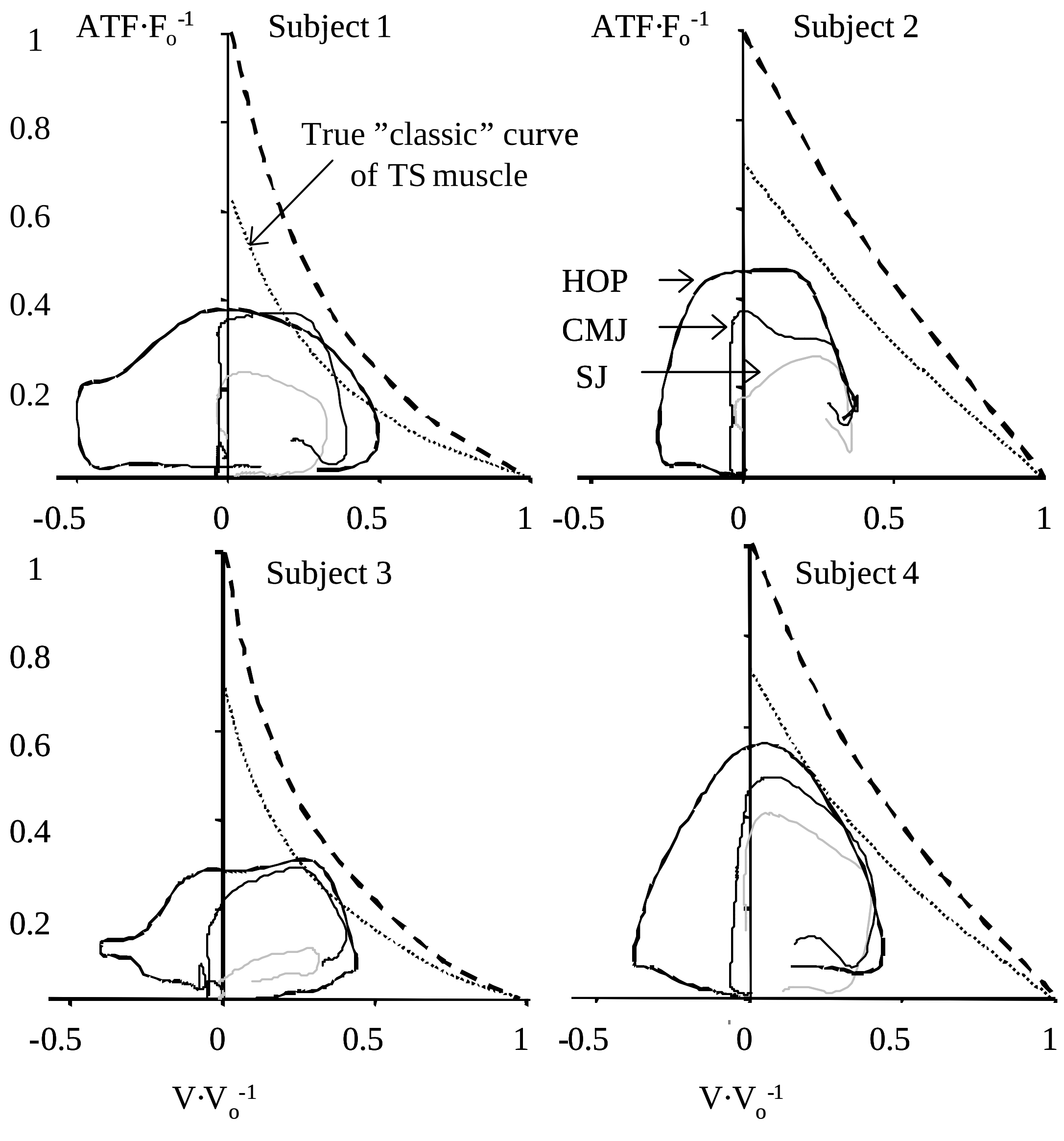

FIGURE 18 Comparison of isokinetic and instantaneous force-velocity relationships from four individuals during squat jump (SJ), counter movement jump (CMJ) and hopping (HOP). Hopping was performed with large knee joint angular displacement. There is possibility for bilateral loading difference in these jumps that were performed on a force plate. The dashed line with higher force values shows the total plantarflexor force and the dotted line represents pure Achilles tendon force calculated by using optic fiber calibration. Scales are normalized to measured maximal plantarflexion force (F_o) and estimated maximal shortening velocity (V_o).

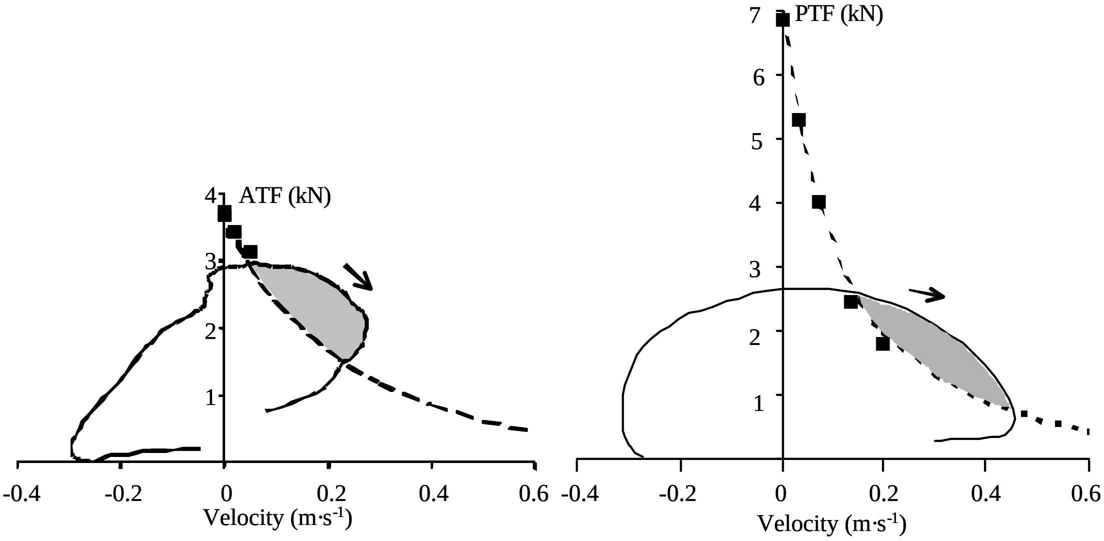

FIGURE 19 Enhancement of triceps surae and quadriceps femoris muscle outputs during hopping with small (left) and large (right) knee joint angular displacement. The black squares indicate the actually measured values and the dashed lines have been constructed by using Hill's equation. The shaded areas illustrate that the concentric muscle output in submaximal hopping exceeded that measured in maximal isokinetic condition.

The enhancement of the output of MTU was further examined by constructing the force-velocity curves for the vastus lateralis muscle fascicle (VI). The results showed that the fascicle force in submaximal jumps reached values close to those produced during maximal isokinetic effort, but did not exceed them. Force in the MTU, however, showed potential enhancement at higher shortening speeds of MTU (Fig. 20). During DJ especially, it was shown that the muscle-tendon interaction made it possible for contractile component to act in high force and low velocity region with the tendon responsible for great shortening velocity of the muscle-tendon unit (III).

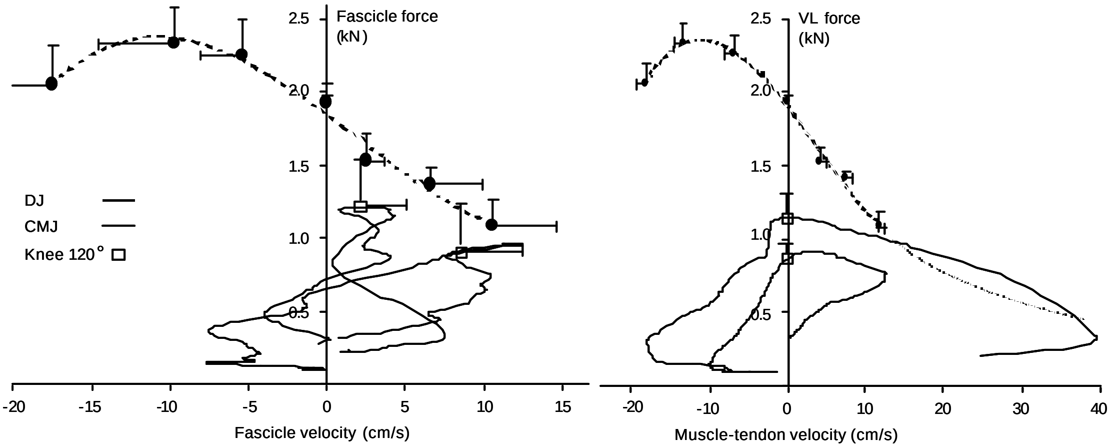

FIGURE 20 Force-velocity curves for vastus lateralis fascicle (left) and muscle-tendon unit (right). Comparisons of the instantaneous curves during drop jump (DJ) or counter movement jump (CMJ) (solid lines) and isokinetic curves (filled circles) showed that muscle output was not enhanced over that in maximal isokinetic condition in either jump type. In DJ, however, the instantaneous MTU force at high muscle-tendon shortening speeds exceeded that extrapolated from isokinetic measurements.

5.2 Fascicle behavior and force enhancement in controlled knee extensions

Figure 21 shows examples of force, knee angle, VL EMG, fascicle and tendinous tissue length recordings during maximal knee extensions. As expected, the fascicles shortened in the concentric action and lengthened in the eccentric action (VI). Velocity had no significant effect on the magnitude of length change in ECC or in CON (Fig. 22). In stretch-shortening cycle the fascicles lengthened prior to shortening (Fig. 23) (V). The magnitude of lengthening in the eccentric phase was greater ($p<0.05$) than shortening in the concentric phase.

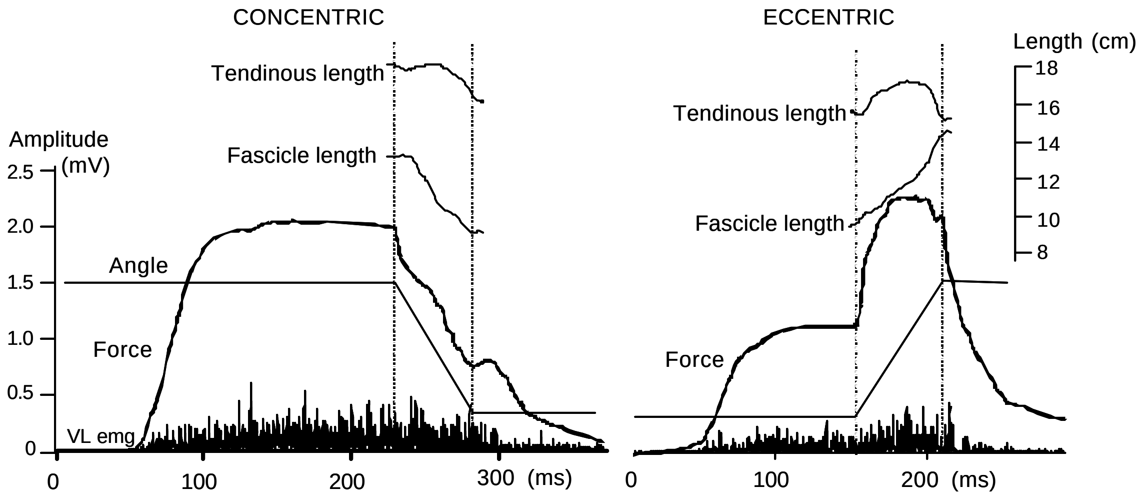

FIGURE 21 Vastus lateralis EMG, knee extension force, knee angle, fascicle length and tendinous tissue length recordings during maximal concentric (left) and maximal eccentric conditions (right). Velocity in this example was 120°· s^{-1}.

Concentric force production in knee extension movement was enhanced in SSC as compared to pure shortening action (V). The force enhancement was significant ($p<0.05$) at knee angle of 115° although the force prior to the concentric phase was smaller ($p<0.05$) in SSC than in CON. The force enhancement was not associated with differences in EMG activity but the fascicle behaved differently between the conditions. In eccentric phase of SSC the VL fascicle was actively lengthened being significantly longer at the beginning of shortening in SSC than in CON (Fig. 22). During the concentric phase the fascicle shortened more in SSC than in CON in a way that at the knee angle of 115° the difference in was not anymore significant.

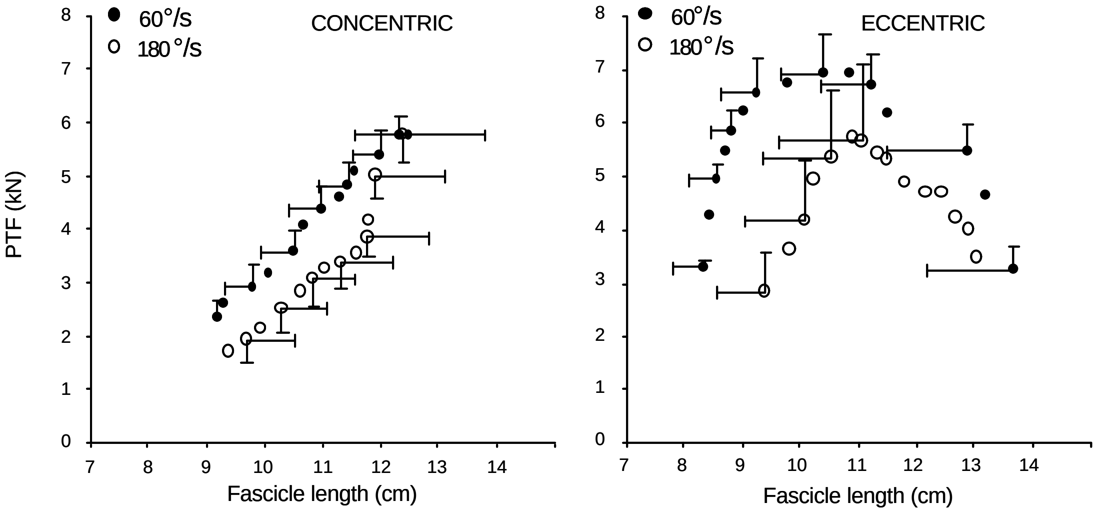

FIGURE 22 Relationships between patellar tendon force (PTF) and fascicle length during concentric (left) and eccentric (right) conditions at 60 and 180°· s-1. Average (SE) for 4 subjects is given.

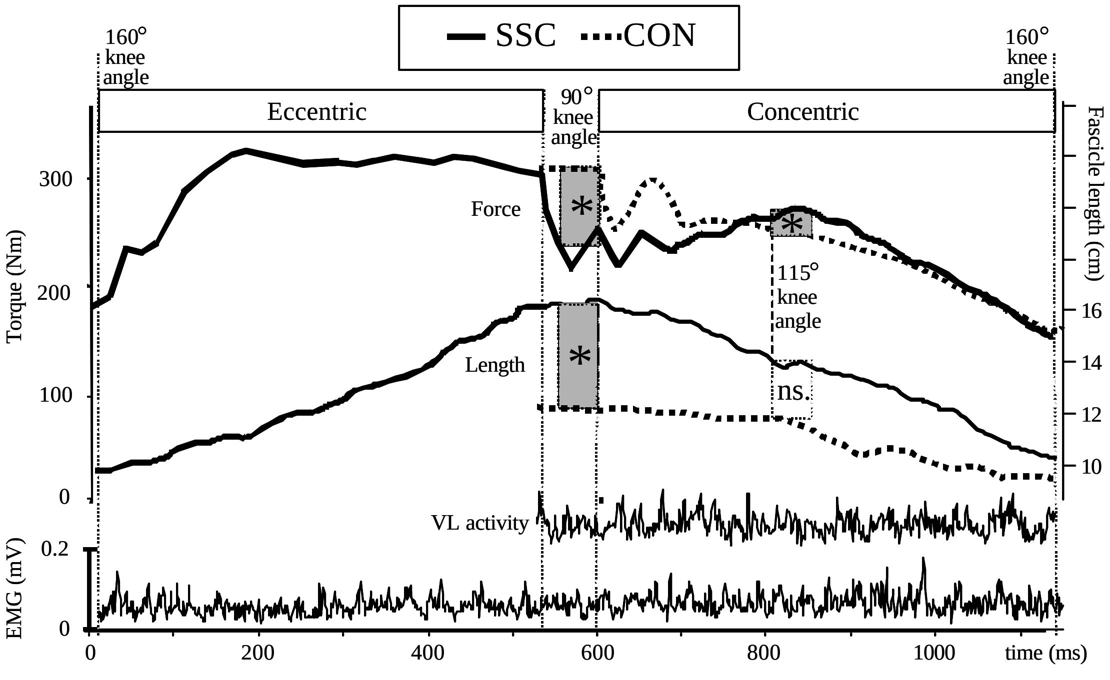

FIGURE 23 Torque (upper curves), fascicle lengths (middle) and rectified vastus lateralis EMG activity in SSC (solid lines) and in pure concentric (CON) knee extension. During the eccentric phase of SSC the fascicles lengthened actively being significantly (*p<0.05) longer prior to the concentric phase than in CON. The torque increased in the eccentric phase but dropped in the subsequent 80 ms transition phase to a lower level as compared to the pre-activity torque level in CON. During the concentric phase at a knee angle of 115° the force was higher in SSC than in CON, but no significant differences in fascicle length or EMG were found.

6 DISCUSSION

Main findings of the present study can be summarized as follows:

1) Tendomuscular output in the concentric phase of CMJ was related to the force at the end of stretching phase in both TS and QF muscles. With similar EMG activity level, a greater concentric power output could be achieved in CMJ than in SJ. Modeling soleus muscle-tendon interaction showed that tendon stretch and recoil occurred in both SJ and CMJ. In CMJ, stretch-shortening cycle in the active muscle compartment was not particularly efficient (I).

2) Increase in jumping intensity did not alter the loading patterns but peak ATF and PTF were increased. In small-amplitude hopping with different intensities a jumping height where the concentric phase is most economical, as measured by EMG-to-ATF ratio, could be found. At this low jumping height the frequency was close to preferred frequency of hopping (II).

3) The Achilles tendon was primarily loaded in small-amplitude hopping whereas patellar tendon forces were greater in large-amplitude jumps, such as CMJ and hopping with great knee joint angular displacement during the ground contact phase. In hopping with different amplitudes the peak stretching velocities and activity patterns remained similar in QF muscle in spite of different magnitude of stretch in the muscle. For the TS muscle, however, there were several possible control strategies (II).

4) Enhancement of concentric force production after pre-stretch was demonstrated in maximal, constant velocity knee extensions. Force enhancement was related to fascicle length behavior but was not associated with differences in EMG levels (V).

5) In all the examined SSC exercises, the fascicles first stretched and then shortened. The magnitude of length change was, however, dependent on movement type and contraction intensity. For example, in CMJ the length change was considerably greater than in DJ where the activity level, and consequently, the stiffness was greater. (III, VI).

6) Instantaneous force-velocity curve of the muscle-tendon unit could exceed that recorded in maximal isokinetic conditions. The enhancement of muscle output was predominant in the normal hopping conditions as compared to the sledge jumps, and could be seen both in the triceps surae and in the quadriceps femoris muscle groups. In the sledge jumps, no enhancement of muscle output was found at the fascicle level (VI).

7) Comparison of the force and kinematic methods to estimate tendinous tissue length change during locomotion produced the same patterns of behavior but the magnitudes of length change differed considerably. The absolute changes in length and in strain were greater using kinematic method as compared to force method (IV).

6.1 *In vivo* behavior of muscle and tendon during jumping

6.1.1 Muscle-tendon interaction

Muscular output depends on interaction between muscle and tendon with a given force, activity level, length and velocity. In this regard human subjects may show individual activity patterns and several patterns of behavior may be found during different natural movements. Also, stiffness of elastic structures may vary (Voigt et al. 1995a) and have an effect on the magnitude of stretch in the fascicles (Yamamoto 2000). In bilateral jumps, MTUs were found to act as springs (I, II) or work generators (I, see also Fig. 16), whereas in sledge performances they were mainly work generators (III). Measurement and modeling of muscle and tendon length changes in the knee and ankle extensor muscles showed that in SJ, the soleus muscle compartment (I) or VL fascicle (III) shortened throughout the movement. First, at low levels of force, shortening of the muscle lengthened the tendon when the force was increasing. When the force was decreasing, both components shortened. These findings are similar to behavior of gastrocnemius muscle during maximal SJs (Kurokawa et al. 2001). Thus, tendon stretching and recoil energy can have an effect on tendomuscular output in the SJ also. In CMJ, both the tendon and muscle lengthened prior to shortening. During muscle lengthening, however, the activity level was quite low. Consequently, the storage of elastic energy within the muscle compartment could not have been significant because it requires an active stretch with sufficient force (Cavagna et al. 1968, Cavagna 1977). Furthermore, the transition between stretching and shortening phase was long in CMJ. This fact further suggests that the role of active stretch in creating beneficial conditions for the utilization of elastic energy in the muscle was only minor in these submaximal performances. In bouncing jumps, such as DJ and hopping, the effectiveness of SSC depends on the loading pattern (force), activity level, duration of the transition phase, and magnitude of length change. In drop jumps where the activity level was higher than in CMJ, the VL fascicles were stiffer bearing greater forces but undergoing smaller length changes. This benefits elastic mechanisms but also myoelectrical potentiation through stretch reflex response (see 6.2).

Both in CMJ and in DJ, the fascicles started to shorten while the tendinous tissue and the entire MTU was still lengthening (Fig.13). This was because the EMG activity was increasing and, probably because of the force-length relationship. For example, when the fascicles operate in the ascending limb of the relationship as shown in paper III, the fascicles gain force potential during the stretch and are strong enough to elongate the tendinous tissues also in the beginning of the shortening phase. This behavior delays the beginning of shortening of the tendinous tissue to the late push-off phase, when the recovered recoil energy compensates muscle fiber shortening velocity (6.2.2).

It must be noted that the behavior of one muscle group cannot be generalized to represent function of other muscles. Also task dependency of muscle function needs to be emphasized (Gollhofer & Kyröläinen 1991). Different activity patterns and amount of length change vary considerably between different muscles (see Voigt et al. 1995b, Bobbert et al. 1996). Muscle specific analysis is of great importance especially when mono- or biarticular muscles are compared (Prilutsky & Zatsiorsky 1994). However, simple models are sometimes useful because parameter estimation may be reduced. In the present study, the muscles of quadriceps femoris and triceps surae muscle groups were often lumped to act as a simple functional unit. Consequently, there was no need to estimate the relative contribution of different muscles to the directly measured patellar and Achilles tendon forces, respectively. Therefore, the loading patterns are reliable in shape and represent true forces produced by these muscle groups *in vivo.*

6.1.2 Effects of intensity and movement amplitude

The loading patterns remained similar at all intensities but changes in magnitude of force and duration of performance were observed with increased effort. Also Komi et al. (1992) observed increases in peak Achilles tendon force with increased running velocity. Alterations in knee joint angular movement during the ground contact phase, or increase in jumping height did not cause dramatic changes in the control strategy of QF muscle during hopping. The TS muscle, however, showed several possibilities in this regard. In large amplitude hopping, the EMG activity was similar between eccentric and concentric phases while in small amplitude hopping major activity was found during the eccentric phase. Furthermore, the small amplitude hopping was characterized with faster stretching velocity of TS muscle and shorter contact time (II) having the criteria for effective SSC that are 1) a well-timed pre-activation, 2) short and fast eccentric phase and 3) immediate transition between stretch and shortening phases (Aura & Komi 1987, Bosco et al. 1981, Komi & Gollhofer 1997). It must be noted, however, that in the present study (II) the relative length changes in the muscle and tendon compartments were not estimated for each subject (see example in Fig. 14). Because passive tendinous structures and active muscle respond differently to stretch it is impossible to know where these conditions occur in the muscle. The abovementioned conditions together with high force in eccentric phase are beneficial for elastic energy storage in the muscle (Cavagna 1977) while elastic storage in the tendinous tissue depends on the magnitude of elongation and force in the end of the stretch. The concentric phase with decreasing EMG activity and force was the elastic energy could be recoiled (Lou et al. 1999, Ettema 1996b). The benefit of elastic energy in economizing the concentric performance had an optimum at medium jumping heights. This optimum, where EMG-to-ATF ratio was lowest, occurred at hopping frequency of 2.0 Hz that is reportedly close to preferred frequency (Melvill Jones & Watt 1971) at which natural resonant frequency can be of advantage (Wilson et al. 1996). Also Taylor (1985) has shown that at preferred hopping frequency the role of elastic energy is maximized and use of metabolic energy is minimized.

In order to increase jumping height more input to muscle is required to achieve powerful performance, as shown in the present study (II). The same behavior was seen in experiments by Moritani et al. (1991) where the ground contact phase was kept constant and frequency of jumping was decreased with simultaneous increase in hopping height. These data suggest that economy of the shortening phase is compromised for power production as shown in controlled animal studies (Curtin & Woledge 1996). Besides increasing muscle input in the concentric phase, also force in the end of eccentric phase is related to powerful concentric performance (I) (Bobbert et al. 1996, Takarada et al. 1997a).

6.1.3 Classical vs. instantaneous force-velocity relationships

The classical force-velocity relationship describes a fundamental property of a skeletal muscle. During natural locomotion, however, the basic relationship measured with constant, maximal activity differed considerably from instantaneous recordings (Figs. 19, 20) as shown previously by Gregor et al. (1988). Differences stem from constantly changing muscle activity and length, and from variable load applied on the muscle during locomotion. In this context it must be emphasized that the basic force-velocity relationship is a property of a contractile component, and that the measurement of instantaneous length changes, from where the velocities are derived, are often measured in the level of MTU as done in the study by Gregor et al. (1988). In the present study, the comparison of the force-velocity curves at the level of muscle fascicle and MTU reveal dramatic differences between the curves (Fig.

20). Although the output of MTU was greater than that extrapolated from isokinetic measurements, the output in the fascicle level was not. This does not mean that the enhancement of power output would not occur in the contractile level at all; in fact, it has been demonstrated in isolated mouse muscles that the lack or presence of enhanced output is dependent on the type of muscle. By comparing force-velocity curves Barclay (1994, 1997) showed that the curves measured during sinusoidal cyclic contractions exceed the classical curve in mouse soleus muscle but not in extensor digitorum longus muscle. These differences in muscle's performance also relate to differences in efficiency between muscles. In intact muscle groups the muscles act synergistically and the interaction between tendon and the muscles during locomotion may lead to misinterpretations about muscle's performance if architectural or functional differences between muscles are not considered.

The measurement of classical force-velocity relationship is especially difficult in human studies where linear velocities of a muscle must be derived from joint angular motion. Furthermore, measurement of the relationship requires that there are no changes in the length of series elastic element. This may be accomplished by allowing the maximally activated muscle to shorten against a constant force during which there are no changes in tendon length. When measuring force production of human muscles *in vivo*, these conditions are not, however, easily met. Without direct measure of fiber or fascicle lengths it is difficult to isolate the contribution of contractile and elastic components. Because muscle fiber or fascicle velocity does not correspond to MTU velocity or joint angular velocity even at constant muscle activation level, the true performance of a muscle is not revealed by conventional isokinetic measurements (Ichinose et al. 2000).

By estimating length changes in both MTU and fascicle level, the present study showed that the concentric output of MTU could be greater in submaximal locomotion as compared to that measured under maximal activation in isokinetic condition. The following chapter discusses the possible mechanisms that might be involved in the SSC related performance enhancement.

6.2 Mechanisms of performance enhancement in SSC

In search for mechanisms of the enhanced performance during shortening phase of SSC, previous conditions in the eccentric phase must be known. In respect to the muscle-tendon interaction, there are several possibilities how MTU may function. On the one hand, when the MTU lengthens, the tendon may be responsible for lengthening almost entirely (Roberts et al. 1997) as was the case in DJ on the sledge (III). This requires high activity in the muscle fibers and is most likely to occur in MTU actuators having large tendon-to-fiber length ratio. On the other hand, muscle and tendon may both lengthen. In some studies, continuous muscle fiber shortening has been reported although the

MTU is lengthening (Griffiths 1991). In the present study also, this phenomenon was seen during late braking phase of CMJ and DJ on the sledge (Fig. 13). Diversity of the reported behavior can reflect variety of explored experimental conditions or differential behavior amongst species and examined muscles in different tasks. In line with previous literature, the submaximal performances of the present study suggest that activation mechanics and use of elastic energy affected the performance enhancement and economy of the movement (Anderson & Pandy 1993, Bosco et al. 1981, 1982b, Thys et al. 1975). Furthermore, results from maximal knee extensions of the present study show possible involvement of force-length properties in enhancing the muscle output.

6.2.1 Role of neural input

Results from both triceps surae and quadriceps femoris muscles suggest that the same concentric power output could be achieved with less EMG activity in the CMJ as compared to SJ. Comparison of the submaximal CMJ and SJ with progressively increasing jumping height showed that the enhancement of SSC performance cannot be solely explained by increases in muscular activity (I). What, then, is the role of activation? Bosco et al. (1982b) pointed out individual differences in activation mechanics in maximal SJ and CMJ performances. In some subjects, the performance potentiation could be attributed mainly to increased activity; while in other subjects the potentiation through elastic mechanisms was suggested (Bosco et al. 1982b). In bouncing jumps that are performed with short contact time, the muscles are activated well before the ground contact (Avela et al. 1994, Dyhre-Poulsen et al. 1991, Gollhofer & Kyröläinen 1991). This pre-activation is very important in creating sufficient MTU stiffness prior to stretching of the muscles (Gollhofer et al. 1984, 1992). Then, the stretch imposed to activated and stiff muscles upon ground contact allows tendon elongation with storage of elastic energy. A fast stretch can also activate reflex response to enhance the activity and stiffness further (Komi & Gollhofer 1997, Nichols & Houk 1976). The reflex function has been shown to be very significant in natural human performances. Dietz et al. (1979) have demonstrated that in submaximal running the EMG activity can be dramatically greater as compared to value obtained during maximal isometric voluntary contraction. Furthermore, SSC performance has been shown to be reduced after blocking the stretch reflex (Kilani et al. 1989). In the present study, a high level of activity and force in DJ had a positive effect on muscle stiffness. Consequently, fascicle length changes were smaller in DJ and in repetitive CMJs than in normal CMJ (III, V). This enabled the fascicles to take advantage of the high force and low velocity region of the force-velocity curve while the tendon was responsible for high shortening velocity of the entire MTU (III, VI).

High forces are consequence of high activity level. The force in the end of eccentric phase had a positive effect on concentric power output in TS and QF muscles (I). This has been shown also in previous studies (Bosco et al. 1981, Bobbert et al. 1996, Takarada et al. 1997a). As joint moments are greater at the beginning of concentric phase of CMJ than in SJ, the performance enhancement brought by SSC of muscle function has been attributed mainly to the greater time available in CMJ for force generation (Bobbert et al. 1996). In submaximal conditions of the present study, however, it was clearly demonstrated that the force could continue to increase also during the shortening phase in CMJ (I). Therefore, although the high force at end of stretch favors concentric power output, it cannot alone be responsible for the performance enhancement phenomenon in standing jumps.

6.2.2 Elastic recoil

It has been known for long time that the elastic compliance in MTU enables metabolic energy savings (Alexander & Bennet-Clark 1977). The mechanisms through which the elasticity affects the performance are not, however, well understood (see target article by Ingen Schenau et al. 1997 and subsequent responses). The diversity of emphasis of the role and mechanisms by different researchers may be related to the multi-component origin of elasticity within the muscle-tendon unit. In the contractile level, the active cross-bridges are generally accepted to have in series elasticity (Huxley and Simmons 1971, Cavagna et al. 1994). However, the elastic energy stored in the cross-bridges during stretch is fully abolished by minute changes in length and cannot have major importance in locomotion *in vivo* (Brown & Loeb 2000, Edman & Tsuchiya 1996). Although the single fiber or single muscle studies do not support considerable elastic contribution from cross-bridges there is evidence that slow and fast twitch muscles may benefit differently from SSC. Bosco et al. (1982) have shown that subjects with higher percentage of fast twitch fibers benefited more from small amplitude movements. The subjects having more slow twitch fibers were able to utilize elastic energy better. The differences in utilizing the elastic energy may be related to the fact that fiber types have different stiffness, the slow ones being stiffer because of longer cross-bridge cycle, because they have fewer sarcomeres in series than in fast twitch fibers (Gregory et al. 1978, see also Goubel and Marini 1987), and because slow muscles have greater amount of cross-linked collagen (Kovanen et al. 1984). In the present experiments fastest transition between stretching and shortening of the fascicles occurred in DJ (VI). Therefore, if there were elastic mechanisms acting in the muscle compartment, most likely they would operate during DJ.

In spite of vast literature on elasticity within the active component, the storage of elastic energy in tendon is much more significant during natural locomotion (Alexander & Bennet-Clark 1977, Herbert & Crosbie 1997, Morgan et al. 1978). In tendon, differences in stiffness have effects on speed of force transmission and on usage of elastic energy in SSC. Compliance of tendon structures has been reported to have a favorable effect on usage of the elastic energy (Cavagna 1977, Kubo et al. 1999, 2000). It may be that a stiff muscle in series with a compliant tendon benefits from elastic mechanisms most. This has been suggested by Hof et al. (1983) who studied muscle-tendon interaction during human walking. He was able to show that in a concerted contraction, where activation is matched to the imposed load in order to keep the length of the contractile component constant, elastic recoil is considerable. Consequently, only little negative work is lost, fibers may operate near plateau of the force-length relationship, shortening speed is reduced and high power peaks may be delivered. In the present study, muscle stiffness was high in DJ where it was shown that shortening velocity of MTU was enhanced considerably by tendon action (III, VI). This demonstrates the dramatic effect that the tendon recoil can have in natural locomotion. Several experiments on animal locomotion have also stressed the importance of storage and recoil of elastic energy in tendinous tissues (Alexander & Vernon 1975, Biewener & Baudinette 1995, Gregor et al. 1988, Morgan et al. 1978, Roberts et al. 1997). However, while elastic recoil can be important in enhancing efficiency and performance through muscle-tendon interaction, it may not be responsible for increased maximal jumping performance (Anderson & Pandy 1993).

6.2.3 Other mechanisms

Mechanisms that could also affect performance enhancement are contractile potentiation and length-dependent behavior of the muscle. Potentiation of the contractile machinery depends on muscle length. Ettema et al. (1992) have shown that the effect of contractile potentiation is amplified when the muscle shortens from longer lengths while conversely being negatively influenced by the velocity of shortening. They showed also that at short muscle lengths a small but significant force enhancement in pre-stretch conditions was found only with lowest shortening velocity. Consequently, in the present study, a small amount of potentiation could have been present in DJ, where the fascicles operated at short lengths and low velocity (III, VI). However, this potentiation may not be responsible for the enhanced output of MTU that occurred at higher shortening velocities during late push-off phase of DJ. This is because the shortening of the fascicles started sooner than shortening of MTU and the transient effects of stretch-induced force-enhancement are abolished very rapidly (Edman et al. 1978, Noble 1992). To be more specific, the transient effects that last shorter time than residual effects are also greater in magnitude and thus, are more likely to have noticeable contributions to performance. Although Edman (1997) has suggested that residual force-enhancement component could contain a mechanism for improved SSC performance, others have not observed the entire phenomenon (Brown & Loeb 2000). In summary, even if there is contractile potentiation, the magnitude would be small and therefore, it may not be primarily responsible for SSC enhancement *in vivo*. Furthermore, in CMJ, the role of contractile potentiation is even more questionable because the transition between lengthening and shortening was slower, and potentiation is most prominent when the fascicle velocity changes rapidly (Brown & Loeb 2000). This does not mean that contractile potentiation does not have significance at all; on the contrary, it may well play a role in regulating the relative changes in muscle and tendon lengths during locomotion.

Apart from contractile potentiation, another mechanism may be considered in CMJ. In CMJ, both ATF and PTF started to increase during the unweighting phase, due first to the passive stretch and then during the active braking phase. During the initial passive stretch, both tendon and muscle may be expected to lengthen (Kawakami et al. 1998, Narici et al. 1996). Consequently, the muscle length, hypothetically, could be positioned on the descending limb of the force-length curve prior to activation. Then, when activity starts, the muscle shortens and moves towards the optimum length and gains force generating capacity (Gordon et al. 1966). Although the VL fascicles were identified to operate at shorter lengths during CMJ on the sledge (III), this mechanism may be operative in other conditions or muscles. Furthermore, this mechanism supplemented by increasing neural activity will magnify the potentiation effect.

Normally, when the muscle is allowed to shorten with constant activity the force decreases. This force decrease has been shown to depend on the initial length, the phenomenon being more marked on the ascending limb of the force-length relationship (Meijer et al. 1997). Comparison of VL fascicle lengths in SJ and CMJ showed that in CMJ the shortening phase started at longer (ns.) fascicle length although the knee joint angle was the same in both jumping conditions (III). Also, in maximal knee extensions the fascicle length was greater ($p<0.05$) prior to the concentric phase in SSC than in CON. These results suggest that the decrease in force production capacity is less when the shortening is initiated at longer muscle length. In fact, the present results in maximal knee extension show enhanced concentric performance in SSC as compared to CON, and suggest that the enhancement may be related to modified length-tension properties together (Huijing 1998) with longer initial fascicle length prior to shortening (V). The various mechanisms explained above stress the importance to consider the interplay between muscular activation, force, length, velocity, and elastic mechanisms in enhancing SSC performance.

6.3 Methodological considerations

6.3.1 Optic fiber force transducer

Optic fiber as a transducer of tendomuscular forces was first reported by Komi et al. (1996) who tested the method in rabbit Achilles tendon. First experiments where this method was applied to humans were reported in abstract form in 1995 (Komi et al.) and in first articles were published in 1998 (Arndt et al. 1998, Finni et al. 1998). Although the calibration was linear up to maximum effort in a report by Finni et al., high force region was of concern in the study by Arndt et al. Since those experiments the method has been improved and the insertion and calibration procedures have been further explored. However, also in the series of experiments of the present thesis it was observed that in some cases high Achilles tendon forces could cause permanent deformation of the optic fiber. Consequently, the calibration curve was not linear or was shifted to lower output range (Figure 5D). This was, however, observed only in a few subjects.

The reason for differential response in Achilles tendon among subjects may be partly explained by its architecture. Individual differences in the degree of medio-posterior rotation of the tendon may stress the optic fiber differently in high force region. Subjects with greater rotation may be more susceptible for permanent deformation of the fiber. Therefore, it is of great importance to perform careful calibration procedures when Achilles tendon forces are recorded, as described in 4.3.1.3. Further advances in ATF calibration could include the use of ultrasound in confirming that only soleus and gastrocnemius are activated during the stimulation calibration procedure. Thus, the true triceps surae contribution would be confirmed. Furthermore, it would be possible to stimulate gastrocnemius muscles selectively, and investigate the relative contribution of mixed (gastrocnemius) and slow (soleus) muscle on the Achilles tendon force.

In the case of the patellar tendon, the fiber response was highly reproducible even after high loading. It may be assumed that the tendon architecture allows more even stress distribution along the fiber going through the tendon. Therefore, in spite of the thicker tendon, measurements of patellar tendon forces can be performed also during strenuous activities.

An important finding was that the natural locomotor patterns, as observed with EMG, reaction force and kinematic recordings, were not disturbed by the presence of optic fibers in situ (Fig. 9). This confirms that the method is applicable for natural locomotion studies. As a technical detail, optic fibers with different properties could be used for different purposes. For example, fiber with high sensitivity could be used for measuring low force levels. When maximum forces are of interest, another type of fiber could be selected. In the present study, individual differences in the sensitivity of fiber output in very low force levels was found (Fig. 5A). In some subjects the low force level region could not be measured accurately, but at forces used during the jumping performances, the fiber responded as expected. Also these individual differences in sensitivity may stem from differential tendon structures.

6.3.2 Use of ultrasound for fascicle length determination

Ultrasound technique has recently become very popular in fascicle length measurements (e.g. Chow et al. 2000, Fukunaga et al. 1997b, Herbert & Gandevia 1995, Kawakami et al. 2000, Kumagai et al. 2000). Reliability of fascicle length and angle measurement has been confirmed by comparing manual measurement from cadavers (Kawakami et al. 1993, Narici et al. 1996) and reproducibility has been confirmed in several studies (Fukunaga et al. 1997, Kawakami et al. 1993, Kawakami et al. 1995). The resolution of the measurements depends on the used probe and the analyzing method. With the current technique, the resolution depends on the image size, as the digitizing procedure allows resolution in pixels no matter how small the image is. The width and depth of the image was adjusted for optimal visualization of VL without compromising the maximum possible scanning frequency of 42 Hz. The most critical aspect in fascicle length determination in the present study was the estimation of entire length. The parallelogram model used requires that the fascicles and aponeurosis are straight. However, curved fascicles have been reported especially in the triceps surae muscle (Maganaris et al. 1998) although linear models have also been used (Chow et al. 2000). In vastus lateralis muscle the curvature has been taken into account in some studies by using digital curvimeter for length measurements (Ichinose et al. 1997, 2000, Kawakami et al 1993, 1998). In relaxed VL muscle the curvature can be considerable but even a small amount of tension straightens the fascicle so that it is almost linear (see figures in Fukunaga et al. 1997a, 1997b, Kubo et al. 1999). With the method used in the present study, the effect of error in estimating the length was shown to be smallest in the mid thigh region where the images were taken (III). This can be seen also from constructed image of entire VL muscle in Fig. 1 of Ichinose et al. (1997). The problem of estimation could be resolved by using wider probe. Unfortunately, a wider probe requires that the scanning frequency be compromised with commercially available probes at the present time. Furthermore, during movement a wider probe would help only little because the entire length of VL fascicles cannot be visualized throughout the unrestricted movements. In jumping conditions especially, the fascicle, being fully visible in initial position, moved in relation to skin where the probe was fixed. As the same fascicle was followed throughout the movement it did not remain within the visualized area. Consequently, estimation was needed. Figure 24 illustrates how the linear estimation may differ only slightly as compared to the naturally occurring curved situation. In the present study, the average error of estimation was 4% ranging from 2 to 7%. An additional precaution of fascicle measurements during locomotion is that the full visibility of fascicles may be abolished when the skin moves in relation to the fascicle. If the fascicle cannot be seen, the probe position needs to be corrected for accurate length determination. With the above reasoning and limitations in mind, the present method was found suitable for determining fascicle lengths during human movement.

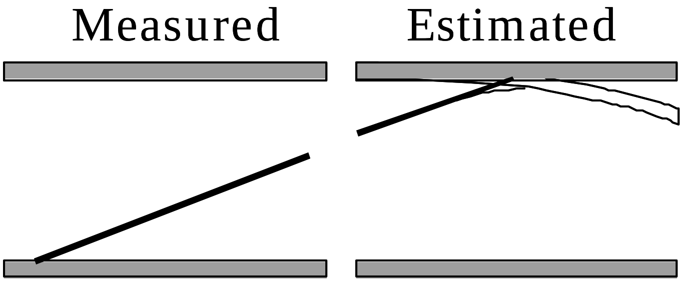

FIGURE 24 Schematic presentation of fascicle length determination (see also model in Fig 7). Measured fascicle length (thick line, left) was added to the estimated length using linear model (thick line on the right). However, the linear model did not differ significantly from the true condition where both the fascicle and aponeurosis curve (thin lines). Superficial and deeper aponeuroses are illustrated with oblique lineation.

6.3.3 Modeling the length of elastic components

A clear distinction between the two methodological approaches, the force and the kinematic method, in estimating the tendinous tissue length during locomotion is that although both of them showed the same pattern of behavior, the magnitude of length change was considerably different (IV). The high strain values obtained with the kinematic method may be explained by the fact that the method takes into account not only the thick tendon but also the aponeurosis. In addition, the compliance may be affected by pennation and unequal distribution of fascicle length change along the muscle length. Thus, the reported high strain values are not surprising because strain in the aponeurosis has been reported to be greater than in the thick tendon both during passive and active loading (Lieber et al. 2000). Furthermore, Fukunaga et al. (1997a) have shown that at given contraction level the fascicle shortening, and consequently, the tendinous elongation, is pronounced with extended knee joint angles, as in the present study, as compared to more flexed position.

According to a review by Zajac (1989) tendon stress in the non-linear toe region may vary form 5 to 30 MPa and strain from 1.5 to 4 %. Maximum stress in the tendon was found during DJ corresponding to 40 MPa with 4.9 % strain calculated from the force method. If we can consider that the force method describes better the force-length relationship of thick tendon it may be possible that the tendon was stretched to operate in a stiffer region at some point of the movement. As the kinematic measure includes also the aponeurosis the present results are in line with the concept of Kawakami and Lieber (2000) that aponeurosis could be the major source for in-series compliance, not the tendon.

Both methods contain several parameters that are subjected to error. The kinematic method with 10 % uncertainty was found to be more unreliable than the force method with uncertainty of 1 %. In the kinematic method most critical measures were the fascicle angle and the amount of fascicle length that was estimated. This error may be reduced considerably when the entire fascicle can be visualized throughout the motion in the ultrasound image as explained in 6.3.2. The force method was most sensitive to resting length (lo). Therefore, we further tested the model with VL tendon lengths measured from entire VL images but the results were not affected. As the uncertainties could not explain the difference between the methods, it can be concluded that the two approaches yield different measures. Tendon length changes are better described with the force method whereas kinematic method includes compliance of the aponeurosis as well.

Tendon elongation has been measured previously by means of ultrasonography in isometric condition using a reference marker on the skin (Fukashiro et al. 1995a, Maganaris & Paul 2000). However, the marker may not provide a stable enough reference in order to determine tendinous tissue length changes reliably during normal locomotion. The kinematic method with *in vivo* fascicle length measurements and muscle-tendon length estimations introduced here was shown to produce the same pattern as could be predicted from quadratic tendon force function. Although the magnitude of length change and strain were different the methods introduced here may be feasible for estimating the patterns of tendinous tissue length change during locomotion. In fact, this technique has been applied to measure gastrocnemius tendon length during walking in a recent report by Fukunaga et al. (2001). They reported tendon length changes to be around 1 cm in a walking cycle. During walking, however, simultaneous action of knee and ankle joints does not cause great changes in MTU length in the biarticular gastrocnemius muscle whereas the changes are more pronounced in a monoarticular vastus lateralis muscle (Pierrynowski & Morrison 1985). This can also explain the great length changes observed in the tendinous tissue of VL muscle during jumping exercises (III).

6.4 Perspectives

The results showed that the behavior of muscles is very much different during natural human locomotion with voluntary neural activity as compared to that expected from the classical force-length-velocity relationships found in maximally activated conditions. These differences arise from several factors such as history dependent behavior of force production that is not considered in most of the models that are used in examining muscle function. Therefore, experimental results should be compared with models for purpose of validity and development. *In vivo* tendon force and fascicle length recordings provide a very good possibility for this comparison during human movements.

Individual differences in voluntary activity level and patterns may sometimes be a source for heterogeneous results and hinder general conclusions from human studies. In search for mechanisms, the possibility is to use electrical stimulation to activate the muscle using the same relative amount of activity for each subject. A project where activity is standardized with electrical stimulation and fascicle length behavior is examined in pure concentric and stretch-shortening cycle muscle action is in progress.

7 PRIMARY FINDINGS AND CONCLUSIONS

1) The results from submaximal jumping performances support earlier views that elastic recoil and muscle activity play an important role in the concentric phase of SSC exercise. It was demonstrated that the MTU output could be enhanced in submaximal SSC performance over that found in maximal isokinetic measurements. The mechanisms behind the effective muscle output and the enhanced performance depend on type of the exercise and muscle of interest. In a multi-joint movement, the enhancement cannot be attributed to any single factor alone. Especially, the interaction between muscle and tendon components may be organized in a manner that takes advantage of the force-length properties of the muscle differently depending on the level and pattern of neural activity (I, III, V, VI).

2) Enhancement of concentric force production after stretch was found also in maximal knee extension exercises. This enhancement was not related to differences in EMG activity but may be attributed to modified length-tension properties together with longer initial fascicle length prior to shortening. These observations, in addition to those from submaximal jumping exercises (III), further suggest that it is important to consider length dependent behavior of muscles when examining factors affecting enhanced performance in SSC exercise (V).

3) Results from hopping with small knee joint displacement suggest that there may be a particular frequency and jumping height at which the elastic bouncing is best utilized and at the same time the concentric phase is most economical. It seems that naturally selected jumping frequency and appropriate input to muscles are important in factors for economical SSC performance. Results also support earlier observations that the economy of the shortening phase must be

compromised at some point in order to produce more power and improve the jumping height (II).

4) In all the examined SSC exercises where the MTU stretched prior to shortening the VL fascicle behaved the same way. The magnitude of length change was, however, dependent on the movement type and contraction intensity. In comparison of CMJ and DJ, the greater muscular activity reduced the magnitude and velocity of fascicle length change during the DJ. Because changes in MTU length were of same magnitude in both conditions, tendon stretching and shortening played a very important role in enhancing the velocity of the entire MTU in the push-off phase of DJ. It must be noted, that the energy stored in tendinous tissues during DJ did not come only from "free" gravitational potential energy, but from the active and stiff contractile elements (III, VI).

5) Tendinous tissue compliance has significant consequences on muscle function during locomotion. Methods for estimating muscle and tendon length changes are, however, mainly based on models where parameters from cadaver studies are used. In the present study, two models were tested and supplemented by *in vivo* recordings of fascicle lengths and tendon forces. The force and kinematic methods for estimating tendon length changes gave different results: the former characterizing external tendon behavior and the latter contained measure from both internal and external tendons. The utility of these methods depends on various estimations. Although both methods are applicable to dynamic movements, further testing is required to improve accuracy of the kinematic method, especially, because it provides a non-invasive tool for examining tendinous tissue behavior during human locomotion (IV).

YHTEENVETO

Ihmisen luonnollisessa liikkumismallissa lihaksen voimia tuotetaan venymislyhenemissyklin (SSC) tavoin. SSC:ssa aktiivinen lihas ensin venyy ja tätä seuraa välittömästi lihaksen lyheneminen. Lihaksen lyhenemisvaihe on SSC:ssa tehokkaampi ja taloudellisempi kuin tilanteessa, jossa lyhenemisvaihe aloitetaan ilman aktiivista esivenytysvaihetta. Usein SSC:tä on tutkittu seuraamalla lihasjännekompleksin pituudenmuutoksia. Kuitenkin lihaksen ja jänteen pituudenmuutosten vuorovaikutus luonnollisessa liikkeessä on erittäin monimutkainen johtuen mm. tahdonalaisen aktiivisuustason ja lihakseen kohdistuvan kuorman jatkuvasta vaihtelusta liikkeen aikana. Täten pelkästään lihas-jännekompleksia tutkimalla ei voida saada riittävän tarkkaa tietoa siitä, millä työtavalla lihas toimii, ja kuinka paljon voimaa, työtä ja tehoa lihakset tuottavat jokapäiväisissä liikkeissämme. Tässä tutkimuksessa käytettiin ainutlaatuista kuituoptista jännevoima-anturia akilles- ja patellajänteen kuormittumisen tutkimisessa, sekä ultraäänitekniikkaa lihassolukimppujen (fascicle) pituuksien mittaamisessa erilaisissa submaximaalisissa hyppelysuorituksissa ja maksimaalisissa polven ojennuksessa. Tutkimuksen tarkoituksena oli selvittää 1) jänteiden kuormittumismalleja sekä lihassolukimppujen käyttäytymistä erilaisissa liikkumistilanteissa, 2) miten voima-pituus- ja voima-nopeus -riippuvuussuhteet eroavat luonnollisessa liikkumistavassa ns. klassisesta tilanteesta, 3) miten tahdonalaisen aktiivisuuden taso sekä lihas-jännekompleksin pituudenmuutoksen suuruus vaikuttaa lihastyön tehokkuuteen ja taloudellisuuteen, ja 4) mitkä tekijät vaikuttavat suorituskyvyn potentoitumiseen SSC lihastyötavalla. Lisäksi vertailtiin kahta eri menetelmää jänteen pituudenmuutoksen arvioinnissa dynaamisen liikkeen aikana. Tutkimussarjasta tullaan julkaisemaan kuusi erillistä raporttia (I-VI). Tutkimuksen päälöydökset ja johtopäätökset voidaan tiivistää seuraavasti:

Submaximaalisessa, SSC:tä hyödyntävässä esikevennyshypyssä tarvittiin vähemmän lihasaktiivisuutta saman tehon saavuttamiseen hypyn konsentrisessa vaiheessa kuin puhtaassa konsentrisessa hypyssä. Esikevennyshypyssä konsentrisen vaiheen teho korreloi eksentrisen vaiheen lopussa tuotettuun voimaan. Kuitenkin lihasvoima ei välttämättä ollut huipussaan vielä eksentrisessä vaiheessa, vaan jatkoi kasvua konsentrisessa vaiheessa, johtuen mm. lihasaktiivisuuden kasvusta. Täten kirjallisuudessa esitetty seikka, että esikevennyksen hyöty tulisi vain ja ainoastaan siitä, että se mahdollistaa suuremman voiman ja aktiivisuuden jo ennen konsentrista vaihetta (Bobbert et al. 1996), ei ole yleistettävissä kaikkiin SSC suorituksiin. Tulokset viittaavat siihen, että esikevennyshypyn etu puhtaaseen konsentriseen hyppyyn tulee ainakin osittain voima-pituus -riippuvuussuhteen hyödyntämisestä. Voima-pituus-riippuvuuden mukaisesti lihas ei menetä voimantuottokapasiteettiaan lähtiessään lyhenemään pidemmältä lihaspituudelta niin paljon kuin lihas, joka on lyhyempi ennen konsentrista vaihetta. Verrattaessa lihassolukimppujen pituuksia ennen konsentrista vaihetta, olivat lihakset esivenytyksen jälkeen pidempiä kuin isometrisen tilanteen jälkeen sekä submaksimaalisessa hyppytestissä että maksimaalisessa polven ojennuksessa. Esivenytyksen tuoma pituusetu voitiin täten hyödyntää välittömästi seuraavassa konsentrisessa vaiheessa. Koska näissä mittauksissa lihas-jännekompleksin pituudenmuutoksia kontrolloitiin siten, että ennen konsentrista työvaihetta niiden pituus oli sama sekä esikevennystilanteessa että puhtaassa konsentrisessa tilanteessa, johtuivat lihassolukimppujen pituuksien erot lihaksen ja jänteen keskinäisestä vuorovaikutuksesta.

Pudotushypyssä ja hyppelyissä jänteen ja lihaksen vuorovaikutus korostaa elastisen energian hyödyntämistä. Esiaktiivisuus ja voimakas aktiivisuus kontaktivaiheessa minimoivat lihaspituuden muutokset ja mahdollistavat lihaksen toiminnan suurella voimalla ja hitaalla supistumisnopeudella. Täten jänne voi venyä varastoiden huomattavan määrän elastista energiaa, joka vapautetaan konsentrisen vaiheen lopussa, kun aktiivisuus ja voima pienenevät. Tulokset osoittavat jänteen olevan erittäin merkittävässä roolissa suuren supistusnopeuden saavuttamiseksi lihas-jännekompleksin tasolla, ja täten myös tuotetun tehon kasvattamisessa ponnistuksen loppuvaiheessa. Tämä tulos havainnollistettiin vertailemalla voima-nopeus -riippuvuussuhteita sekä lihassolujen että lihas-jännekompleksin tasolla. Lisäksi hyppelyissä mitattuja hetkellisiä voima-nopeus -käyriä verrattiin maksimaalisissa isokineettisissä suorituksissa mitattuihin ns. klassisiin voima-nopeus -kuvaajiin. Vaikka lihas-jännekompleksin voimantuotto olikin tietyissä tilanteissa suurempaa submaksimaalisessa hyppelyssä kuin maksimaalisessa vakionopeudella tapahtuvassa liikkeessä, ei potentoitumisilmiötä ollut havaittavissa lihassolukimppujen tasolla.

Luonnollisesti valittu hyppelytaajuus ja tarkoituksenmukainen lihasaktiivisuus ovat tärkeitä seikkoja liikkumisen taloudellisuuden kannalta. Tulokset viittaavatkin siihen, että on olemassa tietty taajuus ja hyppykorkeus, jolla elastisen energian hyödyntäminen on tehokkainta ja samanaikaisesti suorituksen konsentrinen vaihe on kaikkein taloudellisin. Tutkimustulokset tukevat aikaisempia havaintoja siitä, että konsentrisen vaiheen taloudellisuudesta pitää tinkiä, jos päämääränä on tehokas suoritus.

Jänteen pituudenmuutoksia dynaamisen liikkeen aikana arvioitiin kahdella tavalla: 1) suorien jännevoimamittausten perusteella, ja 2) lihassolukimppujen ja lihas-jännekompleksin pituuksien mittaamisen perusteella. Jännerakenteiden pituudenmuutokset olivat malliltaan samanlaisia riippumatta käytetystä menetelmästä, mutta muutoksen suuruus erosi huomattavasti. Paksun jänteen pituudenmuutoksia kuvasi paremmin voimaan perustuva arviointi, kun taas kinematiikkaan perustuva mallintaminen sisälsi pituudenmuutokseen myös aponeuroosin, joka on huomattavasti joustavampi kuin paksu jänne. Täten maksimivenymät olivat 5 tai 15 % lepopituudesta käytetystä menetelmästä riippuen.

Tämän tutkimussarjan perusteella voidaan sanoa, että vaikka lihaksen perusriippuvuussuhteet voimantuoton, pituuden ja supistusnopeuden välillä ovatkin universaaleja, luonnollisessa liikkeessä vaikuttava tahdonalainen aktiivisuus aiheuttaa lihaksen ja jännekomponentin välillä monimutkaisen vuorovaikutuksen. Tämän vuoksi supistuvan komponentin tekemää työtä on vaikea kvantifioida tarkasti ulkoisten mittausten perusteella luonnollisen liikkeen aikana. Lisäksi yksilölliset erot lihasrakenteissa ja opituissa aktiivisuusmalleissa vaikeuttavat pitkälle meneviä yleistyksiä erityisesti submaksimaalisissa liikkumistilanteissa. Tämän tutkimussarjan tulokset ovat osoittaneet, että menetelmälliset edistysaskeleet mm. suorien jännevoimien ja lihaspituuden mittaamisessa mahdollistavat lihaksen voimantuottoon vaikuttavien tekijöiden monimutkaisten vuorovaikutussuhteiden tutkimisen ihmisen liikkumisen aikana.

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