Chapter 4: Effects of Stretch Load and Preactivation on Muscle Performance during SSC –A Simulation Study

Introduction

In natural locomotion or exercise conditions, the human muscles seldom perform a pure form of isometric, concentric, or eccentric contractions. The nature muscle behavior is more often a stretch-shortening cycle (SSC), which is a combination of eccentric and concentric contractions (Komi, 2000). It is well documented that this type of muscle action enhances muscle mechanical output (Bosco & Komi, 1979; Cavagna et al., 1968; Komi & Bosco, 1978). Several mechanisms have been proposed to enhance performance during SSCs (van Ingen Schenau et al., 1997a, 1997b). These mechanisms include: 1) time available for force development (van Ingen Schenau et al., 1997a); 2) increased contribution of the stretch reflex (Komi & Bosco, 1978); 3) reutilization of elastic energy (Bosco et al., 1981; Komi & Bosco, 1978); and 4) potentiation of the contractile machinery (K.A. Edman et al., 1978; Ettema et al., 1992). To date, however, no consensus exists as to the exact contribution of these enhancement mechanisms (Cavagna, Kamarek, Citterio, & Margaria, 1971; van Ingen Schenau et al., 1997a, 1997b).

The stretch load has been reported to affect SSC performance. To obtain different stretch loads during the SSC, and a direct proportional relationship between stretch load and mechanical output during the concentric contraction, drop jumps performed at various heights have been examined in many studies (M. F. Bobbert, P. A. Huijing, & G. J. van Ingen Schenau, 1987; Bosco et al., 1981; Komi & Bosco, 1978). Drop height determines the downward velocity of the body's mass center (M. F. Bobbert et al., 1987), and thus influences muscle stretch velocity. Higher stretch velocity may increase the amplitude of the stretch reflex (Kallio et al., 2004) and the amount of the storage of elastic energy (Cavagna et al., 1968). Therefore, initially increasing stretch load may enhance muscle mechanical output. Komi and Bosco (Komi & Bosco, 1978) reported that jump height, as determined by the rise of center of gravity, increased when the drop height was increased from 26 to 62 cm in male participants from 20 to 50 cm in female participants. However, the contribution of stretch reflex and elastic energy are controversial in the literature (Bobbert, 1990; Komi, 2000; van Ingen Schenau et al., 1997a), and it is still not clear how the different stretch loads (velocities) affect stretch reflex and elastic energy to regulate the mechanical output.

While the stretch speed, the stretch amplitude, and interaction between fascicle and tendon directly (M.F. Bobbert, P.A. Huijing et al., 1987b; M.F. Bobbert, P.A. Huijing, & G.J. van Ingen Schenau, 1987; Komi & Bosco, 1978; Komi & Gollhofer, 1997; Takarada, Iwamoto et al., 1997) influence the muscle mechanical output, these factors are determined by the stretch load (downward velocity of the body's mass center at the moment of ground contact) and muscle activation level. The muscle activation level during eccentric contraction, in turn, will depend on the preactivation level if the same rate of muscle activation development is produced during SSCs. The high preactivation of the leg extensors and successively higher activation during the eccentric phase result in improved performance in SSC (Kyrolainen & Komi, 1995). For maximum SSC like drop jumps, if we assume muscles exert their maximal capacity to produce mechanical output under each condition and the initial muscles' lengths are same among conditions, the stretch load and preactivation may be the only factors regulating muscle mechanical output. Although the significance of the preactivation effect on SSC performance is convincing

(Kyrolainen et al., 1999), no study has quantified the effects of preactivation on muscle mechanical output during SSC under different stretch load.

Isolated muscle experiment is a common way to investigate the basic muscle functions. Performance enhancement following stretch is also observed in isolated muscle experiments (Cavagna et al., 1968; K.A. Edman et al., 1978; K. A. Edman & Tsuchiya, 1996; Herzog & Leonard, 2002; D. L. Morgan, 1990; Takarada, Iwamoto et al., 1997). In this type of experiment there is limited or no external tendon, no stretch reflex and 100% activation level during preactivation. These limitations make it difficult, if not impossible to describe the effects of stretch load and preactivation on muscle mechanical output. Muscle function may also be studied in vivo measurements of the muscle force using buckle type transducers (Komi, 2000) and optic fibers (Finni, Komi, & Lepola, 2000; Komi, 2000). However, there are some ethical and technical problems associated with these methods. Ultrasonography is an noninvasive method to measure the tendon and fascicle length changes during human movement (Finni et al., 2003; Kurokawa, fukunaga, & Fukashiro, 2001), but the tendon stretch measurement is not very accurate and derived velocities are rather noisy (Hof, 2003) because the low recording frequencies limit movement speed (Bohm, Cole, Bruggemann, & Ruder, 2006). Inverse dynamics is a common method used to determine joint moment and power during dynamic movement. However, this method cannot estimate directly muscle force and length change. Even if the muscle force can be estimated by using a muscle model, options for stretch load and preactivation levels are very limited and cannot be precisely controlled.Using a computer simulation to investigate the effect of stretch load and preactivation seems the best option to avoid these drawbacks.

The purpose of this study was to investigate the effects of stretch load and preactivation on muscle mechanical output. More specifically, gain in height, peak power, force at the start of concentric contraction and work production under different stretch loads and preactivation levels were examined. We hypothesized high stretch load needs a high preactivation to maximize the mechanical output.

Methods

A Hill-type (Hill, 1938) muscle-tendon complex model (MTC) (Nagano, Komura, & Fukashiro, 2004) (Fig. 1) was used for this study. The model consisted of three elements, a contractile element (CE), a series elastic element (SEE) and a parallel elastic element (PEE). CE represents the active part of muscle that is capable of voluntary contraction. SEE represents all series elasticity. The passive SEE transmits the forces from the CE to the load and is responsible for most of the elastic energy stored in the MTC. The series elasticity of the muscle fiber itself in the cross-bridges and myofilaments is neglected because the strain of the cross-bridges is very low at a giving muscle force (D. L. Morgan, Proske, & Warren, 1978) and the length of the external tendinous tissue is much longer than muscle fiber (Bobbert, Huijing, & van Ingen Schenau, 1986; van Ingen Schenau et al., 1997b). Therefore, although CE and SEE should be recognized as behavior models rather than anatomical models, in this study the SEE approximately represents the extern tendon and CE approximately represents muscle fibers (fascicle) of the MTC.

In this model, the proximal end of the CE was fixed (Figure 4.1). A weightless supporting object, keeping at the same position until the release time, was affixed to the distal end of the SEE. A weight with a downward velocity, representing the stretch load, landed on the supporting object at the release time. The downward and lifting of this mass through the SSC of the MTC corresponds to jump.

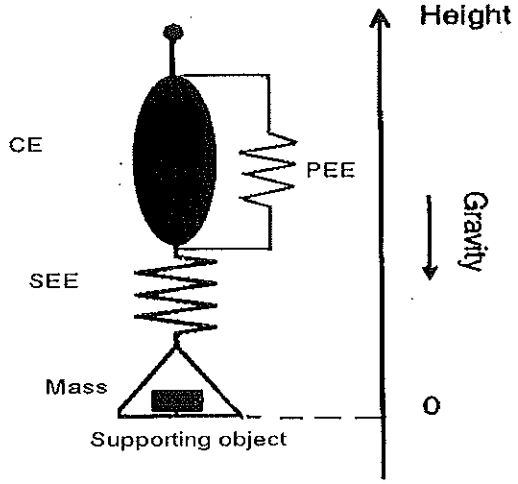

Fig. 4.1 The Hill-type muscle tendon complex consisted of two components: contractile component and series elastic component. (Adapted from Nagano et al., 2004.)

The magnitude of the CE force produced depends on four separate relationships(Gladwell, 2004), including stimulation-activation (SA), force-activation (FA), force-velocity (FV), and force-length (FL). SEE behavior was characterized by an undamped and non-linear force-extension relationship.

Stimulation-Activation

Physiologically, motor neuron action potentials (APs) trigger motor unit action potentials (MUAPs) that travel along muscle fibers. These MUAPs travel through the transverse tubule system to the sarcoplasmic reticulum, where they cause the release of calcium ions into individual sarcomeres. This process can be considered the stimulation (Gladwell,2004). The action-myosin complex responds to the calcium ion influx by changing from its resting state to an activated state. This is the activation part. The stimulation dynamics is difficult to ascertain, so some authors (Nagano et al., 2004; pandy, Zajac, Sim, & Levine, 1990) simplified it using "on" (100% stimulation) and "off" (0% stimulation) to represent the entire process. This on and off model cannot be used to study preactivation. Some studies used normalized surface EMG to represent stimulation dynamics. However, EMG is still a very fuzzy way to represent the stimulation because it is an output signal of the muscle rather than the stimulation input (Bobbert, Gerritsen, Litjens, & Soest, 1996). Another option is to use a constant rate of stimulation development. A rate of 2.2/s was used in a countermovement jump study (Bobbert & Casius, 2005). Although this constant rate may be different with the real stimulation dynamics, it does not favor any experiment condition. We therefore felt that the fixed rate of stimulation development was suitable to investigate the effect of preactivation and stretch load.

The exact shape of the relationship between stimulation (S) and activation (q) can be estimated by the following differential equation (He, Levine, & Loeb, 1991)

$$\dot{q} = (S - q) \cdot (t_1 \cdot q + t_2) \qquad (4.1)$$

where

$$t_2 = \frac{1}{t_d} \text{, } t_d \text{ is time constant for de-activation (65 ms)} \qquad (4.2)$$

$$t_1 = \frac{1}{t_a} - t_2 \text{, } t_a \text{ is time constant for activation (35ms)} \qquad (4.3)$$

For modeling purposes, both stimulation and activation will be placed on relative scales that range from 0 to 100%. In this study, the stimulation will be allowed to rise from different preactivation levels at a constant rate to its maximal value (van Zandwijk, Bobbert, Munneke, & Pas, 2000).

Force-Activation

Activation is a state in which force can be produced rather than an actual force level because the actual force level depends not only on activation, but also on the kinematic state of the CE. For modeling purposes, we consider the conceptual force-activation relation is direct and linear and actual force level will be determined by the kinematic state of the CE. For example, 20% activation can produce twice force compared to 10% activation when the kinematic states of the CE are same.

Force-Velocity

The CE force-velocity relation (Nagano & Gerritsen, 2001; Van Soest & Bobert, 1993) is expressed for the CE concentric contraction adopted from the Hill (Hill, 1938)equation:

$$Vce = -Factor \cdot L_{CEopt} \cdot \left(\frac{(F_{iso} + \alpha) \cdot \beta}{\frac{F_{CE}}{F_{MAX} \cdot q} + \alpha} - \beta \right) \tag{4. 4}$$

where Factor =Min (1, 3.33*q), α=0.41 and β=5.2, F_{CE} is force produced by CE. FMAX is the Maximum isometric force CE can produce at the optimum length. Fiso is the isometric contraction force with 100% activation.

For CE eccentric contraction phase,

$$V_{ce} = -L_{CEopt} \cdot \left(\frac{c_1}{\frac{F_{CE}}{F_{MAX} \cdot q} + c_2} - c_3 \right) \tag{4.5}$$

Where c1, c2, c3 were parameters to specify the shape of the eccentric force-velocity relationship:

$$c_2 = -F_{ISO} \cdot F_{asympt} \tag{4.6}$$

$$c_1 = \frac{FACTOR \cdot \beta \cdot (F_{ISO} + c_2)^2}{(F_{ISO} + \alpha) \cdot Slopefactor} \tag{4.7}$$

$$c_3 = \frac{c_1}{F_{ISO} + c_2} \tag{4.8}$$

where Fasympt is the asymptotic maximum force value in the eccentric phase. Slopefactor is the ratio between eccentric and concentric derivatives dF/dVCE at VCE=0. Fasympt=1.5, Slopefactor =2.0 were used (Van Soest & Bobert, 1993).

Force-Length

The force-length relationship of the CE was modeled as a parabola where the maximal force capability occurs at an optimal muscle fiber length (Gordon, Huxley, & Julian, 1966). The mathematical form of the CC force-length relationship can be expressed as following (Nagano & Gerritsen, 2001; Van Soest & Bobert, 1993):

$$F_{iso} = c \cdot \left(\frac{L_{CE}}{L_{CEopt}} \right)^2 - 2 \cdot c \cdot \left(\frac{L_{CE}}{L_{CEopt}} \right) + c + 1 \qquad (4.9)$$

where

$$c = \frac{-1}{width^2} \qquad (4.10)$$

LCEopt is the optimum CE length. L_{CE} is the CE length. Width is length range of force production relative to LCEopt on the on the ascending limb (half of length range of the parabola). Width=0.55 (Nagano & Gerritsen, 2001) was used in this study.

The force extension relationship of the SEC is expressed as following (Van Soest & Bobert, 1993)

$$F_{SEE} = F_{MAX} \cdot \left(\frac{\Delta L_{SEE}}{Stiff \cdot L_{slack}} \right)^2 \qquad (4.11)$$

where FSEE is SEE force production, ΔL_{SEE} is SEE deformation, L_{slack} is SEE slack length, and stiff is the SEE strain at maximum isometric force. Stiff was set at 4% (Nagano & Gerritsen, 2001; Van Soest & Bobert, 1993), which is in the range of values from in vivo Ultrasonography measurement (Magnusson, Aagaard, Dyhre-Poulsen, & Kjaer, 2001).

The force extension relationship of the PEE is expressed as follows (Delp, 1990)

$$F_{PEE} = F_{MAX} \cdot \left(\frac{L_{CE} - L_{CEopt}}{0.47 \cdot L_{CEopt}} \right)^3 \qquad (LCE>LCEopt) \qquad (4.11)$$

where F_{PEE} is PEE force production. PEE produces force only when CE length is great than CE optimal length.

Parameter values of the muscle tendon complex, such as maximal isometric contraction force of the CC (Fmax), optimal length of the CC (Lceopt) were calculated from the mean value of the six major leg muscle groups used in jumping simulation studies, i.e. Hamstrings, Gluteal muscles, Rectus femoris, Vasti, Gastrocnemius, Soleus (Bobbert & Casius, 2005). This procedure was performed to ensure parameter values are within normal physiological range.

Table 4.1. Muscle Parameters

Muscle	F_{MAX}(N)	Width %	L_{CEopt}	L_{slack}
GM	3700	36	0.12	0.19
BF	1700	70	0.1	0.4
RF	2000	80	0.16	0.35
VA	7000	34	0.09	0.25
GA	1400	56	0.06	0.42
SO	4100	58	0.1	0.35
Mean	3317	55	0.1	0.3

Note: FMAX and Width are adopted from (Van Soest & Bobert, 1993). LCEopt plus Lslack is the muscle resting length (Gerritsen, Van den Bogert, Hulliger, & Zernicke, 1998).

Algorithm

The CE was activated at a one particular level before release. Through this process, the CE will be shortened and the SEE will be stretched. When CE length below than optimal length, PEE does not produce any force. The CE and SEE forces are equal. After the system reached its equilibrium, t = release, the supporting object was released and stimulation was rising at 2.2/s until reach the particular level (see experiment conditions). The flow chart of modeling process is presented in Figure 4.2.

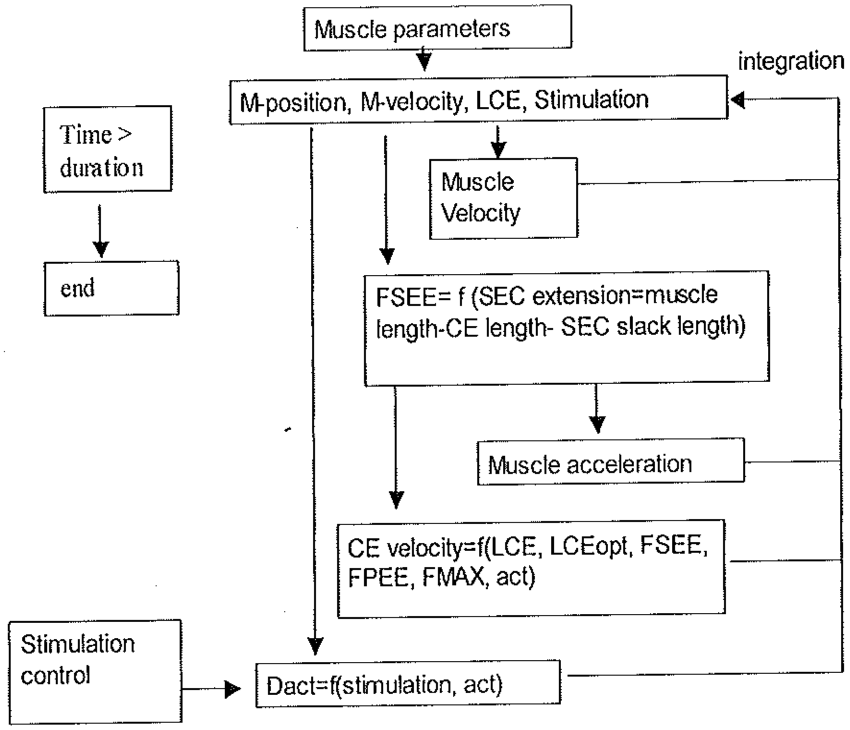

Figure 4.2 Flow chart of the modeling process. Figure 2 Flow chart of the modeling process. Integration of M-velocity, M-acceleration, CE velocity, and first derivative of activation (Dact) will output muscle distal position, muscle velocity, CE length, and activation level.

Experimental Conditions

Experiment 1

The stimulation raise from 0 to a specific preactivation level: 0% (no preactivation occurs), 10%, 20%, 30%, 40%, 50%, and 60% with a development rate of 2.2/s. Before release time, active state in each condition was stabilized at the particular preactivation level. When t = release, the MTC was released and the mass with a downward velocity landed on the supporting object. At the same time, stimulation was raising again at 2.2/s until preactivation level plus 30% maximum possible stimulation level. When t = 0.8s, the stimulation was dropped to zero.

During sprinting, the maximum muscle stretch velocity can reach close to 1.5m/s (Komi, 2000). Therefore, we set the downward velocity of mass from 0 to 1.5 m/s with 0.1/s increment. These velocities represent stretch loads and equal to the initial MTC stretch velocities. In the following sections, the term "stretch velocity" was used to represent the stretch load level.

Experiment 2

After release, the stimulation was rising until 90% maximum possible stimulation level. Some low preactivation level may not reach 90%. All other parameters are same with experiment 1.

Results

Figure 4.3 shows an example of simulation results. In this trial, the preactivation was stabilized at 40% before the mass hitt the supporting object with the initial velocity of 0.8 m/s. Then, the stimulation increased until 90% of maximum possible level of stimulation. From the time history of the mass position, we can see the muscle-tendon complex (MTC) underwent stretch-shortening cycle (SSC). From the initial to the lowest mass position, the MTC was stretching with negative mass velocity and MTC was producing negative power. From the lowest position to the highest position of the mass, the MTC was doing positive work. Therefore, the mass velocity and MTC power in this period were positive. The distance from the initial to the highest mass position is defined as the gain in height. The curves are similar to those of other experiment conditions.

Stimulation, Active State, and Gain in Height in Experiment 1

Figures 4.4 and 4.5 present the development of stimulation and active state respectively. For each preactivation level, the active states stabilized at a certain level. After the release time, active state rose and stabilized at level of preactivation plus 30% of maximum possible level of active state. The gain in height (Figure 4.6) produced by the MTC varied with the change of preactivation level and the initial stretch velocity. At low preactivation levels (0% and 10%), the MTC reduced the gain in height when the initial stretch velocities increased. When the initial stretch velocity increased further, the MTC could not go back to the initial position. At medium preactivation levels (20% and 30%), the gain in height suddenly dropped at a particular stretch velocity, then increased with stretch velocity. However, for the high preactivation level conditions (40%, 50% and 60%), the MTC always responded the increased stretch velocities positively. The greatest gain in height, 0.0496 m, was occurred at 60% preactivation with 1.5 m/s stretch velocity. For a particular stretch velocity, generally, the higher preactivation condition generated a greater gain in height.

Stimulation, Active State, and Gain in Height in Experiment 2

In experiment 2, for low preactivation conditions (0% and 10%), the gain in stimulation (Figure 4.7) exceeded 60% but the stimulation level never reached 90% of maximum possible level of stimulation. The active state (Figure 4.8) also increased about 50%. Accordingly, the gain in height (Figure 4.9) averagely increased 104% (0% preactivation) and 60% (10% preactivation) compared to experiment 1. More importantly, those low preactivation conditions could survive from much higher initial stretch velocities. However, the gain in height decreased with a greater stretch velocity at these levels.

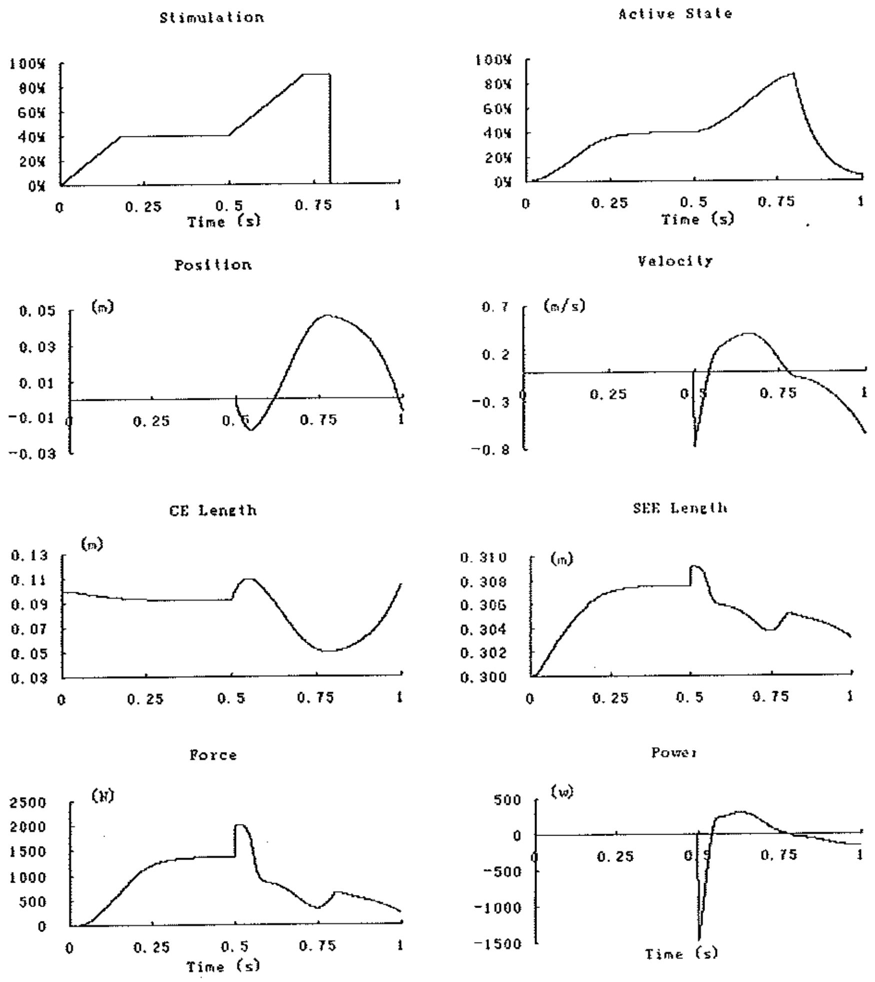

Figure 4.3. Exemplar time histories of stimulation, active state, mass position, mass velocity, CE length, SEE length, Force and power 40% preactivation with the initial stretch velocity of 0.8 m/s.

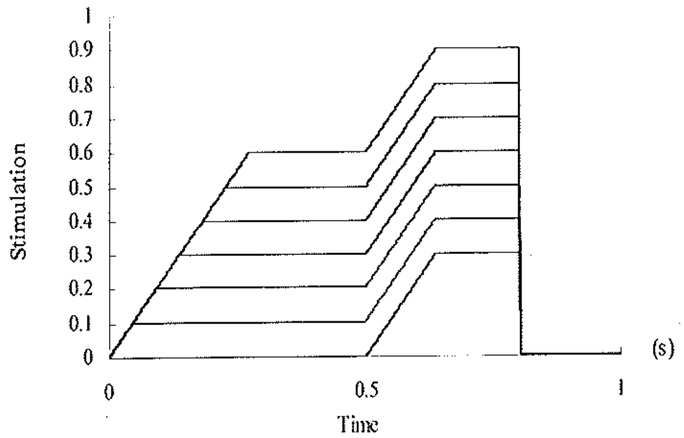

Figure 4.4. Stimulation developments in experiment 1. From low to high, each curve represents the condition with preactivation level of 0%, 10%, 20%, 30%, 40%, %50%, 60% respectively.

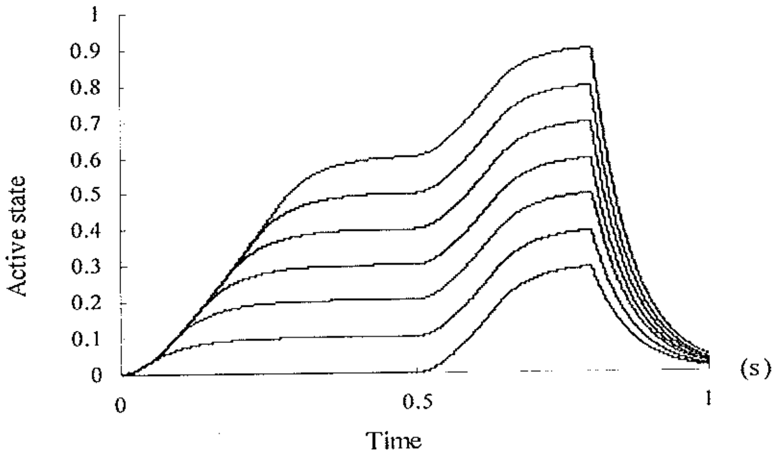

Figure 4.5. Active state developments in experiment 1. From low to high, each curve represents the condition with preactivation level of 0%, 10%, 20%, 30%, 40%, %50%, 60% respectively.

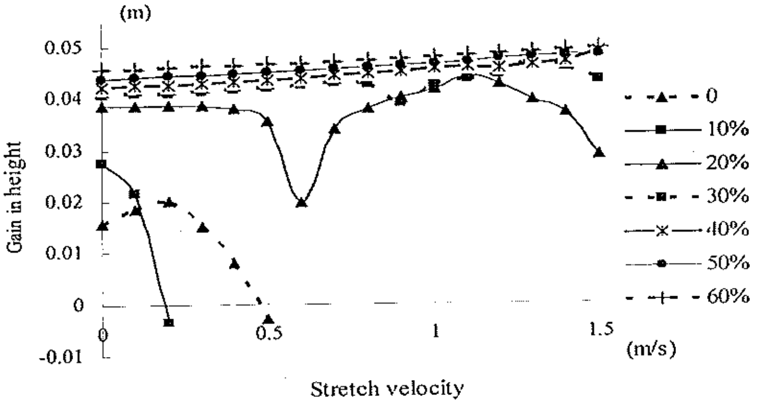

Figure 4.6. Gain in height achieved by the mass in the experiment 1 with 0 – 60% signifies the levels of preactivation.

For 30%, 40%, 50% and 60% preactivation conditions, the stimulation reached 90%, therefore the difference in peak stimulation was eliminated. However, difference in active state was still existed among different preactivation conditions. For most stretch velocities, the higher preactivation was associated with a higher gain in height. But the differences in gain in height were not significant. Although the gain in height only increased 3.4% (30% preactivation), 3.4 % (40% preactivation), and 2.14% (50% preactivation) when preactivation level increased to 60%. On the other hand, the gains in height contributed by stretch velocities were much greater. When stretch velocity increased from 0 to 1.5 m/s, the gain in height increased 11.7% (30% preactivation), 15.4% (40% preactivation), 11.9% (50% preactivation), and 8.5% (60% preactivation).

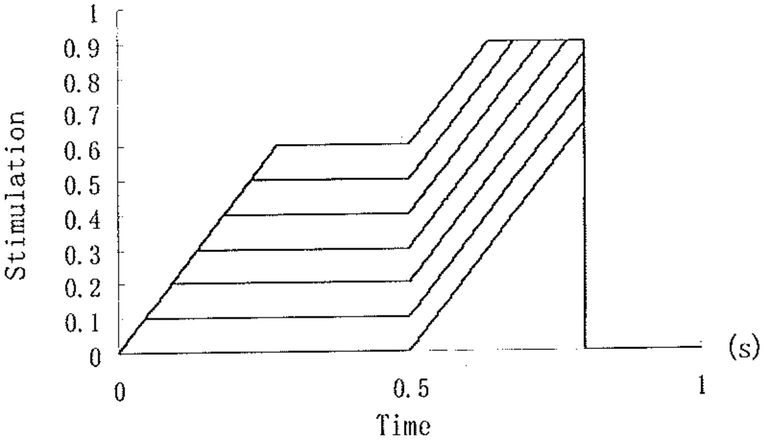

Figure 4.7 Stimulation developments in experiment 2. From low to high, each curve represents the condition with preactivation level of 0%, 10%, 20%, 30%, 40%, %50%, 60% respectively.

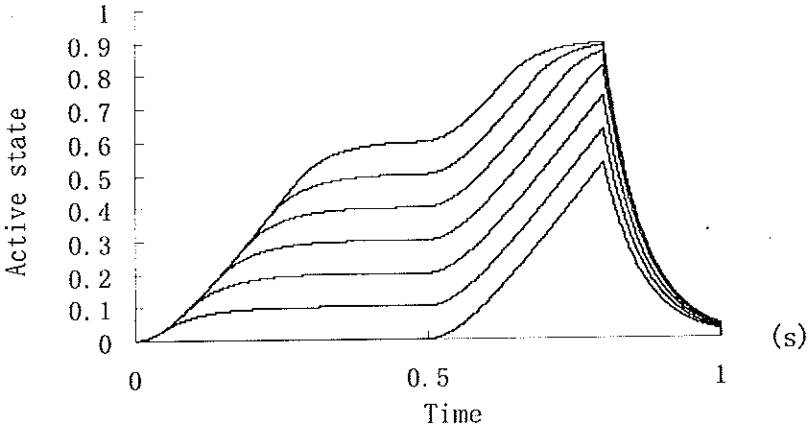

Figure 4.8. Active state developments in experiment 2. From low to high, each curve represents the condition with preactivation level of 0%, 10%, 20%, 30%, 40%, %50%, 60% respectively.

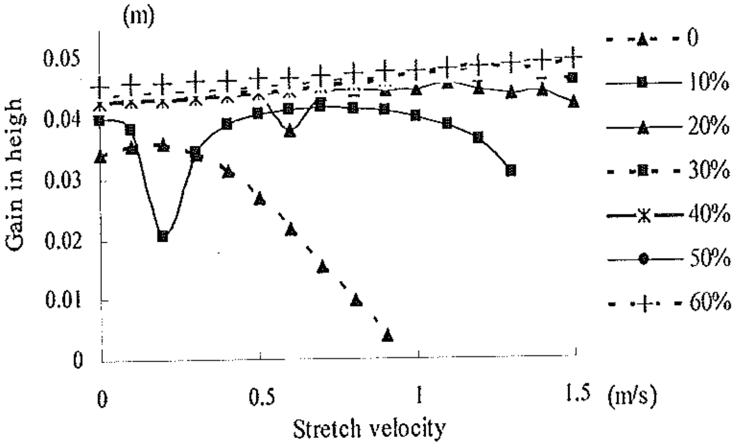

Figure 4.9. Gain in height achieved by the mass in experiment 2, with 0 – 60% signifies the levels of pre-activation.

Force Level at the Start of Concentric Contraction, Peak Power and Work Output in Experiment 2

Because the difference in force, power, and work between experiment 1 and experiment 2 is very small, we just present results from experiment 2 to illustrate the changes in force, power and work output. Figure 4.10 shows the force level at the start of concentric contraction obtained from experiment 2. A crucial stretch velocity was observed in 10% (0.2m/s), 20% (0.6m/s), 30% (0.9m/s), 40% (1.2), and 50% preactivation level conditions. Below this stretch velocity, force was insensitive to the stretch velocity but highly correlated with preactivation level. Beyond this stretch velocity, a small increase of stretch velocity resulted in a dramatic increase of force. This crucial stretch velocity has a higher value in the higher preactivation condition. But no crucial stretch velocity was observed in 60% preactivation level. The highest force (5387 N) occurred in 20% preactivation condition and was almost two times of that occurred in 60% preactivation . We also observed that the force produced by PEE started to play a major role at those crucial velocities (Figure 4.11).

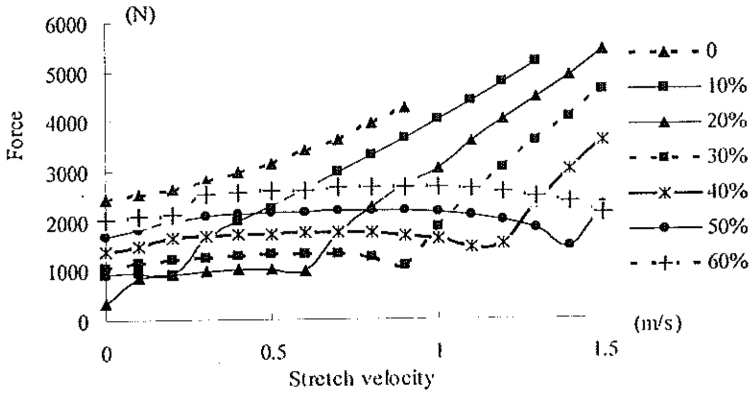

Figure 4.10. Force at prior to the start of concentric contraction with 0 – 60% signifies the levels of pre-activation.

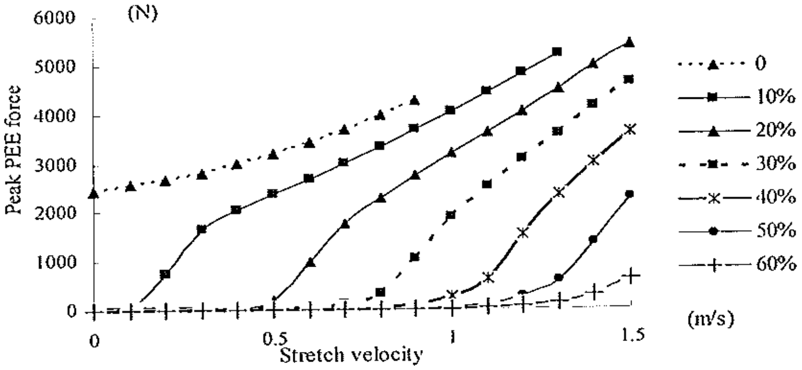

Figure 4.11. Maximum force produced by PEE with 0 – 60% signifies the levels of pre-activation.

A crucial stretch velocity was also observed in peak power (Figure 4.12). When stretch velocity was below 0.6 m/s, the highest peak power was produced at 0% preactivation level. When stretch velocity exceeded 0.7 m/s, a sharp rise of peak power was observed at 20% preactivation. At this preactivation level, when the stretch velocity increased to 1.5 m/s, the peak power reached 2075 w, which was the highest peak power observed in the experiment 2. However, the gain in height was only 58% of the greatest gain in height in experiment 1. The sharp rise of peak power was also observed in other preactivation conditions. Therefore, no correlation between peak power and preactivation level seems to exist.

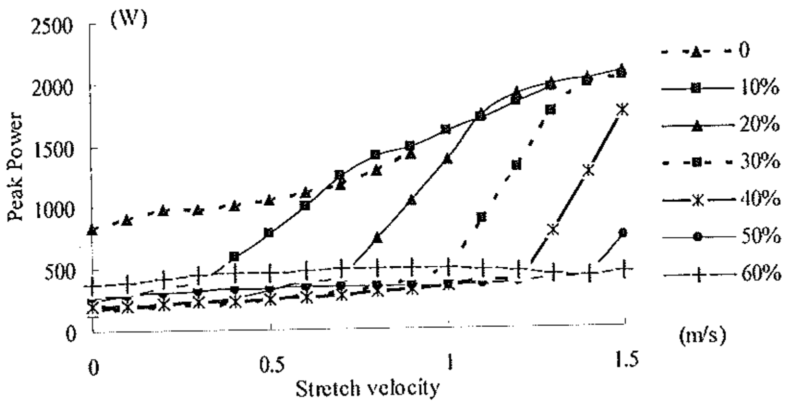

Figure 4.12. Peak power with 0 – 60% signifies the levels of pre-activation.

Figure 4.13 shows net, negative and positive work of MTC. Because those values are very close for 30%, 40%, 50% and 60% preactivation levels, for the clarity of figures, only 0%, 10% and 40% preactivation are showing in figures. 0% and 10% represent low preactivation, while 40% represent high preactivation level. The net work of MTC (4.13 A) decreased with increasing stretch velocity regardless the preactivation level. The net work of MTC was even decreased to negative with further increasing stretch velocity. On the other hand, for a particular stretch velocity, a higher preactivation contributed to a higher work production. This higher net work production was due to less negative work (4.13 B) rather than greater positive work associated with high preactivation. Figure 4.14 A shows that the changes in net work of MTC were mainly driven by CE. The net contribution of SEE (Figure 4.14B) was only 2.5 J regardless stretch velocities. However, this 2.5 J can really make a difference when CE produces all most identical amount work for different preactivation levels. The contribution of PEE to work production (Figure 4.14 C) was so small that it can be ignored.

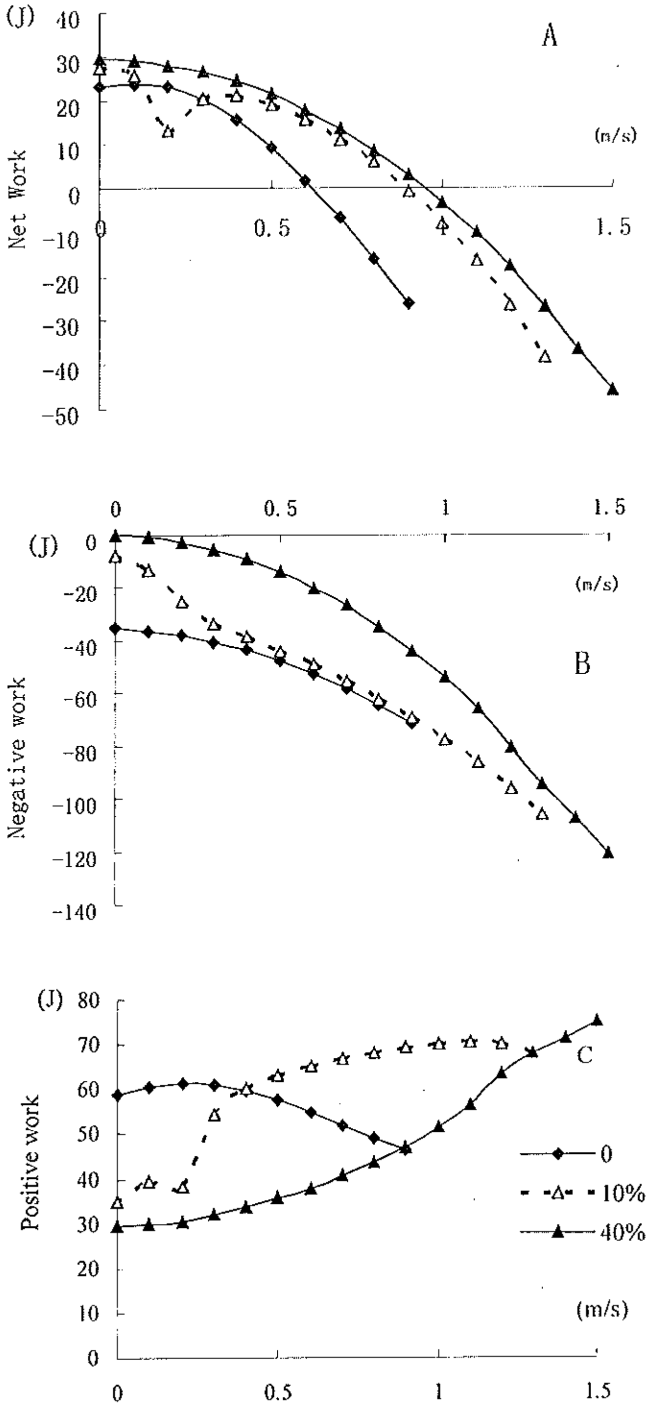

Figure 4.13. Net work (A), negative work (B) and positive work produced by MTC with 0 – 40% signifies the levels of pre-activation.

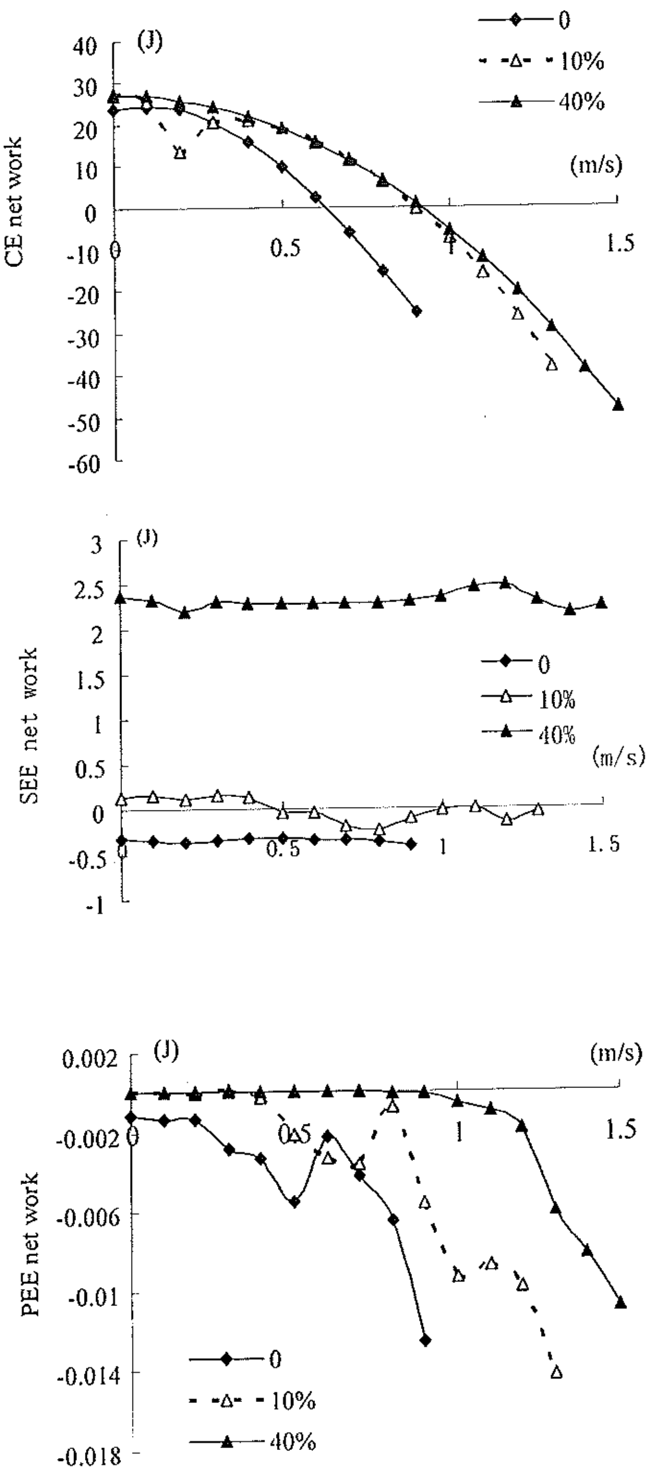

Figure 4.14. Net work of CE (A), SEE (B) and PEE (C) with 0, 10, and 40% signifies the levels of pre-activation.

Discussion

In the literature, it is widely accepted that preactivation and stretch load are two important factors for mechanical enhancement during SSCs. However, no studies have evaluated the interaction of these two factors quantitatively at the MTC level. Because of technical and ethical issues, it is difficult to measure MTC force and velocity in vivo. Therefore, a classic Hill-type MTC model was built to investigate effects of preactivation and stretch load on muscle mechanical output during SSC.

All muscle parameters used in the model are within human physiological range. Thus, the model reproduced reasonable phenomenon capable of being produced by humans. Consistent with results of our previous studies, this simulation study showed that increasing preactivation level, especially for low preactivation levels (0%-30%), dramatically enhanced muscle performance for all stretch velocities tested. One the other hand, stretch velocity enhanced muscle performance only with high preactivation levels. Conversely, with low preactivation levels (0-30%), increasing stretch velocity reduced muscle performance, which was in line with finding in our previous studies and other studies on human subjects (M.F. Bobbert, P.A. Huijing, & G.J. van Ingen Schenau, 1987; Bobbert & Ingen Schenau, 1990; Komi & Bosco, 1978). Stretch velocity was found to enhance power output. The "ceiling effect" of muscle performance enhancement associated with stretch load (velocity) was also observed in some conditions, though not all conditions. The force-velocity relationship determines the fundamental mechanical properties of MTC. The force-velocity curve obtained from this simulation study (Figure 15) is very similar with the curve recorded in an *in vivo* study. Overall, although assumptions were made and some muscle enhancement mechanisms were not included in this model, the model was realistic and valid for this study.

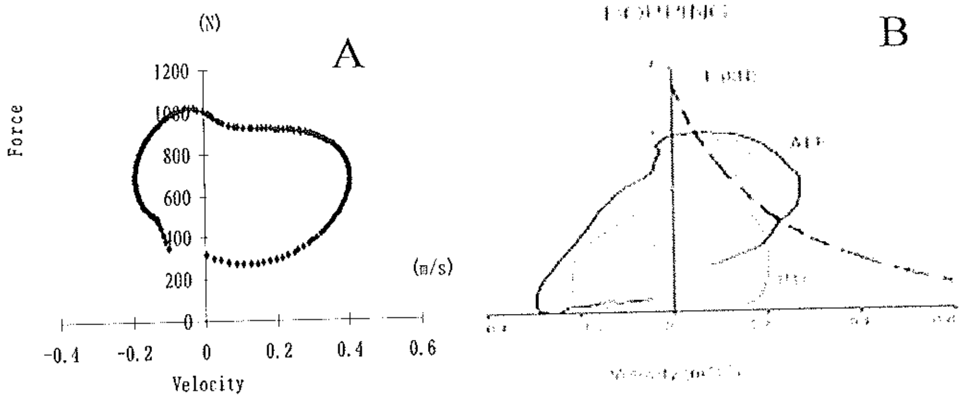

Figure 4.15. Force –velocity relationships of MTC from the present study (A) and an in vivo recording (B) adopted from Komi (2000).

In both experiment 1 and experiment 2, a higher preactivation was found to enhance the gain in height. However, the magnitude of enhancement is smaller in experiment 2. The input difference between experiment 1 and experiment 2 is stimulation development. Experiment 1 allowed additional 30% stimulation adding to the preactivation level and active state also stabilized at addition 30% level. Therefore, the maximum active state was 30%, 40%, 50%, 60%, 70%, 80%, and 90% respectively.

Experiment 2 allowed stimulation increase for 0.3 s or stabilized at 90% (0, 10 and 20% preactivation can not reach 90% stimulation level) and difference in peak stimulation for 30%-60% preactivation was eliminated. Due to the time gap between stimulation development and active state development, there was a difference in active state among different preactivation levels. However, this difference was much smaller in experiment 2 compared to experiment 1. Obviously, the effect of preactivation on muscle performance is due to active state development. This explanation is in line with the findings of Bobbert and Casius (Bobbert & Casius, 2005)

In addition to enhancing muscle performance, preactivation has special meaning for fast movements like sprinting, in which the total contact time is only about 90-100 ms (Komi,

2000) and the braking phase may be less than 50ms. However, the rise time of muscle stimulation reported by van Zandwijk et al. (van Zandwijk et al., 2000) is much longer (100ms-300ms). On the other hand, those fast movements generally need to experience a very high stretch load. An in vivo study showed that the maximum stretch velocity of AT-triceps surae complex at a high running speed (9.02m/s) could reach 1.3 m/s. Because of time constraint, stimulation development during ground contact is very limited and the active state level will be exclusively depended on preactivation level. As illustrated in experiment 1, low preactivation conditions (0 and 10%) cannot survive from high stretch velocities. Studies on human experiments (Kakihana & Suzuki, 2001; Kyrolainen et al., 1999) have reported that muscles are highly preactivated before landing during sprinting and long jump. Combined with those findings and the results of this simulation study, it is concluded that a high level of preactivation is a prerequisite for those SSC with high stretch velocity and time constraint. In other words, for explosive movement like sprinting, long jump, high jump, and triple jump, preactivation is not just a matter of mechanical output enhancement, it is a matter of "capable and incapable".

Force level prior to the start of concentric contraction was considered as a major factor influencing the muscle performance. A classic explanation in the literature why countermovement jump height is greater than squat jump height is countermovement allows muscle to reach a maximum value before shortening. Some authors (van Ingen Schenau et al., 1997b) suggested that this difference in force level can explain exclusively the difference in jump height. However, this simple correlation between force level and muscle performance was not found in the present study. Also this force was very sensitive to stretch velocity due to effect of PEE. Because the effect of PEE may be very small in human movement (Bohm et al., 2006; van Ingen Schenau et al., 1997b), we graphed a figure (4.17) presenting conditions without PEE effect. Clearly, this force was in proportion with preactivation. However, the higher force level prior to the start of concentric contraction may not necessarily produce a higher performance. Figure 4.16 shows force-time histories of 30% and 40% preactivation with 0.5 m/s initial stretch velocity. A higher initial force did not promote the whole force-time curve and no more impulse was produced due to a rapid decay was followed (40% preactivation). Two conditions produced almost identical jump height (Figure 4.9). The phenomenon that a higher initial force associated with a rapid force decay was also found in a human subject experiment (Finni et al., 2001). Therefore, although the high force level prior to the concentric phase is an important factor in performance enhancement, it cannot explain total performance enhancement during SSCs.

Contribution of stretch reflex to performance enhancement during SSC has been a controversial topic for a long time (Komi, 2000; van Ingen Schenau et al., 1997a, 1997b).The first key issue in the debate is whether or not the stretch reflex occurs during SSC. In vivo studies using Ultrasonography showed that (Fukashiro, Hay, & Akinori, 2006; Kurokawa et al., 2001) muscle fibers of the MG were not lengthened at all during the counter movement jump and 20 cm drop jumps. Therefore, stretch reflex may not occur at all during those SSCs. Certainly, the stretch reflex will be more likely trigged by a fast stretch. The second key issue in the debate is time delay. Many different time delay durations and two different definitions of delay have been reported (Komi, 2000; van Ingen Schenau et al., 1997b). To our knowledge, there is no stretch reflex simulation model in the literature that can evaluate the effect of preactivation level and stretch velocity on stretch reflex. Therefore, we did not include a stretch reflex simulation model in the present study. Our previous study showed that the stretch velocity may not influence the gain of stretch reflex, but preactivation can significantly increase the gain of stretch reflex, which is consistent with findings reported by Matthews (Matthews, 1986) that the reflex gain increases with preactivation level. Therefore, the contribution of preactivation may be underestimated in the present study.

The storage and reutilization of elastic energy was one of the enhancement mechanisms proposed in the literature (Avis, Toussaint, Huijing, & van Ingen Schenau, 1986; Komi & Bosco, 1978). During stretch, the MTC is doing negative work, part of which is later reutilized for positive work (Bobbert et al., 1996). Although van Ingen Schenau et al. (van Ingen Schenau et al., 1997b) agree that elastic energy can be largely reproduced from the negative work, they argued that the origin of work enhancement is in the CE which can produce more force. They used drop jump as an example to support their argument: if CE cannot produce more force, even if the drop height is increased and more negative work can be produced, the extra work is dissipated as heat. Our results supported this argument. For low preactivation levels, a high stretch increased MTC negative work dramatically, but the positive work did not increase or even decreased (Figure 4.13). Clearly, stretch velocities can enhance positive work done by MTC but only in high preactivation levels.

Because a one-muscle model was used in the present study, some results are different from that of observations in human experiments. First, the gain in height is much smaller than jump height in human experiments. Secondly, peak power has been reported highly correlated with jump height in drop jumps (Horita et al., 2002a) but this correlation was not found in the present study. Other limitations include the lack of stretch reflex incorporation in the model, no joint structure limiting overstretching, and simplified length of CE and SEE as muscle fiber length and tendon length. Those limitations suggest some observations in this study may not be generalized in human movement. However, those limitations likely do not affect our major findings in the present study because most major finds are in line with literature and results of our previous human subjects experiments.

In summary, preactivation and stretch load can affect MTC mechanical output. However, mechanical output enhancement depends on interaction of preactivation and stretch load. Increasing preactivation enhances muscle performance due to raised active state levels. For low preactivation levels, increasing preactivation level can significantly increase gain in height for all stretch velocities we tested, but increasing stretch velocity may decrease the gain in height. For high preactivation levels, mechanical output may not increase or just increase a small amount if preactivation level is increased but stretch load does not change. In contrast, increasing stretch load alone can significantly enhance mechanical output at those high preactivation levels. Therefore, to maximize muscle performance, a high stretch load must correspond to a high preactivation.

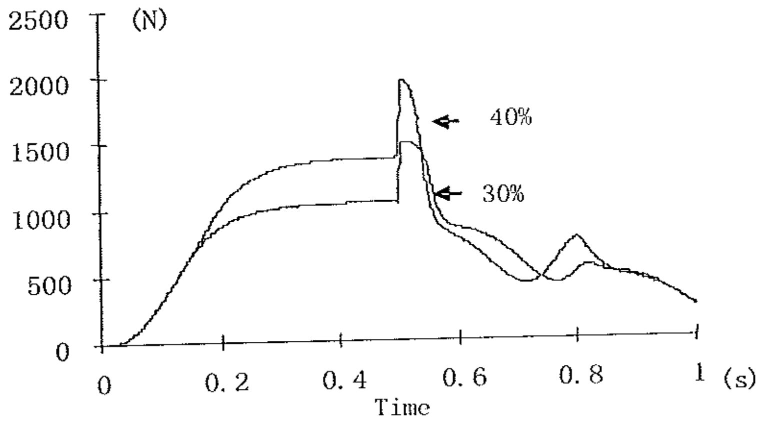

Figure 4.16 Force at the start of concentric contraction in conditions with 0.5 m/s stretch velocity.

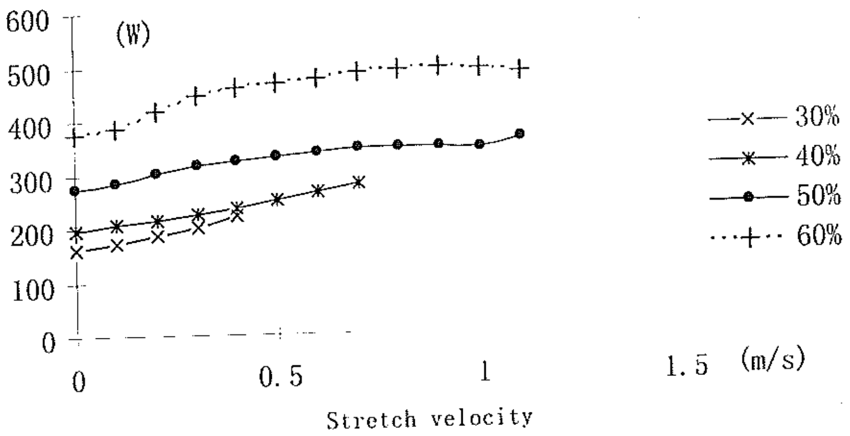

Figure 4.17. Peak power for 30-60% preactivation conditions without PEE effect.

Chapter 5: General Discussion

The purpose of this series of experiments was to better understand the SSC, the most common muscle behavior in human locomotion and explosive exercises. The stretch load and preactivation level as two important factors, which can regulate muscle mechanical output, were systematically examined in this series of studies. Although there are still debates in the literature about the performance enhancement mechanisms during SSC, results from the inverse dynamic study, the EMG study and the stimulation study are believed to provide an insight into the contributions of stretch load and preactivation on maximizing muscle mechanical output. The findings from this series of studies will not only contribute to scientific advancement but may also inspire innovational movement strategies and training practices (van Ingen Schenau et al., 1997b).

Overview of Results

In the literature, drop height is the most common way to adjust stretch load and then regulate the mechanical output (Bobbert, 1990; M.F. Bobbert, P.A. Huijing, & G.J. van Ingen Schenau, 1987; Komi & Bosco, 1978). A study (Saunders, 1980) also showed that a horizontal approach preceding vertical jumps (vertical jump and approach were at the same ground level) could increase jump heights. The results of chapter 2 showed that an approach preceding drop jumps could enhance summed peak power approximate 10% regardless of the number of steps. There results were attributed to the knee joint response. This enhancement was hypothesized due to increased preactivation level associated with approach.

This hypothesis was examined in Chapter 3. The results showed that the aEMG of most tested muscles during preactivation phase and downward phase increased with more steps of approach. This increase did not change the antagonist- agonist coactivation ratio, therefore would not attribute to knee joint injury. On the other hand, no aEMG changes were found with different drop heights. Because approach is associated with preactivation level and drop height is associated with stretch load, direct investigation on effects of preactivation and stretch load on muscle mechanical output was performed in Chapter 3.

A Hill-type muscle model was used in Chapter 3 to test muscle mechanical output under combination of different preactivation level and different stretch load. Results showed that for low preactivation levels, increasing preactivation level can significantly increase gain in height for all stretch velocities we tested, but increasing stretch velocity may decrease the gain in height; for high preactivation levels, further increasing preactivation level may not increase gain in height; to maximize gain in height, a high preactivation must accompany a high stretch velocity.

Overall Discussion

Contribution of Stretch Load to Muscle Mechanical Output

A quadratic trend of peak summed power across drop heights observed in the Chapter 2 suggested contribution of stretch load to mechanical output can positive or negative. The critical value between positive and negative effect is the optimal stretch load.

When stretch load is below the optimal load, an increased angular velocity of dorsiflexion with a higher drop height implied that a higher stretch load may enhance the gain of stretch reflex because the effect of stretch reflex is suggested to increase with stretching velocity (Bosco et al., 1981; Kallio et al., 2004). However, there are still debates in the literature about the contribution of stretch reflex (Komi, 2000; van Ingen Schenau et al., 1997b). While there is no doubt that stretch reflex is triggered during stretch, as clear bursts in rectified EMG presented in Chapter 3, the stretch load may not change the gain of stretch reflex as muscular activation did not change with drop height as results showed in Chapter 3. The possible reason is changes of velocities of muscle spindle associated with stretch load are not great enough to regulate the gain of stretch reflex. It is likely that the influence of stretch load on gain of stretch reflex is not necessary to consider as long as stretch reflex is triggered.

Although some authors questioned the amount of elastic energy in human movement, it is convincing that elastic energy will be released to concentric contraction. For same muscular activation level, a higher stretch load will produce more negative work of MTC. However, the amount of positive work done by the MTC was not determined by the negative work produced by MTC. First, the amount of elastic energy stored in elastic elements is not determined by the negative work done by the MTC (van Ingen Schenau et al., 1997b). During the eccentric contraction, the amount of elastic energy stored is smaller than the amount of negative work done by the MTC because CE is doing negative work too. Because effect of PEE is very small in human movement, we just discuss the effect of SEE. The amount of energy stored in SEE can be determined by the force at the start of concentric contraction. Second, the elastic energy released during concentric contraction may be smaller than that stored in SEE due to CE lengthening, which was observed in some conditions of the simulation study. More importantly, influence of stretch load on positive work is strongly depended on the preactivation level. Only at high preactivation levels can stretch load increase positive work.

When the stretch loads go beyond of the optimal value, muscle mechanical output and performance may decrease. This ceiling effect was observed in the first study (Chapter 2).

The possible explanation is reduced shorten range stiffness (Bosco & Komi, 1979) and cross bridges detachment due to over stretch (Flitney & Hirst, 1978; Syme & Grattan, 2002).

Contribution of Preactivation on Muscle Mechanical Output

In explosive exercises, the short duration time limits muscle force development. This slow force development is due to three processes (van Ingen Schenau et al., 1997b): the finite rate of stimulation development (stimulation dynamics); the time delay between stimulation and active state (excitation dynamics); and the time constant of force development in response to active state (contraction dynamics). On the other hand, muscles performing explosive exercises must tolerate huge stretch loads. To increase force of muscles to very high value in a very short time, a high preactivation level is the only solution. As showed in chapter 4, preactivation can move part of three processes before landing. Consequently, stimulation, active state, and force could reach higher values after landing. Even if stimulation could reach to the maximum possible value, preactivation still can contribute to a higher active state level due to stimulation- active state coupling. Therefore, the main function of preactivation is to enhance the active state level during SSCs.

Because reflex gain is related with excitation level of the motoneuron pool (Matthews, 1986), increased preactivation level may enhance amplitude of stretch reflex. In Chapter 3, a higher level of muscular activation associated with a higher preactivation was found. Also, preactivation has been suggested to enhance tendomuscular stiffness (Komi, 2000). Although we could not quantify the relationship between preactivation level and amplitude of stretch reflex in the simulation study due to lack of suitable stretch reflex model, it is convincing that the increased preactivation level potentiates the functional role of stretch reflexes.

The enhancement of mechanical output is very significant when preactivation initially increases. However, further increasing preactivation, the magnitude of enhancement became very small. The conclusion was obtained from the simulation study, but also supported by human subjects' studies. When one approach step was added to drop jump, preactivation level initially increased. Consistently, the greatest difference in mechanical output was found between standing drop jump and drop jump with one approach step. Further increasing approach steps, a further but smaller enhancement was observed. As results showed in Chapter 4, a high preactivation level needs a high stretch load to further enhance muscle mechanical output.

A Small Step Makes a Big Difference: Relevance of the Observations to Application

The preactivation is interpreted as a preprogrammed neuronal activation (Dietz et al., 1978 ; Gollhofer & Kyrolainen, 1991). It was suggested that muscle co-contraction in anticipation of landing (Ingen Schenau G.J.van. et al., 1997b) or pre-landing movements (T. Horita, P.V. Komi, C. Nicol, & H. Kyrolainen, 2002b) can increase the preactivation level. This series studies verified that an approach before jumping is a good strategy to increase preactivation. A small step before jumping makes a big difference. This step may not only increase the mechanical output, more importantly, it also reduces downward duration time and makes the whole action quicker. In many sports, being a little faster than opponents is essential to win the game. In other words, whoever takes advantage of preactivation may have a decisive edge in the competition.

Exercises with an extremely high stretch load may need a very high preactivation. Thus, a small step may not be enough to trigger a very high preactivation. More approach steps associated with fast speed may be an option to further increase the preactivation level.

However, there may not be enough space or time for more approach steps. Certainly, a step preceding an explosive movement is not the only strategy to increase preactivation. A study showed (Horita et al., 2002b) that a small and fast knee flexion before landing may trigger a stretch reflex and raise preactivation level. Other strategies include vestibular and visual inputs (Avela, Santos, Kyrolainen, & Komi, 1994), and verbal instructions (Arampatzis, Bruggemann, & Klapsing, 2001).

To maximize muscle mechanical output, a high preactivation must cooperate with a high stretch load. Drop height is a common way to adjust stretch load in explosive exercise training. Also, a high approach speed can increase stretch load. In some sports, a high drop height and approach speed may not be available to increase stretch load. Generally, athletes use segment movement to increase stretch load. For example, during downward phase, a rapid arm swing up or one leg raise up can produce initial force and increase stretch load.

Future Research

Because a simplified one-muscle model was used in the simulation study, some results are not consistent with human experiments. Ideally, future *in vivo* studies should focus on interactions between tendon and fascicle, muscles coordination, power transfer from proximal joints to distal joins under combinations of different stretch load and preactivation should be performed. In the near future, some in vivo measurements may not be available. Simulation studies will still be a very important method to investigate SSCs. A more complicated, segment-joint model or whole body model should be used. A better estimated SEE and CE length for each muscle could be performed. A more reasonable stimulation dynamic and stretch reflexes could be included in the model.

For application studies, a training study should be performed to examine whether drop jumps with an approach is a better training method for explosive exercises comparing to standing drop jump. To further apply knowledge obtained from this series study to sports, studies should focus on strategies and pre-landing movements that can regulate stretch load and preactivation. Ultimately, general recommendations for maximizing mechanical output and specific solutions for improving athletic performance will be achieved.

Conclusions

While the drop jump has been proved to be a good training method to improve jump performance due to enhanced mechanical output, we found drop jump with an approach can increase mechanical output further and even exceeded the ceiling effect associated with increasing drop height. EMG records showed the approach preceding jumps enhances muscular activity of major leg muscles during preactivation phase and downward phase. The main function of preactivation is to enhance the active state level and facilitate stretch reflexes during SSCs. Only when preactivation level is high, stretch load can increase muscle mechanical output.

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Appendix 1. Expanded Literature Review

1. Introduction

Human muscles often involve sequential lengthening and shortening activities, that is the stretch-shortening cycle (SSC), in our daily locomotion, such as running and walking. The SSC also commonly happens in explosive movements， such as throwing, sprinting and jumping. Experiments have demonstrated that SSCs induce greater contractile force and produce greater mechanical work and power output (Komi, 2000) .These experiments usually first stretch active muscles (pre-stretch) and then immediately allow them to shorten. These experiments have been performed on isolated muscles (Cavagna, Dusman, & Margaria, 1968; Ettema, Huijing, & Dehaan, 1992), as well as on *in vivo* human dynamic movements (Bosco & Komi, 1979; Bosco, Komi, & Ito, 1981; Cavagna, Dusman, & Margaria, 1968; Komi & Bosco, 1978)

Several mechanisms have been proposed to enhance performance during SSCs (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a, 1997b). These mechanisms include 1) time available for force development (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a); 2) contribution of stretch reflex (Komi & Bosco, 1978); 3) reutilization of elastic energy (Bosco, Komi, & Ito, 1981; Komi & Bosco, 1978); and 4) potentiation of the contractile machinery (Edman, Elzinga, & Noble, 1978; Ettema, Huijing, & Dehaan, 1992). A target article by van Ingen Schenau et al. (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a) and subsequent peer commentaries (Edman, 1997; Farley, 1997; Goubel F., 1997; Komi & Gollhofer, 1997) demonstrated a variety of explanations on these proposed mechanisms. The main reason for the variety of explanations is that some study results were obtained from experiments of isolated muscles or single muscle fiber and should not be broadly generalized for human movement (Goubel F., 1997). The different hypotheses indicated that studies focusing on the mechanical properties of muscles operating under *in vivo* conditions were needed. Recent studies investigating SSCs through *in vivo* observation may provide a better insight on this issue. Understanding what roles these mechanisms play in the process of mechanical output enhancement is not only important scientifically but also implies possible movement strategies and training practice (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a).

Scientifically, understanding the integration of mechanics, muscle mechanics, muscle physiology, and neurophysiology is fundamental to increasing our knowledge in human movement (P.V. Komi, 1984). Therefore, we have to understand the effects of the nervous system (e.g. stretch reflex), mechanical factors (e.g. stretch load and stretch velocity), muscle mechanical factors (e.g. elastic energy) and physiological factors (e.g. potentiation of contractile machinery) on the performance during SSCs. And more importantly, we have to understand the interactions between these factors. For example, the role of stretch reflex and inhibitory reflexes with different stretch loads could be identified with a good understanding of interactions between these factors.

From the point of application, a good understanding of mechanisms may cause a revolution in sports techniques. For example, the importance of series elastic component (SEC) as power amplifier has inspired researchers to design a new innovative skate (G. J. Van Ingen Schenau, De Groot, Scheurs, Meester, & De Koning, 1996). On the other hand, an incomplete understanding of mechanisms involved would lead to wrong suggestions for training practice. For example, several authors (Kyrolainen, Finni, Avela, & Komi, 2003; Walshe & Wilson, 1997) suggested that the flexibility training could increase the work output during SSCs with a reduction in the muscle-tendon complex stiffness. However, others studies (Horita, Komi, Nicol, & Kyrolainen, 2002; Kyrolainen, Finni, Avela, & Komi, 2003) showed that the increased stiffness in the beginning of the contact phase was related to a greater performance during SSCs. Obviously, only a comprehensive studying on these mechanisms can lead to correct suggestions for train practice.

This review paper is intended to provide an overview of the theories of mechanisms in the mechanical output enhancement during SSCs. The paper will add the latest knowledge on this issue from *in vivo* studies, as well as important factors such as preactivation and interaction between fascicle and tendinous structures. As a result, the understanding of these mechanisms and these important factors will lead to further research and possible applications.

2. Definition

In order to understand these enhancement mechanisms, several terms are defined and used throughout the manuscript:

2.1 Stretch-shortening cycle (SSC)

The SSC is a muscle action in which the concentric contraction is immediately preceded by an eccentric contraction (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a). During the eccentric contraction, the muscle must be active during the stretch.

2.2 Contractile component (CC)

According to a model proposed by Hill (1938), human skeletal muscles can be described as several different functional parts (Figure 1). Skeletal muscles consist of an active element and passive connective tissue. The active element, modeled as the contractile component (CC) or contractile element (CE) is the part of muscles that is capable of voluntary contraction.

2.3 Series elastic component (SEC)

In the three-component Hill (1938) model (Figure 1), all connective tissue in series with the CC labeled as the series elastic component (SEC or SE). The SEC was located in the tendons (Cavagna, 1977), the cross-bridges (Huxley & Simmons, 1971) and the thin and thick myofilaments. The relative amount of elasticity located in the tendons and the CC depends on the structure of muscle (Cavagna, 1977).

2.4 Parallel elastics component (PEC)

The connective tissue that surrounds the contractile element is viewed as the parallel elastics component (PEC or PE), as seen in Figure 1. The PEC is thought to located within the sarcolemma, endomysium, perimysium, and epimysium (P. V. Komi, 1984).

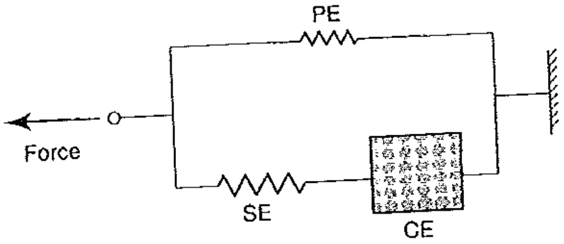

Figure 1. A three-component model of muscle. (From Enoka, 2002)

2.5 Preactivation

The SSC involves an important feature of preactivation (Komi, 2000). Muscles are preactivated before the initial ground contact. The preactivation phase was defined starting from 100 ms (Kyrolainen & Komi, 1995) or 50 ms (Horita, Komi, Nicol, & Kyrolainen, 2002) before the ground contact until the instant of the ground contact.

2.6 Short range elastic stiffness (SRES)

The effect of the short range elastic stiffness is that the tension rises steeply at the initial lengthening. Increasing the range of stretch is likely to decrease the elastic behavior of the muscle (Bosco & Komi, 1979).

2.7 Countermovement jump (CMJ), squat jump (SJ), and drop jump (DJ)

The countermovement jump, squat jump, and drop jump have been employed to study the phenomenon of SSCs (Bobbert, Gerritsen, Litjens, & Soest, 1996). When subjects perform a CMJ, they start from a standing position and make a downward movement before starting to move upward. When subjects perform a DJ, they step off a raised platform and then jump vertically immediately after landing (Bobbert, 1990). Subjects usually achieve a greater jump height in CMJ and DJ than in SJ, in which they start from a semisquatted position and make no countermovement (Komi & Bosco, 1978). Many studies used the comparison between CMJ and SJ to illustrate the effects of countermovement on the mechanical output during SSCs *in vivo* (Bobbert, Gerritsen, Litjens, & Soest, 1996; Bosco & Komi, 1979; Komi & Bosco, 1978).

3. Current theories

3.1 Time available for force development

The first possible explanation for the enhancement of work during SSCs is that it allows muscles more time to develop force (Bobbert, Gerritsen, Litjens, & Soest, 1996; Chapman & Sanderson, 1990; G.J. van Ingen Schenau, 1984; G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a). During a maximal voluntary muscle contraction, it takes time for a muscle to reach its maximum value. For example, during the leg extension task (Bobbert & van Ingen Schenau, 1990), it takes 300-500 ms before 90% of the maximal force is reached. This delay may be due to the limitations in the rate of muscle stimulation by the central nervous system, the time constants of the stimulation-active state coupling, and the interaction between contractile components and series elastic components (Bobbert, Gerritsen, Litjens, & Soest, 1996). In the SJ, the muscles cannot achieve a high level of force prior to the start of a concentric contraction and part of the shortening distance is traveled at a submaximal force. Thus, work produced is less than that in a CMJ, during which the muscles build up the maximum force at the end of countermovement (Bobbert, Gerritsen, Litjens, & Soest, 1996; G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a). This argument is illustrated in Figure 2, which shows the vertical ground reaction force as a function of the height of center of gravity for a CMJ and a SJ (Bobbert & Casius, 2005). The area under the plots reflects the amount of energy contributing to the jump height. Obviously, the area is greater for CMJ than for SJ because a greater ground reaction force can be produced in CMJ over the same distance of upward motion. The shaded area in Figure 2 represents the surplus of effective energy gained in CMJ, which caused a greater jump height in the CMJ.

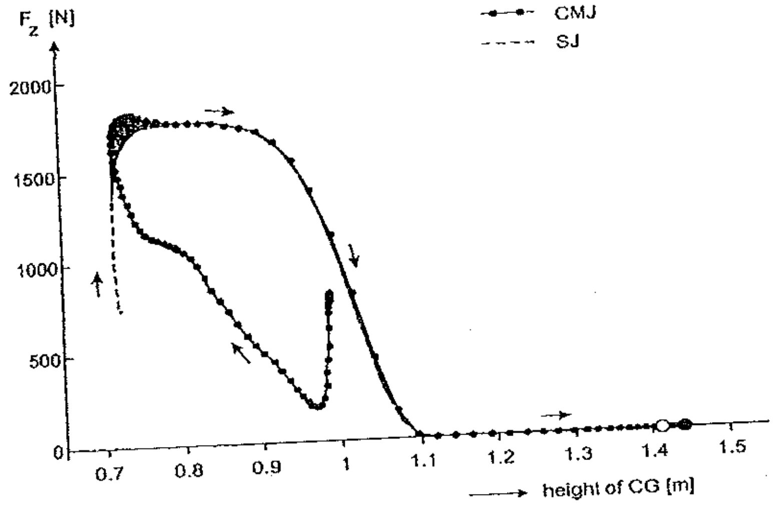

Figure 2. Vertical ground reaction force (Fz) plotted against height of center of gravity for a CMJ and a SJ. (from Bobbert et al., 2005)

This explanation is consistent with the results from other studies. Komi (P. V. Komi, 1984) suggested that subjects rich in fast twitch fibers could benefit from a high speed and short knee-angle displacement, while those slow twitch type subjects could benefit more from the large-amplitude jumps due to the difference in cross bridge lifetimes between fast and slow muscle fibers. Viitasalo and Bosco (Viitasalo & Bosco, 1982) showed the results supporting this argument. The subjects with a relatively large percentage of slow twitch fibers in vastus lateralis (VL) increased their jump height (compared to SJ) more from a countermovement than those with a large percentage of fast twitch fibers. Mero, Jaakkola, and Komi (Mero, Jaakkola, & Komi, 1991) reported that the subjects with a relatively large percentage of fast twitch fibers had a greater rate of force development. Therefore, for those subjects with a large percentage of slow twitch fibers, the relative poor performance in SJ of "slow twitch fibers" subjects could be due to the slow rate of force development which makes muscles traveling a longer distance at submaximal force.

Van Ingen Schenau et al. (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997b) argued that the high force level prior to the concentric phase could sufficiently explain the difference in positive work output between the CMJ and the SJ. To test this argument, it would be necessary to eliminate the effect of unequal force levels prior to the concentric phase and then examine if any difference in force and work output still can be observed. Minetti, Narici, and Cerretelli (Minetti, Narici, & Cerretelli, 1997) proposed an experiment to test this mechanism: A subject is constrained to the ground in the squat position by using a quick-release restraining system; this apparatus releases the subject after he or she develops the highest possible extension force. If this mechanism can sufficiently explain the difference between the CMJ and the SJ, SJ height from this experiment should be equal to that of the CMJ.

There might be some technical difficulties to build such apparatus, but Finni, Ikgawa and Komi (Finni, Ikegawa, & Komi, 2001) did an alternative experiment to test this argument. In their study, maximal concentric knee extension torques were compared in the pre-stretch and the pre-isometric conditions. In the pre-isometric condition, subjects were asked to extend their knee maximally in the isometric pre-loading phase and then sustain the maximum effort throughout the concentric movement. In the pre-stretch condition, subjects were asked to maximally resist a forced lengthening of the quadriceps muscle and then extend the knee joint with maximal effort. Results showed that the maximal knee extension torque was significantly higher in the pre-stretch condition than in the pro-isometric condition at the knee angle of 115° (272 ± 19 vs. 248 ±19 Nm, $P<0.05$), (180° = full knee extension) although the torque prior to the concentric phase was smaller in the pre-stretch than in the pre-isometric condition (268 ± 17 vs. 314 ± 17, $p<0.05$). The torque difference between two conditions diminished when the knee was extended further. The authors also examined average EMG (aEMG) and the fascicle length of VL muscle in both conditions. The fascicles prior to shortening were longer in the pre-stretch condition compared to the pre-isometric condition. Because the decrease in muscle force during the shortening depends on the initial fascicle length (Meijer, Grootenboer, Koopman, & Huijing, 1997), longer initial length may be a potential factor for the greater force observed in the pre-stretch condition. Therefore, although the high force level prior to the concentric phase is an important factor in the enhanced mechanical output, other factors, such as fascicle length, may also play a role in enhancing performance of SSCs.

In the literature, the explanation that SSCs give muscles more time to develop force was explicitly supported by many researchers (D.L. Morgan & Proske, 1997; G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a; Winter, 1997). However, Zatsiorsky (Zatsiorsky, 1997) argued that the performance of fast SSCs can't be explained with time of force development of 300-500 ms. In fast SSCs such as drop jump, muscle stimulation develops in a very short time and the force is much greater than in CMJ. This suggests that other mechanisms may contribute to enhanced mechanical output. First, the muscles may be preactivated in anticipantion of landing (Horita, Komi, Nicol, & Kyrolainen, 2002), therefore the delay in the stimulation and excitation may be eliminated. Also, the high eccentric velocity can increase the force of extensors to a very high value in a very short time (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997b). This high force can contribute to the shortening phase if the eccentric movement is finished in a small distance and short time duration (Bobbert, Huijing, & Ingen Schenau, 1987). For these fast SSCs, other mechanisms such as reutilization of elastic energy rather than the time available for force development may contribute to the enhanced mechanical output.

3.2 Stretch Reflex contribution

The second explanation for the enhanced mechanical output by a countermovement is that the stretch during the countermovement triggers stretch reflexes (Dietz, Schmidtbleicher, & Noth, 1978; Komi & Gollhofer, 1997). Stretch reflexes increase muscle stimulation and muscular stiffness leading to an improved ability to utilize storage of potential elastic energy (Walshe, Wilson, & Ettema, 1998). However, the contribution of stretch reflexes to the mechanical output enhancement during SSCs has been questioned (Gandevia & Burke, 1992; G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a, 1997b). First, it is questionable whether the muscle fibers are lengthened at all during SSCs (G.J. van

Ingen Schenau, Bobbert, & deHaan, 1997a). If there is no lengthening of muscle fibers, there are no muscle spindles lengthening and no trigger of stretch reflexes. Second, it has been shown that the muscle stimulation and excitation may not be enhanced in SSCs *in vivo* (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a). Third, the mechanical effects induced by stretch reflexes would be too late to contribute to the work output enhancement (Gandevia & Burke, 1992; G.J. van Ingen Schenau, Bobbert, & deHaan, 1997b).

3.2.1 Are the muscle fibers and muscle spindles lengthened during SSCs?

Several authors (R. F. Alexander & Ker, 1990; Voigt, Bojsen-Moller, Simonsen, & Dyhre-Poulsen, 1995) suggested that during SSCs, muscles may be involved in a concerted contraction, i.e. the muscle-tendon complex is lengthened but the muscle fibers may remain isometric or even shorten during the pre-stretch. Recently, a noninvasive technique, ultrasonography, has been used for determining the length of fascicles *in vivo.* Kurokawa, Fukunaga, and Fukashiro used this technique (Kurokawa, fukunaga, & Fukashiro, 2001) to determine the change in length of fascicles and tendinous structures of the gastrocnemius medialis (MG) during CMJ. They reported that muscle fibers of the MG were not lengthened at all during the counter movement. Therefore, no stretch reflex of the MG can be triggered. However, it has also been reported that the vastus lateralis muscle fascicles were lengthened during the eccentric phase of CMJ (Finni, Ikegawa, Lepola, & Komi, 2003). These results suggested that different muscles have different fascicle behavior. In addition, the lengthening of fascicle of the MG was also observed in another SSC exercise (Kubo et al., 2000). In this exercise, subjects performed a dorsiflexion followed by a planter flexion (ankle joint angle from 120° to 90°, then from 90° to 120°). These results suggested that stretch reflexes could be triggered in some muscles during SSCs.

3.2.2 Is muscle stimulation and excitation enhanced during SSCs?

Bobbert et al. (Bobbert, Gerritsen, Litjens, & Soest, 1996) compared EMG activity of lower extremity muscles of six volleyball players during the SJ and the CMJ. The results showed that the aEMG during the push off phase was not significantly higher in CMJ than in SJ for any of six muscles (bicep femoris, gluteus maximus, rectus femoris, vastus medialis, gastrocnemius, and soleus). This study provides evidence that questions whether stretch reflexes occur during SSCs. However, Komi and Gollhofer (Komi & Gollhofer, 1997) argued that in normal human movement with high EMG activity, the magnitude and net contribution of reflexes are difficult to measure, but it is much easier to examine the effect of reflexes with a relatively slow passive stretch. Nicol and Komi (Nicol & Komi, 1998) used an in vivo buckle transducer technique to study reflex contribution to Achilles tendon force enhancement during passive dorsiflexion stretches. An ankle ergometer was used to induce passive stretches of the triceps surae muscle group. The subject's foot attached on the top of the ergometer pedal. The passive stretches differed in amplitude (0.06 and 0.12 rad) and mean velocity (0.44 and 1.22 rad/s) of the induced dorsiflexion. They reported that during the stretch at 1.2 rad/s, the Achilles tendon force started to increase 13-15 ms after the onset of the EMG reflex response and the enhancement could be as high as 261% over the pure passive stretch without a reflex response (Figure 3).

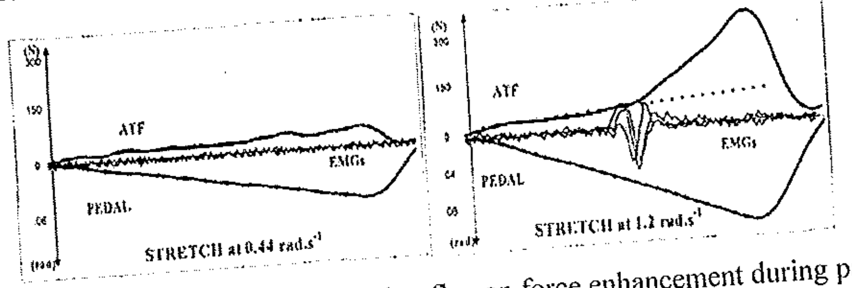

Figure 3 The effect of the stretch reflex on force enhancement during passive stretch. (From Nicol & Komi, 1998)

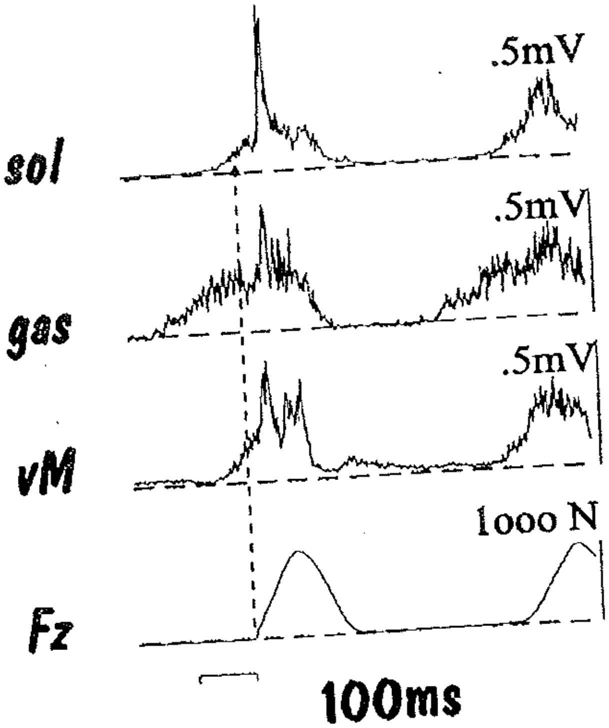

Figure 4 Averaged rectified EMG records of the soleus (sol), gastrocnemius (gas), and vastus medialis (vM) muscles in the drop jump from 60 cm height. (Komi and Gollhofer, 1997)

Komi and Gollhofer (Komi & Gollhofer, 1997) also argued that CMJ is not a suitable model to test reflexes during SSCs in which pre-stretch speeds are relatively low and the switch from stretching to shortening occurs slowly. Those faster activities such as running and drop jump are more likely to be affected by stretch reflexes. Gollhofer, Strojnik, Rapp, and Schweizer (Gollhofer, Strojnik, Rapp, & Schweizer, 1992) reported that during drop jumps, the stretch reflex was visible in all examined muscles, especially in the soleus muscle. Figure 4 illustrates that drop jumps performed from 60 cm introduced clear bursts in rectified EMG records. These records were obtained by averaging the rectified EMG over several trials. The reflex peak is very clear in the soleus muscles, and can be identified for the gastrocnemius and the vastus medialis as well.

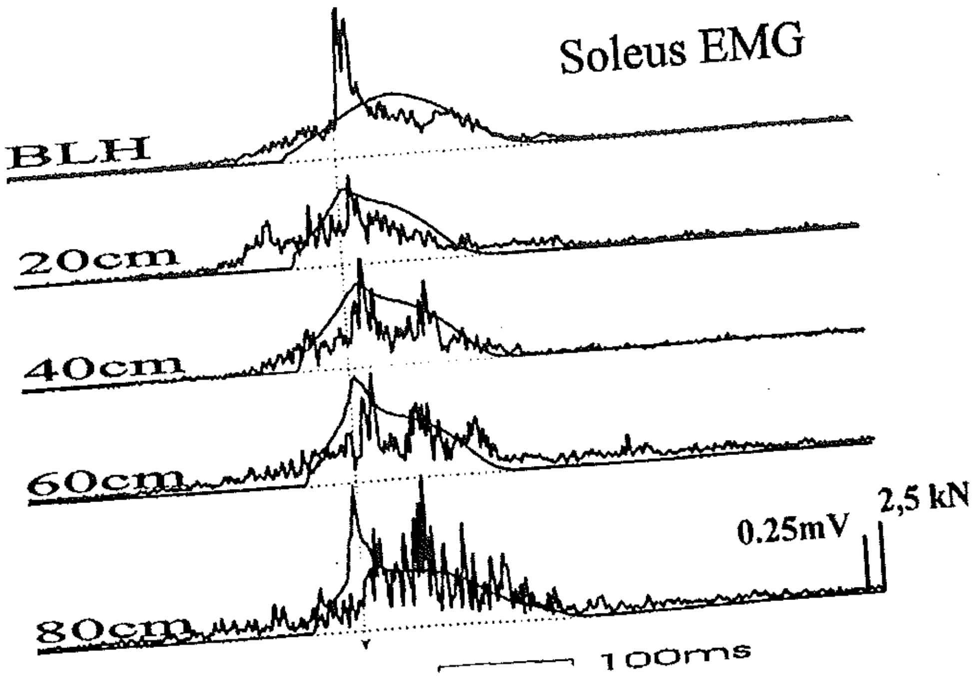

Figure 5 the modulation of the EMG pattern and the ground reaction force with increasing stretch load. (From Komi and Gollhofer, 1997)

It has been shown that stretch reflexes are sensitive to load (Komi & Gollhofer, 1997), fatigue (Gollhofer, Komi, Fujitsuka, & Miyashita, 1987; Nicol, Komi, Horita, Kyrolainen, & Takala, 1996) and the Ia afferent input (Fellows, Domges, Topper, Thilmann, & Noth, 1993). Figure 5 illustrates the modulation of the EMG pattern and the ground reaction force with increasing stretch load. In the highest drop jump (Figure 5) the EMG burst becomes less clear. The reduced reflex activation may be due to increased inhibition from the golgi tendon organ and serves as a protection strategy to prevent muscle injuries (Komi & Gollhofer, 1997). The stretch reflex also can be dramatically reduced during an ischemic blockade, which is used to isolate the Ia afferent information acting on spinal pathways (Fellows, Domges, Topper, Thilmann, & Noth, 1993). This suggests an important role of Ia afferent input in SSCs. Nicol et al. (Nicol, Komi, Horita, Kyrolainen, & Takala, 1996) reported that an exhaustive SSC exercise dramatically reduced the stretch reflex amplitude. Avela and Komi (Avela & Komi, 1998) observed the reductions in stretch reflexes after a marathon run. In the "before marathon" test, the soleus EMG showed a clear stretch reflex in a jump test. However, the stretch reflex disappeared almost completely in the "immediately after marathon" test. These aforementioned studies provide explanations that the pre-stretch may not always trigger a stretch reflex, thus no enhanced muscle stimulation and excitation, and no enhanced mechanical output.

3.2.3 Is the mechanical effects of stretch reflexes too late to enhance the work output?

It is widely accepted that stretch reflexes are likely to occur during the fast movements such as drop jumps and running. However, there is controversy in the literature about whether it would be too late for stretch reflexes to play a functional role in the fast movements. While several authors argued stretch reflexes can have an important role in force enhancement during SSCs, others (Gandevia & Burke, 1992; G.J. van Ingen Schenau, Bobbert, & deHaan, 1997b) argued that these fast movements must be feed forward control and the mechanical effects of stretch reflexes would be too late to enhance the work output.

In the aforementioned example (Figure 3), during the drop jumps performed from 60 cm, the sharp EMG reflex peak occurred about 40-45 ms after the initial ground contact (Komi & Gollhofer, 1997). The total delay between the initial stretch and the subsequent force enhancement would be this 40-45 ms and the delay of 10-12 ms between the onset of reflex EMG and onset of force enhancement, i.e. total 50-55 ms (Komi, 2000). The author argued that in sprinting (the stance phase lasts 90-100ms) as well as in marathon running (the stance phase lasts about 250 ms), therefore, stretch reflexes have enough time to contribute to the mechanical output enhancement in the concentric phase.

Although there is an agreement about the duration of the neural delay, that is 40 ms

(Komi, 2000; G.J. van Ingen Schenau, Bobbert, & deHaan, 1997b), several authors (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997b; Vos, Harlaar, & Ingen Schenau, 1991) argued the delay between the onset of reflex EMG and the onset of force enhancement cannot measure the actual functional delay. This delay , in theory, is zero, i.e. the response of force starts immediately (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997b), therefore the threshold levels of EMG and force should be defined (Vos, Harlaar, & Ingen Schenau, 1991). Furthermore, they argued that the more adequate measure is the delay found by cross-correlating EMG with the corresponding force. They used a method based on cross-correlation techniques to measure the phase shift between EMG and force. The delay at which the highest correlation between EMG and force existed was 90 ms -100 ms. This delay and the neural delay of 40 ms means stretch reflexes may need more than 130 ms to contribute fully to the force enhancement. In the example (Figure 3)of the passively induced stretch reflex on the Achilles tendon force (ATF) presented by Nicol and Komi (Nicol & Komi, 1998): the ATF starts to rise almost immediately but continues to rise beyond the end of the activity. The delay between peak EMG and peak force is even far greater than 90-100ms. Although stretch reflexes can start to contribute to the force and work enhancement before the force reaches the peak value, it is still a question how much work enhancement stretch reflexes could contribute to during fast SSCs (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997b).

3.3. Reutilization of elastic energy

The third explanation in the literature for the work enhancement by a countermovement is the reutilization of elastic energy (Asmussem & Bonde Petersen, 1990; Cavagna & Kaneko, 1977; Hull & Hawkins, 1990; Komi & Bosco, 1978). When the muscle is actively stretched, mechanical energy is absorbed by the muscle. This energy can be dissipated into heat or stored in the SEC and reutilized during the subsequent active shortening (Cavagna, 1977). Although literature shows a lot of evidence in favor of elastic energy reutilization in human movement, two questions still remain: 1) How much elastic energy can be stored and reutilized (G.J. van Ingen Schenau, 1984)? And 2) Does elastic energy enhance the work output (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a)?

3.3.1 Evidence supports elastic energy reutilization

Many isolated muscle experiments have shown muscle elasticity. Even before Hill (Hill, 1938) introduced the concept of SEC, Levin and Wyman (Levin & Wyman, 1927) observed that a muscle could produce a substantial amount of work even at the highest speed and explained that it was due to the elastic element in series with the contractile component of the muscle. Studies (Cavagna & Citterio, 1974; Cavagna, Dusman, & Margaria, 1968; Hill, 1970) also showed that isolated muscles can produce greater force and work during the shortening when they are actively stretched. Cavagna et al. (Cavagna, Dusman, & Margaria, 1968) compared the maximum positive work done by an active muscle during shortening when the muscle shortens from a pre-isometric state (W) and a pre-stretch (W') with the same speed, initial length, and amount of shortening. W and W' were measured at different speeds of stretching and shortening and at different initial length. The ratio W'/W increases with the speed of stretching and shortening and with the length of the muscle up to 2.5 (Figure 6). The higher ratio W'/W at the higher shortening speed provides enough evidence to support that the greater work done after stretch is mainly due to the reutilization of elastic energy stored during the stretch, because it is consistent with that fact that elastic energy can be released at a very high speed by the series elastic component (Cavagna, Dusman, & Margaria, 1968).

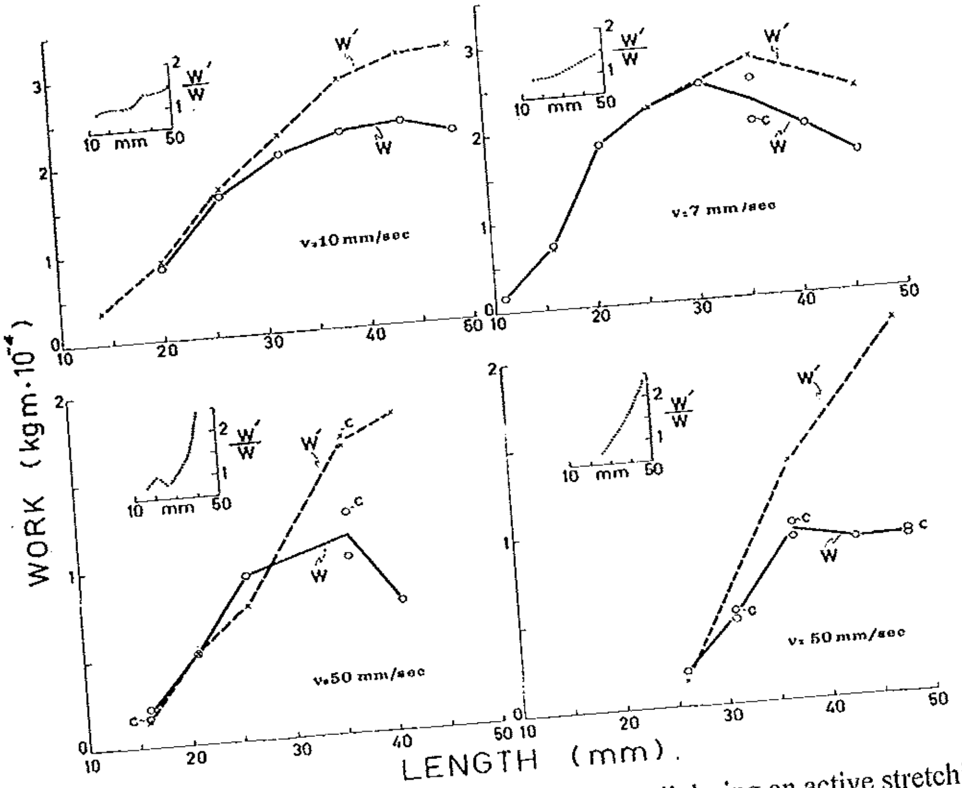

Figure 6 Positive work performed by four toad sartorii during an active stretching, starting from a state of isometric (W) or preceded by an active stretching (W'), is plotted as a function of the length of the muscles (Cavagna et al., 1968).

It is well documented that the storage and reutilization of elastic energy are highly functional to enhance power output in explosive movements, such as sprinting (Cavagna, Kamarek, & Mazzoleni, 1971; Jacobs, Bobbert, & van Ingen Schenau, 1993) and jumping (Asmussem & Bonde Petersen, 1990; Bobbert, Huijing, & van Ingen Schenau, 1986; Cavagna, Kamarek, Citterio, & Margaria, 1971). Cavagna et al. (Cavagna, Kamarek, & Mazzoleni, 1971) reported that in sprinting, the positive power developed at each step increased with speed until 5 m/s and then tended to level at 7 m/s around a value of 1800 watts (Figure 7). This seems to fit the force-velocity relationship of contractile component. At speeds greater than 7 m/s, the positive power output was further increased to 2900 watts at the maximal speed. The onset of this increase of power output coincided with the onset of the negative work produced at each step. According to the force velocity relationship of contractile component, the power reaches the maximum at about 1/3 of the maximal speed of shortening and decreases when the velocity of shortening is increased further (Hill, 1950a). Therefore, under an assumption that the shortening velocities of muscles linearly increase with the speed of running, these results suggest that the high power developed at high speeds is contributed by the reutilization of elastic energy. Elastic energy can provide power output about 1750 W and work of 122 joules (1750*0.07)at the highest speed (34km/hr or 9.4m/s) (Cavagna, 1977).

Studies showed that the countermovement increases the power and work in jumps. Cavagna et al. (1971) reported that the positive work and the jump height increased about 10% by the countermovement, while the average power was about 70% greater in CMJ than that in SJ. The peak ankle joint power output is about 1800 W during a one-legged CMJ and 1200 W (from one leg)during a two-legged CMJ (Soest, van Roebroeck, Bobbert, Huijing, & van Ingen Schenau, 1985). Considered the maximum isokinetic power output is only 200W (Fugl-Meyer, Mild, & Hornsten, 1982), the six times or nine times greater ankle joint power output in CMJ must be mainly explained by the storage and reutilization of elastic energy (Farley, 1997). However, this "power amplifier" effect can also be found in purely concentric contractions, like squatted jumps. The tendons undergoe a stretch-shortening cycle both in CMJ and SJ, thus creating beneficial conditions for the utilization of elastic energy (Finni, Komi, & Lepola, 2000). It was also reported (Iossifidou, Baltzopoulos, & Giakas, 2005) that the peak knee joint power in a SJ was 2255W, almost three times of peak knee joint power in isokinetic test (771 +/- 81W).

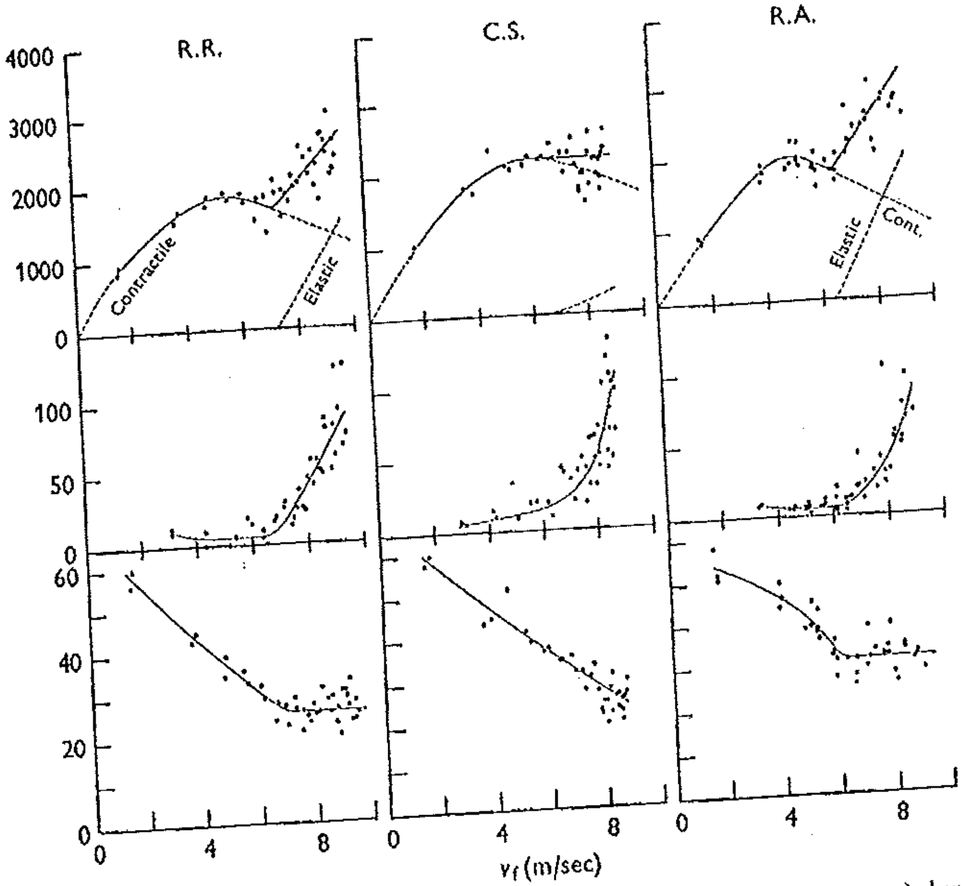

Figure 7 The average power (W) (top) and the average force (kg) (bottom) during the push phase, and the negative work (joule) (middle) done during brake as a function of the speed of the run. (Cavagna et al., 1971)

Experiments have shown that SSC induce greater efficiency of positive work due to elastic energy. Efficiency of positive work usually is defined as "positive work done divided by the chemical energy spent to do it" (Cavagna, 1977). Cavagna, Saibene, and Maragaris (1964) measured the mechanical work in running at speeds of 10-20km/hr (2.78m/s—5.56m/s) when no oxygen debt was occurred. Thus, the net energy expenditure in running could be calculated from oxygen consumption. The efficiency of positive work was measured from the ratio of the positive work divided by the net aerobic expenditure. This efficiency, 0.4-0.5, is greater than the maximal efficiency produced by the contractile component of muscle: about 0.25 (Cavagna, 1977; G.J. van Ingen Schenau, 1984). Biochemical estimations also showed that the efficiency is lower than 0.3 (Stainbsy, Gladden, Barclay, & Wilson, 1980; G.J. van Ingen Schenau, 1984; Whipp & Wasserman, 1969) . This value was calculated from the product of phosphorylative coupling efficiency (0.6) and contraction coupling efficiency (0.5). Other studies also showed the efficiency of running is well above 0.3 (Ito, Komi, Sjodin, Bosco, & Karlsson, 1983; Williams & Cavanagh, 1983). These results suggested that part of the positive work derives from the recoil of elastic elements and does not need the transformation of chemical energy (Cavagna, 1977). In running, kinetic and potential energy decreased in the eccentric phase can be stored in the SEC of leg extensors and at least part of this elastic energy can be reutilized in the concentric phase. Without this reutilization of energy, all mechanical work would have to originate from the contractile elements and all negative work on lengthening muscles would be converted to heat (G.J. van Ingen Schenau, 1984). The efficiency was also found to increase linearly with running speeds from 0.45 at 2.2m/s to 0.8 at 8.9m/s (Cavagna, Kamarek, & Mazzoleni, 1971). This is consistent with the contribution of elastic energy increasing with running speed (Cavagna, Kamarek, & Mazzoleni, 1971). However, Haan et al (De Haan, Van Ingen Schenau, Ettema, Huijing, & Lodder, 1989) reported that the efficiency of isolated rat muscles was only 0.36 when muscles performed concentric contractions preceded by an active pre-stretch. Although this value seems too low to explain the efficiencies of 0.4-0.7 reported for human running (Cavagna, Kamarek, & Mazzoleni, 1971), it was much higher than the efficiency (0.26) of isolated muscles in the pre-isometric condition. Therefore, this result also suggested that the pre-stretch can increase the efficiency with the contribution of elastic energy.

The time delay between eccentric phase and concentric phase has been found to reduce the efficiency in a successive knee bend exercise (Asmussem & Bonde Petersen, 1990). This delay is also called the coupling time (Bosco, Komi, & Ito, 1981). Stored energy can be dissipated as heat if the coupling time is not sufficiently short (Goubel F., 1997). In addition, the efficiency is greater in movements of smaller amplitude (Cavagna, 1977). This is in agreement with the finding that the difference in takeoff speeds between CMJ and SJ is increased when the amplitude of pre-stretch is decreased (Cavagna, 1977). These findings may suggest that the effect of utilization of elastic energy is greater in movements of smaller amplitude (Cavagna, 1977). The relationship between small stretch and greater mechanical output is also consistent with the concept of "the short range stiffness" (Rack & Westbury, 1974). The short range stiffness means that muscles perform like a spring when the length change during stretch is very short. Increasing the range of stretch is likely to decrease the elastic behavior of the muscles due to the possible effect of the reduced short range stiffness (Bosco & Komi, 1979). Also, the actin-myosin interaction in cross bridges could be detached when the muscle is overstretched (Flitney & Hirst, 1978; Syme & Grattan, 2002).

Although the significance of positive efficiency was strongly disputed by van Ingen Schenau et al. (1997a), they stated "We never stated that the disputed efficiencies cannot be taken as evidence for elastic storage. On the contrary! Of course efficiencies of positive work of 40% of high can only be explained by storage and reutilization of elastic energy" (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997b).

3.3.2 How much elastic energy can be stored in muscles and tendons?

From the aforementioned evidence, it can be concluded that elastic energy is stored and reutilized in muscles during SSCs. However, the question how much elastic energy can be stored and reutilized is remaining unclear. Obviously, muscles can not reuse elastic energy that was not previously stored as negative work (G.J. van Ingen Schenau, 1984). The amount of elastic energy stored in the parallel elastic component is small, so we just consider elastic energy stored in SEC. The amount of energy that can be stored is equal to the area bounded by the force-stretch curve of SEC. The force-stretch curve (Figure 8) can be approximated by a power curve (G.J. van Ingen Schenau, 1984):

$$F=ks^{n} \tag{1}$$

where F is force, s is displacement, k and n are constants. Energy can be stored is equal to

$$E=Fs/(n+1) \tag{2}$$

Because the exponential relation for SEC of human calf muscle and tendon can be very closely approximated by Equation 1 when n=2 (A.L. Hof, Geelen, & Van den Berg, 1983), van Ingen Schenau (1984) used n=2 to estimate the amount of elastic energy stored. Then

$$E= (1/3)\, Fs. \tag{3}$$

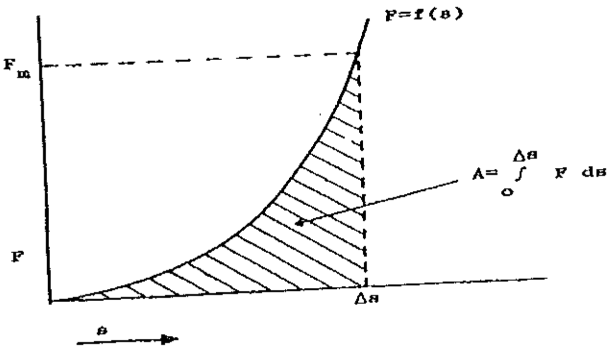

Figure 8 force (F) and displacement (s) curve. (Van Ingen Schenau, 1984)

When the stretch is small, these two equations can be applied for the moment-angular displacement relationship at a joint.

$$E=1/3M\,\Delta\Phi \tag{4}$$

where M is moment, $\Delta\phi$ is angular displacement. In running, the author argued that the hip joint does not show a stretch-shortening cycle during the stance phase, so the storage of elastic energy can only take place in the knee extensors and plantar flexors (Ito, Komi, Sjodin, Bosco, & Karlsson, 1983). When the knee flexion and dorsiflexion in running are about 0.35 rad (20°) and 0.52 rad (30°) and the moments in both joints are about 200 Nm (Luhtanen & Komi, 1978; Winter, 1983), the total storage of elastic energy is equal to (1/3)*200*0.35+(1/3)*200*0.52=58J even if the entire knee flexion and dorsiflexion are used for storage elastic energy and the CC remains constant. This value is much less than 122 J estimated by Cavagna (1977). Although different maximal muscle stretching percentages have been reported, van Ingen Schenau (1984) considered 2% was more realistic. There are two reasons for this consideration. First, Cavagna and Citterio (Cavagna & Citterio, 1974) reported a maximal stretch of 2%. Second, the maximal stretch of a half sarcomere is 11-15 nm, i.e. 1-1.5% of 1 μm (half sarcomere). Thus, the maximal amount of elastic energy can be stored in a `muscle is about 5 J if the muscle length is 20cm and the extreme force is 4000N (1/3*4000*0.2*2%=5.3). To estimate the amount of elastic energy stored in the Achilles tendon, 4000N of maximal force, 5% of stretch (correspondly 16° of dorsiflexion), and 26cm of length were used. The maximal amount of stored energy equals to 17 J (1/3*4000*0.26*5%). The author (1984) further pointed out that the total amount of elastic energy in the leg muscles and tendons would not exceed the 30-40 J during the running or jumping because the tendons of knee extensors are shorter than the tendons of the Achilles tendon. The author (1984) also noted that even this amount of energy cannot be totally reutilized because of viscous properties of tendons. Therefore, the author (1984) concluded that elastic energy plays a minor role in dynamic movements.

The amount of stored elastic energy estimated by van Ingen Schenau (1984) is only about half of that calculated by Alexander and Bennet-Clark (1977). They used a greater force value of 4700N and a greater tendon extension value of 18mm, however, the major difference is that they used a linear force-stretch curve, i.e. n=1 in the Equation (1). Thus E= (1/2) Fs. They calculated the amount of elastic energy in the ankle extensor muscles and the Achilles tendon of one leg of a man running at 3.9m/s. The results showed that the amount of elastic energy stored was 4.1-8.3 J in ankle extensor muscles and 42 J in the Achilles tendon. Thus, if knee extensors can store almost same amount of elastic energy, the total amount of elastic energy in the knee and ankle joint would be close to 122 J during the high speed (9.4m/s) running estimated by Cavagna (1977).

Although Hof and van den berg (1986) agreed that n in Equation 1 should be equal to 2 , they argued that it underestimated the capacities of muscles and tendons for storage of elastic energy. Because van Ingen Schenau (1984) assumed that the SEC stretch is equal to the externally measurable joint rotation. In their view, this assumption is not true because the total SEC length change is the sum of the internal length change $\Delta \Phi_{int}$, caused by a shortening of the CC, and the external length change $\Delta \Phi_{ext}$, caused by an increase of the whole muscle length. Therefore, Equation 4 should be written as

$$E=1/3M\,(\Delta \Phi_{int} + \Delta \Phi_{ext}) \qquad (5)$$

The authors illustrated the external and internal length changes in Figure (9).

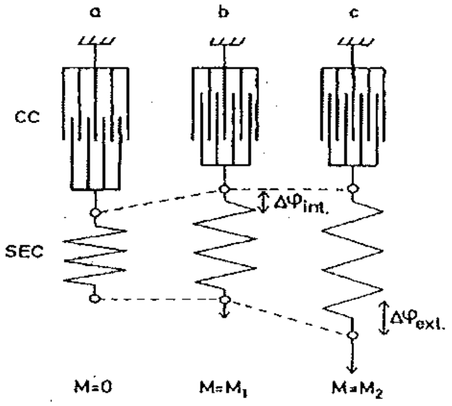

Figure 9. Two-component Hill muscle model in a contraction involving external and internal length changes (Hof & Van Den Berg, 1986).

Phase 1 (from a to b in figure 9): In this phase the muscle contacts isometrically to a low moment M_1. A shortening of the CC stretches the SEC in the length of $\Delta \Phi_{int}$.

Phase 2 (from b to c): In this phase the moment increases from a low M_1 to a maximum M_2 while the muscle is in an eccentric contraction. The length of the CC remains constant during this phase, therefore the lengthening of the SEC is equal to the stretch $\Delta \Phi_{ext}$.

Phase 3: In this phase elastic energy is delivered as positive work in a concentric contraction.

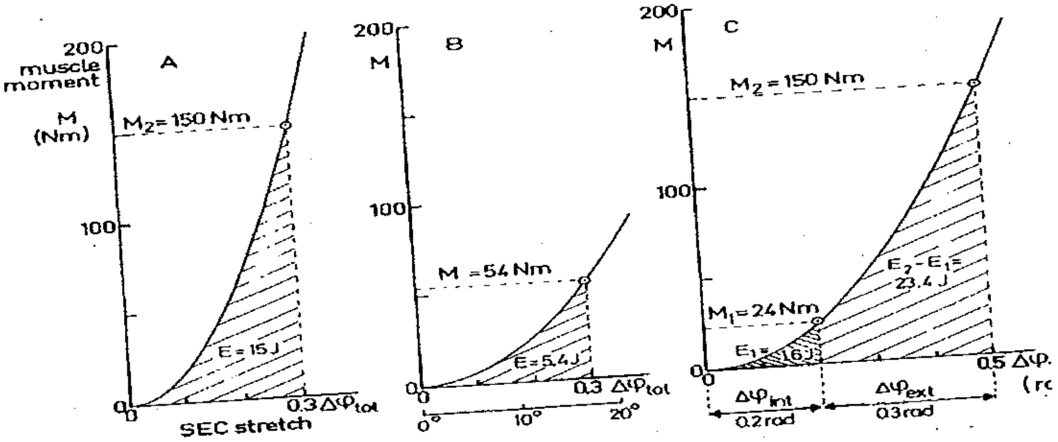

Figure 10. Relation between muscle moment M and stretch of the SEC for the human calf muscle. (Hof & Van Den Berg, 1986).

The authors (1986) illustrated the difference in elastic energy storage when the internal SEC stretch is considered during walking (Figure 10). According to van Ingen Schenau (1984), with $\Delta \Phi_{ext}$ of 0.3 rad at moment of 150 Nm, 15 J of elastic energy is stored (fig 8.A). Hof and Van Den Berg (1986) used k = 600 Nm/rad^2 (experimental value of Hof et al. (A.L. Hof, Geelen, & Van den Berg, 1983)) to calculate the elastic energy storage with a SEC stretch of 0.3 rad. Results showed that only 5.4 J elastic energy could be stored (Figure 8 B). However, the moment of only 54 Nm is not in agreement with the value (150 Nm) found in ature (A.L. Hof, Geelen, & Van den Berg, 1983). Figure 10c showed the amount of elastic energy increased dramatically when the internal length change is considered. An initial moment of 24 Nm stretches the SEC of 0.2 rad while the CC provides only 1.6 J. A further increase of the moment to 150 Nm results in 25 J. The total storage of elastic energy therefore increased from 5.4 J to 23.4 J with the internal SEC stretch. Obviously, a pre-strain requires little contractile work but substantially improves the capacity for elastic energy storage at a given range of motion.

The aforementioned examples are indirect estimates for the elastic properties of human muscle. Hof (1998) reported an *in vivo* measurement of the elasticity curves of the human triceps surae muscle group. This measurement was obtained by the quick-release experiments on a specially developed ergometer. In this controlled-release ergometer, a muscle is shortened at a high but constant speed that should be above the maximum shortening speed of the CC, estimated at 10 rad /s. The movement, up to 1 rad, should be completed within 70 ms to avoid the reflex effect (Allum, Mauritz, & Vogele, 1982). By recording the decline in force as a function of shortening, the force-length relation of the SEC can be obtained (Hill, 1950b). First, the moment and angle were recorded by the ergometer. Next, the moment was corrected for inertia effects, using the acceleration signal. Then, the angle correction for the shortening of the CC was applied to the angle recording. Finally, the passive moment of the antagonists was subtracted from the total moment. Results showed that the SEC moment and length curve can be described by a linear relation, with a stiffness K, preceded by a quadratic curve in the toe region. Stiffness K increases with the level of activation of the muscle. At an ankle moment of 100 N.m, K is 300 ± 40 N m /rad. At moments of 150 and 180 Nm, which correspond to the peak moments in walking at 1.25m/s and running at 2m/s (A. L. Hof, 1990), respectively, the amount of elastic energy stored in the SEC was 23-37 J and 31-57 J. These values suggest that there is enough amount of elastic energy storage to play an important role in SSCs.

3.3.3 Does elastic energy enhance work produced during the concentric phase?

While there is no question about storage and reutilization of elastic energy, some authors (Avis, Toussaint, Huijing, & van Ingen Schenau, 1986; Chapman & Sanderson, 1990; G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a, 1997b) have questioned whether elastic energy enhances work produced during the concentric phase. Their argument is that more elastic energy storage implies a further elongation of the SEC. At the given joint range of motion, the elongation occurs at the expense of the length of CC and consequently reduces the work produced by CC. Van Ingen Schenau et al. (1997a) used a simulation model to illustrate that the total work during the concentric contraction is not determined by the amount of energy stored in the SEC at the start of shortening (Figure 11). The elastic energy stored in the CMJ was 9.7 J more than in the SJ. This is more than 60% of the total extra 15 J of positive work produced in the CMJ. However, they argued that this could not be evidence that elastic energy increases the work production. They used a greater speed of force development in the simulation model to illustrate their argument. The greater speed of force development increased the difference in joint moment and storage of elastic energy between CMJ and SJ. However, the difference in work between CMJ and SJ decreased from 15 J to 5 J (Figure 11).Therefore, the authors concluded that the work enhancement during SSCs is not dependent on elastic energy. Chapman and Sanderson (1990) also demonstrated that work was enhanced when muscle models without SEC were used in simulations.

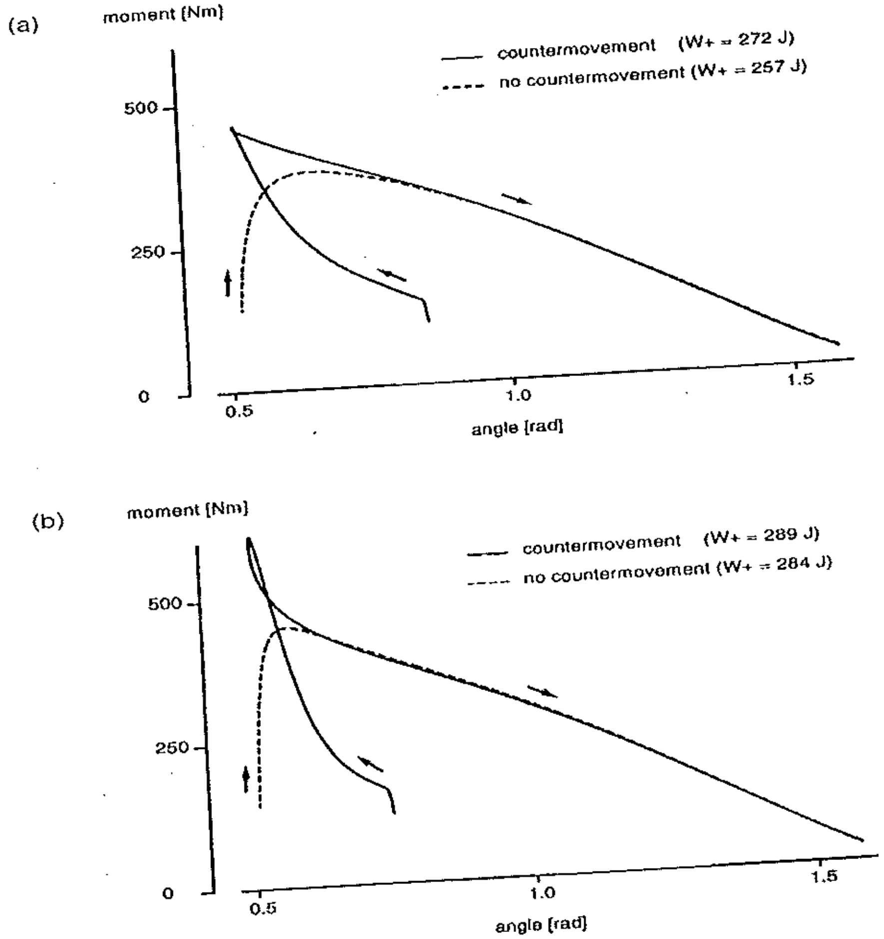

Figure 11 Moment-angle curves obtained in a forward dynamic simulation. Top: Rise of stimulation corresponds to the rise of EMG levels observed in human objects during jumps. Bottom: Rise of stimulation and excitation dynamics doubles. (From Ingen Scheanu et al., 1997)

However, Herzog (Herzog, 1997) argued that van Ingen Schenau and his colleague's statement is not always correct if the SEC is not exclusively associated with tendons. The SEC was thought to be located mainly in the tendons (Cavagna, 1977). However, the SEC is also located within the cross-bridges between actin and myosin (Huxley & Simmons, 1971). Furthermore, some studies have showed that the thin and thick myofilaments have considerable elasticity. The relative amount of elasticity located in the tendons and the CC depends on the structure of muscle (Cavagna, 1977). The force in a single cross-bridge and its work potential depend directly on the x-distance (Figure 12). The average x-distance is increased following a stretch compared to an isometric contraction. Thus, the work potential of the stretched muscle might be greater than that of the isometric muscle. Therefore, increased elongation of the SEC, for a given origin to insertion distance of the muscle, may not decrease work potential of the CC. Herzog (Herzog, 1997) further pointed that if a muscle works on the descending limb of the force-length relation at the start of the concentric contraction, for a given amount of shortening, the work potential might be greater for the muscle with shorter length of CC. The work potential of a muscle during SSC is not equal to the area under the isometric force-length relationship, but this area, conceptually, is proportional to the work performed during the concentric contraction. Therefore, starting from a shorter CC length could possibly favor to work production (Figure 13).

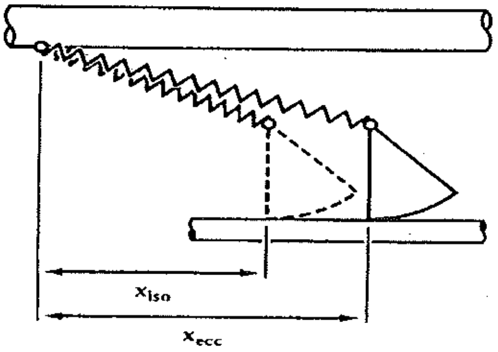

Figure 12. Schematic drawing of two cross-bridges in accordance with the cross bridge model. From Herzog (1997)

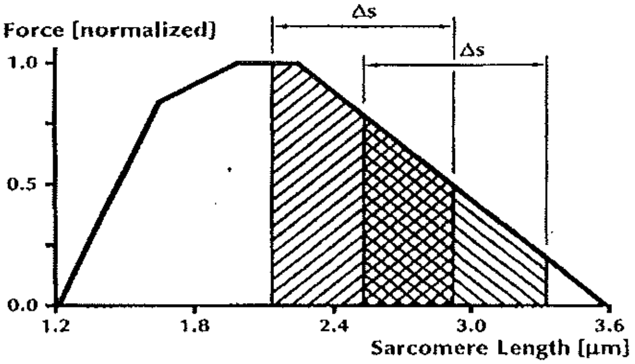

Figure 13. Schematic sarcomere force-length relationship. From Herzog (1997).

Several experimental studies seem to support the statement that the further elongation of SEC reduces the work produced by CC (Avis, Toussaint, Huijing, & van Ingen Schenau, 1986; Chapman & Sanderson, 1990; G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a, 1997b).Takarada, Iwamoto, Sugi, Hirano, and Ishii (1997) tested the effects of eccentric force on the mechanical output during concentric actions. It was reported that both peak and mean power output increased initially with eccentric force, but then began to decline when the eccentric force exceeded 1.8 times the isometric force produced without stretch (Figure 14). The same trend was found in elbow flexion with a pre-stretch (Takarada, Iwamoto, Sugi, Hirano, & Ishii, 1997) and squatting exercise with a countermovement (Takarada, Hirano, Ishige, & Ishii, 1997). Although there is a possible circumstance under which the total amount of work was reduced when the eccentric force exceeded a certain level (Takarada, Iwamoto, Sugi, Hirano, & N., 1997), those results may not provide enough evidence to support the hypothesis that the elongation of SEC reduces the work produced by CC. There is an alternative explanation for the reduced work after increasing the elongation of SEC: cross bridges could be detached when the force exceeds a certain level (Flitney & Hirst, 1978; Syme & Grattan, 2002).

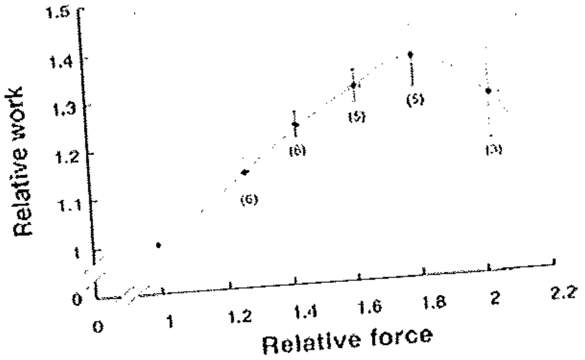

Figure. 14. Relation between peak force developed during stretch and positive work done during shortening in frog single fibers. (from Takarada et al., 1997)

3.4 Potentiation of the contractile machinery

Several studies showed that the contractile component itself is able to exert a greater force when a pre-stretch applied (Cavagna, Dusman, & Margaria, 1968; Ettema, Huijing, & Dehaan, 1992). This enhancement is called the potentiation (Ettema, Huijing, & Dehaan, 1992; Hill, 1970) or potentiation of the contractile machinery (Cavagna & Citterio, 1974; Edman, Elzinga, & Noble, 1978; G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a), in which the force-velocity curve is shifted towards higher force values for a given velocity. Many studies provided evidence for this potentiation. For example, the greater amount of work done after stretching is not entirely determined by the elastic energy stored but partly due to the contractile component itself (Cavagna, Dusman, & Margaria, 1968). When a pre-stretch is applied, muscles can even shorten against loads higher than the maximal isometric force (Cavagna & Citterio, 1974). However, no studies have satisfactorily explained the nature of this potentiation (G.J. van Ingen Schenau, 1984).

During an active stretch in experiments conducted with single muscle fibers, force rapidly increases. But this force then decreases after the stretch is completed and reaches a steady state until the end of activation. (Edman, Elzinga, & Noble, 1978; Edman, Elzinga, & Noble, 1982b; Edman & Tsuchiya, 1996; Herzog & Leonard, 2002; Rassier, Herzog, Wakeling, & Syme, 2003). This force is higher than the maximum isometric force at the corresponding final length (Rassier & Herzog, 2004). So the force enhancement induced by the stretch could be divided into a velocity dependent component and a velocity-independent component. The velocity dependent component, also called a transient component, is consistent with cross-bridge activity since it increases with increasing velocity of stretch and is proportional to the level of activation (Ruiter, Didden, Jones, & Haan, 2000). This transient component can be accomplished if the average force is increased in cross bridges. The possible mechanism is that cross bridges are forced to a state that facilitates force production and stay in this state for subsequent cross bridge cycles (Rassier & Herzog, 2004). Alternatively, this component could be caused by increase in number of attached cross bridges (Rassier & Herzog, 2004). This hypothesis suggested that the active stretch causes a reorientation of thin filaments to a position closer to the thick filaments and therefore increases the possibility of cross bridge attachment (Amemiya et al., 1988). This component could be nearly a doubling of the force produced during the isometric contraction (Ettema, Huijing, & Dehaan, 1992). However, Edman argued against the idea that this component could contribute to the greater force and greater work output in the subsequent concentric phase because the force enhancement will disappear by a small release. Clearly, this component at least can increase muscle's capacity to resist stretch and maintain force enhancement during the muscle fiber isometric contraction. The second component also call steady-state force enhancement (Rassier & Herzog, 2004; Ruiter, Didden, Jones, & Haan, 2000) or residual force enhancement (Edman, Elzinga, & Noble, 1982a; D. L. Morgan, 1994). This component is increased with increasing amplitudes, velocity-independent, and normally appears at sarcomere lengths on the descending limb of the length-tension relation (Edman, 1997; Edman, Elzinga, & Noble, 1982a; D. L. Morgan, 1994; Rassier & Herzog, 2004; Ruiter, Didden, Jones, & Haan, 2000). One possible mechanism is sarcomere length nonuniformity and instability (Julian & Morgan, 1979; D. L. Morgan, 1990, 1994; D. L. Morgan, Whitehead, Wise, Gregory, & Proske, 2000). This mechanism can only appear at sarcomere lengths on the descending limb of the force-length relationship (Edman, 1997). The sarcomere length nonuniformity causes difference in sarcomere length. Most active force is produced by the sarcomeres that are not stretched significantly with greater filament overlap, whereas the sarcomeres with longer lengths and less filament overlap will be supported by parallel elastic component. Thus the force produced by longer sarcomeres will match the short sarcomeres. The final force produced by these two parts would be greater than the force produced during isometric contractions. However, this hypothesis can't explain following observations: 1) a force enhancement was produced by fiber containing uniform sarcomere lengths (Edman, Elzinga, & Noble, 1982b), 2) a force enhancement was observed on the ascending limb of the force-length relationship (Peterson, Rassier, & Herzog, 2004), and 3) the force after stretch is greater than the isometric force produced on the plateau of the force-length relationship (Rassier, Herzog, Wakeling, & Syme, 2003). Therefore, sarcomere length nonuniformity may cause some force enhancement, but other mechanisms, such as engagement of a passive element, may also play a role in the force enhancement (Rassier & Herzog, 2004).

Edman et al. (Edman, 1997) argued that the amplitude of this component may be too small to be a factor that could improve the work output during the shortening phase. However, Ettema and Huijing (Ettema, Huijing, & Dehaan, 1992) found this component could contribute to force enhancement 2-16% for all conditions with different initial shortening lengths and shortening velocities.

Although the effect of the potentiation has been found in isolated muscles, it is questionable how much it can contribute to mechanical enhancement in human dynamic movements, in which activation level is relatively low and some muscle fibers may not be lengthened at all (G.J. van Ingen Schenau, Bobbert, & deHaan, 1997a). However, it seems clear that a greater potentiation may occur in a SSC with a high stretch speed, a short delay after stretch (Edman, Elzinga, & Noble, 1978; Edman, Elzinga, & Noble, 1982a), and a minimized length changes in muscle fibers during shortening.

Recently, several studies investigated the interaction between fascicle and tendinous tissue during SSCs (Finni, Ikegawa, Lepola, & Komi, 2003; Ishikawa, Finni, & Komi, 2003). In these studies, an optic fiber technique was used to directly measure force and the aforementioned ultrasonography was used to directly measure the length change of fascicle and tendinous tissue. These *in vivo* techniques made it possible to study the potentiation of the contractile machinery in human movement. Finni et al. (Finni, Ikegawa, Lepola, & Komi, 2003) reported that compared with the classical force velocity curve, no potentiation was found in the fascicle level of VL during SSCs, but this finding does not completely deny the possibility of potentiation of the contractile machinery presenting in SSCs *in vivo* because only one fascicle was examined and non-uniform stain between fascicles may happen in the muscle (Finni, Ikegawa, Lepola, & Komi, 2003). On the other hand, a power enhancement in the muscle-tendon unit level of VL was observed during hopping (Figure 15) and DJ. In fact, fast SSCs such as DJ or sprint running, the performance enhancement results from the cooperation between fascicle behavior and elastic recoil of tendons (Ishikawa, Finni, & Komi, 2003). It was observed that the tendinous tissue of MG and VL rapid shortened in the push off phase of DJ, while the fascicle shortens isometrically or at a low speed (Finni, Ikegawa, Lepola, & Komi, 2003; Fukunaga, Ichinose, Ito, Kawakami, & Fukashiro, 1997). This suggests that the minimized length change in muscle fascicles facilitates storage and recoil of elastic energy and finally enhances the mechanical output during the concentric contraction. In this view, it may not be significant to discuss whether the elongation of SEC at the expense of CC shortening distance will reduce the work of CC.

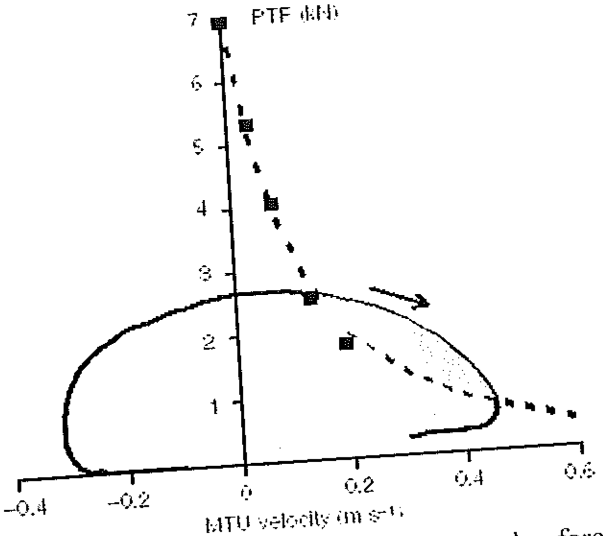

Figure 15 Relation (*in vivo*) between Patellar tendon force and quadriceps muscle–tendon unit velocity during normal bilateral hopping (solid line) and during isokinetic knee extensions. The black squares indicate the actually measured values in maximal knee extensions and the dashed line has been constructed by using Hill's equation. The shaded area illustrate that the concentric muscle–tendon output in hopping exceeded that in the maximal condition at high velocities. (From Finni et al. 2003)

3.5 Importance of preactivation

It has been showed that to prepare muscles to receive high impact force, muscles were strongly preactivated in these explosive movements, such as running (Kyrolainen, Avela, & Komi, 2005; Kyrolainen, Komi, & Belli, 1999; Nummela, Rusko, & Mero, 1994), run-up vertical jumps (Gollhofer & Kyrolainen, 1991; Ishikawa & Komi, 2004; Kamibayashi & Muro, 2005; Young, Wilson, & Byrne, 1999), and long jumps (Kyrolainen, Komi, & Belli, 1999). A high preactivation could be caused by muscle co-contraction in anticipation of landing (Ingen Schenau G.J.van., Bobbert M.F., & A., 1997b) or pre-landing movements (Horita, Komi, Nicol, & Kyrolainen, 2002). The preactivation is interpreted as a preprogrammed neuronal activation part, which has important functions (Dietz, Schmidtbleicher, & Noth, 1978 ; Gollhofer & Kyrolainen, 1991). First of all, it creates a beneficial situation for muscles to develop maximum force in a short time (Ingen Schenau G.J.van., Bobbert M.F., & A., 1997b) . As mentioned in the mechanism of more time available for time available, for those slow movements, it takes about 300 ms to develop the highest force. The force development depends on stimulation dynamics (the development of muscle stimulation), excitation dynamics (the development of muscle active state in response to stimulation), and contraction dynamics (the development of force in response to active state). However, in these fast SSCs, such as drop jumps, the muscles reach the maximum value in less than 100 ms. When muscles are strongly preactivated before landing, the process of stimulation dynamics and excitation dynamics may happen before landing. Therefore, the force could develop very fast after landing. Another function of preactivation is to increase sensitivity of muscle spindles to enhance stretch reflexes (Gottlieb, Agarwal, & Jaeger, 1981), which subsequently increases tendomuscular stiffness (Komi, 2000) and enhances force production (Kyrolainen, Avela, & Komi, 2005). Kyrolainen et al. (Kyrolainen, Avela, & Komi, 2005) reported that at higher speeds, the aEMG activities of the gastrocnemius, vastus lateralis, biceps femoris and gluteus maximus exceeded 100% MVC. This result provided evidence to support that the increased preactivation level potentiates the functional role of stretch reflexes. Recently, Linnamo et al. (Linnamo, Strojnik, & Komi, 2006) reported that the force potentiation is related to preactivation levels. Results showed that the force potentiation was greater at higher stretching velocities but only when maximal preactivation preceded the stretch. At lower preactivation levels the velocity dependence was not observed (Linnamo, Strojnik, & Komi, 2006). The preactivation level can be regulated by required motor task (Horita, Komi, Nicol, & Kyrolainen, 2002), stretch load (Kyrolainen, Komi, & Belli, 1999), fatigue (Nummela, Rusko, & Mero, 1994) , vestibular and visual inputs (Avela, Santos, Kyrolainen, & Komi, 1994), and verbal instructions (Arampatzis, Bruggemann, & Klapsing, 2001).

From the above discussion, it has been showed that there are several critical conditions for a effective SSC: a fast eccentric speed to increase force development and facilitate the stretch reflex, a short lengthening amplitude to take advantage of the short range of stiffness and enhance the storage of elastic energy, a minimized fascicle length change to optimize the release of elastic energy. However, there are dilemmas to maximize the mechanical output. The increased eccentric speed and load could increase force development, but it will overstretch the fascicle, tendon and whole muscle, consequently the power and work output will be dramatically reduced. Also, if the eccentric contraction can be finished in a very short time, the effect of stretch reflex would be too late to improve the mechanical output. A high level of preactivation seems a good solution for these dilemmas. With a high level of preactivation, it takes less time for muscles to reach peak force. Thus, under a high eccentric load and speed, a short stretch range and minimized fascicle length changes are still possible to be realized. The effect of stretch reflex would not be too late to improve the mechanical output because the preactivation can enhance the stretch reflex. Furthermore, one big difference between human dynamic movement and isolated muscle behavior is the activation level. Obviously, all these pre-stretch effects observed in the experiments using fully preactivated muscles would be more likely to happen in SSCs with a high preactivation level. In summary, the preactivation appears to be necessary to enhance EMG activity, potentiate stretch reflexes, and enhance potentiation, therefore, it plays an important role in the SSC performance enhancement (Kyrolainen, Komi, & Belli, 1999)

4. Summary

In the literature, there is not enough evidence to deny any of the four proposed mechanisms contributing to mechanical enhancement during SSCs. It is quite likely a high level of force prior to shortening, stretch reflex, potentiation of the contractile machinery, and the storage and release of elastic energy interact in some manner to produce performance enhancement during SSCs (Cronin, McNair, & Marshall, 2001). The amplitude of enhancement may depend on preactivation, stretch velocity and load, and length change in fascicles and tendons.

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Appendix 2. Consent Form

LOUISIANA STATE UNIVERSITY
CONSENT FORM

Study Title: A Comparison of drop jumps with and without approach run

Performance Site: Biomechanics Laboratory, Room B2, Gym Armory

Investigators: The investigator(s) listed below are available to answer questions about the research, M W F, 1:00 p.m. - 4:00 p.m.

Dr. Li Li (225) 578-2036
Mianfang Ruan (225)578-4395

Purpose of the Study: The aim of this project is to quantify the biomechanics differences between the drop jump with and the drop jump without approach run.

Subject Inclusion: Adults between 18 and 35 years of age with no apparent health problems are allowed to participate in this study.

Number of Subjects: 75

Study Procedures: Each subject will sign a written consent form that is approved by the institutional review board. Next, history of knee and ankle injury will be assessed verbally. Each subject will then have two weeks (three times per week, total six times) jump training and drop jump training, so you will master the correct drop jump technique and reduce the risk of injury. Subjects will be required to wear suitable sports shoes in training. During the formal data collection, you will have 15 minutes to warm up. After warm up, each subject's legs will be cleansed with rubbing alcohol before placement of surface electrodes. Those electrodes will be placed on the surfaces of Gluteus maximus, Rectus femoris, Biceps femoris, Vastus lateralis, Tibialis anterior, Gastrocnemius and Soleus. Additionally, subjects will have five self-adhesive markers (i.e. a reflective ball that tracks joint positioning) placed at the Anterior Superior Iliac Spine, Hip, Knee, Ankle, Metatarsals. Then subjects will be asked to perform drop jumps from five different heights: 0, 13, 26, 39, and 52 cm. combined with four different level of approach run, zero (standing), one, two, and three steps. You will land on a force plate. Totally, you will perform 20 jumps. Kinematics, kinetics and EMG data will be recorded. A spotter will be present during the exercises to ensure subjects' safety.

Benefits There are no direct benefits to the participants. However, information gained from this study may provide biomechanics knowledge to enhance the efficiency of training.

Risks/Discomforts: The risk will be minimal. Subjects who don't have any experience of drop jump may feel nerves and touch ground with their heel while landing, which increase the impact force and may increase the risk. To minimize the risky, the subjects will have two week's (three times a week) jump training before data collection. A spotter will be present during the exercises to ensure participants' safety.

Right to Refuse: Participants may choose not to participate or to withdraw from the study at any time without penalty or loss or any benefit to which they might otherwise be entitled.

Privacy: The results of the study may be published. The privacy of participating will be protected and your identity will not be revealed unless legally compelled.

Financial Information: There is no cost to the participant, nor is there any compensation for participating in the study.

Subject Exclusion: If the answer to any of the following questions is "YES", or those individuals who do not meet the specified age range are excluded from participating in the study.

1). Has your doctor ever stated that you have heart trouble?
2). Do you frequently have pains in your heart or chest?
3). Do you often feel faint or have spells of severe dizziness?
4). Has your doctor ever said your blood pressure was too high?
5). Has your doctor ever told you that you have a bone or joint problem, arthritis that has been aggravated by exercise, or might be made worse with exercise?
6). Is there a good physical reason not mentioned here why you should not follow an activity program even if you wanted to?
7) Have you experienced any knee or ankle injury?

Signatures: The study has been discussed with me and all my questions have been answered. I may direct additional questions regarding study specifics to the investigators. If I have questions about subjects' rights or other concerns, I can contact Robert C. Mathews, Institutional Review Board, (225) 578-8692. I agree to participate in the study described above and acknowledge the investigator's obligation to provide me with a signed copy of the consent form.

______________________________ ________________________

Subject Signature Date

Appendix 3. Computer Programs

```
runmuscle.
% Adapted from Akinori Nagano, Ph.D.
% Computer and Information Division, RIKEN
% June 2003

This program is the main junction for the simulation.
% This program sets up parameter values, initial condition,
% options for the numerical integration,
% calls a numerical integration function
% and draws results.



clear;
close all;

% set up parameter values
grav=9.81; .        % m/s 2,gravity
dur=0.9;            %s, simulation duration
grids=501;
pre=0;
tspan=linspace(0.5,dur,grids);



Fmax=3317;           %N
LCEopt=0.10;     %m
Lslack=0.30;    %m
a_pen=0;            %deg,pennation angle
stiff=0.04;      %stiffness of the SEE
massa=70;
massb=70;        %kg
mus_orig=0;     %m,position of the muscle origin


onset=0.00005;          %s
release=0.5;      %s

%set up initial condition
LCEini = LCEopt *1;
Lslackini=Lslack;


%set up initial condition
```

```
icon=[-LCEini*cos(a_pen*pi/180)-Lslackini;% position    of the mass
-0.50%velocity of the mass
0.1%LCEini;% length of the CE
0]%0.0];% activation level


pars=[mus_orig Fmax Lslack stiff LCEopt massa massb release a_pen onset pre];
% set up options for numerical integration
options=odeset('RelTol',1e-6, 'AbsTol', 1e-9);


% numerical integration
[T,Y]= ode45 ('diffODE', tspan, icon, options, pars);
%draw figures
SEex=max(-Y(:,1)-Lslack-Y(:,3),0.000001);
F=(Fmax/((stiff*Lslack)^2))*SEex.^2;
power=F.*Y(:,2);
PEEX=max(Y(:,3)-LCEopt,0);
FPE=Fmax*((PEEX/(0.47*LCEopt)).^3);
figure (1);

for jj=1:4
    subplot (2,4,jj)
    plot(T, Y (:,jj));
    subplot(2,4,5);
    plot (T,SEex);
    subplot(2,4,6);
    plot(T,F);
    subplot(2,4,7);
    plot(T,power);
    subplot(2,4,8);
    plot(T, FPE);

end

function [Fiso]=calFiso (LCE,LCEopt)
% This function calculates the
% force-length relation of the contractile element.


width=0.55;
c1=-1.0/ (width^2);
c2=-2.0*c1;
c3=1.0 + c1;
LCErel=LCE/LCEopt; %CE length relative to LCEopt
```

```
 Fiso=max(c1*LCErel^2+c2*LCErel+c3,1d-6);% force- length relation

 function [outval]=diffODE (t,inval,options,pars)
 % This function calculates the first derivative of the
 % variables to be integrated.



 %parameter values
 mus_orig=pars (1);
 Fmax=pars (2);
 Lslack=pars (3);
 stiff=pars (4);
 LCEopt=pars (5);
 massa=pars(6);
 massb=pars(7);
 release=pars (8);
 a_pen=pars (9);
 onset=pars (10);
 pre=pars (11);
 mass_pos=inval(1);%position of the massif

 mass_vel=inval(2);%velocity of the mass
 LCE=inval(3);% length of the contractile element
 qq=max(inval(4), 0.0001);%activation level)

 Loi=mus_orig-mass_pos;% muscle origin-insertion length
 FSEE=calFSEE (Fmax, Loi, LCE, Lslack, stiff, a_pen);% SEE force
 FPEE=calFPEE (Fmax,LCEopt,LCE);% PEE force
 %fprintf(1,'%f\n',mass_vel)
 %fileFSEE=fopen('t.txt', 'a');
 %fprintf(fileFSEE, '%.4f',t);
 %fprintf(fileFSEE,'\n');
 %status=fclose(fileFSEE);

 %end
             %if t <release+ 0.1
   mass_acc=(FSEE-massa*9.81)/massa;
   %t>release+0.2;
     %end % acceleration of the    mass


act=pre;% activation input

if t >=onset & t<release %and t <release% full activation after the onset
 act =min(t*2.2,pre);
```

```
 elseif    t>= 0.5 & t<= 0.8
      %act=min(3*(t-release)+pre,0.9);
      %elseif t>0.535 & t<0.57
    act=min(2.2*(t-0.5)+pre,0.9);
    %act=min(3*(t-release)+pre,0.9);
    %elseif t>0.65 &t<0.8
       %act=min(3*(t-release)+pre,pre+0.25);
 elseif t> 0.8
       act=0; % % max(pre+0.3-10*(t-0.1-release),0);
       %else
     % act=1;
 end


ta=0.055;% time constants
td=0.065;
t2=1/td;
t1=(1/ta-t2);
dqq= (act-qq) * (t1*act + t2);%first derivative of the CE activation level










%if t> release+0.3 & -0.0001<mass_pos+0.6 <0.001
 %    mass_acc=0
  %mass_vel=0



  %end
VCErel=calVCErel(LCE, LCEopt, FSEE, Fmax, qq, FPEE,a_pen);
VCE=VCErel*LCEopt;       %CE shortening velocity

if t < release     % no motion before the release
mass_vel = 0;
mass_acc = 0;
end

%SEex=-mass_pos-Lslack-LCE;
```

```
%F=(Fmax/((stiff*Lslack)^2))*SEex^2;
power=FSEE*mass_vel;
powerCE=(FSEE-FPEE)*VCE;
powerpee=FPEE*VCE;
powerSEE=FSEE*(mass_vel-VCE);
fileFSEE=fopen('vce.txt', 'a');
fprintf(fileFSEE,
'%.4f,%.4f,%.4f,%.4f,%.4f,%.4f,%.4f,%.4f,%4f',t,mass_vel,FPEE,VCE,FSEE,power,powerCE,powerpee,p
owerSEE);
fprintf(fileFSEE,'\n');
status=fclose(fileFSEE);


outval=[mass_vel;mass_acc;VCE;dqq];% output first deriva-    tive values


function[FPEE]=calFPEE (Fmax, LCEopt, LCE)
%This function calculates the
%force-length relation of the parallel elastic element.

PEEext=max(LCE-LCEopt,0);%extension of the PEE
FPEE=Fmax*((PEEext/(0.47*LCEopt)).^3); % force-length relation FSEE, Fmax, qq, FPEE, a_pen)
%This function calculates the
%force-velocity relation of the contractile element.

function[FSEE]=calFSEE (Fmax,Loi,LCE,Lslack,stiff,a_pen)
%This function calculates the
%force-length relation of the series elastic element.


SEEext=Loi-Lslack-LCE*cos(a_pen*pi/180);% extension    of the SEE
FSEE=(Fmax/((stiff*Lslack)^2))*(max(SEEext,0)^2);% force-length relation

function    [VCErel]= calVCErel (LCE, LCEopt, FSEE, Fmax, qq,FPEE, a_pen)
%This function calulates the force-velocity relation of the contractile
%element.

%parameter values
Arel=0.41;
Brel=5.2;
Fasympt=1.5;
Slopfac=2.0;
Sloplin=200;
```

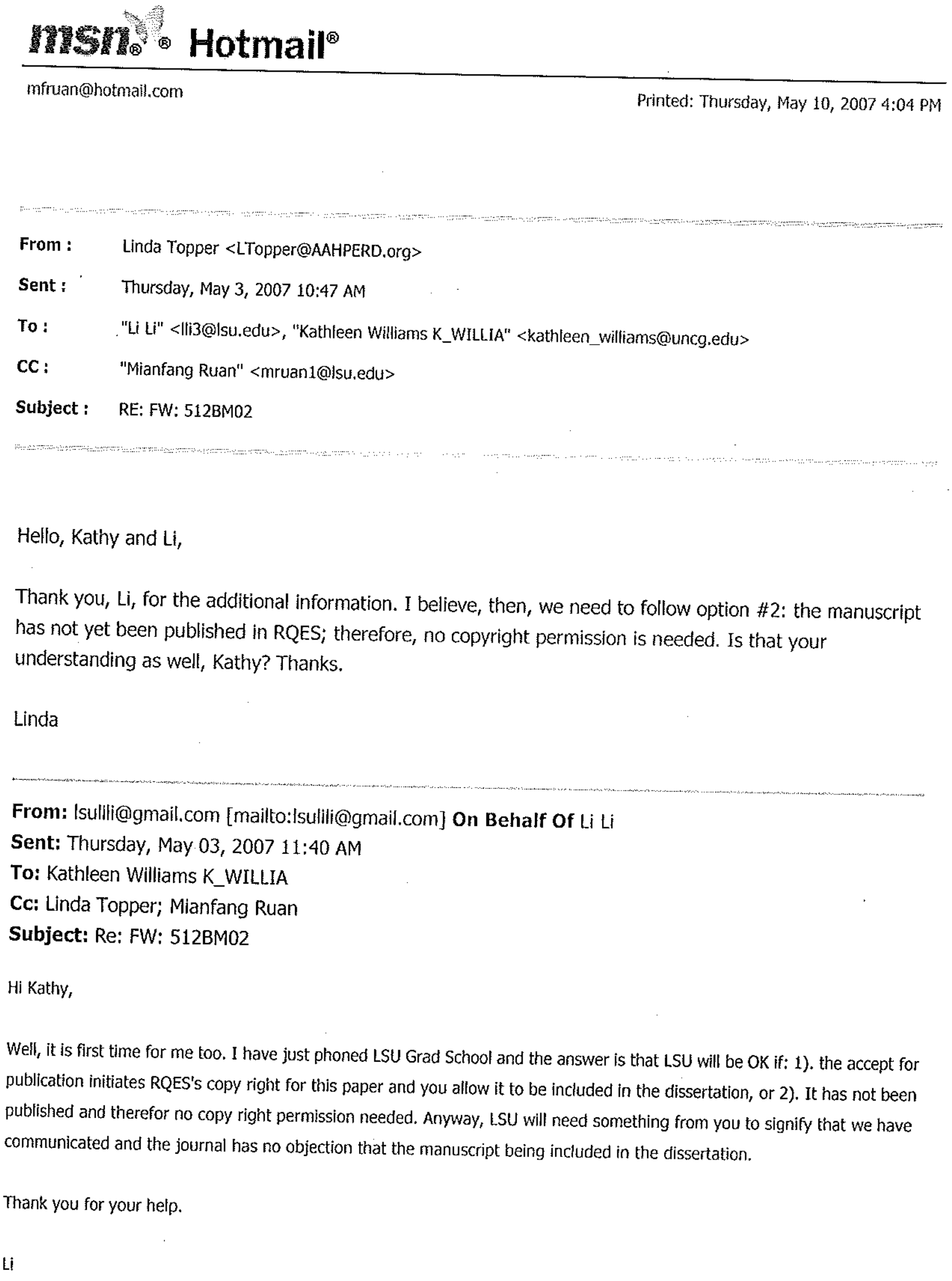
```
%consideration of the effect of the parallel elastic element
if (FSEE/cos(a_pen*pi/180)>FPEE)
FCErel= (FSEE/cos(a_pen*pi/180))/Fmax; %FPEE)/Fmax;
else
 FCErel=0;
end



Fiso=calFiso(LCE,LCEopt);
Factor=min(1,3.33*qq);
%fprintf(1,'%f',Fiso);

if (FCErel/qq<=Fiso) %concentric phase
   VCErel=-Factor*Brel*((Fiso+Arel)/(FCErel/qq+Arel)-1.0);
else% eccentric phase
   c2= -Fiso * Fasympt;
   c1= Factor*Brel*(Fiso+c2)^2/ (Fiso+Arel) /Slopfac;
   c3= c1/ (Fiso+c2);
   if (FCErel/qq <= -sqrt(c1/(Factor*Sloplin))-c2) % slow stretch
        VCErel=-(c1/ (FCErel/qq+c2)-c3);
 else% fast stretch
    VCErel=Factor*Sloplin*(FCErel/qq+c2)+c3+2.0*sqrt(c1*Factor*Sloplin);
end
end
```

Appendix 4. Letters from Publisher



msn Hotmail®

mfruan@hotmail.com

Printed: Thursday, May 10, 2007 4:04 PM

From : Linda Topper <LTopper@AAHPERD.org>
Sent : Thursday, May 3, 2007 10:47 AM
To : "Li Li" <lli3@lsu.edu>, "Kathleen Williams K_WILLIA" <kathleen_williams@uncg.edu>
CC : "Mianfang Ruan" <mruan1@lsu.edu>
Subject : RE: FW: 512BM02

Hello, Kathy and Li,

Thank you, Li, for the additional information. I believe, then, we need to follow option #2: the manuscript has not yet been published in RQES; therefore, no copyright permission is needed. Is that your understanding as well, Kathy? Thanks.

Linda

From: lsulili@gmail.com [mailto:lsulili@gmail.com] **On Behalf Of** Li Li
Sent: Thursday, May 03, 2007 11:40 AM
To: Kathleen Williams K_WILLIA
Cc: Linda Topper; Mianfang Ruan
Subject: Re: FW: 512BM02

Hi Kathy,

Well, it is first time for me too. I have just phoned LSU Grad School and the answer is that LSU will be OK if: 1). the accept for publication initiates RQES's copy right for this paper and you allow it to be included in the dissertation, or 2). It has not been published and therefor no copy right permission needed. Anyway, LSU will need something from you to signify that we have communicated and the journal has no objection that the manuscript being included in the dissertation.

Thank you for your help.

Li

Vita

Mianfang Ruan was born on April 19, 1972 in Ruian, Zhejiang, China. He graduated from Ruian High School in 1990. Following his high school graduation he attended Physical Education department, Hangzhou University, and graduated in 1992. After three years working as a high school P.E teacher, Mianfang Ruan then attended the Shanghai Institute of Physical Education to pursue a Master of Education in sports biomechanics. After graduating from Shanghai Institute of P.E, he worked as an assistant researcher for four years at Shanghai Institute of Sports Science. He left Shanghai in 2002 to pursue his Doctor of Philosophy degree in kinesiology at Louisiana State University. He was the research and teacher assistant during his graduate studies in the Kinesiology Department and the recipient of College of Education Lilian Olson Scholarship. Before graduation, he accepted a research position at American Sports Medicine Institute, in Birmingham, Alabama.