The nature of the stretch–shortening cycle

In Chapter 1 muscle exercises were classified primarily into static and dynamic types. The classification used in Table 1.1 (p. 4) cannot, however, be used to describe the natural form of muscle function. Muscular exercises seldom involve pure forms of isolated isometric, concentric or eccentric actions. This is because the body segments are periodically subjected to impact forces (Fig. 6.51), as in running or jumping, or because some external force such as gravity lengthens the muscle. In these phases the muscles are acting eccentrically, and concentric action follows. By definition of eccentric action, the muscles must be active during the stretching phase. The combination of eccentric and concentric actions forms a natural type of muscle function called a stretch–shortening cycle or SSC (Norman & Komi, 1979; Komi, 1984).

The purpose of SSC is to make the final action (concentric phase) more powerful than that resulting from the concentric action alone. Since Cavagna et al. (1965) introduced the basic mechanisms of work enhancement when an isolated muscle was subjected to active stretch (eccentric action) prior to its shortening (concentric action), considerable scientific work has been devoted to explain the detailed mechanisms of force and power potentiation in SSC. Most of the work has come from experiments with isolated muscle preparations or from mechanical muscle models. These experiments have increased our understanding of this phenomenon, which was simply called elastic potentiation. For details of the current mechanisms of performance potentiation the reader is referred to Chapter 6D.

In vivo demonstration of SSC in natural human locomotion

Whole body exercise involves many joints and groups of muscles. In this complex but well coordinated act each muscle makes its own contribution, usually in the form of SSC action. Identification of SSC for an individual muscle in a particular exercise is often very difficult, and sometimes even impossible. Direct measurements require knowledge of instantaneous forces and changes in muscle–tendon lengths. Methods to calculate length changes separately in muscular and tendon components are not very reliable, and therefore the length is usually expressed for the total segment including both muscular and tendinous material.

Direct in vivo measurement of force requires implantation of a force transducer around the tendon (Fig. 6.52). In vivo registration has been applied primarily in animal experiments and has produced considerable information on the mechanical behaviour of the Achilles tendon (AT), e.g. in cat locomotion (Walmsley et al., 1978). A method which directly records forces on human AT using an implanted transducer has been reported recently (Komi et al., 1987b;
Fig. 6.51 Human walking and running do not resemble the movement of a rotating wheel, where the centre of gravity is always directly above the point of contact and perpendicular to the line of progression. Instead they resemble the action of a ‘rolling’ cube and have considerable impact loads when contact takes place with the ground. Before contact the muscles are preactivated (A) and ready to resist the impact, during which they are stretched (B). The stretch phase is followed by a shortening (concentric) action (C). The lower part of the figure demonstrates the SSC, which is the natural form of muscle function. (From Komi, 1984.)

Fig. 6.52 Schematic diagram showing the position of the ‘buckle’ transducer around the Achilles tendon. (Komi, 1990). This in vivo technique utilizes either an E-form or a buckle-type transducer, of which the latter has proven to be more convenient. The transducer is implanted under local anaesthesia around the AT of adult volunteers. After appropriate calibration procedures the subjects can perform normal unrestricted locomotion including walking, running at different speeds, hopping, jumping and bicycling. In some cases even maximal efforts were performed without any discomfort. All movements were performed either on a long force platform or on a bicycle which had special force transducers on the pedals. Electromyograph (EMG) activities were registered from the major leg muscles. AT force (ATF) and EMGs were telemetered, and all the signals were stored on magnetic tape. The entire measurement lasted 2–3 hours, after which the transducer was removed. Each performance was also filmed at 100 frames – s\(^{-1}\) so that the percent changes of the lengths of the gastrocnemius and soleus muscles could be estimated (Grieve et al., 1978). This estimation was then used to calculate the force–length and force–velocity curves for the two muscles. It must be emphasized that in this analysis the force values represent the two muscles simultaneously because AT is a common tendon for both of them.

Figure 6.53 presents typical results (Komi et al., unpublished observations) of the occurr-
Fig. 6.53 A representative record of the Achilles tendon force and segmental length changes of the gastrocnemius (Ga.) and soleus (Sol.) muscles together with $F_x$ and $F_y$ ground reaction forces and selected EMG activities when the subject was running along a long force platform. The vertical line indicates the beginning of the ground contact as well as of the stretch--shortening cycle (SSC) of the muscles. The upward and downward deflections of the segmental length changes signify, respectively, stretching (eccentric) and shortening (concentric) phases of the cycle. (a) Ball running; (b) heel running.

rence of SSC in gastrocnemius and soleus muscles separately during running. There are several important features to be noted. First, the changes in muscle--tendon length are very small during the stretching phase. This suggests that the conditions favour the potential utilization of short-range stiffness in the muscle (Rack & Westbury, 1974). Second, the segmental length changes in these two muscles take place in phase in both the lengthening and shortening parts of the SSC. This is typical for running and jumping; it has considerable importance because the transducer measures forces of the common tendon for the two muscles. The situation is not so simple in other activities, such as bicycling (Gregor et al., 1991), where the length changes are more out of phase in these two muscles. The third important feature of the example in Fig. 6.53 is that the form of the AT force curve, resembles that of a bouncing ball.

The force--length and force--velocity curves can then be computed on the basis of the curves, as presented in Fig. 6.53. It must be emphasized that in this analysis the force values represent the two muscles simultaneously, because AT is a common tendon for both of them.

Figure 6.54 presents an analysis for the force--length and force--velocity curves during the contact phase in running. The force--length curve demonstrates a very sharp increase in force during the stretching phase, which is characterized by a small change in length. The
right-hand side of the figure shows the force-velocity comparison demonstrating high potentiation during the stretching phase (concentric action). If these curves are compared with the force-velocity curves obtained with isolated muscle preparations (e.g., Hill, 1938) or with human forearm flexors (e.g., Komi, 1973) the dissimilarities are evident. It must be noted that these force-length and force-velocity curves are instantaneous plots during the SSC and may therefore represent more truly the behaviour of the muscles during natural movements. If the subject is running on two occasions at similar speeds, the analysis gives remarkably similar results. Running at near maximum speed (9.02 m·s⁻¹) seemed to result in a lower peak ATP, but the length change in the eccentric phase was much smaller (Fig. 6.54a). The utilized muscle length estimates have shown that running and jumping are not the only activities where SSC can be identified. Recent evidence (Gregor et al., 1987, 1991) has demonstrated that the gastrocnemius and soleus muscles also function in bicycling in SSC, although the stretching phases are not as apparent as in running or jumping.

The in vitro measurement technique for humans has been developed following reports
on animal experiments (e.g. Sherif et al., 1983). Many of these animal studies have included similar parameters to those used in our human studies, such as muscle length, force and EMG. The most relevant report for comparison with present human experiments is that by Gregor et al. (1988); they measured mechanical outputs of the cat soleus muscle during treadmill locomotion. In this study the results indicated that the force generated at a given shortening velocity during late stance phase was greater, especially at higher speeds of locomotion, than the output generated at the same shortening velocity in situ. Thus both animal and human in vivo force experiments seem to give similar results with regard to the force-velocity relationships during SSC. Although the present human experiments cannot include some of the in situ measurements of Gregor et al. (1988), the form of the curves in Fig. 6.54 clearly indicate performance potentiation in the concentric phase of SSC.

The difference between the force-velocity curve and the classical curve in isolated muscle preparations (e.g. Hill, 1938) or in human experiments (e.g. Wilkie, 1950; Komi, 1973) may be due to natural differences in muscle activation levels between the two types of activities; this, however, can only partly explain the deviations. While the in situ preparations may primarily measure the shortening properties of the contractile elements in the muscle, natural locomotion, primarily utilizing SSC action, involves controlled release of high forces, caused primarily by the eccentric action. This high force favours storage of elastic strain energy in the muscle-tendon complex. A portion of this stored energy can be recovered during the subsequent shortening phase and used for performance potentiation. Both animal and human experiments seem therefore to agree that natural locomotion with primarily SSC muscle action may produce muscle outputs which can be very different to the conditions of isolated preparations, where activation levels are held constant and storage of strain energy is limited.

### Mechanical efficiency of SSC exercise

If mechanical outputs of the muscle are enhanced in SSC action the logical consequence should be that the work efficiency is enhanced as well. Mechanical efficiency (ME) has been studied for almost a century and the textbooks of physiology have until recently referred to ME as varying between 20 and 25%. Experiments conducted primarily during the last two decades have shed some doubts on such a relatively low level of ME which varies only slightly. It is now known that the different forms of muscle action have different ME, and that the velocity of shortening or stretching influences its value (e.g. Margaria, 1968; Kaneko et al., 1984; Aura & Komi, 1986a). In addition the SSC alone may introduce very different loading conditions and subsequently different ME.

Conventionally, mechanical efficiency of work (ME) is the ratio of external work performed to the extra energy production:

\[
\text{ME} = \frac{W \times 100}{E - e}
\]

where \(E\) is the gross energy output, \(e\) is the resting metabolic rate and \(W\) is the external work performed.

To examine the ME values of either isolated eccentric or concentric exercises, or their combination, the sledge apparatus (Fig. 6.55) was constructed. The apparatus consists of: (i) a sledge (\(m = 33\) kg) to which the subject is fixed in a sitting position; (ii) a ‘slide’ on which the sledge runs along the slow-friction aluminium track; and (iii) the force-plate placed perpendicular to the sliding surface (for details see Kaneko et al., 1984; Aura & Komi, 1986a, b; Komi et al., 1987a). The relationship between energy expenditure and mechanical work was shown to be linear in a small range of shortening velocities of the concentric exercise (Kaneko et al., 1984), but when the movement velocity was increased (Aura & Komi, 1986b) this linearity was no longer true. For this reason ME of concentric exercise was not constant, but
decreased with increasing shortening velocities. In eccentric exercise, ME increased in all subjects when mechanical work was increased, and in some individuals it reached values over 60% (Aura & Komi, 1986a, Kyröläinen et al., 1990). The evidence suggests that the ME of eccentric exercise is very high but not constant and that great variation between individuals is characteristic. The high efficiency can be improved by increasing stretch velocity, and it can be obtained with low motor unit activation. However, in concentric exercise EMG, energy expenditure and mechanical work change in parallel in slow muscle actions, but increasing shortening velocities will modify these relationships.

Pre-stretching of an active muscle during SSC exercise probably also influences the ME of the positive work phase (concentric action) of the cycle. Accepting that negative work does not have a constant efficiency value, then investigation of the ME of SSC exercise must be preceded by first defining that the ME of pure eccentric exercise is exactly the same in stretching velocity and amplitude as the one to be used in SSC exercise. This method was applied in the sledge apparatus described above by Aura and Komi (1986a). Maximum concentric exercise ($W_{\text{max}}$) was defined as the energy level which the subject is able to exert in one pure concentric action. For each subject the positive work intensity was always kept at 60% of $W_{\text{max}}$, and the preceding eccentric action was varied from day to day. SSC actions were repeated 80 times on each situation at a rate of one every 3 s.

At the beginning of each exercise cycle the sledge was released from a certain distance corresponding to the specific energy level. The height of dropping varied the potential energy of the sledge–subject system and subsequently varied the negative (kinetic) work done during the breakdown. Within each exercise the dropping height was constant, but was varied between exercises, being 20–120% of $W_{\text{max}}$. During contact with the force-plate the subject resisted the downward movement (negative work), and immediately after stopping the
sledge (knee angle 90°) the legs were extended to perform positive work. The effort in positive work was controlled so that the change in the potential energy of the sledge–subject system corresponded to 60% of $W_{\text{max}}$. When the sledge had reached its highest position, two assistants checked that the starting position corresponded to the specific energy level of the negative work. The mechanical efficiencies of the pure negative and pure positive work were measured individually for all of the subjects 1 or 2 days prior to the actual SSC exercises. The formulae for calculating ME during SSC exercises are given elsewhere (Aura & Komi, 1986a).

Figure 6.56 shows how the efficiency of positive work increases in SSC exercise when the pre-stretch load (negative work) is increased. The results therefore suggest that the efficiency of the constant concentric action can be changed considerably by modifying the preceding eccentric stretch load.

The most recent experiments (Oksanen et al., 1990) have questioned the accuracy of estimating the ME of the positive work ($W_{\text{pos}}$) phase in the SSC. In our earlier studies (Aura & Komi, 1986a; Kyröläinen et al., 1990), the calculation of $W_{\text{pos}}$ of ME in the SSC was based on the assumption that the eccentric phase of SSC exercise was the same as in the respective pure eccentric condition. However, EMG activity levels demonstrated that in isolated forms of eccentric action, the EMGs were much lower than in the comparable eccentric phase in the SSC exercise. Thus despite the apparently same mechanical work, the energy expenditure must have been different. This will naturally have introduced errors in the calculation of ME of $W_{\text{pos}}$ in the SSC and the final result will probably be an overestimation. Higher EMG values would imply higher energy expenditure when the two types of eccentric phases, which have the same mechanical work, are compared with each other. However, the use of the sledge apparatus in studying ME of the entire SSC as well as of its two phases is certainly an improvement over the other attempts, which have used a constant value of $-1.2$ (or 120%) (Margaria, 1968) for the eccentric phase ME and then applied it to the calculation of ME in more practical type exercises (e.g. Bosco et al., 1982; Ito et al., 1983).

**Fatigue and training adaptation of SSC exercises**

Fatigue has been examined quite extensively in isolated forms of isometric, concentric or

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**Fig. 6.56** The mechanical efficiency of positive work (+ME) in SSC exercise, related to the pre-stretch intensity ($W_{\text{neg}}$). The subjects performed SSC exercises on a sledge apparatus (Fig. 6.55), in which the take-off (positive work) was always at the same point on the slide bars, but the dropping distance (pre-stretch intensity) was varied on different test days. For details see Aura and Komi (1986b). ●, Male; ○, female.
eccentric actions. Because SSC is probably the only natural form of muscle function, it could be of interest to know how repeated SSCs are receptive to fatigue and how the fatigue phenomenon can be characterized in different parts of the cycle. Unfortunately, however, the literature lacks comprehensive efforts in this regard. The stretch reflex components are expected to play an important role in situations where stretching loads are high or efficient stretch–shortening behaviour is necessary. Under these conditions muscle stiffness must be well coordinated to meet external loading conditions. The sledge apparatus shown in Fig. 6.55 can be used for fatigue experiments using SSCs. In the study by Gollhofer et al. (1987a,b), normal healthy men performed 100 sub-maximal SSCs so that they were lying on the sledge with their heads toward the force-plate. The exercise was then performed with their arms. The results showed that during 100 SSCs fatigue was characterized by increases in the contact times for both the eccentric and concentric phases of the SSC (Fig. 6.57).

![Graph showing EMG data for elbow joint, muscles radialis, biceps, triceps, and force right contact over time](image)

Fig. 6.57 Influence of exhaustive stretch–shortening cycle (SSC) exercises using the arms on EMG records and force–time curves. The subject performed 100 repeated SSCs on a special sledge apparatus (Fig. 6.55), and was lying with the head towards the force plate. Note the increased period of hand contact on the force plate between the first (a) and last (b) of the SSCs. Similarly, the initial force peak during contact increased with increasing fatigue. (From Gollhofer et al., 1987b.)
The force–time curves during contact on the platform were influenced by fatigue so that the initial force peak became higher and the subsequent initial drop of force more pronounced. More interestingly, however, the reflex contribution to sustain the repeated stretch loads became enhanced, especially when measured during the maximal drop-test condition before, and immediately after, the fatigue loading (Fig. 6.58). Thus in a non-fatigue state, the muscles are able to damp the impact in the SSC by a smooth force increase and by a smooth joint motion. However, repeated damping movements followed by the concentric action may eventually become so fatiguing that the neuromuscular system changes its ‘stiffness’ regulation. This change is characterized especially by a high impact force peak followed by a rapid temporary force decline. The enhanced stretch reflex contribution during fatigue could be interpreted to imply attempts of the nervous system to compensate by increasing activation of the loss of the muscles’ contractile force to resist repeated impact loads. Recent studies on marathon running (Komi et al., 1986; Nicol et al., 1991a,b) have confirmed observations of laboratory tests which show that the ground reaction force curves, both during running and in special drop jump tests, imply reduced tolerance to stretch loads as well as loss in the recoil characteristics of the muscles.

It is, however, not known what could trigger the enhanced reflex contribution. One possible candidate could be accumulation of the metabolic products which induce acidosis in the milieu surrounding la-afferent nerve terminals. This hypothesis follows the observation of Fujitsuka (1979) that modulated la-afferent discharges in stretched muscle spindles of isolated frog muscle increased up to twice the value for normal pH conditions when the pH value in the extracellular medium was lowered by 0.1–0.2.

It may not be surprising that the mechanism of SSC fatigue is not well understood. What is astonishing, however, is the fact that the literature lacks comprehensive coverage of the mechanistic events which occur when the muscles are trained for several weeks or months using controlled SSC exercises. There is no doubt that special jumping exercises which utilize the SSC have beneficial effects on strength and power (e.g. Komi et al., 1982). Chapters 9A, 9B and 18 deal partially with the problems of utilizing jumping exercises in power training. In addition to metabolic stimuli in the muscular tissue, training with SSC exercise specifically loads the components
related to stiffness regulation. One of the main purposes of strength and power training is to improve muscle stiffness, especially in the explosive type of force production. It has been proposed (Komi, 1986) that the influence of the length-feedback component (facilitatory reflex), which originates from the muscle spindles, can be enhanced through training. This would improve muscle stiffness during the important stretching phase of the SSC. When the role of the inhibitory force-feedback component (from the Golgi tendon organs) can be simultaneously decreased, the final result is a further increase in muscle stiffness. This would allow the muscle to tolerate greater stretch loads, possibly store more elastic energy, and improve power as well as ME. In this regard Kyröläinen et al. (1991) have demonstrated that a 16-week SSC training improved ME. The greatest changes in ME occurred during higher pre-stretch intensities. The ME values changed from 49.3 ± 12.9% to 55.4 ± 12.1% (P < 0.5) in pure eccentric exercise with the legs as measured on the sledge apparatus. In SSC the corresponding overall ME, including the concentric phase, changed from 39.5 ± 4.6% to 46.1 ± 5.0% (P < 0.1). After training the subjects preactivated their leg extensor muscles earlier, before the impact, thus adding to the possibility of increased power during the braking (eccentric) phase. These observations look promising in explaining the possible potential of training with SSC exercises. Further research projects are, however, needed before conclusive evidence for comprehensive understanding of SSC training is available.

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