

The Unique Action of Bi-Articular Muscles in Leg Extensions

Gerrit Jan van Ingen Schenau, Maarten F. Bobbert, and Arthur J. van Soest

41.1 Introduction

In textbooks on the anatomy of the musculo-skeletal system, both muscles crossing only one joint (mono-articular muscles) and muscles crossing more than one joint (multi-articular muscles) are classified according to the location of their line of action relative to joint axes of rotation (e.g. Williams and Warwick, 1980). For instance, the line of action of the mono-articular vastus medialis passes anterior to the flexion/extension axis of the knee joint, and therefore the muscle is classified as a knee extensor. Similarly, the bi-articular gastrocnemius is classified as a knee flexor and ankle plantar flexor. As such, the gastrocnemius is considered to be an antagonist of the vasti at the knee joint.

This classification method, which is focussed on joint displacements, underlies the majority of contemporary descriptions of muscle actions required to perform a task. For instance, in jumping, hip extension and knee extension occur. Thus, the hip extensor and knee extensor muscles are expected to be active. Unfortunately, if we focus on joint displacements it is difficult to understand why the body is supplied with muscles crossing more than one joint; it seems that such muscles could well have been replaced with sets of mono-articular muscles. Arguing against the classification of muscles as described above, many authors have suggested that muscle actions can only be understood if their effects are studied in a natural environment, taking into account the actions of other muscles, forces on the environment, inertial forces and gravity (e.g. Fisher, 1902; Bernstein, 1967). Following this suggestion, we

have studied jumping, speed skating and cycling using an inverse dynamical approach, and we have identified a number of constraints in the transformation of rotations in joints into the desired translation of the body center of gravity relative to the foot (in jumping and speed skating) or the pedal trajectory relative to the trunk (in cycling). In dealing with these constraints, bi-articular muscles appear to play a unique role by distributing net joint moments and joint powers over the joints.

Both in this chapter and in Chapter 18 (Gielen et al.), this unique role, which often requires co-activation of mono-articular muscles and their bi-articular antagonists, will be explained in the terminology of multi-link models. Before describing our approach, and results obtained using it, some attention is paid to other approaches used in the literature to study the function of bi-articular muscles and co-activation. Also, in order to prevent misunderstandings, attention is paid to some of the concepts used in our approach.

41.2 Possible Actions of

Bi-Articular Muscles

Since Borelli (1685) showed that the force development in the knee joint is influenced by the position of the hip joint, many researchers have advanced ideas about possible actions of muscles crossing more than one joint. The possible action of bi-articular muscles in the lower extremity has in particular been the subject of a lot of speculation over the past century (e.g. Cleland, 1867; Fick, 1879; Hering, 1897; Lombard, 1903; Baeyer, 1921; Fenn, 1938; Markee et al, 1955; Molbech, 1966; Wells and Evans, 1987; Ingen Schenau,

1989). When restricted to bi-articular muscles and actions which cannot be performed by an alternative set of two mono-articular muscles, the following (in part overlapping) functions and advantages of bi-articular muscles have been proposed:

*** *Coupling of Joint Movements***

Many authors have stressed the fact that activation of bi-articular muscles leads to interdependency of the movements in both joints that are crossed (Cleland, 1867; Huter, 1863, 1869; Fick, 1879; Langer, 1879; Elftman, 1939; Markee et al. 1955; Landsmeer, 1961; Winter, 1984; Hogan, 1985; Wells, 1988). If, for example, the hip is extended by the mono-articular hip extensors and the rectus femoris does not elongate, hip extension must be accompanied by knee extension. In a similar way, knee extension can be coupled to plantar flexion via the gastrocnemius muscle. This coupling is known as ligamentous or tendinous action (Cleland, 1867). Especially in animals such as the horse, a number of the bi-articular muscles have only a limited shortening capacity and can to a large extent be regarded as tendons (Bogert et al., 1989). These tendinous muscles allow the more proximally located mono-articular muscles to have indirect actions on joints which they do not pass (Cleland, 1867). As indicated by Cleland (1867) and by Fick (1879), coupling of joint movements by tendinous action of bi-articular muscles has the advantage that most of the muscle mass can be located close to the trunk, thus leaving the distal segments relatively free of muscle bulk. Other proposed advantages of these couplings are the ease of control of multi-joint movements (Hogan, 1985) and the transport of energy from one joint to a more distal joint (Cleland, 1867; Gregoire et al. 1984; see below).

*** *Low Contraction Velocity***

This concept can be seen in the discussions of Cleland (1867), Fick (1879), Duchenne (1867), Fenn (1938), and Gregoire (1984). If hip extension and knee extension occur simultaneously, the shortening velocity of the bi-articular hamstring muscles is lower than that of the mono-articular hip extensors and the shortening velocity of the bi-articular rec-

tus femoris is lower than that of the mono-articular knee extensors. Similarly, the shortening velocity of gastrocnemius is lower than that of mono-articular plantar flexors when knee extension is combined with plantar flexion. At this lower contraction velocity, the muscles are operating in a more favorable region of their force-velocity relationship compared to a situation where origin and insertion are not moving in the same direction. Baeyer (1921) used the term "concurrent movements" to define simultaneous movements in adjacent joints causing origins and insertions of bi-articular muscles to move in the same direction; for the opposite movements he used the term "counter-current movements."

*** *Transport of Energy***

In the above-mentioned simultaneous hip and knee extension it might be said that the mono-articular hip extensors are doing work in extending the knee. In our recent work we defined this process as transport of energy, a concept coupled to our applied multi-link models. Expressed in other words, this transport mechanism was already proposed more than a century ago: Langer indicated in 1879 that the gluteus maximus can support plantar flexion in a leg extension by coupling actions of rectus femoris and gastrocnemius. The same idea was expressed at the same time by Fick (1879) and by other authors later on (Lombard, 1903; Fenn, 1938; Gregoire et al. 1984).

In addition to the above mentioned actions of bi-articular muscles, a number of other actions have been proposed, such as joint stabilization (Markee et al. 1955). However, such actions cannot be judged as unique for bi-articular muscles.

41.3 Co-Activation of Antagonists

From the point of view of joint displacements required in performing a particular task, it seems inefficient to activate antagonists since the force (and work) contribution of the agonists appear to be cancelled out by the antagonists. This apparent inefficiency may have led many to the opinion that such co-contractions should not (or do not) occur in voluntary movements. In this context, it has been stated:

"Nature never works against herself."

(Pettigrew, 1873, cited by Tilney and Pike, 1925)

Several authors have attempted to identify organizational principles which could prevent co-contraction of agonists and antagonists. Descartes (1662) was the first to describe some type of reciprocal inhibition (controlled by "vital spirits") and there have been many supporters since then; especially since Sherrington (e.g. Sherrington, 1909) published his series of papers on this subject (e.g. Fujiwara and Basmajian, 1975; Suzuki et al., 1982; Kumamoto, 1984; Yamashita, 1988; see Smith (1981) for more references).

Since Winslow's work in 1776 (cited by Tilney and Pike, 1925) many have opposed these views. According to Tilney and Pike (1925), Duchenne described co-activations of mono-articular agonists and bi-articular antagonists in 1857 as "Harmonie des Antagonistes": co-activations needed to modify and stabilize the movements. Much experimental evidence has since then been published to show that co-activations of antagonists indeed occur (see Tilney and Pike, 1925 and Smith, 1981 for further arguments and references on this controversy).

In fact, many results of studies of multi-joint movements (such as running, jumping, cycling and standing up from a chair) indicate that co-contractions of mono-articular agonists and their bi-articular antagonists are common rather than exceptional (Andrews, 1987; Elftman, 1939a,b; Gregor et al., 1985; Winter, 1984; Gregoire et al., 1984). In the remaining part of this chapter, as well as in Chapter 18 (Gielen et al.), it will be shown that these co-activations are not in conflict with Pettigrew's statement that "nature never works against herself."

41.4 Constraints in the Transfer of Rotation to Translation

41.4.1 Geometrical Constraints

Since the translational range of motion in human joints is very small, translations of hand or foot relative to the trunk have to be realized by rotations in joints. In the transformation of rotations of segments into translation of segmental end points, constraints are present. Because of these constraints, a particular pattern of coordination of mono- and bi-articular muscles is needed to prevent inefficient utilization of metabolic energy. One of the constraints is that the force exerted on the environment not only needs a magnitude but

also a direction [see also Chapter 9 (Hogan)]. Assuring a particular direction of the external force requires a certain distribution of net moments in the joints. This phenomenon was identified in an analysis of cycling (Ingen Schenau, 1989) and further elaborated for arm tasks in Chapter 18 (Gielen et al.). A second constraint is that joint angles influence the transfer of angular velocities into linear velocities, and the transfer of angular accelerations into linear accelerations. This constraint plays an important role in explosive ballistic movements where the aim of the movement is to obtain a velocity as high as possible in projecting the body center of gravity or an object. Examples are vertical jumping, pushoff in speed skating, and overarm throwing. The constraint was originally identified in the speed skating pushoff (Ingen Schenau et al, 1985) and further elaborated in an analysis of the vertical jump (Ingen Schenau et al, 1987; Bobbert and Ingen Schenau, 1988). It will be illustrated with the help of a simplified example of a push off as outlined in Figure 41.1.

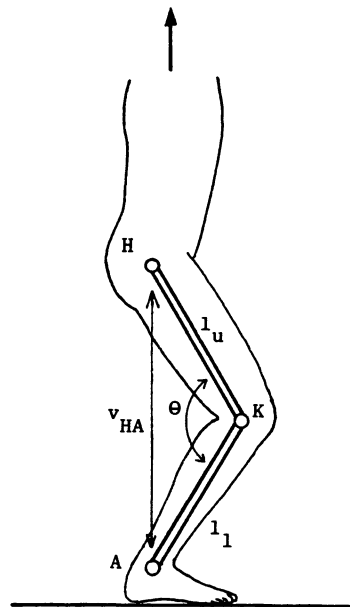


Figure 41.1: The velocity difference between hip and ankle is not only determined by the angular velocity $d\theta/dt$ but also by θ . The more the knee approaches full extension, the smaller is the transfer of $d\theta/dt$ to v_{HA} .

Imagine a pushoff where the trunk is to be accelerated by extending the knee joint without changing the position of the trunk or the foot. Such type of pushoff is required in speed skating: increasing the trunk angle would cause an increase in air friction, and plantar flexion in the leg that pushes off would increase ice friction as the skate of this leg glides forward (Ingen Schenau et al., 1985; de Koning et al., 1989). By taking the time derivative of the distance between hip and ankle, we obtain the vertical velocity of the hip relative to the ankle:

$$v_{HA} = \left[\frac{l_l l_u \sin \theta}{[(l_l^2 + l_u^2 - 2l_l l_u \cos \theta)]^{1/2}} \right] d\theta/dt \quad (41.1)$$

where l_u is upper leg length, l_l is lower leg length, and θ is knee angle. The expression between brackets may be regarded as a transfer function describing the transformation of knee angular velocity into the required translational velocity. This transfer function goes to zero when the knee joint reaches full extension. Thus, irrespective of the knee extension velocity, the translational velocity v_{HA} also goes to zero. Thus, dv_{HA}/dt becomes negative before the knee joint reaches full extension. It follows that the skate will lose contact with the ice before the knee is fully extended, at approximately the instant that dv_{HA}/dt reaches a value of -9.8 m/s^2 . This indeed occurs in speed skating where the skate was found to lose contact with the ice at a knee angle of about 150° (Ingen Schenau et al., 1985). The reason is that at the instant that the decreasing transfer function begins to dominate the (still increasing) angular velocity of knee extension, the relatively heavy trunk pulls the lower leg, foot and skate from the ice since it has already obtained a velocity larger than the decreasing velocity v_{HA} at the last part of knee extension.

Needless to say, the same constraint, referred to as *geometrical constraint* (Ingen Schenau et al., 1987), is present in jumping. The only difference is that the transfer function is more complex because rotation of the trunk and foot are allowed. As a matter of fact, an early loss of contact was demonstrated by Alexander (1989) in a simulation of vertical jumps.

It is important to realize that when the pushoff ends with the knee still flexed, the knee extensor muscles have not shortened fully, and their capacity to do work has not been used fully for the pushoff. If the muscles remain active after takeoff, the work performed by them over the remaining shortening range will be used for a useless increase in rotational energy of segments.

41.4.2 Anatomical Constraint

In addition to the geometrical constraint imposed by the transfer function of equation (41.1), a second constraint is present during explosive pushoffs. This is due to the fact that the angular velocity needs to be reduced prior to full extension. In actual jumping, the knee angular velocity can reach values up to 17 rad/s . If this angular velocity were not actively decelerated to zero, the knee joint could be damaged. To preserve structural integrity of the knee joint, knee flexor activity is needed. This "anatomical constraint" (Ingen Schenau et al., 1987) should be accounted for in protocols used to simulate vertical jumping (see below and Chapter 42 (Pandy)). If Alexander (1989) would have incorporated this constraint in his simulations, he would have found smaller knee angles at the end of the pushoff even in the hypothetical jumps of his model with massless legs.

41.5 Possibilities of Dealing with Constraints

41.5.1 Co-Activation of Mono-Articular and Bi-Articular Muscles

In an actual vertical jump where the jumper is allowed to perform a plantar flexion, the geometrical constraint imposed by the transfer function as well as the anatomical constraint mentioned above can be dealt with effectively by activation of the bi-articular gastrocnemius. This is outlined in Figure 41.2a. The resulting knee flexing moment caused by this muscle reduces the angular acceleration in the knee joint and, due to the tendinous action described earlier, knee extension is now to a certain extent coupled to plantar flexion. It can be said that knee extensors pull on the calcaneus and thus support plantar flexion.

The importance of this tendinous action was demonstrated by a simple physical model as outlined in Figure 41.2b (Bobbert et al., 1987). The mono-articular knee extensors are modelled by a

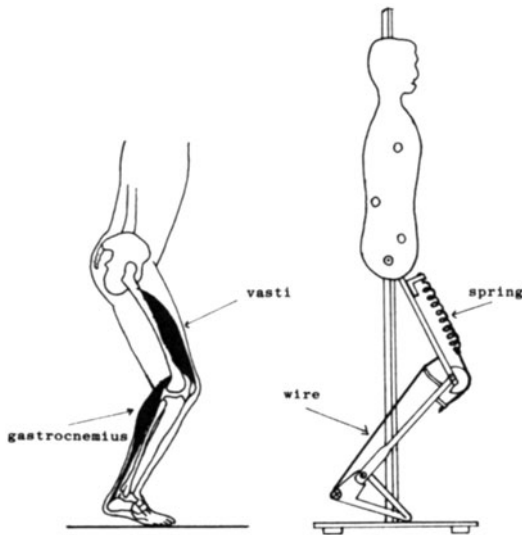


Figure 41.2: *a)* As soon as the velocity difference between hip and ankle can no longer be increased, the gastrocnemius muscle couples a further knee extension to plantar flexion. *b)* The effect of this coupling was demonstrated by a mechanical model ("jumping Jack") where the gastrocnemius is represented by a wire (see text and Bobbert et al., 1987).

spring, which is loaded with a certain amount of potential energy by flexing the knee (pushing the model downwards). The tendinous action of the gastrocnemius is modelled by a stiff wire. The length of this wire can be adjusted in order to simulate variation in timing of the coupling of knee extension and plantar flexion. It was found that when the wire became taut during the pushoff, jumping height was greater than when it remained loose. Moreover, it was found that an optimum occurred in wire length; with wire length adjusted to this optimum (representing optimal timing of the coupling of knee extension and plantar flexion), the model jumped almost twice as high as when the wire remained loose. Also, we performed computer simulations of this type of jumps (Soest et al., 1989) and found that the optimal timing results in a compromise between loosing ground contact too early (which occurs when coupling occurs early in the push off) and increasing the rotational energy in the lower and upper legs uselessly (which occurs when coupling occurs late during the pushoff). These examples suggest that co-activation of antagonists (in this case co-activation of knee extensors and the bi-articular gastrocnemius) can be highly effective in ex-

plosive pushoffs. In an electromyographic analysis of vertical jumping we found that human subjects indeed show co-activation of vasti and gastrocnemius. With these basic principles in mind it is now possible to explain the temporally ordered sequence of muscle activation patterns as observed in those analyses (Bobbert and Ingen Schenau, 1988).

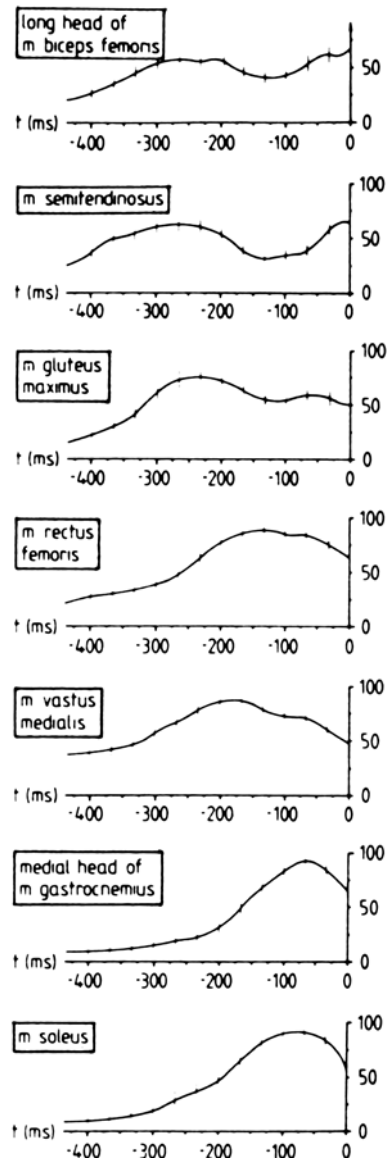


Figure 41.3: Mean muscle activation patterns of 10 experienced jumpers. Time is expressed in ms prior to the end of push off (toe off). Note the periods of co-activation of gluteus maximus and rectus femoris and of vasti and gastrocnemius.

41.5.2 Sequencing of Muscle Activations

Figure 41.3 presents as a function of time mean muscle activation levels of 10 experienced jumpers during the performance of counter movement jumps (see Bobbert and Ingen Schenau (1988) for details regarding this study). For the interpretation of muscle activation patterns one should keep in mind that there is a delay between a change in activation and a change in the mechanical response of the muscle of 80–100 ms (Thomas et al., 1988; Ingen Schenau, 1989b; Vos et al., 1990). These patterns can be shown to be highly functional with help of Figure 41.4, where the orientations of the jumpers' body segments are schematically depicted at four time intervals prior to the end of the pushoff. The thickness of the lines representing muscle actions is drawn in such a way that it gives an impression of the changes in mechanical responses of the muscles.

The vertical acceleration of the center of gravity is initiated by a rotation of the trunk following the increases in activity of hamstrings and gluteus maximus. Some 100 ms later the activity level of the quadriceps muscles is increased while the hamstring activity is decreased. In light of the discussed problems in the transfer of rotations into translation, this seems logical. Because of the large moment of inertia of the trunk, it takes a relatively long time to give this segment a large angular velocity. Activation of the hamstrings helps to increase the angular velocity of the trunk. At the same time, it prevents an early knee extension, which would hamper a fast trunk acceleration (an upward acceleration of the hip because of knee extension would cause an extra inertial force on the trunk). As soon as an increase in trunk rotation can no longer contribute to a vertical acceleration of the body center of gravity, rectus femoris activity is increased and hamstring activity is decreased. The hip flexing moment exerted by rectus femoris helps to reduce the angular acceleration of the trunk, and the power delivered by the gluteus maximus supports knee extension by tendinous action of the rectus femoris. During the last 50–100 ms the knee flexing moment of gastrocnemius helps to reduce the angular acceleration in the knee joint as explained above. In these last 50 ms all leg muscles can contribute to plantar flexion through tendinous actions of rectus femoris and gastrocnemius. The fact that hamstring activity is decreased but not terminated has

most likely to do with the fact that both the hamstrings and the rectus femoris shorten in this movement. This phenomenon was early on described by Lombard (1903), who showed that frogs can jump very efficiently by co-activation of these bi-articular "antagonists."

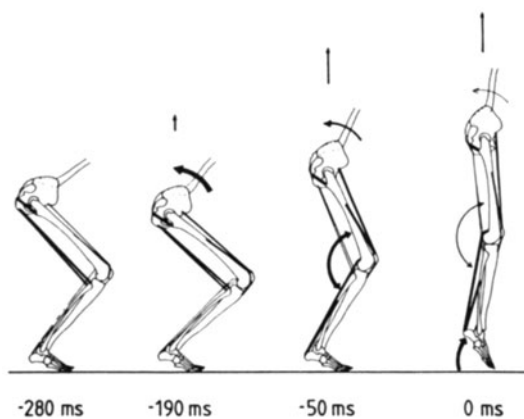


Figure 41.4: A schematic outline of muscle actions as occurring in a sequential order during the pushoff. The thickness of the lines representing the muscles indicates the mechanical responses of the muscles on the changes in activity as presented in Figure 41.3. The curved arrows indicate the major angular accelerations.

A comparable proximo–distal sequence and co-activation of mono– and bi–articular muscles was recently found for the pushoff in the sprint start (Jacobs et al., in preparation). In speed skating, the proximo–distal sequence is not complete: the rectus femoris appears to play a comparable role in transporting energy from the mono–articular hip extensors to the knee, but coupling between knee and ankle is much less pronounced than in jumping and sprinting (de Koning et al., submitted for publication). This is of course due to the fact that speed skaters have learned to suppress a plantar flexion in order to prevent an increase in ice friction.

In an analysis of the overarm throw of female handball players, we also found a pronounced proximo–distal sequence in joint actions (Jöris et al., 1985). Though in that study no muscle activity patterns were obtained, that sequence too is likely to play a role in dealing with the constraints in the transfer of rotations into translations.

In this paragraph on timing it should be stressed that the observed sequence in changes in muscle activation and joint extensions could serve the purpose of transporting energy from joints where it can no longer be used effectively, to joints where it still can. Without these muscles, a proximo-distal sequence is not optimal, as recently shown in computer simulations by Alexander (1989). As indicated above, the actual transfer function between angular velocities in all joints and the translational velocity of the body center of gravity (which has no fixed anatomical location) is much more complicated than what is outlined in the basis of Figure 41.1. Moreover, other constraints may play a role as well (e.g. neurologically based constraints; intrinsic properties of muscles and tendons etc.). This makes it difficult to predict what would be an optimal timing. Moreover, one can imagine that rather large differences in timing exist between subjects, as indicated by Jensen et al. (1989). In our group of not specifically trained subjects, however, we found comparable patterns as for the trained subjects. The only significant difference was a shorter time interval between the onset of hip extension and the onset of knee extension than was found in the trained subjects. Despite the absence of reliable data on intrinsic muscle properties, muscle tendon lengths, tendon compliances and about possible "hard-wired" connections in the central nervous system, an understanding of why one activation pattern is better than another could be obtained by means of direct dynamics. In Chapter 42 (Pandy) such an application is presented for the vertical jump. Comparable results of our own group are presented below. Both Pandy's and our simulation seem to support the proximo-distal sequence.

41.6 Simulations of Vertical Jumping

The concepts presented in the previous paragraphs have been formulated on the basis of an inverse dynamical analysis of jumping. An assumption underlying the formulation of these concepts is that the coordination pattern found experimentally results in a (more or less) maximal jumping height. Experimentally, it is not possible to test this assumption. Also, it is impossible to ascertain from experiment exactly in what way the concepts described interact. Finally, it is not clear whether these concepts are sufficient (in contrast to necessary) to explain the coordination pattern found.

Simulation seems the most promising methodology to tackle these problems. Simulation and optimization of behavior of rather complex systems has become feasible in recent years thanks to a tremendous increase in computational power. In this section, basic ideas are introduced and some results are presented. Basically, direct dynamics simulation of "mechanical" systems can be described as follows [see also Chapter 8 (Zajac and Winters)]:

- 1) Given a position and velocity of the system and neural drive for the current time, the forces acting (usually a function of neural drive, position and/or velocity) are calculated.
- 2) Given the results of (1) plus external loading on the linkage system, and supposing that the equations of motion of the degrees of freedom have been derived in some way (which constitutes the major problem of direct dynamics), the accelerations of the degrees of freedom are calculated.
- 3) Given position, velocity and acceleration of the degrees of freedom, the former two are integrated numerically over a small time interval to yield new positions and velocities of the degrees of freedom. (If a dynamic muscle model is used, the muscle model state variables must also be integrated.)
- 4) Increment time. Given the new values for the state variables, as obtained results of (3), calculate any other parameters that are static functions of the state variables (e.g. other kinematically-related positions and velocities within the assumed linkage system).
- 5) Return to (1).

In our case, the (planar) model consists of four segments (foot, lower leg, upper leg, trunk-head-arms). Driving forces are generated by 6 groups of muscles: GLUtei, HAMstrings, VASti, RECTus femoris, SOLeus and GAStrocnemius. These groups represent the major mono-articular and bi-articular muscles contributing in vertical jumping. Input to these muscles is stimulation, which is transformed into active state using first order dynamics. The muscles are modelled using a three-component Hill-type muscle model. Parameter values for the muscle models are derived from known morphologic characteristics (e.g. number of

sarcomeres in series) and experimental results (e.g. moment-angle relationships). Behavior of the muscle can be described by one first-order differential equation, in which contractile element velocity is calculated as a function of stimulation, contractile element length and total muscle length.

The behavior of the entire system thus defined is simulated using *SPACAR*, a finite element method with deformable links developed at the Technical University of Delft (van der Werff, 1977). All differential equations governing system behavior are integrated simultaneously using a variable order, variable stepsize predictor corrector integration algorithm (Shampine and Gordon, 1975).

For reasons of simplicity, simulations have been restricted to "squatting jumps", i.e. jumps started from a prescribed static squatted position; a countermovement is not allowed. At the start of the simulation, stimulation of the muscles is such that a static equilibrium is maintained.

The question addressed is: At what time should the stimulation of each muscle be switched from the starting value to the maximum value in order to jump as high as possible? This optimization problem is solved using a standard quasi-Newton optimization algorithm (*NAG*).

When comparing the jump performed with optimal timing with experimental data, a number of observations can be made (see Figure 41.5).

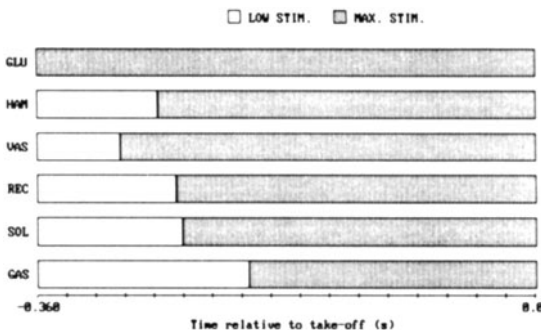


Figure 41.5: Optimal stimulation pattern for a mathematical model incorporating 6 muscle groups, performing a squatting jump from a prescribed static position as obtained from direct dynamics simulation. For all muscle groups, the time at which stimulation was switched to the maximal value was optimized. Time is expressed in seconds prior to the instant of takeoff.

- * in the simulated optimal jump, a clear proximo-distal sequence in stimulation pattern is present; only the hamstrings group is a little out of line;
- * during the major part of the simulated jump, co-activation of monarticular extensors with their bi-articular "antagonists" is present;
- * kinematics of the simulated jump is very similar to the kinematics of experimentally observed squatting jumps (data not shown) except for the final part of the pushoff (see below).

What constraints play a major role in determining optimal timing? This question is currently being investigated in detail using simulation. Here, some observations will be made concerning the constraints discussed earlier in this chapter.

In the first place, the anatomical constraint, forcing a deceleration of joint extension just prior to takeoff, is absent in the model. In the behavior of the model, a continuous increase of the angular accelerations is observed. It can therefore be concluded that the anatomical constraint plays a significant role just before takeoff.

Secondly, the geometrical constraint clearly plays an important role in a fast ballistic movement such as jumping. From the previous paragraphs, it will be clear that a sequential action of the bi-articular rectus femoris and gastrocnemius muscles can contribute in dealing with this constraint (although full joint extension at takeoff probably cannot be reached). From the fact that both in experiment and in simulation such a sequential action is present, it is tempting to think that the stimulation pattern is aimed primarily at solving the problem posed by the geometrical constraint.

However, when performing these simulations it became evident that it is not at all easy to control the direction of the acceleration of the body center of mass. This "directional" constraint has not yet been subject to systematic research. In the near future, we hope to address the influence of this constraint, and the way it relates to the geometrical constraint.

41.7 Redistribution of Joint Moments and Powers

If the actions of bi-articular muscles discussed in this chapter are combined with those in Chapter 18 (Gielen et al.), it is possible to formulate a general role for bi-articular muscles. Generally speaking one might say that bi-articular muscles can redistribute net moments and net power over the joints that are crossed. Power delivered by mono-articular muscles which cross a particular joint can appear as joint power at an adjacent joint. This has been defined as a transport of energy (Ingen Schenau et al., 1987). Unfortunately, because the expression transport of energy has also been used to indicate a flow of energy between segments, our definition appears to cause confusion. The following discussion is intended to prevent misunderstandings.

If the human body is modelled as a system consisting of rigid links connected by joints which predominantly allow rotations, an inverse dynamical analysis, as originally proposed by Elftman (1939a) and applied or further elaborated by many others (e.g. Capozzo et al., 1976; Robertson and Winter, 1980; Aleshinsky, 1986; Bobbert and Ingen Schenau, 1988), yields for each joint a net joint force and a net joint moment. Following Elftman (1939a) a number of authors have constructed an energy balance for each separate segment using the (external) joint forces and joint moments to calculate the flow of energy to the segment which, for rigid segments, should equal the rate of change of mechanical energy of the segment. By constructing these energy balances for all individual segments, these authors were able to calculate flows of energy between segments. It should be emphasized that the transport of energy as discussed in this chapter has nothing to do with these flows of energy between segments [which may be the reason why Pandy (Chapter 42), using the energy flow definition, did not find a unique action for bi-articular muscles in transporting energy]. What is meant here is based on an energy balance of the assembly of all segments together. As shown by Aleshinsky (1986) for running and for the more general case by Ingen Schenau and Cavanagh (1990), a summation of the energy balances for the separate links leads to one energy equation for the entire body. The time

derivative of this equation, called the instantaneous power equation of the system, is:

$$\sum P_{joints} = \sum (F_i \cdot v_i) + dE_{segm}/dt \quad (41.2)$$

The expression on the left-hand side equals the (instantaneous) sum of joint powers (sum of products of joint moment and joint angular velocity). The first expression on the right-hand side equals the power exchange with the environment, calculated as the product of forces external to the entire system (e.g. air friction, force on the pedal in cycling) and the velocity of their points of application. The last expression equals the rate of change of the sum of segmental energies. It should be noted that in this equation the joint forces are no longer present. In fact it shows the origin of power which can be used to fulfill a certain task (increase the mechanical energy of the entire system or do work against the environment). Though joint power is calculated for each joint separately it should be stressed that Eq. 41.2 is only valid for the instantaneous sum of joint powers. This means that a negative power at one particular joint does not necessarily mean that power is degraded into heat or stored in elastic components of muscle-tendon complexes; if the summed power is positive, negative power at one particular joint may appear as positive power in an adjacent joint through action of bi-articular muscles. This is illustrated with the help of Figure 41.6.

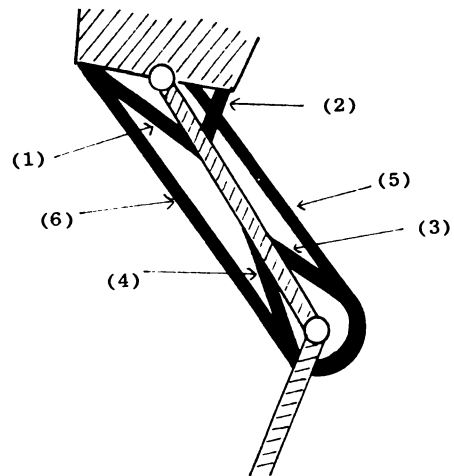


Figure 41.6: Schematic representation of a set of mono- and bi-articular muscles needed to meet the constraints discussed in this chapter and in Chapter 16 (Gielen et al.) for planar two-joint movements.

In the light of the constraints discussed in this chapter and in Chapter 16 (Gielen et al.), the indicated number of mono- and bi-articular muscles is sufficient to control a two bar system in one plane. Now imagine that this two bar system represents the upper and lower leg and that the leg is extended through actions of the mono-articular muscles (1) and (3). Let (1) deliver a moment M_1 with respect to the hip joint and an amount of power P_1 . Let (3) deliver a moment M_3 and power P_3 . If we now also activate the bi-articular muscle (5), the result will be that the net moment in the hip decreases and the net moment in the knee increases. If, for the sake of simplicity, we assume that the extension velocities remain the same and that (5) does not change in length (as the wire in the model of Figure 41.2b), it does not add power to the system while the other two muscles can still deliver the same amount of power. However, the power delivered by (1) does only in part appear as hip joint power since the net moment in the hip is decreased through action of muscle (5). The opposite is true at the knee. Here the power is larger than what is delivered by muscle (3) while muscle (5) in this example does not add power to the system. Note that strong activation of (5) can cause a negative moment (and power) at the hip while (1) is still producing the same amount of positive power. One can easily calculate that the decrease in power due to the decrease in net moment at the hip is exactly equal to the surplus power at the knee. When expressed in net joint powers we defined this phenomenon as a transport of power from hip to knee and basically this should be judged as a contemporary expression of what more than a century ago was defined as a "ligamentous action" (Cleland, 1867). This effect of transport of energy is of course also present if (5) changes in length. The total amount of joint power is then increased or decreased by the amount of power production or absorption by muscle (5). It will not be difficult to realize that activation of muscle (6) will cause a transport of power from knee to hip.

This versatile system makes it possible to redistribute joint moments and joint powers in such a way that the specific task demands are met. For jumping we have seen that this includes a proximo-distal shift in joint power: power is predominantly used in those joints where it can

most effectively contribute to the increase of effective energy of the jumper.

For cycling we found that the shift in net moments was necessary to control the direction of the external force on the pedal in such a way that this force can do work on the pedal [see Ingen Schenau, 1989a, for details on cycling, and Chapter 18 (Gielen et al.) for a more general discussion of this topic].

Though the paper of Cleland came only recently to our notice we feel that he deserves the honor to be explicitly cited in this context. With respect to the effects of the actions of bi-articular muscles he wrote:

".... the total amount of muscular power is made available for overcoming the total amount of resistance, which ever be the joint on which that may to the greatest extent fall." (Cleland, 1867)

41.8 Conclusions and Future Directions

From the phenomena discussed above and those discussed in Chapter 18 (Gielen et al.), the conclusion can be drawn that a wide range of multi-joint movements require not only a control of joint displacements but also a particular distribution of net moments over the joints. These two requirements can to a large extent be judged as independent.

In preventing inefficient eccentric contractions and in interchanging net moments and energy between joints, bi-articular muscles appear to perform unique actions which could not be performed by a set of two mono-articular muscles. This means that the actions of these muscles cannot be qualified on the basis of a simple reference to the joint displacements which they are assumed to support.

The described actions require a co-activation of mono-articular and bi-articular muscles. Such co-activations are not inefficient. Instead, it is only by virtue of these co-activations that specific task demands can be satisfied efficiently. Thus, the co-activations may be qualified as synergistic rather than antagonistic. As such they are not in disagreement with Pettigrew's statement that "nature never works against herself".

On the basis of these conclusions, a number of plans, suggestions and speculations can be formulated to help direct future research.

41.8.1 Ongoing Research

A number of studies have been started to identify constraints in motor tasks other than jumping and cycling, and to determine whether the inter-muscular coordination in these tasks can be understood from the mechanical aim. At present the research focusses on sprinting, running, walking and cycling at different loads and cycle frequencies. In a different set of studies it will also be attempted to quantitate the contributions of individual muscles to the net joint moments and powers, and to determine the amount of power transport via bi-articular muscles. Quantitation is tackled both with inverse and direct dynamics. Much attention is also paid to organizational principles using an experimental setup for leg tasks comparable to that described for arm work in Chapter 18 (Gielen et al.).

41.8.2 Movement Control and Learning

One of the ideas which needs further attention is that the control of mono- and bi-articular muscles is based on different organizational processes. Support for this idea comes from results of analyses of cycling (Ingen Schenau, 1989) and arm tasks [Chapter 9 (Hogan) and Chapter 18 (Gielen et al.)], as well as from other studies in the literature.

Especially from studies of walking, running or jumping cats, it can be deduced that the mono-articular hindlimb muscles seem to act simply as force or work generators while the bi-articular muscles show a considerably more complicated, and task dependent, behavior (Hoffer et al., 1987a,b; Perret and Cabelguen, 1980; Spector et al., 1980; Walmsley et al., 1978). An issue which also needs attention is the importance of sensory information. In many theories on motor control and especially in servo control theories, sensory information is necessary to modulate the α -motoneuron pools. For example, Suzuki et al (1982) suggested that in cycling, especially the bi-articular muscles show a pattern of reciprocal inhibition triggered on the basis of sensory information. Many more of such suggestions have been proposed, mainly based on reflexologic studies (see Smith, 1981 for references). Such reflexologic studies, however, and particularly those based on the characteristics of muscle spindles in lengthening muscles, may have over-emphasized the importance of servo control

(Loeb, 1984). It has been shown that even in tasks with slow or moderate speed one can move well without any sensory information (Taub and Berman, 1968; Loeb, 1984).

In our analysis of experienced cyclists (Ingen Schenau, 1989a) the periods of activation of mono-articular muscles were highly cross-correlated with the periods of muscle shortening, the phase lag being about 90 ms. Since this phase lag agrees with the phase shift between *EMG* and mechanical response of these muscles, it seems that the central nervous system anticipates on the required mechanical responses. This, of course, can only be explained on the basis of an open loop control. In other words: experienced cyclists use a learned movement pattern.

On the basis of these observations and the referred literature our current position with respect to movement organization is that multi-joint movements require a process of learning both position control and control of the distribution of net moments and power over the joints as described in this and Chapter 18 (Gielen et al.). This learning process might occur along the lines described by Chapter 20 (Denier van der Gon et al.).

If it should be confirmed that mono-articular muscles mainly act as force and work generators while bi-articular muscles warrant the correct distribution of net moments and power over the joints, one can imagine that the learning process requires different sources of information for the learning to control these muscles. Learning to control mono-articular muscles might be possible with help of simple muscle length information provided by muscle spindles in lengthening as well as shortening muscles (Burke et al., 1978; Loeb, 1981); learning to control bi-articular muscles, however, might require a variety of multi-modal sources of information.

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