Musculoskeletal properties, coordination and performance in explosive movements

Bobbert, M.F.

published in
Approche Pluridisciplinaire de la Motricité Humaine
2009

Musculoskeletal properties, coordination and performance in explosive movements

Maarten F. Bobbert
Research Institute MOVE, VU University Amsterdam, Amsterdam, The Netherlands.
m.bobbert@fbw.vu.nl

The purpose of this paper is to explain how and why performance in explosive movements depends on musculoskeletal properties and coordination. First, a musculoskeletal model is presented that has muscle stimulation as only independent input, and allows for forward simulation of explosive movements. Subsequently, a theoretical framework is presented for analyzing simulation results: performance depends on muscle work and efficacy, and muscle work production can best be analyzed by looking at contractile element force over shortening distance. To illustrate the approach, it is used to explain how and why performance in vertical squat jumping depends on muscle strength and coordination.
Key words: musculoskeletal model, simulation, jumping

Introduction

Performance in many sports activities depends on the ability of athletes to impart in a single movement high velocity to their hand, foot, or body itself. Examples are punching, throwing, kicking and jumping. Such movements will be referred to as explosive movements in this paper. When asked what factors contribute to performance in explosive movements, athletes, trainers and scientists will immediately answer that both musculoskeletal properties and coordination are important, but there is still a lot of confusion about how and why this is so. The purpose of this paper is to provide a theoretical framework for analyzing performance in explosive movements and for understanding how and why it depends on musculoskeletal properties and coordination. It will become clear that for application of this framework we need access to variables that cannot be measured during actual performances of athletes. Furthermore, manipulations are necessary that cannot be performed *in vivo*. Full access to all variables of interest, and full control over all variables to be manipulated, can only be achieved if movements are simulated using models of the musculoskeletal system that have muscle stimulation as a function of time as their only input. Below, we shall review the steps involved in making such models and in using them to simulate movements. Subsequently, a theoretical framework will be presented for analyzing simulation results. Finally, the simulation approach and the theoretical framework will be used to try and explain how and why performance in an explosive task, squat jumping, depends on muscle strength and coordination.

Simulation of movements using musculoskeletal models

The main reason for resorting to movement simulation is that it allows one to investigate the effects of manipulations or experiments that cannot be performed *in vivo*. The steps involved in the movement simulation approach that we have developed in previous studies are detailed below. References to original sources are provided elsewhere (Bobbert et al. 2008).

1. Formulating a musculoskeletal model that has muscle stimulation as a function of time as the only input

The model that will be used in this paper is shown in Fig. 1. It is a planar model consisting of four rigid segments representing a HAT segment (head, arms and trunk), thighs, shanks and feet. The segments are interconnected by hinge joints representing hip, knee and ankle joints, and the distal part of the foot is connected to the ground in a hinge joint. The model is actuated by six major muscle tendon complexes (MTCs) of the lower extremity: hamstrings, gluteus maximus,

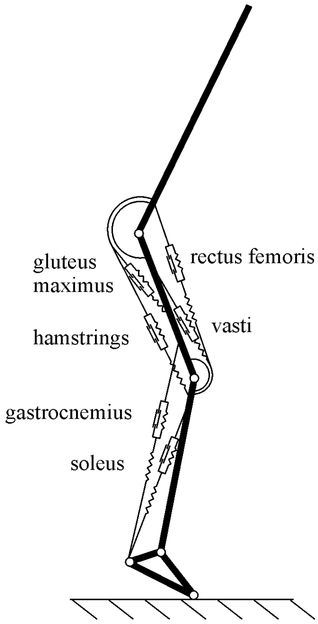

Figure 1. Schematic drawing of the model of the musculoskeletal system used for forward dynamic simulations. The model consists of four interconnected rigid segments and six muscle groups of the lower extremity, all represented by Hill-type muscle models.

rectus femoris, monoarticular vasti, gastrocnemius and soleus. Each MTC is represented using a Hill type muscle model. This muscle model consists of a contractile element (CE), a series elastic element (SE) and a parallel elastic element (PE). The only input of the model is muscle stimulation $STIM$ as a function of time. $STIM$ is a one dimensional representation of the effects of recruitment and firing rate of α-motoneurons, and ranges between 0 and 1.

Mathematically, the model comprises three sets of differential equations (Fig. 2). The first set describes the excitation dynamics, i.e. how stimulation leads to active state. The formulation of these equations was adopted from Hatze (Hatze 1977). For each MTC, there is one first order differential equation: $\dot{\gamma} = f_1(STIM, \gamma)$, where γ is the free calcium concentration. The latter is algebraically related to active state q, the relative amount of calcium bound to troponin, taking into account that CE length ℓ_{CE} affects the sensitivity of the contractile machinery to calcium: $q = f_2(\gamma, \ell_{CE})$.

The second set of differential equations describes the contraction dynamics, i.e. the interaction between contractile elements and series elastic elements. For each MTC, we have some formulation of how force depends algebraically on ℓ_{CE}, CE velocity $\dot{\ell}_{CE}$, and q: $F_{CE} = f_3(\ell_{CE}, \dot{\ell}_{CE}, q)$. Also, we have a relationship between the force of SE and length of SE: $F_{SE} = f_4(\ell_{SE}) = f_4(\ell_{OI} - \ell_{CE})$, where ℓ_{OI} is origin-to-insertion distance, i.e. total length of the MTC. If we ignore the mass of the MTC itself, F_{CE} must equal F_{SE}, so we obtain for each MTC one first order differential equation: $\dot{\ell}_{CE} = f_5(\ell_{CE}, \ell_{OI}, q)$.

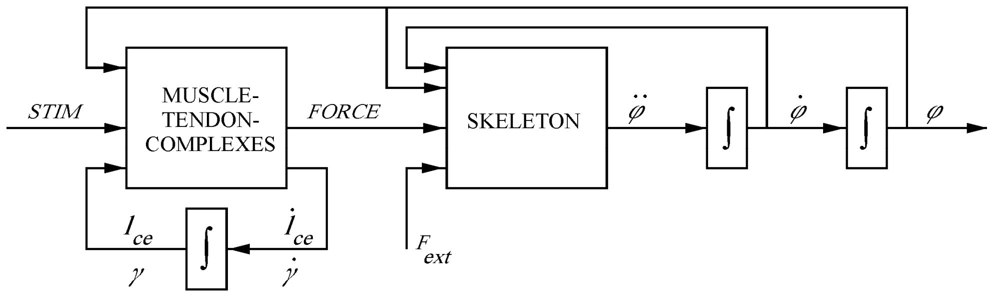

Figure 2. Schematic representation of the mathematical formulation of the musculoskeletal model, which has muscle stimulation $STIM$ as only input. F_{ext}: external forces acting on the system; see text for explanation of other variables used.

The third set of differential equations describes the skeletal dynamics. For each segment there are three equations of motion: $\Sigma F_x = m \cdot \ddot{x}_c$, $\Sigma F_y = m \cdot \ddot{y}_c$ and $\Sigma M = j \cdot \ddot{\varphi}$, where m is the mass of the segment, $\ddot{x}_c$ and $\ddot{y}_c$ are the horizontal and vertical components of the acceleration of the segment's center of mass, respectively, ΣF_x and ΣF_y are the sums of forces acting on the segments in horizontal and vertical direction, respectively, j is the moment of inertia of the segment about its mass center, $\ddot{\varphi}$ is the segment's angular acceleration and ΣM is the sum of moments acting on the segment. The equations of motion are formulated in such a way that we can solve for the angular accelerations of the segments (see Casius et al. 2004 for a user-friendly approach) and if we split up the second-order differential equations into pairs of first-order differential equations, we obtain a total of 8 differential equations for the skeletal system shown in Fig. 1, as long as it is in contact with the ground at the toe.

The final step in the formulation of the model is to describe the interaction between the skeleton and the MTCs. Motion of the skeleton affects the MTCs by changing ℓ_{OI}, an input in the differential equations describing contraction dynamics (f_5). Thus, we need to formulate for each MTC an algebraic relation describing how ℓ_{OI} depends on joint angles: $\ell_{OI} = f_6(\varphi_1, \varphi_2, \varphi_3)$. Each MTC, in turn, affects the motion of the whole skeleton by generating a moment about one or more joints, with muscle moment being the product of MTC force and the moment arm at the joint spanned. At each point in time we have the state of the MTCs so we can calculate their force using f_3, and the moment arms about the joints can be derived directly from f_6 using d'Alembert's principle of virtual work (An et al. 1984).

This then concludes our formulation of a musculoskeletal model that has muscle stimulation as a function of time as the only input. To generate a movement on the basis of a chosen stimulation-time input to the muscles, henceforth referred to as 'control', we simply define an initial state for the model and integrate the differential equations for excitation dynamics, contraction dynamics and skeletal dynamics simultaneously using an Ordinary Differential Equation solver.

2. *Choosing parameter values for the model to make it represent human subjects*

Values for inertial parameters of body segments can be estimated from mass and anthropometrics of subjects using scaling rules (e.g. Yeadon and Morlock 1989). The dependence of ℓ_{OI} on joint angles in the model (f_6) is currently based on results obtained in cadaver studies (e.g. Visser et al. 1990) using the tendon displacement method first proposed by An and coworkers (An et al. 1984). In the future, it may be possible to obtain such information *in vivo* using ultrasound (Maganaris et al. 1998). Hatze's formulation of how $STIM$ leads to active state (f_1 and f_2) has been tested in human calf muscles using electrical stimulation of the tibial nerve and has proven to produce satisfactory results (van Zandwijk et al. 1998). The biggest challenge is to derive the relationships describing how MTC force depends on active state, length and shortening velocity of CE (f_3), and how SE force depends on SE length (f_4). Currently, the relationships in the model are based on what may be called a building-block approach. The idea is to simplify each MTC to a set of parallel units, with each unit consisting of a muscle fiber and a 'tendon fiber' spanning the distance between the ends of the muscle fibers and the bony insertions (Fig. 3). The 'tendon fiber' is taken to behave like a series elastic element SE, and the muscle fibers are taken to behave like a contractile element CE (myofilaments and cross bridges) parallel to an elastic element PE (sarcolemma). The force-length relationship of CE is derived from the sliding filament theory using myofilament lengths measured in human muscle fibers (Walker and Schrodt 1974) and numbers of sarcomeres in series in human cadaver muscle fibers. PE always has the same length as CE and its force-length relationship is derived from measurements on single muscle fibers (ter Keurs et al. 1978); in the model it merely serves to prevent CE from becoming overextended. SE is assumed to have a strain of 4% at maximal MTC force, and SE rest lengths are chosen such that MTCs attain their optimum length at joint angles where human subjects produce their maximum isometric joint moments. The force-velocity relationship of CE is obviously a crucial relationship. The relationships in the model (see van Soest and Bobbert 1993) are currently based on concentric and

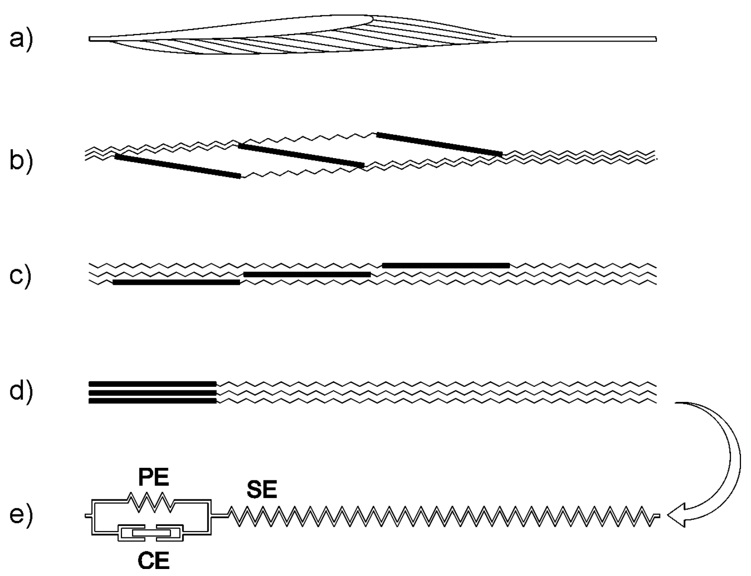

Figure 3. Conceptual steps in simplifying a muscle-tendon complex. a) actual muscle-tendon complex; b) it is assumed that each of the muscle fibers (only three fibers are depicted) is in series with a proximal and a distal portion of a 'tendon fibre'; c) it is assumed that the angle between muscle fibers and the line of pull of the muscle-tendon complex is negligible; d) similar to (c), but this time with the muscle fibers grouped together; e) in the mathematical formulation, the 'tendon fibers' form a series elastic element (SE), and the muscle fibers behave as an elastic element (PE) parallel to a contractile element (CE).

eccentric force-velocity relationships measured in isolated muscles of animals, which have first been reduced to sarcomere force-length relationships of these animals muscles and subsequently have been scaled for human muscles using again numbers of sarcomeres in series in human cadaver muscle fibers. Finally, the maximal isometric force of each MTC is obtained by measuring joint moments that human subjects produce during maximum voluntary isometric contractions, and distributing them over the agonists using the relative physiological cross-sectional areas (PCSAs) and moment arms determined in cadaver studies (Out et al. 1996). This approach assumes that the ratio of PCSAs of muscles spanning a joint and numbers of sarcomeres in series in muscle fibers are similar in human cadavers and in living subjects.

3. Finding the optimal muscle stimulation-time histories and the corresponding maximal performance

This step requires us to reduce the performance of the model to a single criterion number to be maximized or minimized. In studies of vertical jumping, it seems reasonable to use as criterion the height achieved by the center of mass (CM) at the apex of the jump ($y_{CM,apex}$). For the model depicted in Fig. 1 the optimization problem then becomes:

$$-y_{CM,apex} = f_7(STIM_1(t), STIM_2(t), STIM_3(t), STIM_4(t), STIM_5(t), STIM_6(t))$$

(note that optimization routines typically search for the minimum value of an objective function; for this reason, $y_{CM,apex}$ is preceded by a minus-sign). Since *STIM* of each muscle can vary continuously over time, the solution space is infinite and needs to be constrained to find a unique solution. For example, to find the solution for a maximum height squat jump, one may put the model in the squatted posture, find initial *STIM* levels that yield equilibrium in this posture, and then allow *STIM* of each muscle to switch once from the initial level to its maximum. The optimization problem now reduces to:

$$-y_{CM,apex} = f_8(t_{switch,1}, t_{switch,2}, t_{switch,3}, t_{switch,4}, t_{switch,5}, t_{switch,6})$$

(as a matter of fact, since the model starts out in equilibrium, t_{switch} of one muscle may be fixed and only five switching times need to be optimized). This optimization problem can be solved using a simplex search algorithm, simulated annealing, a genetic algorithm, etc. Of these, the genetic algorithm approach is attractive because the solution can be searched using multiple computers in parallel (van Soest and Casius 2003).

4. *Evaluating the performance of the model by comparing it to that of human subjects*

Once the optimal solution for the chosen task has been found, the crucial question is, of course, whether the corresponding movement is similar to the movement displayed by human subjects. If this is not the case, the reason may be that the musculoskeletal model is not valid (it may be missing crucial components or properties), that the optimization criterion chosen is not the criterion that human subjects use, or both. Vertical jumping is an attractive task to study because there will be hardly any discussion about the optimization criterion: maximizing the height of CM at the apex of the jump. And in fact, if squat jumping is chosen as the task of interest, if the optimization problem is reduced to finding only one t_{switch} per muscle, and if $y_{CM,apex}$ is used as criterion, optimal solutions are found that closely resemble the motion pattern found in human subjects performing squat jumps. We did observe that human subjects vary in the rate at which they increase their muscle stimulation, and for this reason we made $STIM$ in our model increase in a ramp-like fashion rather than instantaneously, with the slope of the ramp affecting the duration of the push-off (Bobbert et al. 2008). Fig. 4 presents stick diagrams for experimental and simulated squat jumps. Not only these stick diagrams, but also detailed kinematics and kinetics of the model correspond well to those observed in human subjects; in fact, there even seems to be a reasonably good correspondence between the optimal combination of switch times and onset times of muscle stimulation estimated from EMG in human subjects (Bobbert et al. 2008). For the remainder of this paper we will assume that the model is a valid representation of the parts of the musculoskeletal system that are important in vertical jumping, and that human subjects are indeed trying to maximize $y_{CM,apex}$.

5. *Carrying out the desired manipulation in the model*

The model described in the preceding paragraphs give us full control over all variables. One can change morphological and physiological properties of the model; for example, compliance of SE can be changed, biarticular muscles such as gastrocnemius can be turned into monoarticular muscles, and maximal force and physiological properties of selected muscles can be changed.

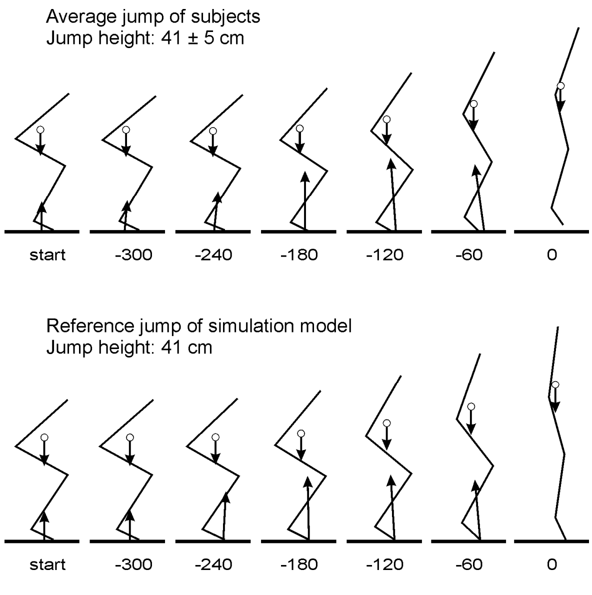

Figure 4. Stick diagrams of average body postures of 8 subjects and of the simulation model for the push off in maximum height squat jumps. Arrows pointing upward represent the ground reaction force vector plotted with the origin in the center of pressure; arrows pointing downward represent the force of gravity, and are plotted with their origin in the center of mass (open circles). Time is expressed in ms relative to the instant of takeoff (time=0).

Furthermore, one can manipulate initial postures and external constraints, and obviously, one can also set out to study the effects of making a countermovement, pushing off with one leg instead of with two legs, and so on.

6. *Finding the new optimal muscle stimulation-time histories and the corresponding maximal performance*

It needs no argument that the theoretical maximum performance that can be achieved by the model in a given task depends on the musculoskeletal properties. This theoretical maximum performance is only achieved, however, if control is optimized. Thus, if one first finds the optimal solution for the model to perform a task and then changes the model without re-optimizing control, the new performance will be submaximal (Bobbert and Van Soest 1994).

7. *Analyzing the simulation results to explain why maximal performance has changed*

It is straightforward to determine to what extent the maximum performance in a given task depends on a given property of the model, on initial conditions, or on other factors. However, the ultimate purpose is to understand why this dependence exists, and this requires an in-depth analysis of simulation results. Below, a theoretical framework will be presented that has proven to be useful in analyzing results of simulation of explosive movements.

A theoretical framework for analyzing performance in explosive movements

Outline of the framework

In explosive movement, a large amount of muscle work is produced in a short time. Hence, it is tempting to analyze simulation results in terms of power over time. However, this approach is hampered by the fact that differences tend to occur in the duration of the movement. For this reason, it is more helpful to use a work-energy approach. Taking vertical jumping as an example: what are the requirements of projecting CM to as great a height as possible? First, we need to realize that a subject can only change the total mechanical energy of CM by pushing against the ground. In the airborne phase, the subject is, by definition, no longer exerting force on the ground, and the total energy of CM remains constant. The total energy of CM may be subdivided into potential energy, vertical kinetic energy (i.e. kinetic energy due to the vertical velocity of CM) and horizontal kinetic energy (i.e. kinetic energy due to the horizontal velocity of CM). In the airborne phase, vertical kinetic energy is transformed into potential energy by the force of gravity. This means that to maximize jump height, we need to maximize the effective energy, i.e. the sum of potential energy and vertical kinetic energy of CM. During the push-off, the muscles perform mechanical work on the segments, thereby increasing the segmental energies, but only part of the segmental energies contributes to effective energy. The rest, horizontal kinetic energy of CM, rotational energy of the segments, and energy due to the velocity of segmental mass centers relative to CM, does not contribute. The ratio of effective energy to total muscle work (total mechanical energy) will be called the efficacy ratio. Let us first focus on the efficacy ratio and then on the factors determining work production by muscles.

The efficacy ratio

The concept of efficacy can best be explained with the help of the simple physical model (Bobbert et al. 1987) schematically shown in Fig. 5. The model consists of four rigid links, just like the model presented in Fig. 1, but the top link can only translate vertically along a rail. There is only one actuator in the model: the spring that crosses the knee joint. The spring may be loaded by pushing the model downwards so that the knee joint becomes flexed, and when the model is

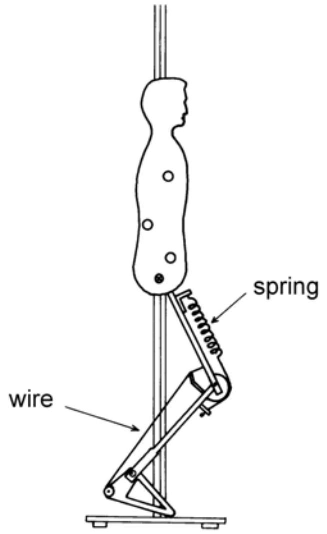

Figure 5. Model demonstrating that performance depends on efficacy.

released the spring force drives the system. There is also a passive element in the model: an inextensible wire, which is embedded like gastrocnemius and may be set at different lengths. When the wire is set at a length at which it does not become engaged during the movement, it obviously has no effect on the motion of the system. When wire length is adjusted so that the wire does become engaged before the knee is fully extended, knee extension becomes coupled to plantar flexion. Experiments with the model demonstrate that when the model is released from a fixed initial height, jump height varies with the length of the rope; there exists an optimum length that maximizes jump height, and jump height decreases both at values above and below optimum length. This result is purely due to the effect of wire length on efficacy, because in all cases the amount of energy released from the spring is the same: at non-optimum wire length, a smaller fraction of the energy released from the spring ends up as effective energy and a greater fraction ends up as rotational energy of the segments at take-off, hence the efficacy ratio becomes smaller.

Factors determining the work produced by muscles

The contractile elements of MTCs are the only elements producing work in the musculoskeletal system. The amount of work contributed by CE of an MTC during a movement is the integral of CE force with respect to CE shortening distance. CE force depends on CE length, velocity, and active state (f_5). One of the fundamental muscle properties is that force decreases with shortening velocity, everything else being equal (Hill 1938). Thus, in order to maximize the work produced by a fully activated muscle during a single contraction, it's shortening distance and active state should be made as large as possible and it's shortening velocity as low as possible. If the muscle is not pre-activated, active state should be built up as fast as possible during shortening. After all, if part of the shortening range is traveled at sub-maximal active state, the force is sub-maximal and so is the work produced. Because building up active state takes time, work production during shortening will benefit if this building up can be done during a preparatory countermovement (Bobbert and Casius 2005). Finally, a muscle can be forcibly lengthened. When CE lengthens while producing force, work output is negative; the energy absorbed by the muscle is converted into heat.

The dependence of squat jump height on knee extensor strength and coordination

Let us now apply the framework presented above to try and understand how and why performance in an explosive task, squat jumping, depends on muscle strength and coordination.

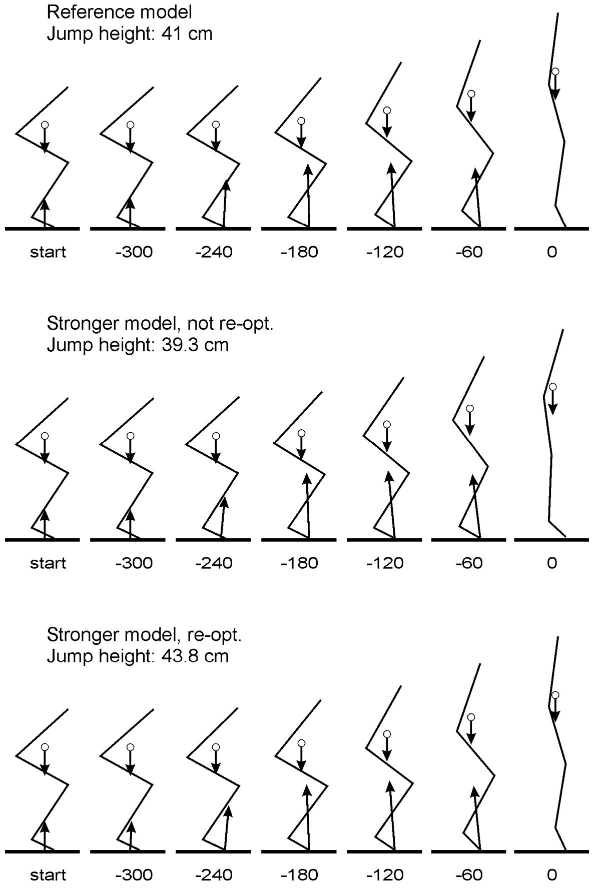

Figure 6. Stick diagrams of the simulation model for the push off in vertical squat jumps for three conditions. ‘Reference model’: a reference set of parameter values was used and control was optimized; ‘Stronger model, not re-opt.’: vasti and rectus femoris were strengthened by 20% compared to reference but control was not re-optimized; ‘Stronger model, re-opt.’: vasti and rectus femoris were strengthened by 20% compared to reference and control was re-optimized. Time is expressed in ms relative to the instant of takeoff (time=0).

Since the kinematics and kinetics of a jump are ultimately determined by muscle stimulation as a function of time, it seems safe to equate coordination with control. To illustrate all arguments presented above, let us devise the following thought experiment that we may simulate with the model (Fig. 6): an athlete has found optimal control for jumping (‘reference model’) but wants to jump higher. The athlete spends 8 weeks in the gym performing leg extension exercises and achieves a 20% increase in quadriceps strength, with all other musculoskeletal properties remaining unchanged. After training, the subject performs a maximum-effort jump, but the ‘old’ control is no longer optimal for the ‘new’ musculoskeletal system (‘stronger model, not re-opt.’). By means of practice, the subject finds the new optimal control solution (‘stronger model, re-opt.’). First of all, we observe that jump height after training but before re-optimization of control is actually less than in the reference model, despite the increased quadriceps strength. The reduction is caused by an 8 J drop in the total work produced by the MTCs (Table 1) and a drop in the efficacy ratio from 87% to

Table 1. Work of muscle-tendon complexes (in J) during the push-off in simulated vertical squat jumps. Values of left and right leg have been added. Conditions are the same as those in Fig. 6.

	soleus	gastrocnemius	vasti	Rectus femoris	gluteus maximus	hamstrings	total
Reference model	85	49	166	8	246	106	659
Stronger model, not re-opt.	70	28	189	26	232	106	651
Stronger model, opt.	86	51	184	12	243	106	682

Reference model: a reference set of parameter values was used and control was optimized;
Stronger model, not re-opt.: vasti and rectus femoris were strengthened by 20% but control was not re-optimized;
Stronger model, re-opt.: vasti and rectus femoris were strengthened by 20% and control was re-optimized.

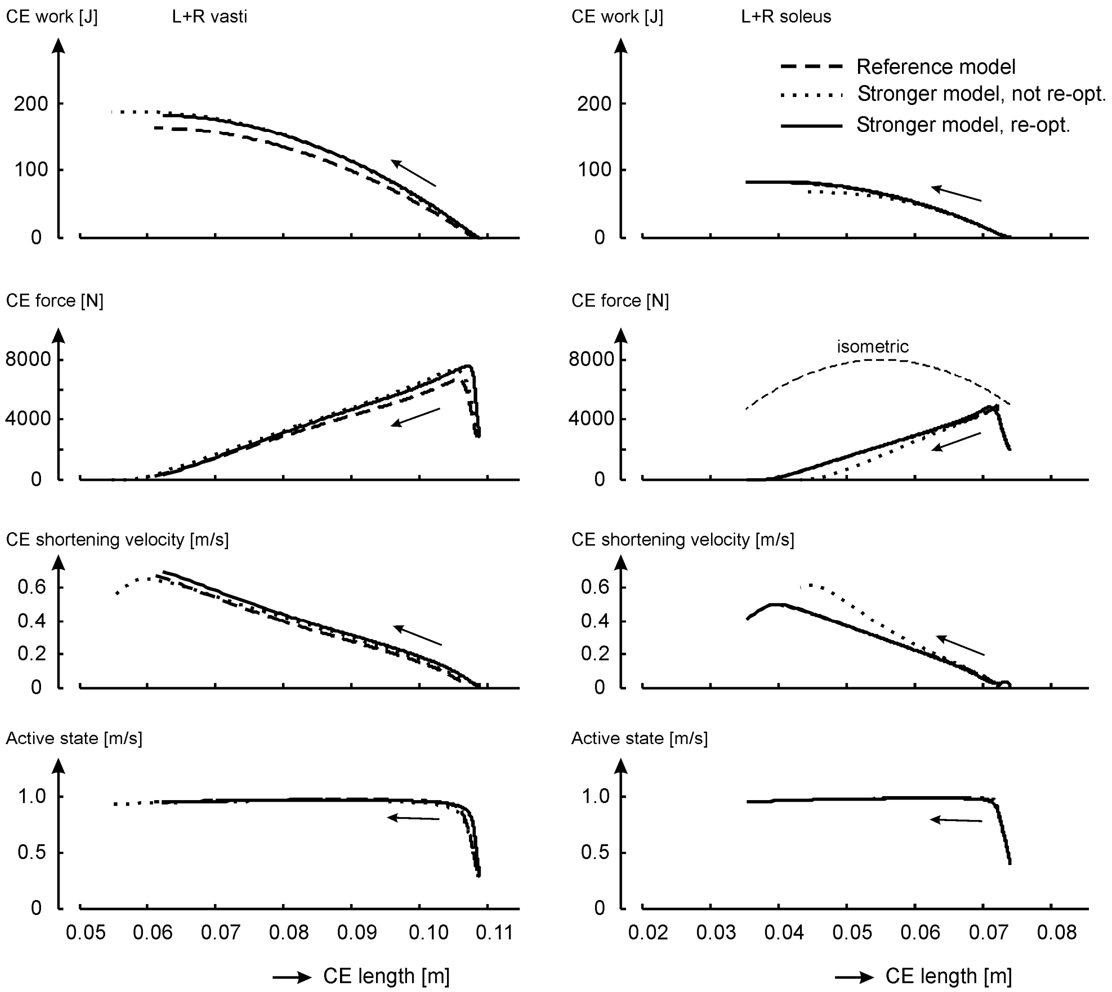

Figure 7. Active state, shortening velocity, force and work of contractile elements (CE) of vasti and soleus as a function of contractile element length for the push off in simulated vertical squat jumps. Values for force and work of left and right legs have been added. Conditions are the same as those in Fig. 6. The parabola labeled 'isometric' represents the force that can be produced at maximum active state and zero shortening velocity. Arrows indicate the direction of time.

86%. Some MTCs produce extra work, but other muscles produce less work (Table 1). The changes in MTC work are almost completely due to changes in CE work and Fig. 7 allows for an analysis of the CE work of vasti and soleus. The increase in CE work of vasti is explained by the fact that these muscles have been strengthened. However, the system now takes off at a smaller plantar flexion angle, so CE shortening distance of soleus is smaller and CE shortening velocity is higher, causing a loss of CE force and CE work. Figure 7 also shows the isometric CE force as a function of CE length, and comparing this isometric force with the actual force it becomes clear that the force-velocity relationship has a major effect on force and therewith work of CE, which is typical for explosive movements. Re-optimization, which primarily results in a slight delay in t_{switch} of the knee extensors, leads to restoration of CE shortening distance and CE shortening velocity of soleus to the values observed in the reference condition.

Conclusions

The musculoskeletal modeling and optimization approach described in this paper leads to simulated vertical jumps that closely resemble vertical jumps performed by human subjects. The theoretical framework presented provides a clear understanding of simulation results: performance depends on muscle work and efficacy, and variations in muscle work production can be explained by examining contractile element force and its determinants, active state and contraction velocity, as a function of shortening distance. The results support the idea that in explosive movements, coordination benefits force and work production by helping to prevent that the shortening velocities of some muscles become disproportionally high (Bobbert and van Soest 2001).

Acknowledgements

The simulation approach described in this paper has been developed in close cooperation with Dr. A.J. van Soest and L.C. Richard Casius.

References

An KN, Takahashi K, Harrigan TP, Chao EY (1984) Determination of muscle orientations and moment arms. J Biomech Eng 106: 280-282

Bobbert MF, Casius LJ (2005) Is the effect of a countermovement on jump height due to active state development? Med Sci Sports Exerc 37: 440-446

Bobbert MF, Casius LJ, Sijpkens IW, Jaspers RT (2008) Humans adjust control to initial squat depth in vertical squat jumping. J Appl Physiol 105: 1428-1440

Bobbert MF, Hoek E, van Ingen Schenau GJ, Sargeant AJ, Schreurs WH (1987) A model to demonstrate the power transporting role of biarticular muscles. Meeting of the Physiological Society, London, U.K. Journal of Physiology 387: 24P

Bobbert MF, Van Soest AJ (1994) Effects of muscle strengthening on vertical jump height: a simulation study. Med Sci Sports Exerc 26: 1012-1020

Bobbert MF, van Soest AJ (2001) Why do people jump the way they do? Exerc Sport Sci Rev 29: 95-102

Casius LJR, Bobbert MF, van Soest AJ (2004) Forward dynamics of two-dimensional skeletal models. A Newton-Euler approach. Journal of Applied Biomechanics 20: 421-449

Hatze H (1977) A myocybernetic control model of skeletal muscle. Biol Cybern 25: 103-119

Hill AV (1938) The heat of shortening and the dynamic constants of muscle. Proc R Soc London B Biol Sci 126: 136-159

Maganaris CN, Baltzopoulos V, Sargeant AJ (1998) Changes in Achilles tendon moment arm from rest to maximum isometric plantarflexion: in vivo observations in man. J Physiol 510 (Pt 3): 977-985

Out L, Vrijkotte TG, van Soest AJ, Bobbert MF (1996) Influence of the parameters of a human triceps surae muscle model on the isometric torque-angle relationship. J Biomech Eng 118: 17-25

ter Keurs HE, Iwazumi T, Pollack GH (1978) The sarcomere length-tension relation in skeletal muscle. J Gen Physiol 72: 565-592

van Soest AJ, Bobbert MF (1993) The contribution of muscle properties in the control of explosive movements. Biol Cybern 69: 195-204

van Soest AJ, Casius LJ (2003) The merits of a parallel genetic algorithm in solving hard optimization problems. J Biomech Eng 125: 141-146

van Zandwijk JP, Bobbert MF, Harlaar J, Hof AL (1998) From twitch to tetanus for human muscle: experimental data and model predictions for m. triceps surae. Biol Cybern 79: 121-130

Visser JJ, Hoogkamer JE, Bobbert MF, Huijing PA (1990) Length and moment arm of human leg muscles as a function of knee and hip-joint angles. Eur J Appl Physiol Occup Physiol 61: 453-460

Walker SM, Schrodt GR (1974) I segment lengths and thin filament periods in skeletal muscle fibers of the Rhesus monkey and the human. Anat Rec 178: 63-81

Yeadon MR, Morlock M (1989) The appropriate use of regression equations for the estimation of segmental inertia parameters. J Biomech 22: 683-689