

**Maarten F. Bobbert, L. J. Richard Casius, Igor W. T. Sijpkens and Richard T. Jaspers**

*J Appl Physiol* 105:1428-1440, 2008. First published Aug 21, 2008;  
doi:10.1152/japphysiol.90571.2008

**You might find this additional information useful...**

---

This article cites 24 articles, 3 of which you can access free at:

<http://jap.physiology.org/cgi/content/full/105/5/1428#BIBL>

Updated information and services including high-resolution figures, can be found at:

<http://jap.physiology.org/cgi/content/full/105/5/1428>

Additional material and information about *Journal of Applied Physiology* can be found at:

<http://www.the-aps.org/publications/jappl>

---

This information is current as of November 26, 2008 .

# Humans adjust control to initial squat depth in vertical squat jumping

Maarten F. Bobbert, L. J. Richard Casius, Igor W. T. Sijpkens, and Richard T. Jaspers

Research Institute MOVE, Faculty of Human Movement Sciences, VU University Amsterdam, Amsterdam, The Netherlands

Submitted 25 April 2008; accepted in final form 15 August 2008

**Bobbert MF, Casius LJ, Sijpkens IW, Jaspers RT.** Humans adjust control to initial squat depth in vertical squat jumping. *J Appl Physiol* 105: 1428–1440, 2008. First published August 21, 2008; doi:10.1152/jappphysiol.90571.2008.—The purpose of this study was to gain insight into the control strategy that humans use in jumping. Eight male gymnasts performed vertical squat jumps from five initial postures that differed in squat depth (P1–P5) while kinematic data, ground reaction forces, and electromyograms (EMGs) of leg muscles were collected; the latter were rectified and smoothed to obtain SREMGs. P3 was the preferred initial posture; in P1, P2, P4, and P5 height of the mass center was +13, +7, –7 and –14 cm, respectively, relative to that in P3. Furthermore, maximum-height jumps from the initial postures observed in the subjects were simulated with a model comprising four body segments and six Hill-type muscles. The only input was the onset of stimulation of each of the muscles (Stim). The subjects were able to perform well-coordinated squat jumps from all postures. Peak SREMG levels did not vary among P1–P5, but SREMG onset of plantarflexors occurred before that of gluteus maximus in P1 and >90 ms after that in P5 ( $P < 0.05$ ). In the simulation study, similar systematic shifts occurred in Stim onsets across the optimal control solutions for jumps from P1–P5. Because the adjustments in SREMG onsets to initial posture observed in the subjects were very similar to the adjustments in optimal Stim onsets of the model, it was concluded that the SREMG adjustments were functional, in the sense that they contributed to achieving the greatest jump height possible from each initial posture. For the model, we were able to develop a mapping from initial posture to Stim onsets that generated successful jumps from P1–P5. It appears that to explain how subjects adjust their control to initial posture there is no need to assume that the brain contains an internal dynamics model of the musculoskeletal system.

coordination; optimal control; simulation model; control strategy

THE PUSH-OFF in a human vertical jump takes <300 ms (4). Taking into account that even the fastest reflexes have latencies of 50–60 ms (11), that the time constant of building up force in maximally fast isometric contractions is well over 100 ms (25), and that positional changes are two time-integration steps away from force, control signals for the push-off in jumping must be generated largely in an open-loop fashion. Since open-loop control of an inherently unstable inverted pendulum-like system such as a human jumper requires very precise control (6), the question may be raised as to how human subjects perform jumps from different initial postures.

When asked to perform a maximum-height squat jump, human subjects tend to assume a specific initial posture. It might be argued that this preferred initial posture, and the associated muscle stimulation pattern for jump execution, have been found through years and years of painstaking practice. Yet subjects seem to have no difficulty whatsoever in perform-

ing squat jumps from initial postures that are different from their preferred position (3, 8). Subjects can, of course, use online feedback to find the muscle stimulation needed for equilibrium in the initial posture, but how do they generate the open-loop control signals for the push-off when the initial posture is different from the preferred one? After all, when the initial posture is different, muscles are at different lengths, so at a given level of stimulation they will produce different forces and joint moments. And even if the muscles were to produce the same forces and the same joint moments as a function of time, these would generate different accelerations at a different posture, and hence the dynamics of the evolving movement would be different (22). In theory, subjects could work around this problem by slowly moving to their preferred posture under online feedback control, but simple observation tells us that this is not what they do. How can we then explain that subjects are able to perform squat jumps from different initial postures without noticeable difficulty? To answer this question, various control strategies may be proposed (for reviews, see Refs. 1, 9), ranging from very simple strategies, such as lookup tables, to strategies that take out a large loan on computational abilities of the brain.

The simplest strategy to control jumping has been proposed by Van Soest et al. (23): subjects might use one and the same stimulation pattern for a range of initial postures and rely for successful performance on the stabilizing properties of their musculoskeletal system during jump execution; the effects of variations in initial posture could be reduced during the push-off by the intrinsic properties of the muscles, with the force-length relationship providing zero-lag negative feedback of joint angles on muscle forces and the force-velocity relationship providing zero-lag negative feedback of joint angular velocities on these forces (22). The feasibility of this control strategy has been explored with a forward simulation model that had muscle stimulation as its only independent input (23). It was found that, indeed, acceptable squat jump performance could be achieved from a range of initial postures using one and the same muscle stimulation pattern. Needless to say, the jump heights achieved from a given initial posture with this stimulation pattern were not the greatest jump heights that could possibly be achieved, but they were never more than 4 cm off (~10% of absolute jump height). The control strategy was therefore called “control that works.” This strategy would merely involve learning, storing, and retrieving a single stimulation pattern, thereby offering a parsimonious solution to persistent puzzles in motor control, such as the storage problem of separate motor programs (19) and the novelty problem, which states that humans are able to successfully make movements that they have never made before (18). To our knowledge, no exper-

Address for reprint requests and other correspondence: M. F. Bobbert, Research Institute MOVE, Faculty of Human Movement Sciences, VU Univ. Amsterdam, Van der Boechehorstraat 9, 1081 BT Amsterdam, The Netherlands (e-mail: m\_f\_bobbert@fbw.vu.nl).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

iments have yet been carried out to test whether human subjects indeed use this “control that works” strategy in vertical jumping.

The control strategies taking out a large loan on computational abilities of the brain, which we find at the other end of the spectrum, rely on internal structural models: inverse kinematics models of the musculoskeletal system for trajectory planning and inverse dynamics models for computation of the time-varying joint moments and muscle stimulation patterns that are necessary to realize desired trajectories (see e.g., Refs. 15, 20). Published data suggest that internal dynamics models are present within the cerebellar circuitry (26), and some researchers have claimed that the use of internal models is the only computational possibility for generating fast and well-coordinated movements (14). However, internal dynamics models are not necessarily inverse dynamics models, and the latter are only useful if control involves trajectory planning in terms of motions of body segments. No evidence has been found so far that control of jumping involves trajectory planning. On the contrary, results of experiments on jumping forward suggest that subjects tend to keep their muscle stimulation pattern constant and let the kinematic pattern simply emerge (17).

The purpose of the present study was to gain insight into the control strategy that humans use in vertical jumping. Our first step was to test the hypothesis that subjects use the “control that works” strategy outlined above. To this end, we had human subjects perform squat jumps from five initial postures that differed in squat depth, i.e., height of the mass center of the body, while we collected kinematic data, ground reaction forces, and electromyograms (EMGs). It will be shown in this article that the hypothesis is not supported: changes in initial posture caused the subjects to adjust their EMG patterns for jump execution. Our next step was to investigate whether these adjustments were functional, in the sense that they contributed to achieving the greatest jump height possible given the initial posture. To this end, we compared the EMG patterns observed in the subjects with optimal control solutions that caused a forward dynamic model to generate maximum-height jumps from the initial postures observed in the experiments. It will be shown that to achieve maximum jump height of the model, changes in the initial posture required adjustments of the muscle stimulation pattern that were similar to adjustments observed in the EMG patterns of the subjects. Finally, we developed for our simulation model a simple mapping from initial posture to muscle stimulation onsets, inspired by the adjustments in EMG patterns observed in the subjects, and we compared its performance to the “control that works” strategy.

## MATERIALS AND METHODS

**Outline of experimental procedures.** This study was approved by the local ethics committee. Eight male subjects participated in the study, all of whom practiced gymnastics once or twice a week and some of whom also participated in other fitness activities once or twice a week. Informed consent was obtained from all subjects in accordance with the policy statement of the American College of Sports Medicine. Characteristics of the group of subjects (mean  $\pm$  SD) were age  $25 \pm 3$  yr, height  $1.82 \pm 0.10$  m, and body mass  $76.7 \pm 7.5$  kg. The subjects performed with their hands on their hips several squat jumps with the instruction to make no countermovement and to jump as high as possible. Each subject was then asked to find for himself the preferred initial posture for a maximum-height jump, and this posture was recorded. Finally, each subject performed four jumps from each of five different initial postures (P1–P5), imposed in

random order, with consecutive jumps separated by 2 min of rest. One of the initial postures, P3, was the posture that the subject preferred for maximum-height squat jumping, and in the other four postures the height of the center of mass of the body (CM) was different from that in P3: 13 cm higher in P1, 7 cm higher in P2, 7 cm lower in P4, and 14 cm lower in P5. The subjects were able to perform jumps from P4 and P5 as required, but most of the subjects could not resist making a small countermovement when performing jumps from P1, and some could not resist doing so when jumping from P2 and occasionally even from P3. As explained in detail below, ground reaction forces were measured with a force plate, sagittal-plane positional data of anatomic landmarks were monitored, and EMGs were recorded from six muscles of the right lower extremity. Jump height, defined as the difference between the height of CM at the apex of the jump and the height of CM when the subject was standing upright with heels on the ground, was calculated from the positional data. Details on the setting of the initial postures and on data collection and processing are provided below.

**Setting of initial postures.** To set the initial postures for the jump and to help the subjects reproduce them, we used the following procedure. In the preparatory phase of the experiment we had each subject perform practice jumps so that he could find his preferred posture. We then asked him to assume the preferred posture and we adjusted the height of a mold fitting the buttocks (Fig. 1). Furthermore, we adjusted the height of a small vertically positioned mirror so that the subject looked himself in the eyes (Fig. 1). Next, we practiced the following jumping procedure: the subject adjusted his body configuration so that his buttocks snugly fit the mold and he saw his eyes in the mirror, the subject maintained this body posture while the experimenter removed the mould, and then the subject performed a maximum-effort vertical jump from this posture. When the subject was accustomed to the jumping procedure, we found the other four postures as follows. We changed the height of the mold by a desired amount and asked the subject to reposition himself with his buttocks snugly fitting the mold, such that he felt able to jump as high as he could from the new imposed initial posture. When the subject had found a comfortable posture at the new height of the mold, the height of the mirror was adjusted so that the subject looked himself in the eyes again. This

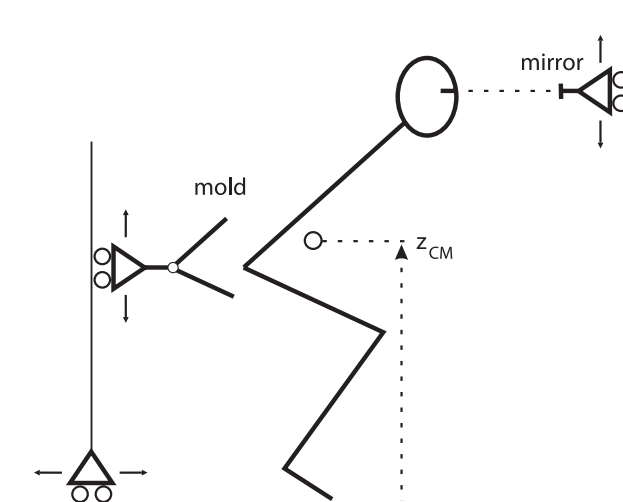


Fig. 1. Schematic representation of the method used to set the initial postures and to help the subject reproduce these postures. The guides for the subject were a mold fitting the buttocks and a small vertically oriented mirror allowing the subject to look himself in the eyes. Both the mold and the mirror were height adjustable. Before the start of a jump from a particular initial posture, the experimenter selected the corresponding combination of mold height and mirror height, the subject adjusted his body configuration so that his buttocks snugly fit the mold and he saw his eyes in the mirror, the experimenter removed the mold, and then the subject performed a maximum-effort vertical jump.  $z_{CM}$ , height of the center of mass (○).

procedure was repeated until we had found the five combinations of mold height and mirror height for the five initial postures.

In the experiment proper, the experimenter selected one of the five initial postures and set the corresponding heights of the mold and the mirror, the subject adjusted his body configuration so that his buttocks snugly fit the mold and he saw his eyes in the mirror, the subject maintained this body posture while the experimenter removed the mold, and then the subject performed a maximum-effort vertical jump from this posture. The subjects had not practiced jumping from P1, P2, P4, and P5 until the first of the four trials in each of these conditions.

**Collection and processing of data.** Ground reaction forces were measured with a force platform (Kistler 9281B, Kistler Instruments, Amherst, NY). The output signals of the platform were amplified (Kistler 9865E charge amplifier, Kistler Instruments), sampled at 200 Hz, and processed to determine the fore-aft and vertical components of the reaction force and the location of the center of pressure.

For kinematic analysis, retroreflective spheres were placed at a point midway (in ventro-dorsal direction) between the sternum and the ninth thoracic vertebra, at the right greater trochanter, at the right lateral epicondyle of the femur, at the right lateral malleolus, and at the right fifth metatarsophalangeal joint. Together, these markers defined the positions of four body segments: HAT (head, arms, and trunk), thighs, shanks, and feet. During jumping, the markers were monitored in three dimensions with four electronically shuttered cameras (NAC 60/200 MOSTV) connected to a VICON high-speed video analysis system (Oxford Metrics, Oxford, UK) operating at 200 Hz. Only sagittal-plane projections were used in this study. The time histories of marker positions were smoothed with a zero-lag 4th-order low-pass Butterworth filter with a cutoff frequency of 8 Hz. The locations of the mass centers of thighs, shanks, and feet were estimated by combining the landmark coordinates with results of cadaver measurements presented in the literature (7). The location of the center of mass of HAT relative to the two markers on this segment was determined as described elsewhere (3). Briefly, the subject first stood upright in equilibrium and then stood in equilibrium with the hips flexed and the upper body oriented horizontally. The force platform provided for each of these postures the center of pressure of the ground reaction force, which in the case of equilibrium equals the fore-aft location of CM. Using the link segment model, we set up two equations for the two known fore-aft locations of CM, which were solved for the two unknown coordinates of CM of the upper body relative to the markers on this segment. Using these coordinates, the location of CM was calculated in all other body configurations found during jumping.

To record EMGs from the muscles of the right leg, pairs of Ag/AgCl surface electrodes (Medi-Trace, Pellet 1801 electrodes, diameter 1 cm, interelectrode distance 2.5 cm) were applied to the skin overlying the most prominent part of soleus, gastrocnemius (caput mediale), vastus lateralis, rectus femoris, gluteus maximus, and biceps femoris (caput longum) muscles, parallel to the muscle fiber direction. The EMG signals were preamplified, transmitted, and further amplified (BIOMES 80, Glonner Electronics, Munich, Germany), high-pass filtered at 7 Hz to reduce the amplitude of possible movement artifacts, full-wave rectified, smoothed with an analog 20-Hz 3rd-order low-pass filter, and sampled at 200 Hz with the analog-to-digital converter of the VICON system. Off-line, the signals were further smoothed with a zero-lag 4th-order low-pass Butterworth filter with a 10-Hz cutoff frequency, to yield smoothed rectified EMG (SREMG). The phase transfer involved in the analog preprocessing of EMG caused SREMG signals to be shifted in time (by  $\sim 7$  ms) relative to the kinematic and kinetic signals. We do not directly relate SREMG signals with kinematic signals. However, we do present graphs showing time histories of SREMG signals together with time histories of the vertical component of the ground reaction force ( $F_z$ ). In preparing those graphs, the time histories of  $F_z$  were run through a digital filter imitating the 20-Hz analog low-pass filter before plotting.

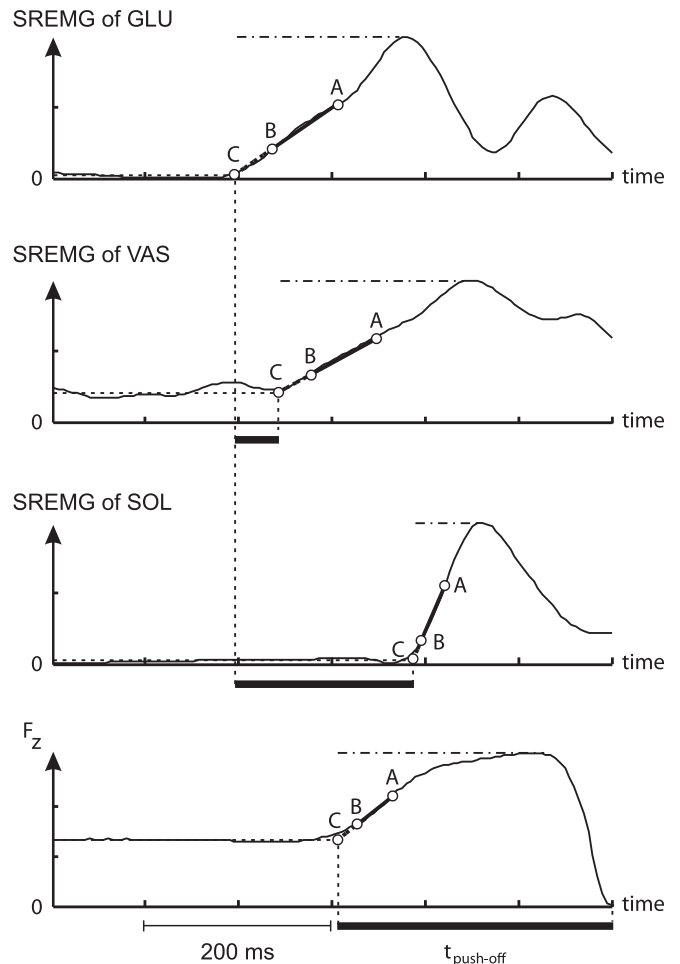


Fig. 2. Illustration of the procedure used for detection of onsets in smoothed, rectified EMG (SREMG) and vertical ground reaction force ( $F_z$ ). For each SREMG signal, we first determined  $SREMG_{ini}$ , i.e., the SREMG level observed while the subject was holding the initial posture (horizontal dashed lines), and  $SREMG_{max}$ , the maximum value during the push-off phase of the jump (horizontal dash-dotted lines). Second, we found point A where SREMG crossed the level  $SREMG_{ini} + 0.5(SREMG_{max} - SREMG_{ini})$ . Third, starting from the latter point and going backwards in time, we found point B where SREMG crossed the level  $SREMG_{ini} + 0.2(SREMG_{max} - SREMG_{ini})$ . Finally, we fitted a line to these 2 points and extrapolated this line backwards to point C where it crossed the level  $SREMG_{ini}$ , with the corresponding time being the SREMG onset. The same procedure was used to find the instant that  $F_z$  started to increase (bottom), which was taken to mark the onset of the push-off. All curves end at the instant that  $F_z$  dropped to 0, indicating takeoff. The horizontal bars below the time axes in the graphs of vastus lateralis (Vas) and soleus (Sol) indicate the SREMG onset of these muscles relative to that of gluteus maximus (Glu), and the horizontal bar below the time axis in the panel of  $F_z$  indicates the duration of the push-off ( $t_{push-off}$ ). For time reference, a 200-ms bar is shown under the graph.

To parameterize the SREMG signals, we decided to determine for each muscle what will henceforth be called an SREMG onset. The procedure that we used to find SREMG onsets is illustrated and explained in detail in Fig. 2. Essentially, we fitted a line to two points on the ascending slope of the SREMG time history and extrapolated this line backwards in time to where the SREMG level equaled the level observed while the subject was holding the initial posture. The same procedure was applied to the time history of  $F_z$  to detect  $F_z$  onset. Finally, for comparisons of SREMG onset patterns, we needed to define a reference point in time. In a previous study (5) it was shown that in squat jumping the rise time of the ground reaction force was closely related to that of the SREMG of gluteus

maximus (Glu). Therefore, it was decided to express all onsets relative to the SREMG onset of this muscle.

**Statistics.** Main effects of initial posture on various variables, among which were jump height and onsets and peak levels of SREMG histories of muscles, were tested to significance with a general linear model ANOVA for repeated measures, and when a significant  $F$  value was found, post hoc pairwise comparisons of means were made with paired-samples  $t$ -tests (SPSS statistical software). The level of significance for all tests was 0.05. Because each subject performed four trials from each initial posture, the first of which was unpracticed, we included trial as a separate factor in the ANOVA. However, neither main effects nor interaction effects were found for this factor, and for that reason we do not present separate results for the four trials. In Tables 1 and 2, we report per variable per condition a mean and a SD, where the latter was calculated over eight values the mean over the four jumps of that subject from a given initial posture.

**Computer simulations of squat jumping.** For simulations of jumps we used the two-dimensional forward dynamic model of the human musculoskeletal system shown in Fig. 3. The model, which had muscle stimulation as its only independent input, consisted of four rigid segments representing a HAT segment, thighs, shanks, and feet. These segments were interconnected by hinge joints representing hip, knee, and ankle joints, and the distal part of the foot was connected to the ground in a hinge joint. In the initial configuration the rotational degree of freedom of the foot was fixed in accordance with the observation that the subjects had their heels on the ground, and we calculated the moment of the ground reaction force relative to the distal part of the foot that was needed to prevent angular acceleration of the foot. The rotational degree of freedom was released during simulations as soon as this moment dropped to zero. In the skeletal submodel, six major muscle-tendon complexes (MTCs) of the lower

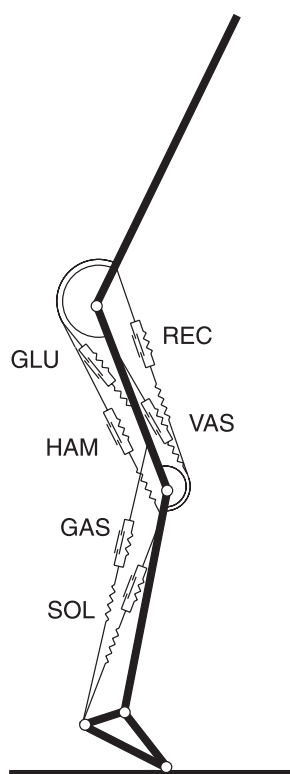


Fig. 3. Model of the musculoskeletal system used for forward dynamic simulations. The model consisted of 4 interconnected rigid segments and 6 muscle-tendon complexes of the lower extremity [hamstrings (Ham), Glu, rectus femoris (Rec), Vas, gastrocnemius (Gas), and Sol], all represented by Hill-type muscle models.

extremity were embedded, which were acting independently (i.e., not mechanically linked by myofascial connections as described in Ref. 13): hamstrings (Ham), Glu, rectus femoris (Rec), monoarticular vasti (Vas), gastrocnemius (Gas), and soleus (Sol). Each MTC was represented by a Hill-type muscle model. This muscle model, which is described in full detail elsewhere (22), consisted of a contractile element (CE), a series elastic element (SEE), and a parallel elastic element (PEE). Briefly, behavior of SEE and PEE was represented with a quadratic force-length relationship. Behavior of CE was more complex: CE velocity depended on CE length, force, and active state, with the latter being defined as the relative amount of calcium bound to troponin (10). Active state was not an independent input of the model but was manipulated indirectly via muscle stimulation (Stim), a one-dimensional representation of the effects of recruitment and firing rate of  $\alpha$ -motoneurons. Stim, ranging between 0 and 1, was dynamically coupled to active state as proposed by Hatze (12), taking into account the length-dependent  $\text{Ca}^{2+}$  sensitivity of the contractile elements (16).

At the start of each simulation, the model was put in an initial posture derived from the subject experiments, and the initial Stim levels were set in such a way that the resultant joint moments kept the system in equilibrium. To find a unique solution for the initial Stim levels, we first assigned a small Stim level to the biarticular Ham, Rec, and Gas, causing them to produce a force of 100 N that took up the slack in SEE. Subsequently, we calculated the Stim levels of the other muscles that ensured equilibrium of the system as a whole. Our motivation for this approach was that it is energy efficient to use primarily the monoarticular muscles to generate the initial joint moments. If, for example, the biarticular Gas instead of the monoarticular Sol were selected to provide the initial plantar flexion moment, an undesired flexion moment of Gas would be introduced at the knee. This undesired moment would have to be compensated by increasing Stim of Vas and/or Rec, thereby raising the total amount of muscle stimulation and, in the real system, cross-bridge cycling and energy expenditure. However, it turned out that SREMG levels of the subjects in the initial postures P1–P5 did not support our approach, and therefore we explored whether the selection of muscle contributions to the initial joint moments affected the main outcome of the study, only to find out that it did not (see RESULTS).

During push-off, Stim of each muscle was allowed only to increase from its initial level toward its maximum of 1. The increase started at Stim onset and occurred at a fixed rate of  $5 \text{ s}^{-1}$  (see Fig. 5). This rate was chosen such that the push-off duration of the jump from P3 (determined as illustrated in Fig. 2, bottom) was the same in the model as in the group of subjects participating in this study. Under these restrictions, the motion of the body segments, and thereby performance of the model, depended on a set of Stim onsets, and the following optimization problem could be formulated: finding the combination of five Stim onsets relative to the fixed onset of Glu that produced the maximum value of the height achieved by CM, and thereby maximum jump height. The optimization problem was solved with a genetic algorithm (24). To get an impression as to whether the solutions found were globally optimal, we performed the optimization for P3 from 10 random initial guesses for Stim onsets. The Stim onsets of individual muscles were found to vary by no more than 3 ms over the 10 solutions, and jump height was found to vary by less than  $2 \times 10^{-5} \text{ m}$ . Since this variation was negligible compared with the variation among conditions, we do not report any error measures for the simulation results.

In addition to finding optimal control solutions for the five initial postures, we explored three possible control strategies. For *strategy 1*, henceforth referred to as the Opt-P3 strategy, we simply took the set of Stim onsets that was optimal for P3 and evaluated this set for P1, P2, P4, and P5. For *strategy 2*, the “control that works” (CTW) strategy, we performed a new optimization as done previously (23): we found the solution that was globally optimal for initial postures P1, P3, and P5, i.e., we found the combination of Stim onsets that produced the best

average jump height over these conditions. This solution was subsequently evaluated for P2 and P4. For *strategy 3*, which was inspired by the experimental findings (see RESULTS) and will henceforth be called the “plantarflexor shift” (PF-Shift) strategy, we also found a combination of Stim onsets that produced the best average jump height over P1, P3, and P5 and evaluated the solution for P2 and P4, but we introduced one extra parameter to be optimized. Specifically, the parameters in the optimization were the “reference” Stim onsets of the muscles as well as a parameter  $d$ , which was used to make the actual Stim onsets of Sol and Gas dependent on the initial height of CM, as follows:

$$t_{\text{Sol}} = t_{\text{Sol,ref}} + d \cdot z_{\text{CM,ini}} \quad \text{and} \quad t_{\text{Gas}} = t_{\text{Gas,ref}} + d \cdot z_{\text{CM,ini}} \quad (1)$$

where  $t_{\text{Sol}}$  and  $t_{\text{Gas}}$  are the actual Stim onsets of Sol and Gas, respectively,  $t_{\text{Sol,ref}}$  and  $t_{\text{Gas,ref}}$  are the “reference” Stim onsets, which were among the parameters to be optimized, and  $z_{\text{CM,ini}}$  is the initial height of CM. This way, the actual Stim onsets of Glu, Ham, Vas, and Rec were equal to the “reference” Stim onsets and hence were the same for all initial postures, while the actual Stim onsets of Sol and Gas varied among P1–P5. Needless to say, in all evaluations of control strategies, the initial Stim levels needed for equilibrium were specific for each initial posture.

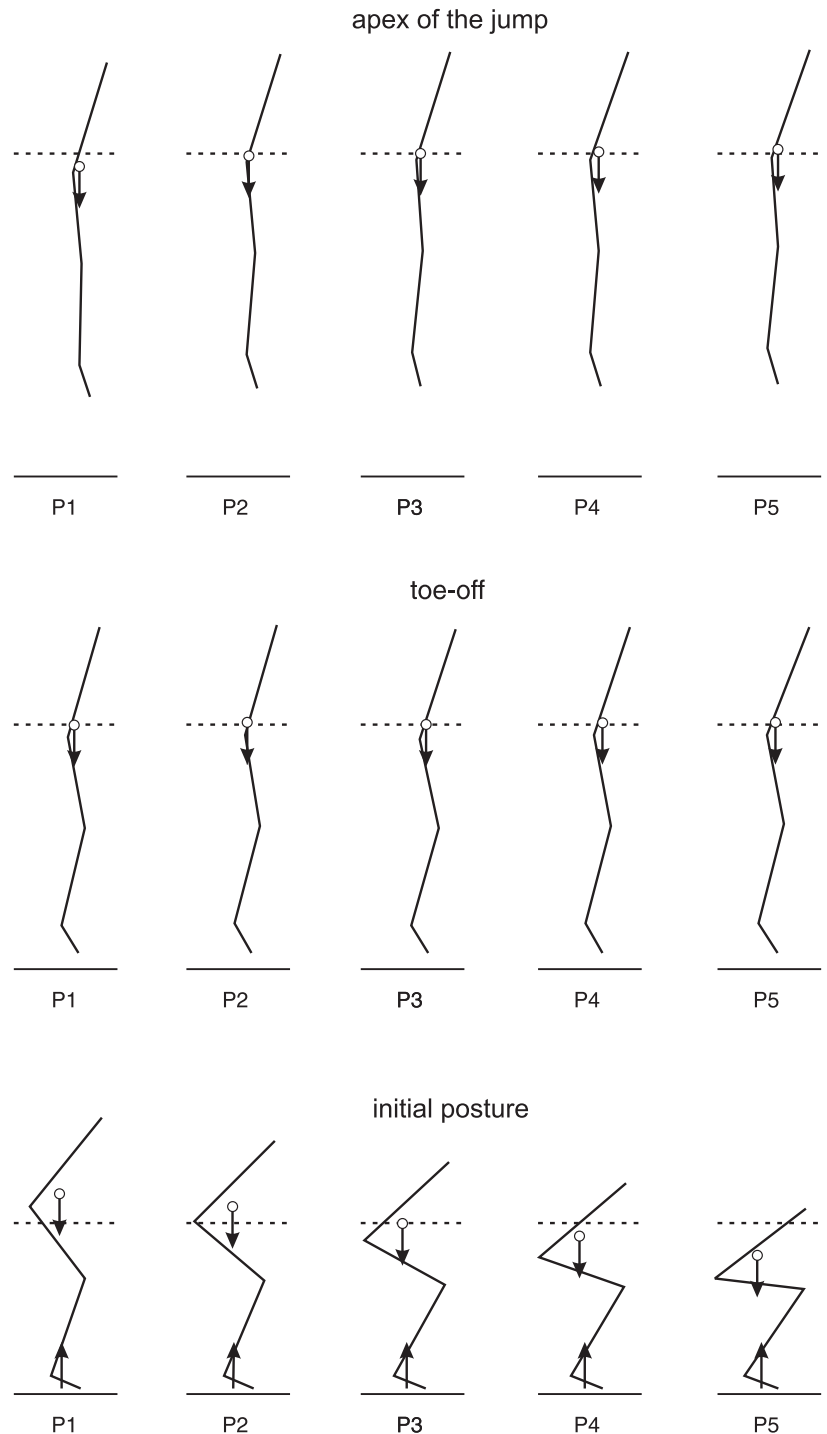


Fig. 4. Average stick diagrams of the group of subjects ( $n = 8$ ) for the squat jumps performed in this study from initial postures P1–P5, with P3 being the preferred initial posture. Stick diagrams are shown for initial posture, toe-off, and apex of the jump (with time proceeding from *bottom* to *top* within columns). In each diagram, the ground reaction force vector is shown with its origin at the center of pressure on the force platform, and the vector of the force of gravity is shown with its origin in the center of mass ( $\circ$ ). To allow for comparison of heights of the center of mass among P1–P5 (see also Table 1), each row of stick diagrams contains a horizontal dashed line (interrupted between columns) that is centered at the height of the center of mass in P3. Note that the foremost foot marker was on the 5th metatarsophalangeal joint, which explains the “premature” upward movement of this marker.

## RESULTS

*Jumps performed by the subjects.* Average body postures and ground reaction forces at selected instants during the jumps are illustrated in Fig. 4, and values of several descriptive variables are presented in Table 1. The initial configuration of the body differed substantially among P1–P5, with the initial height of CM ranging over ~27 cm. As intended, there was a main effect of initial posture on initial height of CM, and pairwise comparisons revealed that all differences were statistically significant (P1 > P2 > P3 > P4 > P5,  $P < 0.05$ ). At takeoff, no differences in height of CM were found. The duration of the push-off, from the onset of  $F_z$  to the instant that  $F_z$  dropped to zero (see Fig. 2), varied substantially among initial postures, ranging from 194 ms in P1 to 384 ms in P5. Again, there was a main effect of initial posture, and pairwise comparisons revealed that all differences in duration of the push-off were statistically significant (P1 < P2 < P3 < P4 < P5,  $P < 0.05$ ); understandably, the push-off duration increased when CM was lower in the initial posture and hence had to be raised over a larger distance during the push-off. Average jump height ranged from 36 cm in P1 to 43 cm in P5. There was a main effect of initial posture, with jump height being less in the higher initial postures than in the lower initial postures (P1 < P2 < P3 = P4 = P5,  $P < 0.05$ ). Interestingly, average jump height was greater (albeit not statistically significantly) in P4 and P5 than in P3, implying that some subjects jumped higher from P4 and P5 than from their preferred posture. This might be a coincidence, or perhaps the preferred posture represents a trade-off between jump height and push-off duration.

Figure 5, *left* and *center*, present mean time histories of SREMG and  $F_z$  for two subjects jumping from initial postures P1, P3, and P5; each curve represents the mean result of four individual jumps from one particular initial posture, and the gray area represents the SE. Two observations can be made. First, for a given subject, the variability in results among the four jumps within each initial posture was sufficiently small that differences among initial postures were clearly distin-

guishable. This was true not only for time histories of  $F_z$  (with the gray area falling within the width of the lines for most of the time) but also for time histories of SREMG. Second, the variation among subjects was large, but consistent changes occurred over P1–P5 in time histories of  $F_z$  and SREMG of the plantarflexors. For example, in *subject 1* SREMG of Gas started to increase almost simultaneously with that of Glu in P5, while in *subject 2* it started to increase some 200 ms after that of Glu in P5, yet in both subjects the burst in Gas started later in P5 than in P3, and later in P3 than in P1. There seemed to be no systematic changes in peak level of SREMG over P1–P5, or in the rate of increase of SREMG.

The qualitative evaluation of the findings obtained in two individual subjects (Fig. 5) was supported quantitatively by statistical analysis of the results of all subjects. Initial posture did not have a main effect on the peak SREMG level during the push-off in any of the muscles ( $P > 0.05$ , results not shown), but it did have a main effect on SREMG onsets (Table 2). There was a main effect of initial posture on SREMG onsets of the plantarflexors, and pairwise comparisons revealed that for Gas all differences were statistically significant (P1 < P2 < P3 < P4 < P5,  $P < 0.05$ ), while for Sol almost all differences were statistically significant (P1 < P2 < P3 < P4 = P5,  $P < 0.05$ ); the greater the distance over which CM was raised during the push-off, the later the SREMG onsets of the plantarflexors occurred. There was also a main effect of initial posture on SREMG onsets of Rec, but pairwise comparisons revealed that the SREMG onset of this muscle only differed between P1 and P2–P4, with SREMG onset of Rec relative to that of Glu occurring later in the latter four conditions.

*Jumps of the simulation model.* Figure 6 presents stick diagrams at selected instants during the optimal jumps of the model from P2 and P5, as well as average stick diagrams of the jumps of the subjects from P2 and P5. Although only the height achieved by CM had been used in the optimization criterion, the kinematics and kinetics of the simulated jumps were very similar to those of the jumps by the subjects. To quantify the deviation in kinematics, we determined in each condition for each body segment at each time sample the error in angle, i.e.,

Table 1. Selected variables describing squat jumps of the subjects and maximum-height jumps of the simulation model from initial postures P1–P5

Variable	Unit	P1	P2	P3	P4	P5	F-Ratio
<i>Jumps of the subjects</i>							
$z_{CM,start}$	m	-0.12 ± 0.03	-0.18 ± 0.03	<b>-0.25 ± 0.04</b>	-0.32 ± 0.05	-0.39 ± 0.06	207.0*
$z_{CM,to}$	m	0.08 ± 0.02	0.09 ± 0.02	<b>0.08 ± 0.04</b>	0.09 ± 0.02	0.09 ± 0.02	1.8
$z_{CM,max}$	m	0.36 ± 0.06	0.40 ± 0.05	<b>0.41 ± 0.05</b>	0.42 ± 0.05	0.43 ± 0.05	13.4*
$t_{push-off}$	ms	194 ± 20	243 ± 38	<b>286 ± 39</b>	332 ± 48	384 ± 49	62.8*
<i>Maximum-height jumps of simulation model</i>							
$z_{CM,start}$	m	-0.15	-0.23	<b>-0.28</b>	-0.33	-0.42	
$z_{CM,to}$	m	0.08	0.07	<b>0.07</b>	0.07	0.07	
$z_{CM,max}$	m	0.31	0.37	<b>0.40</b>	0.42	0.45	
$t_{push-off}$	ms	230	266	<b>289</b>	323	421	

Values for subjects are means ± SD of selected variables describing the squat jumps performed by the subjects ( $n = 8$ ) from initial postures P1–P5. SD was calculated of 8 values, one for each subject, with each value being the mean over 4 jumps of that subject from a given posture. In P3 (bold) the subjects jumped from their preferred initial posture.  $z_{CM,start}$ , height of the center of mass of the body at the start of the jump relative to standing upright;  $z_{CM,to}$ , height of the center of mass of the body at takeoff relative to standing upright;  $z_{CM,max}$ , height of the center of mass of the body at the apex of the jump relative to standing upright;  $t_{push-off}$ , push-off duration, defined as the time interval between the onset of the increase in the vertical ground reaction force (for detection see Fig. 2) and the instant of takeoff. \*Main effect of initial posture occurred ( $P < 0.05$ ). Values for simulation model are for maximum-height squat jumps of the model from the initial postures P1–P5 observed in the subjects.

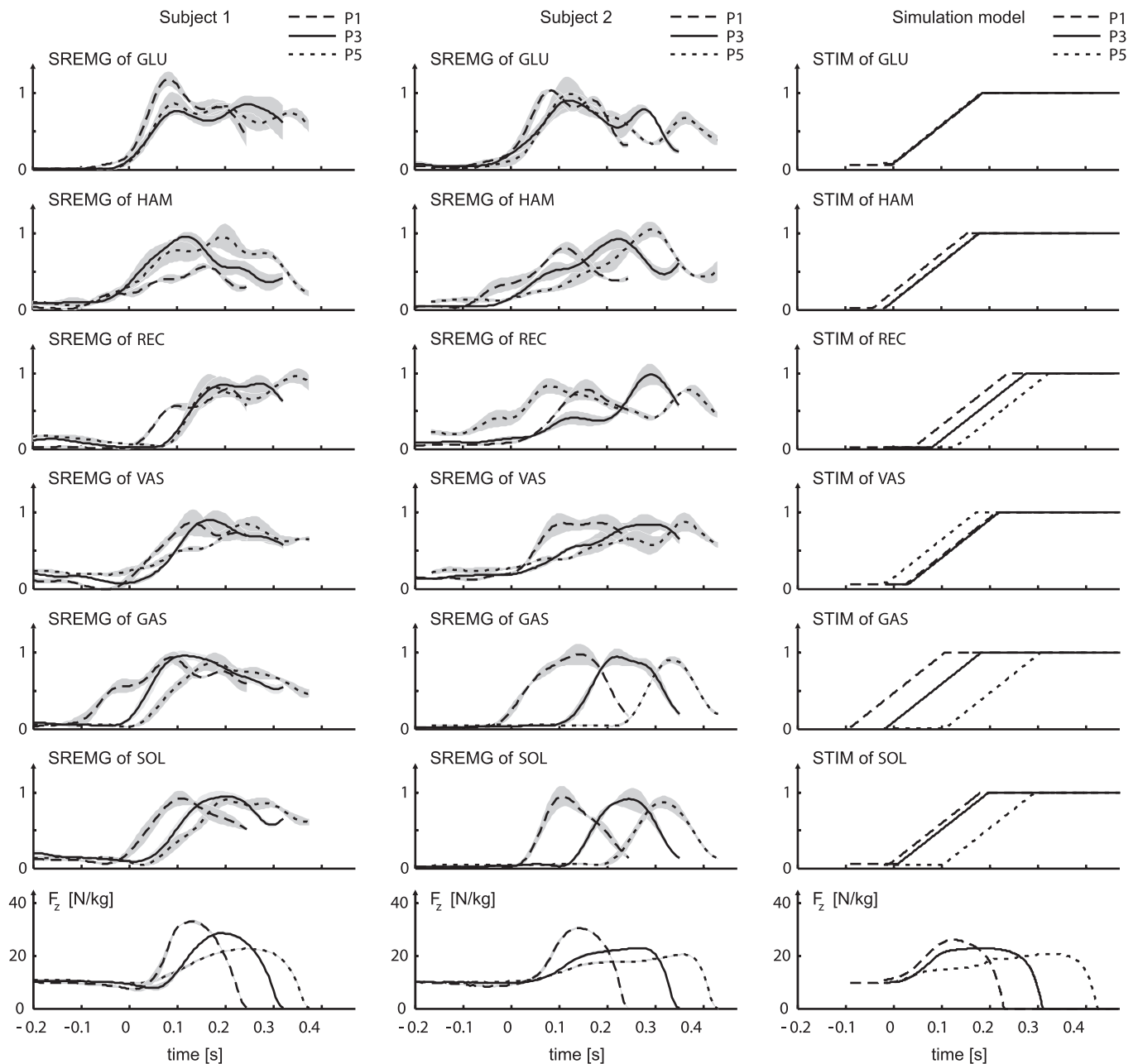


Fig. 5. *Left and center*: time histories of SREMG and  $F_z$  for jumps of 2 subjects from initial postures P1, P3, and P5, with P3 (bold solid lines) being the preferred posture. Each curve represents the mean result of 4 individual jumps from 1 initial posture, calculated after alignment of these individual jumps at takeoff, and the shaded area indicates the SE. SREMG levels have been expressed as fraction of the maximum level found in the 4 P3 trials. Time is expressed relative to the instant that SREMG onsets of Glu occurred, as defined in Fig. 2. *Right*: time histories of muscle stimulation (Stim) and  $F_z$  of maximum-height jumps of the simulation model from initial postures P1, P3, and P5. Time is expressed relative to the instant that Stim onset of Glu occurred.

the difference between the segment angle in the simulated jump and the mean segment angle of the jumps of the subjects. Subsequently, we calculated in each condition per body segment the root mean square (RMS) of the error over all time samples. The highest RMS errors in angles of HAT and thigh occurred in P4 and were 0.093 and 0.101 rad, respectively; the highest RMS errors of shank and foot occurred in P1 and were 0.073 and 0.056 rad, respectively. Relative to the height of CM in upright standing, the height of CM in the initial posture was slightly less in the model than in the subjects (Table 1), because of small differences in anthropometrics between the

model and the group of subjects participating in this study. However, relative to P3, the variations in initial height of CM among initial postures were similar (+13 cm, +5 cm, -5 cm, and -14 cm for P1, P2, P4, and P5, respectively). The average jump height of the model was also similar to that of the subjects, but the variation over initial postures was larger in the model: the model was not able to jump as high as the subjects in P1 and P2 and surpassed the average jump height of the subjects in P5.

Figure 5, *right*, presents time histories of Stim and  $F_z$  for maximum-height jumps of the model from initial postures P1,



Table 2. SREMG onsets in squat jumps performed by subjects from initial postures P1–P5

Muscle	P1	P2	P3	P4	P5	F-Ratio
Ham	-36±71	-4±83	<b>-14±65</b>	3±69	0±62	1.5
Rec	15±31	54±55	<b>67±61</b>	69±75	8±108	3.1*
Vas	5±23	30±48	<b>40±60</b>	10±78	-7±105	1.6
Gas	-82±58	-11±80	<b>51±83</b>	86±88	114±84	60.3*
Sol	-21±54	17±58	<b>56±63</b>	78±78	90±71	15.4*

Values (in ms) are means ± SD of smoothed, rectified electromyogram (SREMG) onsets (for detection, see Fig. 2) in the squat jumps performed by the subjects ( $n = 8$ ) from initial postures P1–P5. All SREMG onsets are expressed relative to the SREMG onset of gluteus maximus. SD was calculated over 8 values, one for each subject, with each value being the mean over 4 jumps of that subject from a given posture. In P3 (bold) the subjects jumped from their preferred initial posture. Ham, hamstrings (m. biceps femoris, long head); Rec, rectus femoris; Vas, vastus lateralis; Gas, gastrocnemius, Sol, soleus. \*Main effect of initial posture occurred ( $P < 0.05$ ).

P3, and P5, to be compared with time histories of SREMG and  $F_z$  of individual subjects (Fig. 5, left and center). Overall, we felt that the model reproduced the salient characteristics of the jumps of the subjects quite successfully. The optimal set of Stim onsets for jumps from the different initial postures is shown in Fig. 7, right. The way in which SREMG onsets changed of the subjects with initial posture was similar to the way in which optimal Stim onsets for the simulation model changed with initial posture (Fig. 7, left).

The question may be raised as to what extent the selection of muscle contributions to the joint moments in the equilibrium initial posture affects the pattern of optimal Stim onsets. Remember that our reference approach to setting the initial Stim levels was as follows: we had the biarticular Ham, Rec, and Gas produce a negligible force of 100 N regardless of initial posture, and we calculated for each initial posture the Stim levels (henceforth referred to as Stim<sub>reference</sub>) of the monoarticular Glu, Vas, and Sol that ensured equilibrium of the system as a whole. However, analysis of the SREMG levels of the subjects in P1–P5 revealed a main effect of initial posture on initial SREMG level of the biarticular Ham and Rec (as well as on the monoarticular Vas and Sol), with SREMG level increasing from P1 to P5. To investigate whether the choice of initial Stim levels affected the pattern of optimal Stim onsets, we tried out an alternative approach to setting initial Stim levels and reoptimized for P1–P5. In the alternative approach, in each initial posture, Ham received Stim<sub>reference</sub> of Glu in that posture, Rec received Stim<sub>reference</sub> of Vas, Gas received Stim<sub>reference</sub> of Sol, and the Stim levels of the monoarticular Glu, Vas, and Sol were recalculated to ensure equilibrium of the system as a whole. In this approach, the initial forces of the biarticular muscles were much larger than 100 N (up to 1,500 N in Ham and up to 1,100 N in Rec and Gas), and they varied with initial posture. Nevertheless, the pattern of optimal Stim onsets was only minimally affected. In fact, the differences among P1–P5 in Stim onsets of Gas and Sol became even more pronounced (relative to the solutions shown in Fig. 7, right, these muscles switched “on” ~15 ms earlier in P1 and ~10 ms later in P5). It seems safe to conclude, therefore, that the main outcome of this study was not affected by the selection of muscle contributions to the joint moments in the equilibrium initial posture.

Figure 8 presents jump heights of the model (Fig. 8, A–C) obtained with the three different control strategies, as well as jump heights of the subjects (Fig. 8D) for comparison. The top of each bar in Fig. 8 pertaining to the model is located at the maximum height that could be obtained from the initial posture

indicated (values in Table 1). Each bar has been filled to the height actually realized from the initial posture with a particular control strategy, so the white area can be interpreted as a deficit in jump height. The Opt-P3 strategy (Fig. 8A) by definition produced maximum jump height in P3, but when evaluated for the other postures jump height dropped substantially, in P5 by >18 cm. The CTW strategy (Fig. 8B), in which one set of Stim onsets was used for all jumps, produced jump heights that were close to maximal for jumps from P1–P3, in accordance with findings reported previously (23). However, for initial postures P4 and P5, jump height was substantially below maximum (up to 13 cm in P5, which was 1 of the 3 postures that had been used in finding the Stim onsets). Inspired by the adjustments that we observed in SREMG onset of the subjects and using an approach similar to that used to find the CTW solution, we performed an additional optimization (using P1, P3, and P5) to find a PF-Shift solution, in which the Stim onsets of Glu, Ham, Vas, and Rec were the same for all initial postures, while Stim onsets of Sol and Gas relative to that of Glu varied depending on initial height of CM (Eq. 1). With an optimal value for parameter  $d$  of  $-0.485$  s/m the results were surprisingly good (Fig. 8C); jump height was deficient by only 2.1 cm when jumping from P1, and even less when jumping from the other initial postures (Fig. 8C). It should be noted that P2 and P4 were not used in the optimization, so that the performance of the model in these jumps gives an impression of the generalizability of the PF-Shift strategy.

## DISCUSSION

The purpose of this study was to gain insight into the control strategy that humans use in vertical jumping. For this purpose, we had subjects perform squat jumps from different initial postures, and we simulated squat jumps from these same initial postures with a forward dynamic model of the musculoskeletal system. Below, we first discuss the results of the experiments, showing that subjects adjusted their control to the initial posture. We then discuss the results of the simulations suggesting that the adjustments of the muscle activation patterns observed in the subjects were functional, i.e., contributed to achieving the greatest jump height possible from the given initial postures. Subsequently, we try to answer the question of why changing the initial posture requires adjustments of the EMG patterns from the perspective of jumping performance. Finally, we elaborate on possible control strategies used by

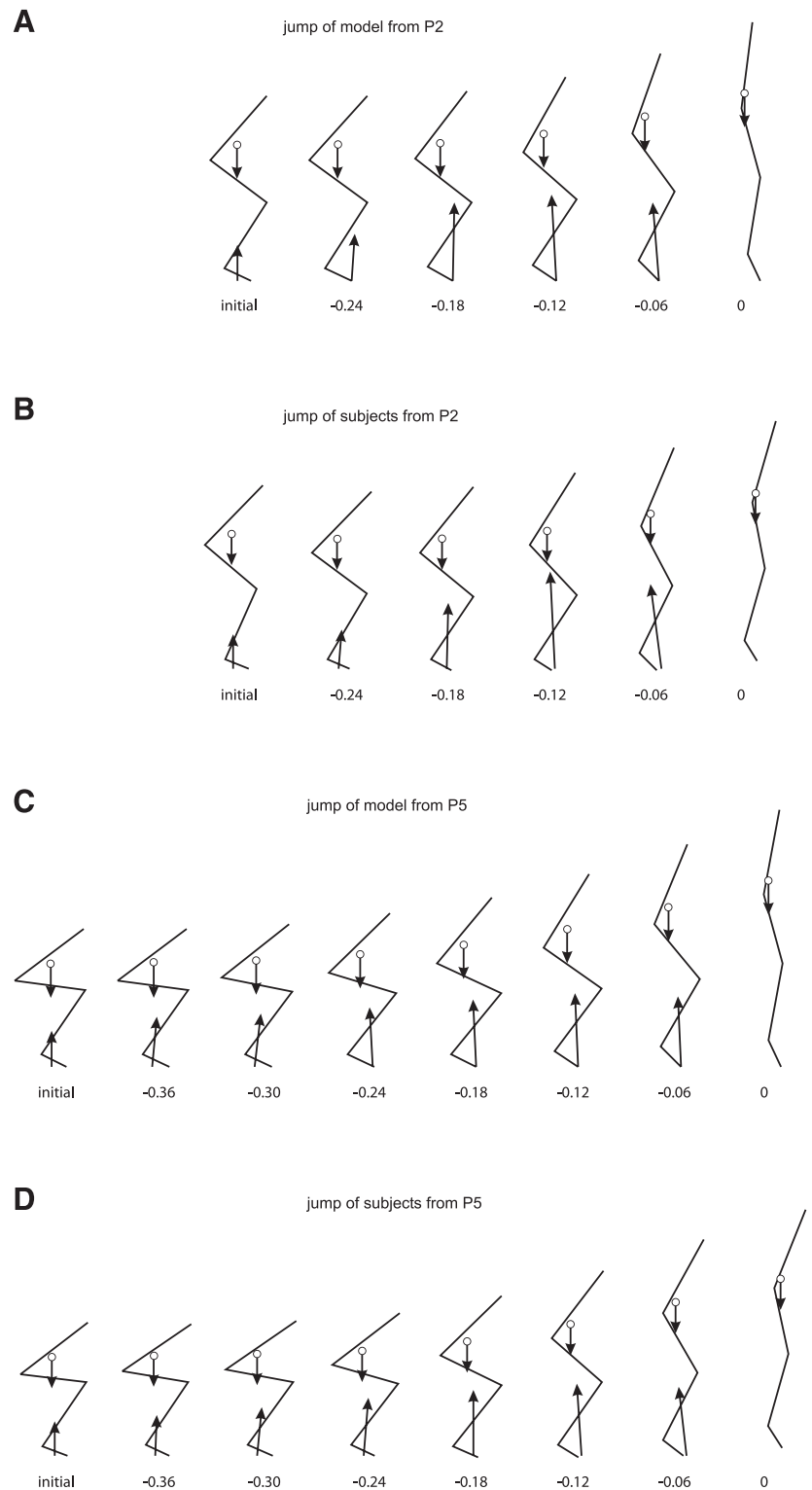


Fig. 6. Stick diagrams of average body postures of the 8 subjects (*B* and *D*) and of the simulation model (*A* and *C*) for the push-off in jumps from P2 and P5. Arrows pointing upward represent the ground reaction force vector plotted with the origin in the center of pressure; arrows pointing downward represent the force of gravity, and are plotted with their origin in the center of mass (○). Time is expressed relative to the instant of takeoff (time = 0).

human subjects, primarily on the basis of the simulation results.

The experimental results leave no doubt that the subjects were able to perform well-coordinated squat jumps from initial postures that differed from the preferred initial posture. Despite the differences in vertical push-off distance and duration among P1–P5 (Table 1), the heights of CM at takeoff were

virtually identical (Table 1), and so were the corresponding body configurations (Fig. 4). Jump height increased by >5 cm from posture P1 to the preferred initial posture P3. While it cannot be excluded that this was due to poor coordination in the jump from P1, it seems plausible that the main reason was the short duration of the push-off in P1, preventing the muscles from reaching a maximal active state and producing maximum

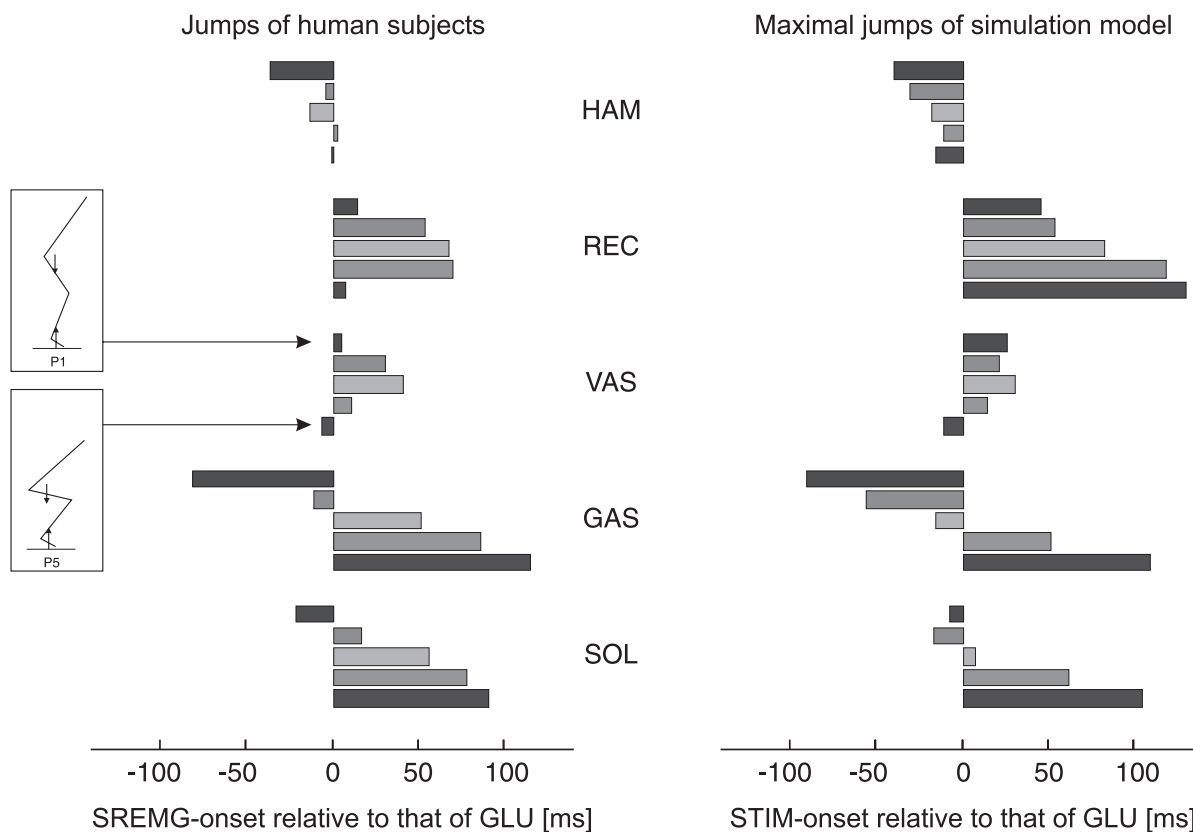


Fig. 7. *Left*: average SREMG onsets as defined in Fig. 2 for Ham, Rec, Vas, Gas, and Sol in the jumps of the subjects from initial postures P1–P5 ( $n = 8$ , see also Table 2); P3 was the preferred initial posture. All values are expressed relative to SREMG onset of Glu. *Right*: optimal set of Stim onsets for jumps of the simulation model from initial postures P1–P5. All values have been expressed relative to the Stim onset of Glu.

force and work (2). The increase in jump height from P3 to P5 was  $<1.5$  cm and not significant, which is in accordance with findings reported in other studies (3, 8). The experimental results also leave no doubt that subjects did in fact adjust their control to the initial posture. The adjustments were not in the amplitude of the neural input to the muscles, but in the onset of this neural input. Statistically significant shifts in SREMG onsets were found in the plantarflexors, and these shifts were very systematic: in P1 the SREMG onsets of Sol and Gas occurred before that of Glu, and from P2 to P4 they were further and further delayed to end  $>90$  ms after that of Glu in P5 (Table 2, Fig. 7). Obviously, we are not saying that individual subjects did not adjust the SREMG onsets of muscles other than the plantarflexors. Such adjustments occurred (see Fig. 5), but they were smaller than those in the plantarflexors and were not sufficiently systematic across subjects to be detected as statistically significant by the ANOVA. In any case, the data clearly show that the “control that works” strategy (23) is not supported.

To get an impression as to whether the shifts in SREMG onsets observed in the subjects were functional, we decided to compare them to changes in Stim onsets in optimal solutions for jumps of a simulation model. The model that we selected has been shown to reproduce the salient characteristics of various types of jumps of human subjects in previous studies (2). The same was true for the jumps of interest in the present study (Figs. 5 and 6), albeit that jump heights in P1 and P2 were below those of the subjects (Table 1). This may be

explained at least partly by the fact that especially in P1 several subjects (for example, *subject 1* in Fig. 5) could not help “cheating” by making a slight countermovement with an amplitude of 1–3 cm in terms of CM height, thereby allowing themselves to build up active state and boost their jump height; when the duration of the jump is small, a notable gain in jump height can be achieved by building up active state during a countermovement (2). The optimal Stim onsets varied to a significant extent among P1–P5, especially in the plantarflexors: for example, the Stim onset of Gas occurred 90 ms before that of Glu in P1 and 109 ms after that of Glu in P5. Analogous results were found by Selbie and Caldwell (21), who simulated countermovement jumps with a model that had joint moments as independent input; they also observed that the optimal sequence of onsets, in their case joint moment onsets, was dependent on the initial posture. When we compare the optimal set of Stim onsets for jumps from the different initial postures of the model with the SREMG onsets observed in the subjects (Fig. 7), two observations may be made: 1) the overall sequence in Stim onsets of the model was very similar to the overall sequence in SREMG onsets in the subjects and, more importantly, 2) the shifts in Stim onsets across the optimal solutions for jumps from P1–P5 were very similar to the shifts in SREMG onsets found in the subjects. The latter leads us to conclude that the adjustments in SREMG patterns to the initial posture observed in the subjects were in fact functional; they did contribute to achieving the greatest jump height possible from the given initial postures. No doubt some readers will feel

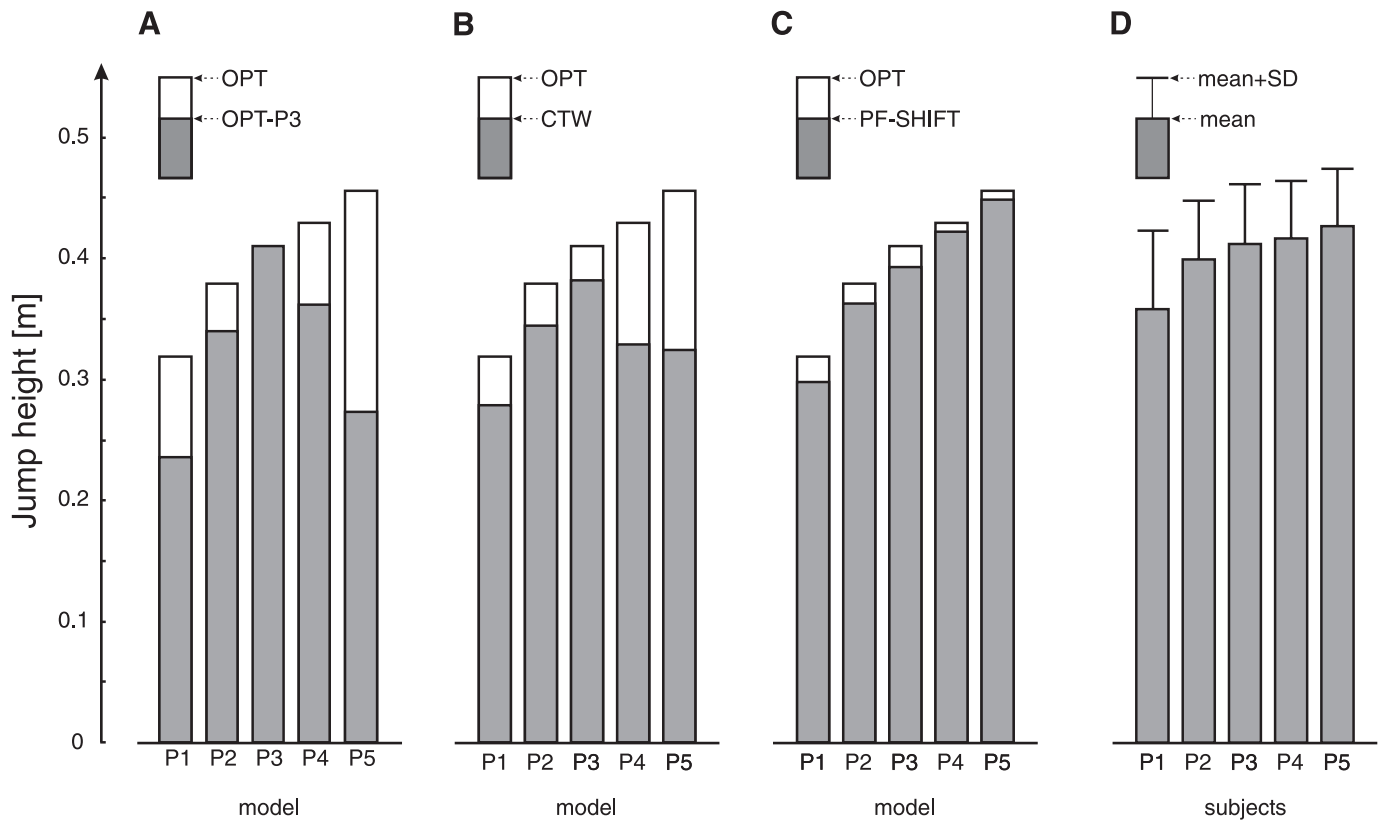


Fig. 8. Jump heights achieved by the simulation model from initial postures P1–P5 using different control strategies (A–C) as well as jump heights achieved by the subjects (D). The top of each bar pertaining to the model is located at the maximum height that could be achieved from the initial posture indicated (values in Table 1). Each bar has been filled to the height actually realized from the initial posture using a particular control strategy, so the white area can be interpreted as a deficit in jump height. Three different control strategies were used for the model. 1) Opt-P3 (A): the optimal combination of Stim onsets for P3 (bold) was simply evaluated for the other initial postures. 2) CTW (B): 1 “control that works” combination of Stim onsets was found that maximized the average jump height achieved over P1, P3, and P5; this combination was simply evaluated for P2 and P4, which had not been used in the optimization. 3) PF-Shift (C): a combination of Stim onsets and a parameter  $d$  was found that maximized the average jump height achieved from P1, P3, and P5 (bold), with  $d$  transforming the initial height of the center of mass into a shift of the Stim onsets of the plantarflexors relative to the other muscles (see Eq. 1); again, the combination found was applied to P2 and P4, which had not been used in the optimization.

that such a conclusion should not be drawn on the basis of a qualitative analysis, and that a quantitative comparison of Stim onsets with SREMG onsets should first be made. In our opinion, however, it would be presumptuous to try and make such a comparison, because our model was designed merely to capture the salient features of the musculoskeletal system relevant for jumping (see Figs. 5 and 6) and not to represent in full detail the real system of the subjects participating in this study.

In the subjects, the adjustments of control to initial posture were achieved primarily via modulation of the onset of plantarflexor activity: the lower CM was in the initial posture, the later the onset of plantarflexor activity occurred. We concluded that these adjustments were functional, because similar adjustments were found in the optimal control solutions for the simulation model. We may go one step further and raise the question of why these adjustments contributed to achieving the greatest jump height possible from the different initial postures. An attractive hypothesis is the following. As explained elsewhere (4), part of the challenge in jumping is to strike a compromise between minimizing the angular velocities of segments to keep the shortening velocities of the muscles as low as possible, so that the muscles can produce as much work as possible, and maximizing the angular

velocities of segments to achieve the highest possible vertical velocity of CM. Striking this compromise requires that the angular acceleration of the proximal segments be restrained in the last part of the push-off by angular acceleration of the distal segments (leading to upward acceleration of the proximal segments, with the moments of the associated inertial forces helping to restrain the angular accelerations of the proximal segments). Angular acceleration of the distal segments during the last part of the push-off is only possible if these segments have not been rotated earlier during the push-off; consequently, the lower the height of CM in the initial posture and hence the longer the duration of the push-off, the more the onset of plantarflexors needs to be delayed.

The reader might wonder at this point whether perhaps the adjustments of control to initial posture have to do with differences among P1–P5 in the initial horizontal distance from CM to the toes. After all, there is a need to bring CM over the toes during the push-off, and the onset of the plantarflexors relative to Glu affects the horizontal motion of CM (5). However, consideration of differences in the initial horizontal position of CM leads to predicted adjustments of control that are opposite to the adjustments actually found. Let us start our argument by noting that if CM is behind the toes in the initial posture, activation of the plantarflexors will lead to backward

acceleration of CM (5). Thus one would expect that if CM were more posterior relative to the toes in the initial posture the plantarflexors would have to be activated later relative to the hip extensors, to allow for sufficient forward motion of CM. We confirmed this expectation by performing two additional optimizations: one for an initial posture  $P3_{\text{post}}$ , obtained by rotating the model in P3 anticlockwise about the ankle joints so that CM was 1.5 cm further backwards relative to the toes, and the other for an initial posture  $P3_{\text{ant}}$ , obtained by rotating the model in P3 clockwise about the ankle joints so that CM was 1.5 cm closer to the toes. And indeed, in the optimal control solution for  $P3_{\text{post}}$  the plantarflexors were activated later relative to Glu than in the optimal solution for  $P3_{\text{ant}}$  (Sol by 24 ms, Gas by 19 ms). Thus if the delay in onset of the plantarflexors in P5 relative to P1 were related to the initial horizontal distance between CM and the toes, this distance should be greater in P5 than in P1. In reality, however, it was smaller: on average the subjects had their center of pressure, and hence the horizontal position of CM, 3 cm closer to the toes in P5 than in P1 (Fig. 4). Thus it seems safe to say that the adjustments of control were not related to differences in horizontal position of CM; in fact, if the horizontal distance between CM and the toes had not differed among initial postures, the adjustments in onset of the plantarflexors would have been even bigger than those reported in Fig. 5, not smaller. Our interpretation remains, therefore, that the adjustments of control are related to the need to restrain the angular acceleration of the proximal segments during the last part of the push-off, as argued above.

According to the results of this study, human subjects use a control strategy for squat jumping that is smarter than the previously proposed “control that works” strategy (23), which was found to break down in P4 and P5 anyway (Fig. 8B). This does not automatically mean, however, that the brain is using a general-purpose, structural dynamics model. Inspired by the adjustments in SREMG onsets observed in the subjects, we explored with the simulation model the effectiveness of what we called the PF-Shift strategy, in which the delay of the Stim onset of the plantarflexors relative to Glu was a function of the height of CM in the initial posture. Obviously, we could also have chosen to make the delay depend on other variables, such as individual joint angles; we merely selected initial CM height for its heuristic value. The alternative strategy (Fig. 8C) was by far superior to the “control that works” strategy (Fig. 8B); in fact, jump height achieved with the PF-Shift strategy (Eq. 1) in P1, P3, and P5 was within 2.1 cm of the maximum height that could be achieved from these initial postures, and the same was true when this simple strategy was used to generate Stim onsets for P2 and P4, which had not been used in the optimization (Fig. 8). Compared with the “control that works” strategy only one extra parameter needs to be learned in the PF-Shift strategy. We tried to represent the PF-Shift strategy in a simple backpropagation network consisting of only one input neuron (initial height of CM), three hidden neurons, and six output neurons (Stim onsets, 1 for each of the 6 muscles). After this network was trained with the sets of Stim onsets found for P1, P3 and P5, the network could not only reproduce these sets on the basis of the initial height of CM but could also interpolate and produce successful sets of Stim onsets for P2 and P4. Thus, to explain how subjects adjust their muscle stimulation patterns to the initial posture

in squat jumping, there is no need to assume that the brain has access to inverse kinematics models of the musculoskeletal system for trajectory planning and inverse dynamics models for computation of the time-varying joint moments and muscle stimulation patterns that are necessary to realize desired trajectories. A parsimonious heuristic model, essentially consisting of a lookup table that maps initial posture to Stim onsets, with interpolation between neighboring entries, seems sufficient.

In the present study, the subjects were not allowed to practice jumping from postures other than P3. In future studies, further insight into the control strategy that humans use in jumping might perhaps be gained by defining a set of initial postures, having subjects make many practice jumps from only a few of the initial postures in the set, and measuring the effects on their performance in jumps from all postures in the set.

#### ACKNOWLEDGMENTS

We thank Dr. Arne Ridderikhoff for his insightful contribution to discussions on issues addressed in this study and for his valuable comments on a draft of this paper.

#### REFERENCES

1. Atkeson CG. Learning arm kinematics and dynamics. *Annu Rev Neurosci* 12: 157–183, 1989.
2. Bobbert MF, Casius LJ. Is the effect of a countermovement on jump height due to active state development? *Med Sci Sports Exerc* 37: 440–446, 2005.
3. Bobbert MF, Gerritsen KG, Litjens MC, Van Soest AJ. Why is countermovement jump height greater than squat jump height? *Med Sci Sports Exerc* 28: 1402–1412, 1996.
4. Bobbert MF, van Soest AJ. Why do people jump the way they do? *Exerc Sport Sci Rev* 29: 95–102, 2001.
5. Bobbert MF, van Zandwijk JP. Dynamics of force and muscle stimulation in human vertical jumping. *Med Sci Sports Exerc* 31: 303–310, 1999.
6. Bobbert MF, van Zandwijk JP. Sensitivity of vertical jumping performance to changes in muscle stimulation onset times: a simulation study. *Biol Cybern* 81: 101–108, 1999.
7. Clauser CE, McConville JT, Young JW. *Weight, Volume, and Center of Mass of Segments of the Human Body*. AMRL Technical Report (NTIS No. AD-710-622). Wright-Patterson Air Force Base, OH: Aerospace Medical Research Laboratory, 1969, p. 69–70.
8. Domire ZJ, Challis JH. The influence of squat depth on maximal vertical jump performance. *J Sports Sci* 25: 193–200, 2007.
9. Dounskaia N. The internal model and the leading joint hypothesis: implications for control of multi-joint movements. *Exp Brain Res* 166: 1–16, 2005.
10. Ebashi S, Endo M. Calcium ion and muscle contraction. *Prog Biophys Mol Biol* 18: 123–183, 1968.
11. Gottlieb GL, Agarwal GC. Response to sudden torques about ankle in man: myotatic reflex. *J Neurophysiol* 42: 91–106, 1979.
12. Hatze H. A myocybernetic control model of skeletal muscle. *Biol Cybern* 25: 103–119, 1977.
13. Huijing PA. Muscular force transmission necessitates a multilevel integrative approach to the analysis of function of skeletal muscle. *Exerc Sport Sci Rev* 31: 167–175, 2003.
14. Kawato M. Internal models for motor control and trajectory planning. *Curr Opin Neurobiol* 9: 718–727, 1999.
15. Kawato M, Furukawa K, Suzuki R. A hierarchical neural-network model for control and learning of voluntary movement. *Biol Cybern* 57: 169–185, 1987.
16. Kistemaker DA, Van Soest AJ, Bobbert MF. Is equilibrium point control feasible for fast goal-directed single-joint movements? *J Neurophysiol* 95: 2898–2912, 2006.
17. Ridderikhoff A, Batelaan JH, Bobbert MF. Jumping for distance: control of the external force in squat jumps. *Med Sci Sports Exerc* 31: 1196–1204, 1999.

18. **Schmidt RA.** *Motor Control and Learning: A Behavioral Emphasis.* Champaign, IL: Human Kinetics, 1982, p. 77–100.
19. **Schmidt RA.** Schema theory of discrete motor skill learning. *Psychol Rev* 82: 225–260, 1975.
20. **Schweighofer N, Arbib MA, Kawato M.** Role of the cerebellum in reaching movements in humans. I. Distributed inverse dynamics control. *Eur J Neurosci* 10: 86–94, 1998.
21. **Selbie WS, Caldwell GE.** A simulation study of vertical jumping from different starting postures. *J Biomech* 29: 1137–1146, 1996.
22. **Van Soest AJ, Bobbert MF.** The contribution of muscle properties in the control of explosive movements. *Biol Cybern* 69: 195–204, 1993.
23. **Van Soest AJ, Bobbert MF, Van Ingen Schenau GJ.** A control strategy for the execution of explosive movements from varying starting positions. *J Neurophysiol* 71: 1390–1402, 1994.
24. **Van Soest AJ, Casius LJ.** The merits of a parallel genetic algorithm in solving hard optimization problems. *J Biomech Eng* 125: 141–146, 2003.
25. **van Zandwijk JP, Bobbert MF, Harlaar J.** Predictions of mechanical output of the human M. triceps surae on the basis of electromyographic signals: the role of stimulation dynamics. *J Biomech Eng* 122: 380–386, 2000.
26. **Wolpert DM, Miall RC, Kawato M.** Internal models in the cerebellum. *Trends Cognit Sci* 2: 338–347, 1998.

