OPTIMAL MUSCULAR COORDINATION STRATEGIES FOR JUMPING

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Abstract—This paper presents a detailed analysis of an optimal control solution to a maximum height squat jump, based upon how muscles accelerate and contribute power to the body segments during the ground contact phase of jumping. Quantitative comparisons of model and experimental results expose a proximal-to-distal sequence of muscle activation (i.e. from hip to knee to ankle). We found that the contribution of muscles dominates both the angular acceleration and the instantaneous power of the segments. However, the contributions of gravity and segmental motion are insignificant, except the latter become important during the final 10% of the jump. Vasti and gluteus maximus muscles are the major energy producers of the lower extremity. These muscles are the prime movers of the lower extremity because they dominate the angular acceleration of the hip toward extension and the instantaneous power of the trunk. In contrast, the ankle plantarflexors (soleus, gastrocnemius, and the other plantarflexors) dominate the total energy of the thigh, though these muscles also contribute appreciably to trunk power during the final 20% of the jump. Therefore, the contribution of these muscles to overall jumping performance cannot be neglected. We found that the biarticular gastrocnemius increases jump height (i.e. the net vertical displacement of the center of mass of the body) by as much as 25%. However, this increase is not due to any unique biarticular action (e.g. proximal-to-distal power transfer from the knee to the ankle), since jumping performance is similar when gastrocnemius is replaced with a uniaxial ankle plantarflexor.

INTRODUCTION

By analysis of experimental data, several investigators have attempted to gain insight into intermuscular coordination during vertical human jumping (Gregoire et al., 1984; Fukashiro and Komi, 1987; van Ingen Schenau et al., 1987, Bobbert and van Ingen Schenau, 1988). Because non-invasive techniques cannot estimate muscle force accurately, previous efforts have focused on manipulating experimentally measurable quantities (i.e. limb-segmental motions, ground reaction forces, and EMG data) to infer action of muscles on the skeletal system. A complementary approach involves augmenting experimental results with predictions from a model of the same task. In this event, the experimental findings can be used not only to guide model development, but also to gain confidence in interpretations derived from the predictions of the model.

Recent work by Bobbert and van Ingen Schenau (1988) and Bobbert et al. (1986a,b) are typical examples of how experimental data are used to infer action of muscles in a motor task. A major hypothesis forwarded by these studies is that jumping performance depends heavily upon the action of biarticular muscles. Specifically, proximal-to-distal power transfer is believed to effect an efficient conversion of rotational motion into translation of the center of mass of the body (Gregoire et al., 1984; van Ingen Schenau et al., 1987). The mechanism by which this is accomplished is purported to be the timely activation of rectus femoris (RF) and gastrocnemius (GAS) just prior to lift-off. Activation of RF supposedly decreases the angular acceleration of the trunk, which, combined with the onset of knee extension, results in power being transferred from the hip to the knee (Bobbert and van Ingen Schenau, 1988). Similarly, activation of GAS near lift-off is said to transfer power generated by the knee extensors (e.g. vasti) to the ankle joint (Bobbert and van Ingen Schenau, 1988). Consequently, Bobbert and van Ingen Schenau (1988) claim that the human musculoskeletal system would be equipped with larger (and therefore heavier) knee extensors and ankle plantarflexors in the absence of biarticular muscles.

Previously (Pandy et al., 1990), we presented a dynamical model of the human musculoskeletal system and used it to compute the optimal controls, body-segmental motions, muscle forces, and muscle activations for a maximum-height squat jump. By analysing this optimal control solution, the present paper aims to provide a better understanding of how intermuscular control and musculotendon dynamics coordinate jumping. Firstly, we compare the response of the model with experimental data recorded from several subjects performing a maximum-height squat jump. After confirming the ability of the model to accurately reproduce the major features of a maximum-height squat jump, we then analyse in detail the optimal control solution. Specifically, our objectives are to quantify the role of both uni- and biarticular
musculotendon actuators during jumping, focusing upon the contribution of muscles to the vertical acceleration and instantaneous power of each segment during the ground contact phase. An understanding of how muscles contribute to power of a segment is important because the integral of power over time determines the kinetic energy of the segment at lift-off, which affects jump height (see equation (7) in Pandy et al., 1990).

METHODS

Experiments with human subjects

Five normal adult males (age 22 ± 2 yr, height 185 ± 3 cm, and body mass 78 ± 4 kg) were chosen as subjects for these experiments. From an initial squatting position, and with hands on hips, each subject performed a two-legged squat jump under the command ‘jump as high as possible’. For three consecutive jumps, force-plate, limb motion, and electromyographic (EMG) data were recorded simultaneously.

Ground reaction forces were measured using an AMTI six-component, strain-gaged force platform, having a first natural frequency of 500 Hz (vertical channel). Horizontal and vertical reactions were sampled at 1000 Hz, as were analog EMG data. Pairs of Ag–AgCl surface electrodes (center-to-center distance 3 cm; circumference 12 mm) were attached to the right lower extremity of each subject to record activity in seven muscle groups: soleus (SOL), gastrocnemius (GAS), tibialis anterior (TA), vasti (VAS), hamstrings (HAMS), rectus femoris (RF), and glutaeus maximus (GMAX) [see Fig. 1 in Pandy et al. (1990)]. The electrical signals were amplified (Grass Instruments Inc., type P511K), and then band-pass filtered (cutoff frequencies 50 Hz and 400 Hz) to minimize errors introduced by noise and motion artifact.

To record the limb-segmental angular displacements of each subject, seven light-emitting diodes (LEDs) were positioned over six bony prominences: fifth metatarsophalangeal joint, calcaneus, lateral malleolus, lateral epicondyle, greater trochanter, and glenohumeral joint. Together these landmarks defined four body segments: the foot, shank, thigh, and trunk. Using the Selcom Selspot II active-marker system, absolute displacements were recorded at 312 Hz (i.e. displacements of each landmark were referenced to a global frame attached to the force platform). All post-processing of the data was carried out on a PDP-11/34 digital computer.

Contribution of muscles to the acceleration and power of segments

The dynamical equations of motion can be used to find the contribution of a muscle to the acceleration of the segments and mass centroid (Gordon et al., 1986; Zajac et al., 1986; Hatze, 1987; Zajac, 1987; Zajac and Gordon, 1989). The equations can also be used to calculate the contribution of muscle to the instantaneous power of segments (e.g. Aleshinsky, 1986). Appropriate to jumping, and using the dynamical equations of motion for the four-segment, planar, skeletal model, the vector of limb-segmental angular accelerations is (Pandy et al., 1990):

\[
\ddot{\theta} = A(\theta)^{-1} \left\{ B(\theta)\dot{\theta}^2 + C(\theta) + DM(\theta)P^T + T(\theta, \dot{\theta}) \right\}. \tag{1}
\]

Each element of the vector \( DM(\theta)P^T \) is the sum of the segmental torques developed by the muscles attaching to or crossing the corresponding body segment. The total contribution of muscles to the vector of segmental accelerations \( \ddot{\theta}_m \) is thus:

\[
\ddot{\theta}_m = A(\theta)^{-1} \cdot DM(\theta)P^T. \tag{2}
\]

Since \( A(\theta)^{-1} \) is, in general, non-diagonal, notice that each muscle force accelerates all body segments. Thus, muscles not directly attached to or spanning a segment still contribute to its acceleration (see Zajac and Gordon (1989) for review).

Knowing the total instantaneous power of a segment (\( \dot{E} \equiv dE/dt, \) which is the time rate of change of the total mechanical energy of a segment) (Meriam, 1975), we computed the contribution of muscles, gravity, and segmental motion (‘inertia’) to the instantaneous segmental power. For example, the contributions to trunk power are (see Appendix):

\[
\dot{E}_{\text{inertia}} = mu(\theta)A(\theta)^{-1} \left\{ B(\theta)\dot{\theta}^2 + mu(\theta, \dot{\theta}) \cdot v_4 \right\}
\dot{E}_{\text{gravity}} = [mg_j + mu(\theta)A(\theta)^{-1}C(\theta)] \cdot v_4
\dot{E}_{\text{muscle}} = [mu(\theta)A(\theta)^{-1}DM(\theta)P^T] \cdot v_4 + F_{RF} \cdot (v_{RF})_{rel} + F_{HAM} \cdot (v_{HAM})_{rel} + F_{GMAX} \cdot (v_{GMAX})_{rel} \tag{3}
\]

Note that \( \dot{E}_{\text{inertia}} \) contains the contributions from the centrifugal and Coriolis forces due to the motion of the body [i.e. the vectors \( B(\theta)\dot{\theta}^2 \) and \( mu(\theta, \dot{\theta}) \cdot v_4 \)], whereas \( \dot{E}_{\text{gravity}} \) results from the gravitational force. \( \dot{E}_{\text{muscle}} \) on the other hand, is the net contribution of muscles to the instantaneous power of the trunk. The net contribution of muscles is composed of contributions from those intersegmental forces acting at the hip joint that arise from muscle forces, as well as from ‘direct’ muscular forces that arise from the insertion of muscle on that segment [e.g. \( F_{RF} \cdot (v_{RF})_{rel} \) (Aleshinsky, 1986)]. Since the matrix \( A(\theta)^{-1} \) appears throughout equation (3), this means that muscles not directly attached to the trunk still contribute to its power. This result follows directly from equation (1), where \( A(\theta)^{-1} \) couples gravity, inertia forces, and muscle forces into all body-segmental motions.

RESULTS

Comparison of model and experiment

The foot, shank, thigh, and trunk angles of the model are plotted in Fig. 1 (heavy solid lines), with the shaded areas representing the range of the subjects’
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Fig. 1. Model (heavy solid lines) and experimental (shaded areas and light solid lines) limb-segmental angular displacements during the ground contact phase of jumping (0–100%). The shaded areas represent the range of experimental data for five subjects performing a maximum-height squat jump, whereas the light solid lines are the computed means of these data. For each subject, 0% of ground contact time defines the instant that the vertical ground reaction force decreases to 95% of body weight. For the model, prior to and at 0% ground contact time, muscle forces are constant to maintain the body statically in the squat. All angles are defined in Fig. 2 of Pandy et al. (1990).

Fig. 2. Model (heavy solid lines) and experimental (shaded areas and light solid lines) ground reaction forces during the ground contact phase. The shaded areas represent the range of ground reaction forces generated by five subjects performing a maximum-height squat jump. The light solid lines are the computed means. Positive force indicates that the body is pushing downwards (top figure), or backwards (bottom figure). No significance should be attached to the two peaks at 75 and 95% of ground contact time in the horizontal ground reaction force of the model (heavy solid line).

In general, there is good agreement between model and experiment. The average jump height and lift-off time for the five subjects were 35 ± 5 cm and 0.60 ± 0.10 s respectively. Corresponding values for the model are 33 cm and 0.50 s. For each subject, 0% of ground contact time was taken to be the instant the vertical ground reaction force decreased to 95% of body weight. Those subjects who jumped higher than the model did so because of their ability to apply a vertical force to the ground for a longer period of time (thereby imparting a larger vertical impulse to the center of mass of the body).

The ground reactions predicted by the model (heavy solid lines in Fig. 2) are also in good agreement with those generated by our subjects. In both cases, peak vertical forces are approximately $2.2 \times$ body weight. Both show the existence of a countermovement prior to upward propulsion, which occurs during the first 40% of jump time (Fig. 2, vertical force; compare thin solid line with heavy solid line). Since the subjects were not told to jump 'straight up', but rather to 'jump as high as possible', it appears that the subjects chose to countermove their bodies because that causes them to jump higher, just as the model predicts. In addition, both the model and the subjects generate a biphasic horizontal ground reaction force (Fig. 2, horizontal force). The latter agreement is particularly encouraging since the horizontal ground force, by being only 30% of body weight, is presumably sensitive to the way the jump is executed.

There are, however, differences in the rates at which the ground reaction forces are applied (compare the light and heavy solid lines near lift-off). Specifically,
the model predicts a steeper increase in the vertical reaction during initial propulsion, together with a more rapid decrease prior to lift-off. Because the angular velocities of the limb segments in the model increase just prior to lift-off (Pandy et al., 1990), the vertical ground reaction decreases very rapidly in an attempt to maximize the impulse applied to the mass centroid. In reality, joint angular velocities decrease near lift-off (Bobbert and van Ingen Schenau, 1988), and thus the measured vertical reaction forces decrease sooner than predicted by our model.

Experimental EMG activity was found to agree qualitatively well with the computed optimal controls (e.g. Fig. 3). However, minor differences were found. For example, the optimal solution predicts GMAX to begin excitation at 30 % of ground contact time and to remain fully active until lift-off (heavy solid line in Fig. 3, GMAX). By comparison, recorded EMG data indicate very low activity of GMAX prior to lift-off (light wavy solid line in Fig. 3, GMAX), presumably to prevent hip hyperextension after lift-off (Bobbert and van Ingen Schenau, 1988). Further, our EMG results suggest that HAMS is activated at lift-off, whereas the optimal control solution predicts inactivity at this time (Fig. 3, HAMS).

Though the foot, shank, and thigh angles of the model compare well with measured data (Fig. 1(a), (b), and (c) show these results to be within 5°), a relatively large difference exists at the trunk [compare heavy and light solid lines, Fig. 1(d)]. The trunk of the model undergoes very little countermovement [less than 5°, Fig. 1(d)] prior to upward propulsion, whereas all our subjects countermove their upper bodies by as much as 10°. One reason why the trunk of the model moves little may be due to the one-segment representation for the trunk. Such a representation may indeed be an unrealistic simplification of body-segmental dynamics [e.g. see Hatze (1981a)], especially if spinal flexure is significantly utilized during upward propulsion. Taking this feature into account will require two or more segments to model the trunk, together with detailed representations of both upper- and lower-back musculature. Such changes will demand an appreciable increase in overall model complexity.

A second explanation for the absence of trunk countermovement in the model involves the parameters chosen to describe the musculotendon dynamics for the actuators spanning the hip (particularly GMAX). Specifically, countermovement may not be tolerated because of the inability of the model to generate sufficient hip moment. With the aim of strengthening the hip musculature of the model, we tried increasing the peak isometric strength of GMAX by 20 %. This increases muscle force (and therefore moment) generated in the range of hip-joint motion experienced during jumping. Unfortunately, increased hip strength has failed to produce the desired increase in countermovement of the trunk in the simulation. In our search to replicate trunk countermovement, we are currently altering the tendon slack lengths of hip muscles, which shift the moment-angle curves (Hatze, 1981b; Hoy et al., 1990). We are also increasing tendon compliance of hip muscles, though countermovement is unlikely to be found since hip muscles are stiff, in an absolute sense, and in a relative sense as well, compared to the muscles spanning either the ankle or knee (Zajac, 1989).

Intermuscular coordination
Since the response of the model replicates the major features of the jump, it can be analysed to understand coordination. We specifically aim to quantify the contribution of muscles to the vertical acceleration and the instantaneous power of the trunk during the ground contact phase. The reason for focusing on the trunk is that it represents approximately 70 % of total body mass. Though the results discussed above indicate that the model is imperfect in replicating the exact response of the trunk [Fig. 1(d)], the model does indeed generate levels and trajectories of horizontal
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Fig. 4. Contributions of all the muscles ('muscle'), gravity ('gravity'), and segmental motion ('inertia') to the total angular acceleration of the trunk (shaded area) computed from the model during the ground contact phase. Notice that muscles dominate, except near lift-off. Positive angular acceleration is a backward rotation of the trunk.

Fig. 5. Contributions of muscles to the angular acceleration of the trunk, thigh, and foot derived from the model during the ground contact phase. The shaded region is the summed effect by all the muscles. UPF is the combined contribution of the uniarticular ankle plantarflexors (SOL and OPF). Light solid lines in (a) are used only for clarity. Positive angular acceleration is a backward rotation of the thigh (b) and foot (c).

Fig. 6. Contributions of muscles to the angular acceleration of the hip, knee, and ankle derived from the model during the ground contact phase. The shaded region is the summed effect by all the muscles. The dashed lines represent the combined effect of TA, HAMS, and RF. Positive angular acceleration is joint extension.
VAS, GMAX, and the uniarticular ankle plantarflexors SOL and OPF (designated by UPF). Of all these muscles, only one (i.e. GAS) is biarticular.

HAMS and GMAX accelerate the trunk towards an upright position (i.e. positive angular acceleration) to counteract gravity [Fig. S(a)], whereas VAS, SOL, OPF, and GAS induce opposing angular accelerations. Activation of HAMS and GMAX (the hip extensors in our model) are therefore crucial to counteracting the effects of gravity on the trunk during the initial phase of propulsion (i.e. the first 60% of the jump). Thus, HAMS and GMAX are excited early (about 20–30% of ground contact time, Fig. 3 HAMS and GMAX) to initiate desirable backward (positive) rotation of the trunk [Fig. 5(a)]. VAS is excited later (about 40% into the jump, Fig. 3 VAS) because it can only induce undesirable forward (negative) angular acceleration of the trunk prior to 80% of ground contact time (Fig. 5(a) VAS). Later (80–100% of ground contact time), positive acceleration from VAS is possible because the body segments are closer to colinearity. VAS can then assist GMAX in positive rotation of the trunk [Fig. 5(a)].

Even though VAS induces a negative angular acceleration of the trunk during 80% of ground contact time, this knee extensor actually accelerates the hip towards extension (Fig. 6(a) VAS) because of the large positive angular acceleration of the thigh it induces (Fig. 5(b) VAS). Since VAS is assumed to be the strongest muscle in the lower extremity [see Table 1 in Pandy et al. (1990)], any action other than hip extension would clearly be undesirable. Thus, GMAX and VAS, the strongest hip and knee extensors in the model [see Table 1 in Pandy et al. (1990)] work together to produce angular acceleration of the knee and hip towards extension [Fig. 6(a)], which acts to accelerate the body mass in the desired direction (upwards).

Unfortunately, the above actions simultaneously accelerate the heel into the ground [see contributions of VAS and GMAX to negative angular acceleration of the foot, Fig. 5(c)]. In response, SOL and OPF [i.e. UPF in Fig. 3(c)] are excited at 50–60% of ground contact time (Fig. 3 SOL and OPF). SOL and OPF also counter the large ankle dorsiflexor accelerations induced by VAS and GMAX [Fig. 6(c)]. Finally, GAS is excited near lift-off (Fig. 3 GAS) to further accelerate the ankle towards plantarflexion [Fig. 6(c)], which arises from the positive acceleration of the foot it induces [Fig. 5(c)]. In so doing, GAS (and the UPF as well) opposes the efforts of VAS and GMAX at this time (e.g. GAS accelerates the knee towards flexion; Fig. 6(b)). Interestingly, the increase in performance resulting from increasing foot angular velocity near lift-off outweighs the undesirable effects (i.e. flexion of the knee and hip rather than extension). That is, the net effect of GAS is to increase the vertical acceleration of the mass centroid of the body, and thus GAS acts to increase the vertical velocity of the body at lift-off.

Role of uni- and biarticular muscles

VAS and GMAX were found to be the major energy producers, the prime movers, of the lower extremity during jumping, since they contribute most significantly to the total energy made available for propulsion (Fig. 7, areas under curves). Note that, in the final 20 percent, the ankle plantarflexors UPF and GAS contribute significantly as well.

A large proportion of the total energy delivered to the segments (Fig. 8, shaded region) resides in the trunk (Fig. 8, compare the areas under the individual curves to the shaded region). In fact, the combined energy of the thigh, shank, and foot amounts to only 30% of the total energy available at lift-off (with approximately half of this belonging to the thigh). Therefore, a large portion (i.e. 70%) of the input musculotendon energy is transferred to the trunk. This is not a surprising result, given that the trunk represents almost 70% of the body mass.
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Fig. 9. Muscular, gravitational, and inertial contributions to the power of the trunk (a), and individual muscular contributions to trunk power (b) and to thigh power (c). (a) Total power of the trunk is the shaded curve. 'Muscle' is the contribution from the muscles, 'gravity' from gravity, and 'inertial' from the motion of all the segments. Notice that muscles dominate. (b) Total contribution from all the muscles is the shaded curve. PF is the contribution of the ankle plantarflexors (SOL, OPF, and GAS). The dashed line is the combined contribution of HAMS, RF, and TA. The area under the curve is the energy developed by each muscle (or muscle group) that is transferred to the trunk. Notice that VAS and GMAX are the major contributors. (c) Total contribution from all the muscles is the shaded curve. PF is the contribution of the ankle plantarflexors (SOL, OPF, and GAS). The dashed line is the contribution from all other muscles. Notice that the ankle plantarflexors are the major contributors to thigh power.

Muscles dominate the contribution to the instantaneous power of the trunk (Fig. 9(a), compare heavy solid curve to the shaded region). However, the contribution of segmental motion approximates the contribution of muscles near lift-off (compare 'muscle' curve to 'inertial' curve at 100 %) because the angular velocities of the segments of the model are quite large then (Pandy et al., 1990). The contribution of gravity is insignificant throughout propulsion.

Of all the muscles, VAS and GMAX contribute most significantly to the instantaneous power of the trunk [Fig. 9(b)], and account for approximately 90 % of the total energy of the trunk at lift-off (summed area under the curves for VAS and GMAX in Fig. 9(b) compared to the area in the shaded region in Fig. 9(a)). Moreover, almost all of the total energy generated by the prime movers VAS and GMAX is made available to the trunk at lift-off (compare the areas under the curves for VAS and GMAX in Fig. 7 and Fig. 9(b)).

The ankle plantarflexors (SOL, OPF, and GAS) make their presence felt only during the final 20 % of the jump (the PF curve in Fig. 9(b)) by contributing about 30 % to the total power delivered by muscles to the trunk (Fig. 9(b), compare the PF curve with the shaded region at lift-off). Note that the 'hump' in the trajectory of total power (Fig. 9(b), 90 % of ground contact time), is due primarily to the contribution of the ankle plantarflexors. In addition, the ankle plantarflexors, by dominating thigh power, except near lift-off, contribute approximately 90 % to the peak power of the thigh, which occurs at about 85 % of ground contact time [Fig. 9(c)]. Because of the combined effects of the ankle plantarflexors on the trunk near lift-off and on the thigh at other times, we conclude that the contribution of the ankle plantarflexors to overall jumping performance cannot be neglected.

Of the ankle plantarflexors, GAS is an important contributor. For instance, it contributes about the same amount of power as SOL and OPF (i.e. approximately 30 %) to each of the thigh and trunk [Fig. 9(b)-(c)]. It should be mentioned that GAS actually delivers power to the thigh, even though it accelerates the knee towards flexion [Fig. 6(b)], because of the substantial power being delivered to the thigh through the intersegmental forces acting at the knee joint. To conclude, of the biarticular muscles, GAS is expected to contribute somewhat to overall jumping performance.

Finally, to assess the dependence of jumping performance on biarticular muscle function, we removed all biarticular muscles from the model [see Fig. 1, Pandy et al. (1990)] and, with only uniarticular muscles available for propulsion, re-computed how muscles would then have to be coordinated to produce as high a squat jump as possible. We found that even though the jump was still coordinated (Fig. 10, stick figures), jump height decreased [compare the solid and dashed lines in Fig. 10 at lift-off (100 %)]. In fact, the net vertical displacement of the mass centroid of the body from standing decreases by 20 %, supporting our previous conclusion that the contribution of the biarticular muscle GAS to jumping performance cannot be neglected. However, we do not feel that the mechanism by which GAS contributes to the jump is any different from that of uniarticular muscles (see below).
jumping (Pandy et al., 1990) in the hope of under-
would go found using the optimization algorithm. The stick figures
dashed lines show how high the mass centroid of the body
given this new set of muscles, another simulated jump was
demonstrates the time histories of all muscle forces, muscle
represents a most important advantage over previous findings (Fig. 3), as well as with previous experimental findings (Gregoire et al., 1984; Bobbert and van Ingen Schenau, 1988).
Gregoire et al. (1984) and Bobbert and van Ingen Schenau (1988) conclude, however, that a proximal-
RF and HAMS were removed from the model and, given this new set of muscles, another simulated jump was
Represents a most important advantage over previous experiments (Gregoire et al., 1984) and Bobbert and van Ingen Schenau (1988). We have found no evidence to support the contention that
masculotendon dynamics coordinate complex human movements. By conducting a detailed analysis of the optimal control solution, we have been able to investigate intermuscular coordination of the squat jump, knowing the time histories of all muscle forces, muscle activation levels, and body-segmental motions. This represents a most important advantage over previous efforts to analyze coordination of jumping, since those efforts focused on relatively small portions of the human musculoskeletal system (Bobbert et al., 1986a, b).
Our optimal control solution has predicted a proximal-to-distal sequence of muscle activation, where muscles spanning the hip (i.e. GMAX and HAMS) are activated first, followed by uniaxial actuators spanning the knee (i.e. VAS) and ankle (i.e. SOL, OPF). This trend is consistent with our experimental

**DISCUSSION**

Though the use of optimal control theory to elucidate the control of the musculoskeletal system is widely appreciated (Hatze, 1976; Davy and Audo, 1987), its full potential has yet to be realized. The major reason is that the human musculoskeletal system has high dimensionality, and exhibits severe nonlinearities. Consequently, even moderately complex optimal control problems encounter serious computational difficulties. We have nevertheless formulated and solved an optimal control problem for maximum-height jumping (Pandy et al., 1990) in the hope of understanding how intermuscular control and muscular tendon dynamics coordinate complex human movements. By conducting a detailed analysis of the optimal control solution, we have been able to investigate intermuscular coordination of the squat jump, knowing the time histories of all muscle forces, muscle activation levels, and body-segmental motions. This represents a most important advantage over previous efforts to analyze coordination of jumping, since those efforts focused on relatively small portions of the human musculoskeletal system (Bobbert et al., 1986a, b).

Our optimal control solution has predicted a proximal-to-distal sequence of muscle activation, where muscles spanning the hip (i.e. GMAX and HAMS) are activated first, followed by uniaxial actuators spanning the knee (i.e. VAS) and ankle (i.e. SOL, OPF). This trend is consistent with our experimental

**Fig. 10. Simulated jump using only uniarticular muscles.**

- **HAMS, RF, and GAS** were removed from the model and, given this new set of muscles, another simulated jump was found using the optimization algorithm. The stick figures show how the body segments should be coordinated during the ground contact phase (0–100%) to achieve the highest possible height with the new muscle set. The heavy solid and dashed lines show how high the mass centroid of the body would go if the body could leave the ground at that time, given that all the muscles, or just uniaxial muscles, are used to coordinate the jump, respectively. The thin dashed line is the standing height of the simulated jumper.

- **Potential jump height** (m) versus ground contact time (Fig. 10). The heavy solid line shows the potential jump height if the body could leave the ground at that time, given that all the muscles, or just uniaxial muscles, are used to coordinate the jump, respectively. The thin dashed line is the standing height of the simulated jumper.

- **% of ground contact time**

- **Potential jump height (m)** in the hope of under-
Moreover, while GAS supplies only a small fraction of the total energy of the trunk at lift-off (i.e. less than 5%), RF and HAMS combine to remove energy from this segment. We claim, therefore, that the absence of GAS is the major factor contributing to the decrease in jump height shown in Fig. 10. In this regard, our results support a previous conclusion (Bobbert et al., 1986b; Bobbert and van Ingen Schenau, 1988) that the contribution of GAS to jumping performance cannot be neglected.

We are, however, opposed to the notion that jumping performance is increased by the unique biarticular action of GAS. Our results do not substantiate the claim that ankle power output is increased significantly as a result of power transferred by GAS from the knee to the ankle. In fact, by delivering power to the trunk and thigh, GAS behaves no differently from any of the uniarticular ankle plantarf lexors (SOL and OPF). So, while it is true that GAS acts to increase jumping performance appreciably (i.e. by as much as 25%), this increase is not a consequence of GAS being biarticular (i.e. the increase is not due to proximal-to-distal power transfer from the knee to the ankle). To support this claim, we offer the following evidence. Upon finding a decrease in performance when only uniarticular muscles are used for propulsion (Fig. 10), we added a uniarticular ankle plantarf lexor that was structurally identical to GAS. With the biarticular capability of GAS to transfer power now removed, we found jumping performance to be restored (and in fact increased).

We conclude, therefore, that GAS is activated near lift-off to increase foot angular velocity (and ultimately the vertical velocity of the mass centroid of the body). More importantly, the action of GAS in this task is no different from that of any other uniarticular extensor muscle; it too transfers power in a proximal direction to the trunk and thigh.

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APPENDIX

The following is a derivation of the equations defining the torque instantaneous power of the trunk. Consider a free-body diagram of the trunk with the following muscles attached: HAMS, RF, and GMAX (Fig. A1). The total instantaneous
power of a segment is given by (Meriam, 1975):
\[ \mathcal{E} = \sum F \cdot v + \sum \tau \cdot \omega \] (A1)
where \( F \) is any external force acting on the segment, \( v \) is the linear velocity of the point on the segment at which the force \( F \) is applied, \( \tau \) is any external torque acting on the segment, and \( \omega \) is the angular velocity of the segment. Using equation (A1), the total instantaneous power of the trunk is:
\[ \mathcal{E}_t = F_4 \cdot v_4 + F_{RF} \cdot v_{RF} + F_{HAM} \cdot v_{HAM} + F_{GMAX} \cdot v_{GMAX} \] (A2)
where \( F_4 \) is the intersegmental force acting at the hip joint; \( v_4 \) is the linear velocity of the hip joint; \( F_{RF}, F_{HAM}, F_{GMAX} \) are forces generated by RF, HAMS, and GMAX respectively; and \( v_{RF}, v_{HAM}, v_{GMAX} \) are the velocities of the points of attachment of RF, HAMS, and GMAX on the trunk. Using Newton’s laws, the intersegmental force \( F_4 \) can be found directly from Fig. A1:
\[ F_4 = -F_{RF} - F_{HAM} - F_{GMAX} + mgj + ma \] (A3)
where \( j \) is a unit vector in the vertical direction (positive upwards). Now write the acceleration of the center of mass of the trunk as:
\[ \mathbf{a} = u(\theta) \hat{\theta} + \nu(\theta, \dot{\theta}) \] (A4)
where \( u(\theta) \) is a \((2 \times 4)\) matrix containing entries which are functions of the limb-segmental angular displacements only; and \( \nu(\theta, \dot{\theta}) \) is a \((2 \times 1)\) vector containing entries which are functions of both segmental angular displacements and velocities. Substitute equation (1) into equation (A4) to get:
\[ \mathbf{a} = u(\theta) A(\theta)^{-1} \left( B(\theta) \dot{\theta}^2 + C(\theta) + DM(\theta) P_T + T(\theta, \dot{\theta}) \right) + \nu(\theta, \dot{\theta}). \] (A5)

Then, substituting equation (A5) into equation (A3) gives:
\[ F_4 = \mathbf{a} - F_{RF} - F_{HAM} - F_{GMAX} + mgj + \mathbf{u}(\theta) A(\theta)^{-1} \left( B(\theta) \dot{\theta}^2 + C(\theta) + DM(\theta) P_T + T(\theta, \dot{\theta}) \right) + \mathbf{v}(\theta, \dot{\theta}) \] (A6)
But the velocity of the point of attachment of a muscle in equation (A2) may be expressed in terms of the hip joint velocity:
\[ v_{RF} = v_4 + (v_{RF})_{rel} \] (A7)
\[ v_{HAM} = v_4 + (v_{HAM})_{rel} \] (A8)
\[ v_{GMAX} = v_4 + (v_{GMAX})_{rel} \] (A9)
where \( (v_{RF})_{rel} \) is the velocity of the point of attachment of RF relative to the hip joint; and similarly for HAMS and GMAX respectively.

Finally, substitute equations (A7)- (A9) into equation (A2) and rearrange to get:
\[ \mathcal{E}_t = \mathbf{a} - F_{RF} - F_{HAM} - F_{GMAX} + mgj + \mathbf{u}(\theta) A(\theta)^{-1} \left( B(\theta) \dot{\theta}^2 + C(\theta) + DM(\theta) P_T + T(\theta, \dot{\theta}) \right) + \mathbf{v}(\theta, \dot{\theta}) \] (A10)
Equation (A10) defines the total instantaneous power of the trunk. The inertial, gravitational, and muscular contributions are:
\[ \mathcal{E}_{inert} = \mathbf{a} - F_{RF} - F_{HAM} - F_{GMAX} + mgj + \mathbf{u}(\theta) A(\theta)^{-1} \left( B(\theta) \dot{\theta}^2 + C(\theta) + DM(\theta) P_T + T(\theta, \dot{\theta}) \right) \cdot v_4 \]
\[ \mathcal{E}_{gravity} = mgj + \mathbf{u}(\theta) A(\theta)^{-1} \cdot C(\theta) \cdot v_4 \]
\[ \mathcal{E}_{muscle} = \mathbf{u}(\theta) A(\theta)^{-1} \cdot DM(\theta) P_T \cdot v_4 \]
Finally, substitute equations (A7)-(A9) into equation (A2) and rearrange to get:
\[ \mathcal{E}_t = \mathbf{a} - F_{RF} - F_{HAM} - F_{GMAX} + mgj + \mathbf{u}(\theta) A(\theta)^{-1} \left( B(\theta) \dot{\theta}^2 + C(\theta) + DM(\theta) P_T + T(\theta, \dot{\theta}) \right) + \mathbf{v}(\theta, \dot{\theta}) \] (A10)