

## MUSCLE COORDINATION OF MOVEMENT: A PERSPECTIVE

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**Abstract**—Multijoint movement requires the coordination of many muscles. Because multijoint movement is complex, kinesiological data must be analyzed and interpreted in the context of forward dynamical models rich enough to study coordination; otherwise, principles will remain elusive. The complexity arises because a muscle acts to accelerate all joints and segments, even joints it does not span and segments to which it does not attach. A biarticular muscle can even act to accelerate one of the joints it spans opposite to its anatomical classification. For example, gastrocnemius may act to accelerate the knee into extension during upright standing. One powerful forward dynamical modeling method to study muscle coordination is optimal control theory because simulations of movement can be produced. These simulations can either attempt to replicate experimental data, without hypothesizing the purpose of the motor task, or otherwise generate muscle and movement trajectories that best accomplish the hypothesized task. Application of the theory to the study of maximum-height jumping has provided insight into the biomechanical principles of jumping, such as: (i) jump height is more sensitive to muscle strength than to muscle speed, and insensitive to musculotendon compliance; (ii) uniaxial muscles generate the propulsive energy and biarticular muscles fine-tune the coordination; and (iii) countermovement is often desirable, even in squat jumps, because it seems both to prolong the duration of upwards propulsion, and to give muscles time to develop force so the body can move upwards initially with high acceleration. The effort necessary to develop forward dynamical models has been so high, however, that model-generated data of jumping or any other task are meager. An interactive computer workstation environment is proposed whereby users can develop neuromusculoskeletal control models, generate simulations of motor tasks, and display both kinesiological and modeling data more easily (e.g., animations). By studying a variety of motor tasks well, each within a theoretical framework, hopefully muscle coordination principles will soon emerge.

### INTRODUCTION

Human movement, performed with its usual gracefulness, demands the coordination of many muscles. Understanding how and why the body coordinates muscles intrigues professionals spanning diverse disciplines, such as sports, the performing arts, engineering, and medicine. For example, as biomechanicians we may attempt to elucidate how the body segments and muscles interact mechanically to execute motor tasks. As motor control neuroscientists we may focus on elucidating the properties of the central nervous system controller. As rehabilitation scientists, we may study human pathological movement to develop musculoskeletal or neurological therapies.

One would think, then, that by synthesizing the collective knowledge from all the disciplines we could postulate (and perhaps agree on) some principles subserving muscle control of movement. I submit, however, that we are far from achieving this goal. Why do muscle coordination properties remain elusive?

I believe the crux of the problem is that we rarely understand (and agree on) how muscles coordinate any one movement, much less a repertoire of movements. And many movements need to be understood before we can hope to postulate broadly applicable muscle

coordination principles. To attain an understanding of muscle coordination of many movements, do we need to just collect more biomechanical and kinesiological data? Though observing how subjects execute a variety of movements is certainly essential to the formulation of hypotheses, it is not sufficient.

A biomechanical model of each movement being studied is also essential. In addition, the models must be sufficiently complex to elucidate muscle coordination principles. Progress will be sustained in movement science by our ability to both develop biomechanical models and record relevant experimental data. For example, often *inverse* dynamical models are hypothesized in order that the net muscle moments about the joints can be estimated from the experimental data. However, *forward* dynamical models offer more potential to studies of multimuscle control of movement (see below, "Integrating Experiments and Models to Study Muscle Coordination"). In movement science, I submit that our ability to construct and use *forward* dynamical models complex enough to study muscle coordination has lagged behind our ability to collect biomechanical and kinesiological data.

In this paper, I will first review why forward dynamical models are so necessary to understand how muscles coordinate a multijoint motor task. Second, forward and inverse dynamics approaches to integrating experiments and models to study muscle coordination will be reviewed. Third, vertical jumping will be used as a case study to show how forward dynamics

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models and optimal control theory can elucidate biomechanical and muscle coordination principles. Finally, I will propose a computer workstation environment whereby forward (and inverse) dynamical models of muscle coordination can be formulated, modeling data generated, and kinesiological and biomechanical data viewed.

#### WHY FORWARD DYNAMICAL MODELS ARE NECESSARY TO STUDY COORDINATION

Because muscle coordination of a multijoint motor task is complex, complex models become necessary in order to interpret experimental data. When very few variables are needed to describe the behavior of a system, often a simple model suffices. For example, when we fit a line to describe the relation between two variables, a linear function is assumed to be the model describing the interaction between these two variables. In multijoint movement, however, not only are many variables needed to describe the musculo-skeletal system, but the relations are nonlinear as well. Furthermore, the interactions among the variables are dynamical (i.e., the position, orientation, and motion of the body segments at some future time depend on their current state as well as on the trajectories of the forces acting on the segments). Let me illustrate the complexity by discussing how muscles affect the

angular acceleration of joints in a multijoint motor task (see review, Zajac and Gordon, 1989).

#### Definition of the 'joint torque' produced by a muscle

Muscles are not *torque* generators (Paul, 1978). Muscles are neither *moment of muscle force* generators. Muscles are, unsurprisingly, *force* generators. They develop forces that act on the segments to which they attach. They are linear actuators, not rotary actuators. Yet we often refer to the "joint torque", or the "moment of force about the joint" developed by the muscle as if this is what the muscle inherently does when, in fact, it doesn't. We strive to consider a muscle to be a rotary actuator because we often visualize intersegmental motion not as translation but rather as rotation (i.e., we visualize motion of the segments by what the joints primarily do, which is rotate). Thus we want to know how muscles act to rotate (cause angular acceleration of) the joints. We know joints, for example, flex/extend, and that muscles act to accelerate joints into, say, flexion/extension.

Consider a uniaxial muscle, which attaches to two segments, and crosses a pin joint (Fig. 1A). Neglecting any friction between the muscle and the segments, or between this muscle and other muscles (these assumptions are almost always invoked), only

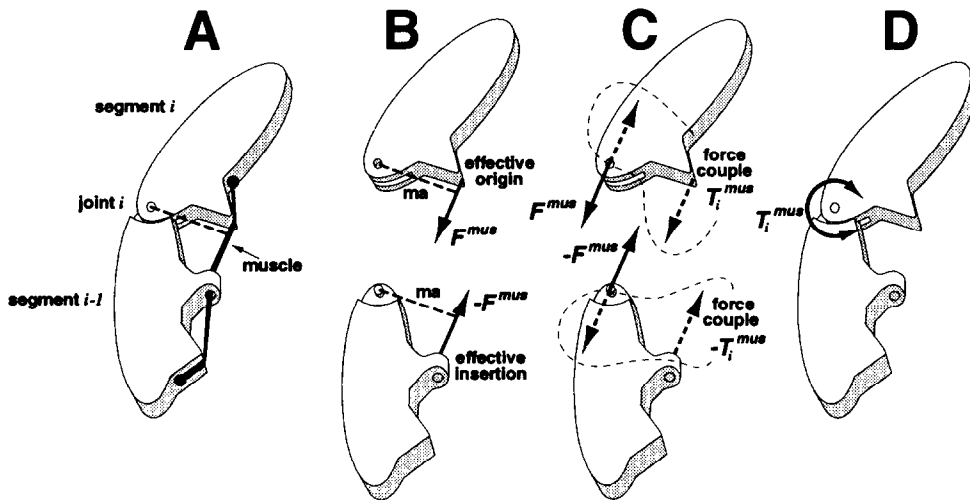


Fig. 1. Equivalent representations of the force in a uniaxial muscle crossing a frictionless pin joint. (A) The path of the muscle is the *heavy solid line*. The shortest distance from the part of the path of the muscle crossing the joint to the joint center is the *dashed line*. (B) This shortest distance is called the moment arm ( $ma$ ) of the muscle. Neglecting muscle path friction, only the forces at the effective origin of the muscle ( $F^{mus}$ ) and at its effective insertion ( $-F^{mus}$ ) affect segmental dynamics. (C) Each of the two forces in (B) can be equivalently represented by a force couple acting on one of the segments. The torques of these two force couples are equal to  $(T_i^{mus} = ma \cdot F^{mus})$ , which acts on segment  $i$ , and  $(-T_i^{mus} = ma \cdot -F^{mus})$ , which acts on segment  $i-1$ . Notice that these two torques are equal to the moments of the two forces in (B) about the joint center. (D) If the pin joint is frictionless, only the two segmental torques in (C), and not the two forces in (C), contribute to the angular and linear accelerations of the segments. These two torques are collectively referred to as the joint torque  $T_i^{mus}$  produced by the force in the muscle. (See text). (Modified from Zajac and Gordon, 1989).

the force of the muscle at its effective origin and the force at its effective insertion will affect segmental dynamics (Fig. 1B). Thus it is assumed that the force in the muscle throughout the rest of its path does not have to be considered to compute how the muscle force affects the acceleration of the segments. Indeed, when we consider a uniaxial muscle as a force generator, as we really should, we often invoke this image; i.e., a muscle developing collinear forces on two segments.

Notice that these two forces ( $F^{mus}$  and  $-F^{mus}$ ) are equal in magnitude but opposite in direction; also that its force of origin ( $F^{mus}$ ), acting on segment  $i$ , produces a clockwise moment about the joint center (equal to  $ma \cdot F^{mus}$ ); and its force of insertion ( $-F^{mus}$ ), acting on segment  $i-1$ , produces a counterclockwise moment (equal to  $ma \cdot -F^{mus}$ ).

When is it sufficient to use just the two moments of muscle force about the joint center to compute how the force in a muscle contributes to the linear and angular accelerations of the segments? To answer this question, recognize that each force of origin and insertion (Fig. 1B) can be equivalently represented by the sum of a force acting at the joint contact point and a force couple acting on the segment (Fig. 1C; Kane and Levinson, 1985, Zajac and Gordon, 1989). The equal and opposite muscle force couples acting on the adjacent segments have associated with them equal and opposite torques (Fig. 1C,  $T_i^{mus}$  and  $-T_i^{mus}$ ). Since the torque of a force couple is the moment of the force couple about any point (Kane and Levinson, 1985), each torque is equal to the moment of the muscle force about the joint center (e.g., torque on segment  $i$  is  $ma \cdot F^{mus}$ ; on segment  $i-1$ ,  $ma \cdot -F^{mus}$ ).

So the question can now be rephrased: when can just the two segmental torques be used to compute how the force in a muscle contributes to the angular and linear accelerations of the segments? This is equivalent to: when will the two compressive forces in the joint caused by the muscle (Fig. 1C,  $F^{mus}$  and  $-F^{mus}$ ) not contribute to the angular or linear acceleration of the segments? The answer is when the pin joint is *frictionless* because then all compressive forces in the joint, including those by muscles, do not affect the motion of the segments (Kane and Levinson, 1985). Thus, only the two torques acting on the two segments have to be used to compute how the muscle force will act to accelerate the segments. It is obvious that the two torques affect the angular acceleration of the segments. The two torques can also be used to calculate the contributions of the muscle force to the linear accelerations of the segments because, in a pin joint, the linear acceleration of one segment relative to another is given by the joint angular acceleration (i.e., the angular acceleration of one segment relative to another), the joint angular velocity, and the joint angle. During a movement, of course, the joint angular velocities and angles are determined from the past angular acceleration trajectories and are, there-

fore, not independent variables (e.g., Fig. 4A, *Forward Multijoint Dynamics*).

For a frictionless pin joint, therefore, the contribution of muscle force to the linear and angular acceleration of one segment relative to another is determined by the torques of the two muscle force couples (or, equivalently, the two muscle moments about the joint) (Fig. 1C). These two torques are, collectively, referred to as the joint torque produced by the muscle (Fig. 1D,  $T_i^{mus}$ ). Thus, it is unimportant to the principles being explicated in the following sections whether the term "muscle joint torque" or "muscle moment about the joint" is used. To me, each term connotes the same meaning and assumptions.

Frictionless pin (and ball-and-socket) models of joints are, of course, only an approximation. Nevertheless, such models often suffice to study multimuscle control of multijoint movement, and how a muscle force acts to accelerate the joints into rotation (e.g., see below). However, studies of multimuscle control of joints exhibiting high friction (e.g., pathology) will require that the compressive forces in the joints be computed. Other studies will require more complex joint kinematics. In some cases it may still be accurate to consider muscles as just joint torque (or moment-generating) actuators. Regardless, it is always best to be rigorous in the use of dynamics (Kane and Levinson, 1985). Thus a muscle should be treated as an actuator generating force at its effective origin and insertion (Fig. 1B), and it should then be subsequently shown that the joint torque (or muscle moment) representation is acceptable.

#### *Anatomical classification and function of muscles*

Muscles are classified according to the directionality of the joint torques they produce. Since the principles to be elucidated below do not depend fundamentally on the details of the kinematics of the joints, frictionless pin joints are assumed. Clearly, a muscle produces a joint torque only at a joint it spans (e.g., only at joint  $i$  in Fig. 1). Soleus is called an ankle extensor muscle because it produces an ankle extensor joint torque (Fig. 2A); gastrocnemius, an ankle extensor/knee flexor muscle because it produces both an ankle extensor and a knee flexor joint torque (Fig. 2B). Thus, from the definitions of joint rotations (e.g., extension and flexion), and from the anatomical position of a muscle with respect to a joint, we can infer the direction(s) of its joint torque(s) (e.g., Fig. 1; Zajac and Gordon, 1989).

Will the direction that a muscle acts to accelerate into rotation a joint it spans be the same as the direction of the joint torque it develops? At times, yes; at other times, no. The rotational direction that a uniaxial muscle acts to accelerate the joint it spans will always be the same as the direction of the joint torque it develops (e.g., soleus acts to accelerate the ankle into extension; i.e.,  $\dot{\phi}_{ankle} > 0$  in Fig. 2A). Thus,

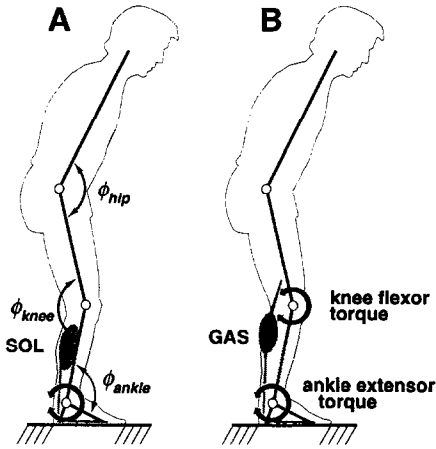


Fig. 2. Classification of muscles according to the directionality of their joint torques. (A) Soleus muscle (SOL) is classified as an ankle extensor muscle because it develops an ankle extensor joint torque; i.e., a counterclockwise torque on the shank and a clockwise torque on the foot. (B) Gastrocnemius muscle (GAS) is classified as an ankle extensor/knee flexor muscle because it develops simultaneously ankle extensor and knee flexor joint torques, with each joint torque producing torques on the segments adjacent to that joint. (See text).

function is consistent with anatomy. If one of the two joints spanned by a biarticular muscle is constrained from moving (e.g., by a brace), then its function, now like that of a uniaxial muscle, will also be consistent with anatomy. However, if both of the spanned joints are unrestrained, the biarticular muscle may act to accelerate one of the two joints it spans opposite to the joint torque it develops at that joint (e.g., gastrocnemius may act to accelerate the knee into extension, or the ankle into flexion; see below).

#### A muscle can act to accelerate joints it does not span

A muscle may act to accelerate the joints it does not span as much or more than the joints it does span. For example, soleus acts to accelerate the ankle, the joint it spans, into extension. But in flat-footed standing near the vertical posture, soleus acts to accelerate the knee into extension twice as much as the ankle because the thigh is accelerated into extension as much as the shank (e.g., referring to Fig. 2A, soleus acts to accelerate the thigh clockwise as much as it acts to accelerate the shank counterclockwise; Zajac and Gordon, 1989). The fact that a muscle can act to accelerate segments to which it does not attach, and joints which it does not span, arises from inertia forces being transmitted from one segment to another via the reaction forces at the joints (i.e., inertial coupling).

To find how much a muscle force contributes to the net angular acceleration of each joint, including the joints the muscle does not span, the dynamical

equations of motion must be found (Kane and Levinson, 1985). The equations of motion specify how the body segments will accelerate subject to the force and torque trajectories acting on the segments. For example, the matrix equations for a frictionless rigid-body model of flat-footed standing (Fig. 2) can be written as (Gordon *et al.* 1988; Kuo and Zajac, 1992):

$$M(\phi)\ddot{\phi} = T^{mus} + V(\phi, \dot{\phi}) + G(\phi) \quad (1)$$

where  $\phi$ ,  $\dot{\phi}$ ,  $\ddot{\phi}$  are the vectors of joint angles, joint angular velocities, and joint angular accelerations of the joints assumed to move (i.e., the ankle, knee, and hip);  $T^{mus}$  is the vector of net joint torques produced by all the muscles crossing the three joints;  $M(\phi)$  is the mass matrix, which depends (among other things) on how body mass is distributed among the segments and the joint angles;  $V(\phi, \dot{\phi})$  is the vector of joint torques due to motion of the segments (i.e., centripetal and coriolis forces); and  $G(\phi)$  is the vector of joint torques due to gravity. (Joint torques from passive soft-tissue, non-muscular joint structures could be added, if desired; e.g., Zajac and Winters, 1990). Segmental translations do not enter into these equations because they can be found from the joint rotations; i.e., translation is not independent from rotation for this rigid-body system. Notice that these equations are the moment balance equations for the three joints. Often these equations are used to find the net muscle joint torques from kinematic data (i.e., inverse dynamics, Fig. 4B; see "Integrating Experiments and Models to Study Muscle Coordination"). The net angular accelerations of the joints are therefore:

$$\ddot{\phi} = M^{-1}(\phi)T^{mus} + M^{-1}(\phi)V(\phi, \dot{\phi}) + M^{-1}(\phi)G(\phi) \quad (2)$$

where  $M^{-1}(\phi)$  is the inverse of the mass matrix (Fig. 4A).

The contribution of a muscle force to the net angular acceleration of each joint can be found from the dynamical equations of motion, if the amount of joint torque(s) produced by the muscle is (are) known. For example, the contribution of soleus joint torque to the angular accelerations of the ankle, knee, and hip during flat-footed standing can be found from equation (2) by setting all joint torques to zero, except the ankle joint torque produced by soleus. Thus:

$$\begin{bmatrix} \ddot{\phi}_{ankle} \\ \ddot{\phi}_{knee} \\ \ddot{\phi}_{hip} \end{bmatrix} = \begin{bmatrix} \alpha_{11} & \cdot & \cdot & \cdot \\ \alpha_{21} & \cdot & \cdot & \cdot \\ \alpha_{31} & \cdot & \cdot & \cdot \end{bmatrix} \begin{bmatrix} T_{ankle}^{SOL} \\ 0 \\ 0 \end{bmatrix} \quad (3)$$

where  $T_{ankle}^{SOL}$  is the extensor joint torque produced by soleus at the ankle, and  $\alpha_{ij}$  ( $i=1,2,3$ ) are the first column elements of  $M^{-1}(\phi)$ . The ankle joint torque developed by soleus therefore contributes  $\alpha_{11}T_{ankle}^{SOL}$ ,  $\alpha_{21}T_{ankle}^{SOL}$ ,  $\alpha_{31}T_{ankle}^{SOL}$  rad/sec<sup>2</sup> to ankle, knee, and hip

angular accelerations, respectively. Notice that the only time soleus will just contribute to ankle angular acceleration is when  $\alpha_{21}$  and  $\alpha_{31}$  are both zero. In fact, from equations (2) and (3), it should be clear that the only way any uniarticular muscle crossing the ankle, knee, or hip will contribute to the angular acceleration of only the joint it spans will be for  $M^{-1}(\phi)$  to be diagonal (and thus also  $M(\phi)$ ). This situation rarely, if ever, occurs. Thus a uniarticular muscle will, in general, contribute to the angular acceleration of at least one joint it does not span in a multijoint motor task.

If the amount of joint torque produced by a muscle is unknown, the amount of angular acceleration of one joint relative to another caused by the force in a muscle can still be computed. For example, the relative joint angular accelerations produced by a force in the soleus muscle during flat-footed upright standing are  $(\ddot{\phi}_{ankle}, \ddot{\phi}_{knee}, \ddot{\phi}_{hip})_{SOL} = (\alpha_{11}, \alpha_{21}, \alpha_{31}) \approx (1:2:1)$  [see equation (3)]. Thus soleus acts to accelerate the knee about 2x more than the ankle and hip in this posture. Because  $\alpha_{i1} > 0$  ( $i=1,2,3$ ), soleus acts to accelerate all three joints into extension.

The contribution of the force in a biarticular muscle to the net angular acceleration of each joint can similarly be found from the summed joint angular accelerations caused by each of the joint torques produced by the biarticular muscle. For example, the contribution of the force in gastrocnemius during flat-footed standing is given by:

$$\begin{bmatrix} \ddot{\phi}_{ankle} \\ \ddot{\phi}_{knee} \\ \ddot{\phi}_{hip} \end{bmatrix} = \begin{bmatrix} \alpha_{11} & \alpha_{12} & \cdot \\ \alpha_{21} & \alpha_{22} & \cdot \\ \alpha_{31} & \alpha_{32} & \cdot \end{bmatrix} \begin{bmatrix} T_{ankle}^{GAS} \\ T_{knee}^{GAS} \\ 0 \end{bmatrix} \quad (4)$$

where  $\alpha_{i2}$  ( $i=1,2,3$ ) are the second column elements of  $M^{-1}(\phi)$ . Notice that the contribution of the force in gastrocnemius to the angular acceleration of each joint is just the sum of the angular accelerations caused by its two joint torques [e.g.,  $(\ddot{\phi}_{knee})_{GAS} = \alpha_{21}T_{ankle}^{GAS} + \alpha_{22}T_{knee}^{GAS}$ ]. Since each of the two joint torques produced by a biarticular muscle acts to accelerate all joints, a biarticular muscle, like a uniarticular muscle, acts to accelerate all joints and segments. However, the angular acceleration of one joint relative to another caused by a biarticular muscle depends on the elements of not just one column of  $M^{-1}(\phi)$ , but on two columns, as well as on the ratio of the joint torques produced by the muscles (or, equivalently, the ratio of the moment arms of the muscle at the two joints) (Zajac and Gordon, 1989).

Finally, it is worth mentioning that the inverse mass matrix [ $M^{-1}(\phi)$ ] is an important geometric transformation because it describes how a joint torque, whether produced by muscles, joint motion, or gravity, affects the angular accelerations of the joints (e.g., see equation (2)). Thus the properties of  $M^{-1}(\phi)$  (or, equivalently,  $M(\phi)$ ) are critical to understanding how

forces contribute to joint angular accelerations. However,  $M^{-1}(\phi)$  depends not only on body inertial parameters and relative segmental orientations ( $\phi$ ), but also on the kinematic constraints (e.g., one or both feet on the ground; hands touching a wall). That is, the equations of motion [and thus  $M^{-1}(\phi)$ ] are, in general, task-dependent. Thus how joint torques are transformed into joint angular accelerations changes from task to task, and how a muscle acts to accelerate the joints also changes from task to task (Zajac and Gordon, 1989).

*A biarticular muscle can act to accelerate the joints it spans opposite to the joint torques it produces*

A consequence of inertial coupling is that a biarticular muscle may act to accelerate one of the joints it spans opposite to the joint torque it produces at the joint (Andrews, 1985; Andrews, 1987; Gordon *et al.*, 1988; Zajac and Gordon, 1989). For example, gastrocnemius may act to accelerate either the knee into extension or the ankle into flexion, even though it develops knee flexor and ankle extensor joint torques (Gordon *et al.*, 1988; Zajac and Gordon, 1989). In fact, during upright standing, gastrocnemius may indeed act to accelerate the knee into extension because its ankle extensor joint torque acts to extend the knee much more than its knee flexor joint torque acts to flex the knee [e.g. from equation (4),  $(\ddot{\phi}_{knee})_{GAS} > 0$  (extension) even though  $\alpha_{22}T_{knee}^{GAS} < 0$  (flexion) because  $\alpha_{21}T_{ankle}^{GAS} + \alpha_{22}T_{knee}^{GAS} > 0$  (extension)]. Of course, in other postures, or in other motor tasks, gastrocnemius may act to accelerate the knee and ankle in one of the other two ways (Fig. 3). All three situations are theoretically possible (Fig. 3). However, gastrocnemius cannot act to accelerate simultaneously the knee into extension and the ankle into flexion (i.e., a biarticular muscle can never act to accelerate both of the joints it spans simultaneously opposite to its two joint torques).

### Summary

Understanding how a muscle contributes to the movement of the segments and joints during multijoint motor tasks is challenging, in part, because a muscle acts to accelerate all segments and joints, sometimes in directions that are antithetical to its anatomical classification. Thus, all muscles contribute to the control of each joint and segment. Furthermore, their contributions may be task dependent. Modeling (e.g., generating the forward dynamical equations of motion) is essential to comprehend multimuscle dynamical control of movement.

### INTEGRATING EXPERIMENTS AND MODELS TO STUDY MUSCLE COORDINATION

Two modeling approaches are used to interpret experimental data. One is based on a forward dynamics representation of the body (Fig. 4A), which emulates how neuromuscular control signals actually

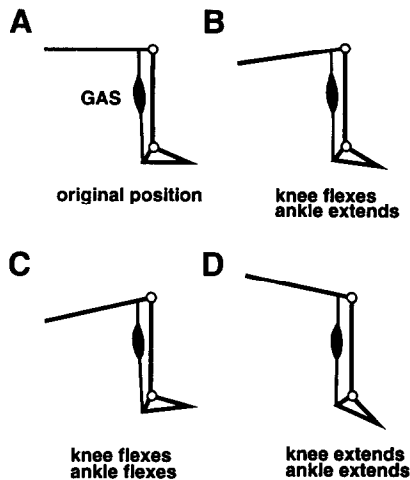


Fig. 3. Angular acceleration of the joints spanned by a biarticular muscle can be opposite to the joint torques it produces. A muscle can act to accelerate the joints it spans only in directions compatible with shortening of the muscle. Three conditions are possible for a biarticular muscle (e.g., GAS). GAS, originally in some position (A), may act to accelerate the knee into flexion and the ankle into extension (B), consistent with its anatomical classification. Or GAS may act to accelerate the knee into flexion and the ankle into flexion (C), or the knee into extension and the ankle into extension (D). The fourth condition (not shown) is impossible because GAS, by shortening, cannot act to accelerate simultaneously both the knee into extension and the ankle into flexion. Which of the three possible conditions (B, C, D) occurs at any instant during a motor task depends on the inertial interactions among the segments at that instant. (See text).

produce movement; the other on an inverse dynamics representation (Fig. 4B) (see review, Zajac and Gordon, 1989; Zajac and Winters, 1990).

#### Inverse dynamics approach

Models based on inverse dynamics have been used extensively. The joint angles of the body are measured (Fig. 4B;  $\phi_1, \dots, \phi_n$ ) and the net joint torques produced by muscles calculated (Fig. 4B;  $T_1^{mus}, \dots, T_n^{mus}$ ). When possible, forces acting on the body, such as from the ground, are measured so as to reduce reliance on velocity and acceleration estimates. Unfortunately, the actual muscle forces (Fig. 4B;  $F^1, \dots, F^m$ ) producing the net muscle joint torques are not resolvable (i.e., muscle redundancy exists) because the moment arm matrix  $R(\phi)$  is not square (Fig. 4B;  $R^{-1}(\phi)$  does not exist). Additional assumptions are then invoked to relate how to distribute the net joint torques at each instant into muscle forces at that instant (e.g., minimize some function of muscle forces using a static optimization algorithm). Unfortunately, these assumptions may have little physiological basis. Even if estimation of these forces was correct, inverse dynamics models cannot be used to ascertain how these forces affect the motion of body joints and segments.

#### Forward dynamics approach

A forward dynamics model must be postulated to study how muscle forces affect motion. Such models are meant to represent how the body actually does produce movement; i.e., how the body transforms neuromuscular excitations (Fig. 4A;  $EMG^1, \dots, EMG^m$ ), muscle force trajectories (Fig. 4A;  $F^1, \dots, F^m$ ), and muscle joint torque trajectories (Fig. 4A;  $T_1^{mus}, \dots, T_n^{mus}$ ), into joint angular accelerations (Fig. 4A;  $\ddot{\phi}_1, \dots, \ddot{\phi}_n$ ) and movement trajectories (Fig. 4A;  $\phi_1, \dots, \phi_n; \dot{\phi}_1, \dots, \dot{\phi}_n$ ). It is important to recognize that the position, orientation, and the motion of the body segments at some instant (Fig. 4A;  $\phi_1, \dots, \phi_n; \dot{\phi}_1, \dots, \dot{\phi}_n$ ) depends on the previous history of applied forces (i.e., on the force trajectories) and not just on the current muscle forces (i.e., the system has dynamics). Thus the future consequence of muscle forces on movement of the body is unaccounted for when static optimization is used, such as with inverse dynamics models to calculate muscle forces. On the other hand, the forward dynamics approach has been employed much less than the inverse dynamics approach because it is difficult to find a set of neuromuscular excitation signals (or muscle forces) that, when provided as inputs to a forward dynamics model, produce a coordinated movement (i.e., a simulation of the movement) (see below).

#### Compatibility of inverse dynamics and forward dynamics models

Can a forward dynamics model that exactly replicates the inverse model be used to find how muscle forces estimated from the inverse model affect motion of the body joints and segments (e.g., Fig. 4A *Forward Multijoint Dynamics*, as a replica of Fig. 4B *Inverse Multijoint Dynamics*)? In theory, yes. In practice, hardly. A test to see if this is reasonable is to apply the estimated muscle force (or net muscle joint torque) trajectories to the forward dynamics model (Fig. 4A) and see if the actual measured movement results. Usually the measured movement is not reproduced because (i) the two models are not exact replicas (e.g., in the inverse model, ground reaction forces may be used in lieu of some kinematics to estimate forces); and (ii) acceleration and velocity estimates from position data are inaccurate, and thus the net muscle joint torque (and muscle force) estimates as well. Nevertheless, such checks on how well inverse-model estimates of muscle forces (or net muscle joint torques) can produce a simulation are rarely done, though such checks seem logical and necessary to study how muscle forces affect body motion.

#### Producing simulations of muscle coordinated movement to best replicate kinesiological data

One way to utilize a forward dynamics approach to study muscle coordination is to produce the best possible simulation compatible with the measured kinetic and kinematic data (Belzer *et al.*, 1985; Chao, 1986). Specifically, the method is to: (i) formulate a

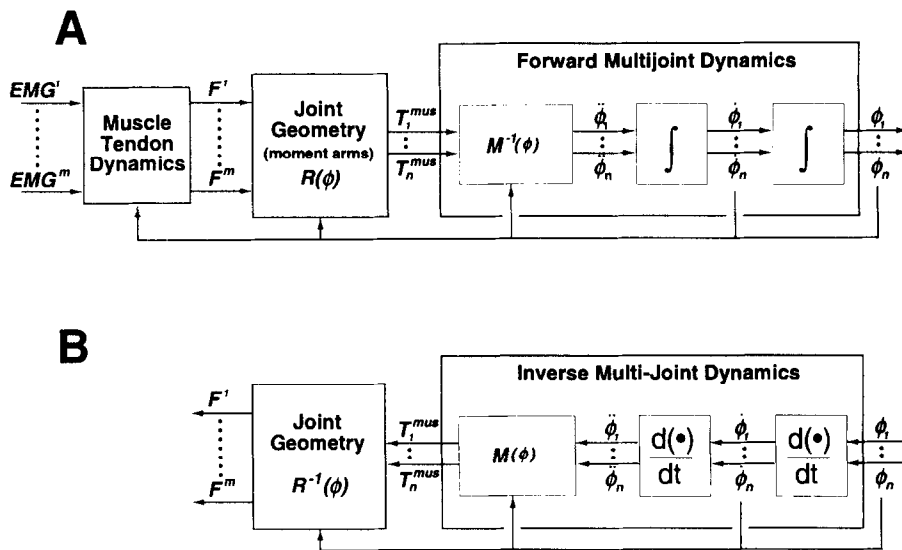


Fig. 4. Forward dynamics (A) and inverse dynamics (B) representation of the musculoskeletal system. (A) The body controls movement by sending neuromuscular excitation signals ( $EMG^1, \dots, EMG^m$ ) to muscles, which low-pass filter these signals (*Muscle/Tendon Dynamics*) to produce forces ( $F^1, \dots, F^m$ ). These forces develop joint torques ( $T_1^{mus}, \dots, T_n^{mus}$ ), which depend on the relation of the muscles to the joints (i.e., joint geometry,  $R(\phi)$ ). The net joint torques ( $T_1^{mus}, \dots, T_n^{mus}$ ) produced by all the muscle forces cause the joints to have angular acceleration instantly ( $\ddot{\phi}_1, \dots, \ddot{\phi}_n$ ), and motion and different angles later ( $\dot{\phi}_1, \dots, \dot{\phi}_n; \phi_1, \dots, \phi_n$ ). The relation between kinetics and kinematics is given by the dynamical equations of motion (*Forward Multijoint Dynamics*). The transformation between joint torques and joint angular accelerations is given by the mass matrix inverse [ $M^{-1}(\phi)$ ], whose properties can be task-dependent and can even change during a motor task. Joints are assumed to be frictionless pin- and ball-and-socket joints, and at least one point on the body is assumed to be stationary. With these assumptions, all the translational accelerations are functions of joint angular accelerations, velocities, and angles. Thus joint angles can be used as the generalized coordinates for the equations of motion (Kane and Levinson, 1985). (B) Net muscle joint torques ( $T_1^{mus}, \dots, T_n^{mus}$ ) can be found from kinematics and the inverse dynamical equations of motion (*Inverse Multijoint Dynamics*). Individual muscle forces cannot be found without additional assumptions because  $R(\phi)$  is not square; so  $R^{-1}(\phi)$  does not exist. (See text). (Modified from Zajac and Gordon, 1989).

forward dynamics model (Fig. 4A); (ii) collect kinesiological data (e.g., body segmental, ground reaction force, and EMG trajectories); (iii) compute the neuromuscular excitation (EMG) trajectories that, when applied to the forward dynamics model, give the best fit to the measurements (e.g., in the least mean-square sense with measurements not necessarily weighted equally); and (iv) analyze the EMG, force, and kinematic simulated trajectories to understand muscle coordination of this task. A dynamic optimization algorithm should be used to compute the neuromuscular excitation inputs (e.g., Fig. 4A;  $EMG^1, \dots, EMG^m$ ) since it considers the future consequences of input control signals on body movement (cf. static optimization, see above). Unfortunately, robust algorithms for solving high-dimensional, complex non-linear optimal control problems are far from well developed (Sim, 1988; Sim et al., 1989a; Pandy et al., 1992). Finally, with this forward dynamics approach, it is important to recognize that one cannot easily gain insight into why the central nervous

system is coordinating muscles the way it does (cf. see below).

#### *Producing simulations of a motor task by modeling its purpose*

Another way to produce a forward dynamics simulation of a motor task in order to study muscle coordination is to pose and solve an optimal control problem based on a *complete* model of the motor task. As with the other use of optimal control (see above), a forward dynamics model must be formulated and a dynamics optimization algorithm used. In this case, however, the purpose of the motor task must also be stated mathematically. The dynamic optimization algorithm is now used to find the control trajectories (e.g., the neuromuscular excitation signals) that best performs the hypothesized purpose of the motor task rather than to find the best fit to the data. In solving this optimal control problem, not only are the neuromuscular excitation signals found, but the consequent muscle forces and body movement as well. Naturally, all these

predicted trajectories (or any function of them), can be compared to kinesiological data. Notice that if the simulation is a reasonable facsimile of the actual behavior, then not only have the kinetics, kinematics, and muscle coordination of the motor task been simulated, but what the person is trying to achieve as well (at least such a postulate would be reasonable).

Of course any simulation of a motor task is imperfect. However, by comparing the simulation with the biomechanical and kinesiological data, insight into those assumptions that ought to be reconsidered is gained. Because *all* components of the motor task must be modeled to produce a simulation of the *motor task*, those assumptions believed to be weak and to which the simulation is affected significantly should be the reconsidered ones (e.g., see "Muscle Coordination in Vertical Jumping: A Case Study").

### Summary

Inverse dynamics, though extensively used, is not an ideal method to study muscle coordination of movement. In contrast, forward dynamics, which represents the way the body actually processes neuromuscular excitation signals to produce movement, is. Optimal control theory, which requires the formulation of a forward dynamics model, can be used to produce movement simulations. These simulations can either attempt to replicate experimental data well, without hypothesizing the purpose of the motor task, or otherwise generate muscle and movement trajectories that best accomplish the hypothesized task. In both cases, the simulations can be analyzed to study muscle coordination. However, simulations generated from models where the purpose of the task is hypothesized have much more potential of providing insight into why the central nervous system is coordinating muscles the way it does. All simulations will, of course, be imperfect. Analyzing these imperfections suggests which assumptions should be reconsidered. As a consequence, a better model of the neuromusculoskeletal control system can be posed.

### MUSCLE COORDINATION IN VERTICAL JUMPING: A CASE STUDY

Maximum-height vertical jumping, starting from either a squat or a standing posture, is a task requiring muscle coordination, first for propulsion, and then for airborne control in preparation for landing. How the body coordinates the body segments and muscles to accomplish propulsion has and continues to be extensively studied (e.g., Asmussen and Bonde-Petersen, 1974; Komi and Bosco, 1978; Bobbert *et al.*, 1986a,b; Bobbert and Ingen Schenau, 1988; Fukashiro *et al.*, 1991; Van Soest and Bobbert, 1991; Voigt *et al.*, 1991). What follows is a review of how we have integrated models and experiments to gain insight into some biomechanical and neuromuscular control issues relevant to jumping propulsion. We define propulsion during jumping to be the time when the feet touch the

ground prior to body lift-off. Propulsion includes, therefore, the time when the body center of mass accelerates upwards (upwards propulsion), as well as any other time prior to lift-off when the body decelerates (downwards propulsion).

The issues to be discussed in regard to propulsion during vertical jumping are:

1. Should lower limb muscles be fully excited? If so, which ones and when?
2. Is jumping height more sensitive to muscle strength, or to speed?
3. Is elastic energy storage important to achieving maximum jumping height?
4. What is the purpose of the initial downward motion (countermovement) of the body?
5. What is the role of uniarticular leg muscles? Of biarticular leg muscles?

### Should muscles be fully excited?

To analyze this question, we solved an optimal control problem based on a model of the motor task; i.e., jump as high as possible. The problem formulated was, given a multisegmental, multimuscle model of a human (or animal), how should the muscles be coordinated for the body's center of mass to reach its highest achievable height (Zomlefer *et al.*, 1975; Zajac and Levine, 1979)? Assuming the feet are never flat on the ground during propulsion, the solution suggested that some muscles (e.g., uniarticular extensors) should be excited as much as possible, others not at all (e.g., uniarticular flexors), and still others switched from one extreme to the other (e.g., biarticular muscles) (Zajac and Levine, 1979).

However, when it is assumed that the feet are initially flat on the ground, the solution suggests that whether the jump starts from a squat (squat jump, SJ) or from a standing posture, where the body initially moves downward (countermovement jump, CMJ), this 'on-off' muscle control strategy should only be implemented just prior to body lift-off when the heels no longer contact the ground (Zomlefer *et al.*, 1975; Levine *et al.*, 1983b, 1987). The reason on-off control does not necessarily apply earlier is that a jumper must coordinate his muscles to avoid premature lift-off of the body. That is, a jumper, in trying to maximize his vertical velocity at lift-off, may want to accelerate upwards at first less than maximally in order to prolong upwards propulsion rather than accelerate maximally outright for a short time (see below). Keeping the feet initially flat on the ground is how a jumper achieves maximum lift-off velocity. (Large changes in jump height occur because of changes in the vertical velocity of the body at lift-off rather than from changes in its height at take-off). This two-phase propulsion strategy (a 'non on-off' strategy before heel-off, and an 'on-off' strategy afterwards) is quite robust to the details of the multimuscle, multijoint model (Levine *et al.*, 1983b); e.g., it is generalizable to any number of segments arranged in an open kinematic linkage (Levine *et al.*, 1984, 1987).



The state trajectories during the 'heel-off propulsion phase' are unique, not only in the kinematics, but in the muscle forces and in the other states used to model muscle dynamics (e.g., muscle activation, Zajac, 1989). For a time preceding heel-off, however, only unique kinematics are required, which can be achieved with a variety of muscle force trajectories (Levine *et al.*, 1983b, 1984, 1987). Prior to this epoch, there is not even uniqueness in the kinematics. Thus the optimal control strategy for maximum-height jumping can, in theory, be partitioned into three rather than two contiguous epochs; however, designing experiments to see if two distinct epochs exist in the 'flat-feet propulsion phase' is difficult (Levine *et al.*, 1987). Nevertheless, kinematic, force-plate, and EMG data from humans and cats jumping to their maximum achievable heights support the overall two-phase propulsion-strategy theory (Levine *et al.*, 1983b, 1984, 1987; Zomlefer *et al.*, 1977; Zajac *et al.*, 1981; Zajac, 1985).

The notion of a perfect separation in strategy before and after heel-off should not, however, be held too strictly. The separation in strategy is based on the assumption that the toes have point contact with the ground after heel-off. But if the toes are considered to be another rigid body being coordinated, then only the epoch subsequent to metatarsal lift-off would demand an on-off control strategy. And of course the feet and toes are not rigid bodies. The major conclusion is that as the physical constraints become inactive during propulsion (e.g., first with the heels and then with the metatarsals losing contact with the ground), muscle coordination should become more stereotyped.

In addition, the notion that some muscles (e.g., uniaxial leg extensor muscles) should be excited just prior to and at lift-off is actually counter to intramuscular EMG recordings, probably because the joints would otherwise hyperextend (Zajac, 1985). Nevertheless, the consequent deceleration of the body center of mass is counter to jumping as high as possible since the strategy of exciting uniaxial extensor muscles fully to lift-off is robust to the details of the model. Of course jumpers might not want to implement exactly the optimal strategy for jumping as high as possible because they may want to jump again (e.g., their joints might otherwise be seriously injured because of hyperextension). Though our models have not included such factors (e.g., reflexes to protect joints), the results from our models support the existence of such protective reflexes.

#### *Is jumping height more sensitive to muscle strength or to speed?*

If you could choose between the two, strengthen your muscles rather than condition your muscles to be faster. This answer follows from solving optimal control problems based on a model of the motor task (i.e., jump as high as possible; Sim, 1988; Sim *et al.*, 1989a), where each problem assumed a different muscle strength or speed (Pandy and Zajac, 1989;

Pandy, 1990). The nominal musculoskeletal model used in the formulation of the optimal control problem consisted of four body segments, and five uniaxial and three biarticular leg muscles, where each muscle was assumed to have both activation and contraction dynamics (Fig. 5; Sim, 1988; Sim *et al.*, 1989a; Pandy *et al.*, 1990). We found that the body-segmental and muscle coordination patterns that should produce the highest height jump resembled those of jumping human subjects (Fig. 6, stick figures; Pandy *et al.*, 1990). Thus, the experimentally observed and theoretically produced ground reaction forces, kinematics, and muscle coordination patterns were found to be quite similar (e.g., Fig. 6). The simulated SJ begins with a countermovement (Fig. 6, 0% to 40% of ground contact time), consistent with how human subjects start their jump (Pandy *et al.*, 1990; Pandy and Zajac, 1991).

Because the simulated SJ emulated human jumping well, we felt comfortable in using the optimal control model to study how sensitive SJ height is to changes in musculoskeletal parameters (e.g., muscle strength and speed). Changes in muscle speed were implemented by changing the intrinsic shortening speed of the muscle fibers in all eight simulated leg muscles (i.e., the speed of the muscle fibers was changed by making

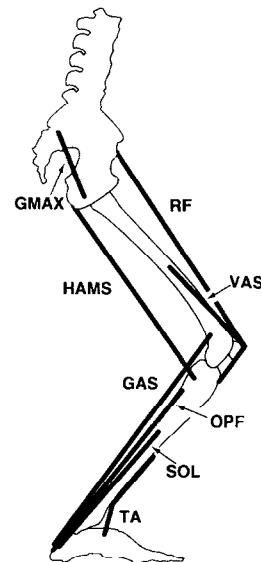


Fig. 5. Musculoskeletal model used in the formulation of an optimal control problem to study maximum height jumping. Sagittal plane motion is assumed. Four body segments represent the multijointed skeleton (feet, shanks, thighs, head-arms-trunk). Eight muscle groups control body movement (GMAX: gluteus maximus and the other uniaxial hip extensor muscles; HAMS: hamstrings; RF: rectus femoris; VAS: vastus lateralis, medialis, and intermedius; GAS: gastrocnemius lateralis and medialis; SOL: soleus; OPF: the other plantarflexor muscles; TA: tibialis anterior and the other dorsiflexor muscles).

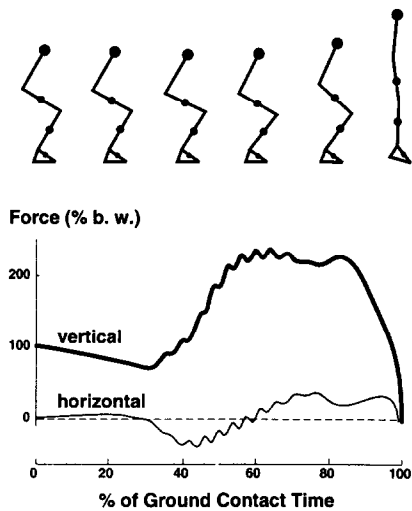


Fig. 6. Optimal control solution for a maximum-height squat jump. Stick figures (and video display of body segmental motion; not shown) show how the body segments should be coordinated during propulsion for the body center of mass to subsequently achieve while airborne its maximum-achievable height. Vertical and horizontal ground reaction forces are similar to those produced by human subjects. Notice that the vertical force initially falls below body weight, indicating that a countermovement may be optimal even in a squat jump (see text). The force oscillations are a result of imperfect modeling of the interaction between the feet and the ground, and computational limitations of the optimization algorithm. (Modified from Pandy *et al.*, 1990.)

fiber speed per unit length faster or slower and not by making the fiber longer or shorter). Changes in muscle strength were implemented by changing the physiological cross-sectional area (and mass) of all muscles and keeping muscle stress the same (cf. changing muscle stress and keeping the area, and mass, the same).

Unsurprisingly, SJ height was found to be higher as muscles become stronger or faster (Pandy and Zajac, 1989; Pandy, 1990). With stronger or faster muscles, the force exerted by the body on the ground was higher, though the duration of the upwards propulsive force was shorter. Nevertheless, the vertical velocity of the body at take-off was still larger, and thus a higher height achieved. Since jump height was found to increase about linearly at about 120% and 60% for a 100% increase in strength and speed, respectively, it seems better to strengthen muscles than to condition muscles to be faster (if that could be possible), at least in a SJ (sensitivity of CMJ height to muscle strength and speed has not been studied).

#### *Is elastic energy storage important to achieving maximum jumping height?*

Data from simulated jumps suggest that storage of elastic energy in musculotendon elastic structures is unimportant to achieving maximum jump height.

Solutions to the multijoint, multimuscle optimal control problem discussed above showed that SJ and CMJ height is insensitive to large and small changes in musculotendon compliance (Pandy and Zajac, 1989; Pandy, 1990; Anderson and Pandy, 1992). Changes in musculotendon compliance were implemented by changing the tendon elastic stress-strain curve (cf. changing tendon length) of either the plantarflexor (Pandy and Zajac, 1989) or the major energy-producing muscles in the jump (Anderson and Pandy, 1992).

The low sensitivity of CMJ height to compliance may seem unexpected. However, series compliance slows the dynamic response of musculotendons, just as slowly-contracting muscle fibers do (Zajac, 1989). If the dynamic response of the musculotendons is slow relative to propulsion dynamics, as is indeed the case in jumping, then changes in musculotendon compliance will affect significantly the responsiveness of the musculotendons. Thus, perhaps the small positive net effect an increase in musculotendon compliance has on jumping height occurs because a large positive effect, resulting from the ability of the musculotendons to store and release elastic energy, is significantly offset by a negative effect, resulting from their inability to develop force fast.

Though simulation data suggest that storage of elastic energy in musculotendons is unimportant to achieving maximum jump height, this is not to say that significant elastic energy is not stored in these structures during propulsion. In fact, simulation data show that high elastic energy is stored in musculotendons and utilized during jumping (Anderson and Pandy, 1992). For example, up to 70% of the energy delivered to the skeleton by plantarflexor muscles was found to come from stored elastic energy, consistent with or even higher than the calculations of others (Bobbert *et al.*, 1986b).

Musculotendon elasticity may, however, enable a CMJ jump to be performed efficiently (Anderson and Pandy, 1992). Simulations show that some of the gravitational energy from standing is indeed stored and utilized in musculotendon elastic structures (Anderson and Pandy, 1992). Furthermore, with increases in musculotendon elasticity, more energy is stored and utilized in these elastic structures and less energy is delivered to the skeleton by the contractile apparatus. Perhaps, as a result, less metabolic energy is utilized. Thus, just as animals can hop efficiently by having compliant tendons (e.g., Alexander and Bennet-Clark, 1977; Morgan *et al.* 1978), it may be that so too could humans if they had compliant tendons.

Could energy be stored in elastic structures other than musculotendons during the countermovement and later be recaptured to enhance lift-off velocity of the body? The feet are a candidate because they are elastic (Ker *et al.*, 1987) and storing energy in elastic structures that make contact with the ground during countermovement, such as the feet, theoretically can

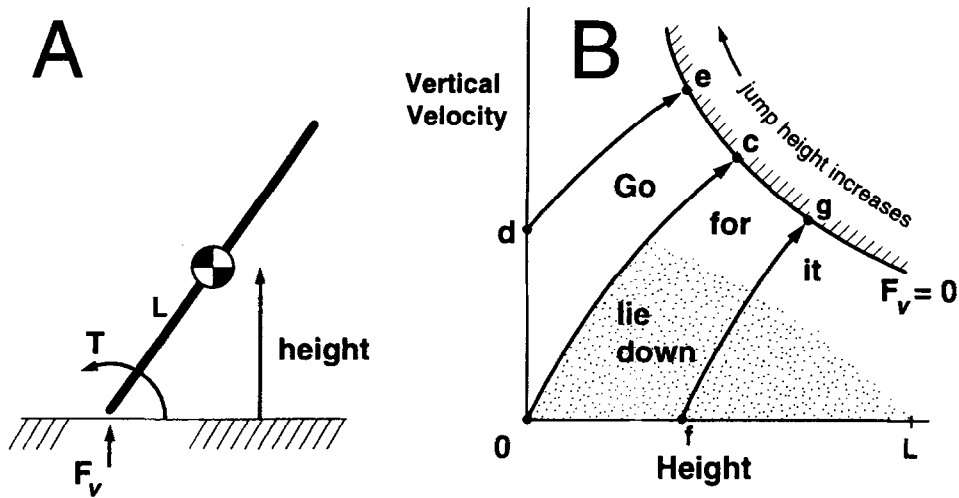


Fig. 7. Optimal strategies for a rod driven by a torque to 'jump' as high as possible. (A) A torque generator  $T$  is assumed to develop only extensor torque on a rod, but the results are generalizable to a flexor/extensor torque generator. The rod is assumed to make frictionless, no-slip point contact with the ground as long as the vertical ground reaction force is positive (i.e.,  $F_v > 0$ ). The rod lifts off the ground ('jumps') when  $F_v = 0$ . (B) The height and vertical velocity of the center of mass (c.m.) of the rod specify the state of the dynamical system since the torque generator is assumed to lack dynamics. From any initial state, the optimal feasible trajectory for propelling the c.m. (or the tip) of the rod as high as possible can be found. For the rod initially flat on the ground and at rest (point  $o$ ) the trajectory is  $oc$ . Point  $c$ , being the rod's height and velocity at lift-off, determines jump height. The rod jumps higher if it has momentum when initially flat (trajectory  $de$ ). The control strategy is to fully excite the extensor torque generator when the initial state resides in the region 'Go for it'. When in the region 'lie down', the strategy is to let the rod first fall to the horizontal resting position (i.e., point  $o$ ) and then fully excite the torque generator (e.g., if the rod is initially at an inclination, point  $f$ , a torque control should be employed that first brings the rod to the horizontal resting position, point  $o$ , which, after the subsequent full thrust, leads to a higher jump, point  $c$ , than what would have been achieved with full thrust outright, point  $g$ ). (See text).

lead to higher jumps (Levine and Zajac, 1984). Future simulations are needed, however, to resolve whether this suggestion is tenable.

#### Why countermove?

In jumping from a full upright standing position the body must first countermove to a squat. In fact, subjects even countermove when they start jumping from a squat, in agreement with simulated optimal jumps (Pandy *et al.*, 1990; Pandy and Zajac, 1991). Many biomechanical and physiological mechanisms potentially interact in executing an optimal countermovement strategy. Also, there may be non-unique optimal strategies in this preparatory phase of the jump (see above). Overwhelming evidence supporting any one mechanism is non-existent. However, as simulations of maximum-height jumping become easier to compute (see "The Future: Will Muscle Coordination Principles Emerge?"), we should be able to gain more insight.

Nevertheless, simulations and analyses of jumping to date have helped to delineate the issues. First, let us remember that in attempting to jump as high as pos-

sible, we want to have as much take-off vertical velocity as possible. We can maximize vertical take-off velocity by either increasing the duration of upwards propulsion (i.e., the time when the body center of mass accelerates upward) or the vertical acceleration of the body during upwards propulsion (i.e., the vertical ground reaction force). Countermoving to a deep squat seems to lengthen upwards propulsion duration. It may also cause higher vertical acceleration, especially at the beginning of the upward movement of the body (Asmussen and Bonde-Petersen, 1974; see later).

Let me describe results from a simple model (Roberts *et al.*, 1979; Levine *et al.*, 1983a) that support the notion that the countermovement enables upwards propulsion duration to be longer (Anderson and Pandy, 1992). The simple model consists of just one segment (a rod) being propelled by a controllable extensor torque generator (Fig. 7A). With this model we formulated and solved analytically an optimal control problem that approximates jumping (Roberts *et al.*, 1979; Levine *et al.*, 1983a). That is, assuming the rod could have any initial kinematic state (e.g., rod height and vertical velocity), we found how a bounded

extensor torque generator must be controlled to propel the rod's center of mass (c.m.) or tip as high as possible. The solution suggests a basic strategy consistent with the more complex models (see above). The more extensor torque the generator can produce (cf. extensor muscle strength), the higher the jump, regardless of the initial kinematic state. If the rod is resting on the ground (cf. the best resting deep squat position), the strategy is to turn the generator on fully throughout propulsion until lift-off (Fig. 7B, trajectory *oc*). (Notice that the two-phase control strategy associated with jumps starting from a deep squat is not predicted from this one-segment model and is, thus, a result of the body being multijointed; see above).

The solution shows that it is better to start the upwards movement of the rod from a horizontal position (cf. a deep squat) rather than from a higher position (Roberts *et al.*, 1979; Levine *et al.*, 1983a) because upwards propulsion duration is longer (Anderson and Pandey, 1992). Therefore, if the rod is initially inclined to the horizontal (cf. not in a deep squat; Fig. 7B, *lie down* region; e.g., point *f*), the optimal control strategy is first to let it fall to the ground to point *o* (cf. countermove to a deep squat) rather than to fully excite the extensor torque generator outright and have the rod be propelled upwards (cf. propel the body upwards without countermovement; Fig. 7B, trajectory *fg*). After the rod falls to the ground, the extensor torque generator should be fully excited until lift-off (i.e., the rod follows trajectory *oc*). The rod now

jumps higher than it would have, had it not at first fallen to the horizontal position (compare point *c* with *g*). Optimal control simulations of jumping using our more complex model of the body suggest that prolongation of the upwards propulsion duration is the key benefit received from a countermovement (Anderson and Pandey, 1992).

The solution also shows that the rod should be exerting as much propulsive torque as possible when it starts upwards from this lowest position, the deep squat (cf. the body should have as much vertical acceleration as possible when it starts moving upwards; Roberts *et al.*, 1979; Levine *et al.*, 1983a). Thus, if the extensor torque generator should behave like a low-pass filter in generating force to neural excitation (and a muscle certainly does since force does not develop instantaneously; Zajac, 1989), then the optimal strategy is to have the extensor torque generator brake the countermovement so that high torque will be exerted on the rod when it reaches the horizontal position. This suggests that the energy-producing muscles of the jump (see below) should be excited not just to brake the fall during countermovement, but brake the fall in such a way that high vertical acceleration of the body is attained as it begins to move upwards (Asmussen and Bonde-Petersen, 1974; Levine *et al.*, 1987).

Finally, other results from this model show that if the rod makes an elastic collision with the ground as a result of a countermovement (cf. the feet being elastic

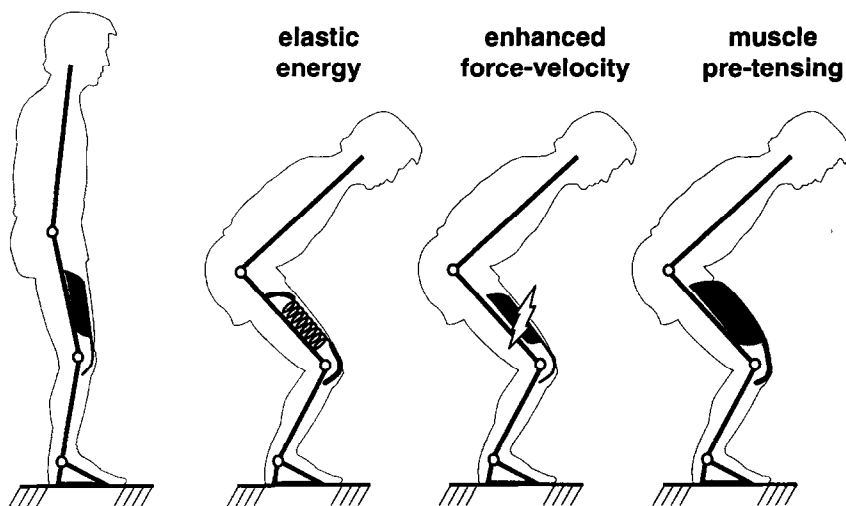


Fig. 8. Cartoon showing three mechanisms for why a countermovement may lead to a higher jump height. Initial upright position of the body before it countermoves is shown at the left. The mechanisms are: (i) *elastic energy*, stored in stretched musculotendinous structures during the countermovement, is subsequently recaptured during upwards movement of the body; (ii) muscle-fiber pre-stretching causes an *enhanced force-velocity* relation during upwards movement of the body; and (iii) a better kinematic and muscle state is reached, such as muscle 'pre-tensing', from which to launch upwards propulsion. Modeling data suggest that the dominant factors affecting jumping height are an enhanced force-velocity relation and muscle pre-tensing. Though elastic energy storage is high in jumping, it is unimportant to performance. (See text).

and the heels slapping the ground during the countermovement), then elastic energy storage and release causes a higher jump (Levine and Zajac, 1984). The reason is that the rod's downward momentum is converted into upward momentum, a better initial state from which to begin upwards propulsion (Fig. 7B, compare point *d* with *o* and trajectory *de* with *oc*).

In summary, it seems that the body should countermove to a deep squat to compensate for the lags associated with muscle force buildup, thereby enabling the body to attain high upwards vertical acceleration at the moment the body moves upwards (Fig. 8, *muscle pre-tensing*). In addition, muscles may be 'temporarily stronger' during upwards movement of the body because of prior stretching of activated muscle fibers during the braking of the countermovement (Fig. 8, *enhanced force-velocity*; Cavagna *et al.*, 1968). Countermovement prolongs upwards propulsion (the time when the body center of mass accelerates upward) and this seems to be very important. Storage and release of energy in elastic ankle, knee, and hip musculotendon structures seems to be not important to

upwards propulsion (see above; Fig. 8, *elastic energy*), though storage of elastic energy in the feet may be.

#### *What is the role of uni- and bi-articular muscles?*

In a SJ, our experimental studies suggest that uniarticular extensor muscles provide most of the propulsive mechanical energy (i.e., they are the prime movers), uniarticular flexor muscles are virtually non-participatory, and biarticular muscles fine-tune the coordination. We found that uniarticular extensor hindlimb muscles of cats jumping to their maximum-achievable height are maximally excited after heel-off, uniarticular flexor muscles are inactive, and biarticular muscles (except gastrocnemius) are deactivated (Zomlefer *et al.*, 1977; Zajac *et al.*, 1981; Zajac, 1985). Prior to heel-off, in preparation for the explosive 2nd propulsion phase of jumping, cat biarticular posterior thigh muscles (i.e., hip extensor/knee flexor muscles) exhibit much more variability than uniarticular posterior thigh muscles (i.e., hip extensor muscles), consistent with the notion that biarticular muscles fine-tune coordination (Zajac, 1985).

Solutions from our multisegmental, multimuscule optimal control model of maximum-height human jumping also suggest that uniarticular extensor muscles are the prime movers and biarticular muscles fine-tune the coordination in both a SJ (Fig. 9; Pandy and Zajac, 1991) and a CMJ (Pandy *et al.*, 1992). Notice the high power and energy (area under the curves) produced by the uniarticular muscles (GMAX, VAS, UPF) and the low power and energy developed by the biarticular muscles (GAS, HAMS, RF). Most of the mechanical energy generated by muscles goes into propelling the trunk because its mass dominates.

Rectus femoris (RF) is excited even though it produces negative work throughout propulsion because the additional work produced by the other muscles as a result of RF being excited more than compensates for its negative work (Zajac and Pandy, 1992). This is what coordination is all about; i.e., muscles working together to achieve a common goal. Recent simulations of CMJs as well as SJs, where changes were made to the musculoskeletal parameters of the optimal control model, suggest that hamstrings play a more significant role as a prime mover than previously thought (Anderson and Pandy, 1992). Gastrocnemius, however, still seems to have the same role as the other plantarflexors (Pandy and Zajac, 1991; Zajac and Pandy, 1992).

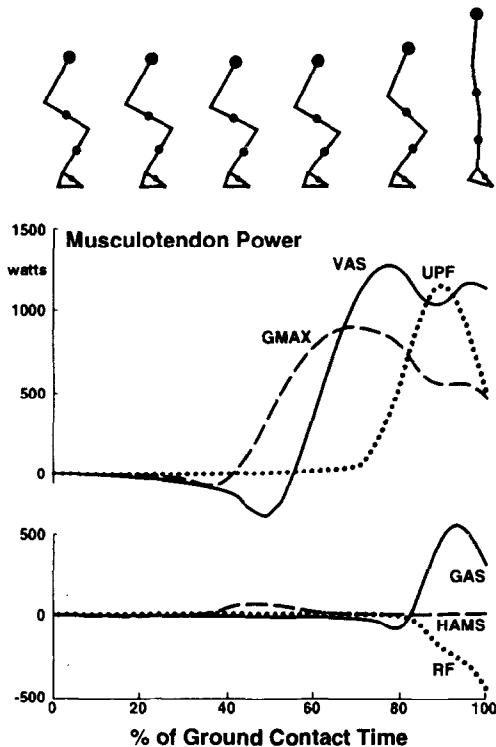


Fig. 9. Musculotendon power during propulsion calculated from the optimal control solution for a maximum-height squat jump. Uniarticular muscles provide most of the power and energy (GMAX, VAS, UPF). Biarticular muscles fine-tune the coordination (GAS, HAMS, RF), especially as lift-off approaches (i.e., lift-off occurs at 100% of ground contact time). UPF (uniarticular plantarflexors) are the SOL and OPF muscles. See Fig. 5 for muscle nomenclature. (Modified from Pandy and Zajac, 1991.)

#### THE FUTURE: WILL MUSCLE COORDINATION PRINCIPLES EMERGE?

Forward dynamics models can be extremely powerful in elucidating task-specific muscle coordination principles (e.g., optimal control models, see above). Why then have only a few motor tasks been studied with forward dynamics models (e.g., jumping, see above; Winters and Stark, 1985; Khang and Zajac, 1989; Yamaguchi and Zajac, 1990; Self-Naraghi and

Winters, 1990; He *et al.*, 1991)? And even for these tasks, why have models not been used more (e.g., to study fully the sensitivity of coordination to musculoskeletal parameters or structure)? The reasons are: (i) the development of a sufficiently complex, realistic, multijoint, multimuscule forward dynamics model of the body requires considerable effort; (ii) the computational time to find how the model-generated movement of the body responds to an assumed muscle excitation pattern is long; (iii) body segments are inadequately coordinated when assumed muscle excitation patterns are applied as inputs to a forward dynamics model (even when the patterns are derived from EMG signals since these signals may just roughly correspond to the neural excitation signals of the muscle model); and (iv) dynamic optimization algorithms to iteratively find an acceptable muscle excitation pattern are few, not robust, and computer-time intensive.

One possible solution is to develop an interactive computer graphics workstation environment that allows simulations of motor tasks to be generated more easily (Fig. 10). This environment could be structured to contain a variety of compatible software modules. Some modules might be commercial software, and others would have to be developed. The environment could be structured so a user would, first, develop a forward dynamics model of a specific motor task (Fig. 10, *State Equations*); second, generate a simulation of the task (Fig. 10, *Simulations*); and third, display and compare the computer modeling data with experimental data (Fig. 10, *Display*).

In this conception, the user would develop a forward dynamics model by user-friendly, menu-driven workstation interaction. The workstation would ensure that all software modules are compatible and transparent to the user. The user would have to learn only one set of nomenclature. Graphic display and animation would facilitate model development. The user would be able to:

- (i) create a musculoskeletal model (e.g., specify the mass and geometry of the body segments, the kinematics of joints, and the musculotendon paths; Delp *et al.*, 1990) (Fig. 10, *Musculoskeleton*);
- (ii) create a dynamical model of how musculotendons generate force from muscle excitation signals (Fig. 10, *Muscle-Tendon*);
- (iii) generate the dynamical equations of motion of the body segments applicable to a specific motor task and the assumed musculoskeletal model (Fig. 10, *Eqns. of Motion*);
- (iv) create a dynamical neural network model (Fig. 10, *Neural Networks*);
- (v) combine these dynamical models of the neural network, the musculotendons, and the body-segments to generate a forward dynamics model (Fig. 10, *State Equations*).

Once the state equations (i.e., forward dynamics model) were generated, the next step would be to generate a simulation (Fig. 10, *Simulations*). To generate a simulation, an appropriate muscle excitation pattern must be applied as an input to the state equations. One approach would be to use observed

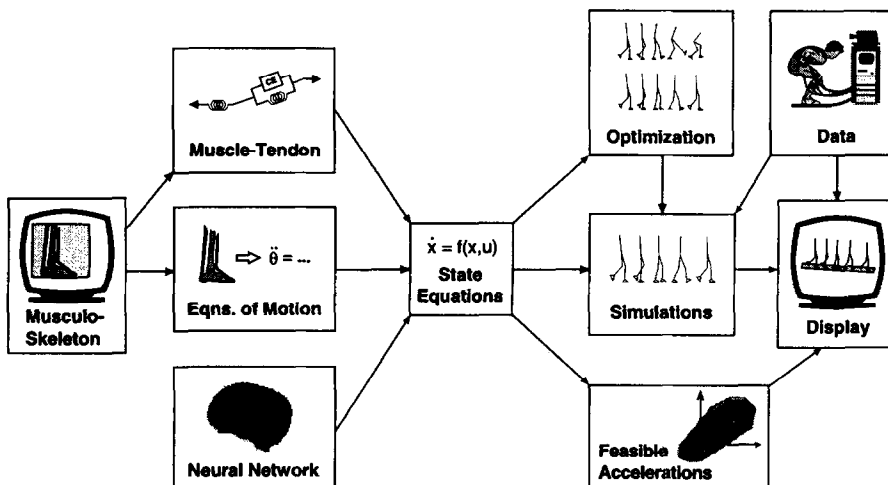


Fig. 10. Proposed interactive computer workstation environment to generate simulations of motor tasks. Modules *Musculoskeleton*, *Muscle-Tendon*, *Eqns. of Motion*, and *Neural Network* allow the user to develop the forward (or inverse, not shown) dynamical models of the neuromusculoskeletal system (the *State Equations*). Kinesiological *Data* and *Optimization* algorithms enable *Simulations* to be generated. Both kinesiological and simulation data can be visualized (*Display*). Bounds on the accelerations achievable in a task (*Feasible Accelerations*) can be computed and displayed. (See text).

EMG patterns from which to estimate an initial guess (Fig. 10, *Data*) and then use a dynamic optimization algorithm (Fig. 10, *Optimization*) to modify this guess until the observed movement and kinetics of the body are simulated as well as possible. The other approach would be to postulate what the purpose of the motor task is and use a dynamic optimization algorithm to find the excitation pattern that best performs the task (See "Integrating Experiments and Models to Study Muscle Coordination").

The final step would be to display either simulation data, kinesiological data, or both (Fig. 10, *Display*). Animations of the body could be one option since coordination is often subtle and requires dynamic visualization of motion of the body segments. Computing bounds on the accelerations the body can achieve in executing a motor task could be another (Fig. 10, *Feasible Accelerations*). Such bounds provide insight into the extent to which the biomechanics or the nervous system dictates movement strategies (Kuo and Zajac, 1992, this volume).

To conclude, we have developed and used forward dynamics models to study muscle coordination, e.g., of jumping (see above), posture (Khang and Zajac, 1989; Kuo and Zajac, 1992, this volume), walking (Yamaguchi and Zajac, 1990), and pedaling (Sim, 1988; Sim *et al.*, 1989b; Levine *et al.*, 1989; Fregly and Zajac, 1989). Unfortunately, the development phase of modeling has been so long that model-generated data have been meager. We believe that an interactive workstation environment to develop models and produce simulations will help circumvent this limitation. The decreased cost of high-powered graphics workstations will also. Perhaps we will soon understand well how muscles control many different motor tasks. Hopefully muscle coordination principles will then emerge.

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