Review

Biomechanics and muscle coordination of human walking Part I: Introduction to concepts, power transfer, dynamics and simulations

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Abstract

Current understanding of how muscles coordinate walking in humans is derived from analyses of body motion, ground reaction force and EMG measurements. This is Part I of a two-part review that emphasizes how muscle-driven dynamics-based simulations assist in the understanding of individual muscle function in walking, especially the causal relationships between muscle force generation and walking kinematics and kinetics. Part I reviews the strengths and limitations of Newton–Euler inverse dynamics and dynamical simulations, including the ability of each to find the contributions of individual muscles to the acceleration/deceleration of the body segments. We caution against using the concept of biarticular muscles transferring power from one joint to another to infer muscle coordination principles because energy flow among segments, even the adjacent segments associated with the joints, cannot be inferred from computation of joint powers and segmental angular velocities alone. Rather, we encourage the use of dynamical simulations to perform muscle-induced segmental acceleration and power analyses. Such analyses have shown that the exchange of segmental energy caused by the forces or accelerations induced by a muscle can be fundamentally invariant to whether the muscle is shortening, lengthening, or neither. How simulation analyses lead to understanding the coordination of seated pedaling, rather than walking, is discussed in this first part because the dynamics of pedaling are much simpler, allowing important concepts to be revealed. We elucidate how energy produced by muscles is delivered to the crank through the synergistic action of other non-energy producing muscles; specifically, that a major function performed by a muscle arises from the instantaneous segmental accelerations and redistribution of segmental energy throughout the body caused by its force generation. Part II reviews how dynamical simulations provide insight into muscle coordination of walking.
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1. Introduction

Humans use their legs most frequently to stand and locomote. Walking is a task that we seek to understand well because it is a most relevant task to humans. This two-part review focuses on the biomechanics and muscle coordination of the legs in healthy adults while walking (for standing, see Ref. [1]). Studies of human locomotion have a long history [2,3] and current understanding

results from the ability to measure EMG activity with surface and indwelling electrodes [4–7] along with the kinematics of the body and the ground reaction force [8]. However, the causal relationships between the measured output variables, such as the kinematics and kinetics, and the measured input variables, such as the pattern of EMG activity, must be determined to further our understanding. Unfortunately, the establishment of these relationships to understand muscle coordination of walking is difficult because many body segments, including the trunk, are being coordinated. Complexity is further enhanced because any one muscle may affect the acceleration and power of all body segments because of dynamical coupling [9].

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We and others [10–12] believe that muscle-based simulations of the walking dynamics are critical to the determination of the causal relationships between EMG patterns and gait kinematics and kinetics. Indeed, simulations have been the cornerstone to the understanding and design of complex multi-input/-output dynamical mechanical systems, such as aircraft, satellites, and weather forecasting. This two-part review emphasizes how simulations of walking from dynamical musculoskeletal models can lead to a comprehension of muscle coordination (see also Ref. [13]).

Before simulation-based coordination principles of walking are reviewed in Part II, this Part I reviews basic kinetic concepts and the advantages and limitations of both traditional Newton–Euler inverse dynamics analyses and dynamical simulations in understanding muscle coordination. Because of the simplicity of the dynamics of pedaling compared to walking, analyses of pedaling simulations are used to show how coordination principles can be deduced from muscle-induced acceleration and segmental power analyses. Emphasis is given to the identification of muscle synergies (i.e. co-excited muscles acting to accelerate the segments differently to accomplish a common task goal), co-functional muscles (i.e. co-excited muscles acting to accelerate the segments similarly), and the redistribution of mechanical energy among the segments caused by individual muscle force generation.

2. Net joint moment, joint intersegmental force, segmental power

A net joint moment is the sum of the individual moments about a joint from the forces developed by muscles and other structures crossing that joint, such as ligaments, as well as those moments due to bone and cartilage contact between segments. When the net joint moment arises primarily from muscles, it is called the 'net muscle moment about the joint'. Net joint moments are often used to assess coordination of movement because their genesis is the muscle forces to a large extent.

The joint intersegmental force, also called the joint resultant force, arises from the acceleration of the body segments and the interaction forces with the environment, such as from the ground or gravity. The joint intersegmental force underestimates the joint contact force, which also includes the compressive forces from muscles, ligaments, and other structures crossing the joint [14]. These compressive forces are, in general, non-contributory to the acceleration of the segments [9]. The term 'joint reaction force' is inconsistently used and sometimes refers to the joint intersegmental force and at other times to the joint contact force.

Segmental power is the time rate of change of the summed potential and kinetic energy of a segment, such as the foot, shank or thigh. Segmental power is computed in one of two ways, either the kinematic or kinetics method. The kinematic method uses the observed or estimated position, orientation, linear velocity and angular velocity of the segment over a short time interval to compute the differential change of kinetic and potential energy of the segment. The kinetic method computes the power at a specific time by summing the power entering and leaving the segment by all forces and moments acting on the segment, which can be found from traditional Newton–Euler inverse dynamics methods. Thus, the two joint-intersegmental forces acting on the segment are multiplied by the respective joint linear velocities, and the two net joint moments acting on the segment are multiplied by their respective joint angular velocity, and all the products summed [15,16]. The methodological problems associated with these two theoretically equal methods have been studied [17]. Specifically, the two methods produce non-equivalent results when either numerical differentiation introduces noise in the kinematic data or when the skin-surface mounted markers placed on the body to measure segment endpoints move inconsistently with rigid body assumptions. Both conditions exist in the analysis of gait laboratory measurements to some degree.

3. Net joint power and individual muscle power

Net joint power is a kinetic quantity computed by multiplying the net joint moment by the joint angular velocity or, equivalently, by the difference in angular velocities of the adjoining segments:

Net joint power

$$= \text{(net joint moment)(joint angular velocity)} \quad \text{(1a)}$$
$$= M_j \omega_j \quad \text{(1b)}$$
$$= (M_j \omega_1)(M_j \omega_2), \quad \text{(1c)}$$

where

$$\omega_j = \text{joint angular velocity} = \omega_1 - \omega_2, \quad \text{(1d)}$$

and ω_1, ω_2 are the angular velocities of the two segments in an inertial reference frame (Fig. 1).

Net joint power is useful because it represents the summed power by the net joint moment to/from all the segments. The sum of all the net joint powers represents the summed power to/from all the segments by all the net joint moments, and thus by all the muscles [18]. However, an individual net joint power does not represent the summed mechanical power delivered to the body segments by the muscles crossing that joint because biarticular muscles crossing that joint also
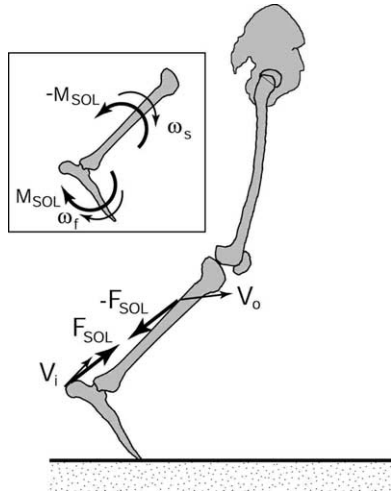
Fig. 1. Muscle force, muscle moment, and muscle power produced by SOL. Total power produced by SOL is $(F_{SOL} \cdot V_i - F_{SOL} \cdot V_o)$, where V_i and V_o are the velocity vectors of its insertion and origin, respectively. Equivalently, SOL power is $(M_{SOL} \cdot \omega_f - M_{SOL} \cdot \omega_s = M_{SOL} \cdot (\omega_f - \omega_s))$, where M_{SOL} is the SOL ankle moment, ω_f, ω_s are the angular velocities of the foot and shank, respectively, and $\omega_f - \omega_s$ is the ankle angular velocity into extension. However, the power delivered by SOL to the foot is not given by $F_{SOL} \cdot V_i$, or $M_{SOL} \cdot \omega_f$, and the power to the shank not by $-F_{SOL} \cdot V_o$, or $-M_{SOL} \cdot \omega_s$, because some of the power produced from SOL is delivered to the trunk and the thigh (see Fig. 2).

contribute to the net powers of the other spanned joints [19,20].

The net power produced or absorbed by a uni- and biarticular muscle, or more precisely the musculotendon complex, is given by Eqs. (2) and (3):

Uniarticular muscle power

$$= (\text{muscle force})(\text{muscle velocity}) \qquad (2a)$$

$$= (\text{muscle force})\{(\text{insertion velocity})$$
$$-(\text{origin velocity})\} \qquad (2b)$$

$$= (\text{muscle moment})(\text{joint angular velocity}) \qquad (2c)$$

Biarticular muscle power

$$= (\text{muscle force})(\text{muscle velocity}) \qquad (3a)$$

$$= \text{muscle force}\{(\text{insertion velocity})$$
$$-(\text{origin velocity})\} \qquad (3b)$$

$$= ((\text{muscle moment at joint 1})(\text{angular velocity of joint 1}))$$

$$+((\text{muscle moment at joint 2})(\text{angular velocity of joint 2})) \qquad (3c)$$

$$= (\text{'muscle power at joint 1'})$$
$$+(\text{'muscle power at joint 2'}) \qquad (3d)$$

Thus, a uniarticular muscle contributes to only one net joint power (Fig. 1) and a biarticular muscle to only two net joint powers. The sum of all the 'muscle powers' at a joint equals the net joint power since the net joint moment is the sum of all the muscle moments (follows from Eqs. (1–3)).

Muscle power is a very useful quantity to compute because it has physical relevance. It represents the summed mechanical power to/from *all* the segments in the system by the muscle.

4. Muscle contribution to joint intersegmental force and segmental acceleration and power

The force generated by a muscle acts to accelerate instantaneously not only the segments to which it attaches and the joints that it spans, but also all other segments and joints [9,21]. For example, when the foot is on the ground, the uniarticular soleus (SOL) acts to accelerate instantaneously the shank and the foot, segments to which it attaches (Fig. 1), and the thigh
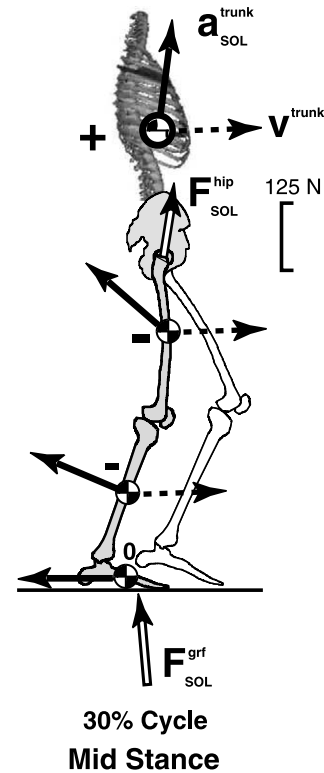

30% Cycle
Mid Stance

Fig. 2. Redistribution of segmental energy by SOL muscle in mid stance while at a nearly constant length. *Unfilled arrows*: Contribution to the hip intersegmental force F_{SOL}^{hip}, and the ground reaction force F_{SOL}^{grf}. Calibration bar applies to these forces. Contribution to the ankle and knee intersegmental forces are similar to the ground reaction force contribution (not shown). *Filled arrows*: Contribution to the linear accelerations of the segments (only trunk labeled, a_{SOL}^{trunk}). Magnitudes are unscaled. *Dashed arrows*: Linear velocity of segments (only trunk labeled, v^{trunk}). Magnitudes are unscaled. Notice motion of segments is mostly forward. Because a_{SOL}^{trunk} has a component collinear with v^{trunk}, SOL acts to accelerate the trunk forward to cause energy flow to the trunk ('+'). SOL-induced acceleration of thigh and shank have a backward component to decelerate these segments ('−'; energy flow < 0). Net effect of SOL on foot is small ('0'). Thus, while acting nearly isometrically, SOL redistributes energy from the leg to the trunk in mid stance. Data are from simulation in Ref. [28].

and trunk, segments to which it does not attach (Fig. 2). Similarly, SOL not only acts to accelerate the spanned ankle joint into rotation, but also the other unspanned joints, such as the knee and hip.

The ability of a muscle force to contribute instantaneously to the linear and angular acceleration of segments and joints far removed from the ones to which the muscle attaches or spans, such as SOL in mid stance (Fig. 2), is due to the dynamic coupling arising from the multiarticular nature of the body. Mathematically, this dynamical coupling arises because the equations-of-motion of the multiarticulated body are coupled. Specifically, the generalized equations-of-motion can often be written as:

$$\mathbf{I}(\boldsymbol{q})\ddot{\boldsymbol{q}} = \boldsymbol{M}^{\text{joint}} + \boldsymbol{G}(\boldsymbol{q})g + \boldsymbol{V}(\boldsymbol{q},\ \dot{\boldsymbol{q}}) + \boldsymbol{F}^{\text{non}}(\boldsymbol{q},\ \dot{\boldsymbol{q}}), \qquad (4)$$

where $\boldsymbol{q}$, $\dot{\boldsymbol{q}}$, $\ddot{\boldsymbol{q}}$ is the vector of generalized coordinates, velocities, and accelerations (e.g. segment angles, angular velocities, angular accelerations); $\mathbf{I}(\boldsymbol{q})$, system mass matrix; $\boldsymbol{M}^{\text{joint}}$, vector of net joint moments ($\boldsymbol{M}^{\text{joint}} = \mathbf{R}(\boldsymbol{q})\boldsymbol{F}^{\text{mus}}$ with $\mathbf{R}(\boldsymbol{q})$, moment arm matrix; and $\boldsymbol{F}^{\text{mus}}$, vector of muscle forces); $\boldsymbol{G}(\boldsymbol{q})g$, $\boldsymbol{V}(\boldsymbol{q},\ \dot{\boldsymbol{q}})$, $\boldsymbol{F}^{\text{non}}(\boldsymbol{q},\ \dot{\boldsymbol{q}})$, vector of gravity, Coriolis and centripetal, and non-muscle terms.

Thus, the accelerations $\ddot{\boldsymbol{q}}$ are:

$$\ddot{\boldsymbol{q}} = \mathbf{I}^{-1}(\boldsymbol{q})\{\boldsymbol{M}^{\text{joint}} + \boldsymbol{G}(\boldsymbol{q})g + \boldsymbol{V}(\boldsymbol{q},\ \dot{\boldsymbol{q}}) + \boldsymbol{F}^{\text{non}}(\boldsymbol{q},\ \dot{\boldsymbol{q}})\};$$
$$(\boldsymbol{M}^{\text{joint}} = \mathbf{R}(\boldsymbol{q})\boldsymbol{F}^{\text{mus}}). \qquad (5)$$

Since $\mathbf{I}^{-1}(\boldsymbol{q})$ is non-diagonal, any one net joint moment M_j^{joint}, or any one muscle force F_i^{mus}, contributes instantaneously to any acceleration $\ddot{q}_k$ in $\ddot{\boldsymbol{q}}$, and thus to all segmental and joint linear and angular accelerations.

Another way to view dynamic coupling is to recognize that a force acting at any one point on the body induces forces instantaneously throughout the body because a joint transmits a force from one segment to the other via the joint intersegmental force. Since each joint intersegmental force $\boldsymbol{F}_j^{\text{interseg}}$ is generally given by:

$$\boldsymbol{F}_j^{\text{interseg}} = \sum_k (\ddot{q}_k \cdot \boldsymbol{f}_k(\boldsymbol{q})) + \boldsymbol{g}(\boldsymbol{q})g + \boldsymbol{w}(\dot{\boldsymbol{q}},\ \boldsymbol{q}), \qquad (6)$$

then it follows from Eqs. (5) and (6) that any one net joint moment, or any one muscle force, contributes instantaneously to all joint intersegmental forces (e.g. SOL in mid stance, Fig. 2).

Consequently, a muscle force also contributes instantaneously to the power of all segments because it contributes to each and every joint intersegmental force, which is apparent by considering a free-body diagram of a segment [22]. For example, SOL, which develops only an ankle extensor moment, acts to reduce the energy of the thigh and increase the energy of the trunk in mid stance (Fig. 2), which are segments to which it does not attach. Importantly, the power of a segment is linear in

the individual muscle forces (or the net joint moments), gravity, and other forces acting on the segments, which is the same as saying that the net power is equal to the sum of all components, because the accelerations and joint intersegmental forces are linear in these components (Eqs. (5) and (6)).

Power analyses offer many advantages. The summed power that a specific net joint moment, or muscle force, contributes to a group of segments can be found because power is a scalar. Conversely, the contribution to the power of a segment by a muscle can be algebraically partitioned into any set of orthogonal translational and rotational directions, such as upward, forward, lateral, fore-aft tilting, etc. The contribution of a muscle to a segment or groups of segments can be compared to the contribution from another force acting on the body, such as that from another muscle or from gravity.

The contribution of a biarticular muscle to segmental accelerations and powers need not be conceptually different from that of a uniarticular muscle. A biarticular muscle similarly acts instantaneously to accelerate all segments and joints and contributes to all segmental powers and joint intersegmental forces [9,21] (Eqs. (5) and (6)). However, whereas a uniarticular muscle will always act to rotate the spanned joint in a direction of the applied muscle moment, consistent with its anatomical classification, a biarticular muscle may act to rotate one spanned joint opposite to its joint muscle moment, inconsistent with its anatomical classification [9], because the muscle moment at the other joint may induce a stronger counter angular acceleration of the joint. Therefore, it is meaningless to attempt to develop a general conceptual classification scheme that assigns muscle function into 'uniarticular' versus 'biarticular' roles [23], though a biarticular muscle may prove to have a unique action on segmental energy flow in any given motor task, just as a specific uniarticular muscle may.

The net power instantaneously delivered by a muscle to either the segment of origin or insertion must be found from the coupled equations of motion and cannot be found from the dot product of its force vector at the origin (insertion) with the velocity vector of the origin (insertion), as given in Eqs. (2b) and (3b) (see also Fig. 1). The reason is that the effects of the muscle contributions to the joint intersegmental forces, which also act on the origin and insertion segments, are not included in the dot product. Similarly, the net power delivered to an adjoining segment by a net joint moment cannot be found from the dot product of the net joint moment vector with the segment angular velocity vector, as given in Eq. (1c). Again the reason is because the effects of the contributions of net joint moment to the joint intersegmental forces are not included. If the net power that a muscle or net joint moment delivers to a segment were given by the terms in Eqs. (2b), (3b) and

(1c), then no power could be delivered to segments to which a muscle does not attach. In general, this is not the case.

Unfortunately, it is often erroneously stated or inferred that a muscle delivers power to or absorbs power from only the segments to which it attaches. Or, conceptually equivalent, that a net joint moment affects power delivery/absorption from only the adjoining segments [16,24–26]. The error seems to arise because of the lack of recognition that the terms in Eqs. (2b) and (3b) are correct when combined for computing muscle power delivered to the entire system, but incorrect when used separately to find the *net* contribution to the segments to which they attach.

5. Transfer of power among segments

It is important to recognize that the primary function of a muscle can be to simply redistribute energy among segments rather than produce or dissipate energy. The redistribution of segmental energy results because the force generated by a muscle creates simultaneous segment accelerations and decelerations throughout the body. Muscle force can cause significant segmental energy redistribution irrespective of whether the muscle produces mechanical work output by shortening (acting concentrically), dissipates energy by lengthening (acting eccentrically), or neither by staying at a constant length (acting isometrically). Though the importance of energy production and dissipation by muscles to task execution has been emphasized [27], the ability of a muscle to redistribute segmental energy seems to be less appreciated.

A muscle undergoing no change in length can redistribute segmental energy by accelerating some segments and decelerating others such that the energy reduction of the decelerated segments equals the energy increase of the accelerated segments. For example, the uniarticular ankle plantar flexor (SOL) decelerates the thigh and the shank and accelerates the trunk causing energy flow from the leg to the trunk while at a nearly constant length during mid stance in walking (∼ 20–40% gait cycle) [28] (Fig. 2). SOL delivers translational power to the trunk because its contribution to the hip

intersegmental force has a component collinear with the translational velocity of the trunk (Fig. 2). Further analysis of the simulation data in Neptune et al. [28] reveals that most of the energy exchange caused by SOL while acting nearly isometrically in mid stance is due to changes in horizontal kinetic energy of the segments (Table 1).

A shortening muscle can also redistribute segmental energy by accelerating some segments and decelerating others, but in this case the energy gain of the accelerated segments exceeds the energy reduction of the decelerated segments by the amount of muscle work produced. For example, SOL during late stance (∼ 40–60% gait cycle) continues to decelerate the thigh and shank and accelerate the trunk while acting concentrically. But the energy gain of the trunk exceeds the energy reduction of the leg because SOL produces work by shortening [28] and also by releasing stored musculotendon elastic energy (see Part II).

A lengthening muscle can also redistribute segmental energy by accelerating some segments and decelerating others, but the energy gain of the accelerated segments is less than the energy reduction of the decelerated segments by the amount of energy dissipated in the muscle and stored in its elastic structures. For example, while acting eccentrically in early stance after heel-strike (0– ∼ 10% gait cycle), the uniarticular knee extensors (vasti group of the quadriceps, VAS) reduce the energy of the leg more than they increase the energy of the trunk because they dissipate energy as they lengthen [29]. Importantly, VAS continues to redistribute significant segmental energy afterwards while acting concentrically. Thus, a consistent function of the uniarticular knee extensors as they lengthen and then shorten in the beginning of stance, defined to be early stance into single-leg support, is to redistribute energy from the leg to the trunk (Fig. 3).

Thus, the concept that a uni- or biarticular muscle can transfer power from one segment to another is physically meaningful and important to the execution of complex motor tasks. Body segments have mass and their kinetic and potential energy can change throughout a movement. Energy flows into or out of the segments and muscles are critical players in this execution by their ability to redistribute segmental energy.

6. Transfer of power from one joint to another by a biarticular muscle: What does it mean?

The concept of a transfer of power by a biarticular muscle from one of its spanned joints to the other [19,20,30–33], which is based on 3, implies that a biarticular muscle can only accelerate/decelerate the segments of origin and insertion and the segment spanned. However, as noted above, a biarticular muscle,

Table 1
Energy flow or power, as measured in Watts (W), by SOL at mid stance

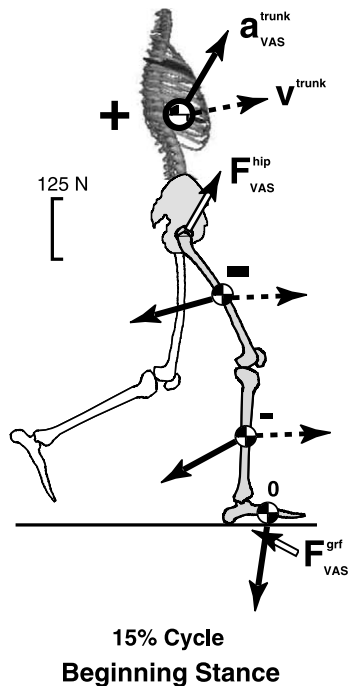|	Trunk (W)	Thigh (W)	Shank (W)	Foot (W)
Horizontal	44	−40	−4	0
Vertical	1	1	1	0
Ant/Post tilting	4	17	−2	3
Total	49	−22	−5	3

Fig. 3. Redistribution of segmental energy by the uniarticular knee extensors (VAS), which first act eccentrically and then concentrically in the beginning of stance, i.e. early stance into single-leg support. *Unfilled arrows*: Contribution to the hip intersegmental force F_{VAS}^{hip} and the ground reaction force F_{VAS}^{grf}. Calibration bar applies to these forces. Contribution to the ankle intersegmental force is similar to the ground reaction force contribution; contribution to the knee intersegmental force is similar in magnitude but oriented upward and slightly backward (both unshown). *Filled arrows*: Contribution to the linear accelerations of the segments (only trunk labeled, a_{VAS}^{trunk}). Magnitudes are unscaled. *Dashed arrows*: Linear velocity of segments (only trunk labeled, v^{trunk}). Magnitudes are unscaled. Notice motion of segments is mostly forward. VAS accelerates the trunk forward and upward ('+' energy flow) while decelerating the thigh and shank ('−' energy flow). VAS lengthens in early stance, and then, after momentarily undergoing no change in length, shortens; but its action to redistribute energy is unchanged. Thus, VAS redistributes energy from the leg to the trunk irrespective of whether it is acting eccentrically, concentrically, or neither. Data are from simulation in Ref. [28].

like a uniarticular muscle, affects the power of all the body segments because it contributes to all intersegmental forces. Thus, inferences of muscle coordination based on the concept of a transfer of power by a biarticular muscle from one of its spanned joints to the other [4,30,32–36] must proceed with caution.

The concept of transfer of power from one spanned joint to the other by a biarticular muscle seems to have developed because mathematical relevance was mistaken for physical relevance. It is important to recognize that one type of relevance does not necessarily imply the other. The net power produced/absorbed by the muscle can indeed be computed by Eqs. (3a), (3b), (3c) and (3d); that is, they all have mathematical relevance in computing muscle power, a physical quantity. But the net power provided by the muscle to the segments adjoined to the two spanned joints is not given by the terms in Eq. (3b)

because the contributions to the segment power from the muscle's contribution to the joint intersegmental forces do not appear in Eq. (3b). Thus, the terms in Eq. (3b) have no physical relevance in this context. Further, Eq. (3d) would seem to suggest that a muscle moment can deliver power to a joint, as if the joint can do work. But a joint is a workless constraint and does not absorb or deliver energy.[1] This is not to say that a muscle moment cannot contribute to the intersegmental force of the spanned joint; it does, and when the contributed force is multiplied by the joint translational velocity, the power delivered to the two adjoining segments by its contribution to this intersegmental force is indeed given. But this quantity is not given by 3, and is not the quantity referred to when transfer of power from one joint to another is mentioned. Finally, the proponent of the phrase, 'transfer of power from one joint to another by a biarticular muscle', has recognized the confusion and states that this phrase is not to be used to infer how the net joint moments transfer power among segments [37].

Of course biarticular muscles do produce moments simultaneously at the two spanned joints, and this must be considered when assessing their role in coordination of locomotion. The energy flow among the segments caused by a biarticular muscle force is the summed energy flow caused by its two moments. Force production by a biarticular muscle might, therefore, be advantageous to the execution of a locomotor task because its force generation might cause energy to be exchanged among the segments in a manner unachievable by the action of any single uniarticular muscle. Or, a biarticular muscle might produce an end-point force to accelerate an object in a direction different from a uniarticular muscle [38], such as the crank in pedaling [38] (see below). The challenge is to discover what biomechanical and neural control advantages are offered by biarticular muscles.

7. Inverse dynamics to compute net joint moments and powers, joint intersegmental and contact forces, and individual muscle forces

The traditional Newton–Euler inverse dynamics method is commonly employed in locomotion analyses to compute the net joint moments, net joint powers, and net joint intersegmental forces (see reviews [11,31,39–41]). The foot, shank and thigh are assumed to be rigid

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[1] Rigid body frictionless joints are assumed here, as well as in virtually all studies of muscle function. Of course, joints with friction can absorb and dissipate energy and 'power absorbed by a joint' has meaning. But that is not usually the context in which the term appears in studies of muscle coordination.

body segments connected by joint articulations. Measured ground reaction forces and observed or estimated segmental accelerations are inserted into the Newton–Euler equations of motion ($\bar{F} = m\bar{a}$, $\bar{M} = I\bar{\alpha}$), starting at the foot and solving for the ankle joint intersegmental force and net ankle moment. Then the Newton–Euler equations for the shank, and lastly the thigh, are solved to compute the net joint moment and joint intersegmental force at the knee and hip.

An advantage of the traditional inverse dynamics method is that a model of the segments proximal to the thigh, such as the trunk segments, do not have to be modeled in order to compute the net joint moment and joint intersegmental force at the ankle, knee and hip because, in effect, their kinetics are included in the ground reaction force. In the presence of noisy data, a least-squares approach can be used to best estimate the net joint moments and forces [42]. Other more computationally complex methods using the equations-of-motion of the body segments have also been developed to compute the net joint moments and joint intersegmental forces [43,44]. The advantage of these methods is that independent estimations of segmental velocities and accelerations are not required; the disadvantage is that at least one segment representing the head, arms, and trunk (HAT) must be included in the model. Of course a HAT segment must be assumed and its kinematics measured or estimated if the traditional inverse dynamics approach is to be used to compute HAT segmental power.

The calculation of net joint moments using the traditional inverse dynamics method is useful in orthopaedics where the net joint moments of healthy individuals are compared to the moments of individuals with musculoskeletal pathologies [45]. Andriacchi and co-workers have shown that the pre-surgical knee adduction moment of the osteoarthritic knee can be used to predict disease severity [46], success of high tibial osteotomy [47,48], effects of drugs on knee loading [49], and can assist in the design of knee braces [50]. The computed net joint moment at the knee has utility in functional testing of the anterior cruciate ligament deficient knee [51], and in understanding gait adaptations and the dynamics of pathological motion in individuals with anterior cruciate ligament deficient knees [52–55]. Estimation of net joint moments from inverse dynamics has been useful to the design of total hip replacements since the net hip moment and motion are correlated with proximal femoral bone mineral density [56] and pain [57] in individuals with hip osteoarthritis.

Knowledge of joint contact force, which has typically been estimated by combining additional methodologies with the traditional inverse dynamics method, is also important in orthopaedic applications, such as the design of total joint replacements and understanding the functional adaptations specific to a design [45,58,59]. Joint contact force is the sum of the joint intersegmental force, which is estimated directly from the traditional inverse dynamics approach, and the compressive joint force caused by muscle forces and forces in the soft tissues in the joint, which is estimated using additional methodology. This additional methodology is structured to decompose the net muscle moments, which are found from the traditional inverse dynamics approach, into individual muscle moments using static optimization. The individual muscle forces are then determined from the moments using a musculoskeletal model of moment arms. The joint compressive forces are then estimated from these muscle forces and information about the lines of action of each force.

Static optimization to decompose the net joint moments into individual muscle moments or muscle forces has a long history [60–62], but can have problems when applied to study muscle coordination [63,64] because of the low confidence in the optimization criterion inherent in this approach [65–68] and the inability of most of these methods to predict co-contraction among antagonistic muscles [68,69]. Nevertheless, predictions of hip contact force with such methods have been useful to prosthetic design (see excellent reviews [45,58]). The comparison of predicted hip contact force using net-joint-moment decomposition procedures with direct measurement of hip contact force from instrumented hip prostheses in patients [59,70,71] indicates hip contact force may be more predictable than previously assumed. Also, Anderson and Pandy [72] recently showed that muscle forces in walking estimated from net joint moments using static optimization are similar to the forces given by the dynamic solution that had generated the net joint moments. Though this study suggests that static optimization may indeed have more potential than realized, it is unclear how muscle force estimation would vary with expected errors in net joint moments computed from traditional inverse dynamics, with the number of joint moments computed, or with the optimization criterion used. Finally, EMG activity is often recorded in gait studies [4,5,31,73,74]. But this information has generally not been very helpful to the quantitative estimation of muscle force during dynamic multijoint motor tasks [75,76], though EMG processing methods have been developed to estimate muscle forces in static single-joint tasks [77,78] and, in rare circumstances, in walking [79,80].

8. Limitation of inverse dynamics in understanding muscle coordination

One limitation of the traditional Newton–Euler inverse dynamics method is the uncertainty in estimates of mechanical energy expenditure by muscles based on

segmental energy flow computations. Uncertainty exists because of intercompensation due to biarticular muscles and the recovery of stored elastic energy [81–86]. Though attempts can be made to account for these effects in the calculation of mechanical energy expenditure [87,88], substantial problems still exist [89].

Even if the net joint moments/powers computed from inverse dynamics, such as during walking, could be decomposed into the contributions from individual muscles as described in Section 7, individual muscle contributions to the acceleration of the segments and joints and to the joint intersegmental forces cannot be found. The reason is that the Newton–Euler equations for the leg segments are an incomplete set of dynamical equations-of-motion of the body; specifically the equations-of-motion of the HAT are unspecified. The force in a leg muscle, for example, affects the acceleration of all segments, including the HAT, and this effect on the HAT acceleration in turn affects the leg segment accelerations. Thus the Newton–Euler equations for the leg segments, by themselves, cannot be used to decompose the acceleration of a segment, including a leg segment, into the individual muscle or net joint moment contributions. This greatly limits traditional inverse dynamics from identifying the role of individual muscles in coordinating the body segments [45].

9. Understanding muscle coordination with dynamical models and simulations

The key to understanding muscle coordination is to find the contributions of individual muscles to the movement of the individual body segments and objects in contact with the body. A major step toward fulfilling this objective is to find the instantaneous contributions of individual muscles to the acceleration and power of the segments. Various approaches can be used to find the instantaneous contributions by individual muscles or individual net joint moments. In each of the approaches a complete set of dynamical equations-of-motion of the whole body is needed, or, stated simply, a dynamical model of the body is needed (Eq. (5)). The approaches differ by whether net joint moments or individual muscles forces are used, whether the muscle forces are derived with or without musculotendon models, and whether dynamical simulations are produced or not.

One approach is to apply the net joint moments computed from traditional Newton–Euler inverse dynamics to a dynamical model of the body. In walking, the model might assume the foot, shank, and thigh are rigid bodies, which are the same assumptions used with the traditional inverse dynamics method to compute the net moments. However, the ankle, knee and hip joints of both legs, a HAT segment, and the foot-ground interaction also need to be modeled, for example; thus,

additional assumptions to those required in the traditional inverse dynamics approach are invoked. The resulting dynamical equations-of-motion of the body segments and the interaction of the feet with the ground would then constitute the dynamical model of the body. In this example of a walking model, the net joint moments at the ankle, knee, and hip serve as the inputs to the dynamical model [90].

A better understanding of coordination can be obtained if the net joint moments computed from traditional Newton–Euler inverse dynamics are decomposed into individual muscle forces and these forces applied to the dynamical model of the whole body. The decomposition of the net joint moments into individual muscle forces can be accomplished by generating a musculoskeletal model of muscle moment arms and applying static optimization methods, in which case the optimization criterion for net joint moment decomposition has to be invoked; for example, the criterion might be minimization of muscle fatigue, stress, or peak forces. When muscle forces are estimated, joint contact forces can also be computed and the individual muscle contributions found, which are important to a variety of orthopedic applications (see above, [91]).

Simulations are unnecessary to compute the *instantaneous* contributions of individual net joint moments or muscle forces to the accelerations and power of a segment (Eq. (5)) because only a dynamical model has to be constructed and the inputs known, such as the net joint moments or muscle forces. The computations can be executed independently at each instant during the motion. However, the resulting accelerations and powers may be inconsistent with the desired motion because of potential mismatches between the dynamical properties of the model and the applied net joint moments or muscle forces.

Conversely, dynamical simulations are desirable because they overcome this limitation and provide compatibility among the computed *trajectories* of the net joint moments or muscle forces, the measured kinematic and kinetic *trajectories*, and the derived whole body dynamical model over the region of the locomotor cycle simulated. Thus, dynamical simulations are the best analytical tools available for extracting *trajectories* of unmeasurable quantities, such as muscle-induced accelerations and powers during walking.

Simulations based on a dynamical model of the body that includes the dynamical properties of individual muscles provide even more insight into muscle coordination. When the whole body dynamical model includes models for muscle and tendon, the simulation is testing for the compatibility of the measured kinematics, kinetics, and EMG patterns with not only the model of the body segments but also the model of the muscle, tendon and muscle moment arm properties.

The potential of simulations derived from a dynamical model of the body that includes muscle and tendon properties to deduce coordination principles has long been recognized [92,93]. With a muscle-based dynamical model, muscle excitations serve as the inputs instead of muscle moments or forces. A muscle-based dynamical model requires, therefore, that the anatomical and physiological properties of each muscle and tendon and the body segmental interactions be specified [13]. Methods for developing musculoskeletal models and the dynamical equations-of-motion of the body segments, which are the constituents of a dynamical musculoskeletal model, have been developed [94–96]. Thus, with muscle-based dynamical simulations, not only can the kinematics and energetics of the segments be 'dissected', but the kinematics and energetics of muscles and tendons as well. Simulations derived from dynamical models driven by muscles can, therefore, be analyzed to find the causal relationships between muscle excitations and the kinematics and kinetics of the task [13,21,97].

10. Generating dynamical simulations

One of the most difficult aspects of generating muscle-driven dynamical simulations compatible with experimentally observed kinesiological measurements is finding an appropriate muscle excitation pattern. Using EMG measurements as the excitation inputs is rarely successful due to the lack of fidelity in the EMG measurements and the inaccuracies in the dynamical properties of the musculoskeletal model. Therefore, two primary approaches have been employed to find the muscle excitation trajectories to drive the simulations [21]. Both use optimization theory and a dynamical model to iteratively find the muscle excitations to produce the desired trajectories [13].

One approach of generating a muscle-driven simulation requires that the objective of the motor task be specified, in which case the optimization algorithm finds the muscle excitations to fulfill this assumed task objective [98–106]. No experimental observations of the motor task are required. The confidence in the dynamical model and in the specification of the task objective is ascertained by how well the simulation-generated kinematics, kinetics, and excitation patterns agree with measurements from subjects performing the same task. For maximal-type events, such as jumping as high or pedaling as fast as possible, a putative objective function is easily postulated. But during sub-maximal tasks, identifying the task objective is much more difficult because it is likely to be multi-factorial, such as the simultaneous minimization of energy expenditure, joint loading and muscle fatigue. Thus, it is most difficult to determine if the difference between the simulation and experimental trajectories is due to the

dynamical model, the definition of the task being performed, or the unmodeled neural control constraints [97]; however, see Pandy et al. [107] for how this approach can be used to determine the task objective. Nevertheless, in self-selected-speed overground walking, it seems that minimization of metabolic energy per unit distance traveled may be a reasonable performance criterion [102,104].

The other approach for generating a muscle-driven simulation does not require that the objective of the motor task be specified, but rather uses measurements obtained from subjects executing the task to find the muscle excitation trajectories. An optimization algorithm finds the muscle excitations such that the simulation-generated trajectories of the kinematics and kinetics, and perhaps muscle excitations, match the measurements as well as possible [108]. The confidence in the dynamical model is evaluated by how well the simulation-generated trajectories, called the 'optimal tracking solution', match the measurements. The challenge in this method is how to specify the relative importance or weighting of each measurement because different weightings produce different muscle excitation patterns and thus tracking solutions. One method is to weigh the measurements proportional to their variability [108]. The confidence in understanding coordination mechanisms depends in part on their robustness to the different tracking solutions.

11. Limitation of dynamical simulations

An important feature of a simulation derived from a dynamical model of the body is the ability to systematically study the sensitivity of the conclusions of an investigation to uncertainty in model parameters, or even in the structure of the model itself. Thus, investigators using simulations have the ability to assess their confidence in the muscle coordination principles advocated.

The importance of performing sensitivity studies to ascertain the level of confidence in the conclusions on muscle coordination derived from simulation data cannot be overstated. The reason is that many assumptions are inherent to the construction of a muscle-based dynamical model of the body. These include the physiological properties of muscles and tendons, musculotendon paths, properties of the joints, the rigid and compliant structural and inertial properties of the body segments, and the interaction of the body with its environment, such as the ground. The construction of the simulation requires, in addition, the specification of the muscle excitation signals that can vary in modeled complexity. Therefore, much effort must be taken to assure the model is valid for the investigation of interest, including comparison with experimental data and sensi-

tivity analyses and perturbation tests to see if the model responds like the real system [109].

Sensitivity studies are required because musculoskeletal data are sparse and some characteristics of the simulation may be quite sensitive to uncertainty in musculoskeletal parameters. To date, most simulation analyses are based on a generic musculoskeletal model. A generic model of muscle and tendon scaled by few muscle architectural parameters is often assumed [110]; but the anatomical and physiological data for specifying the parameters are scant. Musculotendon paths are also based on limited data [96,111–116]. Data and techniques to describe body-segmental mass and inertial properties, even subject-specific ones, do exist however [117–119]. The scientific question being studied determines the specific musculoskeletal or other model-building data most desired, and the simulation-based sensitivity studies must be structured for such determination. Nevertheless, our unpublished data suggest that uncertainty in muscle moment arms of the biarticular muscles and the active and passive force–length curves of individual muscles limit our ability to deduce the detailed function of muscles in moderate-speed motor tasks.

Subject-specific models are expected to generate data that will assist the clinical gait-lab team in making subject-specific recommendations regarding surgical interventions and rehabilitation strategies. However, the development of subject-specific musculoskeletal models, especially models of the joints, muscles, and tendons, is most challenging. Nevertheless, recent studies have demonstrated the feasibility of constructing subject-specific musculoskeletal models by using medical image data to determine muscle moment arms [114,115,120–123], calculate muscle volumes and limb inertial parameters [124,125], estimate muscle physiological cross-sectional areas [126,127], measure muscle pennation angles and fascicle lengths [127,128], and describe bone geometry [115,129–131]. But these techniques can be computationally intensive and incorporating the data into subject-specific musculoskeletal models is not trivial. However, it is likely that these techniques will be refined and algorithms developed to generate subject-specific models efficiently.

12. Deducing coordination by analyzing muscle-induced segmental powers and accelerations

A major step toward understanding muscle coordination of a multisegmented body is to analyze the role of individual muscles in accelerating the segments and controlling the energy flow among the segments. In this Part I, we illustrate how muscle-induced accelerations and powers can be analyzed to understand coordination of seated pedaling rather than walking

because of the relative dynamic simplicity of pedaling. Pedaling has fewer mechanical degrees-of-freedom because the hips can be considered stationary and the foot path is constrained by the pedal trajectory. Part II reviews how similar analyses can lead to an understanding of coordination of walking.

In pedaling, muscles have to produce energy over the crank cycle and deliver the energy to the crank to overcome crank resistance and inertia. Muscles deliver power to the crank by developing a crank force tangential to crank rotation, called 'a tangential crank force' (F_{tang} in Fig. 4). Power delivered to the crank is calculated by multiplying the crank angular velocity by the crank torque, which is the tangential crank force times the crank arm length. The energy delivered to the crank over the crank cycle (0–360° crank angle, Fig. 4), which is the external work done on the environment in a cycle, can be calculated by integrating crank power over the cycle.
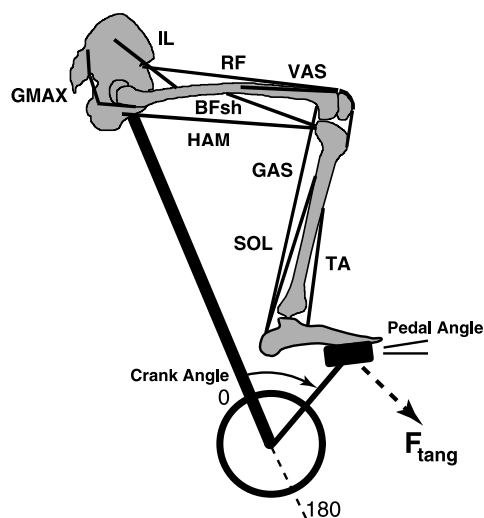

Fig. 4. Kinematic chain, crank and pedal angles, and leg muscle groups in pedaling. Pelvis is assumed stationary in seated pedaling. Thigh, shank, foot and crank move according to a five-bar linkage. Pedal angle is the orientation of the pedal and foot relative to the horizontal. Positive pedal angle is shown. Crank angle is the forward rotation of crank relative to the seat tube. 0° = crank closest to hip; 180° = crank furthest from hip; 0–180° is leg extension; 180–360° is leg flexion. Muscles combined into nine groups to represent the major uniarticular and biarticular leg muscles contributing to sagittal plane motion: GMAX, 'uniarticular' hip extensors (e.g. gluteus maximus); IL, 'uniarticular' hip flexors inserting on pelvis or trunk (e.g. iliacus, psoas); RF, biarticular thigh muscle, rectus femoris; BFsh, uniarticular knee flexor, biceps femoris short-head; HAM, posterior biarticular thigh muscles, the hamstrings; VAS, uniarticular knee extensors, vastus group: medialis, lateralis, and intermedius; GAS, biarticular plantar flexors, the medial/lateral gastrocnemius; SOL, 'uniarticular' ankle plantar flexors inserting on foot (e.g. soleus); TA, 'uniarticular' ankle dorsiflexors inserting on foot (e.g. tibialis anterior). The tangential crank force F_{tang} is the component acting to accelerate the crank; see also inset in Fig. 7. The radial crank force, which is not shown (see Fig. 7), is non-contributory to crank rotation.

Pedaling simulations that replicate the kinematics, kinetics, and EMG activity [108,132,133] have been used to analyze the effect each muscle force has on accelerating the leg and crank at each phase of the crank cycle [98,134]. For this review, a dynamical simulation was generated so data discussed would be perfectly consistent amongst themselves since a complete set of these data is not published in one source. Each muscle was excited at a constant level over a specific region or phase of the crank cycle found using optimal 'tracking' (see above). Muscle excitation levels and phasing were adjusted by an optimization algorithm so the pedal angle, the tangential and radial crank forces, the crank power, and the hip, knee and ankle powers and moments would be well replicated (Fig. 5; average error ± 1 SD) [108,132]. Principles of muscle coordination derived from this simulation agree with published results of previous pedaling simulations [22,98,134,135].

The primary muscles producing the energy cannot alone deliver the energy to the crank because they cannot directly generate a tangential crank force. The uniarticular knee (VAS) and hip (GMAX) extensors contract during leg extension (0–180° crank cycle) to produce considerable work output. Yet the energy delivered to the crank by them is much less (Fig. 6). During leg extension, the tangential crank force is instead largely produced by the uni- (SOL) and biarticular (GAS) plantar flexors (Fig. 7A). Therefore, SOL and GAS deliver considerable energy to the crank; however, they themselves produce little energy (Fig. 6).

Thus, muscles work in synergy to deliver energy to the crank (Fig. 6). This synergism becomes particularly apparent when the individual muscle contributions to segmental energetics are analyzed. GMAX delivers almost all the energy it produces during leg extension to the leg and very little to the crank (Fig. 8 GMAX: area under solid line $\approx$ area under dashed line; dotted line ≈ 0) because its contribution to the tangential crank force is negligible (Fig. 7A). SOL and GAS redistribute segmental energy approximately concurrently by reducing leg energy and increasing crank energy (Fig. 8 SOL, GAS: area under dashed lines < 0; area under dotted lines > 0). The redistribution of energy caused by SOL and GAS is large compared to the energy produced by them (Fig. 8 SOL, GAS: area under solid line is small). The uniarticular knee extensors (the vasti group, VAS) also work in synergy with the plantar flexors during leg extension because much of the energy produced by VAS is delivered to the leg (Fig. 8 VAS: area under dashed line > 0), though a comparable amount is delivered directly to the crank because VAS does contribute to the tangential crank force (Fig. 8 VAS: area under dotted line > 0; Fig. 7A). Besides the uniarticular hip, knee and ankle extensor synergism during leg extension, the uniarticular hip and ankle flexors work in synergy during leg flexion (Fig. 6).
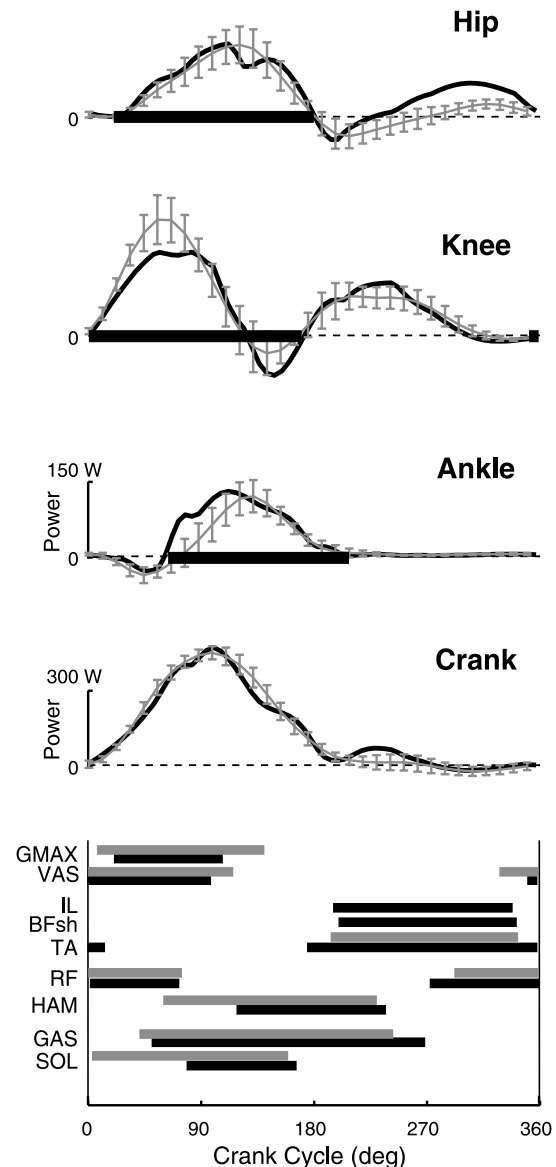

Fig. 5. Comparison between simulated and experimental hip, knee and ankle powers, crank power, and EMG phasing during the crank cycle at a workload of 264 J and a cadence of 60 rpm. Experimental data [139] are the subjects' average ± 1 SD (gray lines; no SD shown for phasing). Simulation data (solid lines) are from a muscle-based dynamical simulation; see text. Propulsive energy to the crank occurs during leg extension; i.e. area under *Crank* power during 0–180° is positive and area under 180–360° ≈ 0. Extensor muscle moments generate high energy during leg extension; i.e. areas under *Hip*, *Knee*, and *Ankle* power over 0–180° are very large. Hip and knee flexor moments generate some energy during leg flexion; i.e. areas under *Hip* and *Knee* power over 180–360° are positive. Black horizontal bars along abscissa in the power graphs indicate when the hip, knee, are ankle are extending. Gravity and inertia forces contribute to crank torque and power some during leg extension and retard propulsion in leg flexion (not shown; [134]).

An analysis of muscle contributions to the acceleration of the segments complements the energy flow analysis. An understanding of the muscle contributions to maintaining the foot nearly horizontal explicates
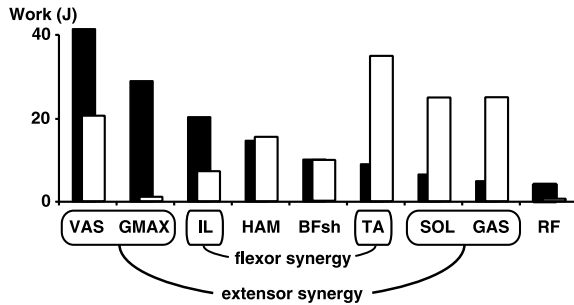
Fig. 6. Work output from each muscle group over the crank cycle computed from the simulation. *Filled bars*: Work produced by each muscle of the ipsilateral leg. *Unfilled bars*: Energy delivered to the crank from the muscle's contribution to the tangential crank force. Some muscles (HAM, BFsh) deliver the energy produced directly to the crank (filled bars equal to unfilled bars) but most muscles deliver less or more energy. VAS, GMAX, and IL accelerate the leg and thus deliver far less energy to the crank than produced (unfilled bars lower than filled bars). SOL, GAS, and TA deliver far more energy to the crank than produced (unfilled bars much higher than filled bars). The additional energy delivered to the crank arises because the leg is decelerated and the crank accelerated, causing energy to be redistributed from the leg to the crank. An 'extensor synergy' and a 'flexor synergy' are identified, enabling the work output of the energy-producing muscles to be delivered to the crank; see text. From Ref. [140].

further the need for muscles to work in synergy in pedaling. Consider leg extension. GMAX acts to accelerate the ankle joint in a distal direction collinear with the long axis of the shank (refer to Fig. 7A and consider the movement of the leg and crank when a clockwise

moment is applied to the thigh). Because of the low mass of the foot, if no other muscles were generating force, GMAX would act to accelerate the foot quickly into dorsiflexion and the knee quickly into extension, and no tangential crank force would be developed. But the plantar flexors (SOL and GAS) are approximately co-excited with GMAX and also generating force. Their muscle forces, should they act in the absence of force generation by GMAX, would accelerate the foot quickly into plantar flexion and the knee quickly into flexion, and tangential crank force would be developed. In effect, by acting in opposition with GMAX on the foot and knee during leg extension, the plantar flexors stiffen the ankle to prevent the ankle from 'collapsing' and the knee from over extending. The leg and crank can thus continue along their desired trajectories and the energy produced by GMAX can be delivered to the crank.

Because the uni- (SOL) and biarticular (GAS) plantar flexors work primarily co-functionally by stiffening the ankle and generating a tangential force, no distinct role can be attributed to the biarticular plantar flexors, in contrast to the deductions stated by analyzing net joint powers and transfer of joint power in the absence of simulations [30]. In fact, a simulation without GAS can also replicate well the measured kinematics and kinetics as long as SOL excitation is increased (Fig. 8). The reason SOL can replace GAS function is because each acts to accelerate one segment relative to the others
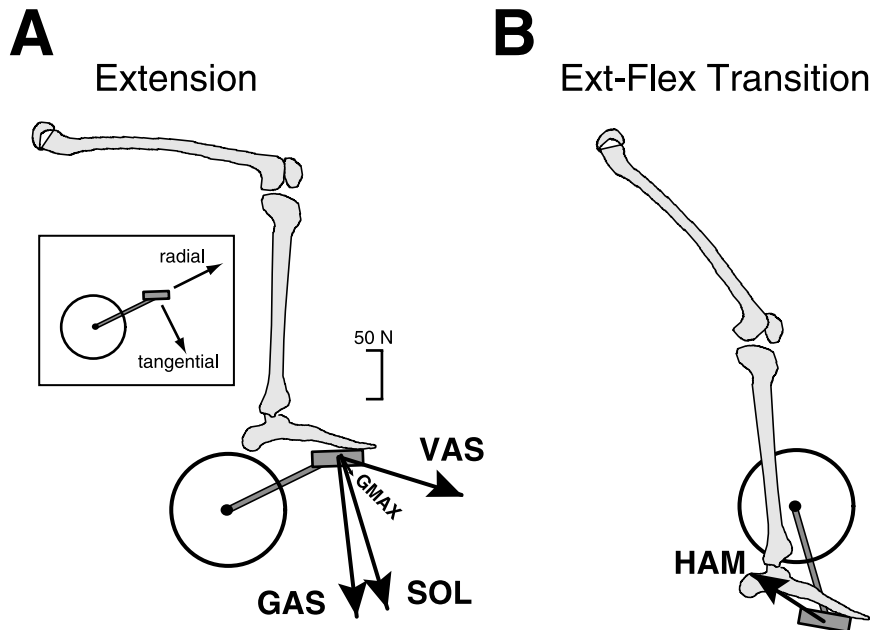

Fig. 7. Pedal reaction forces by active muscles at midpoint of leg extension (A) and near full leg extension (B) derived from the pedaling simulation. (A) *Extension*: Most tangential crank force (see inset for definition) is produced by SOL and GAS. SOL and GAS proportion is even higher at later crank phases in leg extension. GMAX produces little crank force; VAS some. Other muscles, if active then, such as RF and HAM (not shown), also produce little crank force. Yet the muscles producing high work output during leg extension are GMAX and VAS, not SOL and GAS (Fig. 6). Synergistic action by SOL and GAS thus ensures the energy produced by GMAX and VAS is delivered to the crank. (B) *Extension-to-flexion transition*: Only HAM produces a tangential crank force; see text. Modified from Ref. [140].
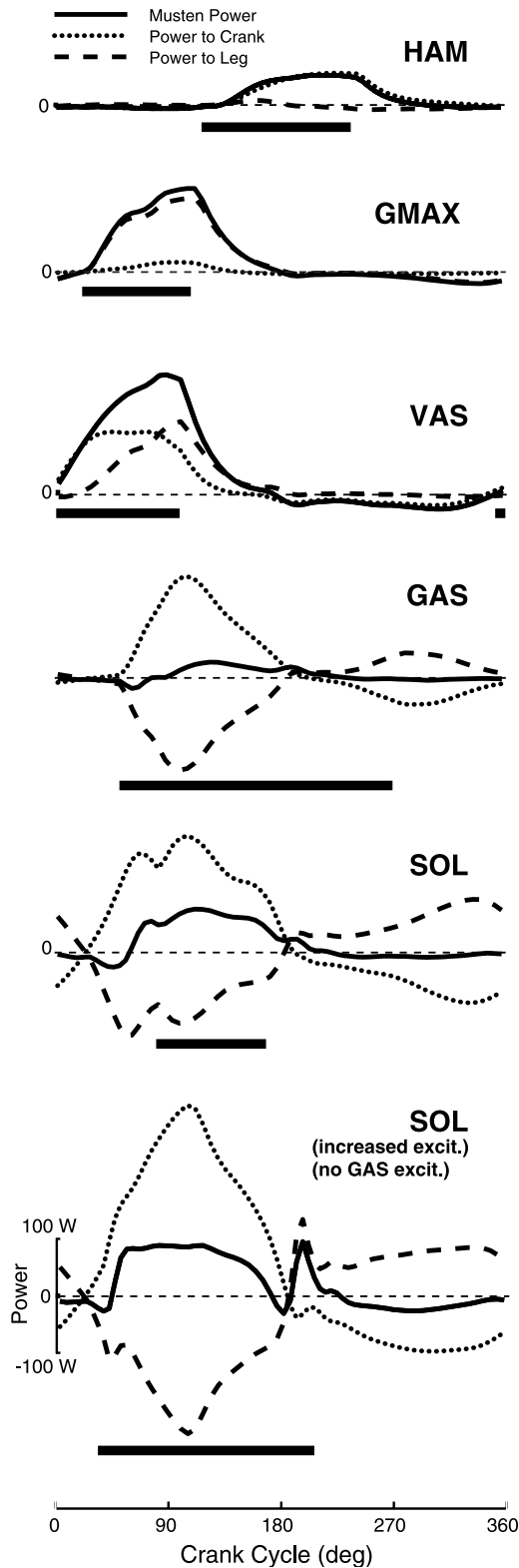
Fig. 8.

deceleration of the crank during the leg extension-to-flexion transition, which occurs near 180° [134,135]. In fact, virtually all the energy produced by HAM is delivered to the crank (Fig. 6; Fig. 8 *HAM*: dotted line ≈ solid line). Thus, HAM develops a large tangential crank force (Fig. 7B). The energy flow caused by HAM is always in the same direction, distally to the crank, even though the net hip and knee joint powers change direction over this interval (Fig. 5, 135–225°). Based on these examples of GAS and HAM function in pedaling, and also in jumping [99,136,137], we conclude that attempts to deduce coordination of energy flow by muscles based on the concept of transfer of joint powers are problematic.

13. Limitation of muscle-induced acceleration and power analyses

Though segmental acceleration and power found in dynamical simulations can be decomposed into the instantaneous contributions from individual muscle and gravity forces acting on the body segments, for example, the 1st and 2nd terms on the right-hand side of Eq. (5), the deduction of coordination principles from these decompositions must proceed with caution. The muscle-induced accelerations and powers are a snapshot in time of the contributions of individual forces acting on the body segments to accelerate them and redistribute power among them. These snapshots are taken without regard to the cumulative effects the past muscle and gravity force trajectories have had on the system behavior. The Coriolis and centripetal, and non-muscle forces in Eq. (5) ($V(q, \dot{q})$, $F^{non}(q, \dot{q})$) are position- and velocity-dependent arising from the previous trajectories of muscle forces and gravity, and from the initial position and velocity state. Thus, it is generally inappropriate to integrate the instantaneous contribu-

Fig. 8. Energy flow or power to the crank and the leg segments by muscles responsible for energy delivery to the crank during leg extension (0–180°) and the transition into leg flexion (near 180°) derived from the simulation. *Solid lines*: Power produced by the musculotendon actuator; area under a solid line is the energy produced by the actuator. *Dotted and dashed lines*: Power delivered to the crank and leg, respectively. Power delivered to contralateral leg ≈ 0 (not shown). Black horizontal bars indicate when the muscles are excited in the simulation. Near the limb transition, HAM delivers all the energy it produces to the crank. During leg extension, GMAX powers the leg and VAS powers both the leg and the crank. GAS and SOL deliver much more power to the crank than they produce because they reduce the power of the leg by decelerating it. Thus, GAS and SOL work synergistically to ensure the energy produced by GMAX and VAS is delivered to the crank. If SOL excitation is increased, it alone without any excitation of GAS can execute the required transfer of energy from the leg to the crank ("SOL increased excit; no GAS excit."). Thus, GAS and SOL are co-functional in pedaling.

approximately equally and neither produces much energy over the crank cycle.

The biarticular hamstrings (HAM) do, however, have a unique role in pedaling, which is to resist the

tions, such as the induced accelerations from $\mathbf{I}^{-1}(\boldsymbol{q})\mathbf{R}(\boldsymbol{q})\boldsymbol{F}^{\mathrm{mus}}$, to find how muscle forces change the velocity, position, and energetics of the segments because of their unaccounted for contributions to the changes in the Coriolis and centripetal, and non-muscle forces.

At times the Coriolis, centripetal, and non-muscle forces may be small compared to the muscle and gravity forces; that is, $\mathbf{R}(\boldsymbol{q})\boldsymbol{F}^{\mathrm{mus}}+\boldsymbol{G}(\boldsymbol{q})g$ dominates the right hand side of Eq. (5). Therefore, it may be reasonable under these circumstances to integrate the instantaneous accelerations and powers induced by individual muscle forces and gravity over a time interval to estimate how individual forces change the velocity, position, and energetics of the segments over this interval. In pedaling at moderate cadences, the Coriolis, centripetal, and non-muscle forces are indeed small [22,134].

In walking, initial attempts to explore the usefulness of muscle-induced acceleration and power analyses to understand coordination, using assumptions like those to study pedaling, seem promising (see Part II). One difficult problem, however, has been to find the individual muscle and gravity contributions to the ground reaction force during stance, such as the contributions to $\boldsymbol{F}^{\mathrm{non}}(\boldsymbol{q},\,\dot{\boldsymbol{q}})$ in Eq. (5), because ground reaction forces are high. One method has been, in effect, to integrate the individual force contributions to the acceleration of each ground contact element over a short interval compared to the gait cycle to find their effects on the velocity and position of each element, and thus to the force in each element [28]. This method appears reasonable as long as the ground contact elements are 'stiff' compared to the rest of the system dynamics.

14. Concluding remarks

The major goals of this Part I review were to critique methods used to deduce muscle coordination principles in human walking, and use pedaling to show how dynamical simulations can elucidate principles of co-ordination of leg muscles. The utility of a dynamical simulation is not in the simulation per se, but rather in the analyses of the simulation data. Simulation analyses can determine the mechanical energy produced by each muscle, the energy stored in musculotendon elastic elements, and the instantaneous contribution of individual muscles to the acceleration and mechanical energy flow or power of the individual body segments and the objects in contact with the body, such as the crank in pedaling. Thus, the causal relationship between the measured kinematics and kinetics and the measured pattern of EMG activity can be estimated.

We emphasized that a major locomotor function performed by a muscle arises from the instantaneous segmental accelerations and powers throughout the body caused by its force generation. The segmental accelerations and powers induced by a muscle include not only those resulting from the muscle exerting force on the segment of origin and insertion but also those resulting from the muscle's instantaneous contribution to the joint intersegmental forces and the ground reaction force, or, in general, any external object constraining the motion of the body. This complete set of muscle-induced forces dictates how the muscle accelerates the body segments. The muscle-induced accelerations cause the system energy to flow among the segments and the body segments to move.

The directionality of the instantaneous induced forces, and therefore accelerations, caused by a muscle at an instant in the locomotor cycle is determined only by the configuration of the body segments [22]. The magnitude of the muscle force scales the muscle-induced forces and accelerations but has no effect on the directionality of the induced forces and accelerations. Thus, if a muscle force should be higher at a given instant in the cycle, with body configuration and moment arms unchanged, each induced force and acceleration would be proportionally higher. The power delivered to one segment relative to another by the muscle depends not only on the relative induced accelerations but also on the relative motion of the segments. Thus, the relative muscle-induced segmental powers depend on the configuration of the body segments and their relative motion at that instant. The force generated by a muscle also scales the muscle-induced segmental powers; thus, the relative distribution of segmental power induced by the muscle is the same.

In assessing muscle function, it is important to recognize that the exchange of segmental energy caused by the forces and accelerations induced by a muscle may be more significant to locomotor task execution than its energetic state. A specific muscle may be critical to the energy exchange among segments because, when it generates force, the resulting set of induced forces acting on the segments is necessary for the exchange to occur. It may be, therefore, that the muscle is excited in this locomotor epoch irrespective of its ability to produce energy by acting concentrically (shortening), absorb energy by acting eccentrically (lengthening), or neither by staying at a constant length.

Muscles may have to participate in the energy exchange among the body segments, the contact objects, and musculotendon elastic elements because inertial and gravitational forces alone are insufficient to achieve the task goals. These latter forces are insufficient when the summed mechanical energy state of the system is not constant over the locomotor cycle. However, we believe that fluctuation in the system energy does not represent a failing on the part of the nervous system to produce a well-coordinated movement. Rather we posit that it represents a solution to the complex problem of select-

ing the muscle coordination that fulfills both the instantaneous task requirements and the overall task goals given the limited range of induced forces and accelerations the muscles can create over the locomotor cycle.

Muscle coordination is required because no one muscle can execute all the required biomechanical functions. Fundamentally, this is due to the articulated nature of the body. In pedaling, for example, the uniarticular hip extensors (GMAX) are important 'energy-producing muscles'. Thus, they develop force while shortening during leg extension. But they cannot alone deliver the energy to the crank because they cannot contribute directly to the tangential crank force. The force produced by these shortening muscles causes joint intersegmental forces that act instead to accelerate the leg and deliver energy to it. There is no other phase of the crank cycle where these muscles can shorten and produce high work output. Thus, the uni- and biarticular plantar flexors (SOL, GAS) must generate force to allow the delivery of GMAX-produced energy to the crank. In addition, they must induce appropriate joint intersegmental forces that act to oppose the strong acceleration of the leg caused by GMAX. Thus SOL and GAS are, in effect, 'energy-transfer muscles'; they allow for the transfer of energy from the leg to the crank. Clearly, muscles important to the transfer of energy among the body segments need not be biarticular.

Muscle coordination in locomotion is, generally, a temporal process. Muscles produce energy and deliver it to accelerate some but usually not all of the segments, thereby increasing the energy state of the accelerated segments. Other muscles later decelerate the segments to transfer energy to other accelerated segments. Thus muscles act in sequence to restore and remove energy from segments to fulfill the kinematic requirements of the task.

At times during the locomotor cycle, however, muscle coordination is predominantly an instantaneous process. In this case muscles work together at the same time, in synergy, to perform different segmental energetic functions to achieve a task goal unobtainable by one muscle alone. By definition, then, synergistic muscles must be co-excited. In pedaling, which can be considered a locomotor-like task [135,138], the uniarticular hip extensors (GMAX) are synergistic with the ankle plantar flexors (SOL and GAS). Without the synergistic action of the plantar flexors, the foot would dorsiflex during leg extension when GMAX contracts and the energy produced by GMAX would not be delivered to the crank.

Sometimes muscles that are co-excited execute the same segmental energetic functions. The muscles are then co-excited and co-functional. In pedaling, for example, SOL and GAS are co-excited during leg extension and both transfer energy from the leg to the crank. SOL and GAS also shorten somewhat and deliver their energy to the crank. Thus SOL and GAS are co-functional while co-excited.

We hope this Part 1 review has demonstrated that simulations derived from muscle-based dynamical models can be extraordinarily helpful in:

- interpreting experimental kinematic, kinetic, and EMG data;
- understanding multi-joint biomechanics;
- finding the contribution of individual muscles to the acceleration and power of each body segment, the joint intersegmental forces, and contact forces;
- understanding how the energy developed by muscles is delivered to the body segments and environment;
- understanding muscle coordination; and
- identifying muscle synergies.

Part II reviews how dynamical simulations provide insight into muscle coordination of walking.

Acknowledgements

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