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Individual muscle contributions to support in normal walking

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Abstract

The purpose of this study was to quantify the contributions made by individual muscles to support of the whole body during normal gait. A muscle's contribution to support was described by its contribution to the time history of the vertical force exerted by the ground. The analysis was based on a three-dimensional, muscle-actuated model of the body and a dynamic optimization solution for normal walking. The results showed that, in early stance, before the foot was placed flat on the ground, support was provided mainly by the ankle dorsiflexors. After foot-flat, but before contralateral toe-off, support was generated primarily by gluteus maximus, vasti, and posterior gluteus medius/minimus; these muscles were responsible for the first peak seen in the vertical ground-reaction force. The majority of support in midstance was provided by gluteus medius/minimus, with gravity assisting significantly as well. The ankle plantarflexors generated nearly all support in late stance; these muscles were responsible for the second peak in the vertical ground-reaction force. The results showed also that centrifugal forces act to decrease the vertical ground-reaction force, but only by minor amounts, and that resistance of the skeleton to the force of gravity is no larger than 1/2 body weight throughout the gait cycle.
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1. Introduction

The vertical ground-reaction force is measured routinely in gait labs, and its characteristic shape is well known for normal gait. Saunders et al. [1] proposed six kinematic determinants to explain the smooth and energy-efficient trajectory that the body's center of mass undertakes during normal bipedal gait. Because the trajectory of the center of mass is determined by the time history of the resultant ground-reaction force, they suggested that the pattern of the ground-reaction force is an important indicator of how well the body is able to execute the six determinants. Saunders et al. [1] further suggested that irregularities observed in the ground-reaction force may be valuable to clinicians in the diagnosis and treatment of gait pathologies.

It has been decades since the work of Saunders et al. [1] was published, yet we still do not have a comprehensive and quantitative picture of how muscles contribute to the vertical ground-reaction force and therefore to support, even during normal gait. Considerable insight in this area has been offered by a number of researchers, but findings have been limited because the analyses have largely not been based on estimates of muscle forces. Winter [2] based his observations on similarities between the shape of the ground-reaction force and the sum of the net extensor moments applied at the hip, knee, and ankle. Sutherland et al. [3] inferred the role of the ankle plantarflexors by administering a tibial nerve block and observing the resulting changes in the ground-reaction force. Perry [4] used detailed analyses of kinetic and EMG data to form hypotheses about the roles of individual muscles. Mochon and McMahon [5,6] and Pandy and Berme [7–9] used simplified dynamic models of the body to study the effects of various gait determinants on the vertical ground-reaction force, but their models did not include the influence of muscles.

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More recently, Kepple et al. [10] used a dynamic analysis to quantify the contributions of joint moments to support of the upper body. Their analysis did not address the contributions made to the support of the whole body, and, because their model did not have muscles, they were not able to examine the roles of individual muscles. Neptune et al. [11] did use a muscle-actuated simulation of gait to investigate the roles of the ankle plantarflexors; however, they too examined the contributions to support of the upper body rather than the whole-body center of mass. In addition, Neptune et al.'s [11] model was two-dimensional, which meant that they were unable to examine the actions of muscles outside the sagittal plane.

Despite limitations, these studies have established some expectations for how some muscles contribute to the vertical ground-reaction force. There is broad consensus that the second maximum observed in the ground-reaction force is due largely to the forces exerted by the plantarflexors during late stance, also referred to as push-off or role-off [2–5,7–12]. However, an explanation for the shape of the ground-reaction force during early stance (or weight acceptance) and midstance has been less definitive. It is generally accepted that the hip and knee extensors make important contributions during early stance [2,6,8–10], but the relative importance of muscles like the vasti, gluteus maximus, hamstrings, and rectus femoris has not been established. Mochon and McMahon [6] hypothesized that the abductors likely make substantive contributions to support during midstance, but Kepple et al.'s [10] results do not substantiate this claim. With regard to the influence of other muscles known to be active during the gait cycle, such as tibialis anterior, adductor magnus, iliopsoas, and erector spinae [4], few quantitative data are available to evaluate the contributions these muscles might make to support. In addition, we note that the skeleton likely offers some contribution to support in resistance to gravity, but this contribution also has yet to be quantified.

We believe an important next step in our understanding of basic gait mechanics is establishing a direct connection between the actions of muscles and the well-known shape of the vertical ground-reaction force. The analyses performed in the present study are based on a three-dimensional, muscle-actuated model of the body and a detailed dynamic optimization solution for normal gait [13,14]. The specific questions we address are: (1) how do muscle forces, gravitational forces, and centrifugal forces (i.e. forces arising from rotations of the body segments) contribute to the vertical ground-reaction force generated during normal gait?, and (2) which muscles contribute most significantly to the time histories of the vertical ground-reaction force and the vertical acceleration of the center of mass?

2. Methods

2.1. Musculoskeletal model

The body was modeled as a 10 segment, 23 degree-of-freedom linkage [15]. The first 6 degrees-of-freedom were used to define the position and orientation of the pelvis relative to the ground. The remaining 9 segments branched out in an open chain from the pelvis. The head, arms, and torso were represented as a single rigid body that articulated with the pelvis via a ball-and-socket joint located at approximately the third lumbar vertebra. Each hip was modeled as a ball-and-socket joint, each knee as a hinge joint, each ankle-subtalar joint as a universal joint, and each metatarsal joint as a hinge joint. The directions of the knee, ankle, subtalar, and metatarsal joint axes were anatomical and based on in-vivo and cadaveric measurements [15,16]. The inertial properties of the model segments were based on anthropometric measures obtained from five healthy adult males (age 26 ± 3 yr, height 177 ± 3 cm, and mass 70.1 ± 7.8 kg) [17].

Each foot in the model was represented by a toes segment hinged at the metatarsal joint to a hindfoot segment. Interactions of the feet with the ground were modeled using a set of five spring-damper units distributed under the sole of each foot [15]. Four spring-damper units were placed at the perimeters of each hindfoot segment, and one unit was placed at the distal tip of each toes segment.

The model was controlled by a total of 54 musculo-tendinous actuators [15]. Each leg was controlled by 24 actuators. Relative movements of the pelvis and upper body were controlled by 6 abdominal and back actuators. Each actuator was modeled as a 3-element, Hill-type muscle in series with tendon [18]. Excitation-contraction coupling was modeled using a first-order differential equation that related the time rate of change of muscle activation to muscle excitation [19]. The muscle parameters, as well as the origin and insertion sites, were based on data reported by Delp et al. [20]. Ligament action was included to prevent anatomically infeasible joint angles from arising during a simulation. Ligament torques were modeled by exponential curves [21]. For details relating to the model, see Anderson and Pandy [15].

2.2. Dynamic optimization solution

A fixed-final-time dynamic optimization problem was solved for one cycle of normal gait [13]. The gait pattern was assumed to be bilaterally symmetric, so it was necessary to simulate only one half of a gait cycle. The initial states for the model were obtained by averaging kinematic and force platform data obtained from the 5 subjects noted above. The final time for the dynamic

optimization problem was fixed to the average time taken by the five subjects to complete one half of a gait cycle, which was 0.56 s.

The performance criterion was chosen to be the total metabolic energy consumed divided by the change in position of the center of mass in the direction of progression. The metabolic energy consumed by each muscle was calculated by summing five terms: basal metabolic heat, shortening heat, activation heat, maintenance heat, and mechanical work [22]. A penalty function was appended to the performance criterion to prevent hyperextension of the joints [13].

The excitation history of each muscle was parameterized by 15 nodal points, and these nodal points, together with the initial activation level for each muscle, served as controls in the dynamic optimization problem [19]. The controls were allowed to vary continuously between zero (fully off) and one (fully on).

The dynamic optimization problem was minimally constrained: only those constraints necessary to ensure a repeatable gait cycle were imposed [13]. Specifically, terminal boundary constraints were applied to the joint angular displacements, joint angular velocities, muscle activation levels, and muscle excitation levels so that the states at the end of the simulation were approximately equal to those at $t = 0$. Because only one half of the gait cycle was simulated, terminal states for the left side of the body were constrained to equal the initial states for the right side of the body, and vice-versa.

The joint angular displacements, ground-reaction forces, and muscle excitation patterns predicted by the dynamic optimization solution were similar to the same measures obtained from the subjects. For details concerning the dynamic optimization problem and solution, see Anderson and Pandy [13].

2.3. Decomposition of the ground-reaction force

Any force applied to the body contributes to the support generated during gait because that force is transmitted to the ground through the joints and bones of the skeleton [23,24]. The equations of motion for a musculoskeletal system allow one to compute the accelerations of the generalized coordinates resulting from the application of the various forces:

$$\ddot{\vec{q}} = \vec{I}(\vec{q})^{-1}\{\vec{C}(\vec{q},\ \dot{\vec{q}}^2) + \vec{G}(\vec{q}) + \Gamma\rightarrow(\vec{q},\ \dot{\vec{q}}) + \vec{R}(\vec{q})\vec{f}_M$$
$$+ \vec{S}(\vec{q})\vec{f}_S(\vec{q},\ \dot{\vec{q}})\} \qquad (1)$$

Here, $\vec{q}$, $\dot{\vec{q}}$, and $\ddot{\vec{q}}$ are vectors of the generalized coordinates, speeds, and accelerations, respectively; $\vec{I}(\vec{q})^{-1}$ is the inverse of the system mass matrix; and the terms inside the curly brackets are various sources of force. In this study, the sources of force were: $\vec{C}(\vec{q},\ \dot{\vec{q}}^2)$, a vector of generalized forces arising from centrifugal forces; $\vec{G}(\vec{q})$, a vector of generalized forces arising from

gravity; $\dot{\Gamma}(\vec{q},\ \dot{\vec{q}})$, a vector of applied ligament torques; $\vec{f}_M$, a vector of applied muscle forces; and $\vec{f}_S$, a vector of applied spring-and-damper forces that represented the interaction of the feet with the ground. $\vec{R}(\vec{q})$ is a matrix of moment arms for the muscles, and $\vec{S}(\vec{q})$ is a matrix of partial velocities for the applied spring forces; these two matrices convert the muscle and spring forces into generalized forces [25].

To quantify how muscle forces and other sources of force contributed to support during the gait simulation, we viewed the forces developed by the foot-ground springs as reactions to the 'action' forces applied within the system:

$$\vec{f}_S = \vec{f}_S{}^C + \vec{f}_S{}^G + \vec{f}_S{}^\Gamma + \vec{f}_S{}^M, \qquad (2)$$

where $\vec{f}_S{}^C, \vec{f}_S{}^G, \vec{f}_S{}^\Gamma$, and $\vec{f}_S{}^M$ are the contributions made to the spring forces by the centrifugal, gravity, ligament, and muscle forces, respectively. Thus, the action forces in the system were the centrifugal, gravity, ligament, and muscle forces, and the reaction forces were the forces due to the foot-ground springs.

When a biomechanical system is in rigid contact with the environment, performing the decomposition indicated in Eq. (2) is a relatively straightforward procedure. For example, one might simulate the foot-flat phase of gait by fixing, or welding, the foot to the ground. In this case, the equations of motion would not include the spring force terms that appear in Eq. (1). The ground reaction force would still be present, but implicitly so, and would exist to enforce the kinematic constraints of the weld joint. The contribution of each action component to the ground reaction force could then be found by solving for the reaction force at the weld joint when each action force is applied in isolation. For example, to find the contribution to the ground reaction force made by the ith muscle force, f_{M_i}, one would set all other action forces to zero, apply f_{M_i} to the skeleton, and solve for the forces needed to enforce the constraints of the weld joint. The resultant of these constraint forces would be $f_S{}^{M_i}$.

When contact with the environment is modeled using a spring, performing the decomposition is more complex. The reason is that the force response of a spring is not instantaneous, but requires a finite time interval to allow the states (i.e. $\vec{q}$ and $\dot{\vec{q}}$) to change. However, if a spring is sufficiently stiff, its force response will be very rapid and, as a result, rigid contact assumptions can be applied with reasonable approximation.

To perform the decomposition for the dynamic optimization solution, we assumed that the springs used to model the foot-ground interaction were stiff enough to allow the rigid contact approximation to be invoked. That is, we constrained each spring point in contact with the ground to have zero acceleration. This approach converts the spring decomposition problem into a standard decomposition problem that one has

when the model is in rigid contact with the ground (e.g. when the foot is welded, hinged, or otherwise rigidly joined to the ground). One can think of this approach as replacing the actual equations of motion for the system with a sequence of plausible equations of motion that approximate how contact of the model with the ground could be simulated. For example, when transitioning between foot-flat and heel-off, the equations of motion should transition between a set of equations in which the foot is welded to the ground (foot-flat) to a set of equations in which the metatarsophalangeal joint is hinged to the ground (after heel-off). To approximate all the variations of foot-ground contact that can occur in a 3D gait simulation with two feet, many different sets of equations of motion (~ 10 in our case) would be needed. Constraining the spring points is one possible way of making the appropriate transitions between plausible equations of motion using only the original equations of motion. The critical aspect of this approach is that the motion of the foot be constrained in a way that is consistent with the manner in which the foot actually accelerated during the recorded or simulated movement.

The specifics of the decomposition method we used now follow. If $\vec{p}_{S_i}$ is the inertial position of a point at which the ith spring force is applied, rigid contact requires that $\ddot{\vec{p}}_{S_i} = \vec{0}$. Now $\ddot{\vec{p}}_{S_i}$ can be computed using Eq. (1) and can be thought of as some function Ψ_i of $\ddot{\vec{q}}$. Therefore, the condition for rigid contact can be expressed as

$$\ddot{\vec{p}}_{S_i} = \Psi_i(\ddot{\vec{q}}) = \vec{0}. \tag{3}$$

Let $\vec{f}_\alpha$ be some action force that occurred at time t in the simulation, and let $\vec{f}_{S_i}{}^\alpha$ be its contribution to the ith spring force at time t. Further, let $\ddot{\vec{p}}_{S_i}{}^\alpha$ be the acceleration caused at the ith spring point by $\vec{f}_\alpha$ and let it be computed as follows:

$$\ddot{\vec{p}}_{S_i}{}^\alpha = \Psi_i(\vec{I}(\vec{q})^{-1}\{\vec{A}(\vec{q})\vec{f}_\alpha + \vec{S}(\vec{q})\vec{f}_{S_i}{}^\alpha\}), \tag{4}$$

where $\vec{A}(\vec{q})$ is the matrix of partial velocities appropriate for $\vec{f}_\alpha$, the elements of $\vec{q}$ have been set to their simulated values at time t, $\dot{\vec{q}}$ has been set to zero, and all action forces in the system except $\vec{f}_\alpha$ have been set to zero. Note that to perform the decomposition for the centrifugal forces, the elements of $\dot{\vec{q}}$ should be set to their simulated values at time t and all other action forces set to zero. Then, from Eq. (3), the condition $\vec{f}_{S_i}{}^\alpha$ must satisfy is

$$\ddot{\vec{p}}_{S_i}{}^\alpha = \vec{0}. \tag{5}$$

Eq. (5) must be enforced simultaneously for a set of n spring points $[\vec{p}_{S_i}; \; i = 1, \cdots, n]$ that appropriately constrain the equations of motion. We chose the set of enforced spring points to be all springs that had a vertical component of force that exceeded 1% of body weight.

Enforcing Eq. (5) is numerically challenging, so we phrased the problem as a parameter optimization problem in which the controls were the set of reaction spring components $[\vec{f}_{S_i}{}^\alpha; \; i = 1, \ldots, n]$ and the performance criterion was to minimize

$$J_S = \sum_{i=1}^{n}(\ddot{\vec{p}}_{S_i}{}^\alpha \ddot{\vec{p}}_{S_i}{}^\alpha + \vec{f}_{S_i}{}^\alpha \vec{f}_{S_i}{}^\alpha). \tag{6}$$

When the first term in Eq. (6), $\ddot{\vec{p}}_{S_i}{}^\alpha \ddot{\vec{p}}_{S_i}{}^\alpha$, is minimized, Eq. (5) is satisfied or nearly so. The second term in Eq. (6), $\vec{f}_{S_i}{}^\alpha \vec{f}_{S_i}{}^\alpha$, was added to avoid difficulties in the event that more than three spring points on a single rigid body were in contact with the ground. Since only 3 points are needed to fully specify the orientation and position of a rigid body, when more than 3 points are constrained there is a redundancy in the distribution of the constraint forces across $\vec{f}_{S_i}{}^\alpha$. Adding the term $\vec{f}_{S_i}{}^\alpha \vec{f}_{S_i}{}^\alpha$ pushes the solution toward an even distribution of the constraint forces.

Finally, we note that the assumption of rigid contact is only an approximation. In general, there will always be some nonzero acceleration of the spring points in a simulation. To account for these nonzero accelerations, we introduce a fictitious reaction component, $\vec{f}_S{}^I$, which we call the inertial component. The quantity $\vec{f}_S{}^I = \Sigma_{i=1}^{n}\vec{f}_{S_i}{}^I$ is the force necessary to generate any nonzero acceleration of the spring points and was computed by minimizing

$$J_S = \sum_{i=1}^{n}((\ddot{\vec{p}}_{S_i}{}^I - \ddot{\vec{p}}_{S_i})(\ddot{\vec{p}}_{S_i}{}^I - \ddot{\vec{p}}_{S_i}) + \vec{f}_{S_i}{}^I \vec{f}_{S_i}{}^I) \tag{7}$$

where $\ddot{\vec{p}}_{S_i}{}^I = \Psi_i(\vec{I}(\vec{q})^{-1}\vec{S}(\vec{q})\vec{f}_{S_i}{}^I)$ and $\ddot{\vec{p}}_{S_i}$ is the actual acceleration of the ith spring point that occurred during the simulation. If the assumption of rigid contact is good, the magnitude of $\vec{f}_S{}^I$ will be small.

We applied the above described decomposition methodology to quantify the contributions made to the vertical ground-reaction force by the centrifugal forces, by the skeleton in resistance to gravity, by all the muscles taken together, and by each muscle taken separately. From these results, we then computed how each of these sources of force contributed to the overall acceleration of the center of mass of the body.

3. Results

Muscles made the largest contribution to support, accounting for 50–95% of the vertical ground-reaction force generated in stance (Fig. 1, Muscle+Ligaments). The passive transmission of force through the joints and bones in resistance to gravity accounted for 20–50% when the foot was flat on the ground, but made much smaller contributions before foot-flat and after heel-off
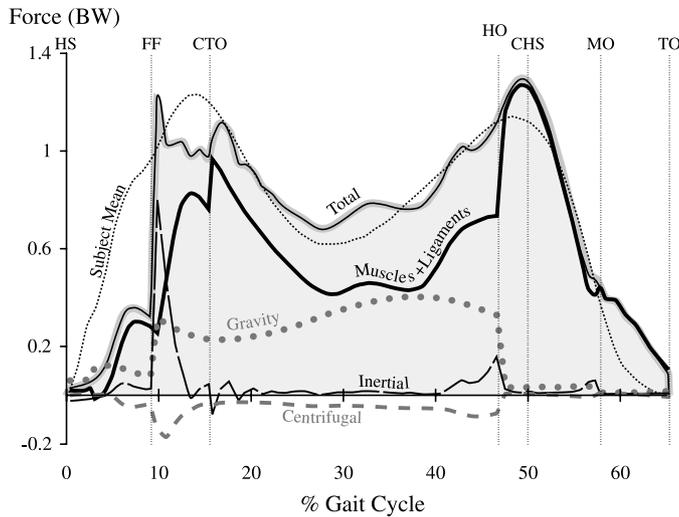
Fig. 1. Contributions of inertial forces (Inertial), of centrifugal forces (Centrifugal), of the resistance to gravity provided by the bones and joints of the skeleton (Gravity), and of muscle and ligament forces (Muscles+Ligaments) to support during normal gait. The thick gray line is the vertical ground-reaction force obtained from the dynamic optimization solution for gait [13]. Total (thin black line) was obtained by summing Inertia, Centrifugal, Gravity, and Muscles+Ligaments. The mean vertical ground-reaction measured for the subjects are shown as a dotted line (Subject Mean). The marked kinematic events are: HS, heel-strike; FF, foot-flat; CTO, contralateral toe-off; HO, heel-off; CHS, contralateral heel-strike; MO, metatarsal-off; and TO, toe-off. BW is body weight (BW = 696 N for the model and the subject mean).

(Fig. 1, Gravity). Centrifugal and inertial forces contributed little throughout stance, except for a brief period after heel-strike when the fore-foot slapped the ground and generated large impact forces (Fig. 1, Inertial at 9% of the gait cycle). The muscles of the contralateral leg contributed no more than 15% to the vertical ground-reaction force, indicating that the support provided by a limb is generated mainly by the muscles of that limb (Fig. 2, Contra. Muscles).

Summing the contributions of inertial, centrifugal, gravitational, and muscle forces gives the total vertical ground-reaction force applied to the leg (cf. Total with thick gray line in Fig. 1). This is an important result to verify, for it is a necessary (although not sufficient) condition for establishing the validity of the methodology used to perform the decomposition of the ground-reaction force.

Since muscles dominate the vertical ground-reaction force, analyzing individual muscle contributions to the vertical ground-reaction force affords further insight into how support is generated in walking. The ankle dorsiflexors, gluteus maximus, vasti, and posterior gluteus medius/minimus generated the majority of support in early stance. Just after heel-strike, but before foot-flat, support was provided mainly by the ankle dorsiflexors (Fig. 3A, DF). From foot-flat to just after contralateral toe-off, gluteus maximus, vasti, and pos-
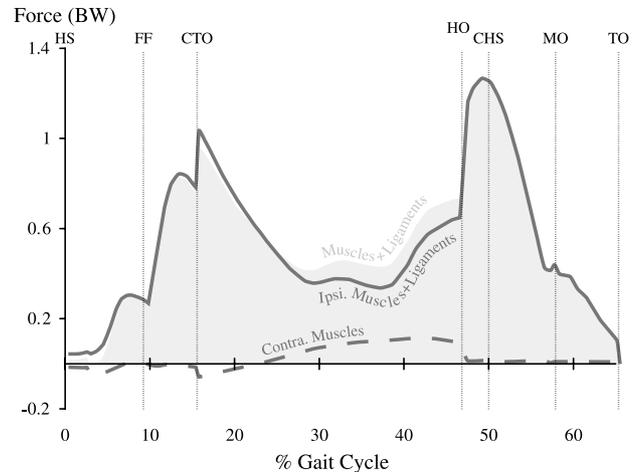

Fig. 2. Contributions to the vertical ground-reaction force of the muscles of the ipsilateral leg (Ipsi. Muscles+Ligaments) and the muscles of the contralateral leg (Contra. Muscles). The shaded region represents the total contribution of all the muscles and ligaments in the model to the vertical ground-reaction force (Muscles+Ligaments). The curve defined by this region is the same as the curve labeled Muscles+Ligaments in Fig. 1. The marked kinematic events are defined in Fig. 1.

terior gluteus medius/minimus contributed most significantly to the vertical ground-reaction force (Fig. 3A, GMAX, VAS, and GMEDP). Thus, these 3 muscle groups were responsible for the first maximum seen in the vertical ground-reaction reaction.

With a significant assist from the passive resistance of the joints and bones to gravity, anterior and posterior gluteus medius/minimus generated nearly all support evident in midstance (cf. GMEDA and GMEDP in Fig. 3B with Gravity in Fig. 1). Posterior gluteus medius/minimus provided support throughout midstance, while anterior gluteus medius/minimus contributed significantly only toward the end of midstance.

Soleus and gastrocnemius generated nearly all support in late stance (Fig. 3C, SOL and GAS). Thus, the ankle plantarflexors were mainly responsible for the second maximum seen in the vertical ground-reaction force. Soleus generated roughly twice as much support as gastrocnemius. The ligaments crossing the metatarsal joint generated all support from metatarsal-off to toe-off (Fig. 3C, Ligaments). Of all the ligaments that were included in the model, only the ligaments that acted at the metatarsal joint contributed substantially to the vertical ground-reaction force. In humans, it is likely that muscles whose tendons cross the metatarsal joint, rather than ligaments, are actually responsible for the contributions made to the vertical ground-reaction force after metatarsal-off.

The biarticular muscles, particularly hamstrings and rectus femoris, contributed very little to support (Fig. 4, HAMS and RF). Other muscles in the model also contributed very little to support, despite developing large forces. These muscles included erector spinae, the
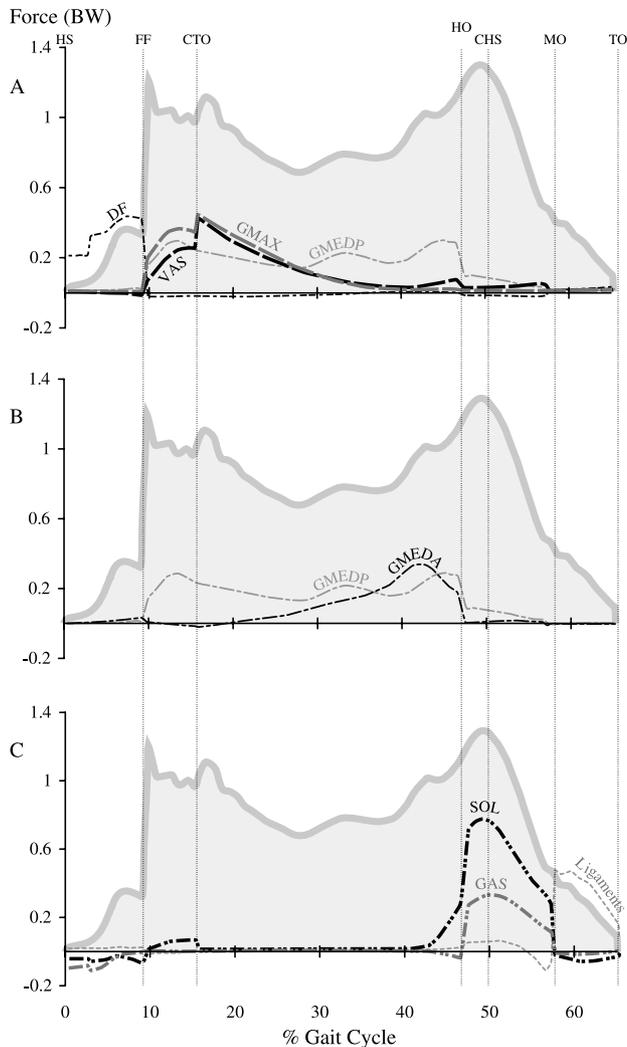
Fig. 3. Muscles contributing most significantly to support in the model. The shaded region represents the vertical ground-reaction force obtained from the dynamic optimization solution. Shown are the major contributions made by muscles in early stance (roughly HS to CTO in A), midstance (roughly CTO to HO in B), and late stance (roughly HO to TO in C). The marked kinematic events are defined in Fig. 1. Symbols used to represent the various muscle groups are DF (ankle dorsiflexors), GMAX (medial and lateral portions of gluteus maximus combined), VAS (vasti), GMEDA (anterior gluteus medius/minimus), GMEDP (posterior gluteus medius/minimus), SOL (soleus), and GAS (gastrocnemius). Ligaments represents the support generated by all the ligaments in the model.

internal and external obliques (not shown), adductor magnus, and iliopsoas (Fig. 4). Iliopsoas, in particular, developed a substantial amount of force during late stance but did not make either positive or negative contributions to support at this time (Fig. 4).

A muscle's potential for generating support can be described by its contribution to the vertical ground reaction per unit of muscle force. This quantity was calculated by dividing each muscle's contribution to the vertical ground-reaction force by the time history of force developed by the muscle. Gluteus maximus, vasti,
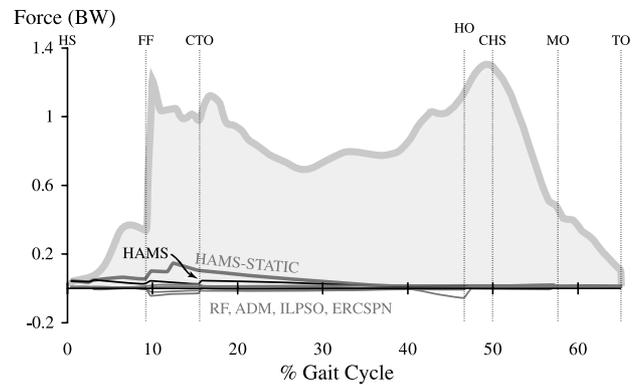

Fig. 4. Muscles that contributed relatively little to support in the model. The shaded region represents the vertical ground-reaction force predicted by the dynamic optimization solution. Shown are the contributions made by hamstrings (HAMS), rectus femoris (RF), adductor magnus (ADM), Iliopsoas (ILPSO), and erector spinae (ERCSPN). ADM, ILPSO, and ERCSPN all developed relatively large forces in the model, but contributed very little to support. HAMS-STATIC is the contribution that hamstrings would make if static optimization rather than dynamic optimization were used to estimate muscle forces during gait. HAMS-STATIC was obtained by multiplying the curve labeled HAMS in Fig. 5A by the time history of force obtained for hamstrings using static optimization (see Fig. 5 in Anderson and Pandy [14]). The marked kinematic events are defined in Fig. 1.

and gluteus medius/minimus had the greatest potential for generating support in early stance (Fig. 5A and B, GMAX, VAS, and GMEDP at 9–15%). During mid-stance, the muscles most able to generate support were gluteus maximus, vasti, soleus, and gluteus medius/minimus; posterior gluteus medius/minimus could generate support throughout midstance, while anterior gluteus medius/minimus was able to contribute only very early in stance (before foot-flat) and at the end of midstance (cf. GMEDA and GMEDP in Fig. 5B). Support in late stance could be given mainly by soleus and gastrocnemius (Fig. 5C, SOL and GAS). Hamstrings had potential for generating support from early stance to midstance, while rectus femoris could contribute mainly during midstance (Fig. 5C, Hams and RF). The back and abdominal muscles could not provide significant support at any time (not shown in Fig. 5).

The body's center of mass experienced a range of vertical accelerations that oscillated about zero during the course of a step and that were brought about mainly by the interplay of gravitational and leg-muscle forces (Fig. 6A, Total). Muscles accelerated the center of mass upward to counteract the downward acceleration of gravity (Fig. 6A, Muscles+Ligaments and Gravity). Gravity did not accelerate the center of mass downward at g (-9.8 m/s^2) because of the resistance offered by the transmission of forces to the ground by the skeleton. Centrifugal forces did not contribute much to the
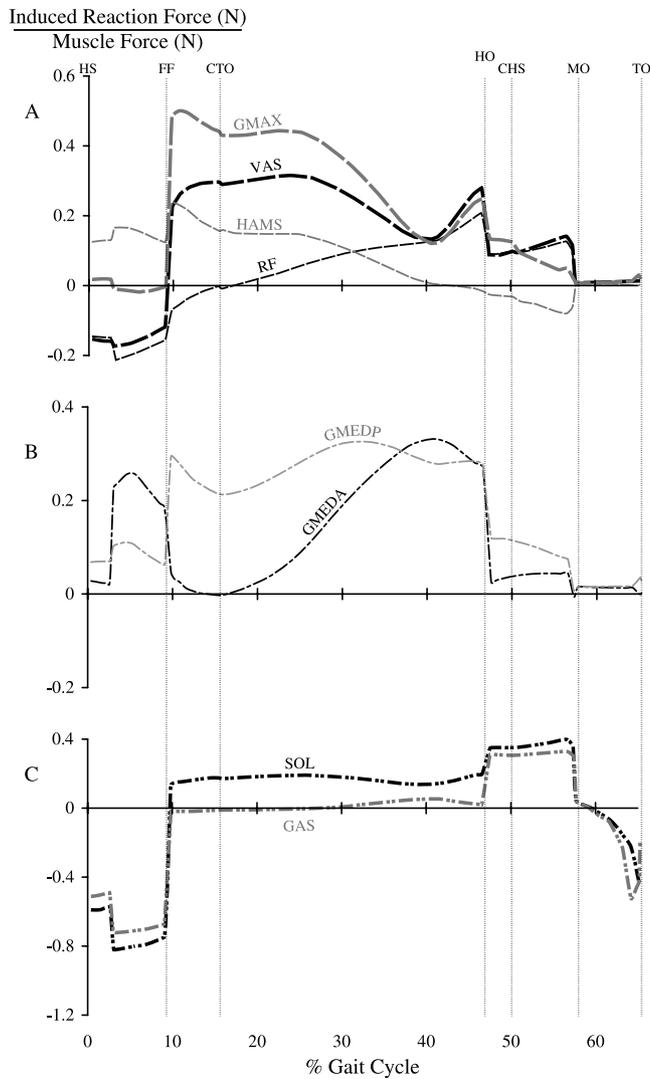
Fig. 5. Potential of some muscles to contribute to support in walking. There are no units for the quantities represented on the vertical axes because a muscle's potential for contributing to support is given by the absolute contribution of that muscle to the vertical ground-reaction force divided by its force. Shown are some of the hip and knee extensors and flexors (A), hip abductors (B), and plantarflexors (C). Muscle symbols are defined in Fig. 3 and Fig. 4. The marked kinematic events are defined in Fig. 1.
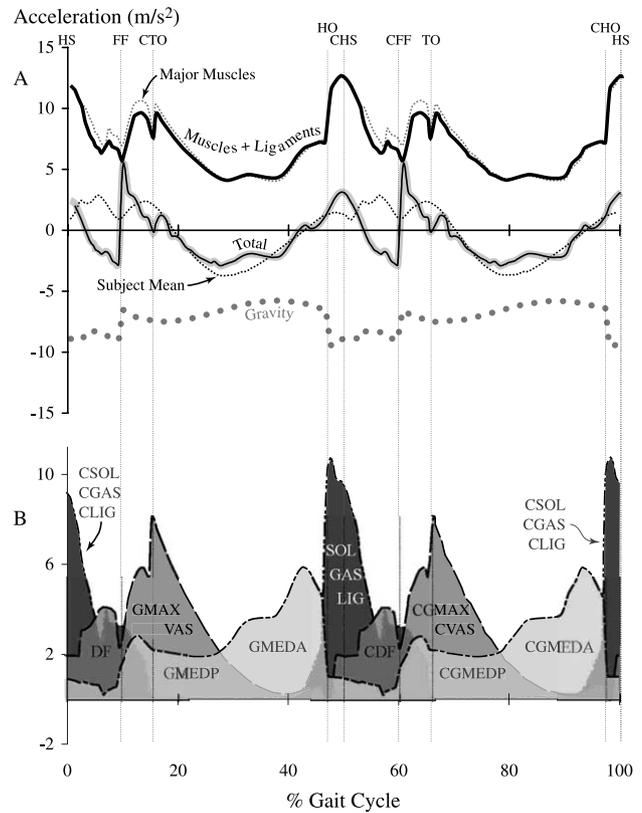
Fig. 6. (A) Contributions of muscle forces and ligament torques (Muscles+Ligaments, thick black line) and of the resistance to gravity provided by the skeleton (Gravity) to the net vertical acceleration of the center of mass of the model (Total, thin black line). Major Muscles (gray dotted line) represents the total contribution of the major contributors to support in the model, specifically DF, GMAX, VAS, GMEDA, GMEDP, SOL, and GAS (Fig. 3). The black dotted line passing through the net vertical acceleration of the center of mass of the model is the mean vertical acceleration of the center of mass of the subjects (Subject Mean). (B) Contributions of individual muscle groups to the net vertical acceleration of the center of mass of the model. Muscle symbols used are as follows: CDF, dorsiflexors of the contralateral leg; CSOL, soleus of contralateral leg; CGAS, gastrocnemius of contralateral leg; CLIG, ligament contributions through the contralateral leg; CGMAX, gluteus maximus of contralateral leg; CVAS, vasti of contralateral leg; CGMEDA, anterior gluteus medius/ minimus of contralateral leg; CGMEDP, posterior gluteus medius/ minimus of contralateral leg. All other symbols are defined in Fig. 1 and Fig. 3.

vertical acceleration of the center of mass (not shown in Fig. 6).

Only the muscles of the leg in contact with the ground contributed significantly to the vertical acceleration of the center of mass (cf. Fig. 2). In double-leg stance, the center of mass was accelerated upward firstly by the plantarflexors of the contralateral leg and dorsiflexors of the ipsilateral leg, and then by the combined actions of the gluteus maximus, vasti, and gluteus medius/ minimus of the ipsilateral leg (Fig. 6B, HS to CTO). In midstance, gluteus maximus, vasti, and gluteus medius/minimus of the ipsilateral leg continued to accelerate the center of mass upward, but their actions were insufficient to overcome the downward pull of

gravity, and so the body accelerated downward during this time (Fig. 6B, 20–40% of gait cycle). The plantarflexors of the ipsilateral leg caused a net upward acceleration of the center of mass just prior to heel strike of the contralateral leg (Fig. 6B, SOL, GAS, and CLIG at 45–60%).

4. Discussion

Although the issue of support has been addressed previously, most notably by Winter [2], Mochon and McMahon [5,6], Pandy and Berme [7–9], Perry [4],

Kepple et al. [10], Meinders et al. [26], Riley et al. [12], and Neptune et al. [11], detailed knowledge of how individual muscles generate support has not emerged until now. Each of the above studies, except Neptune et al. [11], considered only the contributions of the net joint moments to support. The analysis presented by Neptune et al. [11] considered the actions of individual muscles, but only in the sagittal plane.

The musculoskeletal model used in the present study permitted motion of the limbs in all three anatomical planes, and it also permitted the execution of all six gait determinants as proposed by Saunders et al. [1]. Also, because the model was actuated by 54 lower-extremity muscles, the dynamic optimization solution afforded the opportunity to quantify the contributions made by these muscles to the vertical ground-reaction force and, therefore, to the acceleration of the whole-body center of mass.

Perhaps contrary to what one might expect, the passive resistance of the skeleton to the force of gravity was less than 50% of body weight throughout stance and less than 10% of body weight when the stance foot was not flat on the ground. These results should not be interpreted to mean that gravity exerts a force on the body that is less than one body weight (BW); indeed, gravity always exerts a force of 1 BW. The Gravity component shown in Fig. 1 represents the ground-reaction force that would arise if the body were acted on by gravity alone, and its magnitude is a function of the orientations of the limbs and how the feet are in contact with the ground (see Appendix A for a simple example). During midstance, when the feet were flat on the ground and the stance leg was fairly straight, the downward force of gravity was resisted by compressive forces that were transmitted effectively through the bones and joints to the ground. This gravity-induced reaction force reached its maximum when the knee joint was at its peak extension at about 38% of the gait cycle (Fig. 1, Gravity). It remained less than 1/2 BW, and sometimes dropped close to zero, because the orientations of the limbs and nature of the foot contact permitted large downward accelerations of the limbs. When the foot was not flat on the ground, reaction forces could not be transmitted effectively through the bones to the ground without the actions of muscles; therefore, before foot-flat and after heel-off, the gravity-induced reaction force was very small.

Centrifugal forces did not contribute much because the angular velocities of the joints are relatively small in walking (i.e. maximum joint angular velocities were around 6 rad/s). Furthermore, centrifugal forces acted primarily to reduce the vertical ground-reaction force because these forces are always directed away from the centers of joint rotation, and ultimately the ground. This behavior is more easily understood in the case of a simple pendulum (Appendix A).

If the skeleton did so little to resist the downward force of gravity and the centrifugal reaction components were so small, it follows that the burden of maintaining support must have been borne mainly by the muscles in the model. This is indeed what we found. In fact, almost all of the muscular support was generated by relatively few of the 54 muscles in the model: the dorsiflexors, gluteus maximus, vasti, gluteus medius/minimus, soleus, and gastrocnemius (Fig. 3). Consistent with the findings of Winter [2], Mochon and McMahon [6], and Kepple et al. [10], the hip and knee extensors were the main contributors to support in early stance, although prior to foot-flat the dorsiflexors made important contributions as well. Also consistent with the findings of Mochon and McMahon [6], the abductors were the main contributors to support in midstance. Finally, consistent with what has been found by many, the plantarflexors were the main contributors in late stance [3,4,6–8,10–12].

The event of foot-flat marked an important transition in function for the dorsiflexors, gluteus maximus, and vasti (Fig. 3A). Prior to foot-flat, nearly all support was provided by the dorsiflexors. At foot-flat, when the downward motion of the forefoot was resisted by the ground, the burden of support shifted sharply to gluteus maximus and vasti. It is well known that the dorsiflexors are active during weight acceptance, and it is intuitively appealing to think of them as resisting the downward fall of the forefoot during this time [4]. Our findings suggest that in doing so, they also make important contributions to support. What is perhaps not so intuitive is that prior to foot-flat gluteus maximus and vasti cannot contribute positively to support at all. According to our analyses, the potential to contribute to support prior to foot-flat is close to zero for gluteus maximus and negative for vasti (Fig. 5A, GMAX and VAS prior to FF). This means that other muscles must be responsible for generating a positive ground-reaction force prior to foot-flat. Interestingly, hamstrings, like the dorsiflexors and unlike gluteus maximus and vasti, have the potential to contribute positively to support prior to foot-flat and might offer some compensation for weak dorsiflexors (Fig. 5A, HAMS prior to FF).

A closer look at the contributions made by the posterior and anterior portions of gluteus medius/minimus emphasizes that the function of a muscle can depend strongly on body position. Anterior gluteus medius/minimus (GMEDA) developed forces as large as the posterior portion (GMEDP) throughout the gait cycle, yet GMEDA contributed almost nothing to support during early stance (Fig. 3B). The reason is that GMEDA possessed a moment arm at the hip that acted to flex the hip as well as abduct it. These two actions opposed one another and prevented GMEDA from generating support in early stance, no matter what its force (Fig. 5B, following FF). As stance progressed

and the hip extended, GMEDA's hip flexion moment arm fell close to zero so that this muscle became more of a pure abductor and made a contribution to support that was similar in magnitude to GMEDP.

The biarticular rectus femoris and hamstrings did not provide much support in the model. The explanation is twofold. First, the forces predicted for these muscles by the dynamic optimization solution, and also by a static optimization solution, were small compared to the forces predicted for the uniarticular hip and knee extensors [14]. Second, the capacities of hamstrings and rectus femoris to contribute to support were somewhat less than the capacities of gluteus maximus and vasti (Fig. 5A).

A number of other muscles in the model developed substantial forces and yet did not contribute significantly to support. They included adductor magnus, erector spinae, and iliopsoas (Fig. 4). As has been hypothesized by others, the adductors are likely involved in controlling the lateral displacement of the pelvis (the sixth determinant of gait [1]), the trunk muscles are likely important for maintaining the upright posture of the trunk, and iliopsoas is probably important for swing initiation [4]. Further analysis of the dynamic optimization solution should clarify the functions of these muscles.

Our findings may be limited in several respects. First, the ground-reaction force predicted by the model is somewhat different from force platform measurements commonly obtained from normal subjects. Most notably, prior to foot-flat the model ground-reaction force rises too slowly. We believe this slow rise was because the dorsiflexors in the model did not exert enough force during this time. Had the dorsiflexors exerted more force, our findings would have likely changed in two ways: (1) the dorsiflexors would have made a larger contribution to support prior to foot-flat and (2) the spike in the inertial component that appears in response to the fore-foot slapping the ground (Fig. 1) would have been reduced.

Second, our results for the contributions of individual muscles to the vertical ground-reaction force are only as good as the predictions for the muscle forces themselves. In general, we believe these predictions are reasonable [14]; however, there is a possibility that the muscle coordination pattern predicted for soleus is atypical. In our model, the dynamic optimization solution predicted that soleus should develop large forces only during late stance, whereas EMG activity for soleus is often observed for much of stance, although at low levels [4]. Based on the results of Fig. 5C, we note that soleus did have the capacity to contribute to the vertical ground-reaction force during midstance. Therefore, had soleus developed larger forces during midstance, we would have found it to have made a larger contribution to support during this time, which would

have been more consistent with the findings of Kepple et al. [10], Neptune et al. [11], and Riley et al. [12].

Third, the findings presented here likely possess some sensitivity to the decomposition methodology that was used. While our approach is not a perfect solution to the decomposition problem, we believe it is adequate. It satisfies the necessary condition of superposition and is not sensitive to the tuning of any particular parameter. The drawback of the method is that rigid contact between the foot and the ground is assumed. Rigid contact between the foot and the ground (i.e. zero acceleration of the foot relative to the ground) was rarely precisely true during the gait cycle; however, since the foot-ground springs were stiff and damped, it was approximately true for much of the gait cycle. The inertial term described in Section 2 quantifies the force necessary to generate any non-zero acceleration of the foot, and is a measure of how accurate the assumption of rigid contact really was. During the walking simulation, the inertial term was large only for the short period between the onset of foot-flat and just before opposite toe-off (Fig. 1, 9–13%). During the rest of the simulation, therefore, we believe the assumption of rigid contact was reasonable.

By conducting a detailed analysis of a dynamic optimization solution for normal gait, a simple picture of how muscles contribute to support has emerged that substantiates the findings and hypotheses of others. Muscles do most of their work in accelerating the body's center of mass upward when both feet are on the ground [27]. It is clear also that support of the center of mass is brought about by the precisely timed actions of only a few major muscle groups: the ankle plantarflexors and dorsiflexors, the hip and knee extensors, and the hip abductors. The dorsiflexors of the ipsilateral leg and the plantarflexors of the contralateral leg act initially to accelerate the center of mass upward just after heel strike (Fig. 6B, HS to FF). Thereafter, the hip extensors, knee extensors, and hip abductors of the ipsilateral leg provide support until early single-leg stance (Fig. 6B, FF to just after CTO). During midstance, only the hip abductors are needed to generate the necessary level of support as the body is then accelerated downward under the force of gravity (Fig. 6B, 20–40% of gait cycle). The phasic cycle of muscle action is completed when the ankle plantarflexors of the ipsilateral leg are called upon to accelerate the center of mass upward prior to contralateral heel strike (Fig. 6B, HO to CHS).

Finally, a motivating aspect of this work is the potential it offers to link specific features of the ground-reaction force to the actions of individual muscles. As modeling techniques advance and decomposition methodologies are refined, we are hopeful that this kind of analysis can be applied on a subject-specific basis to yield information useful for improving the diagnosis and treatment of gait pathologies.

Acknowledgements

Appendix A

We use the simplest model of walking, a single inverted pendulum, to show how gravity and centrifugal forces can contribute to the vertical reaction force exerted by the ground. This model has been used extensively to study the mechanics and energetics of walking [5,7,28]. The equation of motion for the pendulum is

$$(ml^2 + I)\ddot{\theta} + mgl\cos\theta = 0, \tag{A.1}$$

where m and l are the mass and length of the pendulum, and θ is the angle which the pendulum makes with the ground. The vertical component of the ground-reaction force is given simply by:

$$F_{gy} = m\ddot{y}_{cm} + mg \tag{A.2}$$

where $\ddot{y}_{cm}$ is the acceleration of the center of mass of the body, which is assumed to be lumped at the tip of the pendulum. The acceleration of the center of mass can be expressed in terms of the angular displacement, θ, angular velocity, $\dot{\theta}$, and angular acceleration, $\ddot{\theta}$ of the pendulum, thus:

$$\ddot{y}_{cm} = l(\cos\theta\ddot{\theta} - \sin\theta\dot{\theta}^2). \tag{A.3}$$

Substituting Eq. (A.3) into Eq. (A.2) gives

$$F_{gy} = mg + ml(\cos\theta\ddot{\theta} - \sin\theta\dot{\theta}^2). \tag{A.4}$$

The angular acceleration of the pendulum can be eliminated from Eq. (A.4) by solving for $\ddot{\theta}$ from Eq. (A.1) and substituting the result into Eq. (A.4). The resulting expression for the vertical ground-reaction force is

$$F_{gy} = -ml\sin\theta\ddot{\theta} + mg\sin^2\theta. \tag{A.5}$$

Fig. 7 shows the contributions made to the vertical ground-reaction force by the centrifugal force, $-ml\sin\theta\dot{\theta}^2$, and by gravity, $mg\sin^2\theta$. Gravity's contribution to the vertical ground-reaction force depends only on position, the value of θ; velocity's contribution is determined by both the instantaneous position and velocity of the pendulum, θ and $\dot{\theta}$. Gravity dominates the vertical ground-reaction force (compare Gravity with Total in Fig. 7). The centrifugal force remains
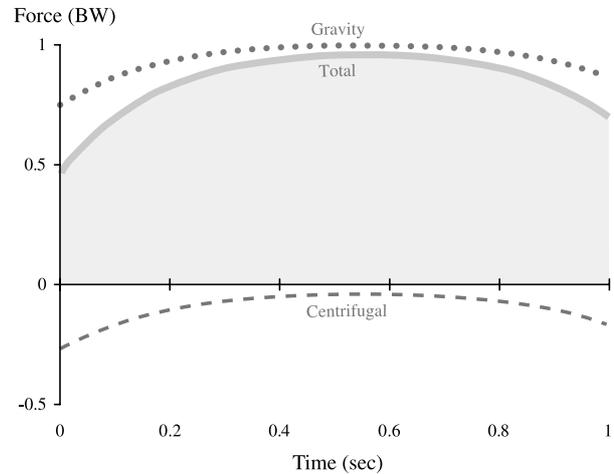

Fig. 7. Contributions of gravitational forces (Gravity) and centrifugal forces (Centrifugal) to the vertical ground-reaction force (Total) generated by the single pendulum model.

relatively small because the angular velocity of the pendulum was chosen to be around 1 rad/s in order to get the time of swing about right for walking at a natural cadence [5].

In this simple example, the resistance of the staff of the pendulum to the force of gravity is much greater than the resistance offered by skeleton during the walking simulation (Fig. 1, Gravity). In fact, it was equal to one body weight when the pendulum was exactly vertical ($\theta = 90°$) (Fig. 7, Gravity, at about 0.5 s). The reason for the difference between the pendulum and the skeleton is that the skeleton has many more joints and, during normal walking, the joint angles are never such that the bones of the skeleton are arranged perfectly vertically, one on top of the other. Rather, there is always some amount of bend in joints that allows the limbs to accelerate downward, just as the pendulum accelerates downward when it is not exactly vertical.

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