Neuromusculoskeletal Computer Modeling and Simulation of Upright, Straight-Legged, Bipedal Locomotion of *Australopithecus afarensis* (A.L. 288-1)

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ABSTRACT   The skeleton of *Australopithecus afarensis* (A.L. 288-1, better known as "Lucy") is by far the most complete record of locomotor morphology of early hominids currently available. Even though researchers agree that the postcranial skeleton of Lucy shows morphological features indicative of bipedality, only a few studies have investigated Lucy's bipedal locomotion itself. Lucy's energy expenditure during locomotion has been the topic of much speculation, but has not been investigated, except for several estimates derived from experimental data collected on other animals. To gain further insights into how Lucy may have walked, we generated a full three-dimensional (3D) reconstruction and forward-dynamic simulation of upright bipedal locomotion of this ancient human ancestor. Laser-scanned 3D bone geometries were combined with state-of-the-art neuromusculoskeletal modeling and simulation techniques from computational biomechanics. A detailed full 3D neuromusculoskeletal model was developed that encompassed all major bones, joints (10), and muscles (52) of the lower extremity. A model of muscle force and heat production was used to actuate the musculoskeletal system, and to estimate total energy expenditure during locomotion. Neural activation profiles for each of the 52 muscles that produced a single step of locomotion, while at the same time minimizing the energy consumed per meter traveled, were searched through numerical optimization. The numerical optimization resulted in smooth locomotor kinematics, and the predicted energy expenditure was appropriate for upright bipedal walking in an individual of Lucy's body size. Am J Phys Anthropol 126:2–13, 2005.   © 2004 Wiley-Liss, Inc.

Evidence from fossils and footprints suggests that our human ancestors started walking on two legs rather than four between 3–5 million years ago (Alexander, 1984; Charteris et al., 1982; Lewin, 1983). The skeleton of *Australopithecus afarensis* A.L. 288-1 (commonly known as "Lucy"), recovered in 1974 from the Hadar region of Ethiopia (Johanson and Taieb, 1976; Johanson et al., 1982), is by far the most complete record of locomotor morphology of early hominids currently available (Conroy, 1997) (Fig. 1). Some researchers (Latimer and Lovejoy, 1989, 1990; Lovejoy, 1988; Lovejoy et al., 2001) suggested that these fossil fragments provide evidence that Lucy may have walked upright with legs kept relatively straight, in a manner similar to that in which humans walk today. Crompton et al. (1998) also arrived at that conclusion by examining kinematic simulations of Lucy. Kramer (1999), as well as Kramer and Eck (2000), performed similar analyses, and concluded that human-like upright locomotion by Lucy may have been as efficient as the upright locomotion of modern humans. On the other hand, there is evidence suggesting Lucy may have walked in a manner similar to that in which chimpanzees walk today, i.e., locomotion with bent hips and bent

knees (Stern and Susman, 1983; Stern, 1999; Susman et al., 1984). Therefore, further research is required to better understand the form of locomotion employed by this human ancestor.

Although several studies support the contention that Lucy may have walked upright like humans do today (Latimer and Lovejoy, 1989, 1990; Lovejoy, 1988; Lovejoy et al., 2001), most of these studies are based solely on the morphological features of Lucy's skeletal remains. Obviously, it is impossible to examine the locomotion of *A. afarensis* experimentally. This is unfortunate, as physiological and biomechanical data would greatly enhance the anthropological understanding gained through examining fossil remains. This is one of the reasons why many

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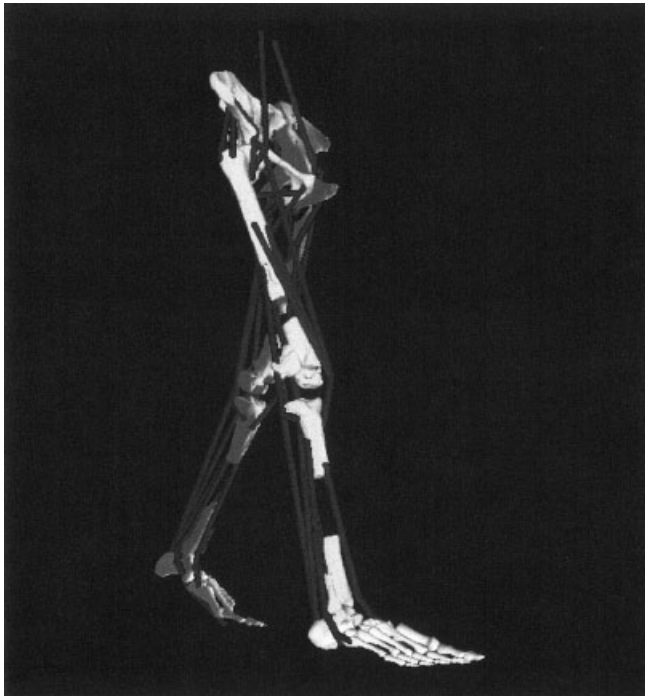E-mail: a-nagano@postman.riken.go.jp

Fig. 1. Lucy's neuromusculoskeletal model consists of 9 segments (HAT, thighs, shanks, feet, toes; see Table 1) and 10 joints (20 degrees of freedom). Each leg has 26 Hill-type muscles (52 muscles in total) (Table 2). Lucy's bone casts were scanned using a laser digitizer (Model 3030, Cyberware, Inc., Monterey, CA), and then imported into a workstation (Silicon Graphics, Inc., Mountain View, CA). Muscle origin, insertion, and via-points were digitized using SIMM (Musculographics, Inc., Santa Rosa, CA). Foot geometry displayed above is a human foot scaled to dimensions used in this study, based on other *A. afarensis* specimens (Latimer et al., 1982).

researchers investigated the locomotion of currently available creatures (e.g., chimpanzees), hoping to gain insights regarding the locomotion of human ancestors (Aerts et al., 2000; Crompton et al., 1996; D'Aout et al., 2002; Fedak et al., 1982; Grasso et al., 2000; Heglund et al., 1982; Jenkins, 1972; Tardieu et al., 1993; Taylor and Heglund, 1982; Taylor et al., 1982).

The methodology of computer modeling and simulation is very useful for addressing questions where direct measurements are not practical, or as in the current case, not possible. Developments in the field of computational biomechanics make it possible to generate detailed neuromusculoskeletal models of modern humans (Anderson and Pandy, 1999, 2001). Using this methodology, it was possible to generate an equally detailed neuromusculoskeletal model of Lucy (Nagano, 2001). This model has mathematical representations of Lucy's skeletal, neural, and muscular subsystems. Therefore, it was possible to account for individual muscle actions, including muscle energy expenditure, during locomotion. Other investigators recently used computer models to study Lucy's locomotion, but details of the neuromuscular system were not included.

Crompton et al. (1998) reported on a computer modeling study in which Lucy's possible locomotor patterns were evaluated. Although this study took a novel step in the application of advanced biomechanical techniques to the field of anthropology, the computer simulation model used by Crompton et al. (1998) lacked predictive power, in that it was not actuated by mathematical representations of the lower limb muscles. Instead, preassigned kinematic patterns served as inputs to the model, and then joint moments and reaction forces acting between segments were calculated using inverse dynamics (Winter, 1990). Kramer (1999) and Kramer and Eck (2000) performed similar analyses using a model of Lucy's skeletal system. Segmental mechanical energies (sums of potential and kinetic energies) of individual segments were calculated, based on kinematic data derived from modern humans. As the models used in these preceding studies (Crompton et al., 1998; Kramer, 1999; Kramer and Eck, 2000) were driven by preassigned kinematics, as opposed to being driven by the neural excitation of model elements representing individual muscles, the insights that could be gained were limited in scope. For example, it was impossible to calculate the energy consumed by muscles during locomotion. The "energetic" features of Lucy's locomotion discussed in these studies implicitly relate only to mechanical energy expenditure, which exhibits poor correlation with metabolic energy expenditure in walking (Martin et al., 1993).

Therefore, in this study, we tested the hypothesis that Lucy walked in a human-like manner, with a similar energy cost, by generating a full three-dimensional (3D) reconstruction and forward-dynamic simulation of upright (i.e., human-like) bipedal locomotion of this human ancestor. In this simulation study, the entire neuromusculoskeletal model was driven solely by neural inputs (muscle activation profiles) to each of the muscles as a function of time. As a result, characteristics of reconstructed bipedal locomotion can be attributed solely to the inherent properties of the neuromusculoskeletal system, and are not dependent on a priori assumptions about the resulting kinematics. As Stern (1999, 2000) noted, results of computer modeling and simulation studies are affected by underlying assumptions and parameters used in the development of the model. With this in mind, only two primary assumptions were made in this simulation study, which are as straightforward as possible (see Methods).

Gross metabolic energy expenditure is believed to be an important criterion for animal locomotion (Hoyt and Taylor, 1981; Nishii, 2000; Ralston, 1958; Sparrow and Newell, 1998; Waters and Mulroy, 1999). Sparrow and Newell (1998) reviewed the literature in this area, and concluded that minimization of metabolic energy expenditure may be the most important factor in the organization of large-scale movement production, including locomotion. Recent simulation work of walking in modern hu-

TABLE 1. Lucy's body segmental parameter values

	HAT[4]	Thigh	Shank	Foot-L[2]	Foot-H[3]
Mass (kg)[4]	17.539	4.452	1.449	0.389	
Length (m)	0.491	0.281[5]	0.241[6]	0.168[7]	0.042[8]
CM (m)[4]	0.208	0.101	0.105	0.067	0.021
I_{xx} (kg · m^2)[4]	0.2563	0.0479	0.0060	0.0002	
I_{yy} (kg · m^2)[4]	0.0369	0.0092	0.0007	0.0010	
I_{zz} (kg · m^2)[4]	0.2426	0.0466	0.0058	0.0009	

[1] Head, arms, and trunk.
[2] Foot length.
[3] Foot height.
[4] Total body mass was assumed to be 30.12 kg (Crompton et al., 1998). Mass, position of center of mass, and moment of inertia of each segment were estimated referring to human body segmental parameter data (de Leva, 1996). $_{xx}$sagittal axis; $_{yy}$longitudinal axis; $_{zz}$transverse axis.
[5] Jungers (1982).
[6] Geissmann (1986).
[7] Jungers (1988).
[8] Latimer et al. (1982).

mans (Anderson and Pandy, 2001; Umberger et al., 2003) also showed that minimization of the cost of locomotion does indeed lead to movement patterns that mimic normal human walking. Some researchers further suggested that the origin of bipedal locomotion itself is tied to improvements in locomotor economy over quadrupedal forms (e.g., Leonard and Robertson, 1997; Rodman and McHenry, 1980), although there is certainly no agreement on this point (e.g., Steudel, 1996; Taylor and Rowntree, 1973). Since metabolic energy expenditure is an important factor in biomechanical assessments of locomotion, Lucy's reconstructed 3D upright bipedal locomotion was evaluated in terms of total energetic cost. The main purpose of this study was to evaluate whether or not Lucy could have walked in a human-like manner (upright, straight-legged locomotion) with an energetic cost similar to that in modern humans.

METHODS

The reconstruction started by laser-scanning fossil fragments to obtain 3D bone geometries. Even though Lucy's 3D bone geometries are available, gaps in the femur and tibia (Fig. 1) make it difficult to determine segment lengths. Several researchers estimated segment lengths from other morphological features of these fossils, such as the width of the tibial plateau. The most frequently referenced value was selected for each segment (Table 1). As foot morphology is not available for Lucy, the morphology was obtained by scaling down the values for A.L. 333-8 (Latimer et al., 1982). Lucy's *relative* body segment inertial parameters (Table 1) were based on relations reported for humans (de Leva, 1996). This assumption seems reasonable, given that *A. afarensis* had many morphological features similar to those of modern humans (Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990; Lovejoy, 1988; Lovejoy et al., 2001).

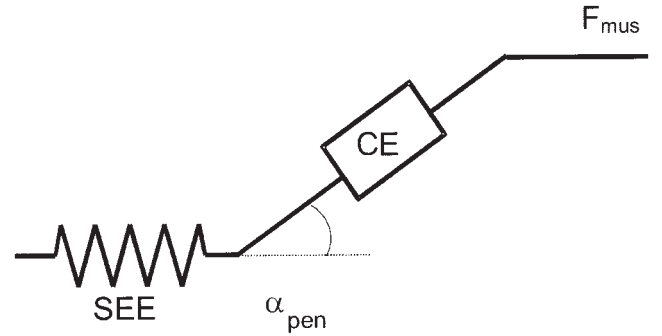Five joints were defined in each leg. The hip joint was designed as a triaxial joint. All other joints

(knee, ankle, subtalar, and metatarsophalangeal joints) were designed as monoaxial hinge joints. Passive joint properties, due to structures such as ligaments and joint capsules, were based on experimental data from human subjects (Riener and Edrich, 1999). The passive joint restraints make a very small contribution during an activity such as walking, but help prevent the joints from assuming nonphysiological postures (e.g., excessive knee joint hyperextension). The distance between the two hip joints, which is markedly larger (in a relative sense) for Lucy than for modern humans, was determined based on the geometry of Lucy's bones. This resulted in a horizontal distance between the right and left hip joint centers of 0.118 m, which is consistent with Lucy's estimated pelvic inlet width (0.132 m) also determined through reconstruction of her skeleton (Rak, 1991).

The neuromusculoskeletal model (Fig. 1) included a total of 52 lower extremity muscles (26 in each leg) that acted upon the skeletal subsystem. The lower extremity model encompassed all major bones, joints, and muscles that have a physiological cross-sectional area (PCSA) larger than 14 cm^2 (Friederich and Brand, 1990). The static and dynamic properties of the 52 muscles were represented using a muscle model of the type by Hill (1938). The Hill-type model consisted of a contractile element representing all muscle fibers, and a series elastic element representing all elastic components in series with the contractile element (CE) (Fig. 2). The force-length-velocity relations of the contractile element (Hill, 1938), as well as the nonlinear force-length property of the series elastic element, were implemented. Mathematically, the behavior of each muscle was represented by two ordinary differential equations (ODE): one ODE per muscle was used to describe the delay between muscle activation signals and muscle active states (He et al., 1991). A second ODE per muscle was used to describe the contractile dynamics, because force in the CE is a function of both CE length and CE contractile velocity. A detailed mathematical description of this

Fig. 2. Each muscle is represented mathematically by a Hill-type muscle model, which consists of a contractile element (CE) representing all muscle fibers (F_{mus}), and a series elastic element (SEE) representing all series elasticity, including tendon. Effect of muscle fiber pennation angle (α_{pen}) was also considered.

TABLE 2. *Lucy's muscle parameter values*

Muscles[1]	F_{MAX} (N)[2]	$L_{CEop \ (m)}$[3]	α_{pen} (degrees)[4]	L_{slack} (m)[5]
ILIA	448.6	0.0544	6.5	0.0488
PSOA	494.2	0.0561	7.5	0.1587
GMAX	1,149.6	0.0784	3.3	0.0731
GMED	1,200.2	0.0366	9.0	0.0767
GMIN	518.0	0.0294	10.5	0.0548
ADDL	437.1	0.0448	3.5	0.0694
ADDM	1,111.8	0.0613	4.2	0.0334
ADDB	324.2	0.0460	0.0	0.0379
PIRI	394.9	0.0140	9.5	0.0845
QUAD	403.8	0.0292	0.0	0.0277
RECF	619.5	0.0401	14.0	0.3033
BFEL	394.3	0.0574	7.0	0.2444
SEMM	668.1	0.0542	16.0	0.2526
SEMT	335.6	0.0659	6.0	0.2573
VASL	928.9	0.0577	13.0	0.1966
VASI	1,182.6	0.0534	2.5	0.1915
VASM	964.4	0.0553	7.0	0.2075
BFES	117.4	0.0889	15.0	0.0744
GASM	1,012.7	0.0218	6.5	0.2569
GASL	286.2	0.0401	17.5	0.2442
TIBA	337.8	0.0401	12.0	0.1489
SOLE	3,736.4	0.0160	32.0	0.1963
TIBP	525.8	0.0184	19.0	0.1775
PERL	493.3	0.0222	5.5	0.2409
PERB	392.5	0.0186	12.0	0.1102
FHAL	370.7	0.0262	19.0	0.2280

[1] Implemented muscles are (from top to bottom): m. iliacus (ILIA), m. psoas major (PSOA), m. gluteus maximus (GMAX), m. gluteus medius (GMED), m. gluteus minimus (GMIN), m. adductor longus (ADDL), m. adductor magnus (ADDM), m. adductor brevis (ADDB), m. piriformis (PIRI), m. quadratus femoris (QUAD), m. rectus femoris (RECF), m. biceps femoris caput longum (BFEL), m. semimembranosus (SEMM), m. semitendinosus (SEMT), m. vastus lateralis (VASL), m. vastus intermedius (VASI), m. vastus medialis (VASM), m. biceps femoris caput brevis (BFES), m. gastrocnemius medialis (GASM), m. gastrocnemius lateralis (GASL), m. tibialis anterior (TIBA), m. soleus (SOLE), m. tibialis posterior (TIBP), m. peroneus longus (PERL), m. peroneus brevis (PERB), and m. flexor hallucis longus (FHAL). Parameter values were obtained by scaling human muscle data (Friederich and Brand, 1990).
[2] Maximal isometric contractile element force.
[3] Optimal contractile element length.
[4] Pennation angle.
[5] Series elastic element unloaded length.

model can be found in a preceding study (Nagano and Gerritsen, 2001). Both muscle activation and contraction dynamics were coded in FORTRAN, compiled, and linked to DADS-3D (LMS CADSI, Coralville, IA) through the USER.FORCE option.

Parameters to specify muscle characteristics were estimated by scaling human muscle data (Friederich and Brand, 1990) (Table 2). Specifically, the PCSAs were scaled to fit Lucy's body size and multiplied by a specific tension of 31.5 N/cm^2 (Brown et al., 1998) to calculate maximal isometric contractile element force values (Table 2). The fascicle length data were regarded as the optimal contractile element (i.e., muscle fiber) length for human muscles, and were scaled to fit Lucy's body size (Table 2). Muscle pennation angles were also derived from Friederich and Brand (1990) (Table 2). Unloaded lengths of series elastic elements were calculated such that optimum muscle force could be produced in the middle of the range of motion of the joint(s) it crosses (Anderson and Pandy, 1999, 2001).

Lucy's 3D bone geometries were imported and assembled using SIMM software (Musculographics, Inc., Santa Rosa, CA) (Fig. 1). Muscle origin, insertion, and via-points were located and digitized by combining Lucy's skeletal geometry with a knowledge of human gross anatomy (McMinn et al., 1995; van Wynsberghe et al., 1995). Relative locations between the origin, insertion, and joint center of rotation determine the biomechanical action of each muscle. Several morphological features of Lucy's skeleton, especially those of the pelvis, are distinctly different from those of modern humans (Abitbol, 1995; Berge, 1994; Lovejoy et al., 1999; Rak, 1991); thus, this procedure did not simply produce a scaled-down human. Instead, it produced a musculoskeletal geometry that was unique to *A. afarensis*. For example, because of the shape of Lucy's pelvis (wider than that of modern humans; Rak, 1991), Lucy's lower limb muscles have larger moment-generating capacity in the coronal/transverse plane than in humans. As rotation of the pelvis in the transverse plane is an important determinant of gait (Saunders et al., 1953), this difference potentially has great impact on the mechanisms underlying Lucy's locomotor abilities. Therefore, the present model has individual muscles that are scaled directly from modern humans (because no soft-tissue information is available for Lucy), but an overall musculoskeletal geometry that is uniquely Lucy's.

An unrestrained simulation of hominid locomotion requires a model of foot-ground interaction. The basic equation used to describe foot-ground forces was adopted from Anderson and Pandy (1999):

$$GRF_y = \alpha_1 \cdot \exp(-\alpha_2 \cdot (y - \beta_1))$$
$$- \frac{\alpha_3 \cdot y}{1 + \alpha_4 \cdot \exp(\alpha_5 \cdot (y - \beta_2))} \quad (1)$$

where GRF_y is the vertical component of ground reaction force, and y is the vertical position of the foot/ground contact point (floor = 0.0 m). As the foot of the model contacts the floor, a ground reaction force is developed according to Equation 1. The viscoelastic parameter values were calculated through numerical optimization such that a computer simulation of a drop-test for a single mass on this particular ground reaction force model gave results similar to those of pendulum tests on human heel pad tissue (Aerts and DeClercq, 1993). The optimization resulted in the following parameter values: $\alpha_1 = 1.039$ N; $\alpha_2 = 491.804$ m^{-1}; $\alpha_3 = 963.321$ Nm$_{-1}$ $\alpha_4 = 44.715$ (no units); $\alpha_5 = 706.924$ m^{-1}; $\beta_1 = 0.857 \times 10^{-4}$ m; and $\beta_2 = -2.325 \times 10^{-3}$ m. Five contact points in each foot (2 on the heel, 2 on the metatarsophalangeal joint, and 1 on the toe) were modeled (Anderson and Pandy, 1999; Nagano, 2001).

The only inputs to the neuromusculoskeletal model were 52 muscle activation profiles, each spec-

ified by three values: onset time (T_{on}), offset time (T_{off}), and amplitude of activation (ACT) (Nagano and Gerritsen, 2001). Muscle activation profiles in the left leg were assumed to be identical to, but 50% out of phase from the muscle activation profiles in, the right leg. In order to "teach" the model how to walk, muscle activation profiles were numerically optimized (Fig. 3). The goal of the numerical optimization process was to minimize an objective function that consisted of three separate terms: 1) the difference between the simulated posture at the end of the first step and a typical upright, human-like target posture described by segment Euler angles (3 Euler angles of 7 segments = 21 angles) (RMS_{ang}), 2) the difference in the first time derivatives of 21 Euler angles between the beginning and the end of the step (RMS_{angvel}), and 3) the whole body energy expenditure per meter traveled (WBE_{meter}). Whole body energy expenditure (WBE) was calculated as the sum of three components: 1) mechanical work produced by all muscle contractile elements: muscle power integrated over time, 2) heat produced by all muscle contractile elements: the sum of the activation heat (Bolstad and Ersland, 1978; Hatze and Buys, 1997), the maintenance heat (Bolstad and Ersland, 1978; Hatze and Buys, 1997), and the additional heat due to contractile element shortening and lengthening (Constable et al., 1997; Barclay et al., 1993), and 3) an estimate of heat produced by all body tissues not accounted for by the modeled muscles. A detailed mathematical description of the muscle energy expenditure model may be found in a preceding study (Umberger et al., 2003). A decrease in RMS_{ang} value meant that the posture at the left heel strike (LHS) is more similar to the initial posture (at t = 0 sec). A decrease in RMS_{angvel} value meant that the motion at the LHS is more similar to what it was at t = 0 sec. A decrease in WBE_{meter} meant that the locomotion was more economical.

The upright, human-like target posture at the instant of heel strike was derived from Anderson and Pandy (2001). According to the posture, Lucy's step length was 0.320 m. From a regression relation between body height and speed of locomotion (Alexander, 1984; Charteris et al., 1982), Lucy's walking speed was estimated to be 0.615 m/sec. Lucy's estimated stature, i.e., 1.05 m, was substituted in the regression equation to obtain this value. The duration of a full gait cycle (i.e., two steps) was therefore 1.04 sec. Assuming bilateral symmetry, one step of locomotion (i.e., 50% of a gait cycle) was simulated. Initial values of the first time derivatives of segment Euler angles were included as additional parameters in the numerical optimization. However, initial forward velocity of the trunk segment was fixed at 0.615 m/sec. Muscle activation onset times, offset times, and amplitudes that minimized the objective function value were searched using a modification (Lehman and Stark, 1982; Winters et al., 1984) of the global optimization algorithm developed by Bremermann (1970). The optimization process was ter-

minated when the value of the objective function had not improved more than 1% during 600 consecutive function evaluations.

RESULTS

After optimization of the muscle activation profiles, the root mean square of the differences in Euler angles between the final posture and the initial posture (RMS_{ang}) (Fig. 5) was reduced to 5.3°. As noted by Anderson and Pandy (2001), this deviation can be reduced to an arbitrarily small value, but only at a great computational expense. The nonzero final RMS_{ang} value was greater than the maximal intrasubject standard deviation values reported by Dingwell et al. (2001) for sagittal plane joint angles over the stride cycle (up to approximately 4.5°). However, much of the final angular deviation for the model was concentrated in the ankle inversion and metatarsal joint angles, which have a minimal effect on energetic outcomes. The optimization process resulted in smooth kinematics (Fig. 5) and in muscle activation profiles that were qualitatively similar to electromyography recordings during modern human locomotion (Knutson and Soderberg, 1995) (Fig. 4). The gross joint kinematic patterns were found to be similar to data from normal human upright walking (Anderson and Pandy, 2001) (Fig. 5), although there were some subtle differences that likely reflect differences in Lucy's locomotor apparatus.

Whole body energy expenditure per meter traveled was calculated to be 7.7 J/(kg · m). Whole body energy required to make a single step (WBE_{step}) was calculated to be 2.0 J/kg. Dividing this value by the step time (0.52 sec), the whole body rate of energy expenditure per second (WBE_{sec}) was equal to 3.8 J/(kg · sec) (Table 3). This was higher than the rate of energy expenditure for modern human adults walking at the same speed (Table 3), but was similar to data from modern human children of approximately the same body mass as Lucy (Fig. 6) (DeJaeger et al., 2001; Waters and Mulroy, 1999).

DISCUSSION

In the present investigation, we generated the first successful forward-dynamic computer simulations of locomotion in *A. afarensis*. The two basic assumptions of this study were that: 1) Lucy's mass distributions among body segments and shapes of individual body segments were similar to those of modern humans, and 2) the basic mechanisms underlying muscle force production are relatively unchanged from when Lucy inhabited the earth, i.e., they are caused by actin-myosin interaction, and as a result muscles have activation dynamics, and force-length and force-velocity characteristics. As there is no soft-tissue information available for Lucy, it was necessary to make these two assumptions. Based on these two assumptions, full 3D upright bipedal locomotion was reconstructed and sim-
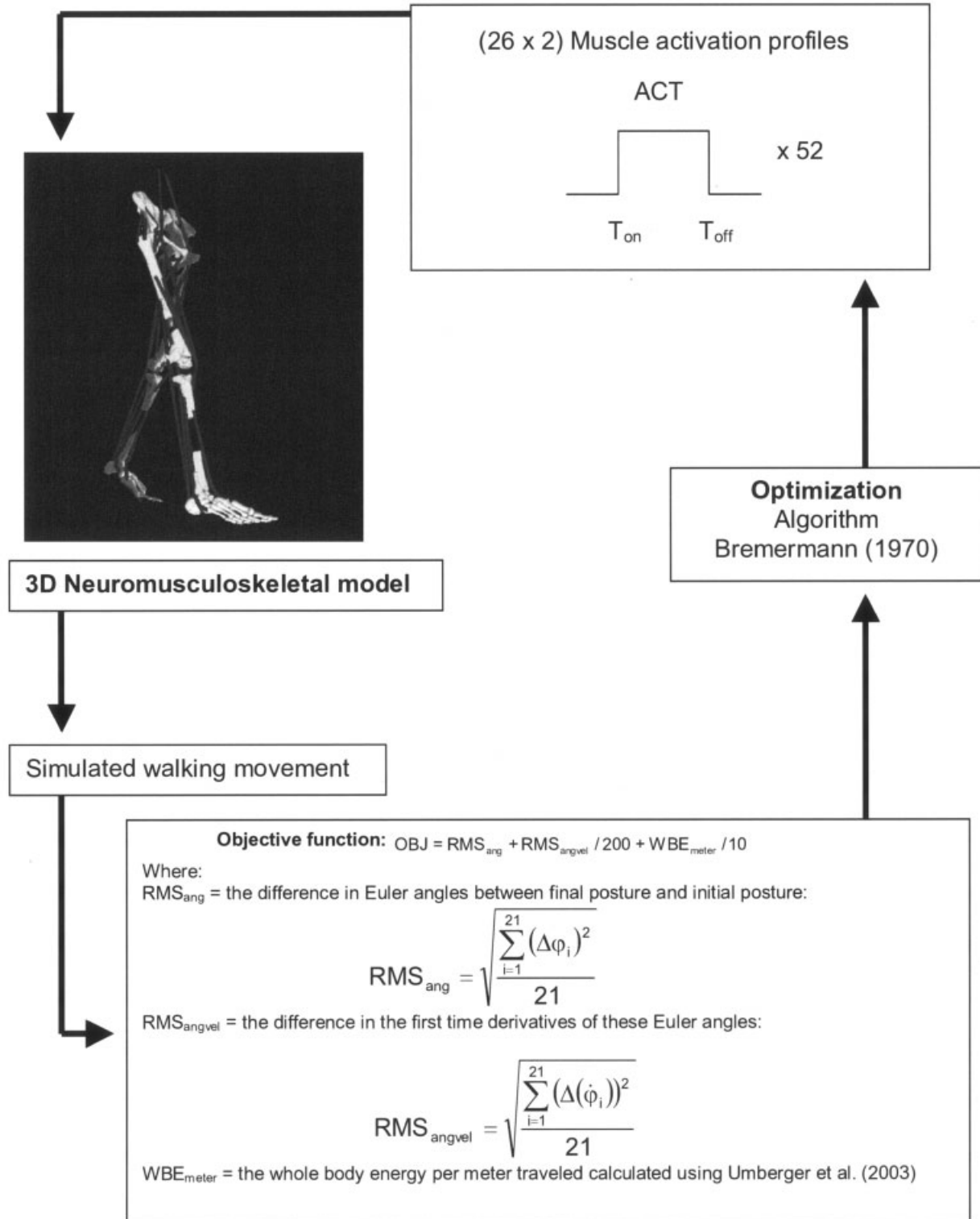
Fig. 3. Flowchart describing details of numerical optimization process. Activation profiles for each muscle were specified by three values: onset time (T_{on}), offset time (T_{off}), and level of activation (ACT). After one step is simulated, posture (Euler angles of segments) and motion (first time derivative of Euler angles of segments) were compared with target data, yielding RMS_{ang} and RMS_{angvel}, respectively. Objective function, i.e., weighted sum of RMS_{ang}, RMS_{angvel}, and WBE (whole body energy expenditure; Umberger et al, 2003), was minimized using a numerical optimization algorithm (Bremermann, 1970).

ulated for this human ancestor. Whole body metabolic energy expenditure was estimated and found to be compatible with data from modern humans of Lucy's size (DeJaeger et al., 2001; Minetti et al., 1994; Waters and Mulroy, 1999) (Table 3 and Fig. 6).
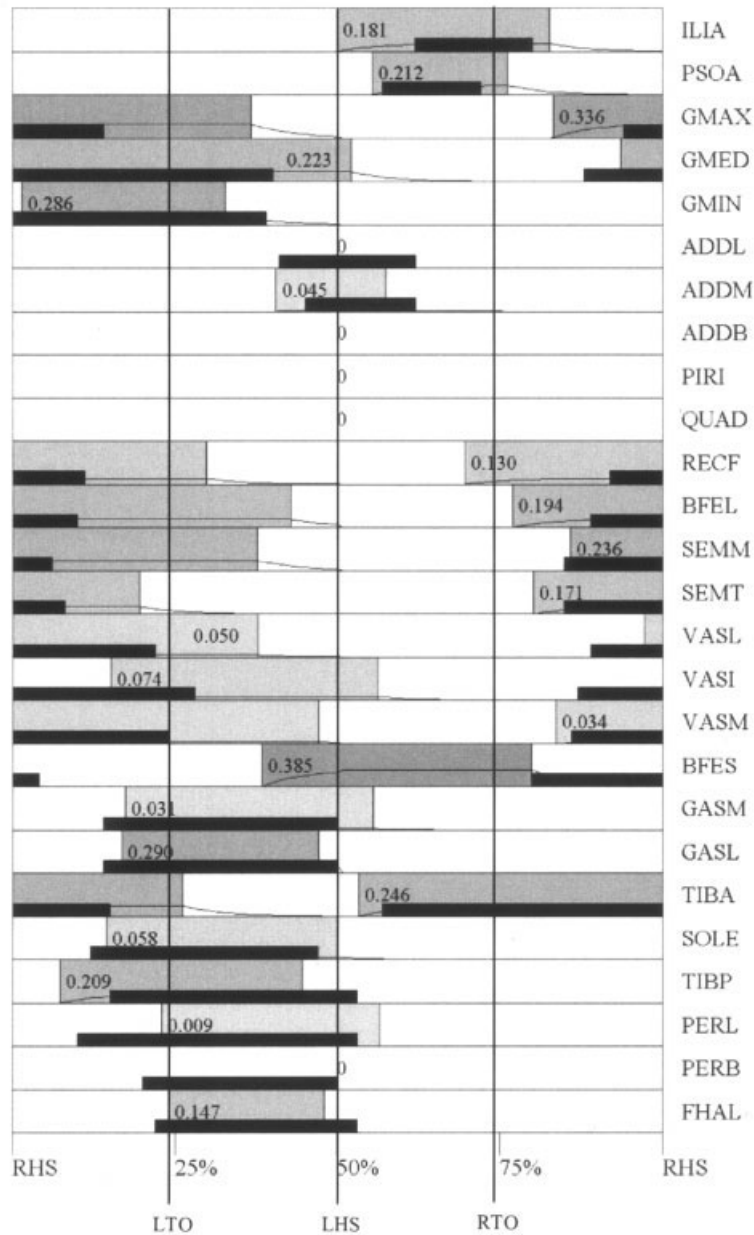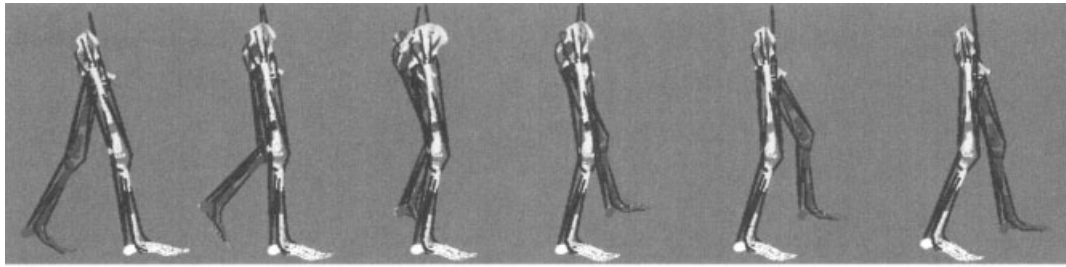
Fig. 4. Sequence of snapshots (top) illustrating kinematics that are results of numerical optimization of all 52 muscle activation profiles. Root mean square of differences in Euler angles between final posture (far right) and initial posture (far left) was reduced to 5.3°. Numerical optimization process resulted in smooth kinematics (top), and resulted in muscle activation profiles (shaded blocks) that showed similar phasing to electromyography recordings during modern human locomotion (one gait cycle, from a right leg heel strike (RHS) to another right leg heel strike (RHS) of the right (stance-swing) leg). RTO, LHS, and LTO stand for right leg toe-off, left leg heel strike and left leg toe-off, respectively. Shading of muscle activation blocks represents amount of activation sent to that muscle (light, small activity; dark, moderately active). Solid lines represent muscle active state. Solid black bars represent electromyography data during normal human locomotion (data collected by D.H. Sutherland et al. at San Francisco Shriners Hospital, and reproduced in Knutson and Soderberg, 1995). Numbers within muscle activation blocks also indicate fraction of maximum activation (1.0 = maximum activation). Largest fraction of activation is found in m. gluteus maximus (33.6%) and in m. biceps femoris caput brevis (38.5%), whereas muscles such as m. piriformis and m. quadratus femoris did not have to be activated at all to produce locomotion illustrated by sequence of stick figures above.
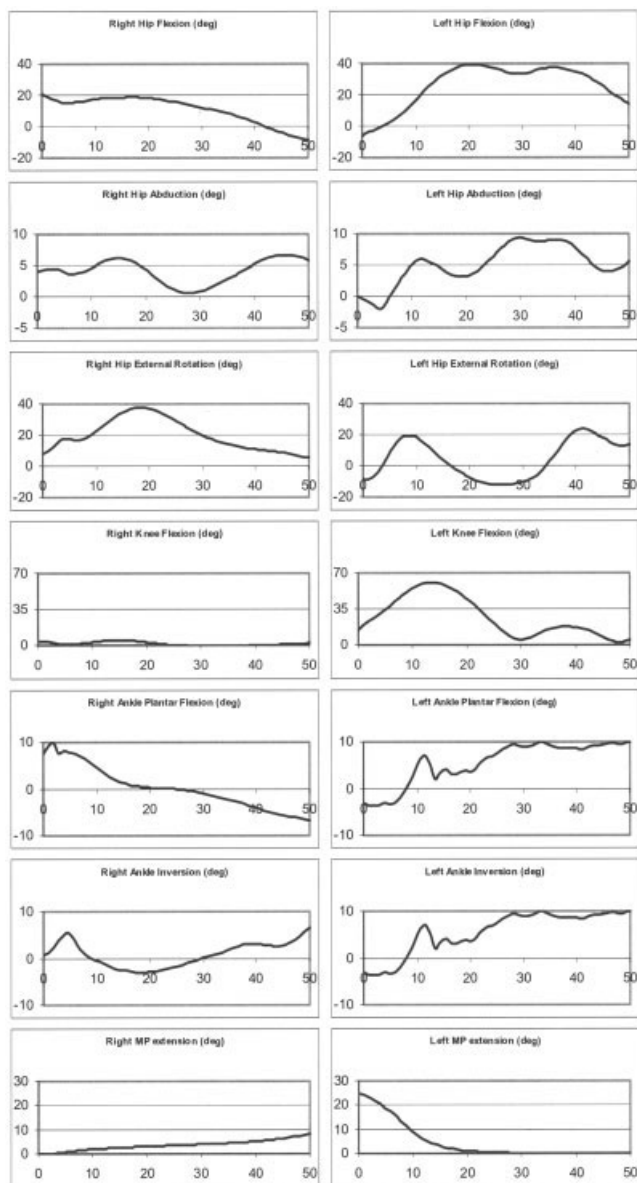
Fig. 5. Joint trajectories as a function of time. X axis corresponds to % of a gait cycle (0–50%). Right leg is stance leg; left leg is swing leg. MP, metatarsophalangeal joint. These trajectories correspond to snapshots in Figure 4. Overall, joint kinematics were similar to comparable data from modern humans (Anderson and Pandy, 2001). However, there were some notable differences, especially at hip joint. These differences were likely due to Lucy's pelvic morphology (see text for discussion); 50% of right leg corresponds to 0% of left leg.

TABLE 3. Results of energy expenditure analysis

Lucy	
Distance traveled	0.259 m
Step time	0.52 sec
Average speed	0.498 m/sec
WBE_{step}[1]	2.0 J/kg
WBE_{meter}[2]	7.7 J/(kg · m)
WBE_{sec}[3]	3.8 J/(kg · sec)
Lucy-humans	
WBE_{sec_Lucy}[3]	3.8 J/(kg · sec)
$WBE_{sec\_modern\ humans}$[4]	3.0 J/(kg · sec)

[1] Whole body energy expenditure per step.
[2] Whole body energy expenditure per meter traveled.
[3] Whole body energy expenditure per second.
[4] Data on energy expenditure during modern adult human locomotion at 0.5 m/sec (DeJaeger et al., 2001; Waters and Mulroy, 1999).
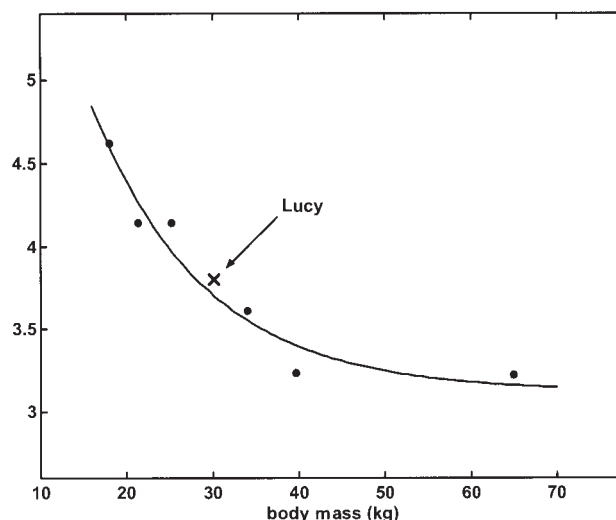

Fig. 6. Dependence of gross metabolic energy expenditure on body mass in modern humans, compared with results obtained for simulated walking in *A. afarensis* in this study. Experimental data points are from DeJaeger et al. (2001) for adults and children walking at same speed as in simulation. Smooth curve is a least-squares exponential fit to experimental data points only. Lucy was less economical than modern adults humans (rightmost data point), but had an energy cost consistent with modern humans of same body mass (8–9-year-old children).

Although a substantial amount of information is available on Lucy's locomotor skeletal characteristics, only a handful of clues are available about her soft tissues (i.e., muscles, tendons, and ligaments) (Haeusler, 2002). For the purpose of this neuromusculoskeletal modeling study, it was necessary to develop mathematical representations for such soft-tissue properties. The parameters to specify these soft-tissue properties were derived by scaling human data. The main justification for this approach is that since *A. afarensis* had many human-like mor-

phological features (Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990; Lovejoy, 1988), it is likely that Lucy's mass distributions among body segments and shapes of individual body segments (i.e., inertial characteristics) showed at least some similarities with those of modern humans. Crompton et al. (1998) performed a kinematic investigation of Lucy's bipedal walking with human-like body segmental parameters and chimpanzee-like body segmental parameters. Those two data sets resulted in similar mechanical output calculations, which suggested that the results of mechanical analyses are not sensitive to those parameter values, as long as Lucy's body proportions are similar to those of either modern humans or chimpanzees (or somewhere in between). The two assumptions made for this study

are simple and straightforward. Also, for every single parameter value used in this study, there is a solid justification for choosing the specific value. Although upright locomotion was considered in this study, there are several morphological features suggesting that *A. afarensis* may have performed locomotion in different forms. Besides upright walking, locomotion with bent hips and bent knees (Berge, 1994; Stern and Susman, 1983; Susman et al., 1984) and knuckle-walking (Collard and Aiello, 2000; Richmond and Strait, 2000) have been suggested. The methodology employed in this study is applicable to investigate these different forms of locomotion, and will be the focus of future research.

Upright bipedal locomotion was successfully generated with the 3D neuromusculoskeletal model (Figs. 4, 5). Lucy's average walking speed was calculated to be 0.498 m/sec (Table 3), which is less than the walking speed of the model at the start of the simulation (0.615 m/sec; originally derived referring to a regression equation represented as a function of body height). This implies that the mechanical configuration of the musculoskeletal model utilized in this study "preferred" to walk at a slower speed than the one obtained by referring to the regression equation. The kinematics of Lucy's locomotion generated in this study (Fig. 5) showed broad similarities with experimental walking data from modern humans (Anderson and Pandy, 2001). In particular, the joint motion profiles for the major sagittal plane components (hip flexion/extension, knee flexion/extension, and ankle dorsiflexion/plantar flexion) were generally similar to the experimental data reported by Anderson and Pandy (2001). It should be noted that a perfect match of the kinematic profiles between this study and Anderson and Pandy (2001) was not expected, as several properties of the model in this study (e.g., muscle line of action, segment lengths) were derived from Lucy's skeletal morphology, whereas the experimental data were from modern humans. In particular, the nonsagittal plane motions at the hip joint exhibited obvious differences. The range of motion of hip joint external/internal rotation was approximately 50° for Lucy, while it was approximately 20° in Anderson and Pandy (2001). This discrepancy may be due to the differences in morphology between Lucy and modern humans. It is likely that Lucy's wide pelvis made it more beneficial for Lucy to perform locomotion with more rotation of the pelvis in the transverse plane, which results in more rotational motions of the hip joint. An increase in rotation of the pelvis about the centerline of the body effectively increases leg length. It should be noted that even when the leg is moving in a parasagittal plane, this effect causes the swing leg to move farther off from the midsagittal plane compared to when the pelvis width is narrower. In this study, this caused the perspective that the swing leg moved away from the midsagittal plane during the swing phase (Fig. 4).

The phasing of muscle activation profiles obtained as a result of the numerical optimization was generally similar to indwelling electromyography data obtained from human subjects (Knutson and Soderberg, 1995) (Fig. 4). For most muscles, the optimized muscle activation patterns were comparable to the corresponding electromyography data (e.g., m. psoas major, m. gluteus medius, m. semitendinosus, m. gastrocnemius lateralis, m. tibialis anterior, and m. soleus). There was also agreement in the lack of activation of m. adductor brevis, m. piriformis, and m. quadratus femoris. On the other hand, in some muscles (e.g., m. biceps femoris caput brevis), the activation in the Lucy model was considerably greater than what is observed in humans. Relatively high activation was observed in m. gluteus maximus, m. gluteus medius, and m. gluteus minimus (Fig. 4). This result is reasonable, as the wider pelvis of Lucy (Berge, 1994) requires a larger hip abduction moment produced by these muscles to keep the trunk upright during the stance phase (Nordin and Frankel, 1980). Although the "primary" action of m. gluteus maximus is hip extension, because of the 3D configuration of the hip joint, m. gluteus maximus also contributes to hip abduction (Jenkins, 2002). The discrepancies that did exist between human walking EMG data and the muscle activation profiles for some muscles may be due to several factors. The most likely one is the difference in skeletal geometry between modern humans and Lucy; however, it cannot be ruled out that some of the discrepancies may be due to muscle activation profiles being specified with only three parameters (onset, offset, and level of activation) as opposed to a continuous profile. Making the muscle activation profiles more continuous by specifying additional activation parameters is technically possible, but comes at a much higher computational cost (Anderson and Pandy, 2001), yet the simulated walking kinematics differ only very little.

In this neuromusculoskeletal modeling and simulation study, several parameter values (e.g., segment inertial parameters, muscle parameters) were scaled from modern humans. However, the only inputs used to control the neuromusculoskeletal system were muscle activation profiles. No constraints or penalties were used to force the muscle activation profiles to be similar to human electromyography data, and the resulting body motion evolved naturally from the forces developed by the active muscles, rather than being predefined. The fact that smooth kinematics were generated with such muscle activation profiles provides further confidence that both the 3D neuromusculoskeletal model and the objective function used in the numerical optimization process captured the fundamental aspects of bipedal locomotion.

Energy expenditure is an important factor in animal locomotion (Hoyt and Taylor, 1981; Nishii, 2000; Ralston, 1958; Sparrow and Newell, 1998; Waters and Mulroy, 1999). Previous simulation studies

(Anderson and Pandy, 2001; Umberger et al., 2003) showed that minimization of the cost of walking a unit distance does in fact lead to realistic simulations of human walking. Therefore, the objective function was formulated to produce an economical walking pattern. The resulting mass-specific rate of energy expenditure (WBE$_{sec\_Lucy}$) (3.8 J/(kg · sec)) was greater than in modern human adults walking at the same speed ($\sim$3.0 J/(kg · sec)) (DeJaeger et al., 2001; Waters and Mulroy, 1999) (Table 3). Thus, Lucy, with a body mass of about 30 kg (Crompton et al., 1998), was predicted to be about 27% less economical than modern human adults. The higher mass-specific energy rate predicted for Lucy appears to be a genuine feature of her locomotion, and not simply an overestimate, as the model of muscle energy expenditure used in the present study yielded accurate predictions of total energy expenditure in simulations of walking for modern human adults (Umberger et al., 2003). This is in contrast to the energy model used by Anderson and Pandy (2001), which overestimated energy expenditure in modern human adults by approximately 50%.

Smaller animals generally have a higher mass-specific cost of locomotion, which is largely related to the higher stride frequencies required to travel at a given speed on shorter legs (Taylor et al., 1982). This phenomenon also seems to apply to walking in modern humans of different body masses. After age 3 years, the higher mass-specific cost of walking in children is mostly explained by body size, as opposed to other developmental factors (DeJaeger et al., 2001). The metabolic energy expenditure calculated for Lucy (30 kg) in this study was intermediate to values from modern humans having body masses of 25 kg (7–8 year olds) and 34 kg (9–10 year olds), placing her close to the regression line for a modern human of her body mass (Fig. 6). The present estimate of Lucy's energy expenditure for walking was also consistent with findings from Minetti et al. (1994) that African Pygmies (body mass $\sim$50 kg) had a higher mass-specific rate of energy expenditure for walking than a group of Caucasians (body mass $\sim$70 kg) across a range of speeds. The fact that our estimate of Lucy's energy expenditure using the present model of upright, bipedal walking was consistent with predictions based on her body size supports the validity of this study, and makes it likely that Lucy could have walked in an upright manner, similar to modern humans today (Crompton et al., 1998; Kramer, 1999; Kramer and Eck, 2000). However, contrary to speculations on Lucy's locomotor efficiency based solely on mechanical energy analyses (Crompton et al., 1998; Kramer, 1999), our metabolic energy assessment suggests that Lucy was actually less economical than modern human adults, although in a manner consistent with her lower body mass.

Regarding other possible forms of bipedal locomotion in *A. afarensis*, Stern and Susman (1983) and Susman et al. (1984) suggested that Lucy might have walked like modern chimpanzees (walking with bent hips and bent knees) instead of modern humans (upright, straight-legged walking). The mechanics of chimpanzee-like walking can be investigated using the same methodology as utilized in this study; however, the results in terms of energetic cost would certainly be that chimpanzee-like locomotion requires considerably more energy, as higher levels of muscle activation are required simply to maintain the bent-hips, bent-knees posture that defines chimpanzee-like locomotion (Crompton et al., 1998; Stern, 1999). The higher energetic cost would have to be outweighed by some other advantage of the bent-hips, bent-knees posture, such as greater postural stability.

CONCLUSIONS

The methodology used in this study (forward-dynamic neuromusculoskeletal computer modeling and simulation) is different from techniques used in earlier modeling studies (Crompton et al., 1998; Kramer, 1999; Kramer and Eck, 2000). In these preceding studies, Lucy's body segmental model was constructed and her bipedal locomotion was driven kinematically using preassigned time histories of joint trajectories. Inverse biomechanical analyses were then performed on those preassigned joint trajectories. In the current study, Lucy's bipedal locomotion was *simulated*, by controlling neural activation patterns sent to the muscles. The present methodology represents a forward approach, in that events flow in the same manner as they occur in the real neuromusculoskeletal system.

The most important contribution of this study to the literature is that this is the first study in which the full 3D upright bipedal locomotion of any of our ancient human ancestors has been reconstructed and simulated, combining laser-scanned 3D bone geometries with state-of-the-art neuromusculoskeletal modeling and simulation techniques in biomechanics. Only two simple, straightforward assumptions were made in the process of model development and simulation. Through this procedure, it was possible to obtain better predictions of Lucy's locomotion (including estimates of her energy expenditure) which had not been possible before. A 3D skeletal model with 20 degrees of freedom was constructed which was actuated by 52 Hill-type muscles. The energy-optimal simulation resulted in a smooth kinematic pattern, and a reasonable energy expenditure estimate, consistent with the dependence of energy expenditure on body mass in modern human locomotion (DeJaeger et al., 2001; Minetti et al., 1994; Waters and Mulroy, 1999). These new dynamic techniques should complement more traditional morphological analyses, and lead to greater insights about the locomotor patterns of extinct hominids. The results of the present study tend to support the notion that Lucy could have walked in a manner similar to that of humans today (walking with an upright posture), with minor variations in

muscle recruitment relating to differences in the shape of the hip region. How likely is it that she did indeed walk in this manner? The neuromusculoskeletal model of Lucy developed in this study provides a means by which other possible dynamic aspects of the locomotion of *A. afarensis* can be studied in the future, and can contribute to the search for an answer to this question.

ACKNOWLEDGMENTS

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