

Muscle mechanical advantage of human walking and running: implications for energy cost

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¹Concord Field Station, Department of Organismic and Evolutionary Biology, Harvard University; Bedford, Massachusetts 01730; ²Department of Integrative Physiology, University of Colorado, Boulder, Colorado 80309; ³Department of Zoology, Oregon State University, Corvallis, Oregon 97331; and ⁴Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois 60637

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Biewener, Andrew A., Claire T. Farley, Thomas J. Roberts, and Marco Temaner. Muscle mechanical advantage of human walking and running: implications for energy cost. *J Appl Physiol* 97: 2266–2274, 2004. First published July 16, 2004; doi:10.1152/jappphysiol.00003.2004.—Muscular forces generated during locomotion depend on an animal's speed, gait, and size and underlie the energy demand to power locomotion. Changes in limb posture affect muscle forces by altering the mechanical advantage of the ground reaction force (R) and therefore the effective mechanical advantage ($EMA = r/R$, where r is the muscle mechanical advantage) for muscle force production. We used inverse dynamics based on force plate and kinematic recordings of humans as they walked and ran at steady speeds to examine how changes in muscle EMA affect muscle force-generating requirements at these gaits. We found a 68% decrease in knee extensor EMA when humans changed gait from a walk to a run compared with an 18% increase in hip extensor EMA and a 23% increase in ankle extensor EMA. Whereas the knee joint was extended (154 – 176°) during much of the support phase of walking, its flexed position (134 – 164°) during running resulted in a 5.2-fold increase in quadriceps impulse (time-integrated force during stance) needed to support body weight on the ground. This increase was associated with a 4.9-fold increase in the ground reaction force moment about the knee. In contrast, extensor impulse decreased 37% ($P < 0.05$) at the hip and did not change at the ankle when subjects switched from a walk to a run. We conclude that the decrease in limb mechanical advantage (mean limb extensor EMA) and increase in knee extensor impulse during running likely contribute to the higher metabolic cost of transport in running than in walking. The low mechanical advantage in running humans may also explain previous observations of a greater metabolic cost of transport for running humans compared with trotting and galloping quadrupeds of similar size.

gait; muscle mechanical advantage; muscle force; metabolic cost

IN THIS STUDY, WE SEEK TO understand whether changes in limb muscle mechanical advantage and muscle force-generating requirements underlie differences in the energy cost of transport during walking vs. running in humans. We quantify changes in a muscle group's effective mechanical advantage, $EMA [= r/R$ (Refs. 1, 2)], that may result from gait-related changes in ground reaction force (GRF) mechanical advantage (R) relative to limb muscle mechanical advantage (r). Based on studies of quadrupedal and bipedal animals, there is evidence that the energetic cost of generating muscular force is an important determinant of the

metabolic cost of locomotion. This has been shown both for changes in metabolic cost during load carrying (39) as well as for comparing differences in cost among animals of different size (25, 37). Thus a change in limb mechanical advantage (mean muscle EMA) that alters the force developed by limb muscles over the period of ground support (muscle impulse) might also help to explain the high energy cost of human running compared with walking (15, 28). We hypothesize that changes in posture that affect muscle force-generating requirements play a substantial role in determining energy use. Nevertheless, other factors such as increased muscle work and an increased rate of force development associated with shorter limb contact time and increased stride frequency are also likely to be important but are not examined here. A recent study (19) has shown that changes in the cost of muscle force generation likely underlie most of the change in cost with speed and load carriage in walking humans. We ask here whether changes in muscle force requirements associated with a change in limb mechanical advantage also occur when humans transition from walking to running.

Although limb muscle mechanical advantage increases significantly with body size in quadrupedal mammals (1, 2), changes in limb mechanical advantage as a function of gait and speed have not been observed. Data for quadrupedal mammals, however, have been largely limited to comparisons of trotting and galloping. The distinctive kinematics (17) and mechanics (9–11, 27) of human walking vs. running suggest that changes in limb mechanical advantage may play a role in determining the energy cost of transport at each gait. In studies comparing a quadruped and biped of similar size, Roberts and coworkers (31, 32) showed that their similar metabolic costs are related to the relative size of limb muscles and the volume of muscle that must be recruited to support body weight during locomotion on four vs. two limbs.

We also seek to evaluate how the generally erect bipedal posture of humans and possible gait-related changes in limb mechanical advantage may relate to comparisons of the energy cost of transport in humans compared with quadrupedal mammals. Early work on the scaling of the energetic cost of transport (40) showed that the transport cost of human running exceeds that for quadrupeds of similar size. This would predict that human runners have a lower limb EMA, requiring them to recruit a larger volume of muscle and generate more force for their weight compared with similar-sized quadrupeds.

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METHODS

Four healthy adult male subjects, who were skilled but noncompetitive runners with no history of musculoskeletal injury, took part in this study. They ranged from 23 to 38 yr of age and weighed 75.0 ± 5.0 kg (means \pm SD; anthropometric data given in Table 1). Subjects gave informed consent, and all procedures were approved by the Harvard University Committee on the Use of Human Subjects. Subjects walked or ran at three self-selected steady speeds within each gait down a 1×40 -m rubber surfaced runway, over a force platform (Kistler model 9261A) located midway along the length of the runway. The subjects' forward velocity was determined at four 1-m intervals by means of infrared photocells (Banner model SMB-800) positioned before and after the force platform. The subjects were also filmed (wearing jogging shorts and running shoes) in lateral view at 100 frames/s by use of a Photosonics 1PL 16-mm camera equipped with an Angeneaux 10×12 zoom lens as they passed over the force platform. The camera was positioned 6.0 m away from the force platform to minimize parallax, which was nevertheless corrected based on the x -position of each joint coordinate relative to the midaxis of the camera and force platform (worst-case correction at the hip: 11.6%). The subjects' pelvis (superior iliac spine), hip (proximal greater trochanter), knee (lateral condyle), ankle (lateral malleolus), and metatarsophalangeal (base of first proximal phalanx) joints were identified by use of 1.0-cm dark ink markers. The markers were placed on the skin over the palpated bony sites, except in the case of the metatarsophalangeal joint, which was marked on the lateral sidewall of the running shoe in line with the base of the first proximal phalanx. A 1-m-long marker was positioned behind the force platform at knee height to serve as a length calibration for the films.

Recordings were made at three speeds ("slow," "preferred," and "fast"), which each subject was allowed to select within each gait. Three trials, in which the subjects' speed varied by less than $\pm 5\%$ of their average forward speed, were selected from those recorded and analyzed at each speed. The outputs of the force platform ["front" vertical, "rear" vertical, and horizontal (fore-aft) forces], together with the output of the photocells and a camera shutter pulse, were sampled at 1,000 Hz via an analog-to-digital converter and entered into a computer for subsequent analysis using customized Pascal software. Front and rear vertical force recordings were used to determine the point of force application, or "center of pressure," on the foot (in the fore-aft direction) and summed to determine total vertical force. Mediolateral ground forces were not analyzed, because only moments in the parasagittal plane of the body were included in the study. This approach ignores frontal plane moments, which may be a substantial component of muscle force requirements during walking and running (19).

Muscle moment arms (r) were determined by palpation of muscle attachments relative to estimates of joint centers of rotation for each subject. These were found to compare well with direct measurements made on fresh cadavers (Table 2) and mounted skeletons of similar stature, as well as values reported in the literature (35, 36, 41, 42). Because we used the same r values for analyzing walking and

Table 2. Cadaver muscle data (mean values for 4 male subjects, average age 78 yr)

Joint and Muscle	Mean r , cm	Mass, kg	Fascicle Length, cm	Pinnation Angle, °	Fiber Area, cm ²
Hip					
Gluteus maximus		0.481	18.7	0	24.8
Semitendinosus		0.109	14.3	0	7.6
Semimembranosus		0.168	7.4	12	23.0
Biceps femoris		0.148	8.3	13	18.8
Total	5.7	0.906	11.7*		74.2
Knee					
Vastus lateralis		0.410	8.0	11	49.9
Vastus intermedius		0.224	7.3	9	31.0
Vastus medialis		0.248	8.4	11	28.6
Rectus femoris		0.128	7.2	13	20.6
Total	5.5	1.010	7.3*		130.1
Ankle					
Lateral gastrocnemius		0.094	5.5	14	17.7
Medial gastrocnemius		0.155	4.6	17	35.1
Soleus		0.326	4.1	17	94.6
Flexor digitorum longus		0.022	4.4	11	7.0
Tibialis posterior		0.068	3.2	14	20.8
Flexor hallucis longus		0.063	5.1	10	11.8
Peroneus longus		0.064	5.5	11	11.2
Peroneus brevis		0.028	3.8	10	7.1
Total	3.7	0.820	4.1*		205.3

*Weighted mean fascicle length (L) of the agonist muscle group as a whole

running, any error in these values will not affect our main goal of comparing posture-related effects on muscle force-generation requirements during these two gaits. In addition to each subject's weight, the following data were also obtained: stature, thigh length, leg length, and foot length. These data (Table 2) were used to calculate the mass and moments of inertia of individual limb segments of each of the subjects by using published anthropometric data (44).

Joint moment analysis and measurement of muscle EMA. Two-dimensional joint coordinate data were obtained by digitizing the films (Summagraphics Plus digitizing tablet, ± 0.1 -mm resolution) and entered into a computer for synchronization with the digitized GRF data. Before analysis of limb segment motion and determination of inertial (M_{inert}) and gravitational (M_{grav}) components of muscle joint moments, the raw coordinate data were first smoothed with a recursive fourth-order zero-lag Butterworth low-pass digital filter with a cutoff of 20 Hz (44). Velocities and accelerations of segment motion were then determined by the finite difference method (3). Muscle moments (M_{GRF}) needed to generate the GRF (in the parasagittal flexor-extensor plane) were calculated from the smoothed joint coordinate data synchronized to the vertical and fore-aft horizontal GRFs sampled for each run. Inertial and gravitational moments at the hip, knee, and ankle were summed with the moment required to generate ground force ($M_{\text{inert}} + M_{\text{grav}} + M_{\text{GRF}}$) to determine the total net moment acting at each joint.

The EMA (1) of muscle extensors to generate a given force on the ground was calculated as the ratio (r/R) of the agonist muscle group's weighted mean moment arm (r) to the moment arm (R) of the GRF acting about the joint (Fig. 1). R is calculated on the basis of the resultant GRF over at any instant in time relative to a joint's center of rotation, and r is calculated on the basis of the moment arms of individual agonist muscles, each being weighted relative to the fiber cross-sectional area (A) of each muscle ($r = r_1 * A_1 / A_{\text{tot}} + r_2 * A_2 / A_{\text{tot}} + \dots + r_i * A_i / A_{\text{tot}}$, where $A_{\text{tot}} = A_1 + A_2 + \dots + A_i$). Measurements of r for individual muscle agonists were only obtained when reliable differences in moment arm could be assessed by palpation (e.g., for the hamstrings: semimembranosus, semitendinosus, and biceps femoris, but not for the quadriceps, which were assumed to have the same

Table 1. Anthropometric data of experimental subjects

Subject No.	Body Mass, kg	Stature, m	Agonist Moment Arm, cm			Segment Moment of Inertia, kg · m ²		
			Hip	Knee	Ankle*	Thigh	Leg	Foot
1	67.4	1.82	5.1	4.5	3.7	0.118	0.052	0.017
2	75.8	1.78	5.5	5.3	4.1	0.119	0.059	0.019
3	76.0	1.88	5.8	5.6	4.3	0.157	0.077	0.024
4	80.6	1.84	5.7	5.2	4.3	0.151	0.071	0.025

*Based on weighted agonist muscle moment arm (r) for triceps surae, flexor digitorum longus, and flexor hallucis longus.

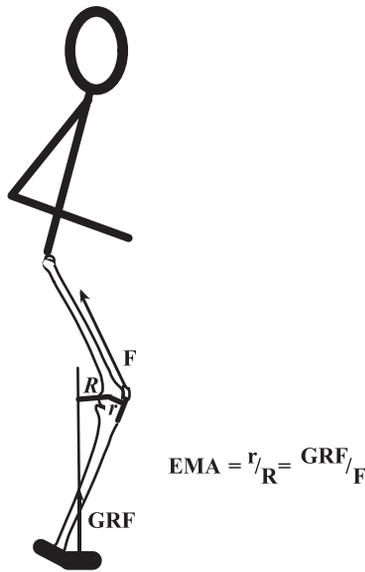


Fig. 1. Limb muscle mechanical advantage (EMA) is defined as the ratio (r/R) of the weighted mean agonist muscle moment arm (r) to the moment arm (R) of the ground reaction force (GRF). Integrated over the period of limb support, this represents the inverse ratio of muscle impulse (F) to ground impulse (GRF; i.e., $\int \text{GRF}/F$).

r). Muscle moment arms were measured at joint angles corresponding to peak M_{GRF} . Although this may underestimate or overestimate muscle forces if r increases or decreases at other joint angles, no systematic effect among limb joints or with respect to joint kinematics as a function of speed and gait is assumed (r is likely to vary most at the knee because of gait-related changes in joint angle, but this cannot be reliably distinguished by palpation). Whole limb EMA was calculated as the average of hip, knee, and ankle EMA. Active agonist muscles during limb support were considered to be the triceps surae at the ankle, the quadriceps at the knee, and the hamstrings and gluteus maximus at the hip. This approach assumes that each agonist muscle generates an equivalent stress (force per fiber cross-sectional area).

Muscle EMA was determined for each joint during the period of support by averaging the R values obtained for each film frame in which joint moments are $>25\%$ of maximum for that stride (this is necessary because of instances in which the GRF vector passes through the joint center, such that R approaches zero and r/R becomes undefined). As defined, muscle EMA specifically relates the ability of an agonist muscle group to produce external moments (M_{GRF}) at a joint and ignores moments produced by segment inertia, which may be substantial, and gravitational moments due to a segment's weight, which are considered to be negligible during ground support.

Time-integrated muscle force (muscle impulse) and estimates of active muscle volume. In addition to measurements of muscle EMA, agonist extensor muscle forces were calculated and integrated over the time course of limb support ($\int F_m dt$) to determine agonist muscle impulses. Muscle impulses were determined to provide an estimate of how changes in force-generating requirements during stance at different speeds and gaits might correlate with differences in energy cost, given that the energy (ATP) utilization of skeletal muscle is dependent on the magnitude and duration of force development (26, 34), in addition to rates of length change and work performed (16, 20). By using inverse dynamics and GRF recordings, muscle forces were calculated during ground contact for each image frame on the basis of analysis of inertial, gravitational, and external moments exerted about each limb joint, accounting for the transmission of force by multisegmental muscles (3, 44). Agonist muscle forces were determined on the basis of a free-body analysis of joint moments required to generate

ground force [M_{GRF} at the ankle (M_a), knee (M_k), and hip (M_h)] by using the following equations (5, 41)

$$M_a = \alpha F_{\text{TS}} r_{\text{TS},a} \quad (1)$$

$$M_k = \alpha F_Q r_{Q,k} - \alpha F_G r_{G,k} - \alpha F_H r_{H,k} \quad (2)$$

$$M_h = \alpha F_H r_{H,h} - \alpha F_{\text{RF}} r_{\text{RF},h} \quad (3)$$

where F_{TS} , F_Q , and F_H are the forces exerted by the triceps surae, quadriceps, and hamstrings (biceps femoris, semimembranosus, and semitendinosus) muscles, and F_G and F_{RF} are the force components exerted by the gastrocnemius and rectus femoris about the knee and hip, respectively; $r_{\text{TS},a}$, $r_{Q,k}$, $r_{G,k}$, $r_{H,k}$, $r_{H,h}$, and $r_{\text{RF},h}$ are the moment arms of the muscles at each joint (a, ankle; k, knee; and h, hip) at the particular joint angle that was measured for each frame. Muscle moments were defined as positive when they acted to extend a joint to produce external ground force.

In addition to assuming that agonist muscle forces were distributed based on equal stress, we assumed no coactivation of monoarticular muscle antagonists, other than that associated with the action of two-joint muscles acting to extend one joint and flex the other. For example, the gastrocnemius extends the ankle but, in doing so, flexes the knee. Consequently, its antagonist flexor moment was included in calculating the net moment produced at the knee and the extensor moment produced by the quadriceps (Eq. 2). This allows the component of force exerted by the gastrocnemius muscle (F_G) to be determined from the total force exerted by the triceps surae (F_{TS}) and the component of force exerted by the rectus femoris (F_{RF}) from the quadriceps force (F_Q). These force components were solved simultaneously from Eqs. 2 and 3 after Eq. 1 was solved.

Muscle impulses were then normalized to the ground reaction impulse $\int (F dt) / \int (\text{GRF} dt)$ to evaluate how much muscle force was required to support a given force on the ground over the duration of limb support at the different speeds within each gait. In effect, this normalized impulse provided a measure of the average muscle force required to exert one body weight of force on the ground. It also corresponds to the inverse (r/R) of the relationship described by muscle EMA (Fig. 1) and has the advantage of allowing a comparison of muscle force-generation requirements with respect to ground force over the entire period of limb support, including those instances when the GRF passes through the joint's center of rotation and $M_{\text{GRF}} \rightarrow 0$, which are ignored in the determination of muscle EMA as defined above.

Because the metabolic cost of locomotion is likely linked to volume of muscle that must be recruited to support an animal's weight while it is running (25, 32), we also estimated the volume of active muscle at each joint. This is important to consider because differences in muscle fiber length affect the volume of muscle needed to generate a given force. Our measurements, however, ignore the cost associated with muscles activated during the swing phase of gait. To estimate the volume of actively recruited muscle at each joint during stance, we used morphological data obtained from fresh lower extremity muscles of four male human cadavers (Table 2; all cadavers were in good musculoskeletal health at the time of their death; however, given their age, substantial muscle wastage had likely occurred). This was done by assuming that muscles exert an equivalent force per cross-sectional area of active fibers (constant muscle stress, σ), irrespective of differences in the velocity of muscle contraction at differing joints. Given this assumption (i.e., that active fiber cross-sectional area of a muscle, $A^* = F/\sigma$), the volume of active muscle (V^* , cm^3) was defined as

$$V^* = A^* L = LF/\alpha \quad (4)$$

where L was the weighted average fascicle length of the muscle group and F was the combined maximum agonist muscle force. L was determined by averaging the agonist muscles' mean fascicle lengths weighted by the mass of each muscle, similar to the calculation of a

weighted agonist muscle moment arm based on muscle fiber area described above (Table 2). The values for L obtained from the cadaver data were then normalized for each subject on the basis of the subject's overall leg length compared with the mean leg length of the cadavers. This resulted in mean values of L for the four experimental subjects being hip 12.1 cm, knee 7.5 cm, and ankle 4.2 cm. This means that muscles with longer fascicles activate a greater volume of tissue per active cross-sectional area and are, therefore, assumed to consume more energy to generate a given force under similar contractile conditions (4, 32).

Although our values for muscle area are substantially less than those reported for younger adults (41), any differences in the absolute measures of muscle mass, fascicle length, and fiber area obtained from the cadavers vs. actual values for the four experimental subjects are not likely to affect our conclusions. Our analysis of how the recruitment of active muscle volume during stance varies as a function of gait depends on the relative size and architecture of the muscles within the limb, which are less likely to differ among groups of subjects than absolute size and architecture. Also, our comparisons of walking and running use the same muscle data for both gaits.

Comparisons between gaits were analyzed using two-way factorial ANOVA. Results were considered significant at a $P < 0.05$ level.

RESULTS

Joint moments. With an increase in speed and change of gait, maximum GRF joint moments (M_{GRF}) increased steadily at the hip, increased sharply when gait changed from a walk to a run at the knee, and remained fairly constant at the ankle (Fig. 2). At the ankle, inertial and gravitational moments ($M_{\text{inert+grav}}$) were small ($<1\%$) compared with GRF moments for both walking and running. At the knee, $M_{\text{inert+grav}}$ were $<9\%$ M_{GRF} during walking and $<15\%$ M_{GRF} during running. At the hip, $M_{\text{inert+grav}}$ averaged 10% M_{GRF} at a walk and 31% M_{GRF} at a run. Consequently, except for the hip at a run, limb muscles primarily acted to generate force on the ground and their role in overcoming segment inertia and gravity was minimal (Figs. 2 and 3). At a walk, the largest net muscle moment acted at the ankle during the latter half of limb support, with smaller moments developed at the hip and knee. In contrast, at a run the largest moment acted about the knee, with smaller moments developed at the hip and ankle.

When all walks were pooled and compared with all runs, peak M_{GRF} at a run was 4.9-fold greater at the knee ($P < 0.0001$, $F = 213.20$), 1.9-fold greater at the hip ($P < 0.0001$, $F = 35.17$; Fig. 2), and not significantly different at the ankle ($P = 0.512$, $F = 0.43$). The increase in M_{GRF} at the knee far exceeded the 1.6 ± 0.2 -fold increase in peak GRF when gait changed from a walk to a run. Consequently, most of the increase in knee moment at a run resulted from the increased flexion of the knee [which increased the GRF moment arm (R) at the knee] during running vs. walking (Fig. 4). During walking the knee flexed relatively little throughout most of the stance phase of the stride (mean range: 154 – 176° , $162 \pm 6^\circ$ at peak moment; $n = 4$ for preferred walk of the four subjects), but during running it is flexed much more (mean range: 134 – 164° , $135 \pm 4^\circ$ at peak moment; $n = 4$ for preferred run). In comparison, the hip operated over a similar range of angles during both walking and running, whereas the ankle was also more flexed during running ($84 \pm 2^\circ$) than walking ($98 \pm 3^\circ$; Fig. 4).

Muscle EMA and muscle impulse. The large increase in knee M_{GRF} when gait changed from a walk to a run was associated

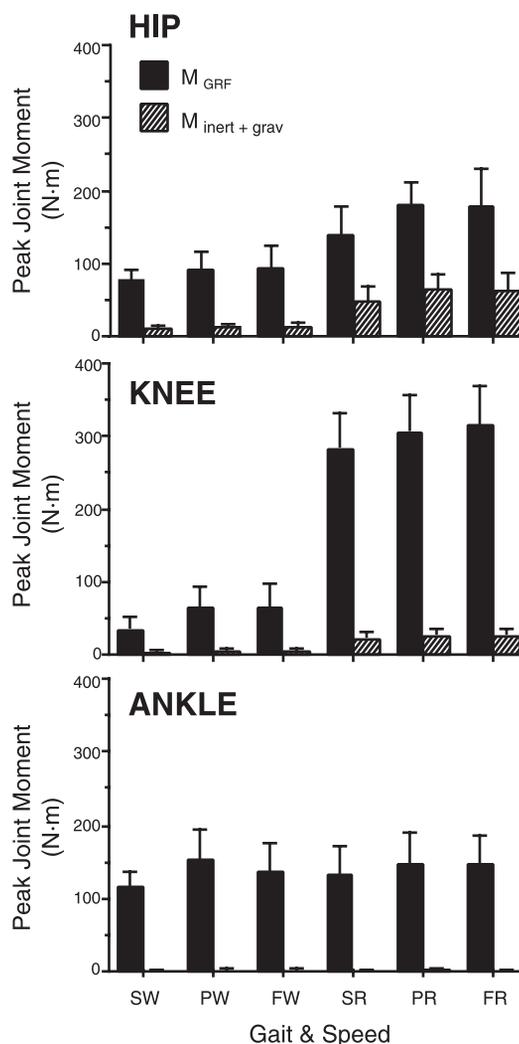


Fig. 2. Histogram of peak joint moments of ground reaction force (M_{GRF}) and inertial and gravitational moments ($M_{\text{inert+grav}}$) vs. relative speed and gait (SW, slow walk; PW, preferred walk; FW, fast walk; SR, slow run; PR, preferred run; FR, fast run) pooled for all 4 subjects. Positive moments correspond to muscle moments acting to extend the hip, knee, and ankle joints during limb support.

with a 68% decrease ($P < 0.0001$, $F = 24.19$, $df = 3, 1$; data pooled among subjects for all walks vs. runs) in the EMA of the knee extensors (quadriceps) (Fig. 5). This was in contrast to increases in muscle EMA at the hip ($+18\%$; $P < 0.05$, $F = 4.20$) and at the ankle ($+23\%$; $P < 0.001$, $F = 21.48$) at a run. The substantial decrease in knee EMA reflected the more flexed position of the knee during running, which increased the moment arm (R) of the GRF.

Partly because of these changes in muscle EMA, when gait changed from a walk to a run, muscle impulse during limb support ($\int F$), normalized to ground impulse ($\int \text{GRF}$), increased 5.2 ± 1.0 -fold at the knee ($P < 0.001$, $F = 21.71$), decreased $37 \pm 7\%$ at the hip ($P < 0.05$, $F = 6.42$), and remained unchanged at the ankle ($P > 0.5$, $F = 0.01$) (Fig. 6). In addition to the reduced knee EMA during running, the increase in knee impulse ratio ($\int F / \int \text{GRF}$) was enhanced by a 32% lower ground reaction impulse during running (265 ± 48 Ns) vs. during walking (389 ± 67 Ns; means of all four subjects averaged for all speed trials within each gait, $n = 12$). Whereas

only 9% of total extensor muscle impulse was produced at the knee during walking, knee extensors generated 39% of total extensor impulse during running, nearly matching that generated by the ankle extensors.

The magnitude of muscle impulse required to overcome moments produced by segment inertia and weight during limb

support was generally much less than that required to counter M_{GRF} . At the ankle the percentage of total muscle impulse due to $M_{inert+grav}$ was $<0.2\%$ at both a walk and a run. At the knee, 20% of total muscle impulse was required to overcome $M_{inert+grav}$ at a walk but only 8% was developed at a run. At the hip, $M_{inert+grav}$ represented 9% of the total hip extensor impulse at a walk and 41% at a run.

Active muscle volume. Because of the differences in mean fascicle length (L , Eq. 4) among hip (12.1 cm), knee (7.5 cm), and ankle (4.2 cm) extensor muscles (adjusted for differences in subject limb length compared with cadaver data reported in Table 2), changes in muscle force-generation requirements resulted in significant shifts in the estimated volume of actively recruited fibers when gait changed from walking to running (Fig. 7). When summed for all three muscle groups, the volume of active muscle estimated to generate force on the ground to counter M_{GRF} increased 2.26-fold when gait changed from a walk (2,237 cm^3) to a run (5,066 cm^3). At a walk, active muscle volume required to generate M_{GRF} was greatest at the hip, being $46 \pm 4\%$ of total, compared with $31 \pm 2\%$ at the ankle and $23 \pm 4\%$ at the knee (Fig. 7A). When gait changed to run, however, the knee extensors represented $49 \pm 8\%$ of the estimated total, compared with $15 \pm 2\%$ at the ankle and $36 \pm 6\%$ at the hip. The greater estimated volume of active muscle at the knee results from the knee extensors having longer fibers than the ankle extensors, despite generating comparable levels of force at a run. The 4.9-fold increase in the active volume of the knee extensors resulted from the decrease in knee EMA and the increase in knee extensor force and impulse at a run vs. a walk.

When accounting for both M_{GRF} and $M_{inert+grav}$, the total increase in active muscle volume at a run was estimated to be 2.42-fold greater than at a walk. At all three joints, the volume of active muscle estimated to generate $M_{inert+grav}$ increased with increasing speed and change of gait, being greatest at the hip and least at the ankle (Fig. 7B). The increase due to inertia and gravity was fivefold greater at the hip and knee at a run vs. a walk, and twofold greater at the ankle. Compared with M_{GRF} , combined inertial and gravitational moments therefore required an additional 6% of active muscle at a walk and an additional 13% at a run.

DISCUSSION

Changes in muscle EMA, muscle impulse, and energy cost vs. gait. We sought to evaluate changes in limb muscle mechanical advantage and its effect on muscle force-generation requirements in the parasagittal plane as humans increase speed and change gait. In contrast to those quadrupeds (1) that have been examined to date and show little evidence of a systematic change in muscle EMA as a function of speed or gait, we observed significant changes as younger adult male humans change gait from a walk to a run. The most dramatic change occurred at the knee, where a 68% decrease in knee extensor EMA resulted in a 5.2-fold increase in knee extensor impulse and a 4.9-fold increase in estimated active muscle volume during running compared with walking. As in other bipeds and quadrupeds, muscle EMA was more consistently maintained within each gait, although in certain instances significant differences between relative speeds were observed.

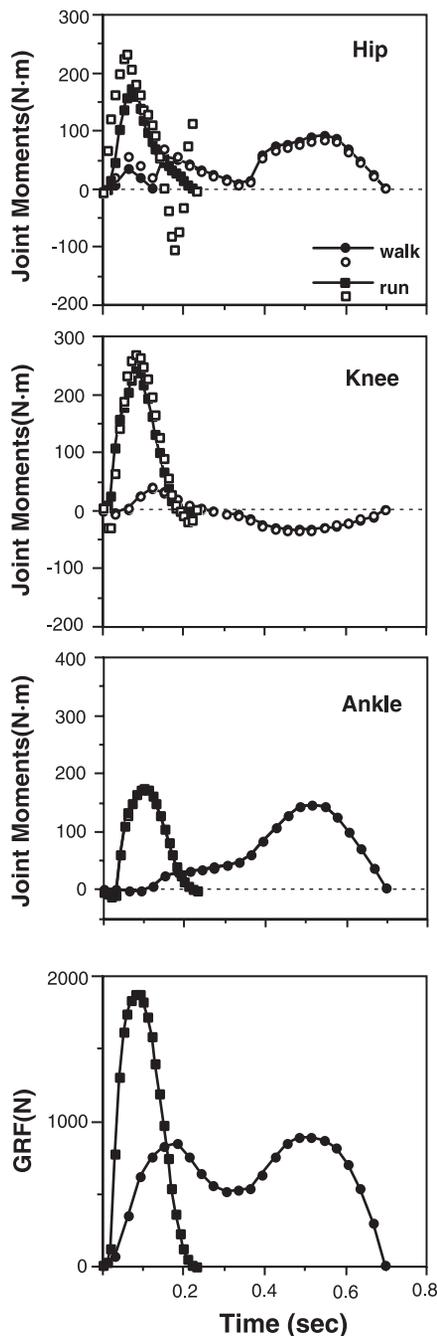


Fig. 3. Representative graphs comparing net muscle moments required to generate the GRF (M_{GRF} , closed symbols) with those also required to lift and accelerate the limb segments ($M_{GRF} + M_{inert+grav}$, open symbols) acting about the hip, knee, and ankle joints vs. the time of limb support for a preferred walk (circles) vs. a preferred run (squares) of 1 subject. Representative records of the magnitude of the GRF vector vs. stance time are shown in the bottom panel for both gaits. Similar patterns were observed for the other 3 subjects. Inertial and gravitational moments at the hip and knee were more variable among subjects than moments developed to generate the GRF (positive, extension; negative, flexion).

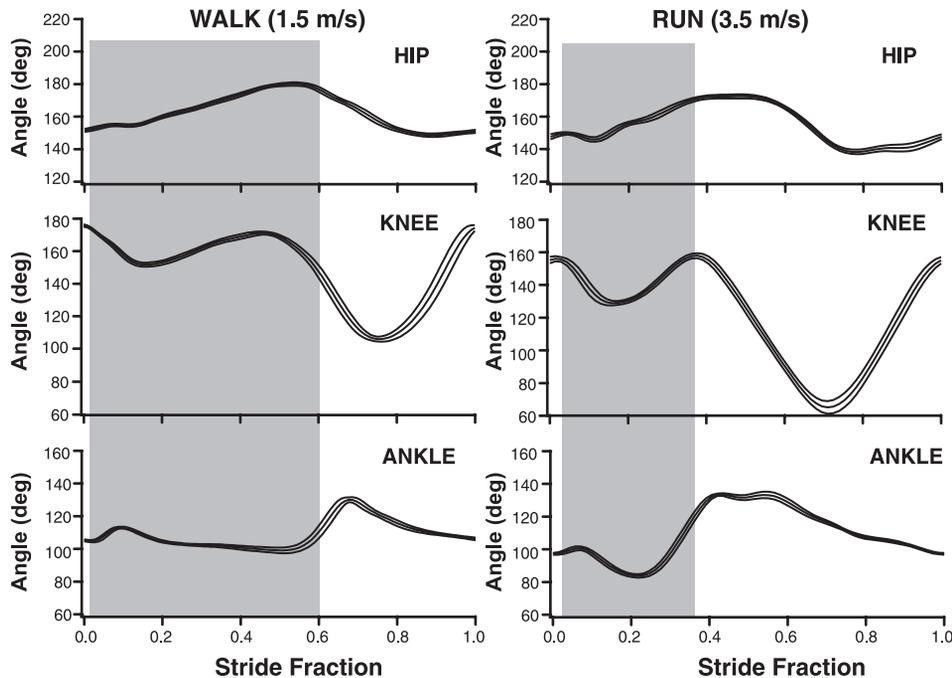


Fig. 4. Representative joint angle changes at the hip, knee, and ankle during walking (PW at 1.5 m/s) vs. running (PR at 3.5 m/s) plotted vs. the fraction of stance. Graphs show mean \pm 1 SD for 8 consecutive strides of *subject 2* normalized for cycle duration. Shaded regions denote the support or stance phase of the stride. deg, Degrees.

The decrease in knee EMA at a run corresponds to previously defined differences in the mechanics of body weight support during walking vs. running, or trotting, and hopping gaits (8). During walking, the knee is extended throughout most of the stance phase of the stride to provide a flexible strut (27) that the body vaults over, exchanging potential and kinetic energy of the body's center of mass to conserve mechanical energy (10). This strategy allows the knee (and hip) to remain more closely aligned with the GRF, lowering the external moment developed at the knee. During running, the knee is held in a more flexed position, associated with the limb's function as a spring (11, 15, 27), which absorbs the impact of the body's weight during landing and allows for the storage of elastic energy at the ankle, within the foot (23), and probably at other sites throughout the leg. This shift in limb function, however, requires a substantial increase in the magnitude of force and total extensor impulse at the knee required to generate the GRF. Because our analysis and results neglect the contribution of force-generation requirements in the frontal plane, our results may differ from those obtained for women and obese runners, whose requirements in the frontal plane are likely greater than those for lean male runners.

At least partly because of these changes in knee joint mechanics in the parasagittal plane, the energy cost of transport in humans is 50–80% greater during running than during walking (15, 28). To assess how the decrease in extensor mechanical advantage may affect this increase in energy cost, we estimated the volume of actively recruited fibers within each agonist muscle group, assuming that all recruited fibers are activated similarly and generate equivalent force per fiber cross-sectional area (equal stress) in the different muscles. We adopted this approach because, in general, longer fibered muscles can be expected to consume more energy to generate a given force per unit time than shorter fibered muscles (31). Although the specific contractile conditions under which a muscle generates force (i.e., its speed of shortening and

whether it shortens, lengthens, or remains isometric) will affect the energy cost of force generation (26), our approach represents a rough first approximation for estimating the volume of actively recruited fibers within a muscle during stance. A similar approach has also been taken by Griffin et al. (19) to examine the metabolic cost of generating force in human walking. Consequently, although the magnitude and rate of muscle force development required to support the body's weight at a particular speed and gait have been shown to underlie the energy cost of locomotion (25, 37), the volume of actively recruited muscle fibers underlying force-generation requirements within the limb during stance is also likely to be a critical influence on energy cost. Consistent with this, Griffin et al. found that the active muscle volume required to generate force on the ground (associated with M_{GRF}) and the rate of generating this force accounted for >85% of the increase in net metabolic rate across moderate walking speeds and load-carrying conditions.

In the present study, when adjusted for differences in muscle fiber length and compared across the gait transition, the knee extensors showed the greatest increase in the active muscle volume needed to generate force on the ground (M_{GRF}), increasing 4.9-fold from $512 \pm 170 \text{ cm}^3$ at a walk to $2,486 \pm 277 \text{ cm}^3$ at a run (23–49% of the total active volume of the three agonist groups combined). In comparison, the hip extensors, which accounted for $1,030 \pm 202 \text{ cm}^3$ of the active muscle volume at a walk (46% of total), increased by 1.77-fold to $1,822 \pm 281 \text{ cm}^3$ at a run (36% of total); and the ankle extensors increased by 1.10-fold from $695 \pm 97 \text{ cm}^3$ at a walk (36% of total) to $761 \pm 81 \text{ cm}^3$ at run (16% of total). These results differ from those reported by Griffin et al. (19), who found that active muscle volume at the ankle (50% of total) exceeded that at the hip (32% of total) at all walking speeds examined. However, this reflects a difference in how we estimated active muscle volume here [based on peak muscle force (F , Eq. 4)] vs. Griffin et al.'s use of time-integrated

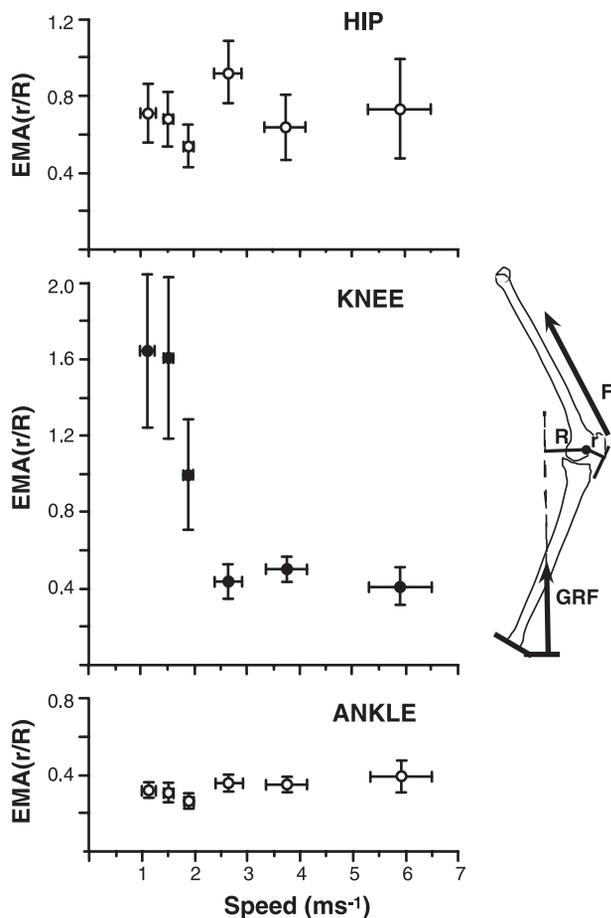


Fig. 5. Representative changes in muscle EMA at the hip, knee, and ankle joints as a function of speed and gait for 1 subject. Error bars indicate ± 1 SD for EMA and for speed (shaded vertical bar indicates approximate gait transition speed). Although the absolute speeds that each subject selected for slow, preferred, and fast speeds within each gait varied among subjects, similar results were obtained for all 4 subjects. Selected speeds varied little among trials within each gait-speed category for each subject ($CV < 0.06$).

muscle force normalized to ground impulse ($\int F_m / \int GRF$, or the inverse of limb EMA) during limb support. Given the several assumptions involved in estimating active muscle volume by either approach, it is difficult to assess which method provides the better estimate of the volume of active muscle recruitment and energy use.

All three joints also showed increases in estimated active muscle volume due to increased inertia during stance as speed increased and gait changed, with the knee and hip being most important. It seems likely, therefore, that a substantial fraction of the observed increase in the energy cost of transport at a run vs. a walk is linked to the increase in muscle impulse and the volume of active muscle at the knee, with a smaller contribution due to inertia at the hip during stance. However, it is important to emphasize that our approach ignores both the cost associated with muscles that are active during the swing phase of gait and how differences in limb support time (or duty factor) affect the cost of muscle force generation. Although increased energy use can be expected with increased motor unit recruitment to generate greater muscle force, energy cost is also likely reduced when the muscles are activated for shorter periods of time. Thus the interacting effects of increased

muscle recruitment but decreased activation duration on energy cost, when humans increase speed and change gait from a walk to a run, remains an important challenge to sort out.

Because our estimate of active muscle volume also ignores changes in the contractile state of the different muscle groups, other factors, such as stride frequency, also likely influence the energy cost of running vs. walking. The increase in stride frequency when humans increase speed and change gait from a walk to a run (preferred walk 0.91 ± 0.07 Hz vs. preferred run 1.37 ± 0.08 Hz) presumably requires the recruitment of faster contracting fibers to develop force more rapidly and shorten at higher velocities. This likely increases the cost of force generation, increasing the overall cost of transport of the body (22, 25). Griffin et al. (19) similarly observed a significant effect of an increase in the rate of force development (based on ground contact time) in relation to the net metabolic cost of walking. In addition, there is evidence that more work may be performed to move the body per unit distance during running than during walking (9, 21), although increased elastic energy storage and return by tendons in running likely supplies some of the increased work (8, 23). Taken together, these

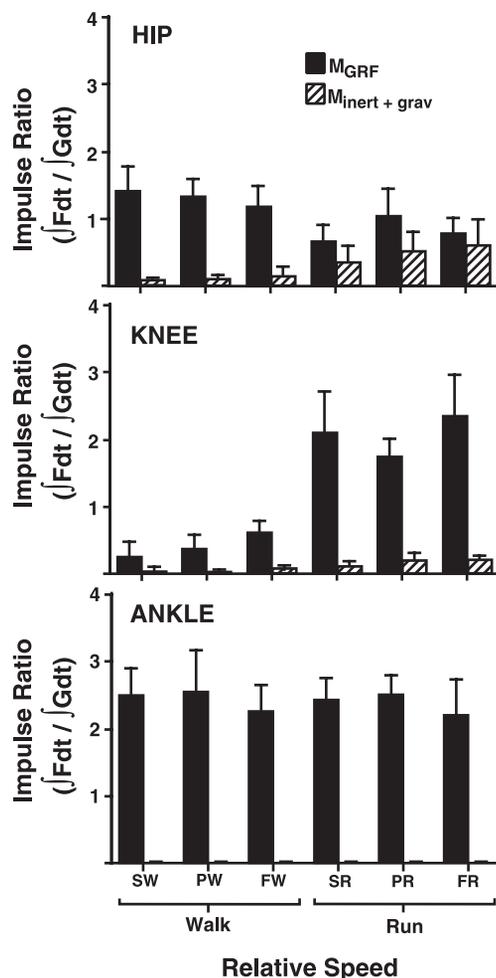


Fig. 6. Histograms of changes in muscle impulse at the hip, knee, and ankle joints normalized for differences in ground reaction impulse ($\int F dt / \int GRF dt$) as a function of relative speed and gait for all 4 subjects combined. Because both are determined over the same time period, $\int F / \int GRF$ effectively measures the average muscle force required to generate 1 body weight of force on the ground. Error bars indicate ± 1 SD.

factors also likely explain much of the difference in the observed increase in the cost of transport of running vs. walking. Nevertheless, our results here suggest that the metabolic cost of generating a substantial increase in quadriceps muscle force during the stance phase of gait likely contributes a major fraction of the increased energy cost of running vs. walking.

Muscle EMA and energy cost vs. size. The mechanical advantage of limb muscles (r/R) increases with body mass in quadrupedal mammals ($\propto M^{0.27}$, 1, 2). The increase in muscle EMA is associated with a size-dependent change to more upright locomotor posture in larger mammals, which reduces mass-specific muscle forces and, thus, peak muscle and bone stress. When compared with that of quadrupedal mammals, the EMA of humans during walking (0.71 ± 0.29 , $n = 104$, pooled for all trials and subjects and averaged for the three joints) fell within the 95% confidence interval (0.592–1.081 at 70 kg body mass) of the regression for the quadruped hindlimb (Fig. 8). However, because of the decrease in knee EMA, average muscle EMA of humans during running (0.52 ± 0.16 , $n = 99$) was significantly less (34%) than that predicted for the hindlimb of a quadruped of similar size (predicted EMA = 0.78). Because the quadruped data are based on mean EMA values obtained for each species over a range of trotting and galloping speeds (for which no discernable change in EMA was observed), the comparison with human walking may be influenced by the difference in gait.

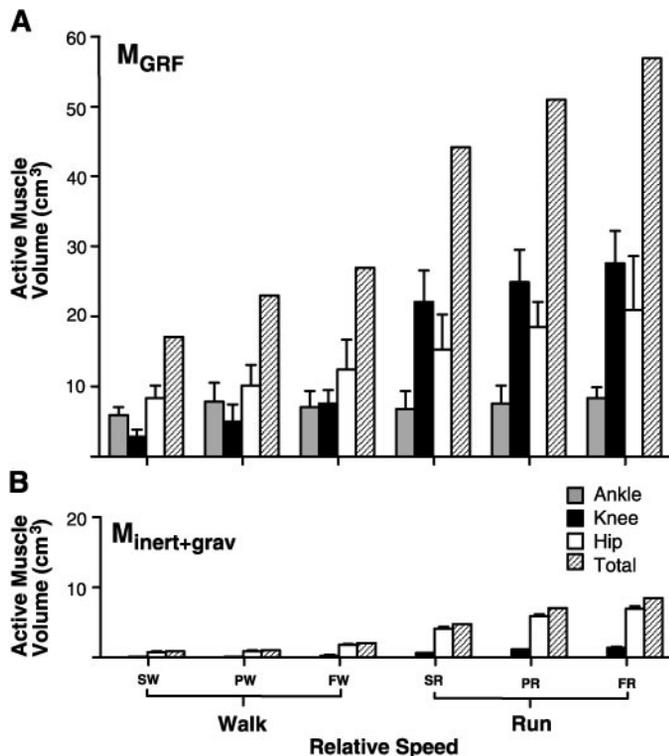


Fig. 7. Estimated active muscle volume as a function of relative speed and gait (see text for details on the calculation of active muscle volume). *A*: active volume of muscles extending the hip, knee, and ankle joints that was required to generate the GRF associated with M_{GRF} , relative to the total volume summed for all 3 joints. *B*: active muscle volume required to lift and to accelerate the limb segments associated with $M_{inert+grav}$. Error bars indicate ± 1 SD.

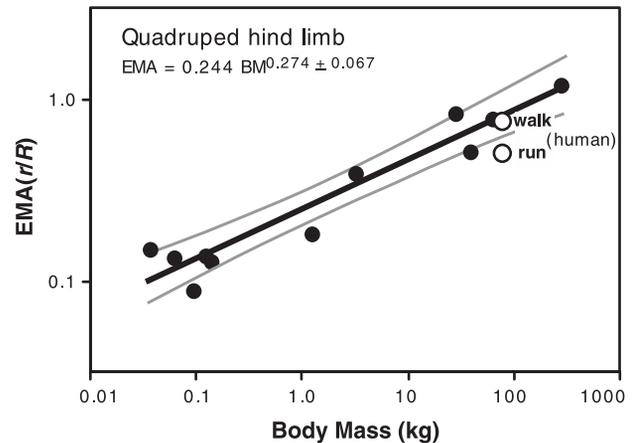


Fig. 8. Hindlimb muscle EMA plotted vs. body mass (BM) on logarithmic coordinates. The thick and thin lines are the least-squares regression slope and 95% confidence interval for the allometric relationship of hindlimb muscle EMA of quadrupedal mammals ($R^2 = 0.91$) originally reported by Biewener (1) and updated with additional species (2). The larger open points denote the averaged EMA of the 4 human subjects for the pooled data at a walk and at a run. Human EMA at a walk falls within the 95% confidence interval of quadrupedal mammals, but it falls outside at a run.

The lower limb mechanical advantage and greater muscle force-generating requirements of humans during running matches previous observations of the greater energy cost of transport of human running compared with quadrupedal mammal trotting and galloping. First noted by Taylor et al. (40) on the basis of data reported for humans (13, 24, 29), with the inclusion of more recent studies of the net (slope or incremental) energy cost in humans during running (6, 12, 30), a mean value of $3.86 J \cdot kg^{-1} \cdot m^{-1}$ is obtained, which is 38% greater than the cost predicted for a trotting or galloping 70-kg quadruped ($2.79 J \cdot kg^{-1} \cdot m^{-1}$) (38). This compares quite favorably to the 35% lower muscle EMA of running humans compared with the predicted muscle EMA of quadrupeds noted above. The similar scaling patterns of forelimb and hindlimb EMA of quadrupeds (1) further supports this interpretation of energy cost of transport based on a comparison of human and quadruped hindlimb EMA.

Although an erect bipedal posture and change in muscle gearing at the ankle joint (7) suggests improved locomotor economy during walking (33) and endurance during running (7), the reduced limb mechanical advantage observed here in running humans supports previous results showing that running incurs a greater cost of transport compared with walking at a preferred speed. Consequently, improved running economy or transport cost was unlikely a key selective factor favoring the evolution of erect bipedalism in humans (7). Furthermore, although differences in the time course of muscle force generation and the rate of force development appear to explain speed- and size-related differences in the energy cost of locomotion within mammals (22, 25), changes in energy cost of transport between walking and running within humans are also likely determined by changes in the magnitude of muscle force generation and recruited volume of active muscle during limb support.

We conclude, therefore, that the greater energy cost during running in humans may be explained in part by the decrease in limb mechanical advantage resulting from the use of more

flexed knee joint during running vs. walking. Whether changes in limb mechanical advantage occur in other species between the mechanically dissimilar gaits of walking vs. running, trotting, or galloping awaits further investigation. To date, such gait-related changes in limb mechanical advantage have not been observed (1, 31). This may reflect the evolution of a unique erect bipedal gait within hominids, which distinguishes modern humans from avian bipeds and mammalian quadrupeds.

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