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Sources of mechanical power for uphill running in humans

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Summary

During uphill running limb muscles must perform net mechanical work to increase the body's potential energy, while during level running the net mechanical work required is negligible as long as speed is constant. The increased demands for work as running incline increases might be met by an increase in power output at all joints, or only a subset of joints. We used inverse dynamics to determine which joints modulate net work output in humans running uphill. We measured joint kinematics and ground reaction force during moderate speed running at 0°, 6° and 12° inclines. Muscle force, joint power and work per step were determined at the ankle, knee and hip using inverse dynamics calculations. We found that virtually all of the increase in work output with increasing incline resulted from increases in net work done at the hip (–0.25±0.23 J kg^{-1}, level, *vs* 0.88±0.10 J kg^{-1}, 12° incline), while the knee and ankle performed similar functions at all inclines. The increase in work output at the hip resulted primarily from a large increase in average net muscle moment during stance (2.07±17.84 Nm, level, *vs* 87.30±13.89 Nm, 12° incline); joint excursion increased by only 20% (41.22±3.41°, level, *vs* 49.22±2.35°, 12° incline). The increase in hip muscle moment and power was associated with a poorer mechanical advantage for producing force against the ground. The increase in hip moment with running incline allows for the production of the power necessary to lift the body. This power may be developed by hip extensors or by transfer of power from muscles at other joints *via* biarticular muscles.

Key words: locomotion, biomechanics, muscle, power, mechanical advantage, recruitment, human.

Introduction

In humans, the extensor muscle mass at the hip is the largest of the three major extensor muscle groups of the leg, yet mechanical measurements suggest that the hip musculature contributes little work during level running. Inverse dynamics measurements during jogging indicate that the net muscle moment and power developed at the hip are substantially lower than for the ankle and knee (Winter, 1983). The low hip moments relative to those at the knee or the ankle are associated with the favorable leverage, or mechanical advantage, for force production at this joint. Limb muscles operate across a skeletal system lever with a fulcrum at the center of rotation of the joint. Any given muscle's mechanical advantage for force production is set by the distance from the muscle line of action to this fulcrum (the in-moment arm) and by the distance from the fulcrum to the ground reaction force vector (the out-moment arm; Biewener, 1989). Hip joint moments are low during ordinary running because the out-moment arm is small, i.e. the ground reaction force vector passes close to the joint center of rotation. Hip muscles must also produce force to overcome the inertia of the limb and to act against co-contracting muscle antagonists, but these forces are generally thought to be low relative to ground reaction based forces (Thorpe et al., 1998). The favorable mechanical advantage at the hip during running may reflect a mechanism for improving locomotor economy. The large extensor muscle mass at the hip must consume considerable metabolic energy when active; a favorable mechanical advantage at the hip may conserve metabolic energy by keeping hip extensor forces low.

Low moments of force at the hip must necessarily limit the power produced at this joint. During level, steady-speed running this lack of mechanical power may have little consequence; the net mechanical power required in each step is close to zero, because there is no net change in the runner's average kinetic or potential energy. By contrast, uphill running requires net mechanical work with each step to increase the body's potential energy. During these activities the low forces developed at the hip could potentially limit the power available from the large hip extensor muscle mass. Power might also be transferred from knee extensors to the hip *via* biarticular hamstrings, but this also requires a net extensor hip moment. Thus, we hypothesized that the average muscle moment at the hip would increase from level to incline running to meet the demands for mechanical power to lift the body.

To determine whether the hip contributes mechanical power to uphill running, we used inverse dynamics to measure hip muscle moments and power during level running and at two running inclines. We also measured muscle moments and power at the ankle and knee to determine the relative contribution of all joints to uphill power output. We predicted that hip net mechanical power output would increase as a function of running incline. We also predicted that increased force and power output at the hip would be associated with a poorer mechanical advantage for force production during incline running.

Materials and methods

Subjects and running protocol

Four healthy male subjects took part in this study. They were between 21 and 34 years of age, with a mean body mass of 78.7±6.5 kg (± S.E.M.). Subjects gave informed consent and all procedures were approved by the Harvard University Committee on the Use of Human Subjects. Subjects ran over separate trackways for the incline and level running measurements. On the level, subjects ran along a 30 m trackway over a force plate mounted flush with the ground. Measurements for 6° and 12° inclines were made on a force plate mounted in an adjustable inclined ramp. The force plate was mounted 5 m from the bottom of the 8 m ramp. The subjects ran at a steady speed over 10–20 m of level ground before ascending the ramp, and descended a ramp at the other end of the trackway after crossing the force plate. Force and position data were recorded for 0°, 6° and 12° inclines. Four photocells mounted at 1 m increments along the trackway were used to determine the speed of the runners. The subjects ran between 3.0 and 3.5 m s^{-1}. Only runs in which speeds between adjacent photocell pairs differed by less than 5% were selected for analysis. Four trials were analyzed for each subject.

Force and video measurements

Force plates (on the level, Kistler model 9261; Amherst, NY, USA; on inclines, AMTI model OR65-6, Watertown, MA, USA) were used to measure ground reaction forces during running. These force plates showed less than 0.5% cross-talk between channels. The inclined force plate was mounted in a stiff steel chassis similar to the apparatus described by Kram and Powell (1989). The unloaded natural frequency of both plates was greater than 150 Hz.

Horizontal and vertical (i.e. parallel and normal to the plate surface) components of the ground reaction force were recorded on computer after A/D conversion on a National Instruments NB MIO 16H A/D board (National Instruments, Austin, TX, USA). Signals were collected through a custom Labview program at 1000 Hz and filtered by a Chebyshev low pass filter with a cut-off frequency of 60 Hz. A manual correction was made for the small phase shift caused by this filter. The force plates used allowed measurement of the center of pressure of the foot. This measurement was calibrated regularly with a known mass and was accurate within 1 cm.

The positions of the hip, knee and ankle joints were marked and recorded with video. The centers of rotation of the three joints were palpated and marked on the skin with black felt-tip marker. A NAC high speed video system operating at 100 fields s^{-1} was used to videotape the runners. For the incline runs, the camera was tilted to the same incline as the force plate, so that the vertical and horizontal axes in the video corresponded to the vertical and horizontal axes of the force plate. Frames were digitized and joint locations were measured using NIH Image software. Raw coordinate data were filtered bidirectionally by a fourth order, zero lag Butterworth filter with a cut-off frequency of 10 Hz (Winter, 1990). Joint angles were determined trigonometrically from joint positions. We assumed that the orientation of the trunk was constant during the stance phase, and used the angle of the leg relative to the horizontal as a measure of hip angle. Force and video data were synchronized by triggering both force data acquisition and the video frame counter (using a custom built circuit) when the runner tripped the first photocell.

Joint moment

We used inverse dynamics to determine net muscle moments (M_m) at the ankle, knee and hip (Elftman, 1939; Winter, 1990). Our analysis included both moments due to limb inertia and rotation as well as ground reaction force-based moments. We used published values of segment masses, moments of inertia, and center of mass locations (Winter, 1990). By convention, net extensor muscle moments are positive and net flexor moments are negative.

We also calculated ground reaction force-based moments independently of limb inertia. This allowed us to determine the moment arm of the ground reaction force, one of the variables that determines the mechanical advantage with which muscles generate force to support the body. By this method, net muscle moments are calculated as the product of the ground reaction force, GRF (in N), and the moment arm of this force, or out-moment arm, R (in m).

$$M_{m(GRF)} = GRF \bullet R\ . \quad (1)$$

R is the orthogonal distance between the resultant ground reaction force vector and the joint center of rotation.

Joint power and work

Net joint power P was calculated from joint moment and angular velocity (ω) according to the equation:

$$P = M_m \bullet \omega\ , \quad (2)$$

where ω is joint angular velocity in radians. By convention extension velocities are positive. Positive power indicates work performed by muscles and tendons, while negative power output indicates work absorbed by muscles and tendons. Net joint work was calculated by integrating the power–time curve during stance. Because elastic elements cannot release more energy than they absorb, the net work performed (positive work minus negative work) during the step represents the minimum work that must be done by muscles.

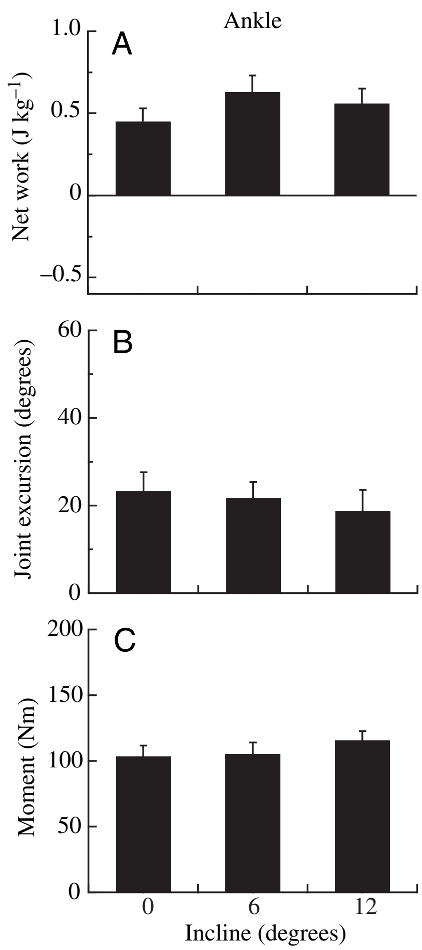

Fig. 1. Net mechanical work (A), net joint excursion (B), and mean joint moment of force (C) at the ankle during the stance period for three running inclines. Values are mean ± S.E.M. (N=4).

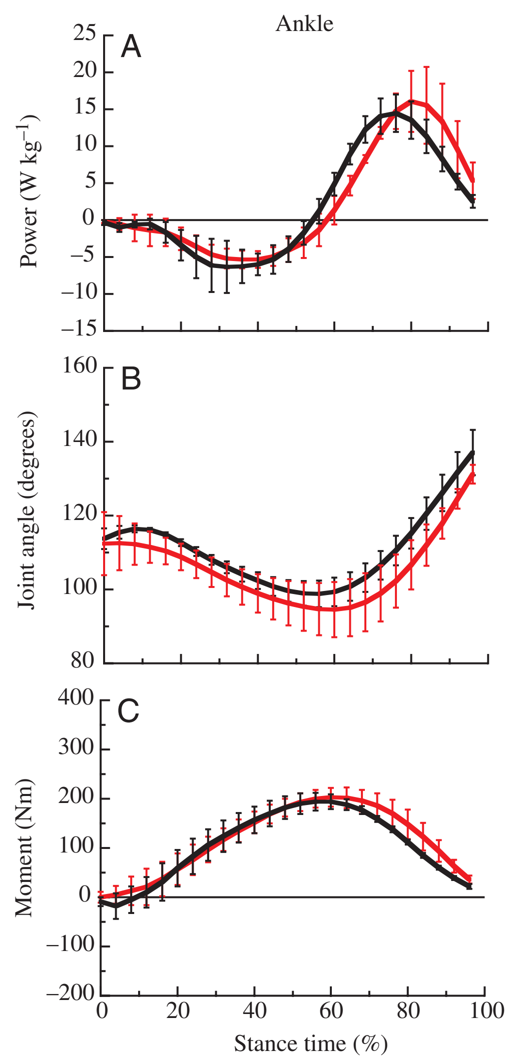

Fig. 2. Ankle power output (A), angle (B) and moment (C) for stance during level running (black lines) and running on a 12° incline (red lines). Data are normalized to the fraction of stance period. Values are mean ± S.D. for 4 subjects.

Statistics

All data are presented as means ± standard deviations (S.D.) or standard errors (S.E.M.). Repeated-measures analysis of variance (ANOVA) was used to determine statistical significance between running inclines.

Results

Net mechanical work developed at the ankle during stance was positive for all inclines, and there was a small but significant effect of running incline on net mechanical work (P=0.022; Fig. 1A). The total angular excursion of the ankle joint during stance, and the mean moment produced, were independent of incline (Fig. 1B,C). Time profiles of joint moment, angle and power during stance reveal that ankle function during incline running was very similar to that of level running (Fig. 2).

At the knee, net work was negative for all inclines, and there was no significant effect of running incline on knee work (Fig. 3A). Although work was unchanged with incline, there was a significant increase in total joint excursion with incline (Fig. 3B), and a decrease in joint moment (Fig. 3C). The increase in joint excursion offset the decrease in joint moment, so that net work produced was independent of incline. Although *net* work was unchanged with incline, it is clear from the time profiles of joint power during stance that the knee developed less positive power and negative power during incline running (Fig. 4). Net work was unchanged because positive and negative power decreased proportionately.

Mechanical work produced at the hip increased dramatically with increasing running incline (P<0.001; Fig. 5A). During level running, net work produced at the hip was not significantly different from zero. Significant positive work was produced at the hip during both 6° and 12° incline running (Fig. 5A). The increase in work output at the hip with running incline was due primarily to an increase in the moment of force developed (Figs 5C, 6C). Average angular excursion of the hip during stance also increased with incline, though the change in

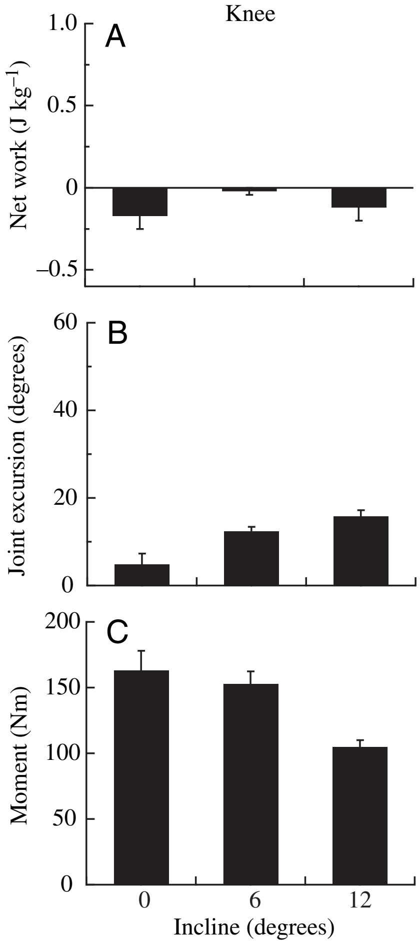

Fig. 3. Net mechanical work (A), net joint excursion (B), and mean joint moment of force (C) at the knee during the stance period for three running inclines. Values are mean ± S.E.M. (N=4).

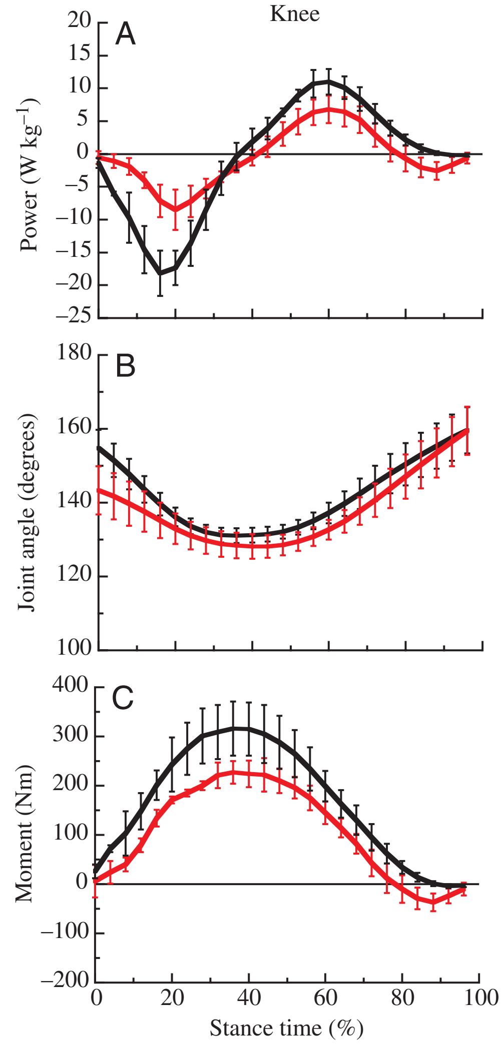

Fig. 4. Knee power output (A), angle (B) and moment (C) for stance during level running (black lines) and running on a 12° incline (red lines). Data are normalized to the fraction of stance period. Values are mean ± S.D. for 4 subjects.

joint excursion was much smaller than the change in joint moment (Figs 5B, 6B).

The increase in extensor muscle moment produced at the hip correlated to a change in the out-moment arm R for force production at the hip. The average moment required at the hip to overcome limb segment inertia was independent of incline (P<0.001). Therefore, we compared the GRF based moment across incline to determine whether increases in average hip moment were due to a change in GRF magnitude or R. There was no significant change in GRF magnitude with incline (Fig. 7), nor was there a significant change in impulse with incline (306±25 Nm s, 311±28 Nm s and 295±25 Nm s for 0°,6° and 12°, respectively). There was a large increase in the average out-moment arm at the hip (R, Eqn 1) with incline (Fig. 8). From level to 12° incline running, the out-moment arm increased by more than fourfold (from 0.022±0.011 m to 0.092±0.006 m; P=0.003).

Discussion

We find that most of the work necessary to propel a runner uphill is produced at the hip. There is a qualitative change in function at the hip from level to uphill running. During level running at the speeds measured here the moments of force at the hip are very small, and net work is negative. From level to a 12° incline, the moments of force increase significantly, until the positive net work performed at the hip represents 75% of the net work performed by the hip, knee and ankle joints. By comparison, there was little change in function at the knee and ankle, with no increase in joint work as the demand for work increased with incline.

Although we find that most of the power necessary to propel a runner uphill is produced at the hip joint, it cannot be concluded from the methods used here that hip extensor muscles alone produce this power. Two-joint muscles can transfer mechanical power from one joint to another (Bobbert et al., 1986; Bobbert and van Ingen Schenau, 1988; van Ingen Schenau et al., 1992; Jacobs et al., 1996, 1993; Prilutsky et al., 1996). During cycling, for example, mechanical power produced by contraction of mono-articular knee extensors can

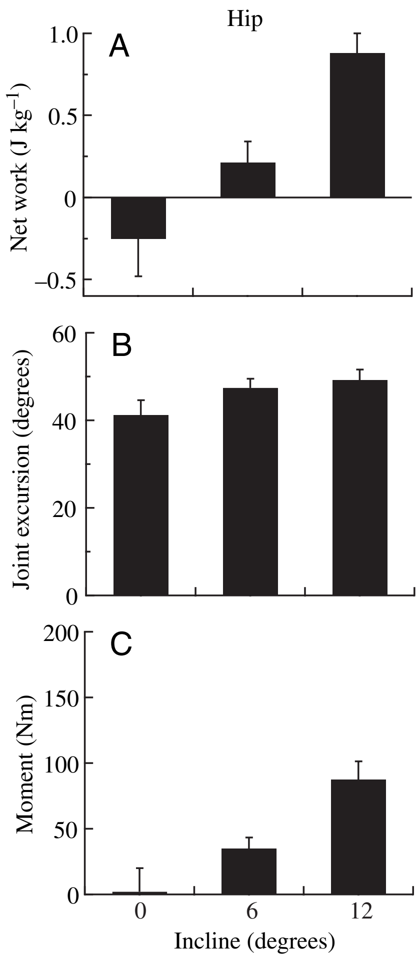

Fig. 5. Net mechanical work (A), net joint excursion (B), and mean joint moment of force (C) at the hip during the stance period for three running inclines. Values are mean ± S.E.M. (*N*=4).

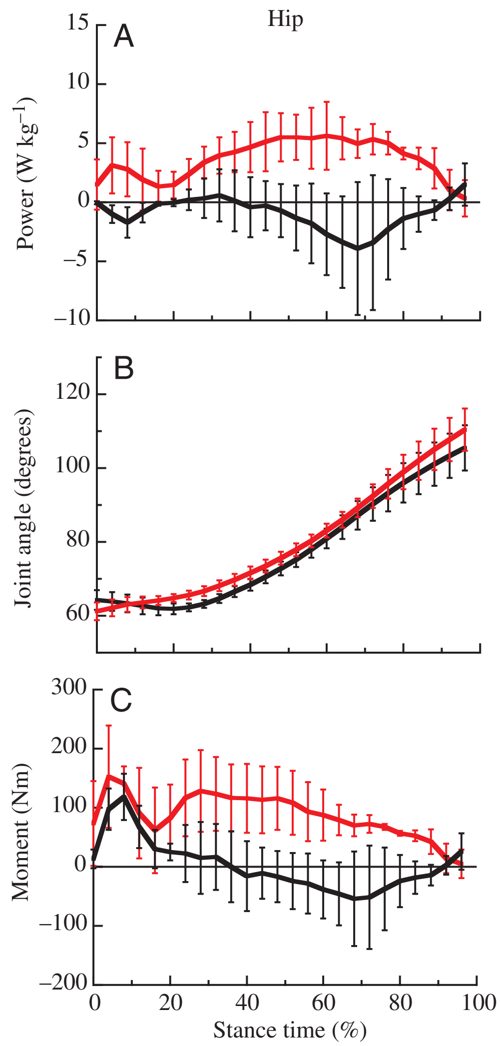

Fig. 6. Hip power output (A), angle (B) and moment (C) for stance during level running (black lines) and running on a 12° incline (red lines). Data are normalized to the fraction of stance period. Values are mean ± S.D. for 4 subjects.

be transferred via the hamstrings to appear as mechanical power at the hip (van Ingen Schenau et al., 1992). Some of the mechanical work observed at the hip in the present study may be produced by contraction of knee extensors. Thus, we can conclude from our measurements of net joint moment that an increase in net moment at the hip is associated with an increase in net work either produced by hip extensors, or transferred by biarticular hip extensors from muscles at other joints (e.g. knee extensors). In either case, an increase in net muscle moment produced at the hip was necessary to increase net hip work.

Because we found no increase in net power output at the knee or ankle with running incline, knee extensors contributed to the increase in net work necessary to run uphill only if they transfer work to the hip *via* the biarticular hamstrings. Estimates of muscle activity from other methods suggest that this may be the case. Sloniger and coworkers (1997a,b) found increased muscle activity, based on Magnetic Resonance Imaging (MRI), in knee extensors with increasing running incline (Sloniger et al., 1997a,b). Glycogen depletion studies also suggest an increase in activity in the vasti group from level to incline running (Costill et al., 1974). The transfer of power from knee extensors to the hip may reflect an important mechanism for overcoming the constraints of force production in a jointed limb. Joint moments are interdependent; an increase in net horizontal force, for example, would tend to decrease knee extensor moments and increase hip extensor moments. It has been suggested that two joint muscles distribute external joint moments across different joints to allow for the coordination of changes in joint moments (van Ingen Schenau et al., 1992). In certain stages of cycling, for example, the transfer of power from the monarticular knee extensors (vasti group) to the hip *via* the biarticular hamstrings allows knee extensors to contribute to pedal power even when net knee moments are low (van Ingen Schenau et al., 1992). Biarticular muscles may play a similar role as the pattern of ground reaction forces change with running incline.

The low joint moments observed at the hip during level running may reflect a strategy for minimizing metabolic energy cost. It has been suggested that the cost of generating muscle

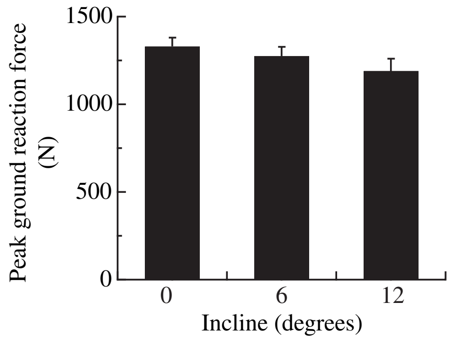

Fig. 7. Average ground reaction force during the stance period for three running inclines. Values are mean ± S.E.M. (N=4).

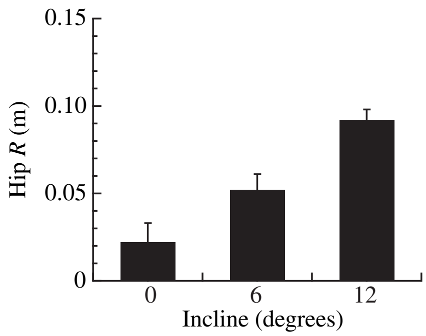

Fig. 8. The mean hip out-moment arm, R, for force production against the ground increased as function of running incline. Values are mean ± S.E.M. (N=4).

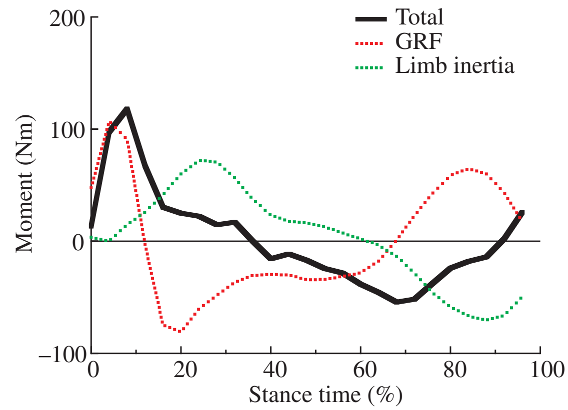

Fig. 9. Ground reaction force-based moments (red) and limb inertia-based moments (green) compared at the hip for level running. The total moment, calculated from inverse dynamics (black), is the same given in Fig. 6. Values are means for 4 subjects, error bars are omitted for clarity.

force determines the metabolic cost of running, and that much of the design of the musculoskeletal system has been shaped by the need to produce force economically (Taylor, 1985, 1994; Kram and Taylor, 1990; Roberts et al., 1997). Several architectural features of the hip extensors suggest that they are poorly suited for producing force economically (Biewener and Roberts, 2000). First, hip extensors have relatively long fascicles (Wickiewicz et al., 1983). For a given force output, longer-fibered muscles are metabolically more costly than short-fibered muscles because a greater volume of muscle must be active (Biewener and Roberts, 2000). Hip muscles may also be disadvantageous for producing force economically because they do not undergo the stretch–shorten cycle that may reduce the energy cost of running by allowing for elastic energy storage and recovery (Alexander, 1988; Cavagna et al., 1964; Taylor, 1994; Roberts et al., 1997). Further, the capacity for elastic energy storage and recovery is likely limited in hip extensors by their relatively small tendons.

Although our measurements of joint moments suggest that hip muscles generate low forces during level running, some values from the literature suggest higher levels of activity in hip muscles. Winter's results for jogging humans were consistent with those of the present study; hip moments were variable, but generally lower than those at the ankle and knee (Winter, 1983). Thorpe et al. (1998) combined measurements of joint moments and muscle cross-sectional area measured from MRI to estimate the average stress in different muscle groups. At slow speeds, their results were generally consistent with the present study; hip muscle stresses were the lowest of all three joints and were only about half those of knee extensors. At higher speeds, however, hip stress values were similar to those of the ankle (Thorpe et al., 1998). Belli and coworkers also found that hip moments were low at moderate speeds but increased substantially with speed, until reaching peak values nearly as high as those for the ankle and knee at runners' maximum speeds (Belli et al., 2002). Sloniger and coworkers estimated muscle activity during very fast level running using contrast shifts in magnetic resonance images (Sloniger et al., 1997a). Their results indicate a very high level of activity of all of the hamstrings, gluteal and adductor muscles (65–90% active; Sloniger et al., 1997a) during horizontal running at an exercise intensity equivalent to 115% of peak oxygen uptake. Electromyographic (EMG) measurements also indicate activity in hip extensors during at least some part of stance (McClay et al., 1990), but it is difficult to make quantitative assessments of absolute magnitude of recruitment and muscle force in different muscle groups from EMG measurements. Together, these results suggest that the low joint moments at the hip observed in the present study for moderate speeds may not hold at fast running speeds. It is unclear from published studies whether the higher hip moments at high speeds result from an increase in ground reaction force-based moments or an increase in inertial moments necessary to swing the limbs faster.

Our results suggest that the primary mechanism for altering joint work with running incline is an increase in joint moment, rather than an increase in excursion. Some increase in joint excursion occurred for the knee, and there was a small increase in hip excursion with incline. Our results for joint excursion at the hip and knee are consistent with Swanson and Caldwell's study of incline running (Swanson and Caldwell, 2000). They found an increase in joint range of motion during stance for the hip, knee and ankle. These results are also consistent with the pattern of change in muscle function observed in individual muscles of running birds. In turkeys (Roberts et al., 1997; Gabaldon et al., 2004) and guinea fowl (Daley and Biewener, 2003), modulation of muscle force is one of the mechanisms utilized to alter mechanical work output for uphill running in distal joint extensors.

Studies of joint moments in running animals have typically used either a pseudo-static approach, in which only ground reaction force-based moments are measured (Biewener, 1989; Roberts et al., 1998; Carrier et al., 1998), or a true inverse dynamics technique, which includes joint moments necessary to overcome inertia of limbs that cyclicly accelerate and decelerate. Only a few studies have reported these values separately to allow evaluation of the importance of the limb-inertia component of joint moments (Biewener et al., 2004; Clark and Alexander, 1975). We found that the inertial component of joint moments was negligible at the ankle and small at the knee. In level running, the average extensor moment due to limb inertia at the knee was only 9.39±2.39 Nm, compared with the total average moment of 162.99±14.94. At the hip, limb inertia moments were on average the same magnitude as GRF based moments (Fig. 9). When the rectified average moment is calculated (to account for moment magnitude independent of sign), the GRF-based rectified moments at the hip are 49.15±11.68 *vs* 52.55±8.03 Nm for limb inertia moments only (for level running). There was no significant change in limb inertia moment with running incline.

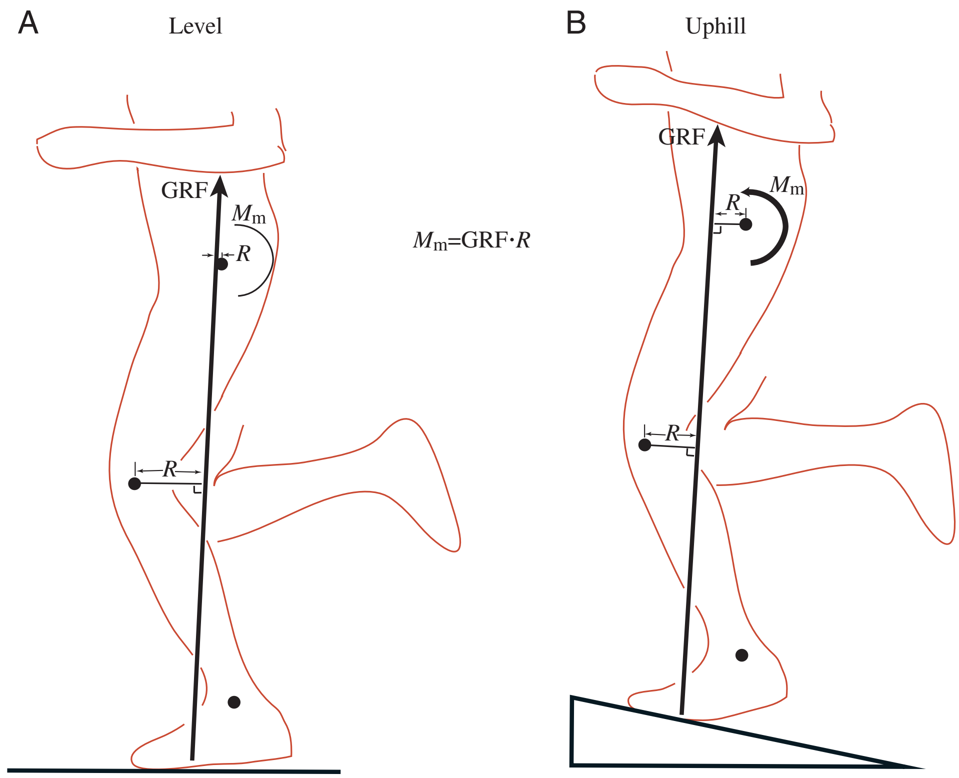

Fig. 10. Diagrams of force and limb position at the midpoint of stance for a level (A) and a 12° incline (B) run. Filled circles indicate the locations of the centers of rotation of the ankle, knee and hip joints. The resultant ground reaction force GRF is closely aligned with the hip during level running (A), resulting in a small out-moment arm (R) and low joint muscle moment (M_m). During incline running (B), the GRF is oriented more forward of the hip, increasing R at the hip and decreasing it at the knee. The increase in R at the hip allows for higher force and work outputs at the hip during incline running. The decrease in R at the knee decreases the external moment and limits the external work that can be done at this joint.

Variable mechanical advantage with running incline

The increase in joint moment with incline observed at the hip was associated with a change in the mechanical advantage with which muscles at the joint produce force against the ground. The mechanical advantage is defined as the ratio of the average of the muscle moment arms acting at a joint, r and the effective moment arm of the resultant ground reaction force, R (Biewener, 1990). In the present study, we measured only the total moment produced at a joint and did not attempt to account for the muscle moment arm or changes in the muscle moment arm that may have occurred across incline. At the hip, the similarity in joint angle patterns across inclines (Fig. 6B) would suggest that muscle moment arms were, on average, similar across inclines. It is the out-moment arm, or the orthogonal distance from the ground reaction force to the joint center of rotation, that increased dramatically as running incline increased. During level running the GRF vector passed very near to the joint center of rotation and as a result the out-moment arm was small and mechanical advantage favorable. During incline running, the GRF was oriented more forward of the hip and the out-moment arm increased, i.e. muscles operated with a poorer mechanical advantage compared with level running (Fig. 10). The increased moment arm at the hip during incline running was associated with higher joint moments and increased work output at the hip for the same change in angle.

The mechanical advantage through which muscles transmit force to the environment is an important determinant of muscle function in nature. Among mammalian runners there is a regular change in mechanical advantage, averaged over all the joints of the limbs, with body size (Biewener, 1989, 1990). The muscle forces required to support body weight are generally lower in large mammals because their upright posture reduces the moment arm of the ground reaction force (R) and improves mechanical advantage (Biewener, 1990). Human runners appear to alter horizontal ground reaction forces to maintain a contstant mechanical advantage when ground reaction forces are altered by simulated reduced gravity (Chang et al., 2000). Recent work suggests that the higher cost of transport in human running *vs* walking may be due in part to runners' poorer mechanical advantage and higher muscles forces associated with a bent-leg posture (Biewener et al., 2004). It has been proposed that variation in mechanical advantage during the course of a single stride may allow muscles to maintain relatively constant contraction velocities even when joint velocity varies (Carrier, 1994; Carrier et al., 1998), and during jumping and accelerations variation in mechanical advantage during single muscle contractions may allow for increased muscle work and enhanced elastic energy storage (Roberts and Marsh, 2003; Roberts and Scale, 2004). The present results suggest a change in muscle mechanical advantage may provide a mechanism for selectively utilizing different muscles for different locomotor tasks. The hip contributes little work for level running because it operates with a favorable mechanical advantage and joint moments are low, while during incline running the mechanical advantage is less favorable and joint moments and work are higher.

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