RESEARCH ARTICLE

Modulation of work and power by the human lower-limb joints with increasing steady-state locomotion speed

Anthony G. Schache[1,*], Nicholas A. T. Brown[2] and Marcus G. Pandy[1]

ABSTRACT

We investigated how the human lower-limb joints modulate work and power during walking and running on level ground. Experimental data were recorded from seven participants for a broad range of steady-state locomotion speeds (walking at 1.59 ± 0.09 m s^{-1} to sprinting at 8.95 ± 0.70 m s^{-1}). We calculated hip, knee and ankle work and average power (i.e. over time), along with the relative contribution from each joint towards the total (sum of hip, knee and ankle) amount of work and average power produced by the lower limb. Irrespective of locomotion speed, ankle positive work was greatest during stance, whereas hip positive work was greatest during swing. Ankle positive work increased with faster locomotion until a running speed of 5.01 ± 0.11 m s^{-1}, where it plateaued at ~1.3 J kg^{-1}. In contrast, hip positive work during stance and swing, as well as knee negative work during swing, all increased when running speed progressed beyond 5.01 ± 0.11 m s^{-1}. When switching from walking to running at the same speed (~2.0 m s^{-1}), the ankle's contribution to the average power generated (and positive work done) by the lower limb during stance significantly increased from $52.7\pm10.4\%$ to $65.3\pm7.5\%$ ($P=0.001$), whereas the hip's contribution significantly decreased from $23.0\pm9.7\%$ to $5.5\pm4.6\%$ ($P=0.004$). With faster running, the hip's contribution to the average power generated (and positive work done) by the lower limb significantly increased during stance ($P<0.001$) and swing ($P=0.003$). Our results suggest that changing locomotion mode and faster steady-state running speeds are not simply achieved via proportional increases in work and average power at the lower-limb joints.

KEY WORDS: Walking, Running, Sprinting, Walk-to-run transition, Elastic strain energy

INTRODUCTION

When walking and running uphill or ascending stairs, the body's potential energy is increased. Similarly, when accelerating (e.g. at the start of a 100 m race), the body's kinetic energy is increased. The power generated during these activities exceeds that absorbed to provide the necessary increase in mechanical energy. In contrast, the body's total mechanical energy does not change during locomotion on level ground at a steady-state speed. Energy will be absorbed and generated by the muscular system during each stride, but the body's net work output will remain zero if speed is kept constant and there is no change in surface inclination. In the present study, we were interested in understanding how the human lower-limb joints modulate work and power during locomotion on level ground for a

broad range of steady-state speeds (walking through to sprinting). For example, is fast running simply achieved by increasing the work done by the hip, knee and ankle joints in a proportional manner? Or are certain joints prioritized, and if so, which joints?

While studies have previously explored how a change in steady-state locomotion speed affects lower-limb joint work and power (Winter, 1983a,b; Ae et al., 1987; Chen et al., 1997; Belli et al., 2002; Teixeira-Salmela et al., 2008; Schache et al., 2011; Farris and Sawicki, 2012a; Pires et al., 2014), no single study has included data for the entire spectrum of speeds that humans can attain. Studies have also quantified the relative contribution from each joint towards the total (sum of hip, knee and ankle) amount of work and power produced by the lower limb during locomotion (Teixeira-Salmela et al., 2008; Rubenson et al., 2011; Farris and Sawicki, 2012a; Stearne et al., 2014); however, locomotion speeds exceeding 4.5 m s^{-1} have not been considered and some inconsistent results have been reported. For example, Rubenson et al. (2011) found the hip to be the dominant power generator during stance when running over ground at 3.3 m s^{-1}, whereas Stearne et al. (2014) found the ankle to be the dominant power generator during stance when running on a treadmill at 4.5 m s^{-1} (irrespective of foot-strike pattern). Furthermore, it is not clear how the relative contributions from the hip, knee and ankle towards total lower-limb joint work and power respond to a change in locomotion speed. Teixeira-Salmela et al. (2008) measured lower-limb joint work across the stride cycle for a range of walking speeds (0.67 to 1.42 m s^{-1}). With faster walking, the relative contribution from the ankle to the total amount of positive work done by the lower limb decreased from 59.8% to 43.5%, whereas the relative contribution from the hip increased from 24.4% to 37.8%. Farris and Sawicki (2012a) measured the relative contributions from each joint to the total average power output by the lower limb across the stride cycle for a range of walking (0.75–2.00 m s^{-1}) and slow running speeds (2.00–3.25 m s^{-1}). In contrast to Teixeira-Salmela et al. (2008), Farris and Sawicki (2012a) found no significant differences in the relative contributions for any joint with faster walking or with faster running. Further research is therefore needed to clarify how the human lower-limb joints modulate work and power with increasing locomotion speed.

We recently investigated human lower-limb joint work when running at steady-state speeds ranging from 3.5 to 9.0 m s^{-1} (Schache et al., 2011). Ankle positive work during stance increased by 30% when running speed progressed from 3.5 to 5.0 m s^{-1}, but it increased by only 10% from 5.0 to 9.0 m s^{-1}. In contrast, hip positive work during swing increased by 70% when running speed progressed from 7.0 to 9.0 m s^{-1}. When analyzing lower-limb muscle function during running for the same range of steady-state speeds, we found similar results (Dorn et al., 2012). Running at speeds up to 7.0 m s^{-1} was largely dependent upon using the ankle plantar flexors to push on the ground with greater force to increase stride length, whereas running at speeds above 7.0 m s^{-1} relied heavily upon using the hip flexors and extensors to increase stride

[1]Department of Mechanical Engineering, University of Melbourne, Melbourne, VIC 3010, Australia. [2]Performance Science and Innovation, Australian Institute of Sport, Belconnen, ACT 2616, Australia.

*Author for correspondence (anthonys@unimelb.edu.au)

List of symbols

$\bar{P}_j^+$	average power generated by the joint
$\bar{P}_j^-$	average power absorbed by the joint
$\bar{P}_{tot}^+$	total average power generated by the lower limb
$\bar{P}_{tot}^-$	total average power absorbed by the lower limb
W_j^+	positive work done by the joint
W_j^-	negative work done by the joint
W_{tot}^+	total positive work done by the lower limb
W_{tot}^-	total negative work done by the lower limb

rate. Based on these observations, we believe that faster running is not simply achieved by proportional increases in lower-limb joint work and power.

The aim of the present study was to investigate how the human lower-limb joints modulate work and power during locomotion on level ground for a broad range of steady-state speeds. We hypothesized that faster locomotion would not be associated with proportional increases in lower-limb joint work and power. To test this hypothesis, we calculated positive (W_j^+) and negative work done (W_j^-) as well as average (i.e. over time) power generated ($\bar{P}_j^+$) and absorbed ($\bar{P}_j^-$) by the hip, knee and ankle during both the stance and swing phases of the stride cycle. These data were then used to calculate each joint's relative contribution to the total (sum of hip, knee and ankle) amount of average power generated ($\bar{P}_{tot}^+$) (and positive work done, W_{tot}^+) by the lower limb as well as the total amount of average power absorbed ($\bar{P}_{tot}^-$) (and negative work done, W_{tot}^-) by the lower limb.

RESULTS

Group mean±1 s.d. steady-state locomotion speeds were: 1.59± 0.09 m s^{-1} (W1) and 2.01±0.08 m s^{-1} (W2) for the two walking

conditions; and 2.08±0.13 m s^{-1} (R1), 3.50±0.05 m s^{-1} (R2), 5.01± 0.11 m s^{-1} (R3), 6.99±0.09 m s^{-1} (R4) and 8.95±0.70 m s^{-1} (R5) for the five running conditions. As locomotion speed increased, joint powers generally maintained similar profiles and differed primarily in magnitude (Fig. 1). However, the hip joint power profile during early stance did change (Fig. 1, top row): a period of power generation occurred during early stance for walking (W1 and W2) and fast running (R4 and R5), whereas a period of power absorption occurred during early stance for slower running (R1, R2 and R3). When analyzing data across the entire stride cycle, both $\bar{P}_{tot}^+$ and $\bar{P}_{tot}^-$ were found to exhibit strong curvilinear relationships with locomotion speed (Fig. 2).

Net joint work

Significant linear relationships were found between locomotion speed and the net work done by the lower-limb joints during stance and swing (Fig. 3). The strongest relationships occurred at the hip and knee during swing. Specifically, net work done during swing increased with faster locomotion at the hip (W_j^+ became increasingly greater than W_j^-), whereas the opposite occurred at the knee.

Lower-limb joint work and average power during stance

The ankle was the dominant source of lower-limb W_j^+ and $\bar{P}_j^+$ during stance (Fig. 4, top row; Fig. 5, top row; Fig. 6, top left panel; supplementary material Table S1). Ankle W_j^+ and $\bar{P}_j^+$ during stance increased 4.1-fold (from 0.32±0.07 to 1.32±0.20 J kg^{-1}) and 23.0-fold (from 1.01±0.24 to 23.00±3.45 W kg^{-1}), respectively, when progressing from walking at 1.59±0.09 m s^{-1} (W1) to sprinting at 8.95±0.70 m s^{-1} (R5). Differences were observed in the way W_j^+ and $\bar{P}_j^+$ during stance responded to an increase in locomotion speed. At the hip, both parameters displayed a similar response, where they
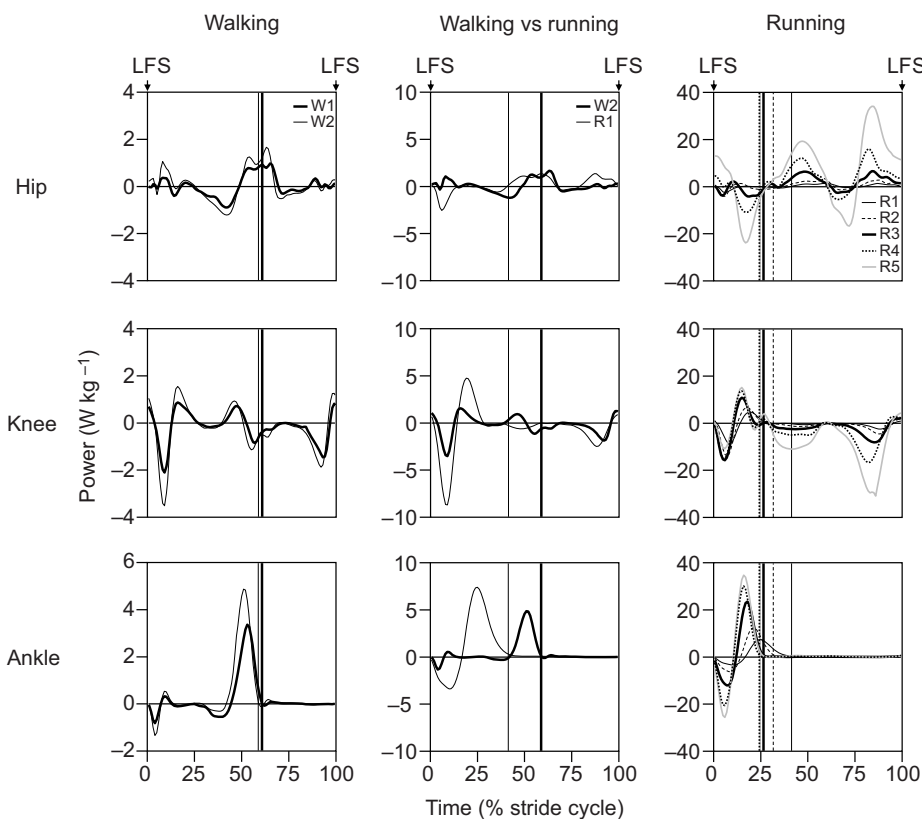

Fig. 1. Group mean power curves for the hip, knee and ankle plotted across a single stride cycle for each steady-state locomotion speed. A stride cycle is from left foot-strike (LFS) to LFS. The top row displays hip power; the middle row, knee power; and the bottom row, ankle power. The left column compares hip, knee and ankle power curves for the two steady-state walking speeds (W1=1.59±0.09 m s^{-1} versus W2=2.01± 0.08 m s^{-1}); the middle column compares hip, knee and ankle power curves for walking and running at the same steady-state speed (W2=2.01±0.08 m s^{-1} versus R1=2.08± 0.13 m s^{-1}); and the right column compares hip, knee and ankle power curves for all five steady-state running speeds (R1=2.08±0.13 m s^{-1} versus R2=3.50±0.05 m s^{-1} versus R3=5.01± 0.11 m s^{-1} versus R4=6.99±0.09 m s^{-1} versus R5=8.95±0.70 m s^{-1}). The vertical lines denote the time (% stride cycle) of toe-off for the various steady-state locomotion speeds. Note the different y-axis scales.
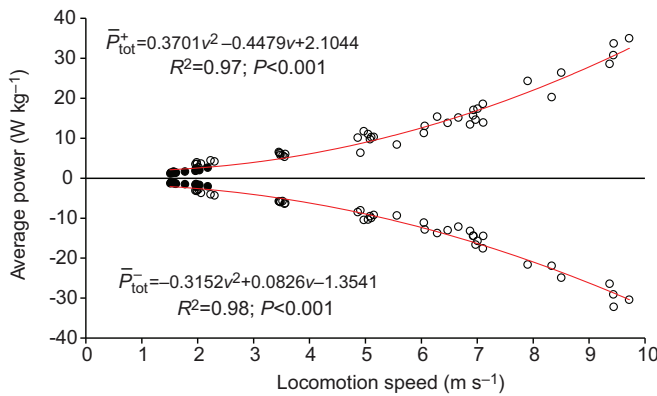
Fig. 2. The effect of steady-state locomotion speed on the total amount of average power generated and absorbed by the lower-limb joints. Total lower-limb average power generation ($\bar{P}_{tot}^{+}$) represents the sum of the average power generated ($\bar{P}_{j}^{+}$) by the hip, knee and ankle across the stride cycle, whereas total lower-limb average power absorption ($\bar{P}_{tot}^{-}$) represents the sum of the average power absorbed ($\bar{P}_{j}^{-}$) by the hip, knee and ankle across the entire stride cycle. See Materials and methods for further details. The circles represent individual participant data: filled circles indicate walking data; open circles indicate running data. The red lines show best-fit second-order polynomial functions describing the relationship between steady-state locomotion speed (v) and $\bar{P}_{tot}^{+}$ (top) as well as $\bar{P}_{tot}^{-}$ (bottom).

increased with faster walking, decreased with a change in locomotion mode, and increased with faster running (Fig. 4, top left panel; Fig. 5, top left panel). However, at the knee and ankle, W_{j}^{+} and $\bar{P}_{j}^{+}$ during stance responded differently. For example, ankle $\bar{W}_{j}^{+}$ during stance increased until a running speed of 5.01±0.11 m s^{-1} (R3) and

then plateaued thereafter at ~1.3 J kg^{-1} (Fig. 4, top right panel), whereas ankle $\bar{P}_{j}^{+}$ during stance continually increased with each increment in locomotion speed (Fig. 5, top right panel). An increase in locomotion speed significantly influenced the relative contributions from the hip and ankle (but not the knee) to $\bar{P}_{tot}^{+}$ (and W_{tot}^{+}) during stance (Fig. 6, top left panel). When switching from walking (W2) to running (R1) at the same speed, the hip's relative contribution to $\bar{P}_{tot}^{+}$ (and W_{tot}^{+}) during stance decreased from 23.0±9.7% to 5.5±4.6%, whereas the ankle's relative contribution increased from 52.7±10.4% to 65.3±7.5%. When running speed progressed from 2.08±0.13 m s^{-1} (R1) to 8.95±0.70 m s^{-1} (R5), the hip's relative contribution to $\bar{P}_{tot}^{+}$ (and W_{tot}^{+}) during stance increased from 5.5±4.6% to 22.1±5.3%.

All three joints contributed to lower-limb W_{j}^{-} and $\bar{P}_{j}^{-}$ during stance (Fig. 4, top row; Fig. 5, top row; Fig. 6, top right panel; supplementary material Table S1). Similar to W_{j}^{+} and $\bar{P}_{j}^{+}$ during stance, differences were also observed in the way W_{j}^{-} and $\bar{P}_{j}^{-}$ during stance responded to an increase in locomotion speed. At the hip, the two parameters responded similarly, increasing with each increment in locomotion speed (Fig. 4, top left panel; Fig. 5, top left panel). However, at the knee and ankle, W_{j}^{-} and $\bar{P}_{j}^{-}$ during stance responded differently. For example, ankle $\bar{W}_{j}^{-}$ during stance peaked at −0.80±0.17 J kg^{-1} when running at 6.99±0.09 m s^{-1} (R4) and then decreased to −0.77±0.17 J kg^{-1} when running at 8.95±0.70 m s^{-1} (R5) (Fig. 4, top right panel), whereas ankle $\bar{P}_{j}^{-}$ during stance increased with each increment in running speed (Fig. 5, top right panel). An increase in locomotion speed significantly influenced the relative contributions from all lower-limb joints to $\bar{P}_{tot}^{-}$ (and W_{tot}^{-}) during stance (Fig. 6, top right panel). When switching from walking (W2) to running (R1) at the same
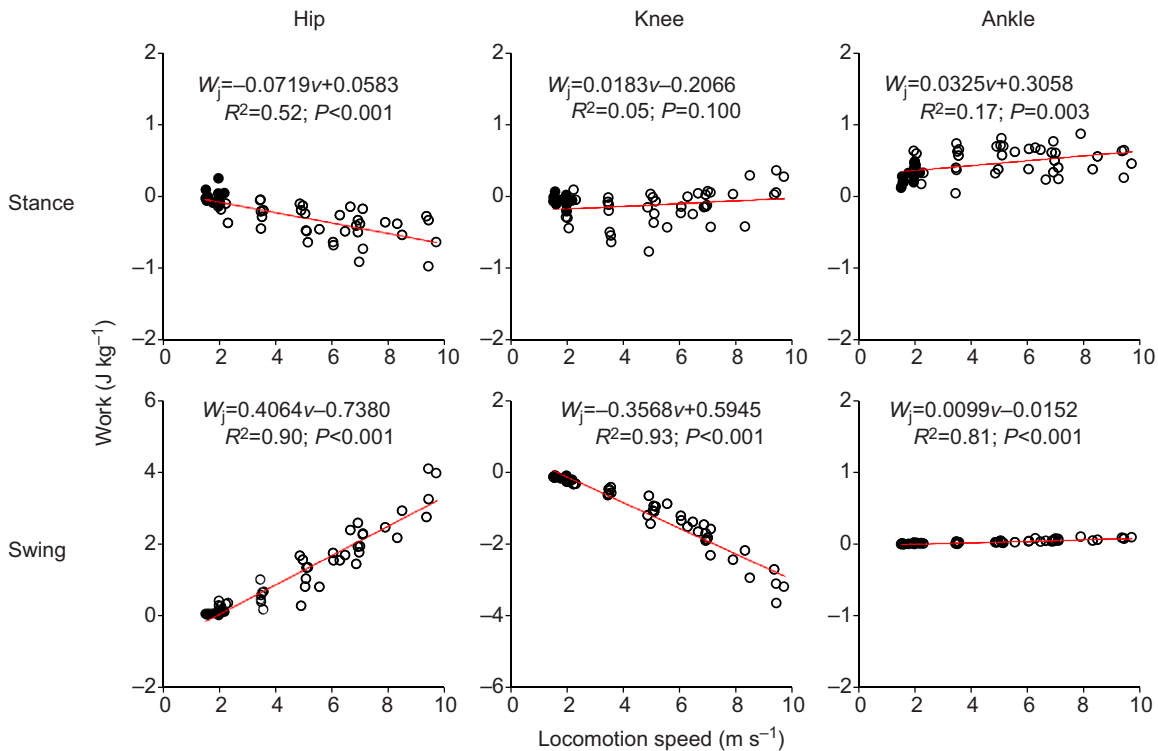

Fig. 3. The effect of steady-state locomotion speed on the net work done by the lower-limb joints. The top row displays the net work done (W_{j}) by the hip (left panel), knee (middle panel) and ankle (right panel) during stance, whereas the bottom row displays positive and negative work done by the hip (left panel), knee (middle panel) and ankle (right panel) during swing. The circles represent individual participant data: filled circles indicate walking data; open circles indicate running data. The red lines show best-fit linear regressions describing the relationship between locomotion speed (v) and net work done. Note the different y-axis scales for the bottom panels.
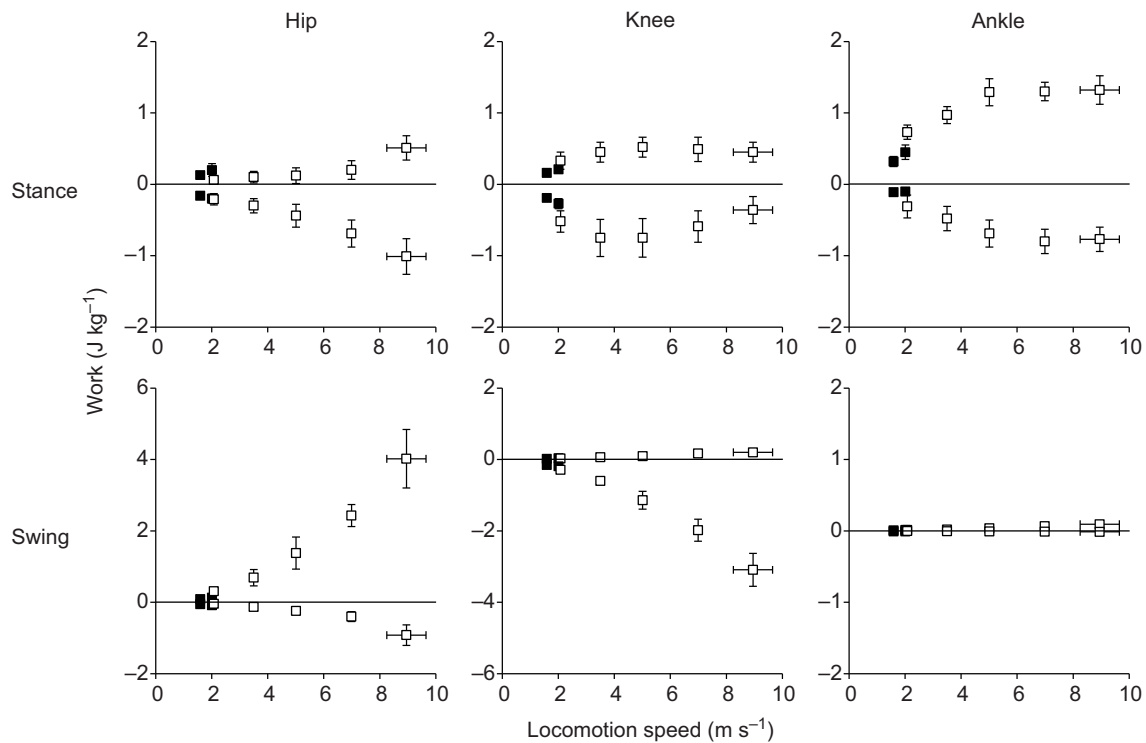
Fig. 4. The effect of steady-state locomotion speed on the work done by the lower-limb joints. The top row displays the positive and negative work done at the hip (left panel), knee (middle panel) and ankle (right panel) throughout the stance phase, whereas the bottom row displays positive and negative work done at the hip (left panel), knee (middle panel) and ankle (right panel) throughout the swing phase. The filled squares represent walking data and the open squares represent running data. Note the different y-axis scales for the bottom panels. Data are means±1s.d. but note that some of the error bars are quite small and are therefore not always discernible in the figure.

speed, the hip's relative contribution to $\bar{P}_{tot}^-$ (and W_{tot}^-) during stance decreased from 34.3±5.7% to 20.1±5.3%. When running speed progressed from 2.08±0.13 m s^{-1} (R1) to 8.95±0.70 m s^{-1} (R5), the hip's relative contribution to $\bar{P}_{tot}^-$ (and W_{tot}^-) during stance increased from 20.1±5.3% to 46.9±6.7%, whereas the knee's relative contribution decreased from 50.5±12.6% to 16.8±9.0%.

Lower-limb joint work and average power during swing
The hip was responsible for producing almost all of the lower-limb W_j^+ and $\bar{P}_j^+$ during swing (Fig. 4, bottom row; Fig. 5, bottom row; Fig. 6, bottom left panel; supplementary material Table S1). Hip W_j^+ and $\bar{P}_j^+$ during swing increased with each increment in locomotion speed. These parameters increased 44.7-fold (from 0.09±0.02 to 4.02±0.82 J kg^{-1}) and 50.1-fold (from 0.46±0.08 to 23.04±5.07 W kg^{-1}), respectively, when progressing from walking at 1.59±0.09 m s^{-1} (W1) to running at 8.95±0.70 m s^{-1} (R5). An increase in locomotion speed significantly influenced the relative contributions from all lower-limb joints to $\bar{P}_{tot}^+$ (and W_{tot}^+) during swing (Fig. 6, bottom left panel). When switching from walking (W2) to running (R1) at the same speed, the hip's relative contribution to $\bar{P}_{tot}^+$ (and W_{tot}^+) during swing increased from 70.0±6.9% to 88.2±2.8%, whereas the knee's relative contribution decreased from 22.7±7.4% to 7.5±2.4%. When running speed progressed from 2.08±0.13 m s^{-1} (R1) to 8.95±0.70 m s^{-1} (R5), the hip's relative contribution to $\bar{P}_{tot}^+$ (and W_{tot}^+) during swing increased from 88.2±2.8% to 92.8±2.6%.

The majority of the lower-limb W_j^- and $\bar{P}_j^-$ during swing occurred at the knee (Fig. 4, bottom row; Fig. 5, bottom row; Fig. 6, bottom right panel; supplementary material Table S1). Knee W_j^- and $\bar{P}_j^-$ during swing increased with each increment in locomotion

speed. These parameters increased 20.6-fold (from −0.15±0.02 to −3.09±0.46 J kg^{-1}) and 24.0-fold (from −0.74±0.12 to −17.77±3.15 W kg^{-1}), respectively, when progressing from walking at 1.59±0.09 m s^{-1} (W1) to running at 8.95±0.70 m s^{-1} (R5). An increase in locomotion speed significantly influenced the relative contributions from all lower-limb joints to $\bar{P}_{tot}^-$ (and W_{tot}^-) during swing (Fig. 6, bottom right panel). When switching from walking (W2) to running (R1) at the same speed, the hip's relative contribution to $\bar{P}_{tot}^-$ (and W_{tot}^-) during swing decreased from 28.0±6.6% to 11.4± 6.3%, whereas the knee's relative contribution increased from 69.2±6.6% to 88.0±6.3%.

DISCUSSION
The present study aimed to determine how the human lower-limb joints modulate work and power during locomotion on level ground across a broad range of steady-state speeds. We hypothesized that proportional increases in lower-limb joint work and power would not be observed with faster locomotion. This hypothesis was generally supported by our results.

Increasing steady-state walking speed
Previous studies have reported that when humans walk at faster steady-state speeds they do so by increasing hip W_j^+ (Chen et al., 1997; Teixeira-Salmela et al., 2008; Pires et al., 2014) and knee W_j^- (Winter, 1983a; Chen et al., 1997; Teixeira-Salmela et al., 2008; Pires et al., 2014), which is consistent with our findings (Fig. 1, left column; Fig. 4). With respect to the ankle, we observed a 40% (0.13 J kg^{-1}) increase in W_j^+ during stance when walking speed changed from 1.59±0.09 m s^{-1} (W1) to 2.01±0.08 m s^{-1} (W2), whereas W_j^- during stance remained of a similar magnitude (Fig. 1;
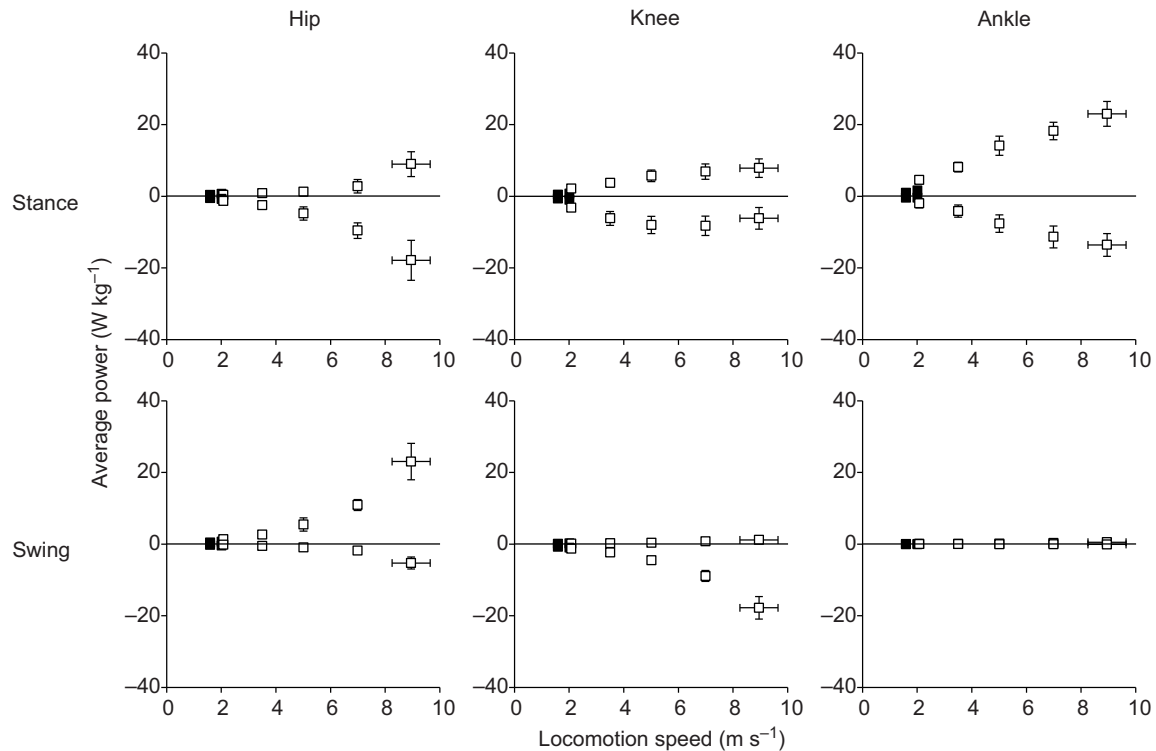
Fig. 5. The effect of steady-state locomotion speed on the average power generated and absorbed by the lower-limb joints. The average power generated by a given joint during stance (or swing) represents the positive work done by that joint during stance (or swing) divided by the stance time (or swing time) multiplied by two. Similarly, the average power absorbed by a given joint during stance (or swing) represents the negative work done by that joint during stance (or swing) divided by the stance time (or swing time) multiplied by two. See Materials and methods further details. The top row displays the average power generated and absorbed by the hip (left panel), knee (middle panel) and ankle (right panel) throughout the stance phase, whereas the bottom row displays the average power generated and absorbed by the hip (left panel), knee (middle panel) and ankle (right panel) throughout the swing phase. The filled squares represent walking data and the open squares represent running data. Data are means±1s.d. but note that some of the error bars are quite small and are therefore not always discernible in the figure.

left column; Fig. 4, top row). Several other studies have reported similar findings (Winter, 1983a; Hreljac et al., 2008; Teixeira-Salmela et al., 2008; Pires et al., 2014). Such behavior suggests that the probable source of the increased ankle W_j^+ during stance with faster walking is greater positive work done by muscles rather than enhanced utilization of elastic strain energy.

Relative contributions from each joint to $\bar{P}_{tot}^+$ (and W_{tot}^+) as well as $\bar{P}_{tot}^-$ (and W_{tot}^-) during walking from the present study are generally consistent with previously reported data. For example, when calculating data for the entire stride cycle, we found the relative contributions from the hip, knee and ankle towards $\bar{P}_{tot}^+$ (and W_{tot}^+) to be 31%, 24% and 45%, respectively, when walking at 1.59± 0.09 m s^{-1} (W1). Teixeira-Salmela et al. (2008) reported relative contributions of 38%, 19% and 44% for the hip, knee and ankle, respectively, for walking at 1.42±0.22 m s^{-1}, while Farris and Sawicki (2012a) reported relative contributions of 42%, 17% and 41% for the hip, knee and ankle, respectively, for walking at 1.75 m s^{-1}. We did not find any of the relative contributions to significantly change with an increase in walking speed during stance or swing (Fig. 6). Thus, overall, faster walking appears to be achieved by proportional increases in lower-limb joint work and average power. While other studies have also evaluated the effect of increasing walking speed on the relative contributions from each joint towards $\bar{P}_{tot}^+$ (and W_{tot}^+) or $\bar{P}_{tot}^-$ (and W_{tot}^-) (Teixeira-Salmela et al., 2008; Farris and Sawicki, 2012a), these studies did not report data for stance and swing separately, making it difficult to compare their findings with those from the present study.

The effect of increasing walking speed on joint work and power has also been explored in other terrestrial animals. For example, Khumsap et al. (2001) measured hindlimb joint kinetics during stance in five clinically sound horses walking at speeds ranging from 0.90 m s^{-1} (slow) to 1.72 m s^{-1} (fast). With faster walking, they found hip W_j^+ during early stance to increase by ∼50%, which is similar to what we observed in the present study for humans. Khumsap et al. (2001) also reported tarsus W_j^+ and W_j^- during stance to increase with faster walking. The equivalent lower-limb joint in humans is the ankle, and we too found ankle W_j^+ to increase with faster walking. However, in contrast to what was observed for the horse tarsus by Khumsap et al. (2001), ankle W_j^- during stance seems to remain independent of walking speed (Winter, 1983a; Hreljac et al., 2008; Teixeira-Salmela et al., 2008; Pires et al., 2014). It is possible that enhanced utilization of elastic strain energy with faster walking is less of a priority for the human ankle compared with the horse tarsus.

Walking versus running at the same steady-state speed
A change in locomotion mode influenced lower-limb joint work and average power. At the hip, the joint power profile during early stance changed from power generation during walking to power absorption during running (Fig. 1, middle column). Hip W_j^+ decreased by 0.14 J kg^{-1} during stance, whereas it increased by 0.18 J kg^{-1} during swing (Fig. 4). Knee joint work during stance increased (Fig. 1, middle column; Fig. 4, top row), with the increase in W_j^- (0.25 J kg^{-1}) exceeding the increase in W_j^+ (0.12 J kg^{-1}). Ankle
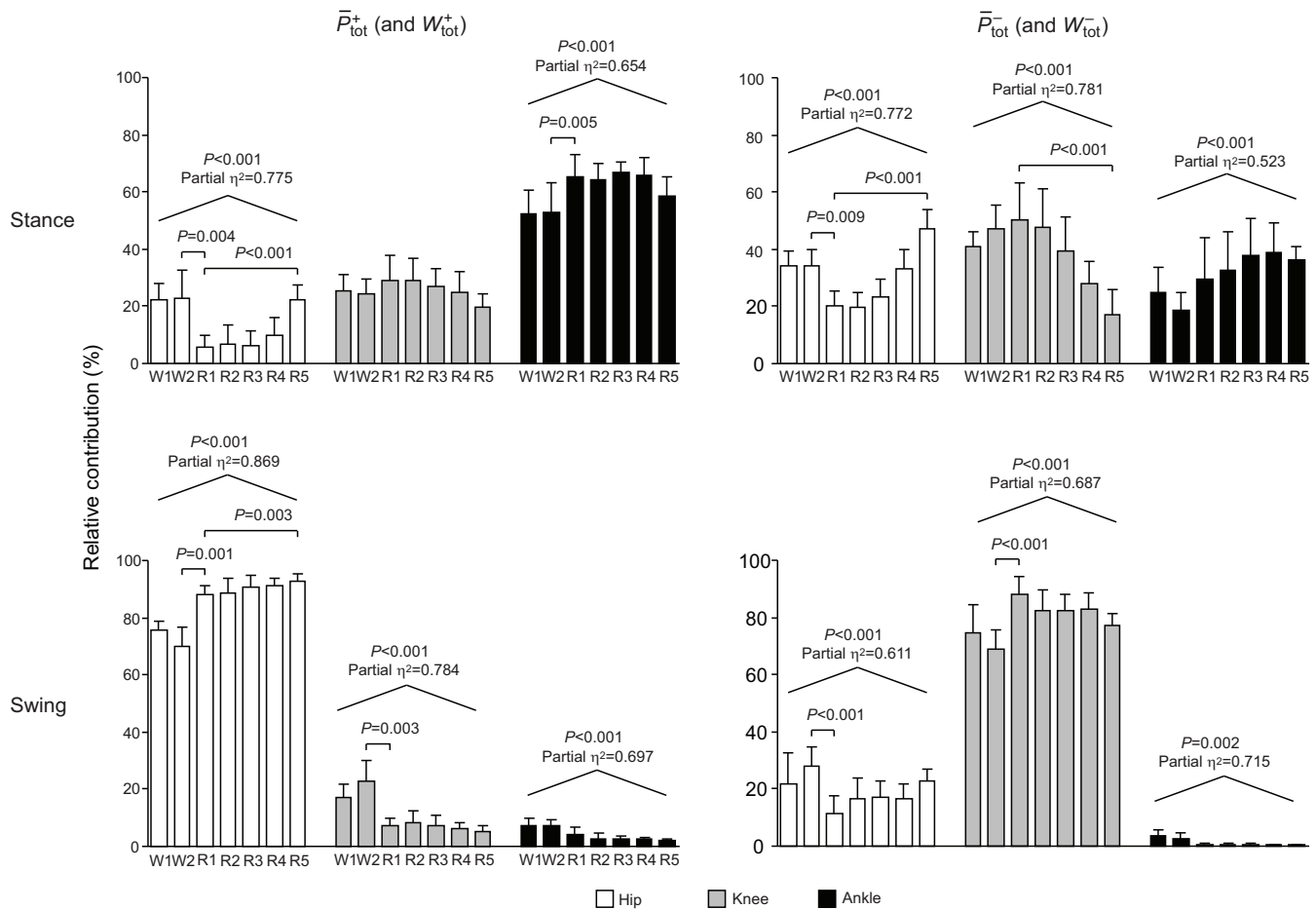
Fig. 6. Relative contributions from the hip, knee and ankle towards the total amount of average power generated ($\bar{P}^+_{tot}$) (and positive work done, W^+_{tot}), as well as the total amount of average power absorbed ($\bar{P}^-_{tot}$) (and negative work done, W^-_{tot}) by the lower limb joints. Contributions to $\bar{P}^+_{tot}$ (and W^+_{tot}; left column) and $\bar{P}^-_{tot}$ (and W^-_{tot}; right column) by the lower limb joints are shown during the stance phase (top row) and the swing phase (bottom row) for all steady-state locomotion speeds. Data are means±s.d. Steady-state locomotion speeds are: W1, walking at 1.59±0.09 m s⁻¹; W2, walking at 2.01±0.08 m s⁻¹; R1, running at 2.08±0.13 m s⁻¹; R2, running at 3.50±0.05 m s⁻¹; R3, running at 5.01±0.11 m s⁻¹; R4, running at 6.99±0.09 m s⁻¹; and R5, running at 8.95±0.70 m s⁻¹. Significant main effects for steady-state locomotion speed at each joint are indicated by the angled lines at the top of the figure. For the joints displaying a significant main effect, the results from the *post hoc* paired *t*-tests of interest (W1 versus W2 – increase in walking speed; W2 versus R1 – switch from walking to running; R1 versus R5 – increase in running speed) are indicated by the horizontal lines with the associated *P*-values. Note that, despite the presence of a significant (*P*<0.01) main effect from the ANOVA tests, none of the *post hoc* paired *t*-tests of interest were found to be significant for the relative contribution from the ankle to: (i) $\bar{P}^+_{tot}$ (and W^+_{tot}) during the swing phase; (ii) $\bar{P}^-_{tot}$ (and W^-_{tot}) during the stance phase; and (iii) $\bar{P}^-_{tot}$ (and W^-_{tot}) during the swing phase (*P*>0.012, all cases).

joint work during stance increased too (Fig. 1, middle column; Fig. 4, top row), but in contrast to what occurred at the knee, the increase in W^-_j (0.21 J kg⁻¹) was less than the increase in W^+_j (0.28 J kg⁻¹). Our results are generally consistent with what has been reported by other studies that have used an inverse-dynamics approach to explore the walk-to-run transition in humans (Hreljac et al., 2008; Pires et al., 2014). For example, when switching from walking to running at the preferred transition speed, Pires et al. (2014) found hip W^+_j during stance to decrease from 0.14 to 0.04 J kg⁻¹ and ankle W^+_j during stance to increase from 0.45 to 0.80 J kg⁻¹. These data are virtually identical to the results of the present study (Fig. 4, top row; supplementary material Table S1).

Farris and Sawicki (2012a) investigated the effect of switching from walking to running at the same steady-state speed (2.0 m s⁻¹) on the relative contributions from each joint towards $\bar{P}^+_{tot}$ across the entire stride cycle. They found the hip's contribution to significantly decrease (from 44% to 32%) and the ankle's contribution to significantly increase (from 39% to 47%). We have expanded upon these findings by reporting: (1) the relative contributions from each

joint towards $\bar{P}^+_{tot}$ (and W^+_{tot}) for stance and swing separately (given that previous studies have demonstrated that at least 70% of the total metabolic cost during locomotion is attributable to stance-phase muscle actions; Gottschall and Kram, 2005; Modica and Kram, 2005; Umberger, 2010); and (2) the relative contributions from each joint towards $\bar{P}^-_{tot}$ (and W^-_{tot}). The relative contributions from each joint were influenced by a change in locomotion mode, especially for the hip (Fig. 6). For example, when switching from walking at 2.01±0.08 m s⁻¹ to running at 2.08±0.13 m s⁻¹, the relative contribution towards $\bar{P}^+_{tot}$ (and W^+_{tot}) during stance significantly decreased at the hip (from 23.0±9.7% to 5.5±4.6%) and significantly increased at the ankle (from 52.7±10.4% to 65.3± 7.5%). Significant differences were also evident for the relative contributions from each joint towards $\bar{P}^+_{tot}$ (and W^+_{tot}) during swing as well as $\bar{P}^-_{tot}$ (and W^-_{tot}) during stance and swing (Fig. 6). These results therefore demonstrate that a change in locomotion mode in humans is not simply achieved via proportional increases in lower-limb joint work and average power, consistent with our main hypothesis.

Our results indicate that humans switch from walking to running by primarily increasing the amount of work done at the knee and ankle during stance. A characteristic pattern in the joint power profile was observed for these two joints, i.e. a period of W_j^- preceding a period of W_j^+ (Fig. 1, middle row). Knee and ankle W_j^- during stance increased 1.9-fold and 3.1-fold, respectively, when switching from walking to running at the same steady-state speed, whereas knee and ankle W_j^+ during stance increased by only 1.6-fold. Does the increase in knee and ankle W_j^- during stance when switching to a running gait reflect enhanced utilization of elastic strain energy? Evidence is available to support this proposition. For example, studies using biomechanical models to predict tendon elastic strain energy in the human lower limb during locomotion have found the storage of elastic strain energy to be greater for slow running compared with fast walking (Sasaki and Neptune, 2006; Farris and Sawicki, 2012b). Furthermore, Cronin et al. (2013) demonstrated that ankle W_j^- during the midstance phase of walking does provide a reasonable estimate of the period when muscle–tendon unit lengthening occurs for the major ankle plantar flexors (soleus and medial gastrocnemius). Because the soleus and medial gastrocnemius muscle fascicles operate isometrically at this time, ankle plantar flexor muscle–tendon lengthening (and thus ankle W_j^-) must be largely attributable to stretch of elastic structures. Consequently, we suggest that the greater knee and ankle W_j^- during stance for running compared with walking at the same steady-state speed observed in the present study reflects (at least in part) increased storage of elastic strain energy in the musculotendon structures surrounding these joints.

Increasing steady-state running speed

When running speed progressed from 2.01±0.08 m s^{-1} (R1) to 8.95±0.70 m s^{-1} (R5), hip W_j^+ and $\bar{P}_j^+$ during swing increased 13.0-fold and 17.2-fold, respectively, and the absolute magnitude of knee W_j^- and $\bar{P}_j^-$ during swing increased 10.7-fold and 14.2-fold, respectively (Figs 4, 5; supplementary material Table S1). Ankle $\bar{P}_j^+$ during stance increased 5.0-fold, but because of decreasing ground contact times, ankle W_j^+ peaked at a running speed of 5.01±0.11 m s^{-1} and plateaued at ~1.3 J kg^{-1} thereafter. These results generally concur with previous findings. For example, Ae et al. (1987) also measured lower-limb joint work for a similar range of steady-state running speeds. While joint work was not calculated for stance and swing separately, they found hip W_j^+ increased 8.5-fold and the absolute magnitude of knee W_j^- increased 4.0-fold when running speed progressed from 2.68 to 9.59 m s^{-1}. Overall, ankle W_j^+ and $\bar{P}_j^+$ during stance would appear to be the dominant mechanism for initially increasing steady-state running speed, but once ankle W_j^+ during stance is maximized around 5.01±0.11 m s^{-1}, then hip W_j^+ and $\bar{P}_j^+$ during swing becomes the dominant mechanism for increasing steady-state running speed towards maximal sprinting.

We found the ankle to provide between 58.3% and 67.0% of $\bar{P}_{tot}^+$ (and W_{tot}^+) during stance across all steady-state running speeds in the present study (Fig. 6, top left panel). This result is quantitatively consistent with that of Stearne et al. (2014), who reported a relative contribution of ~70% for the ankle when running on a treadmill at 4.5 m s^{-1}. However, Rubenson et al. (2011) found the ankle to contribute only one-third of $\bar{P}_{tot}^+$ (and W_{tot}^+) during stance when running over ground at 3.25±0.37 m s^{-1}. It would appear that this disparity is because the participants from the study by Rubenson et al. (2011) ran with reduced ankle W_j^+ relative to the participants in this study, as $\bar{P}_{tot}^+$ across the stride cycle from Rubenson et al. (2011) (~4.8 W kg^{-1}) was similar to that from the present study for

a comparable running speed (6.0±0.4 W kg^{-1} when running at 3.50±0.05 m s^{-1}; see data in Fig. 2). This disparity could be explained by differences in participant characteristics (e.g. recreational versus elite athletes) and/or laboratory configuration. Farris and Sawicki (2012a) also reported relative contributions from each joint to $\bar{P}_{tot}^+$ (and W_{tot}^+) for steady-state running speeds ranging from 2.0 to 3.25 m s^{-1}. Unfortunately, as these authors did not calculate data for stance and swing separately, we cannot compare their results with those from the present study.

With faster running, we found the hip to contribute a significantly greater proportion of $\bar{P}_{tot}^+$ (and W_{tot}^+) during both stance and swing (Fig. 6, left column), whereas the knee and ankle relative contributions did not significantly differ. We also observed that as running speed increased there was a significant shift in the distribution of W_j^- and $\bar{P}_j^-$ amongst the lower-limb joints during stance, whereby the hip's relative contribution towards $\bar{P}_{tot}^-$ (and W_{tot}^-) during stance significantly increased and the knee's relative contribution towards $\bar{P}_{tot}^-$ (and W_{tot}^-) during stance significantly decreased (Fig. 6, top right panel). In other words, with faster running, the energy absorbed by the hip flexors during late stance became greater than the energy absorbed by the knee extensors during early stance. These findings demonstrate that increased steady-state running speed is not achieved by a proportional increase in lower-limb joint work and average power, in support of our primary hypothesis.

It is interesting to compare our data for human running with equivalent data from studies that have investigated the effect of increasing trotting and/or galloping speeds on hindlimb joint mechanics for quadrupedal terrestrials, such as horses (Clayton et al., 2002; Dutto et al., 2006), goats (Arnold et al., 2013) and dogs (Colborne et al., 2006). While the mechanical behavior of a distal joint such as the ankle (or tarsus) is similar for quadrupeds and humans (i.e. a period of W_j^- during early stance followed by a period of W_j^+ during late stance, both of which increase in magnitude with faster speed), distinct differences are evident in the mechanical behavior of a proximal joint such as the hip, especially during stance. For quadrupeds, power is generated and positive work is done by the hindlimb hip for the majority of stance, although this profile appears more accentuated for horses (Dutto et al., 2006) and dogs (Colborne et al., 2006) than for goats (Arnold et al., 2013). As trotting or galloping speed becomes faster, peak hip power generation during stance increases substantially (Colborne et al., 2006; Dutto et al., 2006; Arnold et al., 2013); thus, the hip extensors are important muscles for powering quadrupedal locomotion. In contrast, for humans, the hip generates power during early stance before absorbing a larger amount of power in late stance (Fig. 1, right column). Net work done by the human hip is therefore negative during stance (opposite to quadrupeds) and it increases in absolute magnitude with faster running (Figs 3, 4, top left panel). Hence, the quadrupedal hindlimb hip is a power generator during stance when trotting at a steady-state speed, whereas the human hip is biased towards power absorption during stance when running at a steady-state speed. This difference is likely due to the trunk (and thus center of mass) being located in front of the hindlimb hip for quadrupeds but remaining predominantly above the hip for humans.

Increasing running speed can be achieved by: (1) pushing on the ground with greater force; (2) pushing on the ground more frequently; or (3) a combination of these two strategies (Schache et al., 2014). Which strategy has the greatest influence on determining maximum sprinting speed? Evidence provided by Weyand and co-workers (2000, 2010; Clark and Weyand, 2014)

would suggest that it is a ground force production issue. While our experiment was not specifically designed to evaluate the mechanical limitations of maximal sprinting, our data do lend some support to this conclusion. The ankle plantar flexors generate the bulk of the vertical and propulsive ground forces needed to accelerate the body's center of mass upwards and forwards, respectively, when running (Dorn et al., 2012; Hamner and Delp, 2013; Debaere et al., 2015). We therefore plotted the peak ankle plantar flexor moment during stance versus locomotion speed for all participants and fitted a non-linear regression equation (quadratic polynomial) to the data (Fig. 7). The peak ankle plantar flexor moment reached a maximal limit at a running speed of ~ 7 m s^{-1}. We also found that even though ankle $\bar{P}_j^+$ during stance continually increased with faster running (Fig. 5, top right panel), it did not propagate to greater ankle W_j^+ at the fastest running speeds because of decreasing ground contact times. Ankle W_j^+ during stance peaked at 5.01 ± 0.11 m s^{-1} and plateaued at ~ 1.3 J kg^{-1} thereafter (Fig. 4, top right panel). In contrast, we found that hip $\bar{P}_j^+$ and W_j^+ during swing continually increased with faster running (Figs 4, 5, bottom left panels), which we believe implies that the ability of the hip flexors and extensors to swing the lower limbs faster does not become limited.

Limitations

The present study is associated with several limitations that ought to be acknowledged. First, we used inverse dynamics to calculate lower-limb joint work and average power. It should be understood that work and power data for a given joint represent the net effect of all the muscle–tendon units and passive structures (e.g. ligament and joint capsule) spanning the joint as well as the contact forces at the joint (Farley and Ferris, 1998). Consequently, the work and power derived from the lower-limb resultant joint moments may not necessarily reflect the work and power of individual muscles, as has been previously demonstrated for human walking (Sasaki et al., 2009). Second, analyses were based upon a single trial per locomotion condition for each participant. Multiple attempts were usually completed before a successful trial for a given locomotion condition was obtained. It has been previously demonstrated that fatigue can influence running mechanics (Sprague and Mann, 1983; Nummela et al., 1994; Pinniger et al., 2000; Girard et al., 2011); hence, we monitored the number of trials completed per locomotion condition in an effort to avoid this effect as much as possible. For example, the total number of trials (successful and unsuccessful)
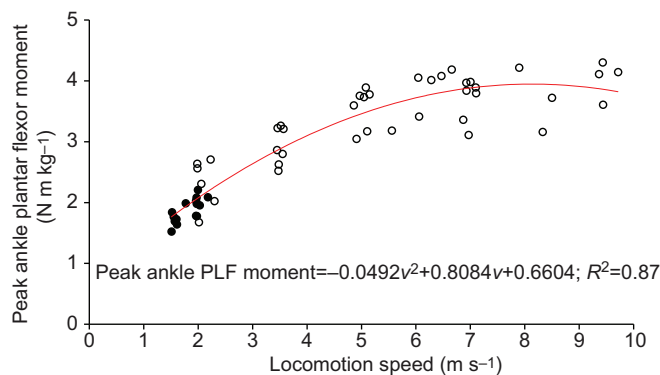
completed by each participant when sprinting (R5) was no more than four. While we acknowledge that a single trial may not adequately represent the generalized performance, we do not believe that this limitation is a substantial issue in the present study. All participants performed a continuous activity to which they were well accustomed. Moreover, we evaluated the inter-trial variability for one of the participants for whom we were able to capture two sprinting trials at an equivalent speed, and data were found to be consistent (Fig. 8). Third, data in this study were obtained from a relatively small number of participants that differed in age, body mass and sex. Nevertheless, all participants were experienced sprinting athletes. While a larger cohort would facilitate generalization of our results, participants did appear to respond to an increase in locomotion speed in a consistent manner. For example, the individual participant data for $\bar{P}_{tot}^+$ and $\bar{P}_{tot}^-$ across the stride cycle displayed very little spread away from the trend line (Fig. 2). It is not envisaged that a larger cohort would have altered our main conclusions.

Conclusions

We investigated how the human lower-limb joints modulate work and power during locomotion on level ground across a broad range of steady-state speeds. Overall, our data indicate that faster locomotion speeds are not achieved by proportional increases in lower-limb joint work and average power. Instead, ankle W_j^+ during
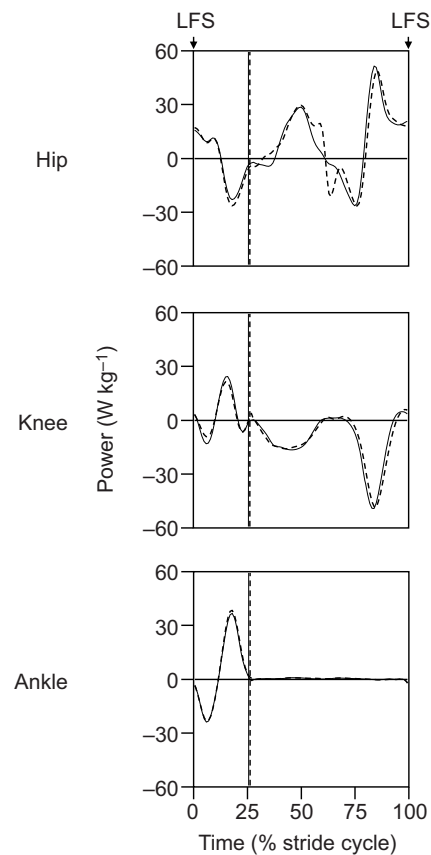
Fig. 8. Lower-limb joint power plotted across a single stride cycle for two separate sprinting trials collected from a single participant. A stride cycle is from LFS to LFS. The running speed for both trials was 9.44 m s^{-1}. The top panel displays hip joint power; the middle panel, knee joint power; and the bottom panel, ankle joint power. The vertical lines denote the time (% stride cycle) of toe-off.

Fig. 7. The effect of steady-state locomotion speed on the peak ankle plantar flexor moment during stance. The circles represent individual participant data: filled circles indicate walking data; open circles indicate running data. The red lines show best-fit second-order polynomial functions describing the relationship between steady-state locomotion speed (v) and the peak ankle plantar flexor (PLF) moment.

Peak ankle PLF moment$=-0.0492v^2+0.8084v+0.6604$; $R^2=0.87$

stance is prioritized when progressing from walking to moderate speeds of running (~5 m s^{-1}), after which hip W_j^+ during swing is prioritized when progressing to sprinting.

MATERIALS AND METHODS

Participants

Seven adult participants were voluntarily recruited for this study. All participants were experienced sprinting athletes and were free from any musculoskeletal injury likely to influence their usual running mechanics. Five men and two women were included, with body mass ranging from 63.0 to 87.4 kg (mean±1 s.d.=74.4±8.2 kg), height ranging from 170.3 to 185.5 cm (177.9±5.6 cm) and age ranging from 19.1 to 42.7 years (26.6± 8.3 years). Ethical approval was obtained from The University of Melbourne and The Australian Institute of Sport.

Experimental data collection

Experimental data were collected while participants walked and ran on an indoor 110 m synthetic running track. A broad range of steady-state locomotion speeds were prescribed *a priori*: walking at a self-selected speed (W1); walking at 2.0 m s^{-1} (W2); running at 2.0 m s^{-1} (R1); running at 3.5 m s^{-1} (R2); running at 5.0 m s^{-1} (R3); running at 7.0 m s^{-1} (R4); maximum sprinting (R5). The locomotion conditions were performed in an incremental order. Locomotion speed over a 20 m distance in the middle of the measurement volume was monitored via timing gates (Speedlight Telemetry Timing, Swift Performance Equipment, Walcol, Australia). Participants were instructed to maintain a constant locomotion speed when moving through the measurement volume. They were allowed to self-select their foot-strike pattern. After each trial, verbal feedback was provided to the participant regarding their recorded locomotion speed. If the desired speed was not achieved, then the participant adjusted their speed accordingly for the next trial. Participants typically required multiple trials per locomotion condition in order to generate at least one trial that was within ±15% of the desired speed. The mean±1 s.d. number of trials completed for both walking conditions was 8.6±1.4, whereas the mean±1 s.d. number of trials completed for all five running conditions was 24.7±2.8.

Hip, knee and ankle joint motions were quantified by recording the three-dimensional trajectories of markers mounted on the pelvis and left lower limb (thigh, shank and foot). Details regarding the specific locations of the markers and the defined biomechanical model can be found elsewhere (Schache et al., 2011). All participants wore running sandals (NIKE Straprunner IV, Beaverton, OR, USA) during testing so that foot markers could be mounted directly on the skin rather than on the outer sole of a shoe. Marker trajectories were recorded using a VICON motion analysis system (Oxford Metrics Ltd, Oxford, UK) with 22 cameras sampling at a rate of 250 Hz. Kinematic data were digitally filtered using a zero-lag fourth-order Butterworth filter (Winter, 2009) with a cut-off frequency of 10 Hz.

Eight force platforms (Kistler Instrument Corp., Amherst, NY, USA) were used to record ground reaction force data. The force platforms were embedded in the laboratory floor in the middle of the measurement volume, and were covered with synthetic running track to disguise their location. Force signals were sampled at 1500 Hz, and were digitally filtered using a zero-lag fourth-order Butterworth filter (Winter, 2009). The chosen cut-off frequency was 10 Hz so as to match that applied to the kinematic data, a procedure that is consistent with published recommendations (Bisseling and Hof, 2006; Kristianslund et al., 2012; Bezodis et al., 2013).

Data analysis

For each participant, a single successful trial at each locomotion speed was identified for analysis. A successful trial was deemed to be one that: (1) contained a complete stride cycle for the left lower limb (i.e. from left foot-strike to the next left foot-strike) with ground contacts occurring in the middle of the force platforms; and (2) was within ±15% of the desired speed (for W2, R1, R2, R3 and R4). Unfortunately, for many participants, we were unable to obtain more than one successful trial at the faster running speeds. In addition to the prescribed speeds, for six participants, we were also able to source another trial from the dataset where the steady-state running speed was between 5.56 and 6.66 m s^{-1}. These additional trials were only

included in plots containing individual participant data (i.e. Figs 2, 3 and 7). In order to determine whether a single trial was likely representative of a given participant's typical motion at a particular steady-state speed, we evaluated inter-trial data variability for one participant from whom we were able to obtain two successful sprinting trials at 9.44 m s^{-1}. Because of larger amplitude joint motions and increased soft-tissue artifact, we expected inter-trial data variability for sprinting to represent a worst-case estimate. Furthermore, we assumed that inter-trial data variability was not substantially different in magnitude amongst the participants given that they were all experienced sprinting athletes.

A standard inverse-dynamics analysis (Winter, 2009) was used to calculate the internal moments developed at the hip, knee and ankle joints for the left lower limb. Body-segment inertial properties were estimated using equations based on segment length and body mass (de Leva, 1996). Mechanical power was calculated using a method similar to that which has been adopted previously (Umberger and Martin, 2007; Rubenson and Marsh, 2009; Rubenson et al., 2011; Farris and Sawicki, 2012a; Stearne et al., 2014). The method involved three steps. First, for each lower-limb joint, the net power across all three planes was determined by taking the product of the net joint moment and joint angular velocity. Net joint power data for each participant were normalized to body mass (W kg^{-1}). Second, the normalized net joint power data were integrated over the duration of the stride cycle to calculate the work done (J kg^{-1}). All periods of positive and negative work were summed independently to determine the overall amount of W_j^+ and W_j^-, respectively. The sum of W_j^+ and W_j^- represented the net work done by a given joint. W_{tot}^+ was calculated as the sum of W_j^+ at the hip, knee and ankle, whereas W_{tot}^- was calculated as the sum of W_j^- at the hip, knee and ankle. Third, W_j^+ and W_j^- were doubled to approximate the output from both lower limbs (assuming symmetry) and then divided by the stride cycle time to determine $\bar{P}_j^+$ and $\bar{P}_j^-$, respectively. $\bar{P}_{tot}^+$ was calculated as the sum of $\bar{P}_j^+$ at the hip, knee and ankle, whereas $\bar{P}_{tot}^-$ was calculated as the sum of $\bar{P}_j^-$ at the hip, knee and ankle.

Previous studies have demonstrated that differences exist in the metabolic cost associated with stance versus swing phase muscle actions during human walking and running, with at least 70% of the total metabolic cost attributable to stance phase muscle actions (Gottschall and Kram, 2005; Modica and Kram, 2005; Umberger, 2010). We therefore calculated all parameters of interest for stance and swing separately. To do so, the second and third steps described above were repeated, except in this instance the time period of interest was stance or swing rather than the entire stride cycle. In order to determine whether or not a change in steady-state locomotion speed influenced the relative contributions of each joint towards $\bar{P}_{tot}^+$ and $\bar{P}_{tot}^-$, we expressed $\bar{P}_j^+$ and $\bar{P}_j^-$ at each joint as a percentage of $\bar{P}_{tot}^+$ and $\bar{P}_{tot}^-$, respectively, for stance and swing separately. Note that these relative contributions are equivalent to those obtained by expressing W_j^+ and W_j^- at each joint as a percentage of W_{tot}^+ and W_{tot}^-, respectively.

Net joint power data for each participant were time normalized as a percentage (0–100%) of a single stride cycle. These data were averaged across participants to generate group mean curves for net joint power at the hip, knee and ankle for each locomotion condition. To evaluate inter-trial data variability, we compared the joint power curves for two separate sprinting trials from a single participant. The ankle and knee joint power curves were virtually identical in profile, whereas variability in the hip joint power curves was evident around mid-swing (Fig. 8). The root-mean-square of the difference between the joint power curves was 5.87, 3.06 and 0.63 W kg^{-1} for the hip, knee and ankle, respectively.

To quantify how $\bar{P}_{tot}^+$ and $\bar{P}_{tot}^-$ across the stride cycle varied with locomotion speed, we fitted non-linear regression equations (quadratic polynomials) to each set of data. To quantify how net work done varied with locomotion speed, we fitted linear regression equations to each set of data. In both instances, goodness of fit was assessed by the coefficient of determination, R^2. One-way repeated-measures ANOVA tests were used to determine whether steady-state locomotion speed had a significant effect on the relative contributions from each joint towards $\bar{P}_{tot}^+$ (and W_{tot}^+) as well as $\bar{P}_{tot}^-$ (and W_{tot}^-) during stance and swing. Where a significant main effect was found, *post hoc* paired *t*-tests were used to determine which locomotion speeds were significantly different from each other. We were specifically interested in the following three *post hoc* comparisons: W1 versus W2

(increase in walking speed); W2 versus R1 (change in locomotion mode); R1 versus R5 (increase in running speed). All statistical tests were performed using IBM SPSS Statistics version 20 (IBM Corporation, Armonk, NY, USA). A conservative level of significance was set at $P<0.01$ given the number of statistical comparisons performed.

Supplementary material
Supplementary material available online at
http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.119156/-/DC1

References
Ae, M., Miyashita, K., Yokoi, T. and Hashihara, Y. (1987). Mechanical power and work done by the muscles of the lower limb during running at different speeds. In *Biomechanics X-B*, Vol. 6B (ed. B. Jonsson), pp. 895-899. Champaign, IL: Human Kinetics Publishers, Inc.

Arnold, A. S., Lee, D. V. and Biewener, A. A. (2013). Modulation of joint moments and work in the goat hindlimb with locomotor speed and surface grade. *J. Exp. Biol.* **216**, 2201-2212.

Belli, A., Kyrolainen, H. and Komi, P. V. (2002). Moment and power of lower limb joints in running. *Int. J. Sports Med.* **23**, 136-141.

Bezodis, N. E., Salo, A. I. T. and Trewartha, G. (2013). Excessive fluctuations in knee joint moments during early stance in sprinting are caused by digital filtering procedures. *Gait Posture* **38**, 653-657.

Bisseling, R. W. and Hof, A. L. (2006). Handling of impact forces in inverse dynamics. *J. Biomech.* **39**, 2438-2444.

Chen, I. H., Kuo, K. N. and Andriacchi, T. P. (1997). The influence of walking speed on mechanical joint power during gait. *Gait Posture* **6**, 171-176.

Clark, K. P. and Weyand, P. G. (2014). Are running speeds maximized with simple-spring stance mechanics? *J. Appl. Physiol.* **117**, 604-615.

Clayton, H. M., Hoyt, D. F., Wickler, S. J., Cogger, E. A. and Lanovaz, J. L. (2002). Hindlimb net joint energies during swing phase as a function of trotting velocity. *Equine Vet. J. Suppl.* **34**, 363-367.

Colborne, G. R., Walker, A. M., Tattersall, A. J. and Fuller, C. J. (2006). Effect of trotting velocity on work patterns of the hind limbs of Greyhounds. *Am. J. Vet. Res.* **67**, 1293-1298.

Cronin, N. J., Prilutsky, B. I., Lichtwark, G. A. and Maas, M. (2013). Does ankle joint power reflect type of muscle action of soleus and gastrocnemius during walking in cats and humans? *J. Biomech.* **46**, 1383-1386.

de Leva, P. (1996). Adjustments to Zatsiorsky-Seluyanov's segment inertia parameters. *J. Biomech.* **29**, 1223-1230.

Debaere, S., Delecluse, C., Aerenhouts, D., Hagman, F. and Jonkers, I. (2015). Control of propulsion and body lift during the first two stances of sprint running: a simulation study. *J. Sports Sci.* doi:10.1080/02640414.2015.1026375.

Dorn, T. W., Schache, A. G. and Pandy, M. G. (2012). Muscular strategy shift in human running: dependence of running speed on hip and ankle muscle performance. *J. Exp. Biol.* **215**, 1944-1956.

Dutto, D. J., Hoyt, D. F., Clayton, H. M., Cogger, E. A. and Wickler, S. J. (2006). Joint work and power for both the forelimb and hindlimb during trotting in the horse. *J. Exp. Biol.* **209**, 3990-3999.

Farley, C. T. and Ferris, D. P. (1998). Biomechanics of walking and running: centre of mass movements to muscle action. *Exerc. Sport Sci. Rev.* **26**, 253-285.

Farris, D. J. and Sawicki, G. S. (2012a). The mechanics and energetics of human walking and running: a joint level perspective. *J. R. Soc. Interface* **9**, 110-118.

Farris, D. J. and Sawicki, G. S. (2012b). Human medial gastrocnemius force-velocity behavior shifts with locomotion speed and gait. *Proc. Natl. Acad. Sci. USA* **109**, 977-982.

Girard, O., Micallef, J.-P. and Millet, G. P. (2011). Changes in spring-mass model characteristics during repeated running sprints. *Eur. J. Appl. Physiol.* **111**, 125-134.

Gottschall, G. S. and Kram, R. (2005). Energy cost and muscular activity required for leg swing during walking. *J. Appl. Physiol.* **99**, 23-30.

Hamner, S. R. and Delp, S. L. (2013). Muscle contributions to fore-aft and vertical body mass center accelerations over a range of running speeds. *J. Biomech.* **46**, 780-787.

Hreljac, A., Imamura, R. T., Escamilla, R. F., Edwards, W. B. and MacLeod, T. (2008). The relationship between joint kinetic factors and the walk-run gait transition speed during human locomotion. *J. Appl. Biomech.* **24**, 149-157.

Khumsap, S., Clayton, H. M. and Lanovaz, J. L. (2001). Effect of walking velocity on hindlimb kinetics during stance in normal horses. *Equine. Vet. J. Suppl.* **33**, 21-26.

Kristianslund, E., Krosshaug, T. and van den Bogert, A. J. (2012). Effect of low pass filtering on joint moments from inverse dynamics: implications for injury prevention. *J. Biomech.* **45**, 666-671.

Modica, J. R. and Kram, R. (2005). Metabolic energy and muscular activity required for leg swing in running. *J. Appl. Physiol.* **98**, 2126-2131.

Nummela, A., Rusko, H. and Mero, A. (1994). EMG activities and ground reaction forces during fatigued and nonfatigued sprinting. *Med. Sci. Sports Exerc.* **26**, 605-609.

Pinniger, G. J., Steele, J. R. and Groeller, H. (2000). Does fatigue induced by repeated dynamic efforts affect hamstring muscle function? *Med. Sci. Sports Exerc.* **32**, 647-653.

Pires, N. J., Lay, B. S. and Rubenson, J. (2014). Joint-level mechanics of the walk-to-run transition in humans. *J. Exp. Biol.* **217**, 3519-3527.

Rubenson, J. and Marsh, R. L. (2009). Mechanical efficiency of limb swing during walking and running in guinea fowl (*Numida meleagris*). *J. Exp. Biol.* **106**, 1618-1630.

Rubenson, J., Lloyd, D. G., Heliams, D. B., Besier, T. F. and Fournier, P. A. (2011). Adaptations for economical bipedal running: the effect of limb structure on three-dimensional joint mechanics. *J. R. Soc. Interface* **8**, 740-755.

Sasaki, K. and Neptune, R. R. (2006). Muscle mechanical work and elastic energy utilization during walking and running near the preferred gait transition speed. *Gait Posture* **23**, 383-390.

Sasaki, K., Neptune, R. R. and Kautz, S. A. (2009). The relationships between muscle, external, internal and joint mechanical work during normal walking. *J. Exp. Biol.* **212**, 738-744.

Schache, A. G., Blanch, P. D., Dorn, T. W., Brown, N. A. T., Rosemond, D. and Pandy, M. G. (2011). Effect of running speed on lower limb joint kinetics. *Med. Sci. Sports Exerc.* **43**, 1260-1271.

Schache, A. G., Dorn, T. W., Williams, G. P., Brown, N. A. T. and Pandy, M. G. (2014). Lower-limb muscular strategies for increasing running speed. *J. Orthop. Sports. Phys. Ther.* **44**, 813-824.

Sprague, P. and Mann, R. V. (1983). The effects of muscular fatigue on the kinetics of sprint running. *Res. Q. Exerc. Sport* **54**, 60-66.

Stearne, S. M., Alderson, J. A., Green, B. A., Donnelly, C. J. and Rubenson, J. (2014). Joint kinetics in rearfoot versus forefoot running: implications of switching technique. *Med. Sci. Sports Exerc.* **46**, 1578-1587.

Teixeira-Salmela, L. F., Nadeau, S., Milot, M.-H., Gravel, D. and Requião, L. F. (2008). Effects of cadence on energy generation and absorption at lower extremity joints during gait. *Clin. Biomech.* **23**, 769-778.

Umberger, B. R. (2010). Stance and swing phase costs in human walking. *J. R. Soc. Interface* **7**, 1329-1340.

Umberger, B. R. and Martin, P. E. (2007). Mechanical power and efficiency of level walking with different stride rates. *J. Exp. Biol.* **210**, 3255-3265.

Weyand, P. G., Sternlight, D. B., Bellizzi, M. J. and Wright, S. (2000). Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J. Appl. Physiol.* **89**, 1991-1999.

Weyand, P. G., Sandell, R. F., Prime, D. N. L. and Bundle, M. W. (2010). The biological limits to running speed are imposed from the ground up. *J. Appl. Physiol.* **108**, 950-961.

Winter, D. A. (1983a). Energy generation and absorption at the ankle and knee during fast, natural and slow cadences. *Clin. Orthop. Rel. Res.* **175**, 147-154.

Winter, D. A. (1983b). Biomechanical motor patterns in normal walking. *J. Motor Behav.* **15**, 302-330.

Winter, D. A. (2009). *Biomechanics and Motor Control of Human Movement*. New York: John Wiley & Sons, Inc.