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Joint-level mechanics of the walk-to-run transition in humans

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Summary

Two commonly proposed mechanical explanations for the WRT include the prevention of muscular over-exertion (effort) and the minimisation of peak musculoskeletal loads and thus injury risk. The purpose of this study was to address these hypotheses at a joint level by analysing the effect of speed on discrete lower-limb joint kinetic parameters in humans across a wide range of walking and running speeds including walking above and running below the WRT speed. Joint work, peak instantaneous joint power, and peak joint moments in the sagittal and frontal plane of the ankle, knee and hip from 8 participants were collected for 10 walking speeds (30 – 120% of their WRT) and 10 running speeds (80 – 170% of their WRT) on a force-plate instrumented treadmill. Of the parameters analysed, three satisfied our statistical criteria of the 'effort-load' hypothesis of the WRT. Mechanical parameters that provide an acute signal (peak moment and peak power) were more strongly associated with the gait transition than parameters that reflect the mechanical function across a portion of the stride. We found that both the ankle (peak instantaneous joint power during swing) and hip mechanics (peak instantaneous joint power and peak joint moments in stance) can influence the transition from walking to running in human locomotion and may represent a cascade of mechanical events beginning at the ankle and leading to an unfavourable compensation at the hip. Both the ankle and hip mechanisms may contribute to gait transition by lowering the muscular effort of running compared to walking at the WRT speed. Although few of the examined joint variables satisfied our hypothesis of the WRT, most showed a general marked increase when switching from walking to running across all speeds where both walking and running are possible, highlighting the fundamental differences in the mechanics of walking and running. While not eliciting the WRT per se, these variables may initiate the transition between stable walking and running patterns. Those variables that were invariant of gait were predominantly found in the swing phase.

Introduction

Why do we switch from walking to running to move faster? This seemingly simple question has received considerable attention yet, whilst several factors have been proposed as triggers for the walk-to-run transition (WRT), their mechanisms remain debated. For example, it has been argued that humans (Margaria et al., 1963; Mercier et al., 1994) and other animals (Hoyt and Taylor, 1981; Rubenson et al., 2004; Watson et al., 2011) switch between walking and running to minimize metabolic energy use. However, some studies in humans have reported that the WRT occurs at a speed when it remains metabolically advantageous to walk, thus putting into question whether energy cost is the underlying determinant of the WRT (Hreljac, 1993a; Tseh et al., 2002). For example, dynamic systems theory acknowledges the importance of minimizing energy expenditure, however, views locomotor economy as a consequence of dynamic stability and not the cause of the transition *per se*. From a dynamical systems perspective, the WRT is influenced by non-specific control parameters that move the system from one stable coordination pattern to another, but does not prescribe these states. As such, the WRT may represent an abrupt shift from walking to running to avoid dynamic instability, initiated by one or more discrete mechanical variables, for example the increase in peak ankle power at the onset of running (Farris and Sawicki, 2011a).

Alternatively, discrete mechanical variables may themselves be directly associated with gait transition, rather than only reflecting the system stability or energetics. Two such commonly proposed explanations for the WRT based on discrete mechanical variables include 1) the prevention of muscular over-exertion (effort) (Hreljac, 1995; Hreljac et al., 2001; Bartlett and Kram, 2008), and 2) the minimisation of peak musculoskeletal loads and therefore the chance of injury (Biewener and Taylor, 1986; Farley and Taylor, 1991; Hreljac et al., 2008). This can occur if variables associated with muscular effort and/or load become elevated when walking above the WRT but are lowered upon switching to running (referred to here as the 'effort-load' hypothesis of the WRT). In humans, the clearest example of these factors influencing gait transition have been identified at the ankle (Farris and Sawicki, 2011b; Hreljac, 1995a; Hreljac et al., 2008; Prilutsky and Gregor, 2001; MacLeod et al., 2014). However, the prevalence of other joints [e.g. the hip, (Minetti et al., 1994)] and associated muscle groups affecting the WRT in humans may be obscured because of a lack of comprehensive information on the simultaneous individual mechanics of all the major lower leg joints across the gait cycle at speeds where both walking and running are possible. Furthermore, which discrete joint mechanical parameters that are most closely associated with gait transition are poorly understood, and in particular, whether joint loading, work, or power have varying influence on the WRT remains untested.

Although these forms of mechanical analyses at the level of the joints do not assess individual muscles directly, they do provide a means to comprehensively assess the end-effect of the lower-limb muscle functions. They also provide a powerful approach by which discrete muscular effort and mechanical loading hypotheses of gait transition can be tested broadly across different joints and muscle groups, and afford further insight into the underlying mechanisms of gait transition. The purpose of this study was, therefore, to assess how discrete joint mechanics impacts the WRT by systematically measuring the effect of speed on lower-limb joint kinetics and mechanical energetics in humans across a wide range of walking and running speeds including walking above and running below the preferred WRT speed. We asked two main questions: 1. How is mechanical work, peak power and/or peak loading (moments) at the individual joints associated with the WRT? 2. Do the individual joints (ankle, knee and hip) affect the WRT differently? Furthermore, in order to better understand the mechanics of switching between walking and running, we also asked which joint work, power and moment parameters exhibit abrupt changes between walking and running, but that do not influence the WRT *per se*. Although not the central question of the present study, these parameters can inform motor control theories, such as dynamic systems theory, as they may represent the behavioural manifestation of higher order control.

In testing these questions we established statistical-based criteria for accepting a variable as satisfying the effort-load hypothesis for the WRT. We analysed variables that can provide a physiological signal for altering gait mechanics including: joint work, peak instantaneous joint power and both peak sagittal and frontal plane joint moments, the former being linked to muscle force required for body support and the latter being linked to lateral stability and ligament loading, and thus may be more closely related to joint injury mechanisms (Besier et al., 2001a; Besier et al., 2001b). We assessed how these mechanical parameters changed with respect to the stance- and swing-phases of gait independently (we only included those variables that represent the major action at the joints in these phases).

Results

Example traces of the group mean joint moment and instantaneous power curves during walking and running at the WRT speeds are presented in Fig. 1. The peak moments and peak instantaneous powers during the stance and swing phases of walking and running that are used in our analyses are identified, as are the joint power bursts that define our joint work variables. Results from the speed/gait series analyses are presented below and group mean data are provided for each variable at each speed in the online supplementary material (Microsoft Excel).

Mechanical work

The majority of joint work variables exhibited a statistically significant increase with speed, with the exception of the ankle stance negative work (see Table 1 for ANOVA statistics including speed main effects from both two-way and one-way *post hoc* analyses). The individual speeds identified as being significantly different between walking and running (*a priori* and *post hoc* analyses) are identified on Fig. 2.

No mechanical work parameters satisfied all the statistical requirements of the effort-load hypothesis of the WRT (see Materials and Methods). The line of best fit for the positive ankle swing work (Fig. 2D) during walking was found to increase above those of running at the WRT speed but did not exhibit a statistically higher value during walking compared to running at the WRT. Table 1 details the ANOVA results and the work variables that satisfied our definition of a general change between walking and running (gait main effect) but which were not identified as satisfying the effort-load hypothesis of gait transition.

Peak instantaneous joint powers

The majority of instantaneous joint power variables exhibited a main effect of speed (ANOVA, Table 2) including both power generation and absorption (Fig. 3). The individual speeds identified as being significantly different between walking and running (*a priori* and *post hoc* analyses) are identified on Fig. 3. From these statistical analyses, the peak positive hip stance power and the peak positive ankle swing power were the only variables identified that satisfied all the statistical requirements of the WRT trigger (Fig. 3C-D). The line of best fit for the peak positive hip swing (flexion) power (Fig. 3F) during walking was found to increase above that of running close to the WRT speed, but did not exhibit a statistically higher value during walking compared to running at the WRT.

The summary of ANOVA results including gait main effects and gait-speed interaction effects on peak powers, and the peak power variables that satisfied our definition of a general change between walking and running (gait main effect) but that did not satisfying the effort-load hypothesis of gait transition are outlined in Table 2.

Peak joint moments

The majority of peak joint moment variables increased with speed during walking, with the only exceptions being the peak knee stance abduction moments (Fig. 4 G) (see Table 3 for ANOVA statistics including speed main effects from both two-way and one-way *post hoc* analyses). The individual speeds identified as being significantly different between walking and running (*a priori* and *post hoc* analyses) are identified on Fig. 4.

The peak hip stance flexion moment satisfied the criteria for the WRT trigger (Fig. 4C, positive values; Table 3). The line of best fit for the peak hip stance extension moment (Fig. 4C, negative values; Table 3) increased above that of running at the WRT, but did not exhibit a significantly larger value for walking compared to running at the WRT after the Benjamini correction for multiple comparisons. The other peak joint moments did not satisfy the criteria for the effort-load hypothesis of the WRT. The summary of ANOVA results including gait main effects and gait-speed interaction effects on peak joint moments, and the peak joint moment variables that satisfied our definition of a general change between walking and running (gait main effect) but that did not satisfying the effort-load hypothesis of gait transition are outlined in Table 3.

Discussion

Humans and other terrestrial animals spontaneously switch from a walking to running gait as they increase locomotor speed. This study aimed to determine the extent by which discrete mechanical variables at the individual joints that can affect muscular effort and musculoskeletal loads are associated with the WRT in humans. The majority of the examined joint parameters showed a general marked increase between walking and running at speeds where both walking and running are possible. However, out of the parameters examined, only three satisfied our statistical criteria of the effort-load hypothesis of the WRT. Mechanical parameters that provide an acute signal (peak moments and peak power) were more strongly associated with the gait transition than mechanical work parameters that reflect the muscular function across a portion of the stride, and were present both at the ankle and the hip.

Which discrete joint mechanical variables might affect the walk-to-run transition?

Previous studies have identified discrete joint kinematics (Hreljac, 1995; Minetti et al., 1994), joint moments (Prilutsky and Gregor, 2001) and peak joint power (Hreljac et al., 2008) that may be linked to the WRT. Because these studies either focused on a sub-set of joints or mechanical variables separately, it is difficult to deduce from them whether each parameter is equally important in the WRT. The current study's comprehensive inverse dynamic analyses indicate that various joint-level mechanical variables are linked to the WRT including both peak joint power and peak joint moments. This might result, in part, because these parameters are each associated with the same muscular actions. For example the required increase in peak positive hip stance power (Fig. 3C) may occur partly due to the increase in peak hip stance flexion moments (Fig. 4C, positive values), as joint power is a function of joint moment.

It is nevertheless interesting that all of the mechanical variables satisfying the effort-load hypothesis of the WRT identified in this study (peak joint power and peak joint moments) are those that can provide an acute physiological signal. This is consistent with the theory that gait transition occurs spontaneously, is initiated within a single stride (Segers et al., 2013), and is triggered by discrete variables that can be acutely sensed. In contrast, joint work reflects the joint's mechanical function over a portion of the stride. Similar to the overall metabolic rate, the longer time over which these variables fluctuate might preclude them from causing the transition step itself [although AMP-activated protein kinase (Winder, 2001) and/or other cellular mechanisms (Clanton et al., 2013) may provide acute sensing of the energy/work state of a muscle]. On the other hand, the increase in joint mechanical work at the ankle and hip during fast walking above that required for running offer a reasonable explanation, together with instantaneous peaks in joint power and moments, why humans avoid walking at these speeds and instead choose to either walk slower or run faster. They might also help explain, in part, the higher cost of walking compared to running at fast walking speeds.

It is likely that the variables consistent with the effort-load hypothesis identified in this study reflect local muscle-level stimuli. These local joint-level effects were, however, not contained to a single phase of the gait cycle. Variables linked to the WRT were identified both in the swing phase (peak positive ankle dorsi-flexion power) and in the stance-phase (peak hip power and flexion moments). Furthermore, the peak hip flexion moments and peak hip power occur at different times during stance. Given that gait transition is likely triggered within a short time frame, it remains unclear whether one of these variables is more strongly associated with the transition, whether each independently affects the WRT at different times, or whether they possibly act cumulatively.

Evidence for both ankle- and hip-based mechanics influencing the walk-to-run transition

Several studies have identified effort (Hreljac, 1995; Hreljac et al., 2001; Hreljac et al., 2008), or fatigue (Malcolm et al., 2009; Segers et al., 2007) in the ankle dorsi-flexors during the swing phase as a main factor influencing the WRT. The findings of this study supports this hypothesis, providing further evidence that ankle dorsi-flexion in swing is a key mechanism affecting the transition from walking to running. Indeed, this study found that the peak swing-phase dorsi-flexion power (Fig. 3D) satisfies the effort-load hypothesis of the WRT transition, with peak power values during walking exceeding those of running at the WRT speed (MacLeod et al., 2014). Our results for ankle swing-phase dorsi-flexion work (Fig. 2D) further indicate that ankle dorsi-flexion mechanics become unfavourable at walking speeds beyond the WRT. It is plausible that the high peak joint power and work are the underlying mechanisms leading to dorsi-flexion fatigue at fast walking speeds and that the reduction of these variables upon switching to running mitigates the fatigue and effort sensed in the muscles.

It has also been argued that stance-phase plantarflexion is a factor contributing to the WRT. Neptune and Sasaki (2005), and more recently Arnold et al. (2013) showed in simulation studies that the ability to generate force is compromised at fast walking speeds because of sub-optimal force-length-velocity characteristics of the triceps surae muscles. Switching to running allowed these muscles to function at a more favourable length and velocity, thus increasing their force capacity. More direct evidence for this has recently been found by combining ultrasound imaging and gait analysis, in which the velocity of the medial gastrocnemius fascicles has been identified as limiting force and power production during walking at the WRT speed (Farris and Sawicki, 2011a). Our speed-series joint-level analysis provides further support for this theory, whereby a plateau in peak instantaneous positive power and plantarflexion moments occurs above the WRT (Fig. 3A, 4A, negative values). The switch to running leads to a marked increase in ankle joint power and plantarflexion moments (Fig. 3A, 4A, negative values) and is in agreement with the higher estimated triceps surae muscle force and power during running at the WRT speed (Neptune and Sasaki, 2005; Farris and Sawicki, 2011a; Arnold et al., 2013). We cannot rule out, however, that the combination of the limitation in plantarflexion torque and dorsiflexion fatigue may contribute to the loss of local dynamic stability at the ankle joint when walking at speeds beyond the WRT (Jordan et al., 2009), and may together reflect a dynamic systems determinant of the WRT as opposed to a discrete ankle joint determinant.

In addition to the aforementioned ankle mechanisms, our study also identified novel discrete hip-based mechanical variables that are associated with the WRT. The increase in peak positive hip stance power and peak flexion moments (Fig. 3C and 4C, positive values) during walking to values above those required for running at the WRT may contribute to the transition to a running gait. It is intriguing to consider whether the sharp increase in the peak positive hip stance-phase power beyond the WRT speed (Fig. 3C) occurs because of the inability of the ankle to produce sufficient stance-phase peak power and joint moments (Fig. 3A and 4A). In this regard, the trigger for the WRT may, in part, be the result of a cascade of mechanical events beginning at the ankle and leading to an unfavourable compensation at the hip, both of which may provide the critical signal for altering gait. Unlike Prilutsky and Gregor (2001) we did not observe a clear unfavourable effect on swing-phase joint moments at fast walking speeds. This may be due to the moderately smaller range of walking speeds in the present study due to the difficulty of our subjects to maintain faster walking speeds. That hip swing-phase mechanics might influence the WRT was, however, supported by the trend of greater peak hip flexion joint power in walking compared to running above the WRT speed (Fig. 3F).

Together, these results suggest that the switch between walking and running may occur not only to reduce effort in ankle muscles, but also in the hip musculature. Some previous support for a hip-based mechanism affecting the WRT can be found from electromyography analyses of the hip muscles (rectus femoris and biceps femoris) at walking and running speeds spanning the WRT speed (Prilutsky and Gregor, 2001). Furthermore, simulation studies in which individual muscle mechanics were predicted for walking and running at and above and below the WRT indicate favourable reductions in peak power and work in hip muscle fibres as a result of switching to running (Sasaki and Neptune, 2006a, 2006b), although this has yet to be shown experimentally in humans. Interestingly, the redistribution of average mechanical power from the hip to the ankle that accompanies the reduction in hip work at the WRT has been suggested to contribute to the greater locomotor efficiency of running (Farris and Sawicki, 2011b). This may occur due the purported greater plantarflexor efficiency during running, and might also contribute to gait selection.

Is injury avoidance a factor in human gait transition?

Whether the elevation in peak hip sagittal plane joint moments (Fig. 4C) would influence the WRT due to an injury reduction mechanism [as has been suggested in horses to reduce tendon loads, (Farley and Taylor, 1991)] is questionable. The increased hip flexion and extension moments are most likely accompanied by an increase in muscle force that, while potentially increasing the effort of locomotion, are at levels that are not expected to pose any significant musculoskeletal injury risk.

More likely to be linked with injury mechanisms are the frontal plane loads at the knee (Besier et al., 2001a; Besier et al., 2001b) and the hip. The present study provides among the first measurements of the response of non-sagittal loading at these joints across speed. Interestingly, while the abduction loading at the knee and hip increase at the same rate with speed during both walking and running, the load level is higher during running at all speeds where both gaits were analysed (Fig. 4). Running may therefore place the joints at larger risk of injury in general, but there is no evidence from our study that frontal plane loading *per se* influences the WRT in a manner to specifically reduce injury risk at the WRT speed.

General effect of gait transition

Whether joint mechanical differences between walking and running are general across all speeds where walking and running are possible, or whether they arise due to a speed related effect has not been extensively examined. Our analysis found that most of the joint parameters in both the sagittal and frontal planes exhibited a marked increase with a shift from walking to running, both below and above the WRT. Furthermore, the majority of variables lacked an interaction effect between gait and speed (Tables 1-3). These findings suggest that, overall, there is an increase in the joint mechanical variables between walking and running that are largely unaffected by speed. Interestingly, those variables that were invariant of gait were predominantly found in the swing phase (Table 1-3). That differences in joint mechanics between walking and running are more predominant in the stance-phase of gait is consistent with the body centre-of-mass paradigms of walking and running (inverted pendulum *vs.* spring mass), which are dictated primarily by stance dynamics (Saibene and Minetti, 2003). We also found some joint variables at the hip and the ankle that exhibited speed-dependent differences between walking and running. For example, the ankle swing-phase work (Fig. 2D), and the peak positive hip stance- and swing-phase flexion power (Fig.

3C and F) and stance-phase moments (Fig. 4C) all lacked a main effect of gait but exhibited an interaction effect between gait and speed (Table 1-3). In these variables there was either a difference between gaits only at faster speeds, or the differences were in opposite direction above *vs*. below the WRT. In this latter scenario, these variables might help explain both the WRT as well as the run-to-walk transition.

While the general increase in these joint parameter magnitudes alone may not explain the WRT, they may however reflect which joint variables are responsible for initiating the transition between stable patterns of coordination (walking/running). As such, while not affecting the WRT *per se*, they may represent the key variables underpinning a dynamic systems interpretation of the WRT and may be representative of the central motor plan for moving between attractor states and avoiding system instability.

Limitations

Our joint-level inverse dynamic analyses represent the net effect of all muscles and structures that span the joints. As has been outlined previously (Sasaki et al., 2009), inverse dynamic analyses do not necessarily reflect the mechanics of individual muscles. We have not taken into account co-contraction between antagonist muscles, force sharing between synergist muscles or the distribution of work and power between muscle fibres and tendon. It is also important to stress that our criteria for the effort-load hypothesis of the WRT to be satisfied is based on the statistical identification of a unique increase in a parameter during walking compared to running at the WRT. This was the case when a parameter for walking first increases above running at the WRT. Whilst these criteria are designed to detect a unique event at the WRT, we cannot rule out that a variable reaches a critical value that influences gait transition without being uniquely identifiable at the WRT speed using the above criteria. They also do not identify other mechanisms that may influence gait transition, such as a restricted capacity for stance-phase peak ankle power and moments output that were evident in our analysis of joint mechanics (Fig. 3A and Fig. 4A). Finally, our analysis of the WRT does not specifically assess whether non-specific control parameters, which may be reflected in our discrete joint measurements, are responsible for the WRT (rather than the discrete variables themselves).

Conclusion

Discrete joint-level mechanisms at both the ankle and hip that are thought to increase muscular effort have been identified as being associated with the WRT in humans. Of the examined variables, only those that provide an acute signal satisfied our effort-load hypothesis of the WRT. We hypothesise that the WRT in humans is dictated, in part, by a limitation in ankle moment and power generation that results in a compensation at the hip that increases the effort in hip muscles above that which is required during running. Finally, our analyses suggest that the differences in joint mechanics between walking and running in most joint-level parameters are consistent across different speeds where walking and running are both feasible gaits.

Materials and Methods

Subjects

8 healthy and recreationally active subjects (m = 4, f = 4), with no history of major lower-limb injury were recruited for this study (age: 24.8 ± 1.8 years; height: 170.0 ± 9.4 cm; mass: 69.6 ± 13.2 kg, mean ± S.D.). All testing procedures were approved by the Human Research Ethics Committee of the University of Western Australia. Written informed consent was obtained from all subjects.

Walk-to-run gait transition speed

All subjects were accustomed to running on treadmills and were initially familiarized to walk and run on a force-plate instrumented split-belt treadmill (Bertec, Columbus, OH, USA). The subject's preferred WRT speed was determined following a protocol similar to those of Hreljac (1993a,b) and Bartlett and Kram (2008). The subjects walked at randomized speeds ranging from 1.5 to 2.5 m.s^{-1} at intervals of 0.1 m.s^{-1} for approximately 30 seconds to one minute per speed. At each speed the subjects were instructed to voluntarily choose between walking and running and were allowed to switch between gaits. The slowest speed where the subjects confirmed running to be their 'most comfortable' gait was selected as the WRT speed. This was repeated three times and the subject's range and average WRT speed was determined (group average 2.00 ± 0.09 m s^{-1}, ranging from 1.90 to 2.10 m s^{-1}).

Three-dimensional (3-D) gait analysis

Experiments were performed on a split belt force-plate treadmill (Bertec, Columbus, OH, USA). Subjects walked at speeds ranging from 30% to 120% of their WRT speed (0.5 to 2.5 $m.s^{-1}$) and ran at speeds ranging from 80% to 170% (1.5 to 3.5 $m.s^{-1}$) of their WRT. For both walking and running, speed increments of 10% were analysed with the subject walking/running at a set speed for at least one minute. Five speeds spanning 80 – 120% of the WRT were performed for both walking and running. The walking and running speeds were randomized to prevent any order effects. Five strides per subject per speed were analysed where the subject maintained their anterior-posterior and medial-lateral position on the treadmill. Individual strides where gait was spontaneously changed between walking and running were not analysed for this study.

Three-dimensional (3-D) ground reaction forces (2000 Hz) and marker position data (250 Hz; 8-camera VICON MX motion-analysis system VICON OxfordMetrics, Oxford, UK) were captured and integrated in Vicon Nexus data acquisition suite (version 1.8.3). Retroreflective markers were placed either on bony landmarks or as part of triad-marker clusters. Single markers were placed on the left and right anterior superior iliac spines, left and right posterior superior iliac spines, left and right head of first and fifth metatarsals, and left and right calcaneus. Triad-marker clusters were placed on the left and right thigh and leg. Three-dimension kinematic and inverse dynamic calculations were computed in VICON Nexus and Bodybuilder (VICON, Oxford Metrics, Oxford, UK) in accordance with the procedures established in Besier et al., (2003), including a functional knee axis and joint center (mean helical axis) and a functional hip center (sphere-fit) calculation. Prior to inverse dynamic modelling, marker position data was filtered using a fourth-order, 12 Hz (walking) and 8 Hz (running) low-pass Butterworth filter, with the filter frequencies selected by performing a residual analysis of filtered vs. unfiltered data (MATLAB, The Mathworks, Natick, MA). Ground reaction force signals were filtered at the same frequency as the kinematic data to prevent joint moment artifacts (Kristianslund et al., 2012).

Joint moments and instantaneous joint power calculations

Joint moments were expressed in the distal segment anatomical coordinate systems as per Besier et al. (2003). Only flexion/extension and adduction/abduction joint moments were used for WRT transition analyses because of the high variability in the long-axis joint loading. Joint powers were computed as the net power across all three joint planes. Joint moments and powers were computed for the right leg and both normalized to body mass (N kg^{-1} and W kg^{-1}, respectively). Numerical values of the peak joint moments and powers were initially identified using Matlab (The MathWorks, Natick, MA). Secondary visual inspection identified whether the peak joint moments and instantaneous peak joint powers corresponded to the physiologically relevant phases of the gait cycle (see Fig. 1).

Joint work

Positive and negative joint work ($W_{j_i}^+$, $W_{j_i}^-$) were calculated for the ankle, knee and hip from the positive and negative values of the instantaneous joint power curves ($P_{j_i}^+$, $P_{j_i}^-$), respectively:

$$W_{j_i}^+ = \int_{t_i}^{t_f} P_{j_i}^+ dt\,,\ \ W_{j_i}^- = \int_{t_i}^{t_f} P_{j_i}^- dt \qquad (1)$$

The work from the individual joints (Eq. 1) was computed for the stance and swing phases independently. Work was normalized to body mass (J kg^{-1}). When clear bursts of positive and/or negative work in the gait phase (stance / swing) were produced separately under net flexion and extension joint moments, both the individual flexion and extension work was computed (Fig. 1). This included positive hip joint work produced during the swing and stance phases, negative work at the hip in stance, negative work at the knee in swing, and the positive work at the ankle in swing. We report the flexion or extension work depending on which parameter represents the primary function of the joint in the gait phase (see Fig. 1).

Testing of the 'effort-load' hypothesis for mechanical variables.

Similar to Hreljac (1993b, 1995), we defined a set of criteria for a mechanical variable to satisfy the effort-load hypothesis of the WRT. Our analysis is based on the hypothesis that the WRT occurs when an 'undesirable' discrete variable surpasses a certain threshold value with increasing walking speed and is lowered by switching to running. A mechanical variable satisfied the effort-load hypothesis of the WRT if it increased with walking speed and first became larger during walking compared to running at the WRT speed such that switching gaits results in a favourable reduction in that variable. This definition is consistent with the criteria of Hreljac (1993b, 1995) whereby a mechanical "trigger" for the WRT is required to increase with walking speed and undergo an abrupt decrease upon switching to running, but with the addition that the stimulus for lowering the variable first occurs at the WRT speed. To assess these criteria of the effort-load hypothesis we first examined the relationships between gait and speed using a two-way (gait: walking and running) by five repeated-measures (speed: 80%, 90%, 100%, 110% and 120% of WRT speed) analysis of variance (ANOVA; SPSS version 21). Significant main effects of speed and gait were assessed ($p < 0.05$) and adjusted for the false discovery rate arising from multiple comparisons (Benjamini adjustment; Benjamini & Hochberg, 1995). The variable was deemed to increase with walking speed when a main effect of speed was detected, or in the event that an interaction effect between speed and gait existed, when a *post hoc* one-way ANOVA limited to walking data exhibited a main effect of speed. Secondly, *a priori* tests were used to establish those speeds where walking data were significantly greater than the running data. Because our criteria asked specifically when the walking data first became greater than the running data we performed a one-tailed paired sample t-test at each speed ($p < 0.05$ with Benjamini multiple comparison adjustment).

General joint mechanical changes between walking and running at different speeds

We also determined those variables that were generally affected by switching between a walking and running gait, but which did not satisfy the effort-load hypothesis *per se*. These variables demonstrated a shift between walking and running gaits at the WRT and other speeds where walking and running were compared. In order to determine if gait had a general effect on the biomechanical variables tested we used the two-way repeated-measures ANOVA described above to assess gait and speed main and interaction effects ($p < 0.05$ with Benjamini multiple comparison adjustment). Variables that exhibited a main effect of gait were deemed to undergo a generalized modification between walking and running. When an interaction effect between gait and speed was found, *post hoc* tests were used to identify significant differences between the walking and running data at individual speeds (two-tailed paired sample t-test; $p<0.05$ with Benjamini multiple comparison adjustment).

Symbols and Abbreviations

WRT, walk-to-run transition; $P^{+}_{j_i}$, $P^{-}_{j_i}$, positive/negative instantaneous joint power; $W^{+}_{j_i}$, $W^{-}_{j_i}$, positive/negative joint work.

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Author Contributions

N.J.P and J.R. designed and conducted the experiment. N.J.P., B.S.L. and J.R. analysed and interpreted the data. N.J.P. and J.R. drafted the manuscript. N.J.P., B.S.L. and J.R. edited and revised the manuscript and approved the submitted version.

Competing Interests

No competing interests declared

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Tables

Table 1. Joint work

Variable	Two-way ANOVA			One-way ANOVA	
	Gait	Speed	Interaction	Walking	Running
Ankle stance (positive) *	**<0.001**	**<0.001**	0.171		
Ankle stance (negative) *	**<0.001**	0.654	**0.004**	**0.005**	0.080
Knee stance (negative) *	**0.002**	**<0.001**	0.363		
Hip stance ext. (positive) *	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.024**
Hip stance flex. (negative)	0.442	0.165	0.611		
Ankle swing dorsi-flex (positive)	0.040	**<0.001**	**<0.001**	**<0.001**	**0.001**
Knee swing flex. (negative)	0.338	**<0.001**	0.536		
Hip swing flex. (positive) *	**0.023**	**<0.001**	0.943		

P values for two-way ANOVA main and interaction effects and one-way ANOVA *post hoc* analyses. Bold numbers signifies statistical differences after Benjamini correction for multiple comparisons. (*) signifies variables that satisfied the definition of a general change between walking and running (gait main effect) but that were not identified as a trigger of gait transition. The group mean joint work data can be accessed through the supplementary material found online (Microsoft Excel).

Table 2. Peak instantaneous joint powers

Variable	Two-way ANOVA			One-way ANOVA	
	Gait	Speed	Interaction	Walking	Running
Ankle stance (positive) *	**0.002**	**<0.001**	**<0.001**	**0.005**	**<0.001**
Ankle stance (negative) *	**<0.001**	**0.004**	0.202		
Knee stance (negative)*	**<0.001**	**<0.001**	0.542		
Hip stance (positive)	0.046	**<0.001**	**0.001**	**<0.001**	**0.004**
Hip stance (negative)*	**0.002**	**<0.001**	0.257		
Ankle swing (positive)	**0.015**	**0.001**	**<0.001**	**<0.001**	0.576
Knee swing (negative)	0.105	**<0.001**	0.385		
Hip swing flex. (positive)	0.555	**<0.001**	**<0.001**	**<0.001**	**<0.001**

P values for two-way ANOVA main and interaction effects and one-way ANOVA *post hoc* analyses. Bold numbers signifies statistical differences after Benjamini correction for multiple comparisons. Bold variable text signifies variables that are identified as walk-to-run transition triggers. (*) signifies variables that satisfied the definition of a general change between walking and running (gait main effect) but that were not identified as a trigger of gait transition. The group mean joint power data can be accessed through the supplementary material found online (Microsoft Excel).

Table 3. Peak joint moments

Variable	Two-way ANOVA			One-way ANOVA	
	Gait	Speed	Interaction	Walking	Running
Ankle stance plantarflexion *	**<0.001**	**<0.001**	**<0.001**	0.223	**<0.001**
Knee stance extension *	**0.001**	**<0.001**	0.387		
Hip stance flexion	0.042	**0.008**	**<0.001**	**<0.001**	0.355
Hip stance extension	0.117	**<0.001**	**0.004**	**<0.001**	**<0.001**
Ankle swing dorsi-flexion *	**0.001**	**<0.001**	**<0.001**	**<0.001**	**0.028**
Knee swing flexion	0.038	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Hip swing flexion	0.037	**<0.001**	0.047		
Hip swing extension	0.321	**<0.001**	**0.008**	**<0.001**	**<0.001**
Knee stance abduction	0.032	0.075	0.505		
Hip stance abduction	0.034	**0.013**	0.387		

P values for two-way ANOVA main and interaction effects and one-way ANOVA *post hoc* analyses. Bold numbers signifies statistical differences after Benjamini correction for multiple comparisons. Bold variable text signifies variables that are identified as walk-to-run transition triggers. (*) signifies variables that satisfied the definition of a general change between walking and running (gait main effect) but that were not identified as a trigger of gait transition. The group mean joint moment data can be accessed through the supplementary material found online (Microsoft Excel).

Figure Captions

Fig. 1. Grouped average moments **(A – F)** and instantaneous powers **(G – L)** for the ankle **(A, B and G, H)**, knee **(C, D and I, J)** and hip **(E, F and K, L)** joints when walking **(A, C, E and G, I, K)** and running **(B, D, F and H, J, L)** at the WRT. The shaded area on the joint moments graphs **(A – F)** represent the S.D. of the group means The dark and light shading on the powers graphs **(G – L)** represent positive and negative joint work, respectively, with group S.D. omitted for clarity. A_{M1} and A_{M2} **(A-B)** indicate the peak ankle stance-phase dorsi- and plantarflexion moments respectively. The peak swing-phase moments have not been indicated on the graph due to the scale. K_{M1}, and K_{M2} indicate the peak knee stance-phase extension and flexion moments respectively, while K_{M3}, and K_{M4} indicate the peak knee swing extension and flexion moments, respectively **(C-D)**. H_{M1} and H_{M2} represent the peak hip stance-phase extension and flexion moments respectively, while H_{M3} and H_{M4} represent the peak hip swing-phase flexion and extension moments **(E-F)**. A_{P1} and A_{P2} represent the peak positive and negative ankle stance-phase power **(G-H)**. The swing-phase power has been not been indicated due to the scale. K_{P1} indicates the peak positive knee stance power, and K_{P2} and K_{P3} indicate the peak negative knee stance and swing power, respectively **(I-J)**. H_{P1} and H_{P2} represent the peak positive and negative hip stance power, respectively, and H_{P3} and H_{P4} represent the peak positive hip swing power during flexion and extension, respectively. The negative knee swing flexion work (performed during net flexion moments in terminal swing) was computed from the K_{P3} power burst; the positive hip stance extension work and negative flexion work (performed during net extension and flexion moments, respectively) were computed from the H_{P1} and H_{P2} power bursts, respectively; the positive hip swing flexion work (performed during net flexion moments in early swing) was computed from the H_{P3} power burst.

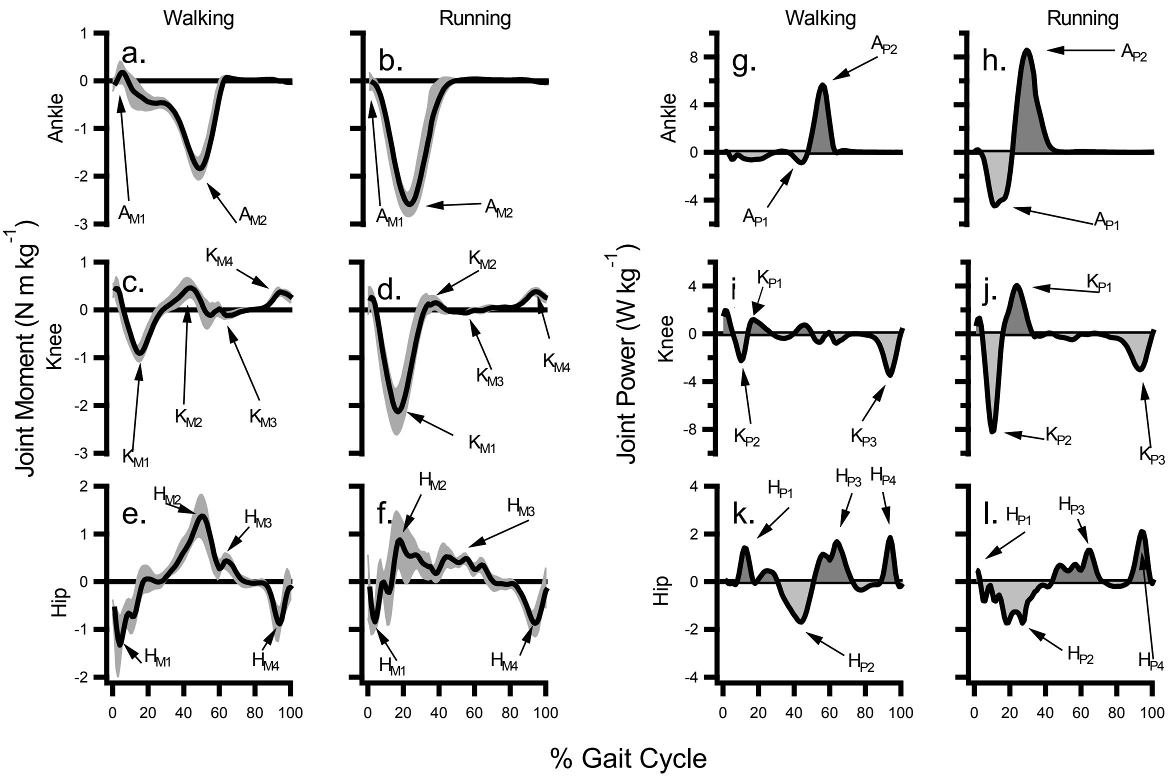
Fig. 2. Joint work (mean ± S.D.) during walking (closed symbols) and running (open symbols) plotted against speed (expressed as a per cent of the WRT speed; 100% depicted by the broken vertical line). Positive and negative ankle **(A)**, negative knee **(B)**, and positive hip stance extension work and negative flexion work (performed during net extension and flexion moments, respectively) **(C)**. Positive ankle swing dorsi-flexion work (performed during net dorsi-flexion moments in swing) **(D)**, negative knee swing flexion work (performed during net flexion moments in terminal swing) **(E),** and positive hip swing flexion work (performed during net flexion moments in early swing) **(F)**. (#) indicates speeds where walking was

significantly greater than running (*a priori tests*). (*) indicates significant differences between walking and running established in *post hoc* analyses (run only when an interaction effect between gait and speed was found). If both *a prior* and *post hoc* significant differences were found only the (*) is labelled.

Fig. 3. Peak instantaneous joint power (mean ± S.D.) during walking (closed symbols) and running (open symbols) plotted against speed (expressed as a per cent of the WRT speed; 100% depicted by the broken vertical line). Peak positive and negative ankle **(A)**, negative knee **(B)**, and positive and negative hip stance powers **(C)**. Peak positive ankle swing power **(D)**, peak negative knee swing power **(E)** and peak positive hip swing power in flexion **(F)**. Circles and squares represent peak positive and negative power, respectively. The (‡) next to the graph heading indicates the variable was identified as a WRT trigger. (#) indicates speeds where walking was significantly greater than running (a priori tests). (*) indicates significant differences between walking and running established in *post hoc* analyses (run only when an interaction effect between gait and speed was found). If both *a prior* and *post hoc* significant differences were found only the (*) is labelled.

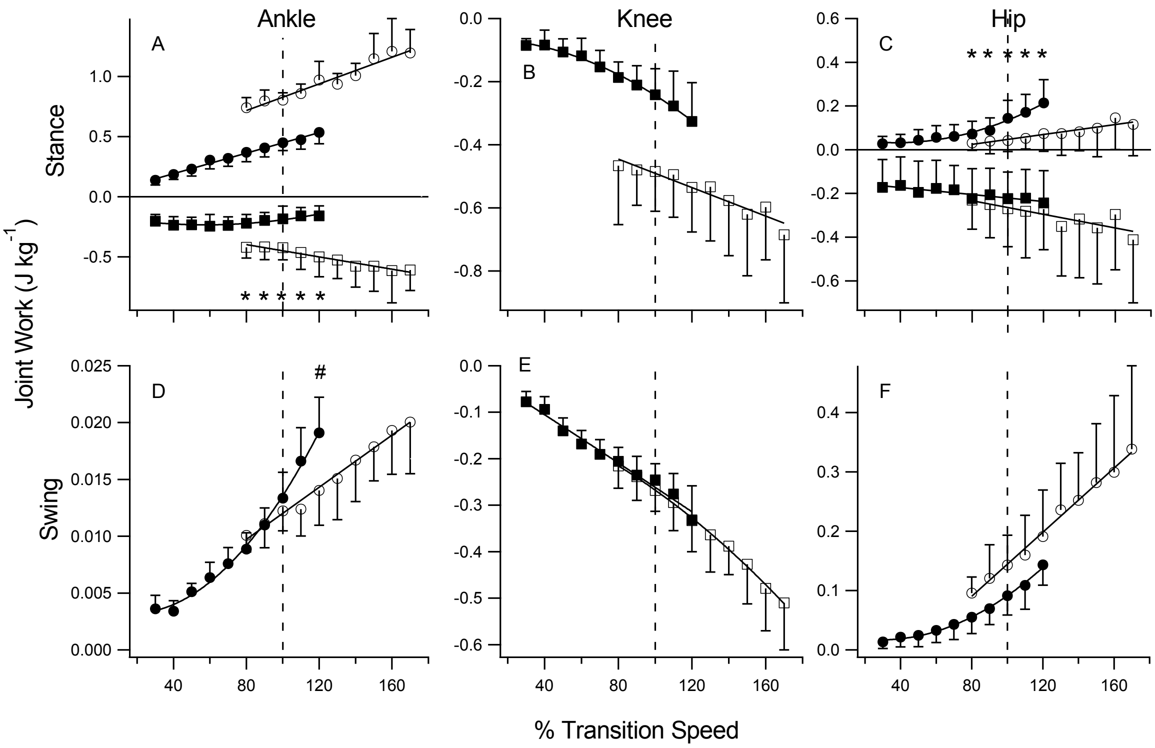
Fig. 4. Peak joint moments (mean ± S.D.) during walking (closed symbols) and running (open symbols) plotted against speed (expressed as a per cent of the WRT speed; 100% depicted by the broken vertical line). Peak ankle stance-phase plantarflexion moments **(A)**. Peak knee stance-phase extension **(B)**, and hip stance-phase flexion and extension moments **(C)**. Peak ankle swing-phase dorsiflexion moments **(D)**. Peak knee swing-phase flexion moments **(E),** and hip swing-phase flexion and extension moments **(E-F)**. Peak knee and hip stance-phase abduction moments **(G – H)**. Positive values (circles) represent net joint flexion moments (dorsi-flexion at the ankle). Negative values (squares) represent net joint extension moments (plantarflexion at the ankle, abduction at the knee and hip). The (‡) next to the graph heading indicates the variable was identified as a WRT trigger. (#) indicates speeds where walking was significantly greater than running (*a priori tests*). (*) indicates significant differences between walking and running established in *post hoc* analyses (run only when an interaction effect between gait and speed was found). If both *a prior* and *post hoc* significant differences were found only the (*) is labelled.

Fig. 1



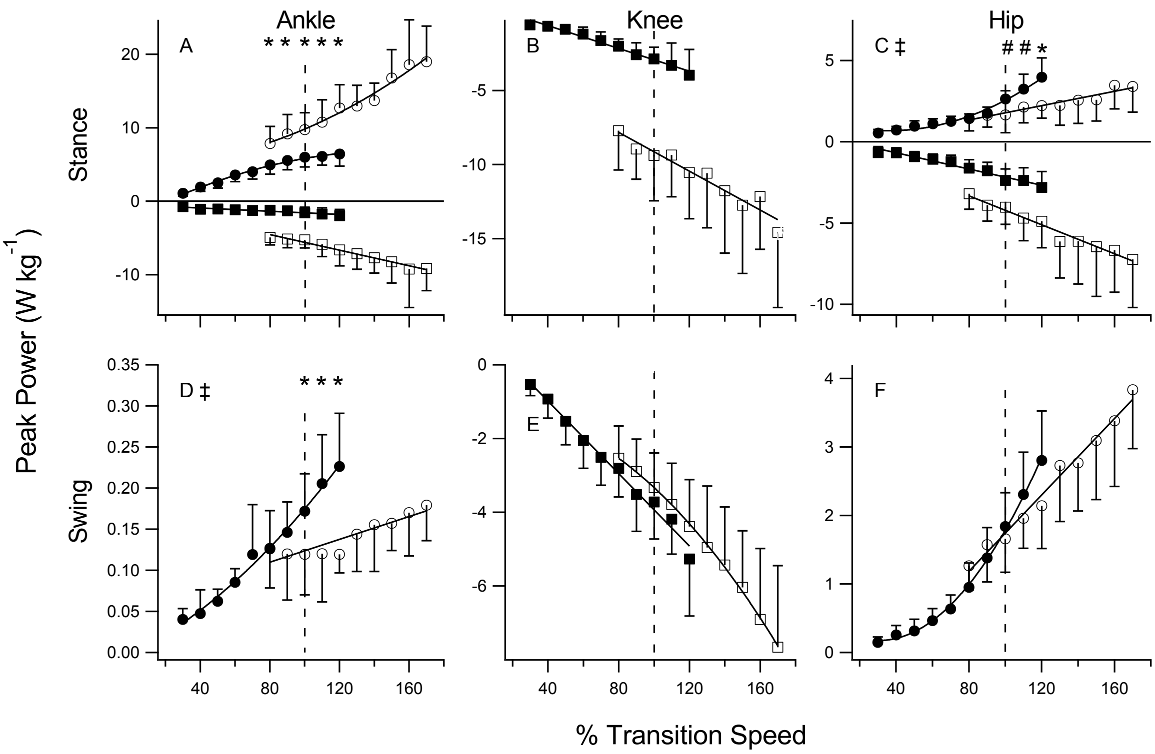
Walking
Running
Walking
Running
Joint Moment (N m kg-1)
Joint Power (W kg-1)
Ankle
Knee
Hip
a.
b.
c.
d.
e.
f.
g.
h.
i
j.
k.
l.
AM1
AM2
KM1
KM2
KM3
KM4
HM1
HM2
HM3
HM4
AP1
AP2
KP1
KP2
KP3
HP1
HP2
HP3
HP4
% Gait Cycle

Fig. 2



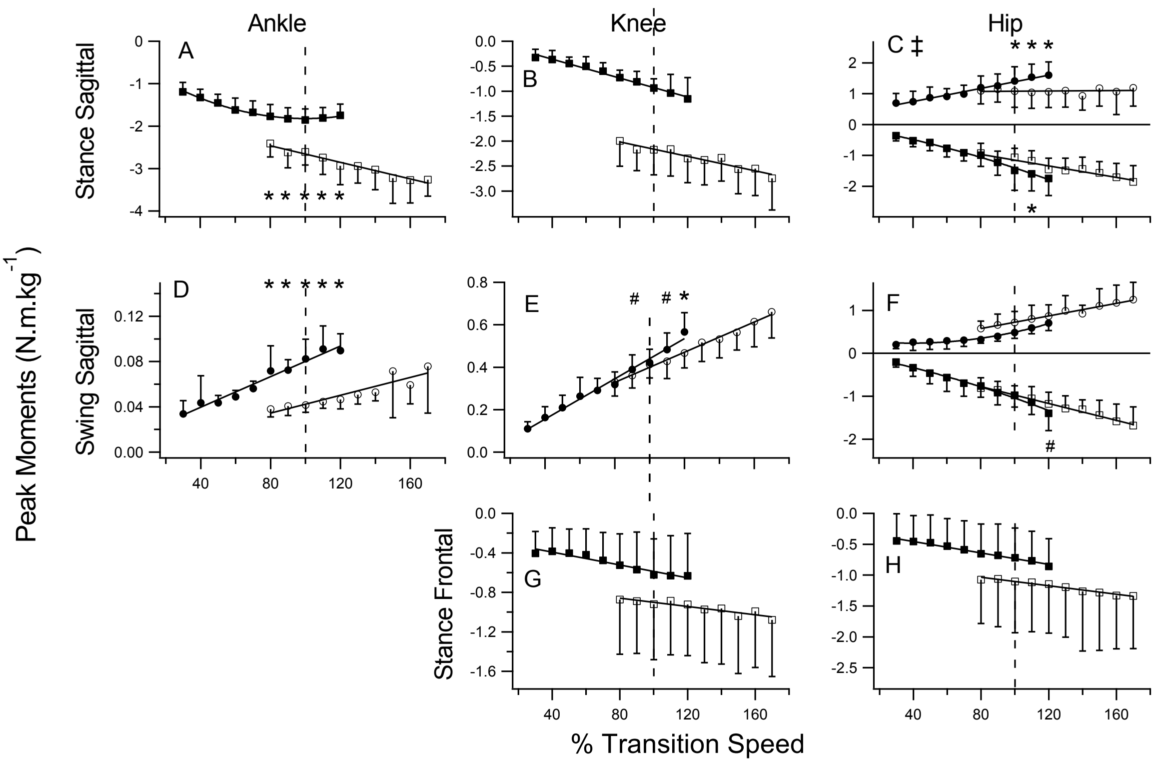
Ankle
Knee
Hip
A
B
C
D
E
F
Stance
Swing
Joint Work (J kg-1)
% Transition Speed
* * * * *
* * * * *
#

Fig. 3



Ankle
Knee
Hip
A
B
C ‡
D ‡
E
F
Stance
Swing
Peak Power (W kg-1)
% Transition Speed
20
10
0
-10
-5
-15
5
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
-2
-4
-6
4
3
2
1
40
80
120
160
* * * * *
* * *
*

Fig. 4



Ankle
Knee
Hip
A
B
C ‡
D
E
F
G
H
Stance Sagittal
Swing Sagittal
Stance Frontal
Peak Moments (N.m.kg^{-1})
% Transition Speed