THREE-DIMENSIONAL KINEMATICS OF THE PELVIS AND HIND LIMBS IN CHIMPANZEE (*PAN TROGLODYTES*) AND HUMAN BIPEDAL WALKING

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Abstract

The common chimpanzee (*Pan troglodytes*) is a facultative biped and our closest living relative. As such, the musculoskeletal anatomies of their pelvis and hind limbs have long provided a comparative context for studies of human and fossil hominin locomotion. Yet, how the chimpanzee pelvis and hind limb actually move during bipedal walking is still not well defined. Here, we describe the three-dimensional (3-D) kinematics of the pelvis, hip, knee and ankle during bipedal walking and compare those values to humans walking at the same dimensionless and dimensional velocities. The stride-to-stride and intraspecific variations in 3-D kinematics were calculated using the adjusted coefficient of multiple correlation. Our results indicate that humans walk with a more stable pelvis than chimpanzees, especially in tilt and rotation. Both species exhibit similar magnitudes of pelvis list, but with segment motion that is opposite in phasing. In the hind limb, chimpanzees walk with a more flexed and abducted limb posture, and substantially exceed humans in the magnitude of hip rotation during a stride. The average stride-to-stride variation in joint and segment motion was greater in chimpanzees than humans, while the intraspecific variation was similar on average. These results demonstrate substantial differences between human and chimpanzee bipedal walking, in both the sagittal and non-sagittal planes. These new 3-D kinematic data are fundamental to a comprehensive understanding of the mechanics, energetics and control of chimpanzee bipedalism.

Keywords: Chimpanzee; Human; Kinematics; Pelvis; Hind limb; Bipedalism

Introduction

Humans are unique among apes and other primates in the musculoskeletal design of their pelvis and hind limbs¹. Our short, wide pelvis and long, heavy hind limbs reflect both our evolution from an arboreal ape as well as selection pressures for an economical, two-legged walking stride (Rodman and McHenry, 1980; Sockol et al., 2007). The common chimpanzee (*Pan troglodytes*) – a facultative biped and our closest living relative – uses a more expensive, flexed-limb gait when moving on two legs. While qualitative differences between human and chimpanzee bipedal walking kinematics have been noted at least since the pioneering work of Elftman (1944), direct quantitative comparisons of their pelvis and hind limb motions are quite limited. Yet, such data are essential for understanding how variation in musculoskeletal structure affects locomotor performance.

The three-dimensional (3-D) kinematics of human walking have been examined and described in considerable detail (e.g. Apkarian et al., 1989; Kadaba et al., 1990; Rose and Gamble, 2006). These studies have revealed important non-sagittal plane motions with direct relevance for understanding joint and muscle-tendon mechanics. For example, measurements of the 3-D motion of the pelvis and thigh are needed for the accurate determination of hip joint kinetics (e.g. Eng and Winter, 1995) and associated skeletal loading (e.g. Stansfield et al., 2003a), as well as calculations of muscle-tendon force and fascicle length change during a stride (e.g. Arnold and Delp, 2011). Given this, accurate 3-D quantification of segment and joint motion has become fundamental to determining the mechanics, energetics and control of locomotor tasks. In chimpanzee bipedal walking,

¹ While “lower limb” is typically preferred in human-specific studies, we use “hind limb” to describe the thigh, shank and foot in both chimpanzees and humans.

qualitative observation indicates that – in addition to their well-known flexed-limb posture – substantial 3-D motions occur about the pelvis and hips (Elftman, 1944; Jenkins, 1972; Stern and Susman, 1981; Stern and Larson, 1993). Yet, no comprehensive joint motion analysis has been undertaken.

Most previous studies of chimpanzee kinematics have been limited to spatio-temporal analyses that focus on a few quantitative metrics, such as stride lengths and durations (Alexander and Maloiy, 1984; Renyolds, 1987; Kimura, 1987, 1990; Aerts et al., 2000; Kimura and Yaguramaki, 2009). Sagittal plane hip, knee and ankle angles have been published for bonobos (D'Août et al., 2002) and, more recently, for common chimpanzees (Pontzer et al., 2014). However, to date, the only multi-plane investigation of chimpanzee pelvis and hind limb motion during bipedal walking is that of Jenkins (1972). Therein, two-dimensional cineradiography taken asynchronously in both sagittal and frontal planes was used to reconstruct the motion of the pelvis, femur, tibia-fibula and foot elements. This approach has the advantage of permitting the direct tracking of skeletal motion, but the published report itself lacks much quantitative detail regarding the timing or duration of the observed kinematics. Further, in this and other studies, no comparable walking data were collected from humans.

Equivalent lab-based measurements of chimpanzees and humans have the potential to improve our understanding of the mechanics, energetics and control of facultative and habitual bipedalism. The aim of this study is to present the 3-D kinematics of the pelvis and hind limb of bipedal walking in both species, as well as compare stride-to-stride, intraspecific and interspecific variation. For completeness, our chimpanzee data are compared to the kinematics of humans walking at similar dimensionless (i.e. relative-

speed match) and dimensional (i.e. absolute-speed match) speeds. The dimensionless comparison minimizes the effects due to differences in body size or speed, while emphasizing those arising specifically from differences in musculoskeletal design between chimpanzees and humans. The dimensional comparison, in contrast, permits an assessment of how sensitive the interspecific differences in 3-D kinematics are to walking speed.

Materials and Methods

Chimpanzee and human subjects

Three-dimensional kinematic data were collected from the pelvis and hind limbs of three male common chimpanzees *Pan troglodytes* (Blumenbach, 1775) (age: 5.5 ± 0.2 yrs; M_b : 26.5 ± 6.7 kg) and three male humans *Homo sapiens* (age: 24.3 ± 2.3 yrs; M_b : 79.2 ± 6.2 kg). The number of human subjects was matched to the chimpanzee dataset to facilitate a comparison of interspecific movement variability. Each bipedal chimpanzee walked across an 11 m rigid, level runway at self-selected speeds, following an animal trainer offering a food reward (Fig. 1). Human data were then collected during walking along a 20 m rigid, level runway at speeds matching the chimpanzee dataset in dimensionless (i.e. relative-speed match) and dimensional (i.e. absolute-speed match) forms. The Stony Brook University Institutional Animal Care and Use Committee and the University of Massachusetts Amherst Institutional Research Board approved all chimpanzee and human experiments, respectively. The human subjects each provided written informed consent before participating in the study.

Chimpanzee training

Each chimpanzee was trained to walk on its hind limbs across the 11 m rigid, level runway at self-selected speeds using food rewards and positive reinforcement. The training regime consisted of mixed periods of walking and resting over approximately 1 hour per day, 3-5 days per week for at least 6 months prior to the start of data collection. The aims of the training regime were to teach each chimpanzee to walk bipedally for multiple strides on command and follow a straight path along the runway through the

calibrated recording volume. Training familiarized the animals with the experimental protocol, thereby reducing random kinematic variance unrelated to musculoskeletal design and/or speed effects. In our view, training was essential to maximizing the comparability of our chimpanzee and human data sets.

Musculoskeletal modeling

Generic musculoskeletal models of the pelvis and hind limb of an adult chimpanzee (O'Neill et al., 2013) and an adult human (Delp et al., 1990) were used for the calculation of the 3-D kinematics (Fig. 2). The chimpanzee and human models include skeletal geometry of the pelvis, as well as the right and left femora, patellae, tibiae, fibulae, tarsals, metatarsals, halluxes (1st digit) and phalanges (2nd-5th digits). The pelvis is assigned six degrees of freedom, permitting rotation in the sagittal (tilt), frontal (list) and transverse (rotation) planes, as well as whole-body translation through the global coordinate space. The 3-D pelvis and hip orientations were quantified using a Cardan angle approach, which is the international standard for quantifying biological joint motion (Cole et al., 1993; Wu and Cavanagh, 1995). Cardan angles are not subject to the errors associated with angles that are projected onto the primary anatomical planes (Woltring, 1991). Projected angles would be especially problematic with the chimpanzees, due to the large amount of transverse plane rotation. The use of Cardan angles requires the a priori specification of a particular rotation sequence. If the rotation sequence is chosen properly, then the angles that are obtained will correspond to the functional anatomical meaning of the joint angles. The orientation of the pelvis relative to the global reference frame was expressed using the Cardan angle rotation sequence:

rotation, list, tilt. This rotation sequence yields pelvis angles that match the functional anatomical meanings of the terms rotation, list and tilt (Baker, 2001). The mobile articulations at the right and left hip have three rotational degrees of freedom. The orientation of the thigh relative to the pelvis was expressed using the Cardan angle rotation sequence: flexion-extension, abduction-adduction, internal-external rotation (Kadaba et al., 1990). As with the pelvis angles, the hip rotation sequence was chosen such that it yielded angles that match the functional anatomical meanings of the terms used to describe them (e.g., abduction-adduction). The knees and ankles (talocrural joints) each have one rotational degree of freedom. The knees and ankles in both the chimpanzee (O'Neill et al., 2013) and human models (Delp et al., 1990) had rotational axes that were parameterized to reflect the anatomy of these joints, rather than having pure mediolateral rotation axes. The rotational degrees of freedom at the knee joints (flexion-extension) are coupled with translation of the tibia relative to the femur to account for the non-circular nature of the femoral condyles. The ankles each have a one degree-of-freedom (plantar flexion-dorsiflexion) revolute joint between the tibia-fibula and talus, with anatomically realistic skewed joint axes. The alignment of the body segments when all angles are equal to zero is shown for both the chimpanzee and human models in Fig. 2.

Marker data collection

A combination of markers placed over anatomical landmarks and clusters of non-collinear markers were applied to the pelvis, thigh, leg and foot to track segment motions for all subjects (Fig. 3). Nontoxic, water-soluble white paint was used for the chimpanzee

markers, while reflective spheres were used for the human markers. Paint markers were applied while the chimpanzees were maintained under general anesthesia in a sterile surgical suite. To facilitate robust identification of anatomical landmarks and help ensure that all the paint markers were visible throughout the experiment, the fur was shaved in the area surrounding each marker location. The number and position of markers used for each species was selected so as to meet or exceed recommendations for rigid segment 3-D kinematics (Cappozzo et al., 1997). Detailed definitions of the chimpanzee and human marker sets are given in Supplementary Online Material (SOM) Tables 1-2.

Marker positions were recorded using synchronized high-speed video cameras. Marker data for the chimpanzees were recorded using a four-camera system recording at 150 Hz (Xcitex, Inc.; Boston, MA, USA), while data for the humans were recorded using an eleven-camera system recording at 240 Hz (Qualisys, Inc.; Gothenburg, Sweden). The calibrated recording volume for the chimpanzee marker data was established using a direct linear transformation approach and a custom-built calibration frame. A wand-based nonlinear transformation approach was used to create the calibrated volume for the human marker data. In all trials, video recording was manually triggered when the chimpanzee or human subject entered the calibrated volume. Marker locations in the videos were digitized using ProAnalyst software (Xcitex, Inc.; Boston, MA, USA) for the chimpanzee dataset and Qualisys Track Manager software (Qualisys, Inc.; Gothenburg, Sweden) for the human dataset. The x -, y -, and z - coordinates of each marker trajectory were filtered using a fourth order zero-lag Butterworth low-pass filter (Winter et al., 1974). The filter cut-off frequency was set to within the range of 4-6 Hz based upon visual inspection of the filtered versus unfiltered data. The specifications and filtered

marker data from each trial were then configured into a file format compatible with OpenSim software (Delp et al., 2007).

Model scaling and kinematics

The generic chimpanzee and human musculoskeletal models were scaled to the size of each subject in OpenSim via a calibration trial (Delp et al., 2007). Since it was not possible to train the chimpanzees to stand quietly in the calibrated volume in a position that permitted a clear view of the full 3-D marker set, a short series of video frames from a walking stride were used for static calibration instead. For our subjects and marker set, the double-support phase of a stride typically provided the most comprehensive view. Human calibration trials were obtained using a more traditional quiet standing posture. In a subset of human trials, we confirmed that the differences in the calibration trial postures had a trivial effect on model scaling, and thus the kinematic results. In both cases, the pelvis was scaled using three or more skeletal landmarks, while each thigh, leg and foot were scaled based on proximal and distal skeletal landmark endpoints. Segment marker clusters were not used for scaling; rather, their precise positioning on a given musculoskeletal model was defined relative to the anatomical markers for each experiment.

An inverse kinematics algorithm was used to determine the 3-D coordinates of the scaled model over the full gait cycle. This was done through a least-squares minimization of the experimentally determined marker positions and the marker positions on the scaled model, subject to constraints enforced by the anatomical models of the joints (Lu and O'Connor, 1999; Delp et al., 2007). This inverse approach differs from traditional

kinematic calculations in some important ways that can be expected to improve the overall quality of the reconstruction of skeletal positions and orientations. Traditional methods treat each body segment separately, which can lead to apparent dislocations at joints due to skin movement artifacts and/or other marker tracking errors. These errors occur when markers displace or rotate relative to the underlying skeletal element, and can be of particular concern for computing frontal and transverse plane motion (Cappozzo et al., 1996). The approach used in this study reduces these errors by computing the 3-D kinematics at all joints simultaneously using scaled, linked models of pelvis and hind limb segments that are constrained to move about realistic joint axes.

Statistics

Four trials per subject were analyzed. All 3-D angular data were normalized to 101 points over one full stride using cubic spline interpolation, facilitating compilation of multiple trials. This also permitted the mean $\pm$ standard deviation (s.d.) of the kinematic curves to be determined per subject and species.

For the chimpanzees, walking speed was calculated as the average of the instantaneous forward velocity of four markers (i.e. 3 pelvis, 1 hip marker) over the full stride. For humans, walking speeds were prescribed ($\pm 3\%$) using photocells positioned at known distances along the runway. Actual walking speeds for the trials selected for analysis were calculated based on the forward velocity of the marker placed over the sacrum. To account for differences in body size among subjects and between species, velocity was made dimensionless by the divisor $(gL)^{0.5}$ and the Froude number (Fr ; v^2/gL) using the base units of gravitational acceleration g and average hind limb length L . Hind limb

length was measured as the height of the greater trochanter marker (see Table S1) from the ground during the middle of the single-support phase of a walk for chimpanzees (L : 0.39 ± 0.02 m) and during quiet standing for humans (L : 0.92 ± 0.05 m). Stance, swing and stride duration were determined based on synchronously collected ground reaction forces (not included herein) recorded from individual foot contacts on an array of four force platforms (Advanced Mechanical Technologies, Inc.; Watertown, MA, USA). Stride length and stride frequency were calculated from speed and stride duration, and were made dimensionless by the divisors L and $(g/L)^{0.5}$, respectively.

To compare the stride-to-stride, intraspecific and interspecific variation of the pelvis and hind limb angles of our chimpanzee and human samples, the adjusted coefficient of multiple correlation (CMC) (Kadaba et al., 1989) was calculated. The CMC represents the correlation of the segment or joint motion among strides for each individual (i.e. stride-to-stride variation) or among individuals (i.e. intraspecific variation). Finally, the balanced chimpanzee and human datasets permits a direct, interspecific comparison of CMCs.

RESULTS

The self-selected, average walking speed was $1.09 \pm 0.10 \text{ m s}^{-1}$ for the chimpanzees, and the matched relative walking speed for the human subjects was $1.66 \pm 0.06 \text{ m s}^{-1}$. These values correspond to identical dimensionless velocities (v) of 0.56 ± 0.06 and 0.56 ± 0.01 , and Froude numbers (Fr) of 0.31 ± 0.06 and 0.31 ± 0.02 for each species, respectively (Table 1). These speeds are close to – but slightly faster than – the preferred overground speeds for human walking, but well below the expected walk-run transition speed (i.e. $v = 0.7$; $Fr = 0.5$; Alexander, 1989; Kram et al., 1997). The chimpanzees and humans walked with stride lengths of $0.78 \pm 0.07 \text{ m}$ and $1.69 \pm 0.15 \text{ m}$ and stride frequencies of $1.43 \pm 0.23 \text{ Hz}$ and $1.00 \pm 0.05 \text{ Hz}$, respectively. The stance and limb-swing durations (of individual limbs) were $0.45 \pm 0.09 \text{ s}$ and $0.27 \pm 0.03 \text{ s}$ for chimpanzees, and $0.64 \pm 0.02 \text{ s}$ and $0.36 \pm 0.04 \text{ s}$ for humans. As such, the duty factors were nearly equivalent.

Pelvis kinematics

Pelvis motion was tracked in the global coordinate system and expressed relative to neutral position (Fig. 2) in the sagittal, frontal and transverse planes using Cardan angles (Table 2; Fig. 4). In the sagittal plane, humans tilt their pelvis forward by a mean peak angle of 7° around which there is a range of motion of 5° ; similarly, chimpanzees tilt their pelvis forward by a mean peak angle of 5° with a range of motion of 8° . In one chimpanzee, the pelvis had a slight backward tilt during the first double-support period and the single support period (Fig. 4A). In the frontal plane, chimpanzee and human pelvis list by similar magnitudes, but in patterns that are out-of-phase with one another.

The chimpanzee pelvis lists 6° downward on the stance side during the support phase, and thus rises by a similar amount on the swing side. In contrast, humans exhibit a more nuanced pattern. During the first double-support period, the human pelvis lists upward on the stance side, exhibits a small oscillation in single-limb support, and then drops downward in the second double-support period, continuing into swing. In the transverse plane, chimpanzees and humans exhibit a similar pattern of internal and then external pelvic rotation, except that for chimpanzees the total magnitude (i.e. range of motion) is much greater. During the stance phase, the chimpanzee pelvis internally rotates by 29° , whereas humans exhibit only 9° of internal rotation. The chimpanzees also exhibit some transverse plane asymmetry not present in humans. Specifically, two of the three chimpanzees rotated their pelvises such that the contralateral hip joint moved forward more than the ipsilateral hip joint. This is apparent in that pelvis rotation angle for two chimpanzees oscillate around a net positive angle, rather than a net zero angle (Fig. 4C).

Hind limb kinematics

The chimpanzee hip is maintained in a more flexed posture throughout the stride than humans (Table 2; Fig. 5). In both species, peak hip extension occurred during the second double-support period, while peak hip flexion occurred during swing phase. Of course, the mean peak hip extension was 25° of hip flexion in chimpanzees, since they never actually reach an extended hip angle (i.e. past neutral position). Unlike chimpanzees, the human hind limb is extended past neutral position for the second half of stance phase and into early swing phase. Chimpanzees reached a mean peak hip flexion angle of 52° at mid-swing. Chimpanzees and humans differ considerably in the frontal plane motion of

the hip. While humans adduct their hips by 9° during the stance phase, due in large part to their valgus knee, chimpanzees consistently maintain their hip in abduction. Chimpanzees exhibited a peak abduction angle of 30° , although some notable variation in pattern and magnitude of hip abduction angle is evident throughout the stance phase. During swing phase, the hip adducts 16° in chimpanzees, indicating that limb swing includes significant non-sagittal plane motion. There are also considerable differences between species in the transverse plane motion of the hip. Chimpanzees exhibit substantial hip rotation throughout the stance and swing phases. The hip begins the first double support period in 35° of external rotation, is rapidly internally rotated by about 25° , and then more gradually internally rotates by an additional 14° throughout the remainder of the stance phase. During the swing phase, the limb is externally rotated back to 35° by heel strike. The human hip exhibits 18° of internal rotation during the support phase and then is externally rotated by a similar amount over the swing phase.

The knee exhibited the greatest range of motion of any joint in both chimpanzees and humans; however, chimpanzees maintain their knee in a more flexed position throughout stance and swing phases (Fig. 5). Of the hind limb joints measured, the knee angles were the most consistent among strides and among chimpanzees. In chimpanzees, the knee is flexed from 20° to 60° in the first double-support phase, maintained at 60° during single support and then begins flexing further during the second double-support period. A small amount of knee extension was observed during single support into the second double-support period in one chimpanzee (Fig. 5G). Humans exhibit a similar pattern, albeit with consistent knee extension during single support, on a more fully extended knee. In both

species, the largest joint excursions occur during limb swing, with the knee reaching peak flexion in the first half of swing phase.

The chimpanzee ankle (talocrural joint) exhibits a larger range of motion than humans over a stride (Fig. 5). This is due to the fact that chimpanzee ‘heel strike’ takes place with the ankle in about 15° of plantar flexion. The ankle dorsiflexes during the first double support phase and then is maintained in a dorsiflexed position throughout single support. The ankle plantar flexes during the second double support period, reaching the neutral position near the stance-swing transition. During the swing phase, the ankle first dorsiflexes, to aid with toe clearance, and then plantar flexes leading up to heel strike. The human ankle, in contrast is maintained near the neutral position for most of the stance phase, except for the second double-support period, during which the ankle is rapidly plantar flexed for push off. To facilitate further comparisons, the mean chimpanzee and human kinematic data presented herein are available at <http://simtk.org/home/chimphindlimb>.

Stride-to-stride and intraspecific kinematic variation

For the chimpanzees and human samples, the coefficients of multiple correlation (CMCs) were smaller between strides than between individuals (Table 3). This indicates that there is more variation among chimpanzees and humans in pelvis and hind limb kinematics than there is within a given individual from one stride to the next. Among individuals, tilt was the most variable pelvic motion in chimpanzees ($r_a^2=0.43$) and humans ($r_a^2=0.58$). For the hind limb, hip adduction was the most variable among chimpanzees ($r_a^2=0.31$), but in humans hip adduction, rotation and ankle flexion had

similar CMC values. Our human results appear to be representative of larger human samples, as they are generally consistent with the CMC results of both Kadaba et al. (1989) and Besier et al. (2003).

Directly comparing the CMC values of our chimpanzee and human samples indicates that, on average, chimpanzees are more variable in their kinematics stride-to-stride (i.e. chimp mean: $r_a^2=0.82$, human mean: $r_a^2=0.97$). That is, a human walking stride is more stereotyped than a bipedal stride of chimpanzees, in both pelvis and hind limb motion. Among subjects, chimpanzees exhibit greater variability than humans in pelvis and hind limb motion as well (i.e. chimp mean: $r_a^2=0.71$, human mean: $r_a^2=0.81$), but not dramatically so. Nevertheless, these interspecific differences do indicate greater variance in the kinematics of facultative bipedalism than habitual bipedalism.

Dimensional vs. dimensionless kinematics

For the dimensional comparison, humans walked at an average speed of $1.08 \pm 0.02 \text{ m s}^{-1}$ (SOM Table 3). This results in a dimensionless velocity (v) of 0.36 ± 0.06 and a Froude number (Fr) of 0.13 ± 0.06 , which is just below the preferred overground walking speed of humans (Rose and Gamble, 2006).

The differences between species in pelvis and hind limb kinematics observed at matched dimensionless speeds were generally maintained when comparisons were done at matched dimensional speeds (SOM Fig. 1-2). The human pelvis and hind limb had lower ranges of motion at 1.08 m s^{-1} than 1.66 m s^{-1} (SOM Table 4); however, the CMC values were nearly the same as the faster speed kinematics, on average (SOM Table 5). This is true for both the stride-to-stride (i.e. dimensional mean: $r_a^2=0.965$, dimensionless

mean: $r_a^2=0.968$) and among subjects variability (i.e. dimensional mean: $r_a^2=0.816$, dimensionless mean: $r_a^2=0.820$). Taken together, these results indicate that the differences between bipedal chimpanzee and human kinematics are maintained across a wide range of walking speeds.

Discussion

The kinematics of chimpanzee bipedal walking have been used to address a number of important issues in studies of human evolution, including the posture, gait and skeletal loading in fossil hominin locomotion. However, these inferences have relied on an incomplete quantitative description of the 3-D motion of the chimpanzee pelvis and hind limb, and have been without any direct, side-by-side comparisons with human walking kinematics. Here, we have carried out detailed 3-D analyses of chimpanzee and human bipedal walking at similar dimensionless and dimensional speeds. These data demonstrate that the kinematics of bipedal walking in chimpanzees are characterized by significant non-sagittal plane motion. The magnitude of this 3-D motion often exceeds that of human walking, especially for the pelvis and hip in the transverse plane. Importantly, these data improve our understanding of the differences between chimpanzee and human bipedalism, as well as our abilities to draw inferences between musculoskeletal structure and function.

At the same dimensionless velocities, chimpanzees use shorter, more frequent strides than humans. However, once differences in hip height are taken into account, chimpanzees actually walk with longer (C: 1.99 ± 0.16 ; H: 1.83 ± 0.10) and less frequent (C: 0.28 ± 0.04 ; H: 0.37 ± 0.02) strides than humans. The relatively long strides in chimpanzees are likely due to both their more flexed hind limb posture as well as their greater amount of pelvic rotation during the single support period. This contrast in spatio-temporal parameters appears to be maintained for walking speeds not measured here (Reynold, 1987; Aerts et al., 2000; Pontzer et al., 2014). An increased stride length per

velocity has been proposed as a potential advantage of bipedal walking with a more flexed hind limb (Schmitt, 2003).

Pelvis motion

Humans generally walk with a more stable pelvis than chimpanzees. In the sagittal plane, chimpanzees walked with a slight anterior tilt of their pelvis, which reached a mean peak value of 5° in single support into the second double-support period. The magnitude of this tilt is less than the 10° reported by Jenkins (1972), but only by a small amount that is likely explained either by variation among animals or differences in methodological approach. This contrasts with 2-D measurements of maximum *trunk* inclination in Kimura and Yaguramaki (2009) and Pontzer et al. (2014), who report much larger values for their chimpanzees. This suggests that a substantial portion of the anterior tilt of the chimpanzee trunk occurs proximal to the pelvis. This is likely due to the absence of lordotic curvatures in the lumbar region of their spine.

The most distinctive difference in pelvis motion between chimpanzees and humans occurs in the frontal plane during the single support period of a stride. It is well known that in human walking, the pelvis drops (lists) on the swing limb side (thereby raising the opposite side). In our human subjects, the pelvis lists a maximum of 8° from neutral position, on average. In contrast, as noted by Jenkins (1972), the pelvis rises on the limb swing side in chimpanzees, listing over the supporting limb. In our chimpanzees, this list reached a mean peak value of 6° from neutral position. This motion likely serves to elevate the swinging limb for foot-ground clearance, as well as maintain the whole-body center of mass over the base of support (i.e. foot) during the single-support period. That

is, pelvis elevation on the limb swing side will move the whole-body center of mass away from the midline and towards the support-side foot, which has a more lateral position in chimpanzees due to their abducted hips and small bicondylar angle.

Chimpanzees exceed humans in the total range of pelvic transverse plane rotation by about three times. Although Jenkins notes that chimpanzees rotate their pelvis around a “vertical axis passing approximately through the hip joint of the propulsive limb” (1972: 877), no measure of the magnitude of this rotation is reported. Interestingly, it has been argued, based on a compass gait model of walking, that a wider pelvis will increase the magnitude of pelvic rotation in order to minimize the vertical displacement of the body center of mass (Rak, 1991). However, chimpanzees exhibit substantial internal-external pelvic rotation when compared with humans walking at the same dimensionless speed, despite their narrower bi-acetabular diameter (Tauge and Lovejoy, 1986). Recent studies of human walking have found that pelvic rotation has a rather small effect on smoothing the body center of mass trajectory, contrary to the theoretical predictions of a compass gait model (Kerrigan et al., 2001). Thus, the greater transverse plane rotation of the pelvis may be due to the more posterior orientation of the iliac blades, or a strategy to compensate for short hind limbs regardless of pelvis width, or both. Among our chimpanzees at least, a greater hind limb length (L) was associated with a larger range of pelvis rotation during bipedal walking.

Hind limb motion

While bipedal chimpanzee and human walking differ – as expected – in hind limb flexion/extension kinematics, these data indicate that equally significant differences exist

outside the sagittal plane. In particular, a full 3-D accounting of hip motion appears to be critical for a comprehensive understanding of the mechanics of both facultative and habitual bipedalism.

In the frontal plane, humans exhibit some adduction during stance and abduction during swing phases; however, in general, the hip is maintained in near neutral position during walking. In contrast, chimpanzees exhibit a maximum of 30° of abduction from neutral position throughout the support phase, resulting in a relatively wide-stance bipedal gait. The abducted hip position in chimpanzees may be linked to the posterior orientation of their iliac blades, as well as the absence of a valgus knee. Regardless, this may serve to increase the base of support in the medio-lateral plane during double-support, and thereby enhance stability and control of whole-body balance in the frontal plane. Of course, when comparing hip adduction angles, the difference in the orientation of the femur with respect to the segment axes must be kept in mind. That is, in neutral position, the chimpanzee femur is nearly vertical, whereas the human femur has a more valgus angle (Fig. 2). In the human model the femur is already in a more adducted posture relative to that of a chimpanzee, so as to maintain knee joint congruence (i.e. femoral condyles to tibial plateau) in both species. Thus, to position the human femur in the same abducted position as in a chimpanzee in the global coordinate system, the difference between species in the neutral position and the bicondylar angle would need to be included. This suggests that the difference between species is even greater than the abduction-adduction hip angles appear, by an amount equal to the difference in bicondylar angle, which is about $5\text{-}10^\circ$ (Tardieu and Preuschoft, 1996).

In the transverse plane, humans experience only a small degree of hip internal-external rotation. In contrast, chimpanzees exhibit their largest hip range of motion in rotation over a stride. This is consistent with Stern and Susman (1981), who observed that chimpanzees internally rotate, rather than abduct, their hip during the stance phase of a bipedal stride. These results demonstrate that the hip is internally rotated by a significant amount (i.e. $\sim 23^\circ$) during the first double-support period of a stride. This internal rotation continues until the initiation of swing phase, at which point the hip begins to be externally rotated by 39° , on average. This substantial external rotation, and simultaneous abduction, is consistent with Stern and Larson (1993), who observed significant non-sagittal plane limb swing in chimpanzee bipedal walking. When comparing the non-sagittal plane hip joint kinematics between chimpanzees and humans, it is important to consider the orientation of the thigh segment. In humans, these motions occur with the femur nearly vertical. Thus, hip abduction-adduction and internal-external rotation correspond closely to motions of the pelvis in the global frontal and transverse planes, respectively. In contrast, these hip joint motions in chimpanzees occur about a femur that is oriented as much as 52° away from the global vertical axis when viewed in the sagittal plane (c.f. Fig. 1) causing non-sagittal hip joint motions to occur about axes that are not closely aligned with the global coordinate system.

The chimpanzee knee is maintained in a more flexed posture than in humans across the entire stride, consistent with the sagittal plane kinematics at the hip indicating a more crouched hind limb posture overall. In humans, during the single support phase, the knee is increasingly extended, while in chimpanzees the knee posture is maintained at a near-

constant position. Only in the second half of limb swing do the chimpanzee and human knee angles approach one another.

The chimpanzee ankle is maintained in a more dorsiflexed posture than in humans for most of a stride. However, chimpanzees exhibit some important differences from humans in the kinematics of heel strike and toe off. Several previous observational studies have noted that chimpanzees – unlike most nonhuman primates, but similar to other African apes – heel strike at the beginning of the support phase of a stride in quadrupedal (Gebo, 1992; Schmitt and Larson, 1995) and bipedal (Elftman and Manter, 1935) walking. Our data indicate that, despite this general similarity in plantigrade foot postures, chimpanzees position their ankle in $\sim 15^\circ$ of plantar flexion at heel strike, rather than in a slightly dorsiflexed position as in humans. Thus, humans must plantar flex the ankle for the foot to lie flat on the ground following heel strike. In contrast, the chimpanzee foot is placed nearly flat on the ground and the ankle begins to dorsiflex immediately after heel strike. This foot posture at ground contact in chimpanzees may help reduce the transient impact force on a non-rigid hind foot that lacks skeletal buttresses, such as a lateral plantar process on the calcaneal tuber. Thus, despite some superficial similarities between species, it appears that the heel strike in human walking is unique. Prior to toe off, during the second double-support period, the chimpanzee ankle undergoes a slower rate of plantar flexion than the human ankle, on average (C: $73 \pm 22^\circ \text{ s}^{-1}$; H: $92 \pm 18^\circ \text{ s}^{-1}$). A greater ankle angular velocity suggests a more powerful push-off in human walking, likely facilitated by our more rigid hind and midfoot (Susman, 1983).

Variation in chimpanzee and human walking kinematics

The data herein indicate that pelvis motion is more variable than hind limb motion in chimpanzees, and that chimpanzees exceed humans in kinematic variation from stride-to-stride. Our human kinematic data appear to be representative of much larger samples (Kadaba et al., 1989; Besier et al., 2003), suggesting that this result would hold with larger intraspecific samples. The greater kinematic variance observed here is likely due to the fact that bipedal walking in chimpanzees is an infrequent locomotor mode and, therefore, requires more kinematics adjustments from one stride to the next. It is possible that the facultative bipedalism of the earliest hominins was similarly variable among strides, at least until the emergence of habitual bipedal walking in australopiths.

The amount of variation in walking kinematics among individuals was on average larger in our chimpanzee than our human sample. This is consistent with the higher adjusted coefficients of variation for bonobo bipedal walking, as compared to humans, reported in a study of sagittal plane hind limb angles (D'Août et al., 2002). The considerable differences between the bonobo and human samples (i.e. un-matched speeds, markerless vs. marker-based joint kinematics, etc.) allowed only limited interspecific inferences; however, the direct correspondence between our chimpanzee and human datasets reinforce and extend these conclusions. As such, these results indicate that there is greater variance in bipedal walking kinematics among facultative bipeds than among habitual bipeds. Greater intraspecific variance in kinematics (and other aspects of bipedal locomotor performance; Sockol et al., 2007) would have been important raw material for natural selection on the gait of the earliest hominin bipeds, at least 6.8-7.2 million years ago (Zollikofer et al., 2005; Lebatard et al., 2008).

Limitations of this study

Studies of the development of human walking kinematics indicate that children over the age of 5 years have an adult-like gait in terms of spatio-temporal parameters, segment motion and metabolic costs, once differences in size are accounted for (Sutherland, 1997; Stansfield et al., 2003b; Weyand et al., 2010). Chimpanzees grow into adults at a faster rate than humans (Zihlman et al., 2004), but are still sub-adult between the ages of 5 and 6 years old. Ontogenetic studies of chimpanzee bipedal walking have found some differences between the spatio-temporal kinematics of sub-adults and adults (Kimura, 1987, 1990; Kimura and Yaguramaki, 2009); however, the extent to which these differences are due to age rather than speed is difficult to make clear, since sub-adult chimpanzees walked at faster dimensionless speeds in these studies. In contrast, the sagittal plane hip, knee and ankle kinematics of chimpanzees walking at identical dimensionless speeds were quite similar between animals ranging in age from 6 to 33 years old (Pontzer et al., 2014). Moreover, ground reaction forces indicate that by the age of 5, chimpanzees exhibit adult-like walking mechanics, independent of speed (Kimura, 1996). More speed-controlled studies of chimpanzee bipedal walking across a range of ages are needed to understand the effect of growth and development on kinematics in this species.

Our analyses did not quantify knee joint abduction-adduction or internal-external rotation during bipedal walking. Although knee motion in locomotion primarily occurs about the flexion-extension axis, studies of the internal anatomy of chimpanzee and human knees suggest that chimpanzees should generally have greater knee joint mobility than humans. This is due to a number of traits, including a single insertion of the lateral

meniscus, a more anterior attachment of the posterior cruciate ligament and the absence of an anterior transverse ligament (Senut and Tardieu, 1985; Aiello and Dean, 1991). However, it is not immediately apparent that these differences in joint anatomy effect abduction-adduction or internal-external rotation ranges of motion at the knee during bipedal walking. Further, it is not clear whether non-sagittal plane knee joint motions can be accurately resolved using skin-based markers (e.g. Reinschmidt et al., 1997).

Implications for fossil hominin bipedal biomechanics

Our study adopts techniques developed in 3-D human gait analysis for the study of chimpanzee bipedalism. These results represent a comprehensive characterization of the kinematics of chimpanzee pelvis and hind limb motion, and a detailed comparison to human walking. More broadly, these results provide insight into how interspecific differences in musculoskeletal structure lead to alterations of 3-D segment motion.

One important difference in musculoskeletal structure between these species is that chimpanzees possess a shorter, less mobile lumbar column than humans. While there is almost no lumbar or sacral fossil material available for a hominin species preceding *Australopithecus afarensis*, it has been argued that the last common ancestor of *Pan* and *Homo* had a much longer lumbar column with six or seven vertebrae, similar to an Old World monkey (e.g. a macaque) (McCollum et al., 2010; Lovejoy and McCollum, 2010; but see Williams, 2012). Further, Lovejoy and McCollum (2010) have proposed that this would preclude the use of flexed-limb postures at any point in hominin locomotor evolution. Yet, even a cursory comparison of our chimpanzee dataset with similar 3-D kinematics from ‘highly-trained’ bipedal Japanese macaques, *Macaca fuscata* (Ogihara et

al., 2010) makes clear that both species walk with a similar flexed-limb posture, despite differences in the number of lumbar vertebra. That is, chimpanzees and macaques are much more similar to each other in 3-D pelvis and hind limb kinematics than either are to humans. Thus, the length of the lumbar region in the last common ancestor of *Pan* and *Homo* – whether it was ‘short-backed’ or ‘long-backed’ – appears to be less consequential for bipedal walking kinematics than some have argued (e.g. Lovejoy, 2005; Lovejoy et al., 2009; Lovejoy and McCollum, 2010; McCollum et al., 2010;).

Finally, our results make clear that facultative bipedalism of chimpanzees is a complex 3-D task that differs from human walking in many important respects beyond flexion-extension of the hip and knee. This is the case for bipedal walking in macaques as well (Ogihara et al., 2010). Thus, the characterization of facultative bipedalism in chimpanzees and other non-human primates as ‘bent-hip, bent-knee’ is a substantial oversimplification of the actual 3-D motion of the pelvis and hind limbs. Nevertheless, a number of studies have used a human crouched gait as a substitute for chimpanzee kinematics (Li et al., 1996) and/or as an experimental design for testing hypotheses about the mechanics and energetics of fossil hominin locomotion (e.g. Crompton et al., 1998; Carey and Crompton, 2005; Raichlen et al., 2010; Foster et al., 2013). A comparison of the 3-D kinematics of human crouched walking and chimpanzee bipedal walking is needed to identify the commonalities that exist outside the sagittal plane hip and knee joint motion. This may further elucidate the contexts in which human crouched walking is a useful experimental design for testing hypotheses about chimpanzee or fossil hominin locomotion.

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FIGURE CAPTIONS

Figure 1. A full bipedal walking stride. A full stride includes both stance and swing phases. The stance phase is divided among the first double support (double support 1), single support, and the second double-support (double support 2) periods. In the first double-support period the right hind limb is the leading limb, while in the second double-support period the right hind limb is the trailing limb.

Figure 2. The local coordinate systems of the (A) chimpanzee and (B) human pelvis and hind limb segments, shown in frontal (left panel) and sagittal (right panel) views. Models are positioned in neutral postures. The x - (yellow), y - (red) and z - (green) axis are positioned at the origins of the pelvis, thigh, shank, and foot segments of each model. Joint angles are expressed as the orientation of the distal segment coordinate system relative to the proximal segment coordinate system. For the pelvis, segment orientation is expressed relative to the global coordinate system.

Figure 3. The anatomical markers and segment marker clusters used for determining the (A) chimpanzee and (B) human kinematics, shown in frontal (left panel) and sagittal (right panel) views. Models are positioned in approximate standing postures. See SOM Tables 1 and 2 for a detailed listing of marker locations.

Figure 4. The pelvis (A-B) tilt, (C-D) list and (E-F) rotation angles (relative to the global coordinate system) over a walking stride (mean $\pm$ s.d.) for the three individual chimpanzees (column 1) as well as chimpanzees (solid blue line) and humans (dashed black line) as groups (column 2). Each stride begins and ends at ipsilateral heel strike. Vertical lines show the average stride event times for the chimpanzees. The broken vertical lines represent contralateral limb toe-off (C: 14%; H: 13%) and the contralateral limb heel strike (C: 48%; H: 51%), which define the double-support and single support phases of a stride; the solid vertical line represents ipsilateral toe off (C: 62%; H: 63%), which defines the start of the swing phase. The human average stride event times were quite similar and therefore are not shown.

Figure 5. The hip (A-B) flexion, (C-D) adduction, (E-F) rotation, (G-H) knee flexion and (I-J) ankle flexion angles over a walking stride (mean $\pm$ s.d.) for the three individual chimpanzees (column 1) as well as chimpanzees (solid blue line) and humans (dashed black line) as groups (column 2). Each stride begins and ends at ipsilateral heel strike. Vertical lines show the average stride event times for the chimpanzees. The broken vertical lines represent contralateral limb toe-off (C: 14%; H: 13%) and the contralateral limb heel strike (C: 48%; H: 51%), which define the double-support and single support phases of a stride; the solid vertical line represents ipsilateral toe off (C: 62%; H: 63%), which defines the start of the swing phase. The human average stride event times were quite similar and therefore are not shown.

Table 1. Spatio-temporal gait parameters in chimpanzee and human bipedal walking.

	v^a (m s ⁻¹)	v^b	Fr^c	stance time (s)	swing time (s)	stride length (m)	stride frequency (Hz)	duty factor
Chimpanzees	1.09±0.10	0.56±0.06	0.31±0.06	0.45±0.09	0.27±0.03	0.78±0.07	1.43±0.23	0.62±0.03
Humans	1.66±0.06	0.56±0.01	0.31±0.02	0.64±0.02	0.36±0.04	1.69±0.05	1.00±0.05	0.64±0.02
^a dimensional velocity								
^b dimensionless velocity								
^c Froude number								

Human data are matched to the chimpanzee data in dimensionless (i.e. relative-speed match) form (mean±s.d.).

Table 2. Joint angle minimum (Min), maximum (Max) and range of motion (ROM = Max – Min) values in degrees.

		Pelvis Tilt	Pelvis List	Pelvis Rotation	Hip Flexion	Hip Adduction	Hip Rotation	Knee Flexion	Ankle Flexion
Chimpanzees	Min	-5±4°	-6±1°	-12±7°	25±9°	-30±3°	-35±3°	-92±2°	-19±8°
	Max	3±3°	6±1°	29±12°	52±6°	-14±7°	4±4°	-14±3°	19±4°
	ROM	8±1°	12±2°	41±13°	27±4°	16±4°	-39±2°	78±1°	38±5°
Humans	Min	-7±2°	-7±2°	-9±5°	-14±3°	-12±6°	-14±3°	0±1°	-18±6°
	Max	-2±1°	8±3°	9±3°	35±5°	9±4°	4±3°	-72±1°	10±5°
	ROM	5±1°	15±0°	18±3°	48±5°	21±3°	18±5°	73±3°	28±6°

Human data are matched to the chimpanzee data in dimensionless (i.e. relative-speed match) form (mean±s.d.).

Table 3. Adjusted coefficient of multiple correlation (CMC) of pelvis and hind limb joint angles.

	Pelvis Tilt	Pelvis List	Pelvis Rotation	Hip Flexion	Hip Adduction	Hip Rotation	Knee Flexion	Ankle Flexion
Chimpanzees ^a	0.557±0.248	0.918±0.082	0.789±0.195	0.890±0.102	0.563±0.250	0.940±0.036	0.978±0.009	0.885±0.030
Among Chimpanzees ^b	0.430±0.217	0.841±0.177	0.732±0.177	0.713±0.044	0.314±0.074	0.897±0.059	0.958±0.011	0.818±0.087
Humans ^a	0.808±0.135	0.994±0.002	0.989±0.004	0.998±0.002	0.996±0.001	0.970±0.017	0.997±0.002	0.991±0.007
Among Humans ^b	0.576±0.194	0.760±0.184	0.819±0.105	0.973±0.016	0.814±0.132	0.828±0.043	0.968±0.022	0.819±0.096

Human data are matched to the chimpanzee data in dimensionless (i.e. relative-speed match) form (mean±s.d.).

^a Correlations between strides within subjects.

^b Correlations between subjects.

CMC mean±s.d. for 4 trials per subject, 3 subjects.

Figure 1

Figure 2

A

B

Figure 3

A

B

Figure 4

Figure 5