Journal of Human Evolution 86 (2015) 32–42

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Three-dimensional kinematics of the pelvis and hind limbs in chimpanzee (*Pan troglodytes*) and human bipedal walking

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ARTICLE INFO

Article history:
Received 6 September 2014
Accepted 20 May 2015
Available online 17 July 2015

Keywords:
Chimpanzee
Human
Kinematics
Pelvis
Hind limb
Bipedalism

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.

1. Introduction

Humans are unique among apes and other primates in the musculoskeletal design of the pelvis and hind limbs.[1] 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, qualitative observation indicates that

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[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.

http://dx.doi.org/10.1016/j.jhevol.2015.05.012
0047-2484/

– 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; Kimura, 1987, 1990; Reynolds, 1987; Aerts et al., 2000; Kimura and Yaguramaki, 2009). Sagittal plane hip, knee and ankle angles have been published for bonobos (D'Aoû t 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.

2. Materials and methods

2.1. Chimpanzee and human subjects

Three-dimensional kinematic data were collected from the pelvis and hind limbs of three male common chimpanzees *P. troglodytes* (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.

2.2. 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 h 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.

2.3. Musculoskeletal modeling

Generic musculoskeletal models of the pelvis and hind limbs 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

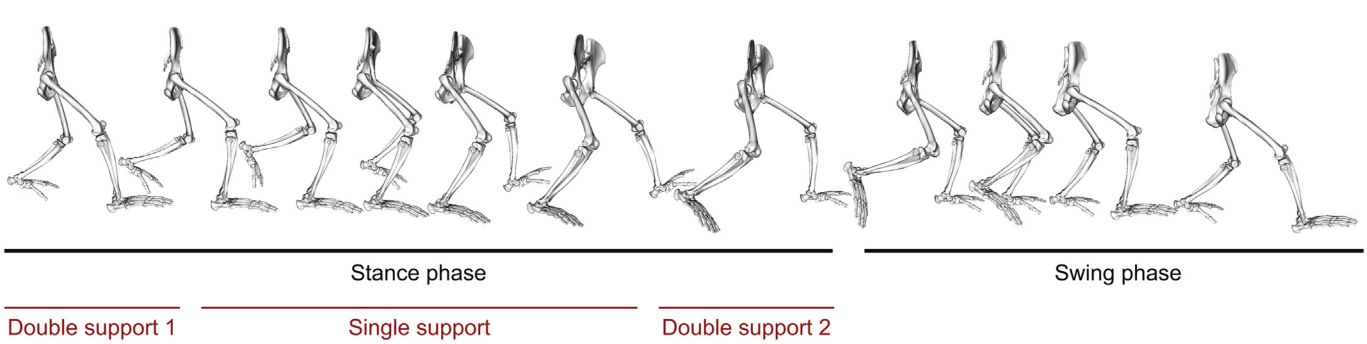

Figure 1. A full bipedal walking stride. A full stride includes both stance and swing phases. The stance phase is divided among the first double support (double support 1), single support, and the second double-support (double support 2) periods. In the first double-support period the right hind limb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