

The Kinematics of Load Carrying in Humans and Great Apes: Implications for the Evolution of Human Bipedalism

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Key Words

Bipedalism · Evolution · Load carrying · Kinematics · Great apes · Locomotion

Abstract

We present a comparison of loaded and unloaded carrying kinematics in humans, common chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), western lowland gorillas (*Gorilla gorilla gorilla*) and Bornean and Sumatran orang-utans (*Pongo pygmaeus* and *Pongo abelii*). Human hindlimb joint and segment angles were collected during treadmill locomotion using infrared motion analysis cameras. Non-human primate fore- and hindlimb joint and segment angles were collected at zoos during free-ranging locomotion using a standard video camera. In quadrupedal locomotion there were small but potentially important changes associated with load carriage leading to a more upright trunk and a shift in shoulder excursion. These changes were exacerbated as locomotion shifts from quadrupedal to tripedal and bipedal gaits when carrying more awkward loads suggesting a possible adaptive sequence. However, food carrying may favour a highly flexed bent-hip bent-knee bipedal gait since it allows simultaneous foraging and hoarding. In bipedal humans no changes in limb kinematics were seen associated with type of load, although asymmetric loads may lead to lateral postural shifts. Carrying may therefore be an important component of the evolutionary shift to habitual bipedalism, although further work is needed to understand the full biomechanical implications.

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Introduction

Bipedalism has long been recognised as one of the most influential adaptations that distinguishes modern humans from our primate relatives. Numerous hypotheses have been proposed to explain the selective pressures and adaptive advantages that gave rise to the adoption of habitual bipedalism. A common element in several of these

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hypotheses is the requirement for the hands to be free; for example, the postural feeding hypothesis necessitates the hands to be free to pick fruit from high branches [Hunt, 1994], and the provisioning model requires pair-bonded males to carry food back to dependent females [Lovejoy, 1981]. Other models also propose an advantage in load carrying including central place foraging [Stephens and Krebs, 1986], tool transportation [Gould and Lewontin, 1979; Videan and McGrew, 2002] and infant carriage once the ability to grasp with the toes had been lost. Doubt has recently been cast on the latter hypothesis because the energetic cost of infant carriage is extremely high compared to more evenly spread loads [Watson et al., 2008]. One of the most prominent explanations for the evolution of bipedality has been the claim that bipedalism is less energetically expensive than quadrupedal walking [Rodman and McHenry, 1980; Sockol et al., 2007]; however, these studies have described a reduction in locomotor economy between human bipedal walking and chimpanzee bipedal and quadrupedal walking as opposed to an improvement in the economy of bipedal walking in apes compared to quadrupedal locomotion. The disparity in energetic cost between human and chimpanzee bipedal walking is accounted for by the finding that leg length is negatively correlated with the energetic cost of bipedal locomotion [Studel-Numbers and Tilkens, 2004]. In a similar study that compared bipedal and quadrupedal locomotion, Taylor and Rowntree [1973] found that the energetic cost of capuchin monkeys and chimpanzees running on a treadmill was the same whether they were running bipedally or quadrupedally. This led to the claim that upright versus quadrupedal locomotion has virtually nothing to do with locomotor efficiency or the evolution of bipedal locomotion in man, a belief still held by some [Sayers and Lovejoy, 2008]. More recent work on chimpanzees has shown that bipedalism in some individuals, although not all, is rather more energetically expensive compared to quadrupedalism [Sockol et al., 2007]. Indeed, it is difficult to draw conclusions from primate energetics. However, the numerous postcranial skeletal adaptations mandating bipedalism present in australopithecines and not present in extant apes include, amongst many others, a rigid non-prehensile hallux, short broad pelvis and pronounced knee valgus [Sayers and Lovejoy, 2008]. These would almost certainly have resulted in improved bipedal economy and may therefore have been a factor in the adoption of a habitual bipedal gait.

In the light of studies on the relative costs of bipedal and quadrupedal locomotion in primates, it is still unclear whether bipedalism confers sufficient biomechanical advantage to justify its selection on the grounds of energetics alone [Taylor and Rowntree, 1973; Richmond et al., 2001; Studel-Numbers, 2001], which strongly suggests that other factors played a key role. Carrying allows animals to adopt central place foraging with resources carried back to a fixed location for consumption and sharing. Most non-human primates spend their days in stable groups, and it is the group as a whole that ranges through the environment. This is particularly apparent in the commonly used models for ancestral hominid behaviour: chimpanzees and baboons [Elton, 2006]. Central place foraging is commonly found in birds and nesting mammals [Stephens and Krebs, 1986] but very rarely seen in non-human anthropoid primates [Chapman et al., 1989]. A change in foraging strategy would have resulted in a large shift in the basic daily activity pattern, particularly in terms of day range and time spent carrying, and thus would have potentially been of great importance to the energy budgets of early hominins. The magnitude of the benefits of this major change in foraging strategy, coupled with greater reliance on bipedalism and carrying could have given the necessary impetus that resulted in anatomical adaptation for bipedality.

Carrying ability has often been studied in non-human primates in relation to tool use [Whiten et al., 1999; Ottoni and Mannu, 2001; Whiten and Boesch, 2001; Mercader et al., 2002]; however, no attempt has been made to research the link between load carrying and fore- and hindlimb kinematics. Amongst primates, the great apes are the most morphologically similar species to early humans and in the absence of experimental kinematic data collection from early humans, apes are preferred as a referential model. We do not suggest that they demonstrate early hominin kinematics, and we appreciate that the various forms of great ape locomotion are just as much the result of natural selection as is human bipedality. However, studies on load carrying in the non-human great apes do provide information on gait selection and mode of load carriage in animals that are not habitual bipeds.

There is considerable interest in the kinematics of load carrying in humans particularly concerning soldiers with military packs [Haisman, 1988] and children with book bags [Hong et al., 2000]. Research has focussed on whether the addition of load perturbs the normal gait pattern. Although studies on energetics show a marked increase in energetic cost [Watson et al., 2008], experiments in which joint angles were recorded during unloaded and loaded walking found little [Ghori and Luckwill, 1985] or no change in lower limb joint angles [Tilbury-Davis and Hooper, 1999], although La Fiandra et al. [2003] did find increased hip excursion with the addition of load. Ghori and Luckwill [1985] found a significant decrease in maximum knee flexion during the swing phase with backpack loads exceeding 20% body mass. They did not however find any changes in knee angle during the stance phase. Balanced loads (rucksacks, weighted jackets and weighted belts) are commonly used weights for experimentation [Robertson et al., 1982; Maloiy et al., 1986; Goh et al., 1997; Tilbury-Davis and Hooper, 1999; Griffin et al., 2003; La Fiandra et al., 2003], and few studies have focussed on lower limb kinematics when carrying light asymmetric loads. The available information shows little difference in lower limb kinematics at low loads but a significant increase in ipsilateral knee flexion with single-hand loads constituting 20% body mass and above [Ghori and Luckwill, 1985]. Significant changes have also been found in the frontal plane angle of the trunk during asymmetric load carrying of single-strap backpacks constituting 17% body mass [Pascoe et al., 1997]. We would therefore expect heavy asymmetric loads, as opposed to light symmetric loads, to elicit the greatest departure from unloaded kinematics.

In order to support or reject the hypothesis that load carrying led to the adoption of bipedal gait in early hominins, quantitative data on the kinematics of carrying are required. Here we present a comparison of loaded and unloaded carrying kinematics in humans, chimpanzees, bonobos, orang-utans and gorillas. The purpose of this study was to test the hypothesis that load carriage influences joint angles (the relative angles between segments) and body segment angles (the absolute angles with reference to the ground) in the 5 species of great ape. Studying load carrying allows us to identify differences between the kinematics of loaded and unloaded locomotion. This enables us to determine whether certain modes of carrying perturb gait more than others. Assuming that large perturbations are more energetically costly than steady locomotion, studying the kinematics of loaded and unloaded walking can provide valuable insight into the energetic costs and benefits of carrying loads. The study of non-human apes in particular provides important information about how habitually quadrupedal and quadrumanous hominoids approach the challenges of load carrying.

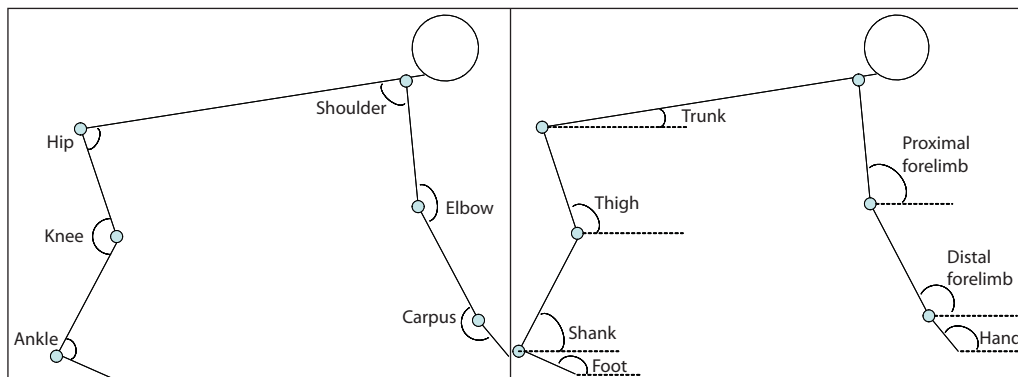


Fig. 1. Anatomical landmarks, joint and segment angles measured on all apes.

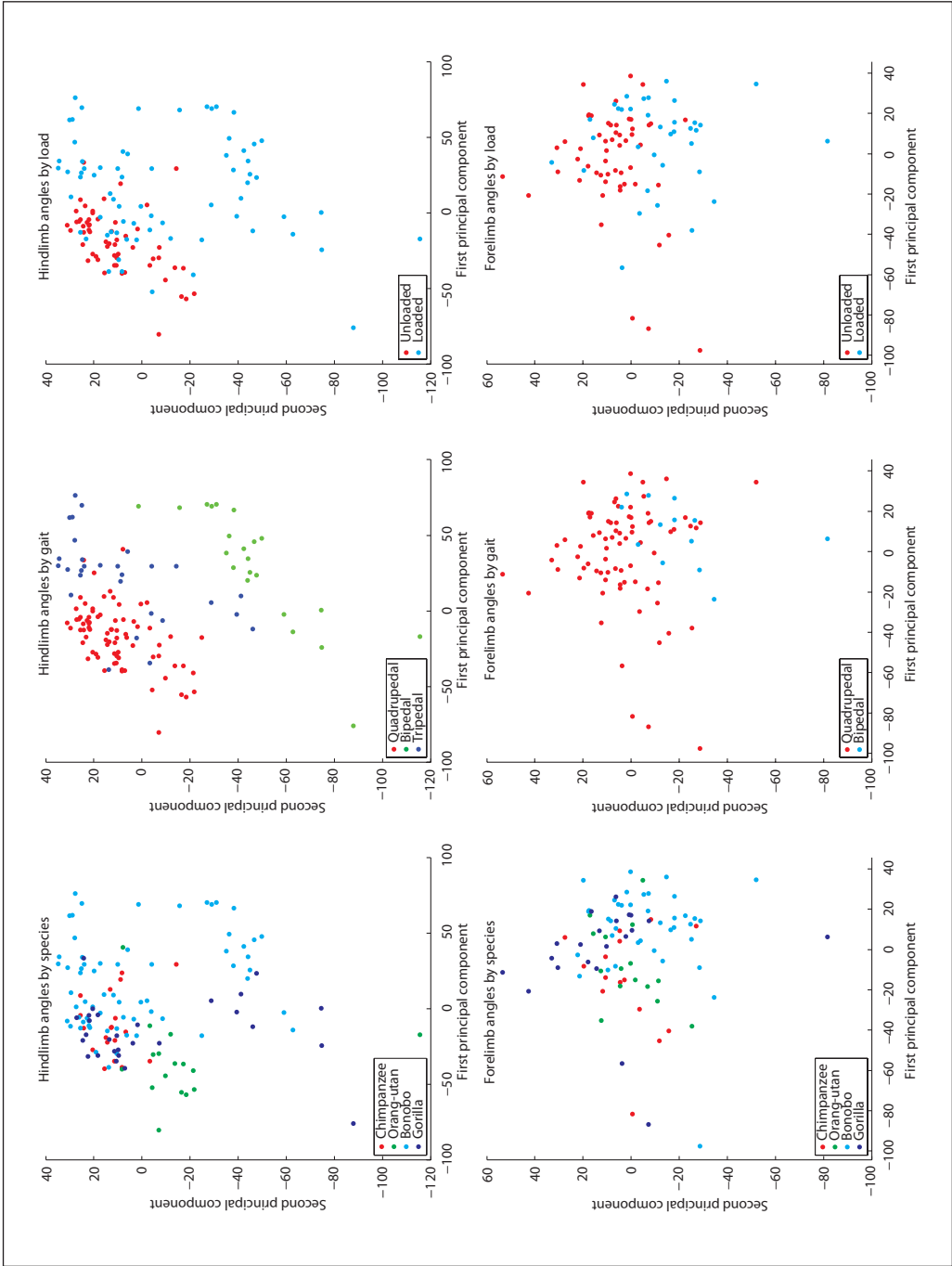
Methods

Non-Human Apes

Kinematic data were collected from common chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), western lowland gorillas (*Gorilla gorilla gorilla*) and Bornean and Sumatran orang-utans (*Pongo pygmaeus* and *Pongo abelii*) from 4 English zoos (Chester Zoo, Twycross Zoo, Porte Lympne Wild Animal Park and Paignton Zoo) and 1 Belgian zoo (Planckendaël Wild Animal Park). All study animals were housed under free-ranging conditions, and items were placed in the enclosures whenever possible to encourage carrying behaviour. The light loads (less than 1 kg) available for carrying were primarily fruit but occasionally included blocks of frozen juice, boxes, bottles, sacks and leafy branches. The exact loads available in this category varied from zoo to zoo. When infants were present, they were often carried by the adults. At Paignton, Porte Lympne and Planckendaël, the gorillas and bonobos were given wooden logs with drilled holes filled with honey, peanut butter and raisins (mass range 5.0–7.1 kg). At Planckendaël, the bonobos were also given ice-filled basketballs (mass 1–3 kg) and sealed drainpipes filled with gravel and walnuts (mass 2.5–3 kg). In compliance with the zoos' ethical guidelines, there was no physical contact with the animals during the study, they did not undergo any training and were unmarked.

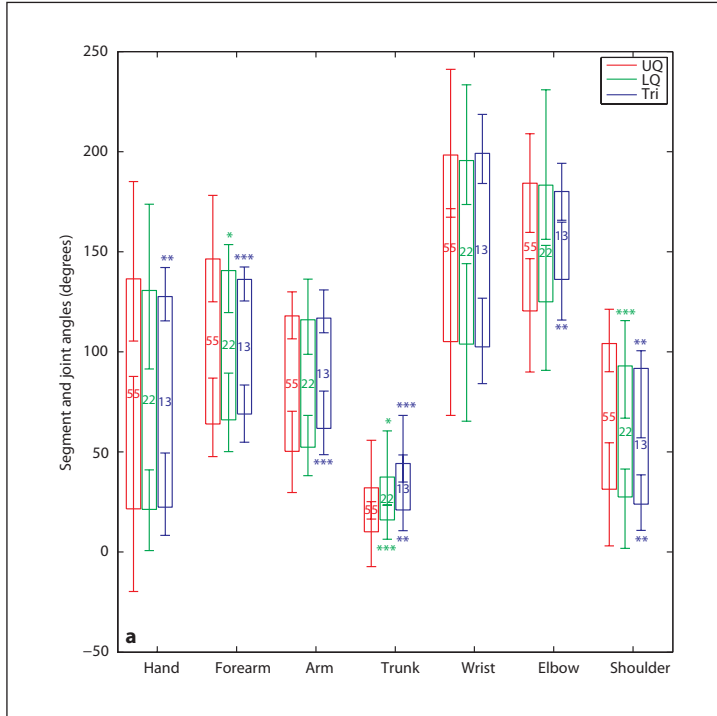
The apes were videotaped in lateral view whilst walking across relatively level areas within their enclosures. Kinematic data were collected using a standard video camera (Sony, NTSC, 29.98 Hz). The camera was levelled and placed perpendicular to the direction of motion of the ape. A sensitivity analysis was performed to show the percentage error associated with kinematic data collected when the ape was not perpendicular to the camera. For a 90-degree joint angle, the error is less than 1% with a camera angle up to 10° from perpendicular. Therefore when the angle of the ape relative to the camera was deemed greater than 10°, the data were discarded. Walking sequences were selected from the video footage. Selected sequences contained walking that was perpendicular to the camera and at a steady speed. The latter was determined by plotting the x-coordinate of the hip marker against time. A linear regression line was fitted to the displacement time data. A straight line plot indicated constant velocity, the data were discarded if the R^2 value fell below 0.97 [D'Aouit et al., 2002, p. 39].

A deinterlacing filter, which removed scan line artefacts, was applied to the video data using Virtual Dub (1.6.18). The separated video fields were then duplicated vertically so the images were resized to their original height. The fields were displayed sequentially resulting in full size images at a frequency of 59.96 Hz. Each frame of video data was digitised using Didge

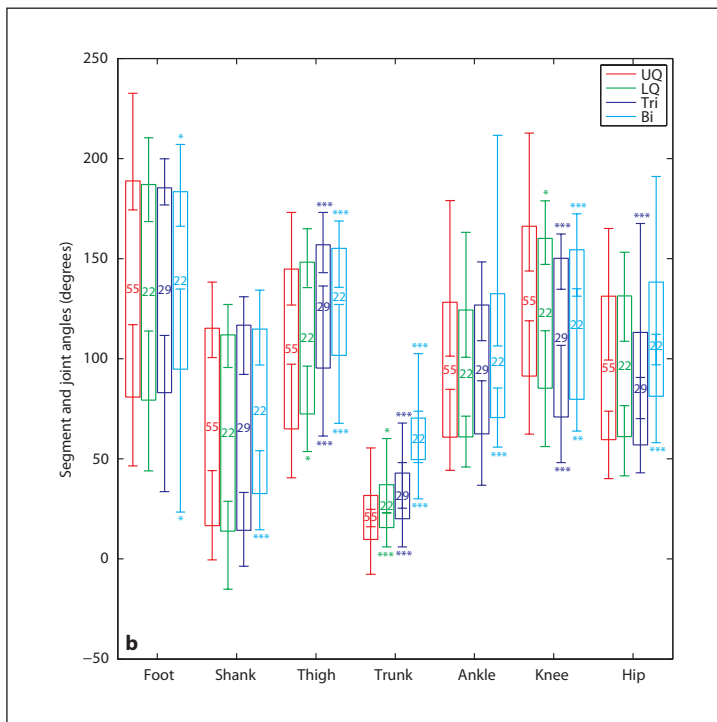


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Fig. 2. Scatter plots of the first and second principal components of the joint excursion and segment angle data for the non-human apes. Individual plots show the groupings by species, gait and load, looking at the hindlimb and the forelimb data separately.



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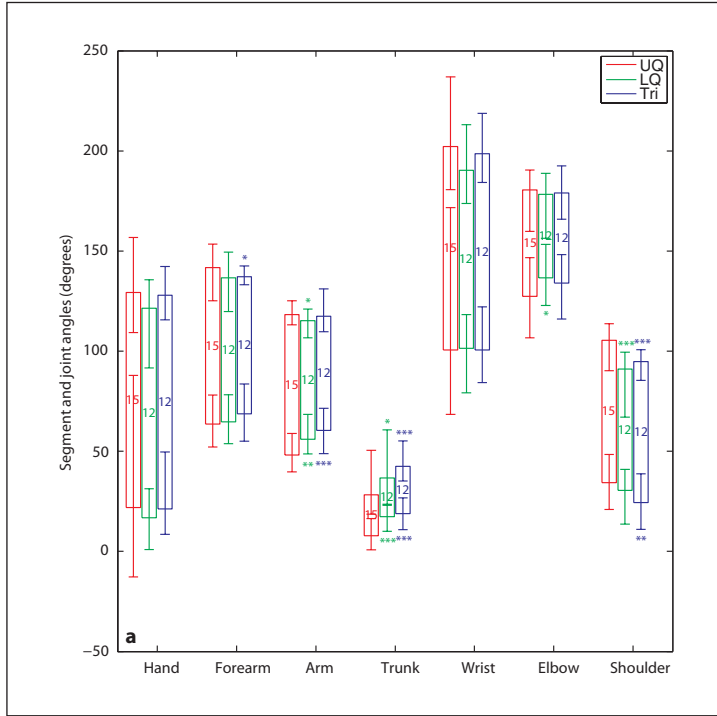
(2.2.0) image digitising software (biology.creighton.edu/faculty/cullum/Didge). The coordinates of the positions of the centre of rotations of the nearside shoulder joint, elbow joint, wrist joint and distal end of the third metacarpal were used to calculate forelimb joint and segment angles. The coordinates of the hip joint, knee joint, ankle joint and distal end of the fifth metatarsal were filtered using at 5 Hz a fourth-order 2-way Butterworth filter. The filtered data were used to calculate hindlimb joint and segment angles (fig. 1). Joint and segment angles were calculated in Matlab (7.1). Due to long grass occasionally covering the hands and feet, locomotion was divided into strides using the x-coordinate of the ankle and carpus joint markers.

Humans

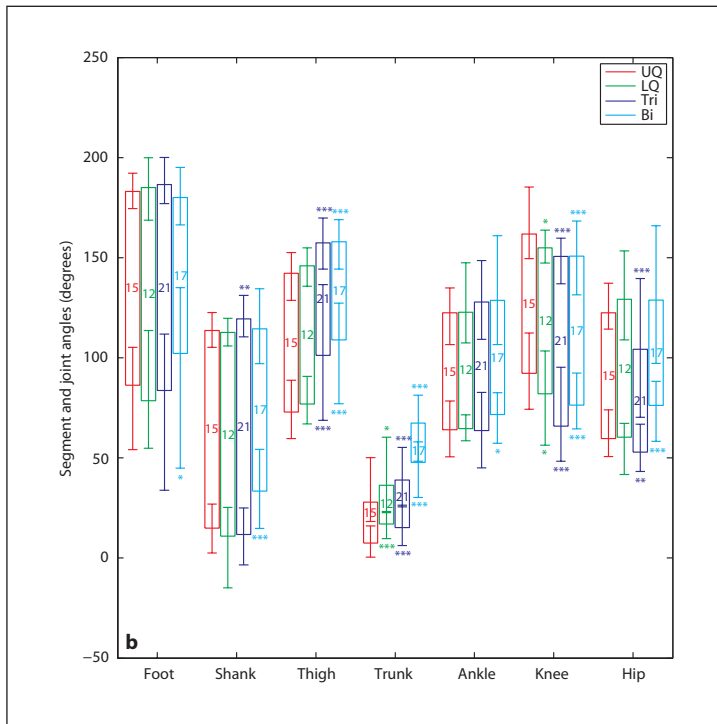
Kinematic data were collected during load carrying in 6 physically fit females of child-bearing age. Joint angles were calculated at the trunk, hip, knee, ankle and foot whilst the participants walked unloaded and walked with 10 kg of additional mass under 4 different carrying conditions. The loads carried were an adjustable weighted vest (Reebok Ironwear), a 5-kg dumbbell in each hand, a 10-kg dumbbell in a single hand and a weighted emergency rescue training mannequin (Ruth Lee, model RL10, www.ruthlee.co.uk). The weighted vest contained flexible rubber weights in small pockets distributed evenly over the front and back. The mass was further adjusted by adding strips of malleable lead to the pockets. The handheld masses were cast iron dumbbell plates with threaded bars and collars. All weights were checked on a laboratory balance, and the mass of the dumbbells was made up to 5 and 10 kg with heavy gauge copper wire. An equal amount of wire was added to each side of the dumbbell and was held in place with tape. The 10-kg dumbbell was carried in a single hand. The emergency rescue training mannequin is manufactured with approximately realistic mass distribution and size, and its mass was made up to 10 kg by hanging a small dumbbell plate around the neck with wire. This hung down the back and was held close to the torso with tape. Further wire was added, evenly distributed, to the top of the legs and held in place with tape. The mannequin wore an all-in-one suit over the added mass which ensured it was comfortable to carry. The mannequin was carried on the hip selected by the participant and remained on the same hip for the duration of data collection. Carrying infants astride the hip is common in many cultures as the hip provides a natural 'shelf' and the position is considered to provide social and sensory benefits for the infant [Jelliffe, 1975]. All the load conditions were 10 kg \pm 1% after adjustment. The average mass carried was about 18% of the participants' mean body mass. The experiments were approved by the University of Salford ethics committee.

All volunteers had a good level of physical fitness. Their ages ranged from 20 to 30 years, masses from 47.9 to 63.2 kg and heights from 1.49 to 1.68 m. Each walking task was carried out on a treadmill (Vison T9250; Vision Fitness, Cottage Grove, Wisc., USA) at a constant speed (3.7 km h⁻¹, 1.028 m s⁻¹) chosen as the speed where the net cost of human walking is minimum [Sellers et al., 2005]. Three-dimensional kinematic data were collected using 10 motion analysis cameras (Proreflex; Qualysis, Gothenburg, Sweden) and passive retroreflective markers. Data were collected at 240 Hz for a 10-second period during each carrying condition. The order of carrying conditions was randomised, and participants were given a minimum of 5 min to become accustomed to walking on the treadmill. Data collection commenced after this period of acclimation and continued for 10 s for each condition allowing 5–10 strides to be recorded. Participants rested for a minimum of 5 min between tasks. The kinematic analysis was performed in Visual 3D (C-Motion version 3.79) which requires a static standing trial in order

Fig. 3. Range plots of the pooled non-human ape data for the forelimb (a) and hindlimb (b). The bars show the mean maximum and minimum joint excursion and segment angles. The error bars show the range of these values. The number in the middle of the bar is the number of samples for each condition. Each condition is compared to the unloaded quadrupedal (UQ) condition using a t test and the significance level indicated: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. LQ = Loaded quadrupedal walking; Tri = tripedal; Bi = bipedal.



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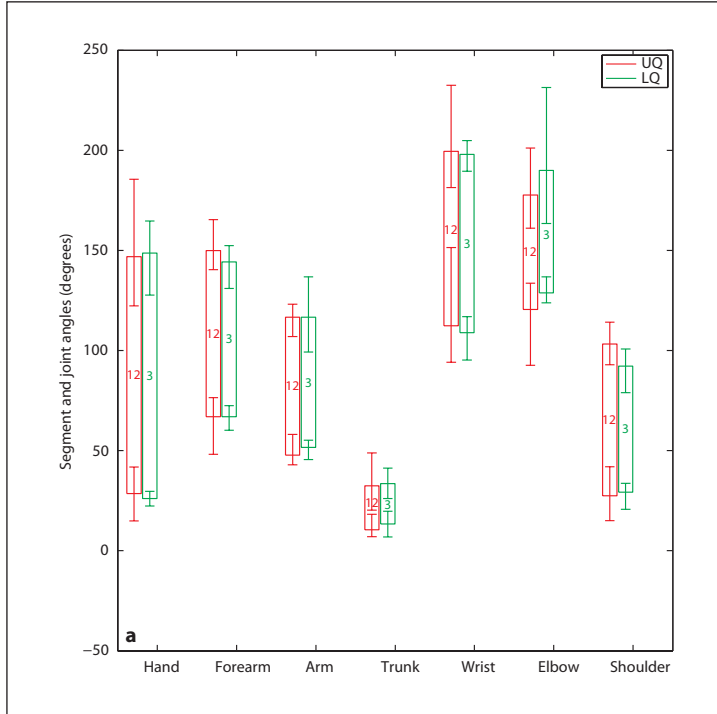


to identify body segment parameters and build a model specific to each participant. A full body marker set composed of anatomical markers and marker cluster plates was initially used to capture a static standing trial. Anatomical markers were placed on repeatable bony landmarks at the proximal and distal ends of each segment (upper arm, lower arm, thigh, shank, trunk and pelvis). The proximal and distal segment markers were then removed leaving the cluster plates (4 markers on a rigid base) to track each segment. Anatomical markers on the calcaneus, first, second and fifth metatarsals were used to define the foot segment. This method of motion capture uses virtual joint centres which reduces measurement error associated with inaccurate marker placement and skin movement over bony landmarks. Heel strike was defined as the lowest point in the trajectory of the calcaneus. A stride was defined as heel strike to heel strike, and this was used to calculate stride length and stride frequency. Joint angles were calculated for each stride and the means of 6 strides per participant were used for statistical analysis. Hip, knee, ankle and foot angles were measured in the sagittal plane. The trunk angle was measured in the sagittal and frontal planes. It was not possible to wear the weighted vest at the same time as the trunk and pelvis segment cluster plates, so trunk and hip angles have not been calculated for the vest load condition. Hip angle was defined as the angle between the pelvis and the thigh, knee angle as the angle between the thigh and the shank, ankle angle as the angle between the shank and the foot, and foot angle as the angle between the foot and the ground. The trunk angle was defined relative to vertical.

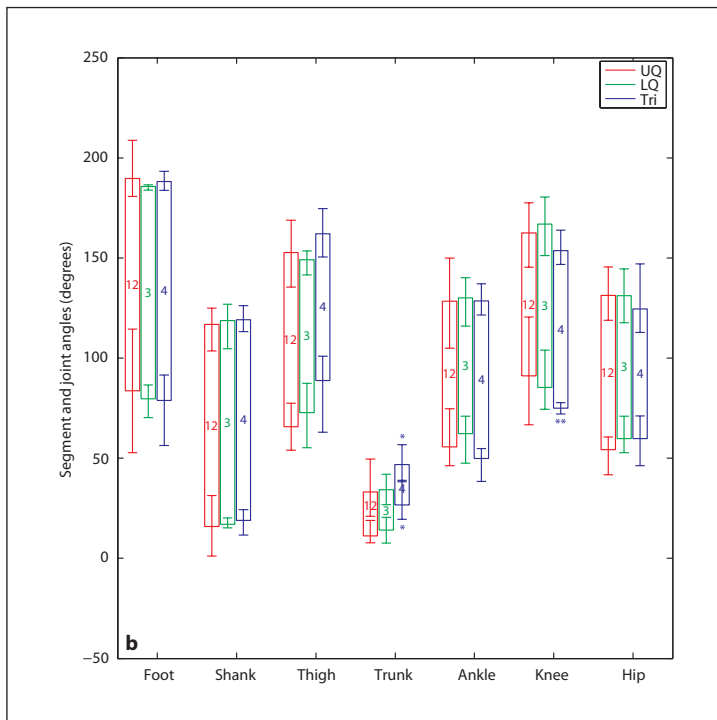
Statistical Tests

Statistical tests were applied in order to test the hypothesis that joint angles under loaded conditions differed significantly from unloaded joint angles. However, it was clear from the initial analysis that light loads made no difference to gait: it would be very surprising if carrying a lettuce leaf in the mouth would have any noticeable effect on gait kinematics, so the loaded situation was defined as a significant load (an infant, log or other large item). Loads were carried by the apes in any combination of ways, dorsally, ventrally and using near- and far-side fore- and hindlimbs during bipedal, tripodal or quadrupedal locomotion. However, it was possible to produce a smaller number of substantial groupings – unloaded quadrupedalism, loaded quadrupedalism, loaded tripodalism and loaded bipedalism – since these covered the vast majority of all occurrences. When comparing data, only limbs that were supporting the weight of the animal were considered, i.e., all limbs for quadrupeds, only the load-carrying 3 limbs for tripeds and only the hindlimbs for bipeds. The minimum and maximum values of each angle were determined for each trial. An initial principal-component analysis was performed to investigate the patterns of variation across all the measured angles in the fore- and hindlimb (fig. 2). These results show that the obvious groupings are by gait rather than species, or by load. Further analysis was performed using pairwise comparisons between the loaded conditions (loaded quadrupedal, tripodal and bipedal) and the unloaded condition (quadrupedal) using both species-specific data and by pooling all species. The sex was not included in the statistical analyses as it has been found previously that there is no interaction between gait and sex in bonobo locomotion [D'Août et al., 2002]. All the animals tested were adult. It should be realised that the sample numbers were very low in some situations, so the chances of a type II error are appreciable. For this reason, it was felt inappropriate to increase this further by using a Bonferroni correction, although, of course, this increases the chances of a type I error.

Fig. 4. Range plots of the bonobo data for the forelimb (a) and hindlimb (b). The bars show the mean maximum and minimum joint excursion and segment angles. The error bars show the range of these values. The number in the middle of the bar is the number of samples for each condition. Each condition is compared to the unloaded quadrupedal (UQ) condition using a t test and the significance level indicated: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. LQ = Loaded quadrupedal walking; Tri = tripodal; Bi = bipedal.



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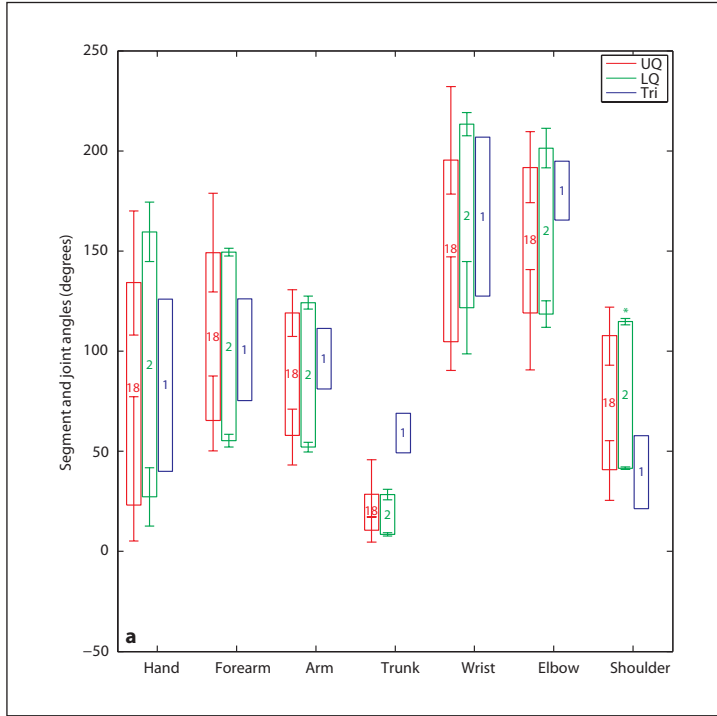


In the human study, 4 participants carried the 10-kg dumbbell in their right hand, and 4 participants carried the mannequin on their right hip. Data from the right and left sides of the body were included in the analysis in order to determine the effect of load on the ipsilateral and contralateral joint angles. In all other conditions data from the right side of the body only were included in the analysis. The minimum and maximum values of each angle were determined for each participant, and these variables were statistically tested across all modes of load carrying for a general effect of load using a one-way repeated-measures analysis of variance (SPSS 13.0) with a Bonferroni post-hoc multiple comparison test (SPSS 13.0) to identify where differences lay. Paired t tests were carried out on equivalent angles from the left and right sides of the body to identify any lateral asymmetry within participants.

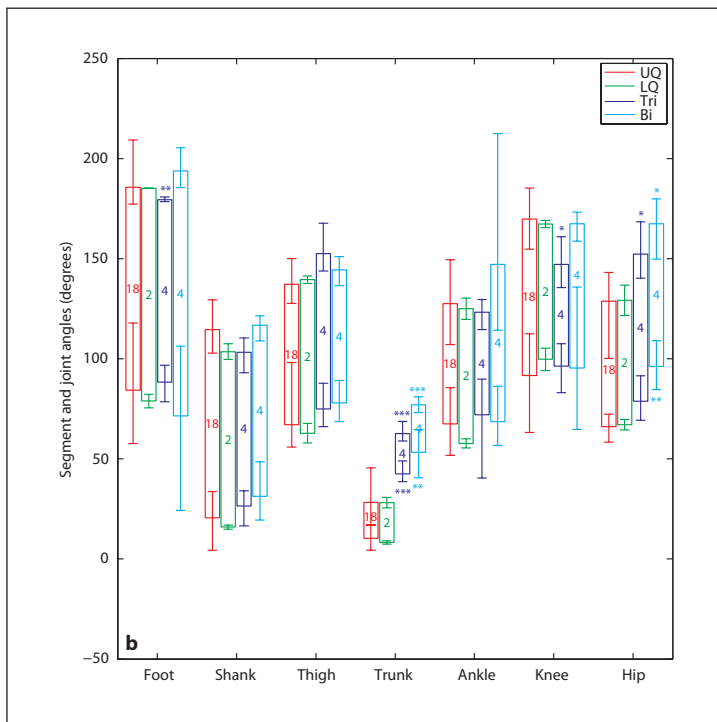
Results

The averaged minimum and maximum joint and segment angles for the non-human primates are presented in figures 3–7. These figures show the mean range of movement for each segment or joint with the range of the limits indicated by the error bars. Variables that were significantly different from the unloaded quadrupedal condition are indicated. Infants of all species were generally carried ventrally but dorsal carrying was also observed. All 5 species of great ape employed tripedal and bipedal locomotion when carrying a load quadrupedally was not possible due to the dimensions or weight of the load although they were able to carry surprisingly heavy loads in the mouth if the dimensions allowed them to get a good grip. In the species-pooled data (fig. 3), the biggest effect is the increased trunk angle for bipedal carrying with a smaller but still significant increase in tripedalism and loaded quadrupedalism compared to unloaded quadrupedalism. This more vertical trunk orientation is associated with significant changes in segment orientation elsewhere in the hindlimb with significant angle increases for bipedalism in at least one joint range limit for the thigh, shank and perhaps foot, with smaller changes for tripedalism and for loaded quadrupedalism. These changes lead to a less vertical thigh segment for tripedalism and bipedalism, and a more vertical shank for bipedalism. This is coupled with a large increase in the minimum hip angle for bipedalism but a reduction in maximum hip angle in tripedalism with a reduced range in both cases. At the knee the range remains similar but is shifted to smaller angles for both bipedalism and tripedalism. The minimum ankle angle is increased for bipedalism. In the load-bearing forelimb, the range of segmental angular movement is significantly reduced in tripedalism compared to unloaded quadrupedalism in all the joints, and this would lead to a more vertical limb posture. In loaded quadrupedalism there is also a suggestion that the forearm is also held more vertically. Joint ranges of movement are significantly reduced in the shoulder for both loaded quadrupedalism and tripedalism with a significant reduction only for tripedalism and at the elbow.

Fig. 5. Range plots of the common chimpanzee data for the forelimb (a) and hindlimb (b). The bars show the mean maximum and minimum joint excursion and segment angles. The error bars show the range of these values. The number in the middle of the bar is the number of samples for each condition. Each condition is compared to the unloaded quadrupedal (UQ) condition using a t test and the significance level indicated: * $p < 0.05$. LQ = Loaded quadrupedal walking; Tri = tripedal.



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Looking at individual species, for the bonobos which have the largest sample size, the picture is very similar to the pooled data. However, in this case the tripedal shank has a significantly higher maximum angle in tripedal carrying which means it is held slightly less vertically and the changes in the forelimb appear less pronounced with only the shifted and reduced ranges of motion at the shoulder associated with a more vertically held arm reaching high significance. For the chimpanzee, the sample size is rather smaller and there were no suitable bipedal bouts recorded. However, the increase in trunk angle with tripedalism is clearly demonstrated, and the tripedal knee also has a smaller minimum joint angle and there are no obvious differences from the common pattern. For the gorilla, the trunk pattern shows a more pronounced vertical posture for the tripedal case as well as for bipedalism, and this is similarly demonstrated in the increase in hip angles for both conditions. The tripedal knee however has a reduced maximum angle, and the foot has a slightly reduced maximum angle too. Finally for the orang-utans there were no suitable tripedal sequences and only a single bipedal sequence. This bipedal sequence does clearly show the more vertical trunk as expected and again much higher hip angles and more restricted thigh movement.

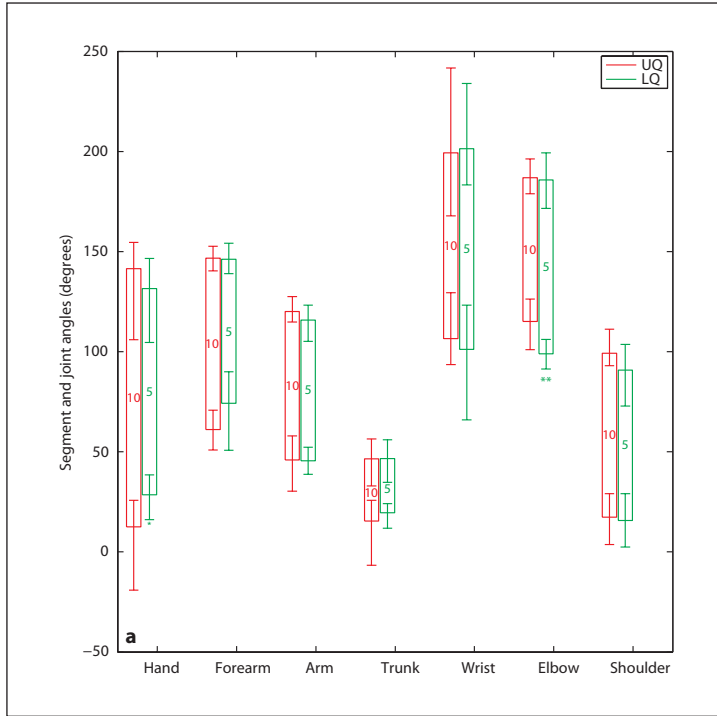
Human Carrying

The human carrying kinematic data are of much better quality than those obtained for the non-human apes. However, the locomotion form was bipedal in all cases, and as can be seen from the principal-component analysis (fig. 8) the bulk of the variation is between individuals and the variation due to the type of load is small. Paired t tests between unloaded data from the left and from the right sides of the body and repeated-measures analysis of variance across the various loaded conditions showed no significance; this finding is summarised in figure 9. However, the situation for asymmetric loads is more complex than this may indicate. For both the one-handed carrying task and the dummy there appeared to be 2 alternative strategies: either the trunk was angled laterally towards the load or it was angled laterally away from the load. This can be seen by the increased angular range for lateral trunk movements in figure 9 but obviously the mean orientation across 6 participants is unchanged since approximately half the participants increased the angle and the other half decreased it.

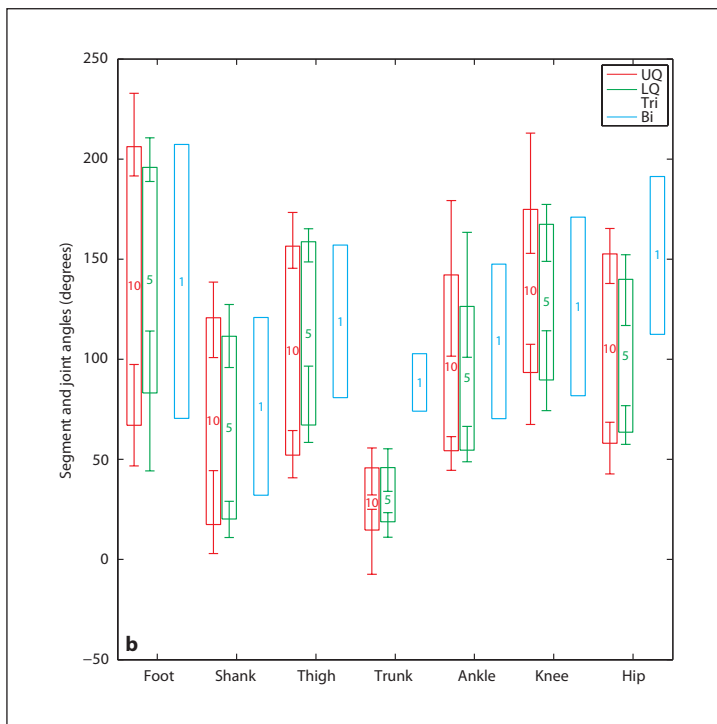
Discussion

The purpose of this study was to determine the influence of load on kinematics. Based on previous load-carrying studies in humans, heavy asymmetric loads would have been expected to have the greatest influence on hindlimb joint angles [Ghori

Fig. 6. Range plots of the gorilla data for the forelimb (a) and hindlimb (b). The bars show the mean maximum and minimum joint excursion and segment angles. The error bars show the range of these values. The number in the middle of the bar is the number of samples for each condition. Each condition is compared to the unloaded quadrupedal (UQ) condition using a t test and the significance level indicated: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. LQ = Loaded quadrupedal walking; Tri = tripedal; Bi = bipedal.



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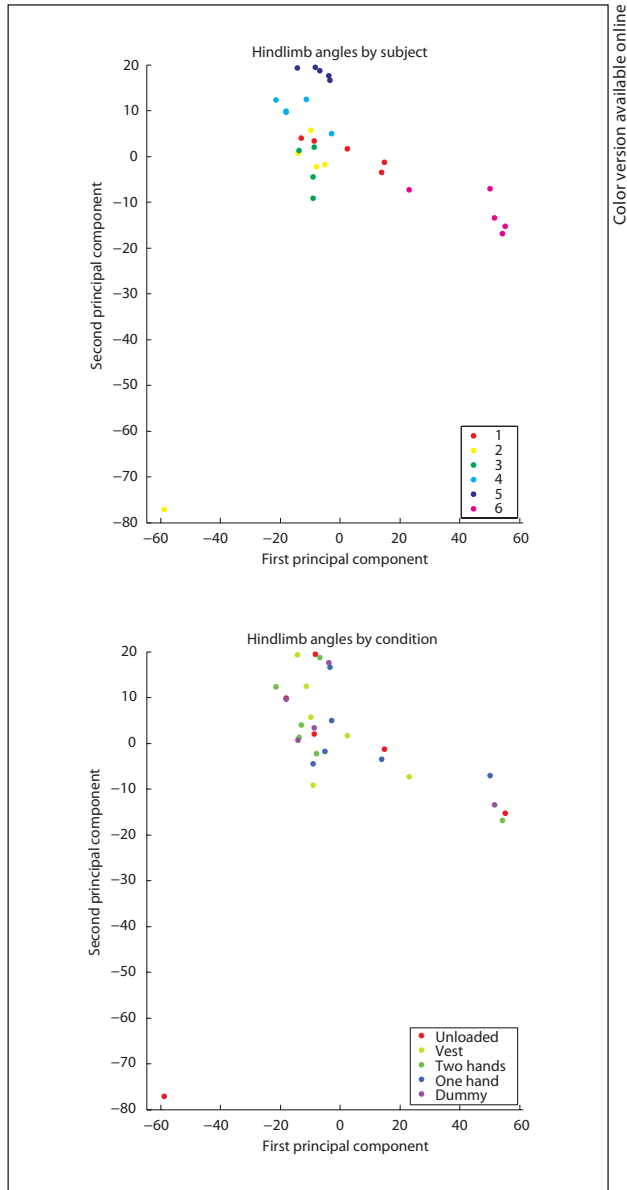
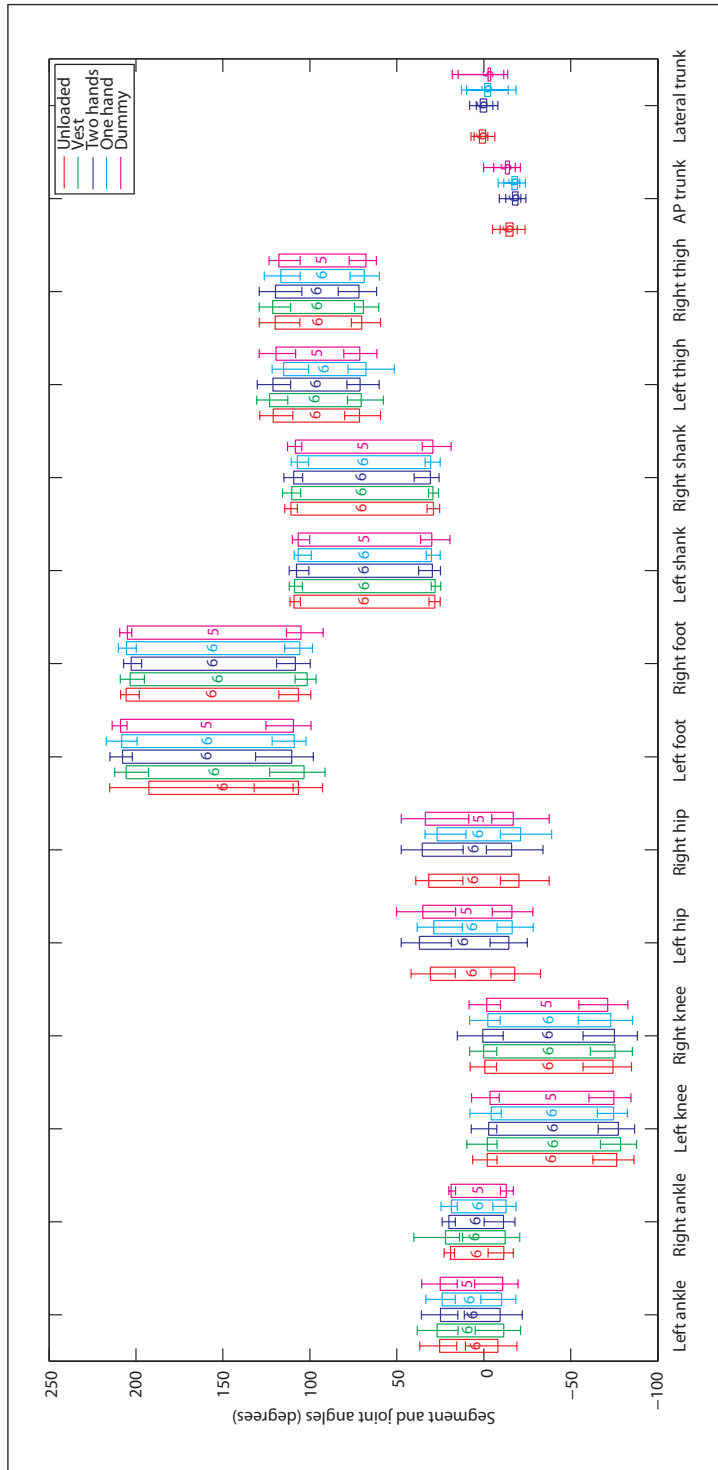


Fig. 8. Scatter plots of the first and second principal components of the joint excursions and segment angle data for humans. Individual plots show the groupings by subject and load condition.

Fig. 7. Range plots of the orang-utan data for the forelimb (a) and hindlimb (b). The bars show the mean maximum and minimum joint excursions and segment angles. The error bars show the range of these values. The number in the middle of the bar is the number of samples for each condition. Each condition is compared to the unloaded quadrupedal (UQ) condition using a t test but none of these comparisons reach significance. LQ = Loaded quadrupedal walking; Tri = tripedal; Bi = bipedal.



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and Luckwill, 1985; Pascoe et al., 1997]. Our data in humans do not support this hypothesis as very little departure from normal kinematics was observed following the addition of loads up to 20% of body weight in either the human or non-human apes. However, there were significant changes in the torso orientation and shoulder joint excursion for loaded and unloaded quadrupedalism in the pooled and bonobo-only cases, indicating that a heavy load may lead to a slightly more vertical trunk orientation with a straighter forelimb. This change becomes more pronounced for tripedal carrying and then reaches significance additionally in the chimpanzee and gorilla data. The trunk becomes yet more vertical in bipedal carrying in all the great ape species. One could certainly postulate this as an adaptive progression towards habitual bipedalism associated with improved carrying capabilities which could be confirmed by investigating the forces and energetics of these different carrying strategies.

However, it is clear that evolution of habitual bipedality is likely to be more complicated than this. In particular some of the bonobo bipedal sequences were very bent over with an extremely flexed hip. Previous studies have indicated a predisposition of bonobos to bipedal walking [Aerts et al., 2000; D'Août et al., 2002], and perhaps the reason why bonobos frequently adopt a bipedal gait is that they can achieve bipedality and the associated use of their hands whilst maintaining the flexed hip posture that they are morphologically best adapted to use. Flexed hip bipedalism was observed during foraging behaviour in which there are obvious benefits to keeping the upper body close to the ground. Such a mode of walking enables hand-to-mouth food delivery as well as gathering food in one hand whilst hoarding with the other. This demonstrates a possible selective pressure in favour of the otherwise energetically unfavourable bent-hip bent-knee (BHBK) walking since this is a gait that maximises foraging success in this circumstance. A reduction in arboreal feeding sites would have occurred as forests receded during the Miocene epoch which would have minimised postural bipedalism [Stanford, 2006] during feeding in trees [Hunt, 1994]. A form of locomotor bipedalism would have become more important as food sources became more dispersed and closer to the ground. Not all bipedal bonobo locomotion resulted in such a highly flexed hip. The lack of any increase in hip or knee flexion during loaded compared to unloaded locomotion may indicate that there is no additional energetic cost associated with load carrying. A previous study has shown that human walking with increased knee and hip flexion (BHBK) results in increased energetic cost [Carey and Crompton, 2005]. Interestingly the energetic cost of walking was also measured during the present human carrying experiment [Watson et al., 2008]. It was found that there was a significant increase in the energetic cost of carrying an asymmetric load compared to an evenly balanced load. The kinematics from the human carrying experiment under all load conditions show little departure from normal, unloaded kinematics despite the increase in energetic

Fig. 9. Range plots of the human data. The bars show the mean maximum and minimum joint excursion and segment angles. The error bars show the range of these values. The number in the middle of the bar is the number of samples for each condition. Each condition is compared to the unloaded quadrupedal condition using a t test but none of these comparisons reaches significance level.

cost. In the light of this previous study on energetics, joint and segment angles are unlikely to indicate changes in energetic cost between loaded and unloaded locomotion. Computer simulations on the energetic cost of BHBK walking have suggested that BHBK gait is even more inefficient when load carrying, and a more effective way to carry a load is to use an upright posture [Wang and Crompton, 2004]. As with all studies on the influence of energetic cost on overall fitness, there are costs and benefits which may not be immediately apparent. In the case of flexed hip bipedalism, the nutritional benefits of increased foraging success could outweigh the increased energetic costs of bipedal BHBK locomotion. There are also biomechanical benefits to walking with compliant limbs. BHBK walking may incur greater energetic cost but it also reduces joint load as peak vertical ground reaction forces are reduced in compliant gaits. A compliant BHBK gait is consistent with early hominin anatomy in which joint surface areas are relatively small [Richmond et al., 2001] and has been proposed as an effective gait for a small hominin with less stabilised joints which was still partially arboreal [Schmitt, 2003].

In the human study the 4 different modes of load carrying evoked few changes in the kinematic parameters studied. Unlike La Fiandra et al. [2003], who reported increased hip excursion with load, we found no significant difference in hip angle. Ghori and Luckwill [1985], who also studied asymmetric load carrying, found no significant difference in maximum flexion of the contralateral or ipsilateral knee at loads below 20% body mass. However, a significant increase in the maximum flexion of the ipsilateral knee was found with asymmetric loads of 20% body mass. With evenly spread backpack loads, Ghori and Luckwill [1985] found a significant decrease in knee flexion during the swing phase with loads above 20% body mass. Our loads constituted about 18% body mass, so the influence of load on kinematics may only become apparent at higher loads. However, Tilbury-Davis and Hooper [1999] found no significant difference in knee flexion or ankle flexion during walking with loads of up to 64% body mass. There is no consistent pattern of alteration in joint or segment angles with the addition of load in the human and non-human subjects. The side on which the load is carried does not appear to influence kinematics in any gait. There are isolated instances of differences in joint angles which may be attributable to the small sample sizes but in general it appears that load has little influence on joint angle. However, whilst not statistically significant, our data did suggest that the lateral orientation of the trunk was affected by heavy asymmetric loads. It is likely that these lateral movements (either of the hips or the shoulders) serve to move the centre of mass of the body + load back between the feet and that it is this postural compensation that leads to the higher metabolic energy costs that we observed particularly in asymmetric carrying [Watson et al., 2008]. This could be tested by measuring ground reaction forces and performing 3-dimensional inverse dynamics, although this is technically challenging.

When comparing limb extension between the different species of great ape during bipedal walking, the orang-utan, although based only on a single case, has the most extended hip and knee joints. Thorpe et al. [2007] have observed highly extended limbs in orang-utans when employing assisted bipedal walking in trees, and based on this finding they have suggested that human terrestrial bipedalism evolved from arboreal assisted bipedalism. Orang-utans appear to use an extended hindlimb when walking bipedally whether assisted or unassisted.

There are a number of limitations of any primarily zoo-based study. A limitation of this study is the variability in the mass of the loads carried. It was not possible to use standardised loads in all cases, and on many occasions we had to rely on opportunistic (and therefore rare) carrying events. Sample sizes were necessarily relatively small and there is always the danger that the data from a small captive sample are not necessarily representative of a more general wild population. In particular certain carrying/locomotor combinations were missing or present for very low numbers for some species which may lead to sampling bias. In addition, the digitisation process for unmarked animals is not very accurate, particularly for the long-haired orang-utans which made it difficult to identify anatomical landmarks. Similarly, long grass sometimes made the hands and feet difficult to see when they were in contact with the ground. This means that small but perhaps important changes in angles may be impossible to detect.

In conclusion, load carrying has small but potentially important effects on quadrupedal locomotion that might lead to an adaptive sequence where the trunk becomes progressively more upright and gait switches from quadrupedal to tripedal and ultimately bipedal locomotion as the carrying task becomes more difficult. However, the major changes in kinematics are associated with the gait change rather than the load itself, and in humans no significant changes in limb angles were seen associated with different types of load, although this study cannot rule out potentially important lateral postural alterations.

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