

1 **The kinematics of load carrying in humans and great apes: implications for the**  
2 **evolution of human bipedalism.**

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15 **Abstract**

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

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# 1 **Introduction**

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3 Bipedalism has long been recognised as one of the most influential adaptations that  
4 distinguishes modern humans from our primate relatives. Numerous hypotheses have been  
5 proposed to explain the selective pressures and adaptive advantages that gave rise to the  
6 adoption of habitual bipedalism. A common element in several of these hypotheses is the  
7 requirement for the hands to be free, for example the postural feeding hypothesis necessitates  
8 the hands to be free to pick fruit from high branches (Hunt, 1994) and the provisioning model  
9 requires pair bonded males to carry food back to dependent females (Lovejoy, 1981). Other  
10 models also propose an advantage in load carrying including central place foraging (Stephens  
11 and Krebs 1984), tool transportation (Gould and Lewontin, 1979; Videan and McGrew,  
12 2002) and infant carriage once the ability to grasp with the toes had been lost. Doubt has  
13 recently been cast on the latter hypothesis because the energetic cost of infant carriage is  
14 extremely high compared to more evenly spread loads (Watson et al., 2008). One of the most  
15 prominent explanations for the evolution of bipedality has been the claim that bipedalism is  
16 less energetically expensive than quadrupedal walking (Rodman and McHenry, 1980; Sockol  
17 et al. 2007) however these studies have described a reduction in locomotor economy between  
18 human bipedal walking and chimpanzee bipedal and quadrupedal walking as opposed to an  
19 improvement in the economy of bipedal walking in apes compared to quadrupedal  
20 locomotion. The disparity in energetic cost between human and chimpanzee bipedal walking  
21 is accounted for by the finding that leg length is negatively correlated with the energetic cost  
22 of bipedal locomotion (Studel-Numbers and Tilkens, 2004). In a similar study that compared  
23 bipedal and quadrupedal locomotion, Taylor and Rowntree (1973) found that the energetic  
24 cost of capuchin monkeys and chimpanzees running on a treadmill was the same whether  
25 they were running bipedally or quadrupedally. This led to the claim that upright versus

1 quadrupedal locomotion has virtually nothing to do with locomotor efficiency or the  
2 evolution of bipedal locomotion of man, a belief still held by some (Sayers and Lovejoy,  
3 2008). More recent work on chimpanzees has shown that bipedalism in some individuals,  
4 although not all, is rather more energetically expensive compared to quadrupedalism (Sockol  
5 et al., 2007). Indeed, it is difficult to draw conclusions from primate energetics. However the  
6 numerous postcranial skeletal adaptations mandating bipedalism present in australopithecines  
7 and not present in extant apes include, amongst many others, a rigid non-prehensile hallux,  
8 short broad pelvis and pronounced knee valgus (Sayers and Lovejoy, 2008). These would  
9 almost certainly have resulted in improved bipedal economy and may therefore have been a  
10 factor in the adoption of a habitual bipedal gait.

11

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

1 in foraging strategy, coupled with greater reliance on bipedalism and carrying could have  
2 given the necessary impetus that resulted in anatomical adaptation for bipedality.

3  
4 Carrying ability has often been studied in non-human primates in relation to tool-use, (Ottoni  
5 and Mannu, 2001, Whiten et al. 1999; Mercader et al., 2002) however no attempt has been  
6 made to research the link between load carrying and fore- and hind-limb kinematics.  
7 Amongst primates the great apes are the most morphologically similar species to early  
8 humans and in the absence of experimental kinematic data collection from early humans,  
9 apes are preferred as a referential model. We do not suggest that they demonstrate early  
10 hominin kinematics and we appreciate that the various forms of great ape locomotion are just  
11 as much the result of natural selection as is human bipedality. However studies on load  
12 carrying in the non-human great apes do provide information on gait selection and mode of  
13 load carriage in animals that are not habitual bipeds.

14  
15 There is considerable interest in the kinematics of load carrying in humans particularly  
16 concerning soldiers with military packs (Haisman 1988) and children with book bags (Hong  
17 et al. 200). Research has focussed on whether the addition of load perturbs the normal gait  
18 pattern. Although studies on energetics show a marked increase in energetic cost (Watson et  
19 al., 2008), experiments in which joint angles were recorded during unloaded and loaded  
20 walking found little (Ghori and Luckwill,1985) or no change in lower limb joint angles  
21 (Tilbury-Davis and Hooper, 1999) although La Fiandra *et al.* (2003) did find increased hip  
22 excursion with the addition of load. Ghori and Luckwill found a significant decrease in  
23 maximum knee flexion during the swing phase with backpack loads exceeding 20% body  
24 mass. They did not however find any changes in knee angle during the stance phase.  
25 Balanced loads (rucksacks, weighted jackets and weighted belts) are commonly used weights

1 for experimentation (Maloiy *et al.*, 1986; Griffin *et al.*, 2003; Robertson *et al.*, 1982; Goh *et*  
2 *al.*, 1997; La Fiandra *et al.*, 2003; Tilbury-Davis and Hooper, 1999) and few studies have  
3 focussed on lower limb kinematics when carrying light asymmetrical loads. The available  
4 information shows little difference in lower limb kinematics at low loads but a significant  
5 increase in ipsilateral knee flexion with single hand loads constituting 20% body mass and  
6 above (Ghori and Luckwill, 1985). Significant changes have also been found in the frontal  
7 plane angle of the trunk during asymmetrical load carrying of single strap backpacks  
8 constituting of 17% body mass (Pascoe *et al.*, 1997). We would therefore expect heavy  
9 asymmetric loads, as opposed to light symmetrical loads, to elicit greatest departure from  
10 unloaded kinematics.

11

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

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## 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 four English zoos (Chester Zoo, Twycross Zoo, Porte Lympne Wild Animal Park and Paignton Zoo) and one Belgian zoo (Planckendael Wild Animal Park) (Table 0). 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 1kg) 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 carried by the adults. At Paignton, Porte Lympne and Planckendael the gorillas and bonobos were given wooden logs with drilled holes filled with honey, peanut butter and raisins (mass range 5.0-7.1kg). At Planckendael the bonobos were also given ice filled basket balls (mass 1-3kgs) and sealed drain pipes filled with gravel and walnuts (mass 2.5-3kgs). 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

1 kinematic data collected when the ape was not perpendicular to the camera. For a ninety  
2 degree joint angle the error is less than 1% with a camera angle up to 10 degrees from  
3 perpendicular. Therefore when the angle of the ape relative to the camera was deemed greater  
4 than 10 degrees the data were discarded. Walking sequences were selected from the video  
5 footage. Selected sequences contained walking that was perpendicular to the camera and at a  
6 steady speed. The latter was determined by plotting the x coordinate of the hip marker against  
7 time. A linear regression line was fitted to the displacement time data. A straight line plot  
8 indicated constant velocity, the data were discarded if the R squared value fell below 0.97  
9 (D'Août et al., 2002: 39).

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11 A deinterlacing filter, which removed scan line artefacts, was applied to the video data using  
12 VirtualDub (1.6.18). The separated video fields were then duplicated vertically so the images  
13 were resized to their original height. The fields were displayed sequentially resulting in full  
14 size images at a frequency of 59.96Hz. Each frame of video data was digitised using Didge  
15 (2.2.0) image digitising software ([biology.creighton.edu/faculty/cullum/Didge](http://biology.creighton.edu/faculty/cullum/Didge)). The  
16 coordinates of the positions of the centre of rotations of the nearside shoulder joint, elbow  
17 joint, wrist joint and distal end of the 3<sup>rd</sup> metacarpal were used to calculate forelimb joint and  
18 segment angles. The coordinates of the hip joint, knee joint, ankle joint and distal end of the  
19 5<sup>th</sup> metatarsal were filtered using at 5 Hz using a 4th order two-way Butterworth filter. The  
20 filtered data were used to calculate hindlimb joint and segment angles (Figs 1a and 1b). Joint  
21 and segment angles were calculated in MATLAB (7.1). Due to long grass occasionally  
22 covering the hands and feet, locomotion was divided into strides using the x coordinate of the  
23 ankle and carpus joint markers.

24

25 *Humans*

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

1  
2 All volunteers had a good level of physical fitness. Their ages ranged from 20-30 years,  
3 masses from 47.9-63.2kg and heights from 1.49-1.68 m. Each walking task was carried out  
4 on a treadmill (Vison T9250, Wisconsin, US) at a constant speed ( $3.7\text{kmh}^{-1}$ ,  $1.028\text{ ms}^{-1}$ )  
5 chosen as the speed where the net cost of human walking is minimum (Sellers *et al.*, 2005).  
6 3D kinematic data were collected using ten motion analysis cameras (ProReflex, Qualysis,  
7 Sweden) and passive retroreflective markers. Data were collected at 240Hz for a ten second  
8 period during each carrying condition. The order of carrying conditions was randomised and  
9 participants were given a minimum of five minutes to become accustomed to walking on the  
10 treadmill. Data collection commenced after this period of acclimation and continued for 10  
11 seconds for each condition allowing 5-10 strides to be recorded. Participants rested for a  
12 minimum of 5 minutes between tasks. The kinematic analysis was performed in Visual 3D  
13 (C-Motion Version 3.79) which requires a static standing trial in order to identify body  
14 segment parameters and build a model specific to each participant. A full body marker set  
15 composed of anatomical markers and marker cluster plates was initially used to capture a  
16 static standing trial. Anatomical markers were placed on repeatable bony landmarks at the  
17 proximal and distal ends of each segment (upper arm, lower arm, thigh, shank, trunk and  
18 pelvis). The proximal and distal segment markers were then removed leaving the cluster  
19 plates (four markers on a rigid base) to track each segment. Anatomical markers on the  
20 calcaneus, 1<sup>st</sup>, 2<sup>nd</sup> and 5<sup>th</sup> metatarsals were used to define the foot segment. This method of  
21 motion capture uses virtual joint centres which reduces measurement error associated with  
22 inaccurate marker placement and skin movement over bony landmarks. Heel strike was  
23 defined as the lowest point in the trajectory of the calcaneus. A stride was defined as heel  
24 strike to heel strike and this was used to calculate stride length and stride frequency. Joint  
25 angles were calculated for each stride and the means of six strides per participant were used

1 for statistical analysis. Hip, knee, ankle and foot angles were measured in the sagittal plane.  
2 The trunk angle was measured in the sagittal and frontal plane. It was not possible to wear the  
3 weighted vest at the same time as the trunk and pelvis segment cluster plates so trunk and hip  
4 angles have not been calculated for the vest load condition. Hip angle was defined as the  
5 angle between the pelvis and the thigh; knee angle - the angle between the thigh and the  
6 shank; ankle angle – the angle between the shank and the foot; foot angle – the angle between  
7 the foot and the ground. The trunk angle was defined relative to vertical.

8

### 9 *Statistical tests*

10

11 Statistical tests were applied in order to test the hypothesis that joint angles under loaded  
12 conditions differed significantly from unloaded joint angles. However it was clear from initial  
13 analysis that light loads made no difference to gait: it would be very surprising if carrying a  
14 lettuce leaf in the mouth would have any noticeable effect on gait kinematics so the loaded  
15 situation was defined as a significant load (an infant, log or other large item). Loads were  
16 carried by the apes in any combination of ways, dorsally, ventrally and using near- and far-  
17 side fore- and hind-limbs during bipedal (bi), tripedal (tri) or quadrupedal (quad) locomotion.  
18 However it was possible to produce a smaller number of substantial groupings: unloaded  
19 quadrupedalism (UQ); loaded quadrupedalism (LQ); loaded tripedalism (LT); loaded  
20 bipedalism (LB) since these covered the vast majority of all occurrences. When comparing  
21 data only limbs that were supporting the weight of the animal were considered: i.e. all limbs  
22 for quadrupeds, only the load carrying three limbs for tripeds, and only the hindlimbs for  
23 bipeds. The minimum and maximum values of each angle were determined for each trial. An  
24 initial principle component analysis was performed to investigate the patterns of variation  
25 across all the measured angles in the fore and hindlimb (Figure 2). These results show that

1 the obvious groupings are by gait rather than species, or by load. Further analysis was  
2 performed using pairwise comparisons between the loaded conditions (LQ, LT, LB) and the  
3 unloaded condition (UQ) using both species specific data and by pooling all species. The sex  
4 was not included in the statistical analyses as there has previously been found to be no  
5 interaction between gait and sex in bonobo locomotion (D'Août et al 2002). All the animals  
6 tested were adult. It should be realised that the samples numbers were very low in some  
7 situations so the chances of a Type II error are appreciable. For this reason it was felt  
8 inappropriate to further increase this by using a Bonferroni correction although of course this  
9 increases the chances of a Type I error.

10

11 In the human study four participants carried the 10kg dumbbell in their right hand and four  
12 participants carried the mannequin on their right hip. Data from the right and left sides of the  
13 body were included in analysis in order to determine the effect of load on the ipsilateral and  
14 contralateral joint angles. In all other conditions data from the right side of the body only  
15 were included in the analysis. The minimum and maximum values of each angle were  
16 determined for each participant and these variables were statistically tested across all modes  
17 of load carrying for a general effect of load using a one way repeated measures analysis of  
18 variance (ANOVA) (SPSS 13.0) with a Bonferroni post-hoc multiple comparison test (SPSS  
19 13.0) to identify where differences lay. Paired t-tests were carried out on equivalent angles  
20 from the left and right sides of the body to identify any lateral asymmetry within participants.

21

## 22 **Results**

23

24 The averaged minimum and maximum joint and segment angles for the non-human primates  
25 are presented in Figures 3-7. These figures show the mean range of movement for each

1 segment or joint with the range of the limits indicated by the error bars. Variables that were  
2 significantly different from the UQ condition are indicated. Infants of all species were  
3 generally carried ventrally but dorsal carrying was also observed. All four species of great  
4 ape employed tripedal and bipedal locomotion when carrying a load quadrupedally was not  
5 possible due to the dimensions or weight of the load although they were able to carry  
6 surprisingly heavy loads in the mouth if the dimensions allowed them to get a good grip. In  
7 the species pooled data (Figure 3) the biggest effect is the increased trunk angle for bipedal  
8 carrying with a smaller but still significant increase for tripedalism and loaded  
9 quadrupedalism compared to unloaded quadrupedalism. This more vertical trunk orientation  
10 is associated with significant changes in segment orientation elsewhere in the hindlimb with  
11 significant angle increases for bipedalism in at least one joint range limit for thigh, shank and  
12 perhaps foot, with smaller changes for tripedalism and for loaded quadrupedalism. These  
13 changes lead to a less vertical thigh segment for tripedalism and bipedalism, and a more  
14 vertical shank for bipedalism. This is coupled with a large increase in the minimum hip angle  
15 for bipedalism but a reduction in maximum hip angle in tripedalism with a reduced range in  
16 both cases. At the knee the range remains similar but is shifted to smaller angles for both  
17 bipedalism and tripedalism. The minimum ankle angle is increased for bipedalism. In the  
18 load bearing forelimb the range of segmental angular movement is significantly reduced in  
19 tripedalism compared to unloaded quadrupedalism in all the joints and this would lead to a  
20 more vertical limb posture. In loaded quadrupedalism there is also a suggestion that the  
21 forearm is also held more vertically. Joint ranges of movement are significantly reduced in  
22 the shoulder for both loaded quadrupedalism and tripedalism with only a significant reduction  
23 for tripedalism and at the elbow.  
24

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

16

### 17 *Human carrying*

18 The human carrying kinematic data is much better quality than that obtained for the non-  
19 human apes. However the locomotion form was bipedal in all cases and as can be seen from  
20 the principle component analysis (Figure 8) the bulk of the variation is between individuals  
21 and that the variation due to the type of load is small. Paired t-tests between unloaded data  
22 from the left and from the right sides of the body and repeated measures ANOVA across the  
23 various loaded conditions showed no significance and this finding is summarised in Figure 9.  
24 However the situation for asymmetrical loads is more complex than this may indicate. For  
25 both the one handed carrying task and the dummy there appeared to be two alternative

1 strategies: either the trunk was angled laterally towards the load or it was angled laterally  
2 away from the load. This can be seen by the increased angular range for lateral trunk  
3 movements in Figure 9 but obviously the mean orientation across 6 participants is unchanged  
4 since approximately half the participants increased the angle and the other half decreased it..

5

## 6 **Discussion**

7 The purpose of this study was to determine the influence of load on kinematics. Based on  
8 previous load carrying studies in humans, heavy asymmetric loads would have been expected  
9 to have the greatest influence on hindlimb joint angles (Ghori and Luckwill, 1985; Pascoe *et*  
10 *al.*, 1997). Our data in humans do not support this hypothesis as very little departure from  
11 normal kinematics was observed following the addition of loads up to 20% of body weight in  
12 either the human or non-human apes. However there were significant changes in the torso  
13 orientation and shoulder joint excursion for loaded and unloaded quadrupedalism in the  
14 pooled and bonobo only cases indicating that a heavy load may lead to a slightly more  
15 vertical trunk orientation with a straighter forelimb. This change becomes more pronounced  
16 for tripedal carrying and then reaches significance additionally in the chimpanzee and gorilla  
17 data. The trunk becomes yet more vertical in bipedal carrying all the great ape species. One  
18 could certainly postulate this as an adaptive progression towards habitual bipedalism  
19 associated with improved carrying capabilities which could be confirmed by investigating the  
20 forces and energetics of these different carrying strategies.

21

22 However it is clear that evolution of habitual bipedality is likely to be more complicated than  
23 this. In particular some of the bonobo bipedal sequences were very bent over with an  
24 extremely flexed hip. Previous studies have indicated a predisposition of bonobos to bipedal  
25 walking (Aerts *et al.*, 2000; D'Aout *et al.*, 2002) and perhaps the reason that bonobos

1 frequently adopt a bipedal gait is that they can achieve bipedality and the associated use of  
2 their hands whilst maintaining the flexed hip posture that they are morphologically best  
3 adapted to use. Flexed hip bipedalism was observed during foraging behaviour in which there  
4 are obvious benefits to keeping the upper body close to the ground. Such a mode of walking  
5 enables hand to mouth food delivery as well as gathering food in one hand whilst hoarding  
6 with the other. This demonstrates a possible selective pressure in favour of the otherwise  
7 energetically unfavourable bent-hip bent-knee walking since this is a gait that maximises  
8 foraging success in this circumstance. A reduction in arboreal feeding sites would have  
9 occurred as forests receded during the Miocene epoch which would have minimised postural  
10 bipedalism (Stanford, 2006) during feeding in trees (Hunt, 1994). A form of locomotor  
11 bipedalism would have become more important as food sources became more dispersed and  
12 closer to the ground. Not all bipedal bonobo locomotion resulted in such a highly flexed hip.  
13 The lack of any increase in hip or knee flexion during loaded compared to unloaded  
14 locomotion may indicate there is no additional energetic cost associated with load carrying. A  
15 previous study has shown that human walking with increased knee and hip flexion (Bent-Hip  
16 Bent-Knee or BHBK) results in increased energetic cost (Carey and Crompton, 2004).  
17 Interestingly the energetic cost of walking was also measured during the present human  
18 carrying experiment (Watson et al, 2008). It was found that there was a significant increase in  
19 the energetic cost of carrying an asymmetric load compared to an evenly balanced load. The  
20 kinematics from the human carrying experiment under all load conditions show little  
21 departure from normal, unloaded kinematics despite the increase in energetic cost. In the light  
22 of this previous study on energetics, joint and segment angles are unlikely to indicate changes  
23 in energetic cost between loaded and unloaded locomotion. Computer simulations on the  
24 energetic cost of BHBK walking have suggested that BHBK gait is even more inefficient  
25 when load carrying and a more effective way to carry a load is to use an upright posture

1 (Wang and Crompton, 2004). As with all studies on the influence of energetic cost on overall  
2 fitness there are costs and benefits which may not be immediately apparent. In the case of  
3 flexed hip bipedalism the nutritional benefits of increased foraging success could outweigh  
4 the increased energetic costs of bipedal BHBK locomotion. There are also biomechanical  
5 benefits to walking with compliant limbs. Bent hip bent knee walking may incur greater  
6 energetic cost but it also reduces joint load as peak vertical ground reaction forces are  
7 reduced in compliant gaits. A compliant BHBK gait is consistent with early hominin anatomy  
8 in which joint surface areas are relatively small (Richmond et al., 2001) and has been  
9 proposed as an effective gait for a small hominin with less stabilised joints which was still  
10 partially arboreal (Schmitt 2003).

11

12 In the human study the four different modes of load carrying evoked few changes in the  
13 kinematic parameters studied. Unlike LaFiandra *et al.* (2003) who reported increased hip  
14 excursion with load, we found no significant difference in hip angle. Ghorri and Luckwill  
15 (1985) who also studied asymmetric load carrying found no significant difference in  
16 maximum flexion of the contralateral or ipsilateral knee at loads below 20% body mass.  
17 However a significant increase in the maximum flexion of the ipsilateral knee was found with  
18 asymmetrical loads of 20% body mass. With evenly spread backpack loads Ghorri and  
19 Luckwill (1985) found a significant decrease in knee flexion during the swing phase with  
20 loads above 20% body mass. Our loads constituted about 18% body mass so the influence of  
21 load on kinematics may only become apparent at higher loads. However Tilbury-Davis and  
22 Hooper (1999) found no significant difference in knee flexion or ankle flexion during  
23 walking with loads of up to 64% body mass. There is no consistent pattern of alteration in  
24 joint or segment angles with the addition of load in the human and non-human subjects. The  
25 side on which the load is carried does not appear to influence kinematics in any gait. There

1 are isolated instances of differences in joint angles which may be attributable to the small  
2 samples sizes but in general it appears that load has little influence on joint angle. However  
3 whilst not statistically significant our data did suggest that the lateral orientation of the trunk  
4 was affected by heavy asymmetrical loads. It is likely that these lateral movements (either of  
5 the hips or the shoulders) serve to move the centre of mass of the body+load back between  
6 the feet and that it is this postural compensation that leads to the higher metabolic energy  
7 costs that we observed particularly in asymmetric carrying (Watson et al. 2008). This could  
8 be tested by measuring ground reaction forces and performing 3D inverse dynamics although  
9 this is technically challenging.

10

11 When comparing limb extension between the difference species of great ape during bipedal  
12 walking, the orang-utan, although based only on a single case, has the most extended hip and  
13 knee joints. Thorpe et al. (2007) have observed highly extended limbs in orangutans when  
14 employing assisted bipedal walking in trees, and based on this finding they have suggested  
15 that human terrestrial bipedalism evolved from arboreal assisted bipedalism. Orangutans  
16 appear to use an extended hind-limb when walking bipedally whether assisted or unassisted.

17

18 There are a number of limitations of any primarily zoo based study. A limitation of this study  
19 is the variability in the mass of the loads carried. It was not possible to use standardised loads  
20 in all cases and on many occasions we had to rely on opportunistic (and therefore rare)  
21 carrying events. Sample sizes were necessarily relatively small and there is always the danger  
22 that the data from a small captive sample are not necessarily representative of a more general  
23 wild population. In particular certain carrying/locomotor combinations were missing or  
24 present for very low numbers for some species which may lead to sampling bias In addition  
25 the digitisation process for unmarked animals is not particularly accurate particularly for the

1 long-haired orangutans which made it difficult to identify anatomical landmarks. Similarly  
2 long grass sometimes made the hands and feet difficult to see when they were in contact with  
3 the ground. This means that small but perhaps important changes in angles may be  
4 impossible to detect.

5

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

13

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15

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- 6
- 7

1 **Figure legends**

2

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

4

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

8

9 Figure 3. Range plots of the pooled non-human ape data. The bars show the mean maximum  
10 and minimum joint excursion and segment angles. The error bars show the range of these  
11 values. The number in the middle of the bar is the number of samples for each condition.  
12 Each condition is compared to the unloaded quadrupedal condition using a t-test and the  
13 significance level indicated: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

14

15 Figure 4. Range plots of the bonobo data. The bars show the mean maximum and minimum  
16 joint excursion and segment angles. The error bars show the range of these values. The  
17 number in the middle of the bar is the number of samples for each condition. Each condition  
18 is compared to the unloaded quadrupedal condition using a t-test and the significance level  
19 indicated: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

20

21 Figure 5. Range plots of the common chimpanzee data. The bars show the mean maximum  
22 and minimum joint excursion and segment angles. The error bars show the range of these  
23 values. The number in the middle of the bar is the number of samples for each condition.  
24 Each condition is compared to the unloaded quadrupedal condition using a t-test and the  
25 significance level indicated: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

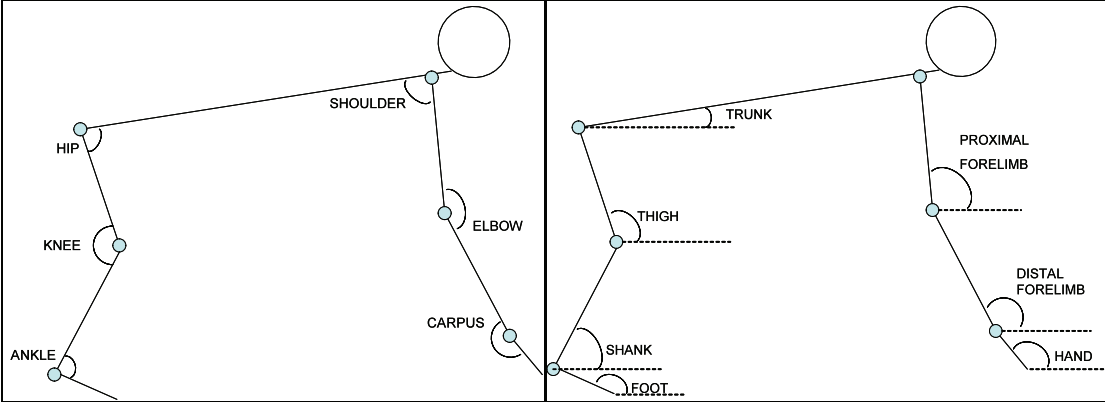
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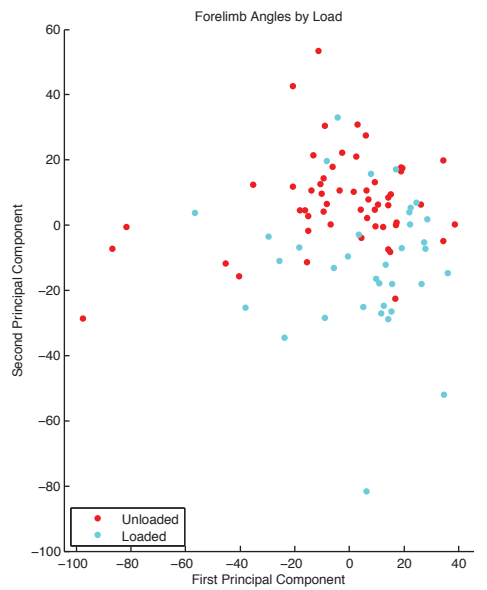
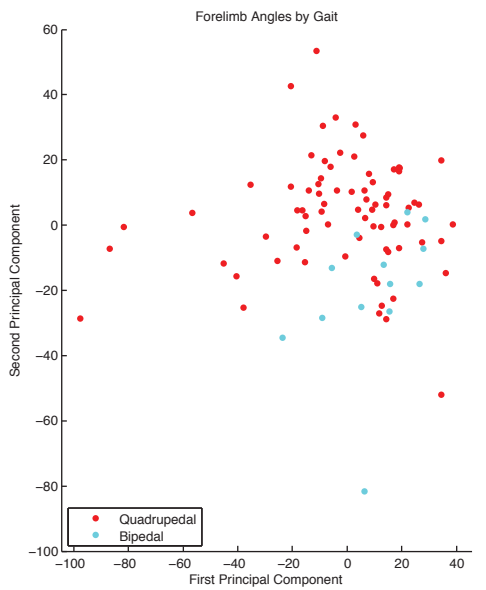
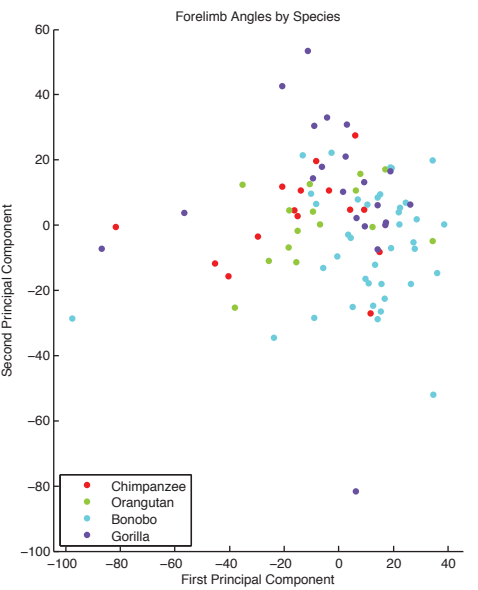
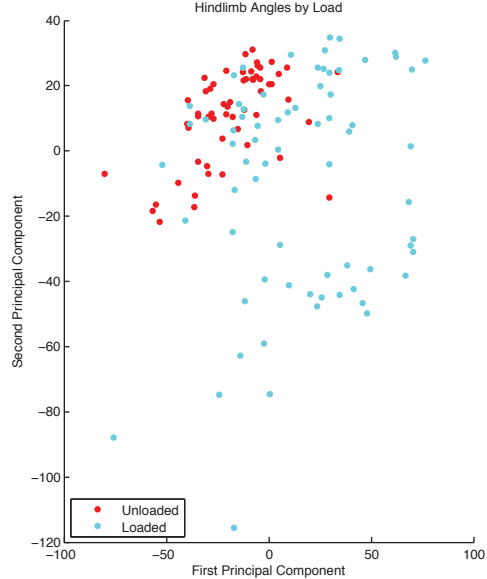
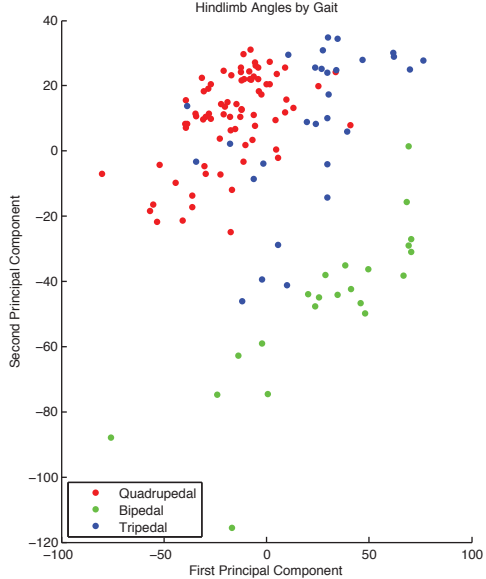
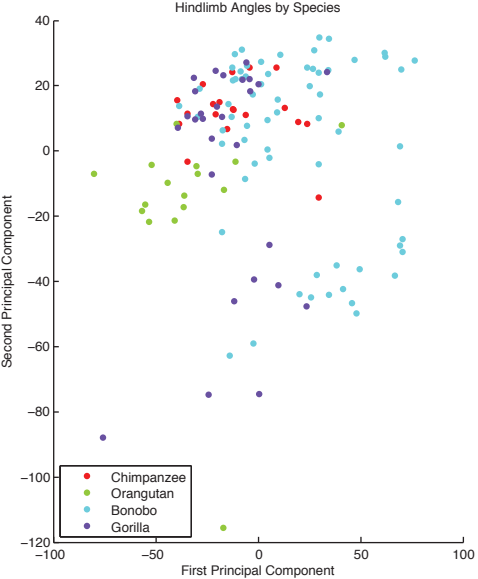
Figure 6. Range plots of the gorilla data. The bars show the mean maximum and minimum joint excursion and segment angles. The error bars show the range of these values. The number in the middle of the bar is the number of samples for each condition. Each condition is compared to the unloaded quadrupedal condition using a t-test and the significance level indicated: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

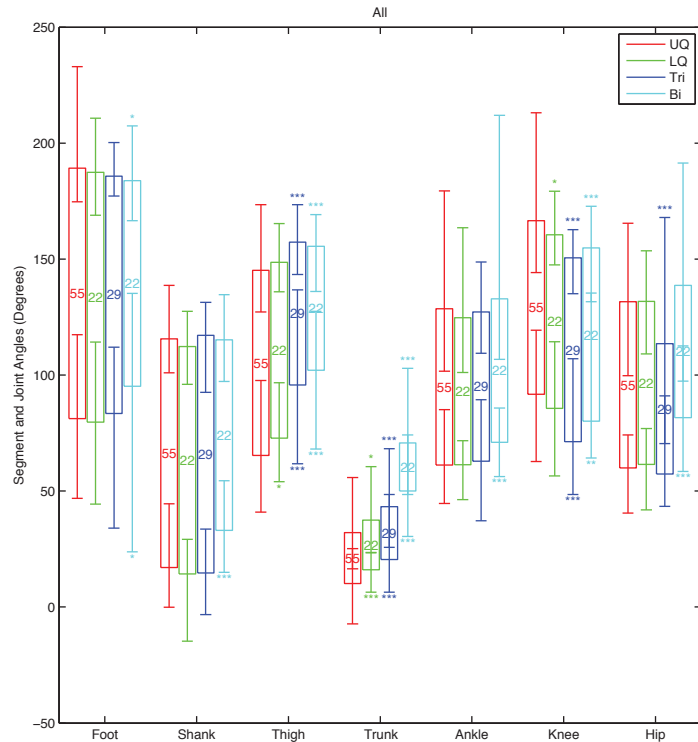
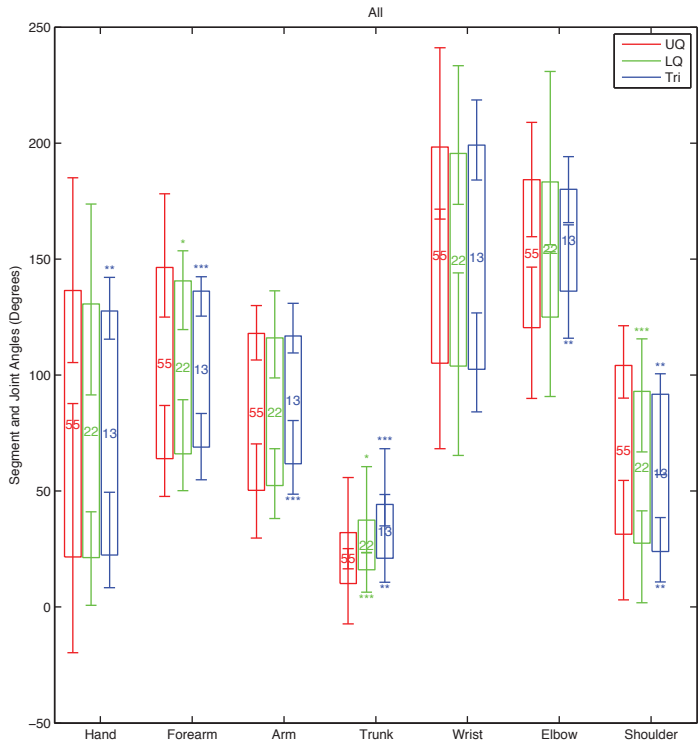
Figure 7. Range plots of the orangutan data. The bars show the mean maximum and minimum joint excursion and segment angles. The error bars show the range of these values. The number in the middle of the bar is the number of samples for each condition. Each condition is compared to the unloaded quadrupedal condition using a t-test and the significance level indicated: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

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

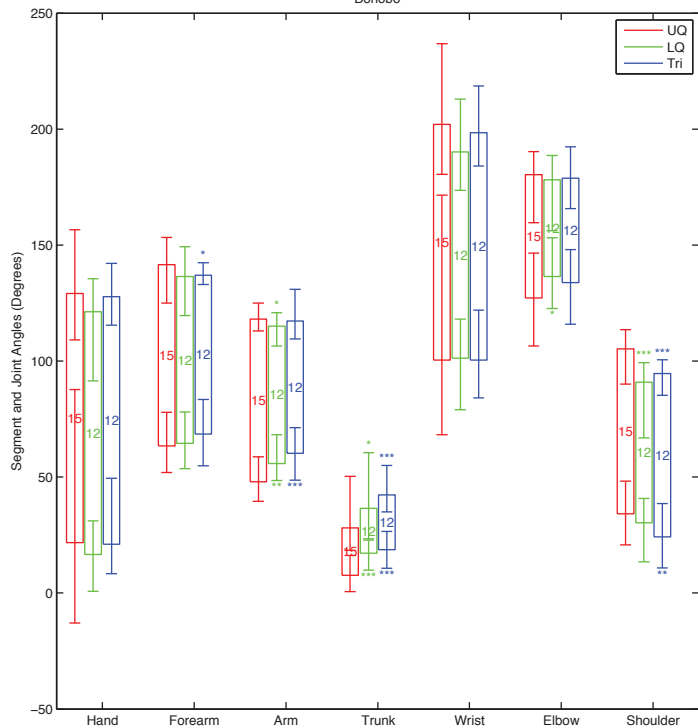
Figure 9. Range plots of the human data. The bars show the mean maximum and minimum joint excursion and segment angles. The error bars show the range of these values. The number in the middle of the bar is the number of samples for each condition. Each condition is compared to the unloaded quadrupedal condition using a t-test and the significance level indicated: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .



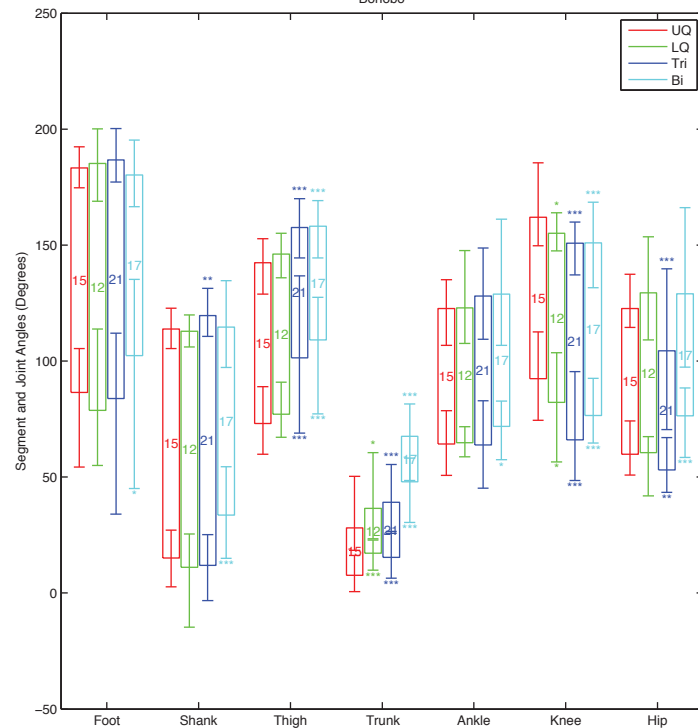


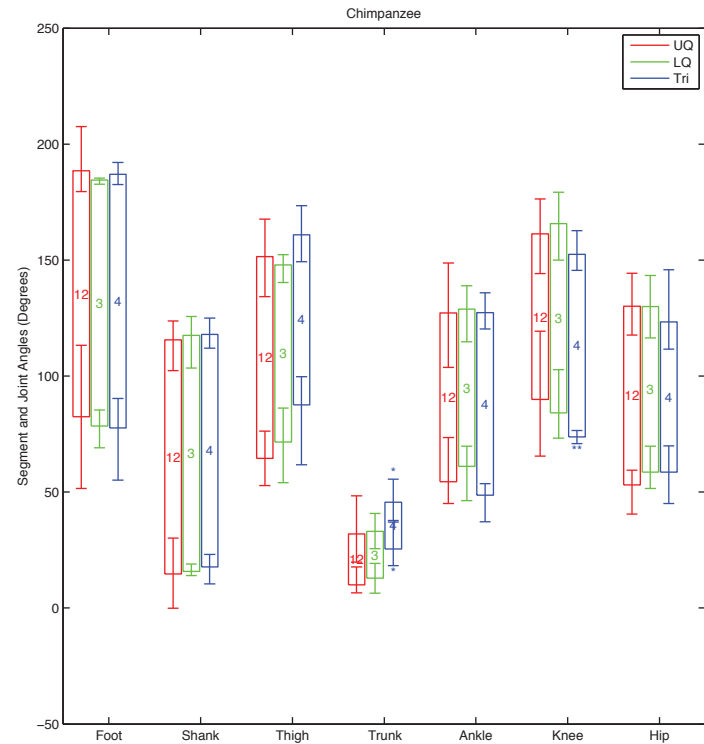
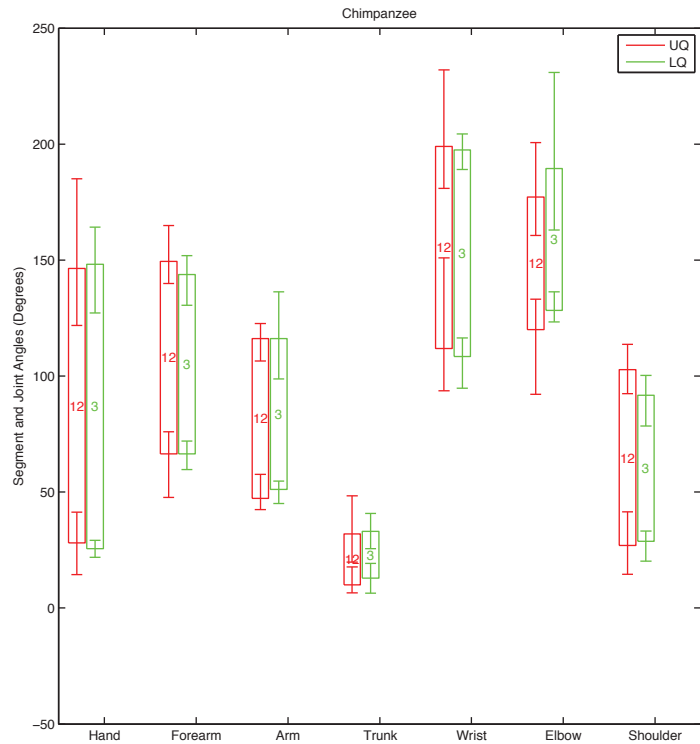


Bonobo

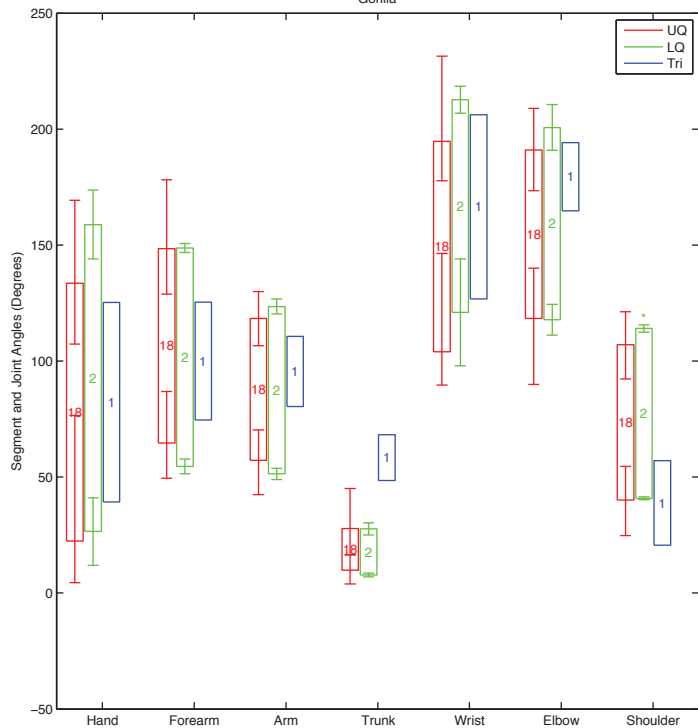


Bonobo





Gorilla



Gorilla

