

Adaptive and phylogenetic influences on musculoskeletal design in cercopithecine primates

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Summary

Broad allometric studies of the musculoskeletal system have frequently sought to explain how locomotor variables have been influenced by body mass. To examine animals that vary widely in body mass, these studies have included taxa that differ in their locomotor adaptations and phylogenetic relatedness. Because these sources of diversity could obscure the effects of body mass, this study was designed to test the effects of adaptive differences in limb proportions and phylogeny, as well as body mass, on locomotor kinematics and extensor muscle mechanical advantage. More specifically, two hypotheses were tested in a sample of closely related animals: (i) that, among animals with similar body mass, those with longer limb segments should adopt more extended limb postures to moderate the joint and midshaft bending moments that they experience, and (ii) that body mass will have similar influences on joint posture and joint moments in closely related and diverse mammalian samples. Three-dimensional kinematic and synchronous force-platform data were collected for six individual cercopithecine

monkeys ranging in mass from 4 kg to 24 kg and at a range of walking speeds. Comparisons among three monkeys with similar body mass but different limb segment lengths reveal a significant effect of limb proportion on posture. That is, animals with longer limbs frequently use more extended limb postures and can have correspondingly lower joint moments. The scaling of locomotor variables across the entire sample of closely related monkeys was generally similar to published results for a diverse sample of mammals, with larger monkeys having more extended limb postures, lower joint moments and greater effective mechanical advantage (EMA) for their limb extensor musculature. Ankle EMA, however, did not increase with body mass in the primate sample, suggesting that clade-specific adaptive differences (e.g. the use of arboreal supports by primates) may constrain the effects of body mass.

Key words: interspecific scaling, kinematics, limb proportions, effective mechanical advantage, cercopithecine, monkey.

Introduction

It is well known that body mass is a primary determinant of locomotor postures and musculoskeletal design. The rationale for this relationship derives from the fact that, while the external forces that an animal experiences are directly related to its body mass (which is proportional to volume), the strengths of the muscles and bones that must resist these forces are proportional to their cross-sectional areas (Galilei, 1638; Alexander et al., 1979, 1981; Biewener, 1982; McMahan, 1975). Because the strength of musculoskeletal support structures does not scale with strong positive allometry in most mammals, including primates, larger animals will either have lower safety factors, and risk bone breakage, or must alter their behavior to moderate the forces and moments that their bones experience (Alexander et al., 1979, 1981; Biewener, 1983; Jungers and Burr, 1994; Polk et al., 2000). There are several behavioral methods that animals may use to moderate the forces that their limbs experience. Animals may decrease their locomotor performance, thereby lowering peak force and strain magnitudes (Rubin and Lanyon, 1984), they may increase the

duration for which their limb is in contact with the ground (duty factor), thereby lowering peak forces for a particular impulse (Alexander et al., 1977), or they may adopt more extended limb postures, thereby increasing the alignment between ground reaction forces (GRFs) and the limb segments (Gray, 1968; Biewener, 1983, 1989). Aligning limbs with the GRF has the combined effects of decreasing the bending loads on bones at the expense of increased axial compression and of moderating the joint moments that extensor muscles must resist. Consequently, larger animals use relatively less muscular force to maintain an erect posture than smaller animals, and larger animals avoid very high tensile bone strains (Biewener, 1983, 1989, 1990).

The majority of the data on size-related changes in locomotor postures and bone strength are derived from broad interspecific allometric analyses. Such studies can often serve to identify fundamental organizing principles that explain much of the variation in biological phenomena. That body mass is an important factor in explaining variation in terrestrial

locomotion is well established and follows from the need for all terrestrial animals to overcome the ubiquitous force of gravity. However, the adaptive and phylogenetic diversity included in such broad samples of mammals may obscure the functional relationship between body mass and locomotor variables. For example, the scaling relationships for joint surface areas for specific clades of mammals differ from those for across-clade comparisons (Godfrey et al., 1991). Consequently, the need for phylogenetic control in comparative and scaling analyses has been increasingly emphasized (Harvey and Pagel, 1991; Felsenstein, 1985; Martins, 1996). In addition, species included in broad interspecific samples frequently vary widely in their locomotor adaptations.

The anatomical specializations related to differences in locomotor behavior may also influence both the limb postures and the mechanical advantage of muscles required to maintain these postures. For instance, the moment arm of the GRF about any joint depends on the relative length of the segments distal to that joint (Fig. 1). Consequently, animals with longer limb segments are predicted to experience higher moments at that joint (compared with shorter-limbed animals) unless they alter their posture to moderate these increased moments.

Limb proportion effects on bone loading and body posture are also implied by the scaling of humeral and femoral cross-sectional properties in three orders of mammal (Polk et al., 2000). When regressed either on bone length or on the product of body mass and bone length, the estimated resistance to bending and compression in the humerus scaled isometrically

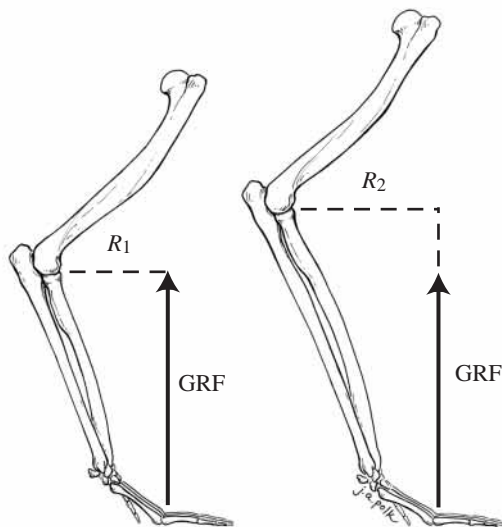


Fig. 1. Rationale for the effects of body proportion on limb posture. Animals with longer limbs will have longer moment arms (R) and will experience increased joint moments compared with shorter-limbed animals [assuming that force magnitude, ground reaction force (GRF), and body posture are constant]. As a consequence, animals with longer limb segments below a joint are expected to adopt more extended joint postures to moderate the joint moments that they experience; that is, the product of GRF and R is smaller for the limb on the left (with R_1) than for the limb on the right (with R_2).

in primates, carnivorans and rodents. This isometric scaling implies either that safety factors are lower in animals with longer forelimbs (with no changes in joint posture) or that behavioral changes must occur to moderate the bending loads that their humeri experience. In contrast, femoral cross-sectional properties scaled with positive allometry, suggesting that the femora of longer-limbed primates may be able to resist increased bending without the need for postural adjustments.

The goal of this study is to test for phylogenetic and adaptive influences on locomotor postures and behavior in a closely related sample of mammals. Adaptive influences on locomotor postures are tested by comparing joint postures and moments among animals that have the same body mass but that differ in their body proportions. Phylogenetic effects will be recognized if the scaling of locomotor variables differs between a phylogenetically restricted and a phylogenetically diverse sample of mammals (Biewener, 1983, 1989). Two specific hypotheses will be tested: (i) that, among animals of similar body mass, those with longer limb segments will have more extended joint postures, lower (or equal) joint moments and a greater effective mechanical advantage for the extensor muscles; (ii) that body mass will have a similar effect on closely related and phylogenetically diverse samples of mammals. That is, animals with a larger body mass will have more extended joint postures, lower (or equal) joint moments and a greater effective mechanical advantage for their extensor muscles (Biewener, 1983, 1989).

Cercopithecine primates are an ideal group in which to examine the effects of body mass and limb proportions. Primates have longer limbs relative to their body mass than most other mammals; they also take longer strides and have greater amounts of forelimb protraction and hindlimb retraction (Alexander et al., 1979; Alexander and Maloiy, 1984; Reynolds, 1987; Larson, 1998; Larson et al., 2000). As a consequence, primates may either experience relatively larger joint moments than other mammals or they should be more likely than other mammals to show limb-proportion-related changes in the mechanical advantage of their limb extensor muscles. The Cercopithecinae is an extremely well supported clade in both morphological and molecular phylogenies (Strasser and Delson, 1987; Groves, 2000; Disotell, 2000), and cercopithecines show a remarkable degree of morphological similarity in their postcranial anatomy (Schultz, 1970). Furthermore, if mass and proportion-related differences in posture are observed between these primate taxa, the results should assist in making functional interpretations about the postures used by some hominin taxa that also differ in both mass and limb proportions (Jungers, 1982; McHenry, 1991).

Materials and methods

This study used six closely related cercopithecine monkeys: one male and one female vervet *Chlorocebus aethiops* (Linnaeus, 1758), patas *Erythrocebus patas* (Schreber, 1775) and olive baboon *Papio anubis* (Lesson, 1827) (Table 1).

Table 1. List of the species, sex and body mass of the six subjects for which data were obtained

Animal	Sex	Body mass (kg)
<i>Chlorocebus aethiops</i>	Female	4.1
<i>Chlorocebus aethiops</i>	Male	5.4
<i>Erythrocebus patas</i>	Female	7.9
<i>Erythrocebus patas</i>	Male	15.7
<i>Papio anubis</i>	Female	15.4
<i>Papio anubis</i>	Male (adult)	24.2
<i>Papio anubis</i>	Male (subadult)	15.4

The subadult and adult male baboon were the same individual.

These monkeys differ fairly widely, both in their body mass (range 4.1–24.2 kg) and in their limb proportions (Fig. 2), for such a closely related group, yet they are the most terrestrial monkeys and use similar locomotor behaviors in natural habitats (Rose, 1973, 1977; Isbell et al., 1998). The male baboon was acquired as a subadult and grew considerably during the study period. Data are included from his adult body mass of 24.2 kg as well as for a subadult stage of 15.4 kg, permitting comparisons among three animals with essentially the same body mass but differing in their limb proportions (male patas, female baboon, subadult male baboon). On the

basis of his dental eruption pattern and body mass, the subadult was approximately 5.5–6 years old at the time of filming (Leigh, 1992; Smith et al., 1994). The subadult did not display the increased variation in limb movement that characterizes immature walking in other taxa (see Kimura, 1987; Sutherland et al., 1988).

The sample size was limited to one male and one female of each species because of the difficulties in housing and training cercopithecine primates as well as the considerable time required to digitize video sequences. Nevertheless, these data are significant because they constitute the first three-dimensional study of locomotor kinematics in non-human primates and, while the results reflect interindividual differences in locomotor posture, the morphological differences among these individuals closely mirror the size and body proportion differences observed between larger samples of these species (Gebo and Sargis, 1993; Strasser, 1992). Thus, the results described below should also reflect interspecific differences in locomotor behavior.

Absolute lengths of the limb segments for each of the three 15 kg monkeys are shown in Fig. 2B. As noted above, the length of the limb segments distal to a particular joint is predicted to be a major influence on the moments experienced at that joint (Fig. 1), and the animals with longer limb segments are predicted to have more extended joint postures (including lower angular excursions and lower protraction and retraction

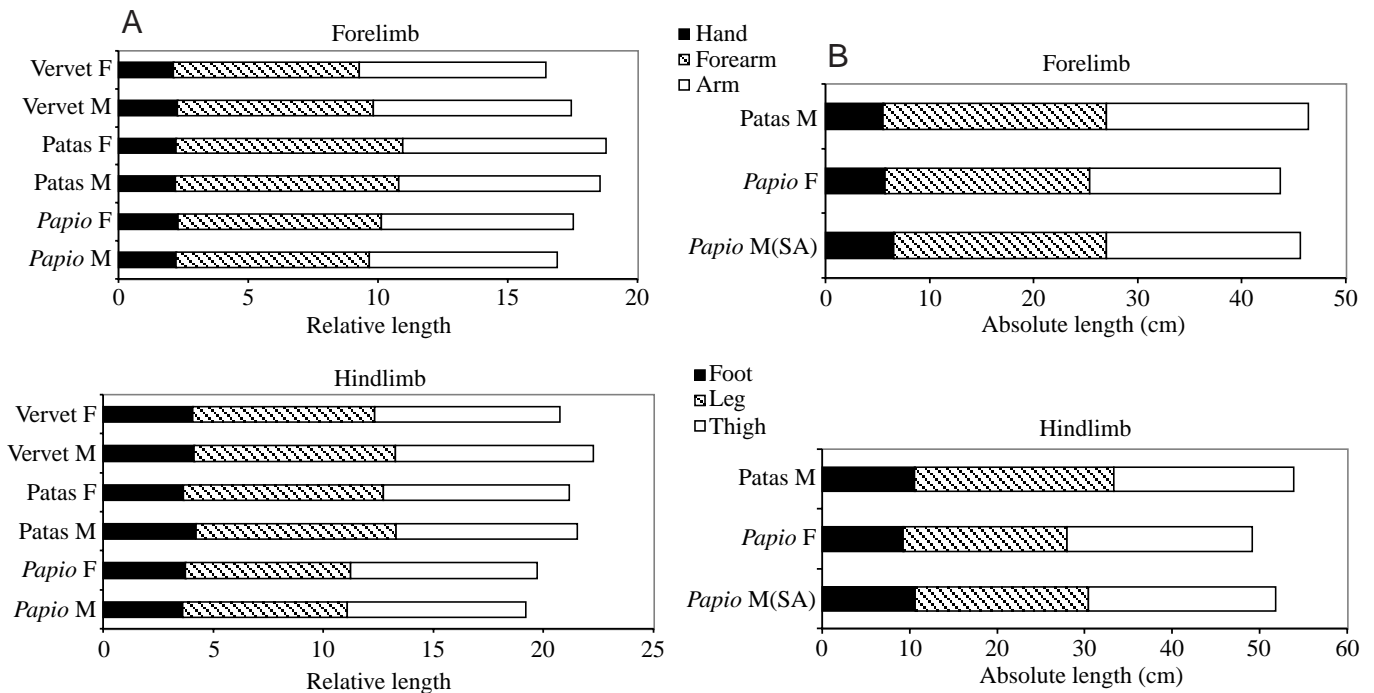


Fig. 2. Body proportions for (A) all adult monkeys and (B) 15 kg monkeys. Relative lengths for adult monkeys were calculated as the length of each segment/(mass)^{1/3}. Proximal segments (arm and thigh) are unshaded, intermediate segments (leg and forearm) are hatched and distal segments (hand and foot) are in black. In the adult monkeys (A), similar limb proportions are found within each species (except for the vervet hindlimb), and the interspecific differences in limb proportions are not well correlated with body mass. The greatest discrepancy in segment lengths between the 15 kg animals (B) is found below the knee, where the patas has longer distal hindlimbs than either baboon (*Papio*). The patas has longer hindlimbs and forelimbs than either baboon, and longer feet and distal forelimbs (forearm + hand) than the female baboon. The patas also has shorter hands than the male baboon. F, female; M, male; SA, subadult.

angles at the hip and shoulder), correspondingly lower or equivalent joint moments and greater effective mechanical advantage for their extensor musculature. The male patas has relatively longer hindlimbs and longer segments distal to the knee than either baboon. The forelimbs, segments distal to the elbow, and feet of the patas were similar in length to those of the male baboon, but these segments were longer in the male monkeys than in the female baboon. The hand segment was similar in length between the female baboon and the patas, while the male baboon had longer hands. The differences in body mass and proportions among these individuals closely reflect the differences observed between larger samples of

these taxa (Gebo and Sargis, 1993; Strasser, 1992). A summary of predicted differences between the three 15 kg individuals is given in Table 2.

Three-dimensional kinematic and ground reaction force data were collected as the animals moved through a Lexan and plywood tunnel (11 m×1.2 m) at the Primate Locomotion Laboratory at SUNY, Stony Brook, USA. A three-camera video-based motion-analysis system (Peak Performance Technologies, Inc., Englewood, CO, USA) was used to measure the three-dimensional positions of reflective markers attached to the shaved skin overlying several bony landmarks (Table 3). Limb segments were defined by connecting adjacent limb markers, and joint angles were measured between adjacent segments. Three-dimensional angles were measured at the wrist, elbow, shoulder, ankle, knee and hip at mid-stance (MS). Protraction and retraction angles were obtained for the arm, forelimb, thigh and hindlimb at touch-down (TD) and lift-off (LO), respectively. Protraction and retraction angles for the forelimb and hindlimb were measured relative to a transverse plane passing through the shoulder and hip, respectively. Angular excursions (AEs) for the arm, forelimb, thigh and hindlimb were calculated as the sum of protraction and retraction angles. Video cameras were shuttered at 1/1000 s or 1/2000 s to avoid motion blur, and cameras were operated at both 60 and 180 Hz for animals weighing more than 15 kg and exclusively at 180 Hz for animals weighing less than 15 kg.

Three-dimensional ground reaction force (GRF) components were measured using a Kistler 9281B force platform (Kistler Instruments, Winterthur, Switzerland) and recorded digitally, at 2700 Hz, using National Instruments hardware and LabView software (National Instruments, Austin, TX, USA). Kinematic and kinetic data were synchronized using an Event-Video Coordinating Unit (EVCU) and Peak Motus software. Synchronization pulses were generated by the EVCU and recorded both on kinematic video tapes and in kinetic data files. The Peak Motus software unites these two data sources, thereby allowing the alignment of a single video frame with the start of the synchronization pulse located in the analog force data file. The absolute accuracy of this synchronization is determined by the frequency of the kinematic data (i.e. maximum alignment errors are less than the duration of one frame). The three-dimensional GRF vector resultant was projected upwards from

Table 2. Predictions for 15 kg monkeys

Variable	Influential body segment	Segment length	Prediction
Joint angles			
Wrist MS	Hand	$m > f = p$	$p = f > m$
Elbow MS	Forearm + hand	$p = m > f$	$p = m > f$
Shoulder MS	Forelimb		
Shoulder TD	Forelimb		
Forelimb TD	Forelimb		
Shoulder LO	Forelimb		
Forelimb LO	Forelimb		
Shoulder AE	Forelimb		
Forelimb AE	Forelimb		
Ankle MS	Foot		$p = m > f$
Knee MS	Leg + foot		$p > m > f$
Hip MS	Hindlimb	$p > m > f$	$f > m > p$
Hip TD	Hindlimb		
Hind limb TD	Hindlimb		
Hip LO	Hindlimb		
Hind limb LO	Hindlimb		
Hip AE	Hindlimb		
Hindlimb AE	Hindlimb		
Joint moments			
Wrist	Hand	$m > f = p$	$p = f \geq m$
Elbow	Forearm + hand	$p > m > f$	$f \geq m \geq p$
Shoulder	Forelimb	$p = m > f$	$f \geq m = p$
Hip	Hindlimb	$p = m > f$	$f \geq m = p$
Knee	Leg + foot	$p > m > f$	$f \geq m \geq p$
Ankle	Foot	$p > m > f$	$f \geq m \geq p$

These predictions relate kinematic variables to limb segment lengths for three 15 kg monkeys: male patas (p), female baboon (f) and subadult male baboon (m). The influential limb segment and the rank order of segment lengths are included in this table with the variable and predicted difference between the animals.

To interpret the prediction $f > m$, for example, indicates that the female is predicted to have a more extended posture (greater joint angle) than the male baboon.

MS, mid-stance; TD, touch-down; LO, lift-off; AE, angular excursion.

Table 3. Bony landmarks underlying kinematic markers

Joint marker locations
Distal end of metacarpal V
Ulnar head
Lateral epicondyle of humerus
Posterior side of acromion
Distal end of metatarsal V
Lateral malleolus
Lateral epicondyle of femur
Greater trochanter
Anterior superior iliac spine

the distal end of the metatarsal or metacarpal (for fore- and hindlimb measurements, respectively). External joint moments were estimated in Peak Motus software, following Biewener (1983), as the product of the GRF magnitude and the (three-dimensional) perpendicular distance between the GRF vector and each limb joint (GRF moment arm).

Anatomical moment arms were measured from lateral-view radiographs for the elbow, knee and ankle as the maximum perpendicular distance between the line of action of the muscle (assumed to be parallel to the long axis of the bone proximal to the joint in question) and the joint center of rotation. Joint centers of rotation for the elbow, knee and ankle were assumed to be the center of the humeral trochlea, the point of contact between the femur and tibia and the anteroposterior center of the tibia's distal articular surface, respectively. Muscle insertion points on the ulna, patella, tibia and calcaneus were confirmed by dissection of conspecific cadaver specimens. Effective mechanical advantages (EMAs) for these extensor (and plantar flexor) muscles were calculated as the ratio of the anatomical moment arm to the GRF moment arm (Biewener, 1989) at the time of mid-support (mid-support was identified when the hip was over the metatarsal or the shoulder over the metacarpal marker for the hindlimb and forelimb, respectively). EMA measurements were obtained for all adult monkeys, but not for the subadult male baboon. In addition, EMA measurements were not obtained for the shoulder, hip or wrist because of the difficulty in measuring muscle moment arms at these joints.

A total of 528 strides at a range of walking speeds comprised the study sample. At least 60 strides were included for each individual monkey to characterize limb kinematics, and at least 30 of these strides included both kinematic and kinetic data (Table 4). Walking speeds are shown in Fig. 3. The male patas tended to use faster walking speeds than the other monkeys while the male baboon tended to use slower speeds. Only walking speeds were included in this analysis since the male baboon would not gallop.

Two general types of comparisons are reported here. First, kinematic and kinetic variables are compared among the three individuals with similar body mass but different limb proportions. Second, kinematic and kinetic variables are scaled across the entire sample of adult primates and compared with those for a diverse sample of mammals. For the first comparison, kinematic and kinetic variables were compared between individuals using either analyses of variance (ANOVAs) or analyses of covariance (ANCOVAs) depending on whether the variables were significantly correlated with speed. For variables not correlated with speed, the significance of differences between individuals was tested using ANOVAs with *post-hoc* comparisons conducted using the least-significant-difference method (Sokal and Rohlf, 1995). ANCOVAs, with speed as the covariate, were used to evaluate differences between individuals when variables were significantly correlated with speed. In the ANCOVA, least-squares means (LSMs) for each individual were

Table 4. Sample sizes

	Total number of strides	Strides with force data
Vervet M	62	36
Vervet F	61	51
Patas M	85	37
Patas F	86	39
Baboon F	62	30
Baboon M (A)	69	38
Baboon M (SA)	103	34
Total	528	265

At least 60 strides were analyzed for each individual to obtain a wide range of speeds. At least 30 of these strides had synchronized ground reaction force data. A single foot contact with the force platform was obtained for each stride, and these were evenly divided between forelimb and hindlimb contacts.

A, adult; SA, subadult; F, female; M, male.

obtained at the mean walking speed, and significant differences in LSMs indicated significant differences between individuals for a particular variable (Green et al., 2000). In the event that a variable was correlated with speed for one individual but not the other, ANCOVA was used to assess the significance of interindividual differences. A Bonferroni correction, $\alpha' = \alpha/k$ (where α is the type one error rate and k is the number of

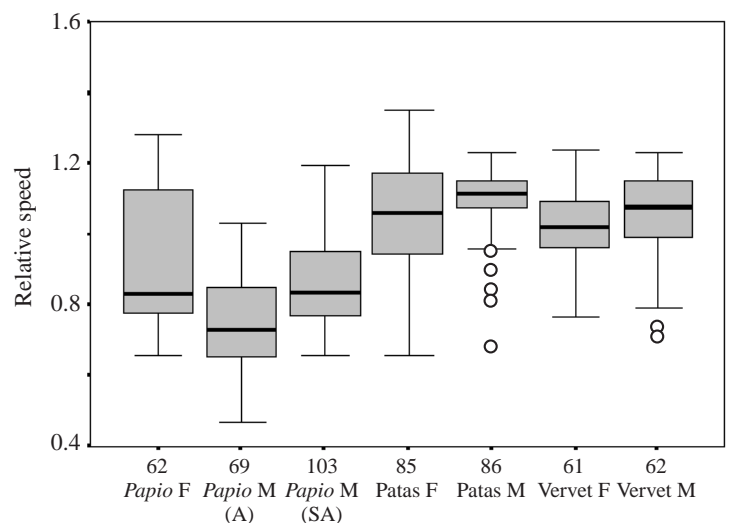


Fig. 3. Range of walking speeds. The range of relative speeds, $v/(gh)^{0.5}$, is illustrated. v is velocity, g is the gravitational constant and h is hip height during quiet standing, adopted by each of the individuals in this study. Walking gaits were used at all speeds in this study. The male patas tended to use faster walking speeds than the other monkeys, while the male baboon (*Papio*) tended to move more slowly. The median speed for each individual is indicated in bold, the shaded box contains the interquartile range (IQR), and whiskers may extend to $1.5 \times \text{IQR}$. Values beyond the whiskers (open circles) are outlying data points. Values of N are given below the box-and-whisker plot. F, female; M, male; A, adult; SA, subadult.

comparisons), was applied to the experiment-wise type-one error rate to make the statistical tests of each variable more conservative (Sokal and Rohlf, 1995).

To evaluate how kinematic variables scaled with body mass across the entire sample of adult primates, it was necessary to obtain values for each variable at comparable speeds. Considerable literature has been devoted to the issue of comparable speeds, and for most mammals comparisons have been made at the trot-gallop transition (Heglund et al., 1974). Unfortunately, primates do not use a classical trotting gait (Hildebrand, 1967; Vilensky, 1989; Larson, 1998) and do not appear to change gait to a gallop for similar mechanical reasons as do non-primates (Demes et al., 1994). Alexander and colleagues (Alexander and Jayes, 1983; Alexander, 1989) have suggested that geometrically similar animals should move in a dynamically similar fashion if they are moving at the same relative speeds (the same Froude numbers). Under such conditions, linear gait parameters should differ by a constant value for animals that are geometrically similar. Similarly, all speeds, frequencies or muscle powers should also be proportional (but with different constants) for animals moving at similar Froude numbers. Thus, to obtain values of kinematic parameters at comparable speeds, ANCOVAs (using relative speed as the covariate) were conducted to obtain the LSM for each variable at the

mean relative speed. These LSM values were plotted against body mass to evaluate how they scaled and to compare them with Biewener's (1989) diverse sample of mammals. Relative speed is measured as the square root of Froude number, $v/(gh)^{0.5}$, where v is velocity, g is the gravitational constant and h is hip height.

Results

Effects of speed on locomotor variables

Pearson product-moment correlation coefficients between kinematic variables and speed are presented in Table 5. In general, with increasing speed, joint postures at mid-stance tend to become more flexed (dorsiflexed for the ankle). Only elbow and ankle angles at mid-stance are correlated with speed for all individuals, and these become more flexed as speed increases. Wrist and knee angles at mid-stance tend to decrease with increasing speed, but the correlations with speed are not always significant, while shoulder angles tend to be more retracted for most individuals (except for the male patas). With more flexed postures at mid-stance, combined with higher GRFs, joint moments for most individuals are positively correlated with speed. Longer moment arms resulting from more flexed postures also lead to lower values of EMA at the elbow and ankle with increasing speed.

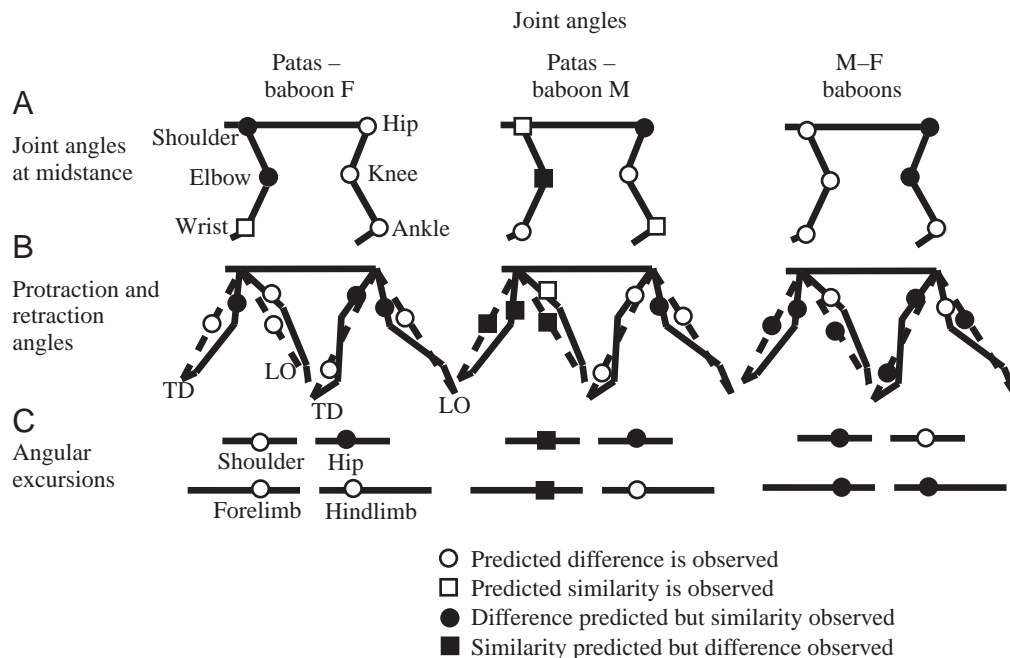


Fig. 4. Differences in joint angles between pairs of 15 kg monkeys. Each stick figure represents a comparison of two monkeys. Markers at each joint (A), limb segment (B) and angular excursion line (C) are shaped to indicate whether a difference in joint angle (or excursion) was predicted to exist between these monkeys (based on the differences in body proportions; see Table 2). Markers are shaded to indicate whether that prediction was observed. Solid lines represent individual limb segments, while broken lines represent either forelimbs or hindlimbs. Monkeys with longer limb segments were predicted to have more extended joint postures and lower protraction and retraction angles than monkeys with shorter limb segments. Markers in B illustrate whether predicted differences were observed in shoulder, forelimb, hip and hindlimb protraction and retraction angles. Markers in C illustrate comparisons between joint angular excursions. Where significant differences exist, the animal with longer limb segments had more extended joint postures at mid-stance, as well as lower protraction and retraction angles at touch-down (TD) and lift-off (LO), respectively. M, male; F, female.

Body proportion effects

Joint angles

Fig. 4 illustrates whether the observed differences in joint angles corresponded with predictions; summary data for these comparisons are shown in Table 6. In general, the joint angles differ between the male patas and female baboon in the direction predicted from differences in limb proportions. That is, the patas, with its longer limb segments, uses more extended joint postures and lower angular excursions than the female baboon. Exceptions are found at the elbow and shoulder at mid-stance, the shoulder at touch-down, the hip at touch-down and lift-off and for hip angular excursion, where no significant differences are observed. Despite the non-significant differences, the direction of the difference was the same as that predicted (except for the elbow angle at mid-stance). For the

comparison of the male baboon with the male patas, predicted differences are most often found for the hindlimb joints, where the patas has more extended knee posture and decreased angular excursions at the hip. The male patas also has more extended forelimb joints and lower forelimb and shoulder angular excursions even though no significant difference was predicted. It should be noted, however, that the subadult male baboon has more extended wrist postures (as predicted by hand length differences), so it is not always the case that the patas has more extended limb postures than the baboons. Where significant differences exist for the comparison between the male and female baboons, they are usually in the direction predicted from limb length differences (e.g. the male, having longer limbs distal to the elbow, has correspondingly more extended elbows). The majority of these results suggest that

Table 5. Pearson product-moment correlation coefficients between kinematics variables and speed for each individual

	Vervet M	Vervet F	Patas F	Patas M	Baboon F	Baboon M (A)	Baboon M (SA)
Angles							
Wrist MS	-0.064	0.208	-0.106	0.260	-0.687	-0.488	-0.639
Elbow MS	-0.557	-0.395	-0.674	-0.575	-0.716	-0.754	-0.452
Shoulder MS	0.280	0.164	0.462	0.262	0.547	0.588	0.582
Shoulder LO	0.121	-0.018	0.298	0.075	-0.032	0.359	-0.095
Shoulder TD	0.097	0.022	-0.497	-0.340	-0.455	-0.259	-0.229
Forelimb TD	-0.142	0.240	-0.195	0.044	-0.186	0.011	-0.186
Forelimb LO	0.119	0.143	0.076	-0.178	0.146	0.185	-0.220
Shoulder AE	0.195	0.005	-0.102	-0.185	-0.381	0.076	-0.334
Forelimb AE	-0.002	0.281	-0.089	-0.169	0.148	0.195	-0.245
Hip TD	0.000	-0.146	-0.095	-0.148	-0.580	-0.102	-0.197
Hindlimb TD	-0.243	-0.134	-0.432	-0.369	-0.695	-0.112	-0.044
Ankle MS	-0.456	-0.393	-0.599	-0.343	-0.341	-0.273	-0.271
Knee MS	-0.108	-0.225	-0.238	0.004	-0.500	-0.739	-0.529
Hip MS	-0.009	0.290	-0.305	-0.049	0.287	0.717	0.222
Hip LO	0.646	0.668	-0.259	0.320	0.495	0.037	-0.090
Hindlimb LO	0.274	0.487	-0.103	0.110	0.237	0.201	-0.242
Hip AE	0.550	0.455	-0.209	0.135	-0.172	-0.073	-0.309
Hindlimb AE	0.120	0.287	-0.360	-0.221	-0.453	0.116	-0.342
Joint moments							
Wrist MS	0.815	0.780	0.641	0.852	0.930	0.103	0.854
Elbow MS	0.788	0.753	0.779	0.819	0.954	0.219	0.695
Shoulder MS	0.603	0.344	0.101	-0.022	0.667	0.118	0.687
Ankle MS	0.780	0.794	0.777	0.712	0.849	0.647	0.224
Knee MS	0.810	0.591	0.463	0.357	0.844	-0.021	0.755
Hip MS	0.298	0.490	-0.155	0.482	0.484	0.509	0.005
Effective mechanical advantage (EMA)							
Elbow	-0.476	-0.421	-0.704	-0.560	-0.891	-0.250	-
Ankle	-0.466	-0.441	-0.364	-0.414	-0.269	-0.559	-
Knee	-0.347	0.201	-0.058	0.033	-0.200	0.231	-

Significant correlations are highlighted in bold print.

Although the correlations were not always significant for all individuals, many joint angles at mid-stance tend to become more flexed with increasing speed (negative correlations for wrist, elbow, ankle and knee, positive correlations for shoulder and hip).

Joint moments increase with speed as a result of the increased limb flexion as well as increasing GRF magnitude.

EMA decreases with speed for the elbow and ankle for most individuals. Knee EMA does not change significantly with speed.

EMA could not be calculated for the subadult male baboon.

GRF, ground reaction force; MS, mid-stance; LO, lift-off; TD, touch-down; AE, angular excursion; F, female; M, male; A, adult; SA, subadult.

mid-stance joint angles differ predictably with differences in limb proportions. Given the subtle differences in limb proportions in this sample, many of the differences are not significant at the $\alpha'=0.017$ level. However, the fact that several of the non-significant results also differ in the predicted

direction suggests that greater differences in limb proportions could have a more substantial effect on locomotor postures. Comparison of protraction and retraction angles and angular excursions reveals a more mixed picture, with angles either not differing (e.g. comparison of male with female baboon) or not

Table 6. Summary data for joint angles and comparisons between the three 15 kg monkeys

	Speed correlation	Patas		♀ Baboon		Subadult ♂ baboon		Patas–♀ baboon	Patas–♂ baboon	♀ Baboon–♂ baboon
		LS mean	95% CI	LS mean	95% CI	LS mean	95% CI	<i>P</i> -value	<i>P</i> -value	<i>P</i> -value
A Analysis of variance (ANOVA)										
Wrist MS	f,m	122.92	120.4–125.5	136.28	132.1–140.6	144.06	140.8–147.4	0.002	0.000	0.002
Elbow MS	p,f,m									
Shoulder MS	f,m	35.32	33.2–37.6	28.56	26.6–30.6	24.89	23.3–26.6	0.000	0.000	0.000
Shoulder LO	n	47.71	46.1–49.3	52.10	51.0–53.3	46.43	45.7–47.2	0.000	0.106	0.000
Shoulder TD	p,f,m									
Forelimb TD	n	25.97	24.9–27.1	27.56	26.7–28.4	27.89	27.3–28.5	0.011	0.002	0.599
Forelimb LO	n	36.09	34.3–38.0	39.90	38.7–41.1	39.36	38.4–40.4	0.000	0.001	0.601
Shoulder AE	f	55.51	53.8–57.3	62.12	60.8–63.5	62.59	61.6–63.6	–	0.000	–
Forelimb AE	n	62.47	60.7–64.3	67.99	66.6–69.4	67.08	66.1–68.1	0.000	0.000	0.000
Hip TD	f	35.54	34.1–37.0	40.03	38.8–41.3	39.60	38.5–40.8	–	0.000	–
Hindlimb TD	p,f	28.10	27.0–29.2	34.98	33.8–36.2	34.18	33.3–35.1	0.000	0.000	0.337
Ankle MS	p,f,m									
Knee MS	f,m	124.33	122.9–125.8	117.61	116.1–119.2	117.50	115.7–119.4	0.000	0.000	0.926
Hip MS	n	16.72	15.0–18.6	19.66	17.9–21.6	18.90	17.6–20.3	0.017	0.049	0.520
Hip LO	p	12.84	11.5–14.4	11.07	9.9–12.4	8.52	7.4–9.8	–	–	0.005
Hindlimb LO	n	31.93	30.5–33.4	37.73	36.8–38.7	37.23	36.1–38.5	0.000	0.000	0.598
Hip AE	m	50.57	49.4–51.8	52.01	51.0–53.0	49.80	48.7–50.9	0.097	–	–
Hindlimb AE	f,m	60.61	59.3–61.9	72.93	71.7–74.2	71.69	70.7–72.7	0.000	0.000	0.166
B Analysis of covariance (ANCOVA)										
Wrist MS	f,m	131.33	127.7–135.0	133.46	130.6–136.4	139.34	136.3–142.4	0.396	0.003	0.005
Elbow MS	p,f,m	132.07	130.3–133.9	133.42	131.6–135.3	138.89	137.3–140.5	0.332	0.000	0.000
Shoulder MS	f,m	29.39	27.1–31.9	31.01	29.0–33.1	26.66	25.2–28.2	0.363	0.075	0.000
Shoulder LO	n									
Shoulder TD	p,f,m	7.51	6.5–8.7	7.98	6.9–9.2	13.62	12.0–15.4	0.595	0.000	0.000
Forelimb TD	n									
Forelimb LO	n									
Shoulder AE	f	57.30	55.8–58.9	61.35	59.7–63.0	61.38	60.0–62.8	0.001	–	0.977
Forelimb AE	n									
Hip TD	f	37.34	35.9–38.8	39.34	37.8–40.9	38.35	37.1–39.6	0.077	–	0.304
Hindlimb TD	p,f	30.14	28.9–31.4	33.79	32.7–34.9	32.97	31.9–34.1	0.000	0.003	0.264
Ankle MS	p,f,m	95.81	93.6–98.1	89.14	87.5–90.8	93.93	92.2–95.71	0.000	0.237	0.000
Knee MS	f,m	127.75	125.8–129.8	116.36	114.6–118.2	115.47	113.9–117.0	0.000	0.000	0.439
Hip MS	n									
Hip LO	p	11.48	9.9–13.3	11.51	10.0–13.3	9.14	8.1–10.4	0.982	0.037	–
Hindlimb LO	n									
Hip AE	m	51.32	50.0–52.7	51.75	50.5–53.1	49.34	48.3–50.4	–	0.042	0.004
Hindlimb AE	f,m	62.42	61.1–63.8	71.93	70.7–73.2	70.66	69.4–71.9	0.000	0.000	0.130

A. Mean joint angles, confidence intervals (CI) and results of ANOVA for each pairwise comparison.

B. Least-squares (LS) means and confidence interval and results of ANCOVA.

Where significant differences between individuals were observed, the *P*-value for the comparison is highlighted in bold print.

The Bonferroni-adjusted type-one error rate was 0.017.

The column Speed correlation indicates whether the variable in question was correlated with speed for the male patas (p), the female baboon (f) or the subadult male baboon (m).

If a variable was correlated with speed for one individual but not the other, the ANCOVA was used to assess the significance of the observed difference. The differences are summarized in Fig. 4.

MS, mid-stance; LO, lift-off; TD, touch-down; AE, angular excursion; n, variable not correlated with speed for any animal.

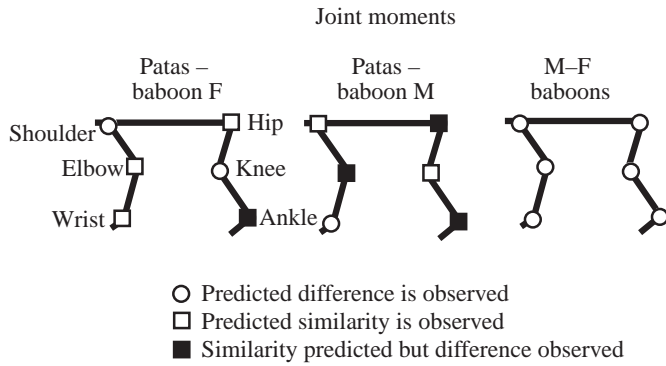


Fig. 5. Joint moments. This figure illustrates the difference in joint moments between each pair of 15 kg monkeys. Joint moments in animals with longer limb segments were predicted to be lower or equivalent to those of shorter-limbed animals. While there are some exceptions, this pattern is generally observed. Most importantly, where difference in limb proportions are greatest (i.e. below the knee), lower joint moments are consistently observed. M, male; F, female.

differing in the manner predicted (e.g. forelimb comparisons for male patas with male baboon).

Joint moments

The joint moment comparisons across the pairs of 15 kg monkeys show a mixture of predicted and unpredicted results (Fig. 5, Table 7). Joint moments depend on the magnitude of the GRF and the moment arm of the GRF about the joint in

question. Animals with longer limb segments were predicted to have similar or lower joint moments than those with shorter limb segments. When moving at the same speed, the subadult male baboon exerted significantly lower ground reaction forces on its forelimb and hindlimb than either the adult female baboon or the male patas monkey. The latter two monkeys do not differ in their GRF magnitudes.

Despite having longer limbs and higher GRF magnitudes, the patas experiences similar or lower joint moments than either baboon (except for comparisons at the ankle for both baboons and at the hip and elbow for the male baboon). The moderation of joint moments for the patas is attained by better alignment between the limb segments and the GRF. In the comparisons between the two baboons, the predicted differences were observed for all joints. The male baboon had lower moments than the female because the GRF magnitude was lower and the male frequently used more extended limb postures (Fig. 4).

Effective mechanical advantage

EMA (Table 7) was measured for the knee, elbow and ankle for all adults but not for the subadult baboon (radiographs were not obtained for the subadult male). The greatest difference in limb proportions between these monkeys is found in the limb segments below the knee, with the patas having longer legs and feet. The male patas has correspondingly more extended knee postures and greater mechanical advantage at the knee than the female baboon. This indicates that the patas requires less muscle force to

Table 7. Summary data for comparisons of joint moments, mid-stance ground reaction force magnitudes and effective mechanical advantage

	Speed correlation	Patas		♀ Baboon		Subadult ♂ baboon		Patas-♀ baboon	Patas-♂ baboon	♀ Baboon-♂ baboon
		LS mean	95% CI	LS mean	95% CI	LS mean	95% CI	P-value	P-value	P-value
Joint moments										
Hip	p,f	1.081	0.875-1.335	0.711	0.576-0.879	0.513	0.430-0.612	0.019	0.000	0.009
Knee	p,f,m	0.475	0.398-0.568	0.840	0.705-1.001	0.407	0.349-0.474	0.000	0.252	0.000
Ankle	p,f,m	1.160	1.025-1.314	0.802	0.709-0.908	0.535	0.480-0.596	0.000	0.000	0.000
Shoulder	f,m	0.414	0.321-0.534	0.880	0.683-1.133	0.590	0.454-0.766	0.000	0.104	0.017
Elbow	p,f,m	1.043	0.933-1.167	0.855	0.763-0.957	0.478	0.425-0.539	0.028	0.000	0.000
Wrist	p,f,m	0.492	0.440-0.551	0.521	0.466-0.583	0.246	0.219-0.276	0.526	0.000	0.000
GRF										
Hindlimb	p,f,m	13.177	12.020-14.445	11.353	10.358-12.445	7.012	6.472-7.599	0.050	0.000	0.000
Forelimb	p,f,m	12.552	11.619-13.559	12.605	11.676-13.609	7.127	6.584-7.714	0.944	0.000	0.000
EMA										
Knee	p,f	0.620	0.518-0.743	0.280	0.236-0.333	-	-	0.000	-	-
Ankle	p,f	0.296	0.278-0.316	0.346	0.325-0.369	-	-	0.004	-	-
Elbow	n	0.526	0.461-0.601	0.312	0.290-0.336	-	-	0.000	-	-

All comparisons were conducted using ANCOVA with the exception of the elbow EMA, which was conducted using an ANOVA (means rather than LS means are presented for this variable).

Comparisons are summarized visually in Fig. 5.

Significant P values are highlighted in bold print. GRF, ground reaction force; EMA, effective mechanical advantage; f, female baboon; m, subadult male baboon; n, variable not correlated with speed for any animal; p, male patas; LS mean, least-squares mean; CI, confidence interval.

maintain its knee joint posture than does the female baboon. At the elbow and ankle, however, the female baboon has greater mechanical advantage than the patas.

Scaling of variables across adult primates

Joint angles

Many of the joint angles at mid-stance do not change

Table 8. Regression equations for least-squares mean values (obtained from ANCOVA with relative speed as covariate) versus body mass

	<i>r</i>	Slope	Intercept	Predicted	Observed
Joint angles					
Hindlimb AE	-0.059	-0.006	1.827	-	0
Hip AE	-0.915	-0.103	1.821	-	-
Hindlimb LO	-0.336	-0.034	1.587	-	0
Hip LO	-0.956	-0.405	1.537	-	-
Hip MS	-0.510	-0.088	1.354	-	-
Knee MS	0.492	0.032	2.045	+	0
Ankle MS	-0.187	-0.011	1.975	+	0
Hindlimb TD	0.153	0.020	1.461	-	0
Hip TD	-0.327	-0.025	1.595	-	0
Forelimb AE	-0.378	-0.032	1.854	-	0
Shoulder AE	-0.692	-0.102	1.892	-	-
Forelimb LO	-0.404	-0.043	1.642	-	0
Shoulder LO	-0.686	-0.136	1.859	-	-
Shoulder MS	-0.723	-0.190	1.685	-	-
Elbow MS	0.692	0.073	2.037	+	+
Wrist MS	0.262	0.020	2.099	+	0
Forelimb TD	-0.206	-0.022	1.442	-	0
Shoulder TD	0.484	0.215	1.609	-	0
EMA					
Knee	0.786	0.359	0.170	+	+
Ankle	0.047	0.002	0.317	+	0
Elbow	0.807	0.312	0.147	+	+
Joint moments					
Hip	0.975	1.191	0.030	-	-
Knee	0.983	1.036	0.035	-	-
Ankle	0.992	1.359	0.024	-	0
Shoulder	0.968	1.305	0.017	-	0
Elbow	0.970	1.156	0.040	-	-
Wrist	0.977	1.121	0.022	-	-

Regression equations were calculated on log-transformed data. Intercepts have been detransformed.

With increasing body mass, knee, ankle, elbow and wrist angles were predicted to be more extended (or plantarflexed), leading to reduced joint moments and increased effective mechanical advantage (EMA).

Shoulder and hip angles at mid-stance, as well as protraction and retraction angles at touch-down (TD) and lift-off (LO), respectively, were expected to decrease with increasing body mass.

Because of the small sample size ($N=6$), significant correlations were rare, and confidence limits on the regression slopes always included the isometric expectation (0 for joint angles and EMA, 1.333 for joint moments). Consequently, allometry was recognized for joint angles and EMA when the correlation coefficient was greater than 0.5 and by the sign of the correlation. Allometry for joint moments was recognized when the slope was less than 1.20. Where substantial deviations from isometry exist for joint angles, moments and EMA (highlighted by the boxes), the deviations were always in the predicted direction.

significantly with increasing body mass across the entire sample of adult primates (Table 8). However, where significant differences are observed, they are most frequently in the direction predicted: larger animals have more extended elbow and shoulder joints at mid-stance. Hip and shoulder angles at lift-off also decrease with increasing body mass, as do the hip and shoulder angular excursions.

Joint moments

Joint moments (Table 8) scale with negative allometry across the sample of adult primates, as predicted. The same pattern of negative allometry is obtained without including data from the adult male baboon, which moved more slowly and had lower GRF magnitudes.

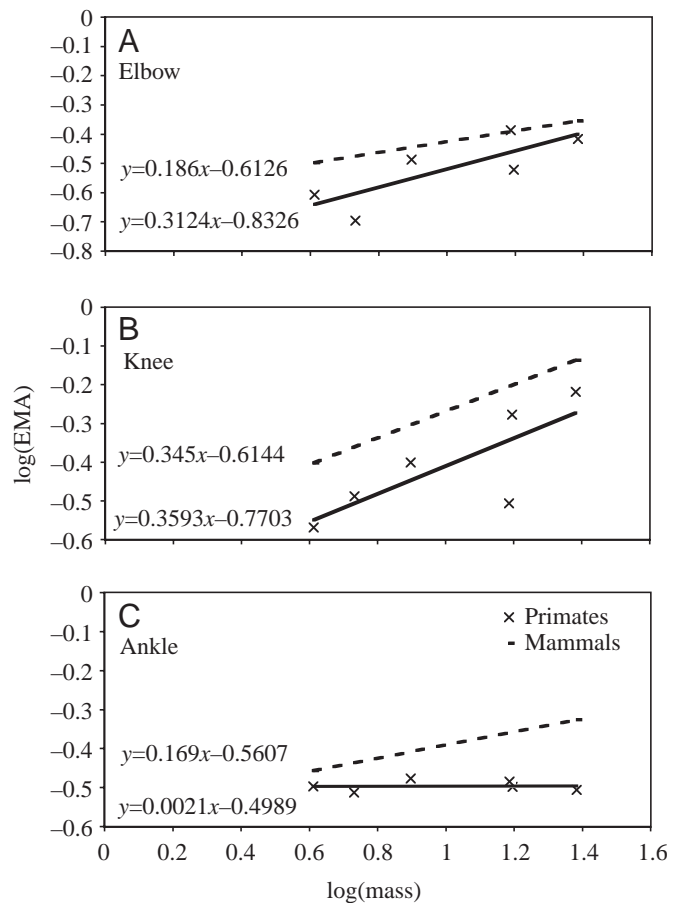


Fig. 6. Effective mechanical advantages (EMA; ratio of anatomical to GRF moment arms, where GRF is ground reaction force) at the elbow (A), knee (B) and ankle (C) for the phylogenetically constrained sample of primates and the diverse sample of mammals from Biewener (1989). EMA for the elbow and knee increase with body mass (in kg) for both primate and non-primate samples. This indicates that body mass has a similar influence on EMA (and consequently on the muscle force required to resist gravity) in the phylogenetically constrained and diverse samples. In contrast, ankle EMA does not increase with body mass in the primate sample, but does increase significantly in the diverse mammalian sample.

Effective mechanical advantage

EMA for the extensor musculature at the knee and elbow increases with increasing body mass, allowing larger animals to use relatively less muscular effort to maintain knee and elbow postures in comparison with smaller animals. The slopes for the knee EMA lines are remarkably similar for the phylogenetically constrained group of primates and for the diverse sample of non-primate mammals (Fig. 6), while the elbow EMA increases with a larger slope in the primate sample than in the non-primate sample. In contrast, the ankle EMA for the primate sample did not change with increasing mass.

Discussion*Do body proportions influence musculoskeletal design?*

Adaptive differences in limb proportions have a predictable and significant effect on the orientation of limb segments at mid-stance at walking speeds, while the limb proportion effect is more equivocal at touch-down and mid-stance. The effect of limb proportions on joint moments and the effective mechanical advantage of extensor muscles is most apparent when the differences in proportions are sufficiently large. Animals with longer limbs tend to use more extended joint postures than those with shorter limbs, presumably moderating the larger mid-stance bending and joint moments they would otherwise incur. The observation that forelimb joint moments were lower in longer-limbed primates corresponds well with the scaling of cross-sectional properties observed by Polk et al. (2000). Humeral polar moments of area, which should reflect an average resistance to bending (Schaffler et al., 1985), and cortical areas that resist compressive and tensile loads both scale isometrically when regressed on bone length (as well as the product of body mass and bone length). Longer-limbed animals may experience greater bending strains and have a higher risk of bone damage unless they moderate bending moments. The similar and lower joint moments observed in the forelimbs of longer-limbed primates suggest such an adaptation. In addition, Polk et al. (2000) observed positive allometry in the scaling of primate and rodent femoral cross-sectional properties (when regressed on bone length and on the product of body mass and bone length), which gives longer femora relatively greater resistance to bending and compression (relative to shorter primate femora). Therefore, longer limbs are not at greater risk of breakage than shorter limbs. Correspondingly, joint moments and midshaft bending moments may not need to be reduced for the femur, which may account for why joint moments are not always lower at the hip in longer-limbed animals. In summary, the combined results of the present study and that of Polk et al. (2000) suggest that joint moments tend to be lower in longer-limbed animals than in shorter-limbed animals but, where such decreases in joint moments are not observed, there may be corresponding increases in bone cross-sectional properties to maintain the strength of the limb bones and to decrease the risk of bone breakage.

The observation that mid-stance joint moments were similar

or lower in longer-limbed animals also has implications for the magnitudes of muscle force required to maintain limb posture. As Biewener (1983, 1989, 1990) has shown, the product of the ground reaction force and the inverse of the effective mechanical advantage can be used to estimate the amount of muscle force necessary to prevent the limb from collapsing into flexion during stance. Only in the knee was the EMA of a longer-limbed monkey greater than that of the shorter-limbed monkey (allowing the longer-limbed animal to exert less quadriceps muscle force). The strongest body proportion signal was expected at the knee joint since the segment distal to the knee is where the greatest difference in body proportions exists. While the EMAs at the ankle and elbow were significantly higher for the shorter-limbed female baboon than for the male patas (in contrast to expectations), the percentage difference between the individuals was rather small.

Limb and proximal segment protraction and retraction angles, and their corresponding angular excursions, do not vary predictably with body proportions. This may result from the fact that the limbs are already quite extended at touch-down and lift-off (Polk, 2001), and the GRF magnitude is relatively low at these times. As a result, joint moments at these times are quite low compared with those at mid-stance (Schmitt, 1999), and joint posture does not need to be modified.

Does phylogeny affect how body size influences musculoskeletal design?

The similarities observed between the phylogenetically constrained sample of primates and the diverse sample of mammals suggest that locomotor variables in both samples respond to the same functional signals. That is, larger animals tend to adopt more extended limb postures and have lower angular excursions than smaller animals. Larger animals also have lower joint moments and correspondingly greater effective mechanical advantages for their elbow and knee extensor muscles than smaller animals. These similarities demonstrate that the pattern of how body size influences knee and elbow kinematics is generally not influenced by the phylogenetic composition of the study sample.

One important and illustrative exception to this similarity between closely related and diverse groups is observed at the ankle, where the EMA did not increase with increasing body mass for the primate sample, but did increase with mass in the non-primate sample. This difference in slopes probably reflects the diversity in foot morphology subsumed within the non-primate sample. That is, because of the phylogenetic diversity of the sample, a wide variety of foot morphology is represented, ranging from the elongated pes of the artiodactyl and perissodactyl taxa to the shorter feet of the rodents. These variations in foot morphology probably require differences in ankle posture either because of mechanical constraints related to body mass or because of the relative lengths of the limb segments; or the differences in posture may simply result from historical events associated with the origin of unguligrade posture in the artiodactyl and perissodactyl clades. If so, the 'mass'-related increase in ankle EMA observed by Biewener

(1983, 1989) may be conflated with similar effects resulting from phylogenetically correlated differences in foot morphology.

In contrast, the cercopithecine monkeys are more uniform in their foot morphology (Strasser, 1992). Perhaps more importantly, in the wild, these cercopithecines are accustomed to spending part of their lives in trees to feed, sleep and escape from predators (Fleagle, 1999), and their feet all possess significant grasping ability. When moving on arboreal supports, even the largest of the monkeys is frequently required to use a semi-plantigrade foot postures (the heel does not contact the substratum) to maintain its grip above branches and avoid falling (Schmitt and Larson, 1995). On terrestrial substrata, monkey foot posture ranges from semi-plantigrade to digitigrade, but ankle postures remains similar between the taxa in this study. Thus, primates may not show a mass-related increase in ankle EMA because their foot postures are constrained by their need to use arboreal supports. Size-related increases in ankle EMA may still be apparent in taxa that are not constrained to be plantigrade or semi-plantigrade, but this question remains to be tested with a sample that demonstrates the appropriate control of phylogenetic and adaptive influences.

Predicting alignment between GRF and limb segments from joint posture

In most cases, more extended limb postures result in lower joint moments. Exceptions to this pattern (in the body proportion comparisons) are found at the shoulder and elbow, where moments at mid-stance are lower for the patas despite the fact that the elbow and shoulder joint angles did not differ between these monkeys (Figs 4, 5). In addition, the ankle and hip moments are higher for the patas monkey than for the female baboon despite the fact that the patas used more extended hindlimb joint posture (Figs 4, 5). These results show that alignment between the limb segments and the GRF is difficult to predict from joint posture alone. These apparent discrepancies between joint angles and moments may be overcome through changes in limb rotation or abduction. For example, decreased shoulder and elbow joint moments, with no change in joint angles, could be accomplished by medial rotation or adduction of the limb. This would decrease the mediolateral (ML) moment arm by bring the limb segments closer to the ML component of the GRF. Similarly, the moments in the hindlimb could be increased through external rotation or abduction. This finding underscores the advantage of recording both three-dimensional kinematic data as well as the ML component of GRFs for animals such as primates that may have greater joint mobility and that are not constrained to parasagittal limb movements during locomotion.

Determinants of joint posture in intra- and interspecific comparisons

Joint posture is clearly influenced by a variety of factors including speed, limb proportions, body mass, joint moments

and substratum use (Biewener, 1983; Inman et al., 1980; Vilensky and Gankiewicz, 1990; Schmitt, 1999). Comparisons among individuals demonstrate that joint postures become more extended as body mass or limb length increases, probably to avoid high joint and midshaft bending moments (see above; see also Biewener, 1983, 1989). Joint moments also increase with speed for most individuals (within a walking gait), yet the changes in posture that accompany speed increases within individuals are in the opposite direction to those observed among individuals that differ in mass. Joint flexion increases with speed in both bipedal and quadrupedal taxa (Table 5; Inman et al., 1980; Vilensky and Gankiewicz, 1990; Gatesy and Biewener, 1991), permitting both more efficient forward motion of the body's center of mass and moderation of peak vertical forces. Smoothing the path of the center of mass has the effect of reducing fluctuations in potential and kinetic energies; the vertical accelerations of the center of mass are decreased, and more efficient forward motion is permitted (Inman et al., 1980; Andriacchi et al., 1982; Andriacchi and Strickland, 1983). Mochon and McMahon (1981) have also shown that increasing knee flexion at mid-stance helps to moderate peak vertical forces.

Increasing limb flexion with increasing speed in intra-individual comparisons may also result from changes in momentum. As speed increases, so does forward momentum; when the limb touches down, a braking impulse is applied, but the limb is not rigid and the joints of the limb may be forced into flexion. The amount of flexion is dependent on limb stiffness, which Farley et al. (1993) have shown to be nearly independent of speed for running gaits. If stiffness is also independent of speed for walking, the limb will flex more at higher speeds than at lower speeds.

Thus, joint posture and joint moments have different relationships in intra- and inter-individual comparisons. Within individuals, increasing limb flexion allows efficient forward motion of the center of mass with increasing speed, at the cost of increasing joint moments. In comparisons among individuals, the limbs are extended to avoid high joint and midshaft bending moments that result from increased body mass or limb length.

In summary, adaptive differences in limb proportions generally have significant and predictable effects on limb design, while phylogenetic effects are more limited. Among animals with similar body mass, longer-limbed monkeys use more extended limb postures at mid-stance than do shorter-limbed individuals. A more-extended posture permits a greater effective mechanical advantage and allows longer-limbed animals to resist gravity with less muscular effort than shorter-limbed animals. Joint postures also tend to increase among closely related animals that differ in body mass, allowing larger monkeys to have a greater EMA at the elbow and knee than smaller monkeys. The increase in elbow and knee EMA in the closely related primate sample is similar to that observed in a diverse sample of mammals (Biewener, 1989), suggesting that body mass is the predominant influence on posture at these joints. In contrast to the general mammalian pattern, ankle

EMAs did not increase with body mass across the primate sample, perhaps because arboreal substrata impose constraints on primate foot posture. The observation that ankle EMA did not increase with body mass suggests that clade-specific adaptive differences may obscure the ubiquitous effects of body mass and that both phylogeny and limb proportions can have significant effects on musculoskeletal design.

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