
Review

Insights into the evolution of human bipedalism from experimental studies of humans and other primates

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Summary

An understanding of the evolution of human bipedalism can provide valuable insights into the biomechanical and physiological characteristics of locomotion in modern humans. The walking gaits of humans, other bipeds and most quadrupedal mammals can best be described by using an inverted-pendulum model, in which there is minimal change in flexion of the limb joints during stance phase. As a result, it seems logical that the evolution of bipedalism in humans involved a simple transition from a relatively stiff-legged quadrupedalism in a terrestrial ancestor to relatively stiff-legged bipedalism in early humans. However, experimental studies of locomotion in humans and nonhuman primates have shown that the evolution of bipedalism involved a much more complex series of transitions, originating with a relatively compliant form of quadrupedalism. These studies show that relatively compliant walking gaits allow primates to achieve fast walking speeds using long strides, low stride frequencies, relatively low peak vertical forces, and

relatively high impact shock attenuation ratios. A relatively compliant, ape-like bipedal walking style is consistent with the anatomy of early hominids and may have been an effective gait for a small biped with relatively small and less stabilized joints, which had not yet completely forsaken arboreal locomotion. Laboratory-based studies of primates also suggest that human bipedalism arose not from a terrestrial ancestor but rather from a climbing, arboreal forerunner. Experimental data, in conjunction with anatomical data on early human ancestors, show clearly that a relatively stiff modern human gait and associated physiological and anatomical adaptations are not primitive retentions from a primate ancestor, but are instead recently acquired characters of our genus.

Key words: primate, locomotion, biomechanics, bipedalism, evolution, force, electromyography, kinematics, human.

Introduction

One of the features that separate humans from all other primates is the habitual use of a bipedal gait. This single feature is seen as such a defining characteristic that skeletal adaptations to bipedalism are used to identify our extinct hominid ancestors. Yet, because of the paucity of the fossil record, the fragmentary nature of fossil remains, and the difficulty of inferring behavior from fossils, significant questions remain unanswered concerning the evolution of human bipedalism. Over the past thirty years, however, experimental analyses of locomotion in humans and other primates have done much to improve our understanding of the mechanics of human locomotion and have provided insights into the evolutionary origins of modern human bipedalism.

When modern humans walk, we vault over relatively stiff lower limbs in such a way that our center of mass is at its lowest point at heel-strike and rises to its highest point at

midstance (Cavagna et al., 1976; Lee and Farley, 1998). This inverted pendulum-like gait allows for an effective exchange of gravitational potential and kinetic energy (Cavagna et al., 1976). The same style of walking is employed by other bipeds and probably by most quadrupeds (Cavagna et al., 1976, 1977; Alexander, 1977; Heglund et al., 1982; Gatesy and Biewener, 1991; Griffin and Kram, 2000; Farley and Ko, 2000; Griffin, 2002). Thus, it might seem reasonable to argue that the evolution of human bipedalism was a logical progression from a relatively stiff quadrupedal walking style to our modern gait. Evidence from numerous experimental studies, however, suggests that the evolution of bipedalism was much more complicated. Understanding the nature of locomotion in our prebipedal primate ancestor (prehominid) and in early hominid bipeds has the potential to provide unique insights into the basic mechanics of walking in humans and other animals.

Table 1. A representative¹ list of experimental studies of primate locomotion

Source	Taxa	Data	Movement(s)
Cartmill et al., 2002	All	T	TQ, AQ
Hildebrand, 1967	All	T	TQ
Larson, 1998; Larson et al., 1999, 2001	All	K	TQ, AQ
Lemelin and Schmitt, 1998	All	K	TQ, AQ
Reynolds, 1985	All	T, FP	TQ
Reynolds, 1987	All	T, K	TQ, TB
Vilensky, 1987, 1989; Vilensky and Gehlsen, 1984; Vilensky and Larson, 1989	All	T, K, EMG	TQ
Aerts et al., 2000	Hom	T	TQ, TB
Chang et al., 1997, 2000; Bertram and Chang, 2001	Hom	FP	AS
D'Aout et al., 2002	Hom	T, K	TQ, TB
Elftman, 1944; Elftman and Manter, 1935	Hom	K, T	TB
Jenkins, 1972	Hom	K	TB
Kimura, 1990, 1991, 1996	Hom	T, En	TQ
Larson and Stern, 1986, 1987	Hom	EMG	TQ, AQ, R
Larson et al., 1991	Hom	EMG	AS, TQ, R
Larson, 1988, 1989	Hom	EMG	AS
Okada and Kondo, 1982; Okada, 1985	Hom	EMG	TB
Prost, 1967, 1980	Hom	K, T	TQ, TB, VC
Shapiro et al., 1997	Hom	EMG, T	TQ
Stern and Larson, 2001	Hom	EMG	TQ, AS
Stern and Susman, 1981	Hom	EMG	TQ, TB, VC
Susman, 1983	Hom	K	TQ, TB
Swartz et al., 1989	Hom	BS	AS
Tardieu et al., 1993	Hom	K	TB
Tuttle and Basmajian, 1974a,b,c, 1977, 1978a,b; Tuttle et al., 1983, 1992	Hom	EMG	TQ, TB, AS
Wunderlich and Jungers, 1998; Wunderlich and Ford, 2000	Hom	Pr	TQ, AQ
Yamazaki and Ishida, 1984	Hom	K, T	TB, VC
Jenkins et al., 1978	NWM	K, C,	AS
Prost and Sussman, 1969	NWM	K, T	IQ
Schmitt 2003a	NWM	FP, K, T,	AQ, TQ
Turnquist et al., 1999	NWM	K	AS
Vilensky and Patrick, 1985;	NWM	T, K	TQ
Vilensky et al., 1994	NWM	T, K	IQ
Fleagle et al., 1981	NWM, Hom	EMG, BS	VC, TQ, TB
Ishida et al., 1985	NWM, Hom	EMG	TQ, TB
Jungers and Stern, 1980, 1981, 1984	NWM, Hom	EMG	AS
Stern et al. 1977, 1980	NWM, Hom	EMG	AQ, VC
Taylor and Rowntree, 1973	NWM, Hom	En	TQ
Hirasaki et al., 1993, 1995, 2000	NWM, OWM	T, K, FP, EMG	VC
Prost, 1965, 1969	NWM, OWM	T	TQ
Kimura et al., 1979; Kimura, 1985, 1992	NWM, OWM, Hom	FP	TQ
Kimura et al., 1983	NWM, OWM, Hom	T	TQ, TB
Schmitt and Larson, 1995	NWM, OWM, Hom	K	TQ, AQ
Vangor and Wells, 1983	NWM, OWM, Hom	EMG	TQ, TB, VC
Wunderlich and Schmitt, 2000	NWM, OWM, Hom	K	TQ, AQ
Demes et al., 1994	OWM	BS	TQ
Larson and Stern, 1989; 1992	OWM	EMG	TQ
Meldrum, 1991	OWM	K, T	AQ, TQ
Polk, 2002	OWM	T, FP, K	TQ
Rollinson and Martin, 1981	OWM	T	AQ, TQ
Schmitt et al., 1994	OWM	EMG	TQ
Wells and Wood, 1975	OWM	K	TQ, L
Schmitt, 1994, 1998, 1999, 2003b	OWM	K, FP	TQ, AQ

Table 1. Continued

Source	Taxa	Data	Movement(s)
Vilensky, 1980, 1983, 1988; Vilensky and Gankiewicz, 1986, 1990; Vilensky et al., 1986, 1990, 1991	OWM	K, T	TQ
Whitehead and Larson, 1994	OWM	K, C, EMG	TQ
Alexander and Maloiy, 1984	OWM, Hom	T	TQ
Shapiro and Jungers, 1988, 1994	OWM, Hom	EMG, T	TQ, TB, VC
Anapol and Jungers, 1987	Pro	EMG, T	TQ, L
Demes et al., 1990	Pro	T	AQ
Demes et al., 1998, 2001	Pro	FP	L
Gunther, 1991	Pro	FP, EMG	L
Ishida et al., 1990	Pro	T, FP	AQ
Jouffroy, 1983; Jouffroy and Gasc, 1974; Jouffroy et al., 1974	Pro	K, C	AQ
Jouffroy and Petter, 1990	Pro	T, K,	AQ
Jouffroy and Stern, 1990	Pro	EMG	AQ
Jungers and Anapol, 1985	Pro	T, EMG	TQ
Schmidt and Fischer, 2000	Pro	K, C	AQ
Schmitt and Lemelin, 2002	Pro	FP	TQ, AQ
Shapiro et al., 2001	Pro	K	AQ
Stevens, 2001; Stevens et al., 2001	Pro	K, T	AQ, IAQ

Pro, prosimian; NWM, New World monkey; OWM, Old World Monkey; Hom, hominoid; All, representative species from all of the above. FP, force plate; K, kinematics; T, temporal characters; EMG, electromyography; BS, bone strain; En, energetics; Pr, pressure; C, cineradiography.

TQ, terrestrial quadrupedalism; AQ, arboreal quadrupedalism; IQ, inclined quadrupedalism (flat substrate); IAQ, inclined quadrupedalism (pole); L, leaping; AS, arm-swinging; TB, terrestrial bipedalism; R, reaching.

¹This is not an exhaustive list of all studies on primate locomotion. I have included those studies that focus specifically on primate locomotor mechanics primarily in a laboratory setting. I apologize to anyone who was excluded.

Reviews of many experimental studies can be found in Fleagle (1979), Jouffroy (1989), and Churchill and Schmitt (2003).

This table does not include studies by anthropologists that focus solely on human bipedalism, such as Li et al. (1996), Schmitt et al. (1996, 1999) or Crompton et al. (1998).

Primate locomotor characteristics

Primates show a remarkable diversity of locomotor behaviors. The apes (gibbons, orangutans, chimpanzees and gorillas) show a particularly wide range of locomotor habits, including acrobatic arm-swinging, quadrumanous climbing, quadrupedal knuckle- or fist-walking, and regular short bouts of bipedal locomotion. Nonetheless, quadrupedalism is the most common mode of locomotion among primates, and the ways in which primate quadrupedalism is similar to or differs from that of other mammals has bearing on the pathways for the evolution of more specialized forms of locomotion, including bipedalism.

Data from laboratory-based studies of primate locomotion, much of which is summarized below, can be of great utility to those working on locomotor mechanics in other vertebrates. To make the reader aware of what data are available, I have included a representative list of major studies of primate locomotor mechanics (Table 1). Below, however, I concentrate only on those studies that bear directly on the unique aspects of primate locomotion and the evolution of human bipedalism.

The walking gaits of primates are known to differ from those of most other mammals in several ways (Fig. 1).

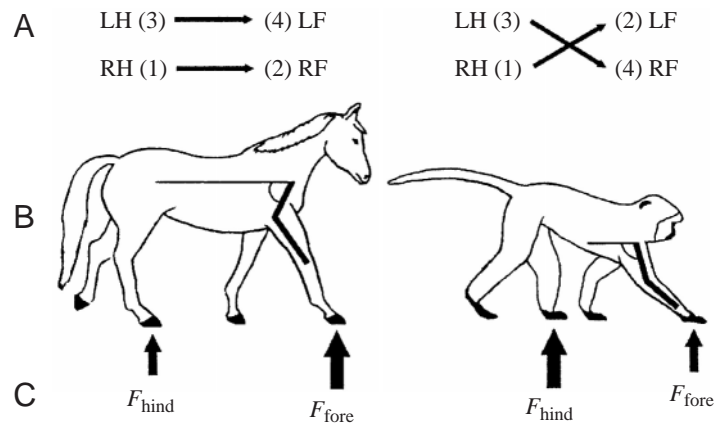


Fig. 1. Summary of the commonly accepted differences that are believed to distinguish the walking gaits of most primates from those of most nonprimate mammals. Nonprimates generally use (A) lateral sequence walking gaits (LH, RH, left and right hindlimb; LF, RF, left and right forelimb), (B) have a humerus that at ground contact is retracted relative to a horizontal axis passing through the shoulder, and (C) have greater peak vertical forces F on their hindlimbs than they do on their forelimbs. Primates show the opposite pattern. From Schmitt and Lemelin (2002), with permission.

First, most primates habitually use a diagonal sequence footfall pattern, in which the footfall of a hindfoot is followed by that of a contralateral forefoot (Muybridge, 1887; Hildebrand, 1967; Vilensky and Larson, 1989; Cartmill et al., 2002). Secondly, primates have a humerus that is relatively protracted at forelimb touchdown (Larson, 1998; Larson et al., 1999, 2001). Thirdly, most primates also have relatively greater peak vertical forces on the hindlimb compared to those on the forelimb (Kimura et al., 1979; Reynolds, 1985; Demes et al., 1994; Polk, 2001, 2002; Schmitt and Lemelin, 2002). Finally, quadrupedal primates appear to use a walking gait involving substantial increases in elbow flexion during stance phase, smaller vertical excursions of the center of gravity, longer contact times, and longer stride lengths compared to other mammals traveling at dynamically similar speeds (Froude numbers) (Alexander and Maloiy, 1984; Demes et al., 1990; Schmitt, 1998, 1999). This more compliant quadrupedal walking style has been documented in a wide range of primates, including the large-bodied quadrupedal apes (Demes et al., 1990, 1994; Schmitt, 1998, 1999; Wunderlich and Jungers, 1998; Larney and Larson, 2003).

Primate locomotor evolution

The gait characteristics thought to distinguish most primates from most other mammals have all been associated directly or indirectly with the mechanical requirements of locomotion on thin flexible branches (Schmitt and Lemelin, 2002; Cartmill et al., 2002; Schmitt, 2003a), an environment thought to be critical in the origin of primates fifty-five million years or more ago (Cartmill, 1974; Fleagle, 1999). This combination of gait characteristics, shown by primates in general and arboreal primates especially, results in a strong functional differentiation between forelimbs and hindlimbs. This may have facilitated the use of forelimbs in tension during climbing and arm-swinging in New World monkeys and apes. This suite of gait characteristics that typify primates may ultimately have played a role in the evolution of bipedalism (Stern, 1971, 1976; Reynolds, 1985; Schmitt, 1998; Larson et al., 2001; Schmitt and Lemelin, 2002).

The first hominids (primates that use a habitual upright bipedal gait) are believed to have evolved in Africa five to six million years ago (Fleagle, 1999; Ward et al., 1999; Senut et al., 2001). Immediately prior to the appearance of hominids, the primate fauna of Africa and Asia was dominated by generalized arboreal quadrupedal primates with a mixture of ape-like and monkey-like traits (Begun et al., 1997). The earliest known hominids (members of the genus *Australopithecus*) were relatively small-bodied compared to modern humans and their skeletons contain a mosaic of features (Fig. 2) (Stern and Susman, 1983; Susman and Stern, 1984; Lovejoy, 1988; McHenry, 1991a; Leakey et al., 1995; McHenry and Berger, 1998; Ward et al., 1999; Stern, 2000; Ward, 2002). Early hominids had primitive, more ape-like features such as relatively small lower limb and vertebral joints, curved fingers and toes, relatively long upper limbs and

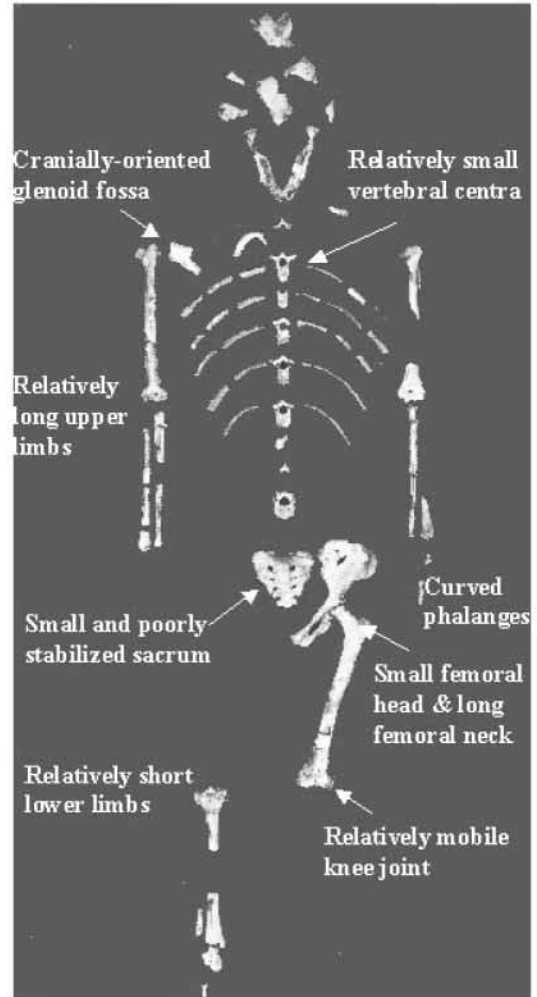


Fig. 2. The skeleton of one individual of *Australopithecus afarensis*. Members of this early hominid species were relatively small and short, with females weighing approximately 30 kg and standing about 1.05 m tall (McHenry 1991b, 1992). These early hominids were gracile with small and loosely stabilized limb and vertebral joints and distinctly curved phalanges (Stern and Susman, 1983), features that are also found in many extant apes. Like living apes, they also had relatively long upper limbs compared to the lower limbs, a condition that is also found in later australopithecines (McHenry and Berger, 1998). Many of the ape-like features of the postcranial skeleton are also found in earlier australopithecines (Ward et al., 1999). Exactly how these features should be interpreted is the subject of considerable debate (Susman et al., 1984; Latimer, 1991; Stern, 2000; Lovejoy et al., 2002; Ward, 2002), although the joint morphology suggests a different loading pattern from that found in modern humans (Stern and Susman, 1983; Schmitt et al., 1996, 1999). The image is modified from Fleagle (1999).

short lower limbs. They also had derived, more human-like features associated with bipedalism, including valgus knees and short, somewhat laterally facing iliac blades. Finally, early hominids also had unique features not found in either apes or humans, such as an exceptionally wide, platypelloid pelvis. There is considerable debate about how these features should

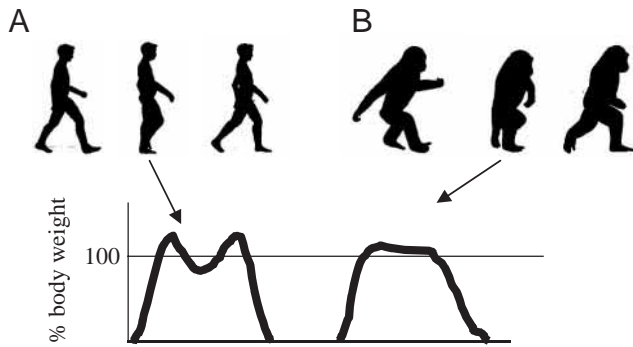


Fig. 3. Illustration of the walking postures (at heel-strike, midstance and toe-off) and vertical ground reaction forces (expressed as % body weight) in a human (A) and a chimpanzee (B). The chimpanzee uses a more flexed hip and knee posture throughout stance phase, has lower oscillations of the center of mass, and generates a flatter, lower vertical peak force curve. Human and chimpanzee redrawn from Elftman (1944); force traces re-drawn from Kimura et al. (1979).

be interpreted (for comprehensive reviews of this debate, see Stern, 2000; Ward, 2002). Some researchers argue that the locomotor mode of these hominids was kinematically distinct from our own (e.g. Zuckerman et al., 1973; Oxnard, 1975; Tuttle, 1981; Stern and Susman, 1983; Berge, 1984, 1991, 1994; Susman et al., 1984; Berge and Kazmeirczak, 1986; McHenry, 1986, 1991a; Duncan et al., 1994; Ruff, 1988; Sanders, 1998; Stern, 2000). Others have argued equally strongly that early hominids walked with a gait equivalent to that of modern humans (e.g. Robinson, 1972; Lovejoy, 1980, 1988; Latimer, 1983, 1991; Latimer et al., 1987; Latimer and Lovejoy, 1989; Crompton et al., 1998). The features of the locomotor skeleton that appear to some to indicate a gait different from that of modern humans and some degree of regular climbing behavior appear as early as 4 million years ago, and are also present in the earliest members of the genus *Homo* (*Homo habilis*) (Susman and Stern, 1982; Susman, 1983; Susman et al., 1984; McHenry and Berger, 1998; Ward et al., 1999). There is much less controversy about the locomotor behavior of later hominids such as *Homo erectus* (appearing about 1.8 million years ago), which exhibit a more modern body form with long hindlimbs and robust joints (Jungers, 1988; McHenry, 1991b). It is widely accepted that *Homo erectus* walked and ran much as we do today (Carrier, 1984; Stanley, 1992; Bramble, 2000; Gruss and Schmitt, 2000, in press).

Gait compliance and the evolution of bipedalism

Since the pioneering studies of the British anatomist Herbert Elftman, it has been recognized that apes and other nonhuman primates differ from humans in the use of a relatively more compliant form of bipedalism (Fig. 3) (Elftman and Manter, 1935; Elftman, 1944; Prost, 1967, 1980; Jenkins, 1972; Okada, 1985; Yamazaki and Ishida, 1985; Reynolds, 1987; Kimura, 1990, 1991, 1996; Aerts et al., 2000; D’Aout et al., 2002). Normal human walking differs from apes, which exhibit habitually flexed hips, knees and ankles during stance phase (Fig. 4). However, when we asked people to walk with minimal oscillations of the center of mass, they adopted deeply flexed lower limb postures like those of most apes (Fig. 4; Schmitt et al., 1996, 1999).

Limb compliance leads to smaller oscillations of the center of mass and alters the magnitude of the peak vertical substrate reaction force and the shape of the force–time plot (Alexander and Jayes, 1978; McMahon et al., 1987;

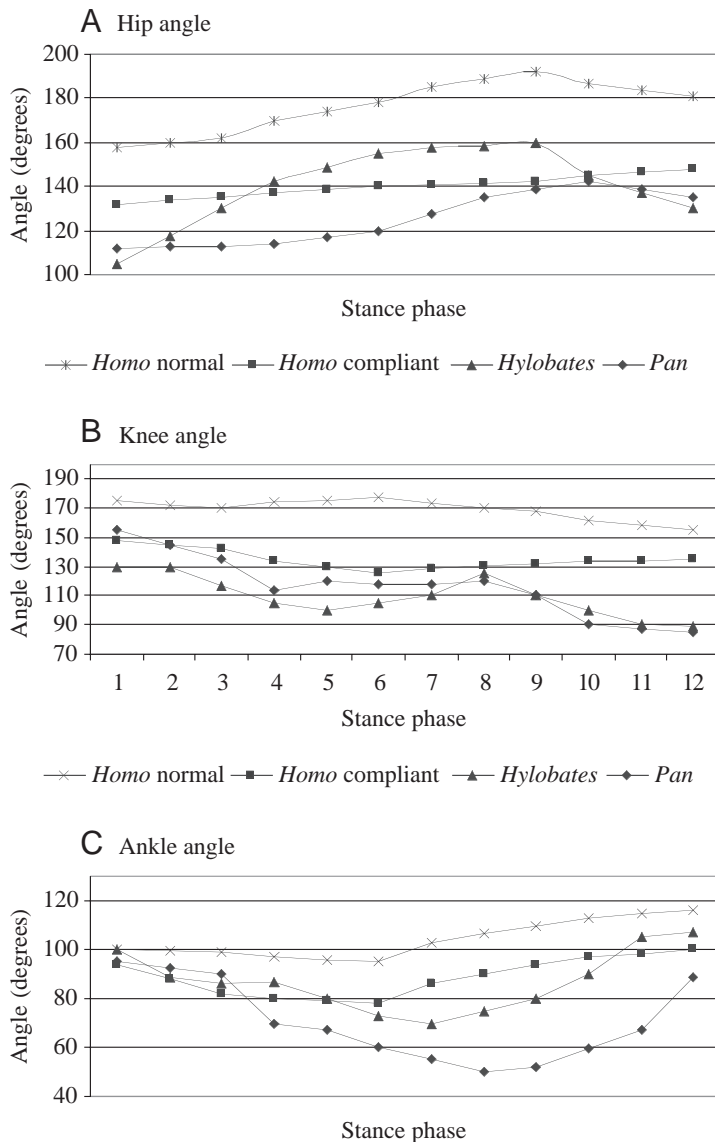


Fig. 4. Angular values for the lower limb joints of humans walking normally and compliantly compared with bipedal walking gaits of the gibbon (*Hylobates lar*) and the pygmy chimpanzee (*Pan paniscus*). The data for the humans were collected at SUNY Stony Brook using the same sample as was used for the maximum walking speed and stride length data presented in Table 2. The data for the gibbon are a composite of data from Prost (1967) and Yamazaki and Ishida (1984). The data for the chimpanzee are from D’Aout et al. (2002).

Alexander, 1992; Schmitt, 1998, 1999; Yaguramaki et al., 1995; Li et al., 1996). During normal walking humans generate a vertical ground reaction force curve with two distinct peaks that are both greater than body weight, although at very slow speeds the force-time curve is relatively flat-topped (Alexander and Jayes, 1978). This force pattern is characteristic of a stiff-legged gait in which the center of mass is highest at midstance and lowest at double support (Fig. 3A). In contrast, nonhuman primates walking bipedally generate single-peaked force curves in which the peak is much closer to body weight (Fig. 3B) (Kimura et al., 1979; Kimura, 1996). Humans walking with more compliant limb postures produce similar force patterns, although the overall mechanics of human compliant walking are still not well understood (Yaguramaki et al., 1995; Li et al., 1996; Schmitt et al., 1996).

Since nonhuman primates typically utilize compliant gaits when they walk either quadrupedally or bipedally, it seems plausible then, that early bipedal hominids would have retained a compliant walking style typical of other nonhuman primates. Postcranial anatomy of early hominids suggests that some of them walked with a deeply yielding knee and hip (Stern and Susman, 1983). But beyond being simply a primitive retention, compliant walking in prehomonids may have had several advantages. Among quadrupedal nonhuman primates, low peak forces and reduced stride frequencies make their locomotion relatively smooth, which helps them avoid shaking flexible branches, thus enhancing their stability and helping them escape the notice of predators (Demes et al., 1990; Schmitt, 1998, 1999). These features may have also allowed primates to maintain mobile, loosely stabilized forelimb joints. Our recent kinematic, force plate and accelerometer studies on human compliant bipedalism (summarized in Table 2) show that humans who adopted a complaint gait achieved longer stride lengths, faster maximum walking speeds, lower peak vertical forces, and improved impact shock attenuation between shank and sacrum compared to normal walking (Schmitt et al., 1996, 1999). These data are consistent with findings of several other studies (Yaguramaki et al., 1995; Li et al., 1996). As a result, my colleagues and I have argued, as did Stern and Susman (1983), that compliant bipedalism may have been an effective gait for a small biped, with relatively small and weakly stabilized joints that had not yet completely forsaken arboreal locomotion (Schmitt et al., 1996, 1999).

Humans who attempt to walk with a compliant gait often find it awkward, however, and some researchers argue that the retention of compliant walking style in early hominids is unlikely because it would be too energetically expensive and raises core-body temperatures (Crompton et al., 1998). It is likely that a modern bipedal walking gait would be more efficient than hominoid-style quadrupedalism or bipedalism (Leonard and Robertson, 1995, 1997a,b, 2001). Some have argued that the costs of locomotion would be especially high for a short-legged hominid (Jungers, 1982; Rodman and McHenry, 1980; but for a contrary view, see Kramer, 1999). However, a review of the literature by Stern (1999) suggests that the differences would have been minor. Moreover, there

Table 2. *The effect of compliant bipedalism on temporal and kinetic variables in humans*

	Normal	Compliant
Average maximum walking speed (m s^{-1})	2.25	3.2
Average maximum stride length (m)	2.1	2.97
Average peak vertical force magnitude (% body weight)	130	112
Average impact shock attenuation (shank g/head g)	3.8	10.1

The data in this table are previously unpublished values collected at the State University of New York at Stony Brook and at Duke University.

Different samples were used for different studies.

The study of maximum walking speed and stride length involved 7 men and 7 women between the ages 19 and 55 (mean = 30) whose height ranged from 1.5 m to 1.94 m (average = 1.7 m).

The study of vertical peak force magnitude involved 7 women and 5 men between the ages of 18 and 55 (mean = 23) whose height ranged from 1.5 m to 1.84 m (average = 1.62 m).

The speed range of the subjects in this study was relatively narrow and subjects walked relatively fast (average speed for straight-legged walking = 2.03 m s^{-1} and for bent-hip, bent-knee walking = 2.13 m s^{-1}).

Finally, the study of impact shock attenuation involved 6 men and 5 women between ages of 19 and 35 (average = 22) whose height ranged from 1.6 m to 1.84 m (average = 1.6 m). In this latter study, average speed for normal walking = 1.78 m s^{-1} and for compliant walking = 1.92 m s^{-1} .

is little evidence that such a compliant bipedal gait in early hominids would have been more energetically costly than that of a quadrupedal prehomonid. Experimental studies have repeatedly shown that there is little difference in energetic costs between quadrupeds and bipeds (Taylor and Rowntree, 1973; Fedak et al., 1977; Fedak and Seherman, 1979; Rodman and McHenry, 1980; Roberts et al., 1998a,b; Griffin, 2002), although a recent study found a 20% increase in cost in macaques (Nakatsukasa et al., 2002). In addition, Steudel (Steudel, 1994, 1996; Steudel-Numbers, 2001), using data on limb length and oxygen consumption for humans and other mammals, concluded that 'increased energetic efficiency would not have accrued to early bipeds' (Steudel, 1996, p. 345). She goes on, however, to point out that 'selection for improved efficiency in the bipedal stance would have occurred once the transition [to modern human bipedalism] was made' (Steudel, 1996, p. 345). In summary, it certainly cannot be convincingly argued that bipedalism in the earliest hominids provided significant savings in energy. By the same token, it is unlikely that a shift to bipedalism induced significant energetic costs relative to the locomotion of a prehomonid primate.

Locomotion of the prehomonid primate

Although a discussion of the selective advantages of bipedalism is beyond the scope of this paper, one other way to understand the pathway through which bipedalism evolved is

to consider the mode of locomotion in the prebipedal prehominid ancestor. The mode of locomotion in the primate that immediately preceded the adoption of upright bipedalism has been a subject of debate since the turn of the last century (for thorough reviews, see Tuttle, 1974; Richmond et al., 2002). Theories concerning the nature of locomotion in the prehominid primate can be divided into three basic groups. The troglodytian model posits a terrestrial, knuckle-walking chimpanzee as the prototype for a prehominid (e.g. Washburn, 1951; Gebo, 1992, 1996; Richmond et al., 2002). Proponents of this model argue for a significant component of terrestrial locomotion in the hominid ancestor (Gebo, 1992) but do not preclude arboreal activity as a significant component of the evolution of bipedalism (Richmond et al., 2002). In addition, some researchers have argued that feeding, not locomotor, adaptations in chimpanzees are critical for the evolution of hominid bipedalism (Hunt, 1994; Stanford, 2002). Supporters of a brachiationist model alternatively suggest that bipedalism evolved from a small-bodied suspensory ancestor similar to gibbons (e.g. Keith, 1923; Tuttle, 1981). Finally, other researchers invoke no specific primate as a distinct model for the prehominid, but argue instead that the mechanical requirements of climbing vertical supports are similar to those required by early bipeds (Stern, 1971; Prost, 1980; Fleagle et al., 1981). Of course, these models are not mutually exclusive, and some have argued for an ancestor with a varied and generalized locomotor repertoire (Rose, 1991). These models can be evaluated using phylogenetic, morphometric, fossil and experimental evidence, but these approaches do not yield consistent results.

The knuckle-walking model has received strong support from molecular data that suggest that chimpanzees and humans are sister taxa (Richmond et al., 2002). The clear phylogenetic relationship between humans and chimps, the latter of which regularly knuckle walk in both terrestrial and arboreal settings (Tuttle, 1974; Doran, 1992) and engage in frequent bouts of terrestrial and arboreal bipedalism (Hunt, 1994; Stanford, 2002), makes it tempting to look only to chimpanzees for understanding the evolution of human bipedalism. This long-standing habit may have hindered our understanding of human evolution because of the difficulty of explaining why a terrestrial quadruped would have evolved into an obligate biped. Furthermore, recent anatomical evidence supporting a terrestrial knuckle-walking ancestor for hominids (Gebo, 1992, 1966; Richmond and Strait, 2000, 2001; Richmond et al., 2002) is not universally accepted (Meldrum, 1993; Schmitt and Larson, 1995; Wunderlich and Jungers, 1998; Dainton and Macho, 1999; Corruccini and McHenry, 2001; Dainton, 2001; Lovejoy et al., 2001).

While phylogenetic evidence points toward chimpanzees, and fossil evidence remains ambiguous, experimental studies of humans and other primates point squarely toward an arboreal, climbing ancestor of hominids, because the mechanics of arboreal climbing and bipedalism are more similar to each other than either is to the mechanics of terrestrial quadrupedalism. Some of the earliest experimental

work on locomotion in apes was carried out independently by Russell Tuttle of the University of Chicago and Jack Stern of the State University of New York at Stony Brook. Tuttle's studies of muscle recruitment patterns in forearm and gluteal musculature in chimps and gorillas led him and his colleague John Basmajian to conclude that terrestrial quadrupedalism did not play a critical role in the evolution of bipedalism. Rather they surmised that 'hominid bipedalism may indeed be rooted in bipedal reaching and branch-running behaviors of relatively small bipedal apes' (Tuttle and Basmajian, 1974a, p. 312).

Stern and his colleagues documented recruitment patterns of forelimb and hindlimb muscles in a variety of ape and monkey species (Stern et al., 1977; Vangor, 1977; Fleagle et al., 1981; Stern and Susman, 1981; Vangor and Wells, 1983). Perhaps the most critical result of their studies was the finding that spider monkeys, chimpanzees and orangutans recruit their lesser gluteal muscles to the greatest degree during stance phase of vertical climbing and bipedalism to produce medial rotation of the femur or to stabilize the pelvis when walking with a flexed hip (Fig. 5). They concluded that a transition from vertical climbing to bipedalism would have involved minimal change in the functional role of thigh musculature. These data, along with additional EMG and bone strain data, led them to conclude that a prehominid primarily adapted for vertical climbing would develop 'hindlimb morphology pre-adaptive for human bipedalism' (Fleagle et al., 1981, p. 360). Ishida et al. (1985) reached the same conclusion in their electromyographic study of bipedal walking in a variety of primate species. The argument that vertical climbing is a 'good intermediate between arboreal behavior and terrestrial bipedalism' (Prost, 1985, p. 301) is further supported by kinematic and electromyographic data on gibbons, chimpanzees and spider monkeys walking bipedally and climbing vertical supports (Prost, 1967, 1980; Hirasaki et al., 1993, 1995, 2000).

Additional support for an arboreal/climbing ancestry for hominids comes from force-plate studies showing that the difference in forelimb and hindlimb peak vertical forces is greatest in highly arboreal primates (Kimura et al., 1979; Kimura, 1985, 1992; Reynolds, 1985; Demes et al., 1994; Schmitt and Lemelin, 2002). More recent studies show that functional differentiation between fore- and hindlimbs is greatest when animals walk on arboreal supports or climb vertical poles (Hirasaki et al., 1993, 2000; Schmitt, 1998; Wunderlich and Ford, 2000). Data on peak plantar pressures in chimpanzees and humans led Wunderlich and Ford (2000) to state that chimpanzee quadrupedal walking on arboreal supports resembles human bipedalism more closely than either chimpanzee terrestrial quadrupedalism or bipedalism. Thus, if reducing the weight-bearing role of the forelimbs is critical to the evolution of bipedalism, it seems likely that the hominid ancestor was an active arborealist. Recent experimental studies associating heel-strike at the end of swing phase with arboreal quadrupedalism (Schmitt and Larson, 1995) and vertical climbing (Wunderlich and Schmitt, 2000) further strengthen this argument.

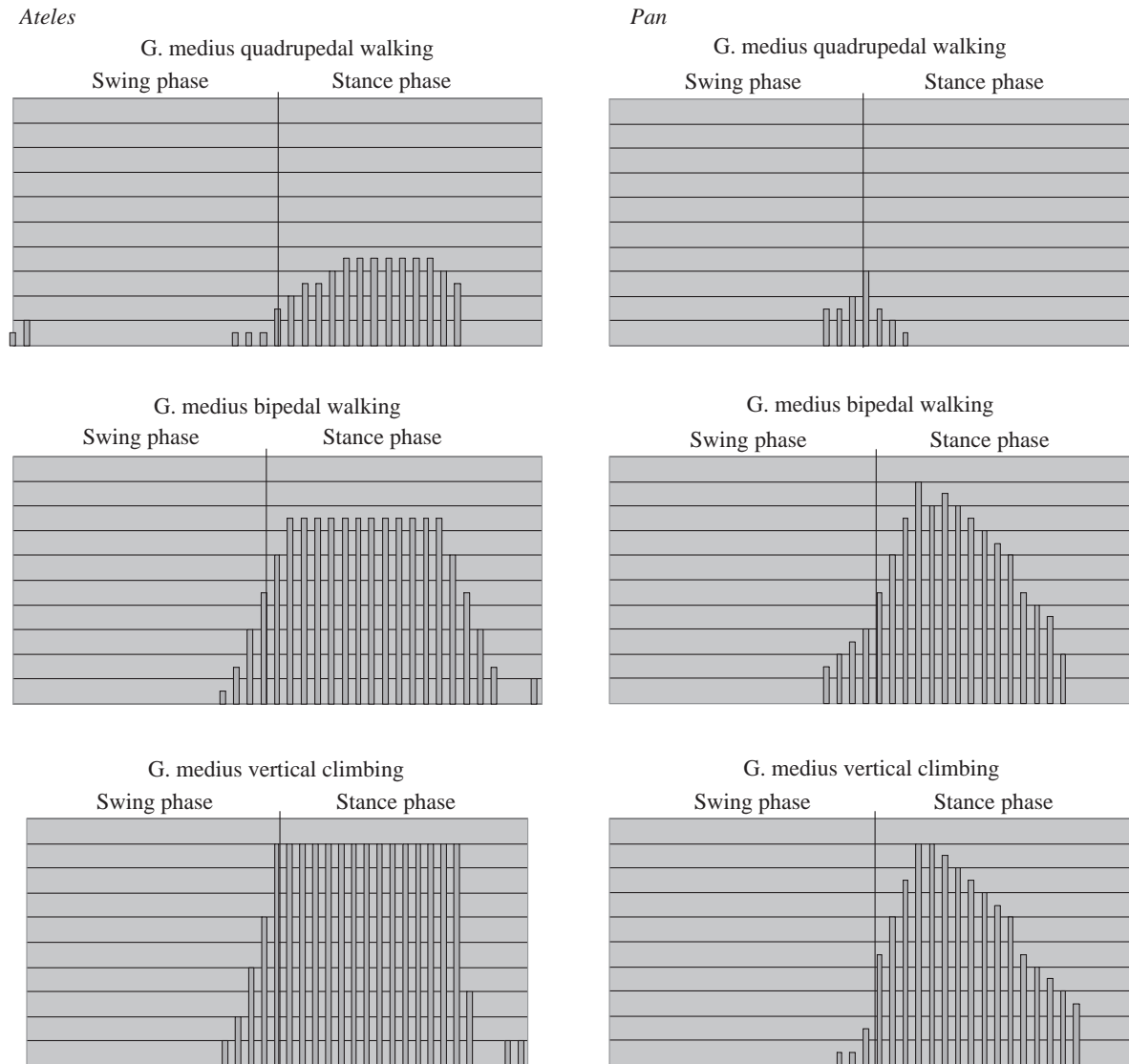


Fig. 5. Electromyographic activity of gluteus medius in spider monkeys (*Ateles* sp.) and chimpanzees (*Pan troglodytes*) during terrestrial quadrupedalism, terrestrial bipedalism, and climbing a large vertical support. The data for the spider monkey are from Fleagle et al. (1981), and for the chimpanzee from Stern and Susman (1983). The graphs follow the approach of Stern et al. (1980). The *x*-axis represents stance and swing phase. The *y*-axis represents activity (expressed as a percentage of maximum muscle recruitment) that occurred 75% of the time during the respective activity. Muscular recruitment increases in both magnitude and duration from quadrupedalism to bipedalism. The recruitment patterns during bipedalism and vertical climbing are similar to each other. The same pattern is found for the orangutan (*Pongo pygmaeus*) for all three behaviors and for the gibbon (*Hylobates lar*) during bipedalism and vertical climbing (Stern and Susman, 1983).

Conclusions

Experimental data collected on humans and nonhuman primates suggest that early hominid bipedalism evolved in an arboreal, climbing primate. The earliest mode of bipedalism included many aspects of locomotion seen in modern humans, but probably did not involve inverted pendulum-like mechanics. This difference in locomotor styles between early hominids and modern humans appears to be associated with small, gracile and poorly stabilized hindlimbs in our earliest ancestors (Stern and Susman, 1983). It seems likely that the shift to a more robust modern skeleton seen in early members of the genus *Homo* reflected the adoption of a relatively stiff-

legged gait. This perspective on the evolution of bipedalism from a relatively compliant to a relatively stiff-legged style changes our understanding of locomotor adaptations in the genus *Homo*. The data described above strongly suggest that a relatively stiff-legged bipedal gait and associated physiological and musculoskeletal adaptations are not inherited from prebipedal ancestors or even from the earliest upright bipeds. These features are instead, specialized characters that evolved relatively recently.

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