External Forces and Torques Generated by the Brachiating White-Handed Gibbon (*Hylobates lar*)

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KEY WORDS: arm-swinging; biped; locomotion; ground reaction force; biomechanics

ABSTRACT We compared the kinetics of brachiation to bipedal walking and running. Gibbons use pectoral limbs in continuous contact with their overhead support at slow speeds, but exhibit aerial phases (or ricochetal brachiation) at faster speeds. This basic interaction between limb and support suggests some analogy to walking and running. We quantified the forces in three axes and torque about the vertical axis generated by a brachiating White-handed gibbon (*Hylobates lar*) and compared them with bipedal locomotion. Handholds oriented perpendicular to the direction of travel (as in ladder rungs) were spaced 0.80, 1.20, 1.60, 1.72, 1.95, and 2.25 m apart. The gibbon proportionally matched forward velocity to stride length. Handhold reaction forces resembled ground reaction forces of running humans except that the order of horizontal braking and propulsion were reversed. Peak vertical forces in brachiation increased with speed as in bipedal locomotion. In contrast to bipedalism, however, peak horizontal forces changed little with speed. Gait transition occurred within the same relative velocity range as the walk-run transition in bipeds (Froude number = 0.3–0.6). We oriented handholds parallel to the direction of travel (as in a continuous pole) at 0.80 and 1.60 m spacings. In ricochetal brachiation, the gibbon generated greater torque with handholds oriented perpendicular as opposed to parallel to the direction of travel. Handhold orientation did not affect peak forces. The similarities and differences between brachiation and bipedalism offer insight into the ubiquity of mechanical principles guiding all limbed locomotion and the distinctiveness of brachiation as a unique mode of locomotion. Am J Phys Anthropol 113:201–216, 2000. © 2000 Wiley-Liss, Inc.

Brachiation is a highly specialized form of bimanual suspensory locomotion. In brachiation, the pectoral limbs are used to locomote beneath a superstrate without the aid of the pelvic limbs or tail and without any interruption by other behaviors such as vertical climbing (Hollihn, 1984). Although orangutans, spider monkeys, and adolescent chimpanzees have been known to exhibit varied levels of suspensory locomotion (Hollihn, 1984; Hunt, 1992; Takahashi, 1990; Tuttle, 1972), the hylobatids (gibbon and siamang) are highly specialized for brachiation and are considered by some to be the only “true brachiators” (Hollihn, 1984). In this study, we quantify the external forces and torques generated during brachiation.

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Received 6 October 1999; accepted 26 May 2000.
by a white-handed gibbon (Hylobates lar). Knowledge of the external forces generated during brachiation provides insight into the mechanics of a unique mode of locomotion and contributes to our general understanding of primate locomotion. Additionally, Bonser (1999) asserts that measuring the forces generated during brachiation will allow for a deeper understanding of how animals assess the mechanical competence of their supporting stratum.

On flat surfaces, terrestrial organisms are able to freely choose foot placement locations suitable for the speed at which they are traveling and so are able to vary both the frequency and the length of their stride. For the brachiator, however, the dynamics of the locomotion must be adjusted to accommodate the predetermined distances between available supports. The forward speed of a running or brachiating animal is equal to its stride length (forward distance covered from one limb contact to the next ipsilateral limb contact) times its stride frequency (strides per unit time). Within the complex environment of the forest canopy, the variability of stride lengths encountered could have a profound effect on the dynamics of locomotion and may be a major constraint on brachiation compared to the relatively unconstrained biped.

Over the past several decades, a large body of literature has documented many details surrounding the morphology, muscular function, kinematics, and behavior of brachiators to relate the musculoskeletal anatomy to the specialized functional requirements of brachiation. Many field observations of gibbons have provided kinematic descriptions of brachiation (Andrews and Groves, 1976; Avis, 1962; Carpenter, 1976; Fleagle, 1974). Several anatomical studies (Andrews and Groves, 1976; Hallgrimsson and Swartz, 1995; Jenkins, 1981; Larson, 1993; Swartz, 1990; Takahashi, 1990) and electromyographic studies (Basmajian, 1972; Jungers and Stern, 1980, 1981, 1984; Larson and Stern, 1986) have also investigated this extraordinary form of suspensory locomotion. Furthermore, there have been biomechanical studies investigating bone strain during brachiation (Swartz et al., 1989), mathematical modeling of brachiation (Preuschoft and Demes, 1984; Swartz, 1989), and metabolism (Parson and Taylor, 1977). These studies provide insight into both the internal physiology and the external behavior of brachiation. Understanding the link between the two, however, requires knowledge of the forces generated by the animal to accomplish these movements. The ability to obtain this critical information from brachiation has recently become available (Chang et al., 1997).

In some respects, brachiation is very similar to bipedal locomotion. It is well known that brachiation consists of individual limb contact cycles in which there is a support phase followed by a non-support, swing phase for each limb (Fig. 1). Therefore, brachiation can be characterized by many of the same kinematic parameters used to characterize bipedal locomotion. At slow speeds, gibbons exhibit a “continuous contact” gait in which there is always at least one hand in contact with a handhold. In this way, continuous contact brachiation is analogous to bipedal walking because there is a portion of the stride in which both limbs are in contact with the support. Thus, the duty factor of each limb (proportion of stride time the limb spends supporting the animal) in both continuous contact brachiation and walking is greater than 50%. At higher speeds, gibbons use a “ricochetal” gait where they exhibit an aerial phase between handhold contacts. There is no double limb support phase as in continuous contact brachiation and the duty factor accordingly drops below 50%. In these respects, ricochetal brachiation is analogous to bipedal...
running, the bouncing gait that bipeds use at higher velocities.

In this paper, we provide a mechanical context for further evaluating the details of the morphological specializations of brachiators and their mode of locomotion. We do so by providing new kinetic information on brachiation and by juxtaposing it against previous theoretical analyses of brachiation as well as existing data on bipedal walking and running. Given the ubiquity of the mechanisms used by walking and running animals, from humans to dogs to cockroaches, a precedent exists for similar mechanisms for minimizing mechanical energy expenditure to exist in all terrestrial, limbed locomotion (Cavagna et al., 1977; Heglund et al., 1982; Full, 1989; Full and Tu, 1991). Bipedal walking and running have been well studied and the mechanics of these gaits are far better understood in comparison to brachiation. By comparing brachiation with a more familiar mode of locomotion, any unique locomotory mechanisms utilized by brachiators can be more easily distinguished. We have recently compared the mechanisms for conserving mechanical energy between both modes of locomotion (Bertram and Chang, unpublished data). Here, we further compare and contrast the external forces and torques generated during brachiation to bipedal walking and running.

The ability to grasp their handholds (i.e., tree branches) allows gibbons to interact with their stratum in a dramatically different way compared to bipeds that rely on surface friction to maintain their foothold with the ground. A high degree of rotation of the body about the vertical axis has been observed in brachiating gibbons (Jenkins, 1981; Stern and Larson, 1993). This indicates that the movements associated with brachiation are not predominantly limited to translations within the sagittal plane as in bipedal gaits, but include a substantial amount of rotation about the long axis of the support limb. This enhanced mobility is mostly due to the presence of a unique ball and socket joint at the wrist (Jenkins, 1981). This specialized morphology allows the gibbon to rotate its body nearly 180° about the vertical axis with each handhold grasp (Stern and Larson, 1993). Considering the unpredictable environment within which gibbons brachiate, it would be advantageous to be able to actively control the amount of rotation about the vertical axis depending upon the orientation of the handhold with respect to the gibbon’s trajectory. To control the amount of rotation about the vertical axis, a gibbon must be able to control the amount of torque it generates and transmits to the handhold about the vertical axis. It has been proposed that gibbons use a substantial amount of supinator and pronator activity at the proximal and distal radioulnar joints to actively generate torques about the long axis of the limb during brachiation (Stern and Larson, 1993). Furthermore, these muscles may be activated differently for different handhold orientations. Whether or not these differences in muscle activity actually change the external torques generated, however, has never been established. The purpose of our study was to compare and contrast the kinetics of brachiation to bipedal locomotion, which is a better understood mode of locomotion. Specifically, we aimed to (1) quantify and document the reaction forces and torques exerted by a brachiating gibbon on its overhead support, and (2) test whether a brachiating gibbon was able to generate different forces or torques for handholds oriented in different directions.

**MATERIALS AND METHODS**

**Animal**

A white-handed, adult female gibbon (*Hylobates lar*, 7.95 kg, 11 years old) was cooperative and available for use. The protocol for this study was approved by the Institutional Animal Care and Use Committee at the State University of New York at Stony Brook, where the animal used in this study was housed and where the data were collected. Two animals were available for use, however, the much older male could not be persuaded to use our handholds. Presumably, this was because our handholds differed too much from the environment to which he had become accustomed, whereas the younger female took readily to our set-up.

The ground reaction forces in human walking and running show a very characteristic pattern that yields predictable trends
with size and speed with little variation between individuals (Munro et al., 1987; Cavanagh and Lafortune, 1980; Nilsson and Thorstensson, 1989; Frederick and Hagy, 1986). In human running, for example, the standard deviation of the peak vertical forces generated against the ground (normalized to body weight) among different individuals is typically less than 10% (Munro et al., 1987). Although data from more animals are needed to quantitatively support our findings, this study represents the only comprehensive and direct measurements of the external forces produced by a brachiating gibbon and provides a unique perspective on the qualitative mechanics of brachiation. Given the stereotypical kinetics observed in human locomotion, the general qualitative trends observed in the current study are likely representative of most gibbons.

**Experimental set-up**

We instrumented a handhold with a force-torque transducer, which could measure forces \((F_v, F_h, F_m)\) generated in three directions and torque about the vertical axis \((M_v)\), where \(v\) is vertical, \(h\) is horizontal, and \(m\) is mediolateral. The instrumented handhold was mounted at the center of a series of identical, non-instrumented “dummy” handholds on the ceiling of an exercise cage (Fig. 2). The total number of handholds for a given trial ranged from three to seven. The length of the exercise cage (6.10 m) limited the potential number of handholds for extended spacings. We recorded video images of the animal’s motion (60 Hz, sagittal view) simultaneously with the force and torque reaction data (500 Hz) to synchronize the kinematic (video) and kinetic (force and torque) data. The details of this set-up followed those outlined in a prior study (Chang et al., 1997).

The data were collected in two 1-week sessions that were separated by a year. The gibbon brachiated freely at its preferred speed across a series of identical and evenly spaced handholds. Handholds were oriented perpendicular to the direction of travel (like the rungs of a ladder). The distance between successive handholds was altered for different data collection trials to provide data from a range of handhold spacings (0.80, 1.20, 1.60, 1.72, 1.95, and 2.25 m). In effect, by changing the distance between hand-

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Fig. 2. Experimental set-up. Transducer data are amplified and stored to computer while video data are taken simultaneously. One channel from the transducer is spliced and sent to a special effects generator that superimposes force trace over the video data to synchronize the two types of data. Exercise arena was 3.71 m wide \(\times\) 6.10 m long \(\times\) 3.56 m high. (Reproduced from Chang et al., 1997, with permission from Company of Biologists, Ltd.)
holds, we were able to directly control the length of the gibbon’s stride (i.e., the distance covered from one hand contact to the subsequent contact with the same hand, or, the distance between three successive handholds). Much of our data and discussion will consider parameters made per brachiation step rather than per stride, because our measurements were made for only one limb. A step was defined as ipsolateral hand contact to contralateral hand contact. We also rotated the handholds to an orientation parallel to the direction of travel (like a discontinuous pole) for two of the handhold spacings (0.80 and 1.60 m). We used these data to investigate any differences in the torques generated for each handhold orientation.

**Data analysis**

Handhold reaction forces were normalized to the time of single hand contact in order to facilitate comparison of reaction force pattern at each gait, velocity, and handhold spacing. Continuous contact was defined as any pass in which a double-hand contact was used at both the beginning and end of contact with the instrumented handhold. We determined this from reviewing the video record. Individual handhold reaction forces for each hand were unknown during the double-limb support phase because only a single handhold was instrumented. The net movement of the center of mass cannot be determined without knowledge of all external forces acting on the body. Therefore, during the continuous contact gait, only portions of the brachiation step where the animal was supported by a single limb were considered. This was reasonable because the peak forces generated during continuous contact brachiation were seen to be generated during the single-limb support phase. Video analysis was used when time of hand contact data were needed for continuous contact brachiation.

Ricochetal brachiation was defined as any pass across the transducer in which we observed an aerial phase between hand contacts. Peak forces for ricochetal brachiation were calculated from these trials. For the integration of accelerations measured in ricochetal brachiation, we rejected trials that did not exhibit a constant forward velocity (i.e., the net change in horizontal acceleration from handhold contact to handhold release was less than 0.2 m s \(^{-2}\)). This criterion typically included trials where the forward velocity changed less than 10% between the beginning and end of hand contact. We calculated the average forward velocity for each trial from video for a complete brachiation step for each run. A step was defined as ipsolateral hand contact to contralateral hand contact.

The handhold reaction forces were very consistent within each brachiation gait. As will be discussed, the peak vertical and peak horizontal handhold reaction forces for each gait did not differ significantly between handhold orientations (Table 1). Therefore, we grouped the reaction force data from both handhold orientations together in our analyses of each brachiation gait.

**Table 1. Summary of average peak handhold reaction components (number of trials in parentheses)**

<table>
<thead>
<tr>
<th></th>
<th>Continuous contact brachiation at 0.80 m spacing</th>
<th>Ricochetal brachiation at 1.60 m spacing</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Perpendicular handholds (4)</td>
<td>In-line handholds (6)</td>
</tr>
<tr>
<td>Vertical force (N)</td>
<td>133.9 ± 9.6</td>
<td>137.8 ± 5.3</td>
</tr>
<tr>
<td>Horizontal propulsive force (N)</td>
<td>42.9 ± 11.7</td>
<td>41.6 ± 11.1</td>
</tr>
<tr>
<td>Horizontal braking force (N)</td>
<td>-42.2 ± 5.0</td>
<td>-39.0 ± 9.3</td>
</tr>
<tr>
<td>Supination torque (N m)</td>
<td>1.61 ± 0.59</td>
<td>1.08 ± 0.53</td>
</tr>
<tr>
<td>Pronation torque (N m)</td>
<td>-1.90 ± 0.76</td>
<td>-1.68 ± 0.48</td>
</tr>
</tbody>
</table>

\(^1\) Data represent mean ± the standard deviation.

\(^*\) Significant difference between handhold orientations (\(P < 0.05\), two-tailed t-test).
The measured forces generated during brachiation were used to derive the instantaneous accelerations, velocities, and positions of the gibbon’s center of mass over the time of contact with the handhold. The horizontal force generated by the animal on the handhold is equal to the body mass of the gibbon times the net forward acceleration. Dividing our measured reaction forces by the gibbon’s body mass thus gave the forward acceleration of the animal’s center of mass. Integrating this acceleration with respect to time gave the relative changes in forward velocity of the gibbon’s center of mass about some constant. The constant of integration for the horizontal velocity was calculated from the force data such that the average forward velocity equaled the average velocity determined from an automated video digitizing and analysis system (Peak Performance Technologies, Inc., Englewood, CO). Average velocity data were calculated from video and agreed well with our force data. Time of hand contact data were previously calculated from video (Bertram and Chang, unpublished data). Similarly, a double-integration of the acceleration with respect to time gave the relative horizontal changes in position of the center of mass during single hand contact. We performed a similar analysis on the vertical force data with the exception that the body weight of the animal had to be accounted for. This procedure is outlined in detail elsewhere for both terrestrial animals (Cavagna et al., 1977) and for brachiators (Chang et al., 1997). We tested for differences in the torque generated about the vertical axis with each handhold orientation using a two-tailed, paired t-test. Significance was determined at $P < 0.05$.

RESULTS

Forward velocity and handhold spacing

The forward velocity of the brachiating gibbon increased almost directly with the spacing distance between available handholds. At handhold spacings equal to or less than 1.20 m, the gibbon moved at slow to moderate velocities and always used a continuous contact brachiation gait (i.e., had at least one hand in contact with the support). At handhold spacings greater than or equal to 1.60 m, the gibbon brachiated at moderate to fast velocities and used a ricochetal brachiation gait (i.e., displayed a non-contact, or aerial, phase during the stride cycle). Using twice the handhold spacing as a surrogate for stride length (i.e., the distance traveled from one hand contact to the next ipsilateral hand contact), we observed a strong relationship between forward velocity and stride length regardless of gait (Fig. 3A). Mean forward velocities for each spacing increased from $0.63 \pm 0.05$ m s$^{-1}$ (mean $\pm$ s.d.) to $2.69 \pm 0.26$ m s$^{-1}$ corresponding to stride lengths of 1.60 m to 4.50 m, respectively.

The frequency of brachiation strides only increased slightly with increased stride length (Fig. 3B). The stride frequency can be calculated by dividing forward brachiation velocity by stride length. Although we observed a range of stride frequencies for each stride length used by the gibbon, there was far less correlation between stride fre-
frequency and stride length compared to the correlation between velocity and stride length. Although the gibbon was able to exhibit a range of velocities and stride frequencies at each stride length, our data show a unique range of preferred speeds associated with each spacing distance and to a lesser extent a preferred range of stride frequencies for each spacing distance.

Handhold reaction forces

The general shapes of the handhold reaction forces for both brachiation gaits were qualitatively similar, but each exhibited quantitative differences in absolute magnitudes of force and durations of contact (Figs. 4A,C). We observed a characteristic rise and fall in the vertical force generated during single-limb support for each gait (Fig. 5A). The gibbon produced a positive horizontal force (propulsion) during the first half of limb support and then a negative force (braking) during the second half for both continuous contact and ricochetal gaits (Fig. 5B). The gibbon generated very small forces in the mediolateral direction and did not exhibit any characteristic patterns (Fig. 5C). The time of handhold contact decreased with speed across both gaits (Fig. 6).

The peak vertical and horizontal forces generated against the handhold changed disproportionately with speed. The peak vertical force increased with average forward velocity, whereas the peak horizontal force increased slightly with speed only during continuous contact brachiation and actually decreased slightly during ricochetal brachiation (Fig. 7). Over the entire range of speeds covered by both gaits, peak horizontal forces changed very little compared to the range of peak vertical forces generated.

Movement of the center of mass during handhold contact

In both brachiation gaits, a negative vertical velocity was seen during the first half of hand contact (the mid-point, M, was defined kinematically as when the support limb was vertical and determined from video). This indicated a downward movement of the animal's center of mass (Fig. 8A). During the second half of the support phase, the vertical velocity was positive, indicating an upward movement of the center of mass.
In both gaits, the fore-aft horizontal velocity increased from initial limb contact until mid-support and decreased thereafter (Fig. 8B). On average, the mediolateral component of velocity was much smaller in magnitude compared to the other velocity components and did not exhibit any characteristic changes (Fig. 8C).

We did not typically observe steady speeds for continuous contact brachiation. The gibbon would often come to a complete stop or even move its center of mass backward while in double-limb support. With its two hands in contact with consecutive handholds, the gibbon would move backward as it stretched its forward limb to its full extent before releasing the back hand. The motion of the center of mass during single-limb contact of continuous contact support, however, characterized a smooth arc centered on the handhold position (Fig. 9).

The total vertical oscillation for a complete step appeared to be greater for ricochetal brachiation than for continuous contact brachiation and from 1.7 to 2.9 m s⁻¹ for ricochetal brachiation. Body weight (BW) is indicated for the vertical reaction force plots. Time of mid-support (M) as determined kinematically when the limb was in the vertical position is indicated in each plot. Note that in many instances during support, especially at higher speeds, the support limb leads the center of mass (i.e., the shoulder appears hyperflexed). This explains why certain inflection points (e.g., instant of zero horizontal force) do not always align with the instant that the limb is vertical (M).
tact brachiation (Fig. 9). Only data during single-limb support are given for the continuous contact gait, which prevented a comprehensive comparison between the two gaits. The ricochetal data, however, do represent a complete gait cycle and, together with the kinematic data, support the idea that vertical oscillations were greater than during continuous contact brachiation. Our video data showed that the gibbon would grasp the handhold in ricochetal brachiation when its center of mass was obviously at a greater overall height than in continuous contact brachiation (the trunk was typically horizontal at the moment of hand contact for the faster speeds). In both gaits, however, we observed the gibbon to have a fully extended support arm at mid-support.

**Torque generated about the vertical axis**

The torques applied to the handhold about the vertical axis indicate either an active supination (positive torque) or pronation (negative torque) of the proximal and distal radioulnar joints (Table 1). In general, peak torques applied to the handhold about the vertical axis during continuous contact brachiation were smaller than those applied during ricochetal brachiation. A difference between handhold orientations was observed only during ricochetal brachiation. The gibbon applied significantly greater torques about the vertical axis (in both supination and pronation) with handholds oriented perpendicular to the direction of travel compared with handholds oriented parallel to the direction of travel ($P < 0.05$).

**DISCUSSION**

**Forward velocity and handhold spacing**

There is a strong relationship between velocity and handhold spacing over a wide range of absolute velocities (0.45–3.25 m s$^{-1}$) and handhold spacings (0.8–2.25 m) for the one gibbon studied. This indicates a basic association between forward velocity and stride length during brachiation. The range of stride frequencies observed at each stride length, however, indicates that the gibbon was able to control its forward velocity to some extent by manipulating its stride frequency. Furthermore, this ability to adjust stride frequency was not heavily influenced by the stride length imposed by the fixed handholds. A similar relationship between velocity and stride length with some variation due to stride frequency has also been observed in humans and terrestrial birds (Cavanagh and Kram, 1989; Gatesy and Biewener, 1991).

On flat surfaces, terrestrial organisms are able to freely choose foot placement locations suitable for the speed at which they are traveling and so are able to vary both the frequency and the length of their stride. For the brachiator, however, the dynamics of its locomotion must be adjusted to accommodate the predetermined distances be-
between available supports. The forward velocity of a running or brachiating animal is equal to its stride length times its stride frequency. Within the complex environment of the forest canopy, the variability of stride lengths could have a profound effect on the dynamics of brachiation and could be a major constraint on brachiation. Our data suggest, however, that a brachiating gibbon is able to adjust its stride frequency for a given stride length to compensate for the constraints of a fixed stride length. In fact, for one atypical trial, the gibbon used an extremely high stride frequency and substantially increased its forward velocity beyond the expected range of speeds for that stride length (Fig. 3). A recent mathematical model of brachiation also found that, even when minimizing energetics, the stride parameters remained rather unrestricted (Bertram et al., 1999). Despite possessing the ability to widely vary stride frequency, however, stride length appears to be a stronger predictor of velocity.

The ease with which the gibbon was able to accommodate a nearly three-fold change forward speeds ranged from 0.5 to 1.3 m s⁻¹ for continuous contact brachiation and from 1.7 to 2.9 m s⁻¹ for ricochetal brachiation. The broken line indicates the average velocity. Time of mid-support (M) as determined kinematically when the limb was in a vertical position is indicated in each plot. Note that in many instances during support, especially at higher speeds, the support limb leads the center of mass (i.e., the shoulder appears hyperflexed). This explains why certain inflection points (e.g., peak vertical velocity) do not align with the instant that the limb is vertical (M).

Fig. 8. Mean velocities of the center of mass over time for continuous contact (left) and ricochetal (right) brachiation. Vertical (A), horizontal (B), and mediolateral (C) velocity components are shown. Time is normalized to either the entire single-limb handhold contact time (continuous contact) or to the complete step time (ricoehetal). Shaded bar indicates proportion of time in single-limb contact with the handhold. Data represent mean (bold lines) ± 1 standard deviation (light lines) for 20 trials of continuous contact brachiation and 19 trials of ricochetal brachiation. Average forward speeds ranged from 0.5 to 1.3 m s⁻¹ for continuous contact brachiation and from 1.7 to 2.9 m s⁻¹ for ricochetal brachiation. The broken line indicates the average velocity. Time of mid-support (M) as determined kinematically when the limb was in a vertical position is indicated in each plot. Note that in many instances during support, especially at higher speeds, the support limb leads the center of mass (i.e., the shoulder appears hyperflexed). This explains why certain inflection points (e.g., peak vertical velocity) do not align with the instant that the limb is vertical (M).
in stride length demonstrates the versatility of its brachiation. Nevertheless, the spacings used in this study were by no means representative of the animal’s full range of stride lengths and should not be taken as an indication of the limits of its maneuvering capabilities in the wild. While brachiating in our test cage, the gibbon generally matched its forward speed to the distance between available supports although it possessed the ability to vary its speed by changing stride frequency. Although this is a fundamentally different approach than that of walking and running animals that alter both stride length and stride frequency to change velocity, both brachiators and bipeds seem to rely heavily on changing stride length to change speed.

**Handhold reaction forces**

The difference in relative position of either a brachiator or a biped relative to its supporting stratum is indicative of the differences in the direction of the horizontal forces applied during the support phase. Gibbons locomote by hanging from pectoral limbs beneath their stratum, whereas bipeds locomote supported by pelvic limbs above their stratum. Once handhold contact is made, gravity acts to accelerate the gibbon forward until mid-support and then it decelerates the gibbon after mid-support. Bipeds, on the other hand, are decelerated by gravity immediately after ground contact and then accelerated forward by gravity during the second half of the step (Cavagna, et al., 1976; Cavagna et al., 1977). For example, recall the fundamental difference in timing of the horizontal braking and accelerating forces for each mode of locomotion.

Much of the difference in gross mechanics of both modes of locomotion can be attributed to simple, passive mechanics. In the horizontal direction, gravity has the oppo-
site effect on the simple pendulum as it does on an inverted pendulum. A typical pendulum swings from some initial height and is accelerated by gravity until it reaches its lowest point, thereafter gravity acts to decelerate the pendulum. An inverted pendulum can be viewed as a mass vaulting over a rigid, massless support exchanging gravitational potential energy for translational kinetic energy as it moves along an inverted pendular arc. Assuming that it has enough initial velocity to reach its maximum height, gravity first decelerates the inverted pendulum until the maximum height is achieved, thereafter gravity accelerates it forward. To a certain degree of success, the basic movements of brachiators have been idealized as a simple pendulum (Preuschoft and Demes, 1984; Swartz, 1989), whereas the movements of bipeds have similarly been idealized as an inverted pendulum (Cavagna et al., 1976, 1977).

Although simple pendulum mechanics are sufficient at a gross level, more detailed analyses are necessary for a better understanding of brachiation biomechanics. A comparison of the mechanical energetics of brachiation, for example, suggests that a fundamental change in mechanical energy utilization occurs when switching from the continuous contact brachiation gait to the ricochetal gait (Bertram and Chang, unpublished data). A mathematical model of brachiation suggests that gibbons may be able to minimize energetic cost by minimizing the collisions when grabbing their overhead support (Bertram et al., 1999).

As in bipedal locomotion, vertical forces generated during brachiation also follow basic rules of mechanics. In order for a gibbon to maintain its vertical position while locomoting through an integral number of strides, it must on average apply a vertical force to the handhold equal to its own body weight. As we observed, the peak vertical reaction forces were generally greater for continuous contact brachiation (2.7 times body weight) than for continuous contact brachiation (1.8 times body weight). Furthermore, the time of handhold contact decreased with faster speeds giving the gibbon less time to apply these vertical forces to oppose the gravitational force (Fig. 7). During ricochetal brachiation, the gibbon generated greater peak vertical forces with less handhold contact time compared to continuous contact brachiation. At slower speeds (i.e., continuous contact brachiation), the gibbon generated the same average vertical force by generating lower peak vertical forces over a longer period of time.

Although gibbon brachiation is similar in many respects to human locomotion, there are several important differences. For example, in continuous contact brachiation, we did not observe the classic “double peak” characteristic of the vertical ground reaction force in human walking (Meglan and Todd, 1994). In human walking, these two peaks have been attributed to the flexion/extension of the stance knee during weight acceptance and to the foot-knee interaction during push-off, respectively (Yamaguchi et al., 1991). This double peak in reaction force, however, seems to be a unique characteristic of human walking and has not been observed in other non-human primates (Kimura et al., 1979; Demes et al., 1994).

The changes in the horizontal forces generated across different speeds show a very different relationship than that seen in terrestrial locomotion. The magnitude of the changes in peak horizontal force across all speeds was relatively small compared to the changes in peak vertical force. The peak horizontal force even slightly decreased over the ricochetal speeds (Fig. 7). In contrast, humans typically generate increasingly greater peak horizontal forces with increased running speed (Cavagna et al., 1976; Cavanagh and Lafortune, 1980; Munro et al., 1987).

The difference in horizontal force generation across speeds suggests a substantial difference in the mechanics of ricochetal brachiation compared to the spring-mass dynamics of bipedal running. The spring-mass model for running animals has been shown to have great predictive value for bipedal locomotion (Blickhan, 1989; McMahon and Cheng, 1990; Farley and Gonzalez, 1996). Such a model has not been successfully used to describe ricochetal brachiation. A mathematical model of brachiation that minimizes collisional losses of mechanical energy while utilizing parabolic free-flight and pendular movement does, however, agree well with data recorded from a bra-
chiating gibbon (Bertram et al., 1999). Additionally, a ricochetal brachiation model of the rotational energies of a gibbon compared with the continuous contact gait agrees with estimates made from kinematic data (Bertram and Chang, unpublished data). Such models provide improved insight into the mechanics of brachiation that functionally diverge from better understood modes of locomotion such as walking and running.

**Vertical displacement of the center of mass**

The vertical displacement of the center of mass was much greater in brachiation than is normally seen in bipedal locomotion. In ricochetal brachiation, the maximum change in vertical position during limb support approached 70 cm, whereas it is typically only about 5 cm or less in the terrestrial locomotion of bipeds (Cavagna et al., 1963, 1964, 1977). The greater vertical movements of the center of mass in brachiation represent a 14-fold difference, which may represent a dramatic difference in the mechanics of the locomotion. Again, these data suggest that ricochetal brachiation may be more accurately modeled using a mechanism other than those used to model the spring-like gait of running or even the pendulum-like gait of walking.

**Gait transition speed**

Although different animals will change gait at quite different absolute speeds, the majority of these differences can be explained simply by differences in size (He-eglund and Taylor, 1988; McMahon, 1975). Making comparisons relative to a dimensionless, or relative, forward velocity (i.e., the Froude number) can often eliminate scale effects on the dynamics of locomotion (Alexander and Jayes, 1983). The Froude number can be calculated as the square of the average forward velocity (in m s\(^{-1}\)) divided by the product of the gravitational constant (equal to 9.81 m s\(^{-2}\)) times a characteristic limb length (in meters). The bipedal walk-run transition for a variety of humans and ground-dwelling birds occurs at a Froude number between 0.4–0.6, where the leg length was measured from the ground to the height of the hip at mid-stance (Alexander, 1977; Gatesy and Biewener, 1991; Kram et al., 1997; Mochon and McMahon, 1980).

If similar principles were operating in both brachiation gaits as is seen in the two bipedal gaits, we would expect brachiators to change gait at the same Froude number. Continuous contact brachiation was observed only at spacings of 1.2 m or less and ricochetal brachiation was observed only at spacings of only 1.6 m or more. Given the correlation between spacing distance and forward speed, we can assume that the transition between the two brachiation gaits occurred at a speed that lies somewhere between the fastest speed at the 1.2 m spacing and the slowest speed at the 1.6 m spacing. If this were the case, our data indicate that the transition from continuous contact brachiation to ricochetal brachiation would have occurred between 1.3 m s\(^{-1}\) and 1.8 m s\(^{-1}\). We can convert these absolute velocities to Froude numbers as previously described using the gibbon’s fully extended pectoral limb length (estimated from video to be 0.55 m measured from handhold to shoulder) as the characteristic limb length. This conversion reveals that the continuous contact-ricochetal transition occurred at a Froude number between 0.3–0.6. This is in good agreement with the bipedal walk-run transition speed observed in both humans and ground-dwelling birds. Bipedal utilize a pendulum-like exchange of mechanical energies to lower the metabolic costs of walking (Cavagna et al., 1977). It has been suggested that continuous contact brachiation also depends upon a similar mechanism (Bertram et al., 1999; Fleagle, 1974; Preuschoft and Demes, 1984; Swartz, 1989). This agreement in relative gait transition speed provides further support that there is a similar speed limitation of the pendular mechanisms for both continuous contact brachiation and bipedal walking.

**Brachiating along a ladder versus a continuous pole**

Unlike terrestrial locomotion, brachiators must be able to locomote on branches oriented at a variety of angles to their direction of movement. The presence of a unique ball and socket joint at the wrist allows the gibbon an enhanced range of wrist rotation (Jenkins, 1981). This greater range of mo-
tion, however, requires that the gibbon must actively control this movement to be able to transmit torques to a handhold during brachiation. Our observation of different peak torques generated about the vertical axis for two different handhold orientations suggests that gibbons do actively control the amount of torque generated on the handhold during ricochetal brachiation (Table 1). The gibbon generated greater torques about the vertical axis of the handhold when they were in the perpendicular orientation, as in the rungs of a ladder. This may suggest different recruitment patterns of the limb musculature as well as different kinetics at the proximal and distal radioulnar joints for brachiation across ladder rungs compared to a continuous pole. Stern and Larson (1993) observed that the supinator and pronator were active during brachiation in gibbons, indicating the possibility of an actively generated torque about the vertical axis. The relatively large mass of the supinator muscle in gibbons compared to non-brachiating primates (Tuttle, 1972) provides further anatomical support for the hypothesis that the gibbon is able to actively generate substantial torques about the vertical axis during brachiation. This represents a major distinction between brachiators and bipeds. Bipeds are not able to grasp the ground that they run on and do not utilize such a mechanism for generating torque against the ground during locomotion.

One study focusing on the vertical torques generated against the ground by human runners, however, indicated that normal human runners typically generate torques on the ground of 12 N m (Holden and Cavanagh, 1991) compared to the pronation torques of 2.8 N m generated by the gibbon during ricochetal brachiation. To gain an appreciation for these values relative to the size of the animal, we can perform a quick calculation by dividing by body weight (human, 697 N, data from Holden and Cavanagh, 1991; gibbon, 78 N) and by a characteristic limb length (human, 0.94 m pelvic limb length, estimated as 53% of average height, see Winter, 1990; gibbon, 0.55 m pectoral limb length). Taking body size into account, we see that the relative torque generated against the ground for gibbons brachiating in a ricochetal gait with perpendicular handholds is more than 3.5 times that of running humans (0.065 versus 0.018, respectively).

In terms of forces, however, gibbons limit substantial force generation to the sagittal plane, as exemplified by the extremely small magnitudes of mediolateral forces generated (Fig. 5). The generation of forces on the handholds did not indicate any substantial effect of handhold orientation and is independent of torque generation. The ability to grasp their support and generate large torques against their handholds allows the gibbons to maneuver within the complex and unpredictable canopy of their habitat without compromising their ability to generate the forces necessary for supporting their body weight and accelerating forward.

CONCLUSIONS

Brachiation and bipedalism are two distinct modes of locomotion, however, the mechanics with which they accomplish movement have in principle many similarities. The use of symmetrical, alternating limb support characterizes both brachiation and bipedalism. The relative difference of swinging beneath an overhead support versus stepping on top of a substrate leads to distinct differences in the force patterns generated by both brachiator and biped. Brachiators accelerate during the first half of limb support and decelerate during the second half of support.

Despite exhibiting a very similar relationship between speed and stride length, the mechanism for controlling speed is different for the two forms of locomotion. Brachiators maintain a relatively constant stride frequency and primarily adjust their forward speed to accommodate the stride lengths dictated by the availability of handholds. Bipeds, on the other hand, are generally able to vary both stride frequency or stride length for a given speed, although running speed is predominantly modulated by varying stride length (Cavanagh and Kram, 1989; Nilsson and Thorstensson, 1989).

In principle, continuous contact brachiation appears to be functionally analogous to bipedal walking, whereas ricochetal brachiation appears to utilize a different mecha-
nism from the spring-mass system used by running bipeds. At the slower gaits, both the continuous contact brachiation and bipedal walking appear to be limited by similar mechanical mechanisms as evidenced by our observation that both modes change gait at the same relative speed. The lack of increase in peak horizontal force with speed and the far greater vertical excursions indicate that ricochetal brachiators may be utilizing a different mechanical mechanism compared to the bouncing gait of bipedal runners. Two different models of brachiation that seem to predict the dynamics of both brachiation gaits also suggest differences between the ricochetal gait and running (Bertram et al., 1999; Bertram and Chang, unpublished data). A clear shortcoming of our study as well as many other empirical and theoretical studies is that brachiation was studied on rigid handholds. In nature, gibbons brachiate beneath compliant branches that are to some degree elastic. As Bonser (1999) suggests, a promising area for further study would include the possible biomechanical contributions of an elastic handhold because it may influence the gibbon’s locomotion.

Brachiation provides a unique comparative model with which to test our general understanding of legged locomotion. It is clear from our data that brachiation is not a comprehensive analog of bipedality. Yet, the many similarities that prevail amidst the differences still point to some basic principles that are likely universal to all limbed locomotion.

ACKNOWLEDGMENTS

This work could not have been completed without the cooperation, facilities, and expertise of the Department of Anatomical Sciences, SUNY—Stony Brook (supported by NSF SBR 9507078 to Susan Larson). We are particularly indebted to Susan Larson, Jack Stern, Brigitte Demes, and Marianne Crisci for assistance with this project. Additionally, we thank the members of the University of California, Berkeley Locomotion Lab, as well as David De Gusta for providing helpful comments and suggestions to this manuscript. The experimental studies described in this paper were supported by grants from the NSF Division of Physical Anthropology (NSF-SBR-9422118 and 9706225 to J.E.A.B.) and from Sigma Xi Grants-in-Aid of Research to Y.-H.C.

LITERATURE CITED


