New Perspectives on Brachiation Mechanics

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ABSTRACT   This review is designed to evaluate and interpret studies relevant to the locomotory mode known as brachiation, particularly as performed by the Hylobatid apes: the gibbon and siamang species. The older literature and its conclusions are evaluated against recent work performed by the author and other research groups working on brachiation models, either computer simulations or physical robots. The gibbon displays two types of brachiation: continuous contact, analogous to walking, and ricochetal, analogous to running. Both brachiation gaits display substantial pendular exchange between kinetic and potential energy. However, the fundamental feature of either of these gaits is the minimization of collisional energy loss. Collisional energy loss due to discontinuities in the trajectory of the center of mass is emerging as key in understanding locomotion using limbs in any terrestrial environment. The insight gained from this perspective applied to gibbon locomotion demonstrates that this is a critical factor in understanding many of the maneuvers employed by these animals, and can provide novel new interpretations of the morphological specializations that characterize the group. It is observed that these animals could brachiate using either totally active (muscle powered) or totally passive (nonmuscular) mechanisms. The active option would be metabolically costly, but provides substantial motion plasticity, while the passive option has the potential for profound economy, but does not allow a means to effectively contend with the inconsistencies present in the animal's natural environment. The conclusion is that the body form of brachiators and the locomotion behaviors they exhibit are a compromise between these two extremes, and these features of the gibbon's biology can only be understood by recognizing the role of collisional enerlgy loss and evaluating both passive and active motion options together. Yrbk Phys Anthropol 47: 100–117, 2004.   © 2004 Wiley-Liss, Inc.

Brachiation is an intriguing form of locomotion for several reasons. The apparent effortlessness combined with the drama of the volatile actions of a ricochetal gibbon careening through the highest branches engenders the same envy in those who have witnessed it as does the freedom and apparent simplicity of bird flight. It has also long been recognized that those primates that are best at brachiation (gibbons and siamangs) share several distinctive anatomical characteristics with humans and the great apes, such as a dorsoventrally flattened thorax, orthograde (upright) posture, and wrist specializations (Lewis, 1971a,; Stern and Oxnard, 1973). Such similarities are of interest because they imply an influence of brachiation on the morphological evolution of the human lineage (Keith, 1923), although closer scrutiny of the phylogenetic evidence stimulates substantial debate (Avis, 1962; Tuttle, 1975; Fleagle et al., 1981; Sarmiento, 1988; Gebo, 1996). Beyond implications regarding human evolution, we are intrigued by brachiators because of their unique ability to move under their support, rather than over it as humans and most other primates do. This reversal of orientation relative to the support makes one question whether the mechanical "rules" governing brachiation are substantially different from those operating in the locomotion of humans, other primates, and other mammals (Tuttle, 1968; Fleagle, 1974; Swartz et al., 1989).

What are the key features that allow effective brachiation? How should the mechanics of brachiation be interpreted? The mechanics of animal locomotion defined in quantitative terms can be complex. In terrestrial locomotion, the use of mechanical analogies has proven effective as a means of translating key features of the complex mechanics into readily understandable concepts. With such analogies, it is possible to gain a sophisticated conceptual understanding of the mechanisms employed to accomplish the mechanical tasks required without getting lost in analytical details. The most common analogies in terrestrial locomotion involve the inverted pendulum, most effectively applied to human walking (Cavagna et al., 1977), and the spring-mass model, applicable to a variety of running systems (Blickhan, 1989). In the inverted pendulum model of

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bipedal walking, higher levels of potential energy (energy of vertical position = mgh, where m is mass, g is the acceleration due to gravity, and h is height) at midstance are converted to kinetic energy (energy of motion = $(1/2)mv^2$, where m is mass and v is velocity) as the following foot contacts the substrate, and this kinetic energy is translated back to potential energy as the center of mass (CoM) is lifted as it approaches midstance once again. The direct exchange between potential and kinetic energy means that these will be out of phase; their levels will vary in reverse of each other. In this way, energy of the previous step contributes to the motions of the subsequent step, just as occurs in the cyclical swinging of a pendulum. However, because the potential-kinetic energy translation requires the action of gravity, and because gravitational acceleration is constant, pendulum-like exchange will have a determined natural frequency that will in turn determine the speed at which cost-effective walking will proceed; this is referred to as the "preferred" walking speed and is approximately 1.1 m/sec for an average human (Sun et al., 1996). At higher walking speeds, this exchange is no longer energetically effective, and it is necessary to switch to an alternate mechanism: the running gait. The spring-mass model describes the bounce-like behavior displayed in symmetrical running gaits and describes an exchange of both potential and kinetic energy with strain potential energy of the limb muscles and connective tissues (Alexander, 1991). In this case, potential and kinetic energy levels vary in phase, in reverse of a pendular system.

How much does brachiation resemble either of the terrestrial gaits? There are obvious pendulum-like aspects to the swinging movements where potential energy is exchanged passively with kinetic energy (Fig. 1A), but models of brachiation relying only on pendular motion do not characterize brachiation well except over a limited speed range (Preuschoft and Demes, 1984; Swartz, 1990; Yamazaki, 1990). On the other hand, the higher-speed ricochetal gait can involve a substantial ballistic aerial phase. Cannon and Leighton (1994) reported that in the wild, gibbons routinely brachiate across canopy gaps of 3 m and have the capacity to cross gaps as large as 9 m. As the name of the gait implies, ricochetal brachiation is characterized by an apparent bouncing between overhead supports (Fig. 1B). Unlike the limbs of terrestrial mammals that employ bouncing gaits such as hopping and running (Alexander, 2002), however, brachiators do not possess long slender elastic tendons that can act as effective strain energy storage and recovery devices to facilitate spring-based bouncing (Jungers and Stern, 1980).

Rather than demonstrating ambiguous mechanical function, brachiation is a remarkably simple example of a fundamental, yet poorly recognized, aspect of the mechanics involved with any animal using limbs to move rapidly across a solid surface, whether above or below. Previous models of locomotion, including brachiation, share one general feature: they focus on the mechanisms by which mechanical energy can be recovered between gait cycles (Cavagna et al., 1977). In contrast, tracking the mechanism of energy loss can, in certain circumstances such as brachiation, provide substantially more insight into how (and why) these animals move as they do (Bertram et al., 1999; Usherwood and Bertram, 2003).

It is generally assumed that muscle action must be responsible for the rapid maneuvers required in brachiation, and that measurement and analysis of the muscle action could lead to insights into how these animals exploit this unique style of locomotion. Although substantial data exist on muscle action in brachiation (Stern et al., 1980; Jungers and Stern, 1980; Stern and Larson, 2002), it has led to surprisingly little insight into the limitations or opportunities provided by using brachiation as a means of locomotion. In contrast, recent work in modeling brachiation, at least in the steady state of continuous speed motion, suggests that all of the basic motions involved in both continuous contact and richochetal brachiation can, under certain circumstances, be provided passively without muscle action (Gomes and Ruina, personal communication).

It is the intention of this review to evaluate the brachiation strategies available to conserve mechanical energy and the possibilities of passive motion, and evaluate their implications for the interpretation of function, form, and ecology of animals using brachiation as means of exploiting a unique habitat.

WHAT IS BRACHIATION?

En route to understanding the mechanics of brachiation, it is necessary to define the term as it will be used here. This is particularly important because some dispute exists about the definition and which species should be characterized as brachiators. This in turn determines what features need to be considered when accounting for the morphological and behavioral specializations that characterize "brachiators."

In its fundamental form, brachiation should simply mean locomotion using the pectoral limbs. However, this simple definition becomes problematic when it is recognized that the only mammals that travel exclusively using their pectoral limbs are bats. Even within those mammals that move against a solid surface, none do so exclusively using the pectoral limbs. The definition of brachiation depends on the degree of pectoral limb dominance in locomotion. Those animals that rely to a greater extent on pectoral limb support than pelvic limb support do so in some form of below-branch suspension. This strategy simplifies the issue of balance because in a hanging posture, the CoM is located under the support and does not generate an overturning moment (Grand, 1972; Cartmill, 1985).

Of the number of mammals that move when hanging under a branch support, a few primates do so
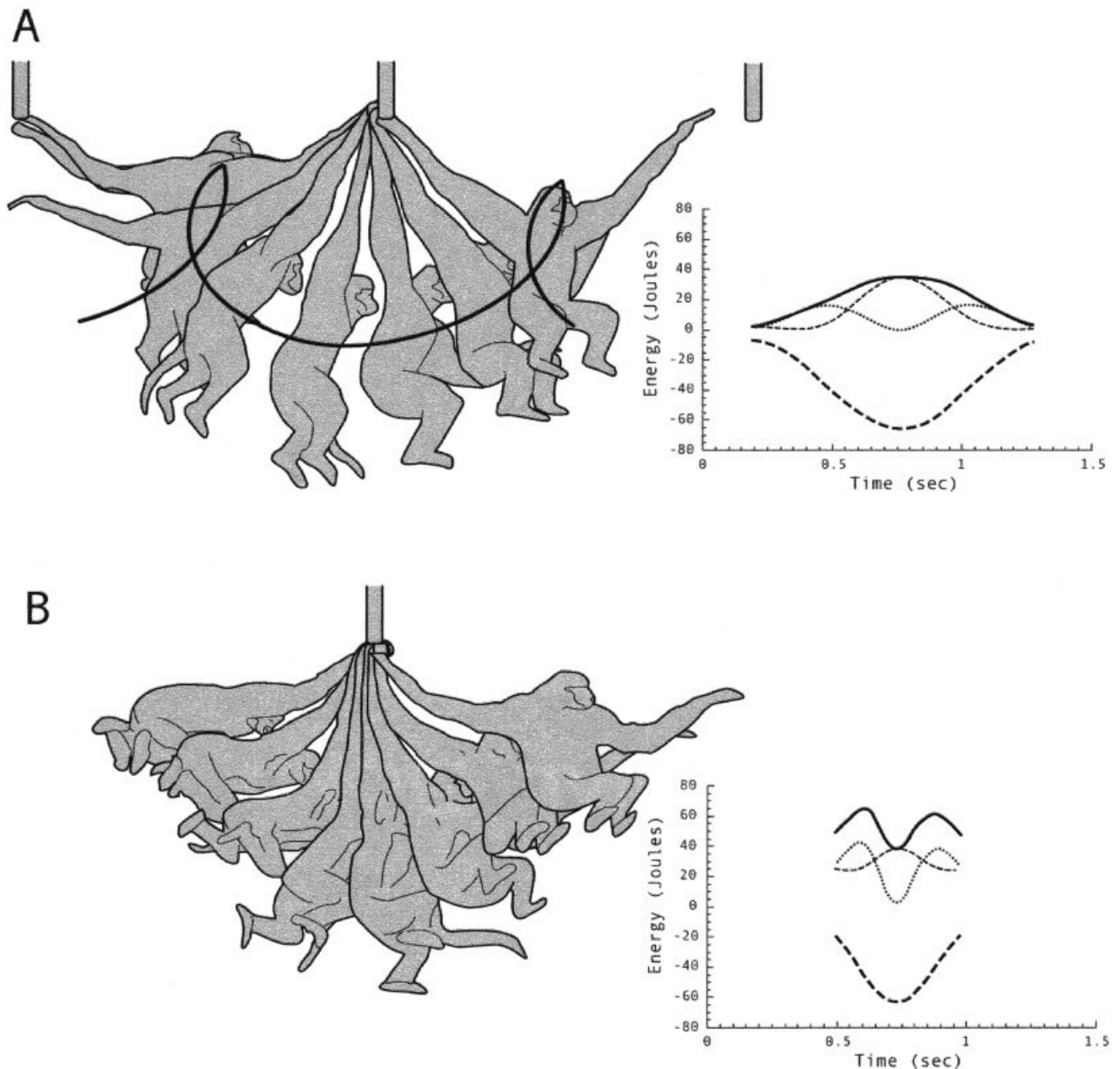
Fig. 1. A: Tracings of a lar gibbon using continuous contact brachiation to move between handholds. When transferring to next handhold, previous handhold is released, and animal's body swings smoothly under support. A large proportion of energy required for this swing is provided by pendular exchange of kinetic and potential energy (**inset**, right). Kinetic (bold solid curve) and potential (bold long dashed curve) energy are out of phase, indicating an exchange as animal converts its vertical position to horizontal speed and back again as swing progresses. Smaller dashed curves under kinetic energy curve in each inset indicate vertical (minimum at midswing) and horizontal (maximum at midswing) components of kinetic energy. Solid curve running through tracing shows path of center of mass. Note that motion is reverse to direction of travel at handhold transition, giving a distinctive looping path. **B:** Tracings of same animal in A, using ricochetal brachiation. Ricochetal brachiation is a rapid gait with a ballistic aerial flight between contacts. In midportion of contact, kinetic and potential energy appear to have some components in phase, as in terrestrial running gaits. However, decrease in translational kinetic energy results from its conversion to rotational kinetic energy as body spins around shoulder at bottom of swing. Curves in inset as in A. Adapted after Bertram and Chang (2001).

depending to an appreciable extent on their pectoral limbs. These are the orangutan (*Pongo*) (Tuttle, 1970), spider monkey (*Ateles*) (Takahashi, 1990), woolly monkey (*Lagothrix*) (Cant et al., 2003), adolescent chimpanzee (*Pan*) (Hunt, 1992), and Hylobatids (Hollihn, 1984). Even within this limited number of animals, substantial differences exist between speed and mode of movement. Orangutans can move exclusively using the pectoral limbs (bimanual overhead motion), but usually do so only briefly (one or two swings) and usually secure a foot support between handholds. Chimpanzees can have

substantial facility with brachiation, even into their adolescent years, but rarely use this mode of locomotion in the wild. Woolly monkeys use an overhead suspensory motion when scrambling through the canopy, but they too employ additional supports with the prehensile tail and pelvic limbs. *Ateles* was reported to use bimanual overhead support for transport, even in the wild, and does so quite capably. However, it is much more common for *Ateles* to supplement the pectoral limb support with prehensile tail support.

Brachiation has been defined as a specialized form of suspensory locomotion in which the pectoral limbs are used to move beneath a superstrate without the intervening aid of tail or hindlimbs, and without the interruption of other suspensory behaviors such as vertical climbing (Hollihn, 1984). By this definition, the Hylobatids are the only "true" brachiators, and in fact the first use of the term is attributed to Owen (1859), by whom it was defined specifically as "locomotion by means of the arms in the manner of gibbons." To some degree, this is a problematic definition because of its circularity: brachiation is what Hylobatids do, and therefore Hylobatids are the only true brachiators.

Studies of the locomotion of any of these canopy-dwelling primates have been limited largely to observations in which the first step to understanding the locomotion modes employed is the categorization of the observed behavior. This has been important in quantitatively determining the extent to which brachiation-like behavior is used in different groups. For instance, gibbons spend approximately 50% of their daily time in locomotion behavior, and of this, brachiation is the mode used in 80% of the instances (Andrews and Groves, 1976). This is a substantial portion of their locomotion and will potentially have an important effect on their adaptive morphology.

The classification of brachiation and related locomotory behaviors has evolved as more thorough documentation has accumulated. Although a variety of primates have been included in the brachiator or semibrachiator category over time, the only genus that persists in dispute is *Ateles*. *Ateles* was classified as a semibrachiator by Napier (1963) and Ashton and Oxnard (1964), and as a brachiator by Erickson (1963) and Ashton et al. (1971). Mittermeier and Fleagle (1976) evaluated the locomotion of *Ateles* and *Colobus* and concluded that the term semibrachiator was ill-advised because it does not describe a true functional group, the differences between semibrachiators being greater than their similarities. Still, *Ateles* does employ below-branch suspensory locomotion activity (Mittermeier and Fleagle, 1976) and can use bimanual, swinging progression, including even a brief aerial phase (Turnquist et al., 1999). *Ateles* and Hylobatids also share numerous morphological characteristics of the arm and shoulder (Jenkins, 1981; Takahashi, 1990; Hallgrimsson and Swartz, 1995; Gebo, 1996; Young, 2003), which may argue for functional similarity in their use. When

describing the locomotion of *Ateles*, perhaps it is best to follow Priemel (1937), whose classification can be translated as "prehensile-tailed brachiation."

The progress in evaluating arboreal locomotion in primates parallels that in terrestrial gait studies, where early work involved a quantitative description of the motions involved (Marey, 1874; Muybridge, 1887; Hildebrand, 1968), with later characterization of the mechanics responsible (Bekker, 1956; Rashevsky, 1948; Willems et al., 1995; Donelan et al., 2002). From the perspective of a thorough mechanical understanding, it is sometimes found that similar-appearing gaits actually function through fundamentally different means for fundamentally different reasons. For example, kangaroos and kangaroo rats appear to move in a remarkably similar saltatory hopping motion, but the mechanics underlying these motions differ. Biewener and Blickhan (1988) found that the limb morphology and saltatory hopping in kangaroo rats provide the means to accelerate very quickly and erratically, presumably helping to avoid predation in the exposed habitats of their arid habitat, but do not function to store and return energy economically. In contrast, Dawson and Taylor (1973) demonstrated that this same hopping motion in larger kangaroos provided for economical travel at remarkably high rates of speed through a mechanism dependent on strain energy cycling (Morgan et al., 1978). To avoid analogous confusions that arise from similar-appearing but functionally distinct locomotion behaviors, brachiation should be classified according to mechanical function and the degree to which it is accomplished, rather than simple descriptions of relations between limb contacts. It is only through this means that a worthwhile interpretation of the morphological specializations that characterize brachiators will be accomplished. To date, comparable mechanical analyses of gibbons and spider monkeys do not exist. Presumably by finding a mechanical definition of brachiation in Hylobatids, who are at least uncontested brachiators, it will be possible to compare the degree to which the arboreal locomotion of other species exploit these functional opportunities.

What then are the fundamental mechanics of brachiation in Hylobatids? The obvious swinging motion of a gibbon under an overhead support strongly suggests pendulum-like motion. Pendular motion is an attractive concept because it implies the possibility of passive exchange between potential and kinetic energy, i.e., the basic function of pendular motion and the reason pendulums are such effective motion machines (Fig. 1A). That is, except for relatively small losses due to friction and air resistance, the mechanical energy of one portion of the swing is available for spontaneous transfer to other portions of the motion (Preuschoft and Demes, 1984). This transfer is dependent on gravitational forces that ultimately provide the "potential" for motion in the form of potential energy.

By using passive pendular exchange, then, it is anticipated that brachiation could be a remarkably

efficient gait. Analysis of the metabolics of brachiation, at least in spider monkeys (*Ateles*), does not readily verify this expectation (Parsons and Taylor, 1977). These latter data, carefully generated by a reputable laboratory, have confounded the analysis of brachiation for some decades now. Unfortunately the measurements were generated with the sole definition of brachiation being a restriction to bimanual overhead locomotion. At the time the study was designed, there was no understanding of what factors might contribute to the mechanical cost of brachiation, and the study was limited to an analysis of metabolic cost under conditions of unknown impact on the mechanics of brachiation. As the following discussion will indicate, a number of factors could influence the effectiveness of such a study.

One major consequence of pendular energy exchange is that the most effective swing period (time required for one complete swing) is determined by the geometry of the mass distribution around the swing pivot (usually considered the handhold or wrist). Other swing periods are possible, but they require the substantial addition of mechanical energy; in biological systems, the addition of mechanical energy requires the investment of metabolic energy. Unless gibbons invest substantial metabolic energy (wherein pendular motion is no longer cost-effective), pendular exchange should imply a limited range of swing periods or stride frequencies. Since gibbon pectoral limbs have a finite length, this should mean that in continuous contact brachiation, forward speeds should also be restricted. Although swing frequencies and forward speeds that match such expectations can be observed in continuous contact brachiation (Preuschoft and Demes, 1984; Swartz, 1990; Yamazaki, 1990), active gibbons in an adequate brachiation environment appear quite unrestricted in both step length and speed of progression.

How do these animals circumvent the restrictions imposed by the physical consequences of their pendular swinging? Kinematic analysis of siamang brachiation (Fleagle, 1974) indicates that, not surprisingly, these animals employ clever redistributions of their mass during the swing to allow conversions of their angular momentum (a measure of the rotational motion of the system and the product of angular velocity and mass distribution in a rotating system) to increase angular velocity (rate of rotation around the pivot point). However, the speed changes possible using these mechanisms cannot account for the large changes in speed observed, and other detailed reports of brachiation in gibbons do not indicate a dependence on systematic leg flexion and extension. For instance, Jungers and Stern (1984, p. 122) reported, "Unlike the siamang, our gibbons were never observed to extend and flex their hindlimbs alternately during brachiation."

Using a specially designed dynamic force and moment system, basically a force plate designed to be fixed to the ceiling with a handhold attached, Chang et al. (1997) were able to directly demonstrate that gibbons swing in a very pendulum-like manner, exchanging gravitational potential and translational kinetic energy when using continuous contact brachiation (Fig. 1A). However, this instrument indicated that faster brachiation using the ricochetal gait showed much more complex interactions of potential and kinetic energy (Fig. 1B; Bertram and Chang, 2001).

In ricochetal brachiation, periods of aerial noncontact occur between handholds. Recognizing that horizontal velocity remains constant during this ballistic aerial phase, Preuschoft and Demes (1984) interpreted this as a method of increasing forward speed. That is, assuming that even though the swing phase is determined by pendular exchange, the intervening ballistic travel provides the opportunity to increase forward speed because forward velocity does not decrease during the aerial phase as it does during the latter half of the contact phase. This is in fact the case, but the problem is that gravity still requires adequate vertical velocity at the end of the swing to allow the animal to remain airborne until it reaches the next handhold, i.e., for long enough to reap the advantages of being without a contact. If the system operates on an exchange of potential and kinetic energy (i.e., pendular motion), the requirement for vertical velocity at release does not allow for an advantage in horizontal travel. That is, the farther the next handhold, the greater the component of available kinetic energy that must be converted to vertical velocity to stay in the air against the action of gravity, but the more kinetic energy that is converted to vertical velocity, the less that is available for horizontal travel. Even with no losses in the system, beyond a certain optimum value it is a predicament of diminishing returns (note that this optimum value will form the basis of an alternative model of brachiation that will be discussed below). However, if the available kinetic energy were adequate to cover the distance between handholds, it would be possible to cross an extended distance. It is an unusual pendulum indeed that has substantially more kinetic energy than potential energy. But, of course, this is just what a rapidly brachiating gibbon is.

THE MISUNDERSTANDING OF BRACHIATION AS A PENDULAR SYSTEM

The discussion above should indicate that both major gaits of brachiation (continuous contact and ricochetal) have potential and kinetic energy exchange. Such pendular exchange, however, is not adequate to explain why gibbons move as they do or what limits their function or influences their morphology. As pointed out by Swartz (1990), pendular aspects of motion are not exclusive to brachiators. In order to understand brachiation, it is necessary to recognize that pendular exchange will occur in a swinging system regardless of morphological detail, so design to "be" a pendulum need not be a large

influence on brachiator form. Likewise, passive motions will occur in a swinging system unless actively cancelled by specifically applied torque forces.

It is to any animal's advantage to limit the energetic cost of locomotion. One method to accomplish this is to recover energy from previous steps using an exchange mechanism, i.e., the energy recovery strategy. An alternate method, and one that has substantially more potential to reduce the cost of a locomotion method like brachiation, is to limit the original loss of energy. But where does the energetic cost of brachiation originate?

Pendular exchange refers to the reversible conversion of one type of energy to another, i.e., gravitational potential energy exchanged with translational kinetic energy. In this case, losses must be attributed to only pivot friction and air resistance (Jungers and Stern, 1984; Preuschoft and Demes, 1984). Air resistance is certainly of negligible concern in the case of a brachiating Hylobatid. Pivot friction can also be negligible. Mammalian joints are noted for their low friction, at least within the normal range of motion. The free motion of the wrist joint in a gibbon, for instance, can be noted by the continued free swinging of an animal that stops while holding a branch. That this motion is passive is verified by the small torque forces measured at the handhold (Chang et al., 2000). However, it must be remembered that if necessary, a gibbon can increase its pivot friction to quite high levels through muscle action of the grip and across the wrist (Jenkins, 1981).

Unfortunately, the pendular perspective of brachiation neglects a major factor determining the mechanics of this style of locomotion. When moving from one support to the next, mechanical energy losses can occur due to interaction with the support at the transition between handholds. Note that the reference here is to mechanical and not metabolic energy losses. However, in order to maintain constant motion, any mechanical energy losses must be replaced; in biological systems, this requires metabolic energy contributions through muscle action. In this discussion, it is assumed that the animal will benefit from using a locomotion strategy in which mechanical energy loss is minimized, provided the locomotion goals of the animal are achieved.

## WHERE IS MECHANICAL ENERGY LOST IN BRACHIATION?

Although it might seem that identifying where energy is lost in locomotion is trivial, it is actually quite difficult to determine. Even within human walking, the muscle action that we recognize as the effort used to perform this task occurs largely to reduce and replace energy lost by other means. Recent studies showed that much of this loss is due to discontinuities of the center of mass trajectory at the transition between foot contacts (Kuo, 2002). In mechanics, a discontinuity in CoM path is termed a collision (Chatterjee and Ruina, 1998).

Collisions with the supporting surface may at first appear an obscure factor in locomotion, but it is likely dominant in determining the energetics of motion using limb contacts. To appreciate its potential for determining locomotion cost for a brachiator, consider a child on a swing. This is a well-known situation in which the advantages of pendular swinging as a low-cost means of maintaining cyclical motion are obvious. The advantages only apply over a specific range of motion, however. If the individual becomes overexuberant and the swing arc becomes too high, gravity will draw the CoM of the individual down through the swing arc (Fig. 2A). This results in a jerk when the swing cords (the tension supports for the swing) reach their limit, causing a discontinuity in CoM motion. This will substantially reduce the energy available for the swing because energy is lost to the collision, regardless of the physical properties of the swing suspending lines. The energy loss in this case results from a tension collision: tension because it is tension in the suspension lines of the swing that results in the discontinuity in CoM travel, and it is the discontinuity that is the collision that results in a loss of energy. A simple test on a playground swing demonstrates that even relatively small tension collisions result in the loss of a substantial component of the energy available for the remaining swing.

In order for forward progression in brachiation to occur in an energy-effective manner, energy loss due to tension collisions at the transition between handholds must be minimized. A brachiating animal does have the capacity to actively flex and extend joints, applying force to the support and altering the position of the CoM, and these complexities and the opportunities they provide will be discussed below. However, the key factor involved with effective brachiation is the CoM path at transition, and this must be understood in order to evaluate the consequences of other maneuvers the animal may employ. For this basic aspect of brachiation mechanics, it is adequate to consider the animal as a simple point mass located at the end of a massless arm: the point-mass model of brachiation (Bertram et al., 1999).

It may seem ridiculous to reduce a complex athletic animal like a gibbon to a simple point-mass at the end of a massless arm, but even this remarkably simple model contains the essence of the mechanical features that determine effective brachiation. As such, it forms the foundation of the more complex movement possibilities that the active capabilities of the animal provide. The key feature of this model is simple: in order to minimize energy loss in brachiation, the transition between handholds must allow the CoM to continue on a smooth trajectory (Fig. 2B). In continuous contact brachiation, this will occur if the end of the previous swing arc during support by one limb is coincident with the arc of the following swing. Even though the CoM trajectory changes direction at the transition, it does so at zero velocity; therefore, no collision occurs. In ricochetal
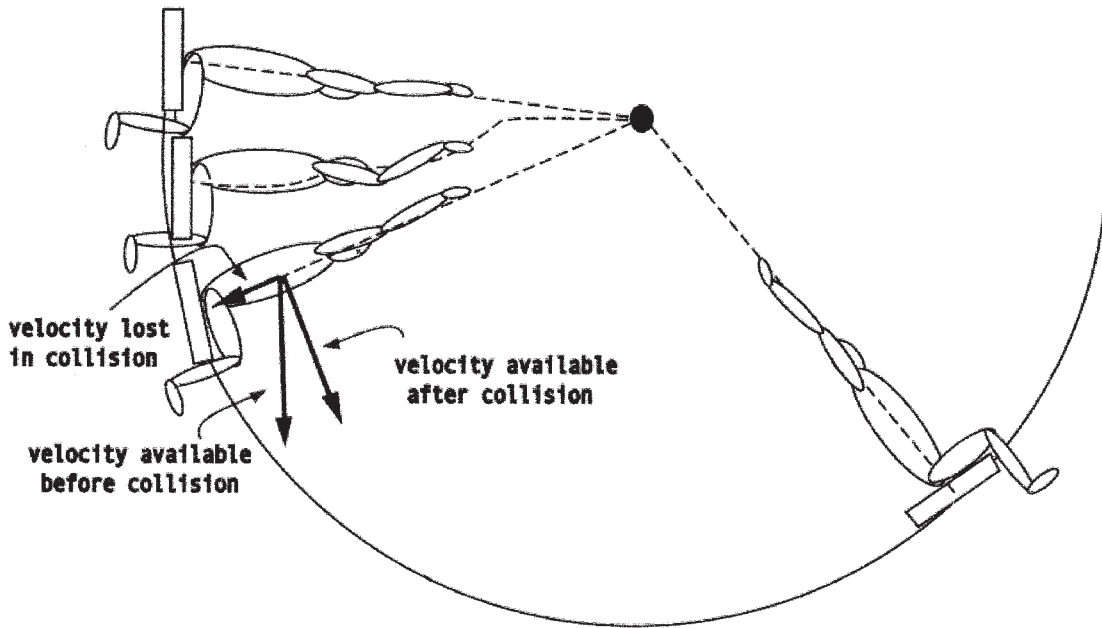
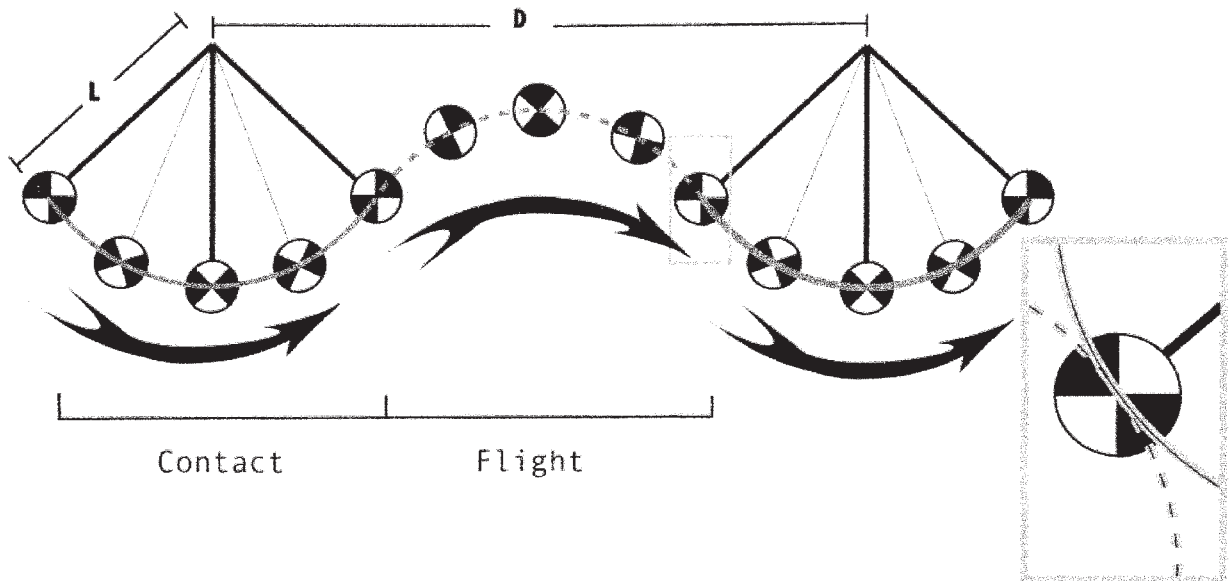**Fig. 2. A:** Tension collision in a playground swing. If individual swings too high, gravity will draw center of mass directly downward and within swing arc of fully extended swing cord supports. When cords again reach their limit, CoM path of individual will be abruptly altered. This discontinuity will result in loss of component of velocity vector in line with cords, leaving only that perpendicular to maintain motion along swing arc. Energy loss will result in lower swing height. **B:** Collisional energy loss as described in A can be avoided in brachiation if parabolic path of aerial phase and circular arc of contact phase are coincident at transition (**inset**). Under this circumstance, transition is smooth, and no energy loss occurs. Note that these criteria can be satisfied for continuous contact brachiation as well, if transition between swing arcs is made when CoM has zero velocity. Under these circumstances, continuous contact brachiation is simply a special case of ricochetal brachiation when velocity at initiation of aerial phase and its length are nil. The distance between handholds is labeled D and the length from the handhold to the center of mass of the swinging gibbon is labeled L. Redrawn after Bertram et al. (1999).

brachiation, the trajectory of the CoM at the end of the ballistic aerial phase must be coincident with the swing arc around the handhold when support is transferred to that handhold. In this case, the transition can occur with appreciable velocity, but no energy need be lost if there is no discontinuity in the CoM trajectory when the animal transitions between aerial and support phases of the "step." From a mechanical perspective, continuous contact and ricochetal brachiation are not fundamentally different; the continuous contact point-mass model is just a specific case of the ricochetal brachiation model, in which velocity at transition and flight distance between handholds are nil.

Direct measurement of the interaction of a brachiating gibbon with the handhold confirms that it uses a pendular exchange at slow brachiation speeds, but then transitions to an alternate gait at higher speeds when brachiating ricochetally (Bertram and Chang, 2001). Although the potential-kinetic energy changes over the course of contact in ricochetal brachiation have some superficial similarity to those of a spring-mass system, i.e., some aspects of potential and kinetic energy changes are in phase, the changes taking place during contact also have some distinct differences from normal bouncing (Fig. 1B, inset). If neither the pendulum nor the spring-mass systems characterize the fundamental mechanics of ricochetal brachiation, what mechanical analogy captures the functional aspects of ricochetal brachiation?

In many regards, the bounce-like characteristics of gibbon brachiation resemble the skipping of a stone on a calm water surface. In both cases, the trajectory of the CoM is smoothly diverted from a downward fall to an upward ballistic aerial phase, but these changes are not mediated by strain energy storage and return as required by a spring-based system. The energy is available not because it has been stored and returned (as in a spring), but simply because it was not lost in the first place (note that the apparent "bouncing" of the stone on the water surface cannot involve spring-like energy recovery, because neither the water nor the stone can store and return the required energy). For both the skipping stone and brachiating gibbon, energy will be available for the subsequent flight, provided the diversion of motion direction is smooth and does not extract too much energy. In the case of the stone, the water forms the trough that diverts the direction of the stone, but energy loss due to fluid viscosity will result in an inevitable decrease in energy that will decrease the flight distance between contacts as they progress. This is not necessarily the case for brachiation, where the contact between the overhead support and the arm causes the same change in direction of the CoM that the water causes for the stone. For the gibbon, if the transition from the aerial to contact phase is smooth, energy loss from the collision will not occur. Under certain circumstances, ricochetal brachiation with long aerial components, termed "bimanual saltatation" (Tuttle, 1968), recognized as an important means of crossing large gaps by gibbons, may be akin to simply "skipping" through the high canopy.

For continuous contact brachiation, the most effective transition will occur if the handholds are spaced so that the previous swing arc naturally ends at a point coincident with the arc of the next swing. This will occur for handholds that are spaced slightly less than the full arm spread of the animal, so that the CoM position is slightly lower than the handholds, but both handholds can be reached simultaneously with fully extended pectoral limbs. This will be approximately 1.2 m for an average-size gibbon (a surprisingly long distance for an animal of less than 10 kg mass). Analysis of the mechanical transfers in a brachiating gibbon shows that under these handhold spacing conditions, the pendular action of the animal is maximized (Bertram and Chang, 2001), and presumably this will be correlated with a minimization of metabolic energy expenditure. No direct measurements of metabolic cost exist for this circumstance (but it is this type of understanding that is needed to appropriately evaluate the metabolic cost of brachiation, in contrast to the conditions used by Parsons and Taylor, 1977).

Ricochetal brachiation has an intervening aerial phase between handholds. For any given handhold spacing, there are an infinite number of parabolic flight trajectories that would put the path of the CoM in alignment with the swing arc at contact (thus eliminating collision loss in the transition) (Fig. 3A). The specific trajectory selected will have consequences for the speed of travel and tension in the supporting hand and arm (Bertram et al., 1999), but presumably one of this set of trajectories would have advantages over the others. Determining the optimization using the point-mass model is not trivial. A good candidate should be the specific energetic cost of transport (energy use per unit weight and unit distance traveled). However, all of the trajectories that satisfy the criterion for coincidence between aerial and swing paths at transition have the same energetic cost: theoretically zero, because each involves no mechanical energy loss. Alternatively, it might be useful to consider the total energy of the moving system: if an animal starts and stops while using a locomotion technique that requires high energy levels, these high energy levels must be actively generated at start-up, and they must be absorbed at stopping. If large, such changes in energy state would be an unnecessary burden on the animal. For the family of trajectories indicated in Figure 3A, the low fast-progressing trajectories and the high slow-progressing trajectories both have high total energy levels. The intermediate trajectories have the lowest total energies and also involve the lowest tension force in the supporting limb, because the angular velocity around the handhold is not as rapid as either the low or high trajectory options require. Not surprisingly, the model indicates that total energy is
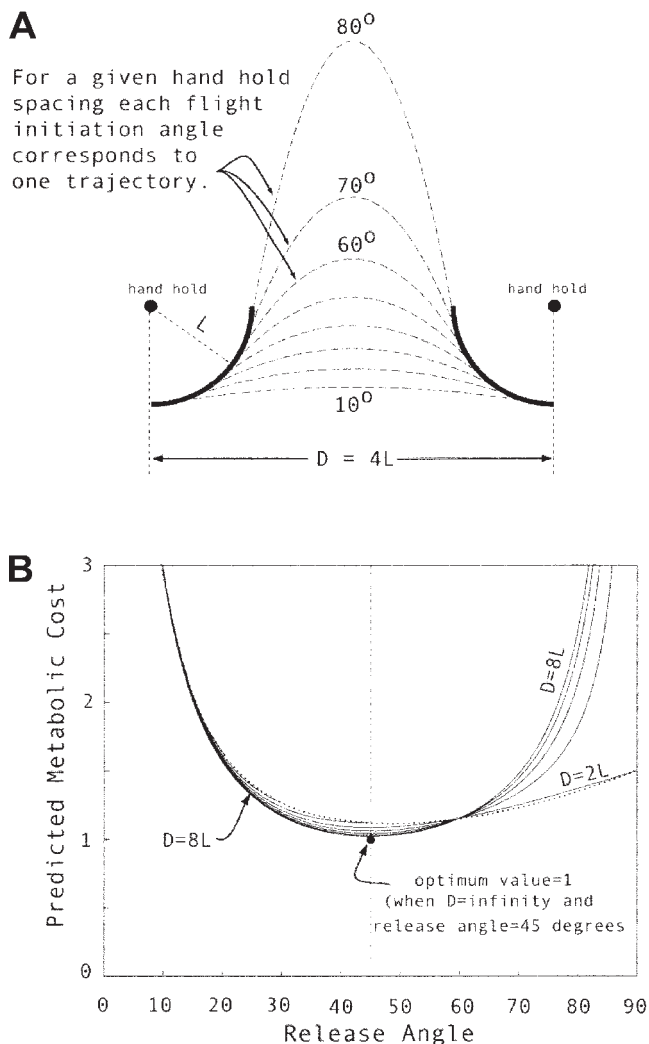
A

For a given hand hold spacing each flight initiation angle corresponds to one trajectory.

hand hold   hand hold

D = 4L

B

Predicted Metabolic Cost

D=8L

D=8L

D=2L

optimum value=1
(when D=infinity and
release angle=45 degrees

Release Angle

Fig. 3. **A:** For any given handhold spacing, here illustrated as four times distance from animal's CoM to its hand, an infinite number of ballistic trajectories could satisfy smooth transition required to avoid collisional energy loss. Each of these options is not equivalent, however. High and low angle releases both require high kinetic energy levels. High speeds required for these options have consequences for tension loads on supporting limb and metabolic cost of operating required musculature. **B:** Relationship between predicted metabolic cost of locomotion and release angle in brachiation (after Bertram et al., 1999). Cost is high for both low and high release angles because high velocities required to satisfy collisionless transition demand high support limb muscle tensions that change rapidly. Continuous contact brachiation is less costly than ricochetal for release angles over 60°, for handhold spacings in which both continuous contact and ricochetal brachiation are possible. Cost is inversely related to handhold spacing, a conclusion inferred by Preuschroft and Demes (1984). In this analysis, locomotion cost is minimized for handhold spacing of infinity because unlimited travel would occur for effort of a single contact. This is not possible because of extreme tension loads that would be required in initial contact. However, trade-off between cost-free aerial phase and increasing costs of support as handhold spacing increases is demonstrated by small variation between cost levels for different spacings. Dotted curve indicates unique continuous contact solution. Each curve is generated for a specific handhold spacing (D). Solid curves not specifically labeled indicate handhold spacing between 2–8 L, where L is fully extended distance from hand to CoM of animal. Redrawn after Bertram et al. (1999).

minimized for a release angle of 45°, agreeing with intuitions regarding the longest range for a projectile launched with a given energy level. In this case, optimization during the support phase matches optimization during the ballistic phase.

Of interest in considering how these factors might influence the behavior of a brachiating animal is the fact that, although a distinct optimum exists, the function is remarkably flat near the optimum (Bertram et al., 1999). This means that release angles other than the optimum do not incur a substantial energetic cost. For instance, for a handhold distance of twice the animal's arm length, release angles between 30–60° have a cost within 20% of the optimum. This implies that, provided the animal satisfies the smooth transition at the following contact, it is not rigidly restricted in the path selected to do so. This is the case except for large interhandhold distances; as ballistic flight distances increase beyond four times the animal's pectoral limb length, given the assumptions of this analysis, the energetic consequences of employing anything but the optimum release angle become greater.

Other considerations may also be important in determining the effectiveness of a particular ricochetal flight strategy. Terrestrial locomotion analyses suggest that one primary determinant of overall locomotion cost is the metabolic cost of activating and deactivating musculature (Kram and Taylor, 1990). If this also holds for brachiation, and the metabolic cost of generating a brief isometric tension during support in a gibbon is proportional to the level of tension in the supporting limb, then the metabolic cost per unit distance would be proportional to peak tension divided by the distance between muscular contractions. The distance between contractions would be handhold spacing (Bertram et al., 1999). For this measure of cost, the function is again minimized at a release angle of 45°, but once again it does not imply substantial extra cost until the release angle moves beyond the 30–60° range (Fig. 3B). Interestingly, this calculation suggests that the metabolic cost of brachiation should be almost independent of handhold spacing (each curve in Fig. 3B indicates a specific handhold spacing, and there are negligible differences between the absolute cost value of each). Such predictions are yet to be verified experimentally, but this remarkable insensitivity to handhold spacing may be a key factor in the success of brachiation. The natural habitat of brachiating forms, the canopy of tropical and subtropical forests (Carpenter, 1976; Andrews and Groves, 1976), is likely the most three-dimensionally complex of any that must be dealt with by a mammal using limb contacts to move. Although most experimental analyses are conducted with consistently spaced handholds, it is likely the animal's ability to contend effectively with handhold opportunities that differ substantially from one contact to the next that provides the opportunity to deal with its complex natural environment.

ASSESSING COLLISIONAL LOSS IN BRACHIATION

What evidence exists that minimizing collisional energy loss is a major determinant of effective brachiation, and that gibbons use this locomotion strategy? The direct evidence exists in two forms that compare the timing of gibbon behaviors when brachiating to predictions of the collision minimizing models (Fig. 4).

A variety of behavioral predictions can be derived from the simple point-mass model of gibbon brachiation (Bertram et al., 1999). Some of these predictions provide admittedly ambiguous results, where the data do not reflect details of the model in a compelling way, even if they also do not differ greatly from the model's predictions. This is the case, for instance, for the relationship between average forward velocity and handhold spacing. In this case, the observed data overlap with the model predictions for both continuous contact and ricochetal brachiation, but the data could just as readily be described by a single linear relation (Vel_{av} (m/sec) = 1.43 Spacing (m) − 0.47; R^2 = 0.942). This is in contrast to the specific predictions of the point-mass model where continuous contact and ricochetal brachiation each have individual curvilinear solutions that plot within the scatter of observed gibbon brachiation behavior. This likely indicates that the simple model precisely predicts behavior in a manner that is lost within the variability of the actions of the complex, active gibbon. On the other hand, comparisons are available for functional relationships where the predictions of the model for continuous contact and ricochetal brachiation are quite distinct (Bertram et al., 1999). Note that the predictions of this particular model depend on the collision minimization feature of brachiation, so matching gibbon behavior with the prediction can be taken as indirect evidence that collision minimization is a factor in brachiation. Even with the minimal point-mass model, some predictions match brachiation behavior well. For instance, the relation between time of contact with the handhold and the maximum velocity of the animal, which occurs at the bottom of the swing, has features that match the simple model predictions (Fig. 4A). Time of contact is a particularly relevant feature of locomotion because it defines the time available for muscle activity and determines what the muscles must accomplish in order to provide an appropriate upward impulse to counter the downward effects of gravity. In this case, the model predictions for continuous contact and ricochetal brachiation differ substantially, and this allows an effective comparison of the model even with the inevitable variability of real gibbon brachiation behavior. In ricochetal brachiation, observed gibbon handhold contacts form a tight cluster around the model's prediction (Fig. 4A). Although there is some loose association between the continuous contact prediction and observed behavior (which also predicts col-
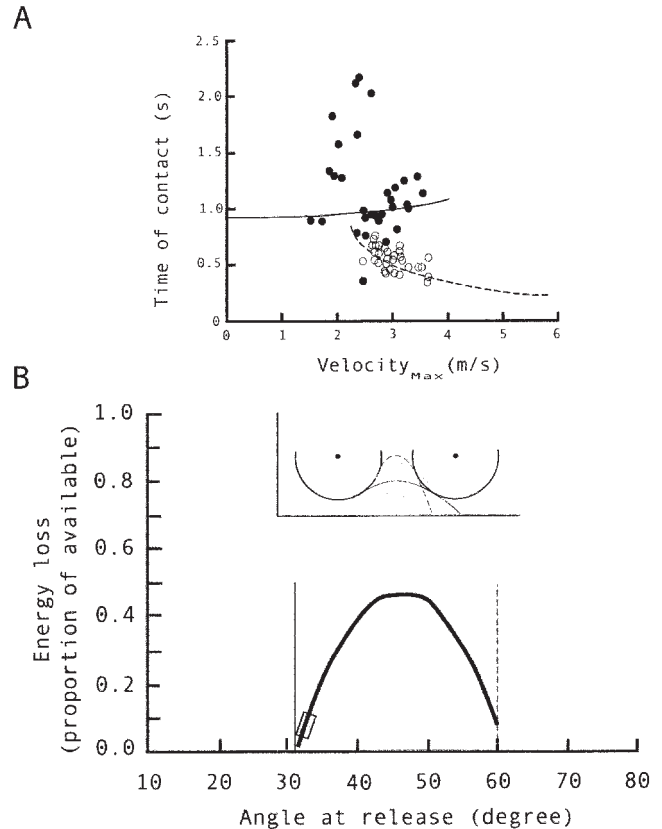

Fig. 4. **A:** Time of handhold contact plotted against maximum swing velocity for collisionless point-mass models (solid line, continuous contact; dashed line, ricochetal) and for brachiation by a lar gibbon (solid circles, continuous contact; open circles, ricochetal). Model predictions closely match behavior for ricochetal gait, where collision-mediated energy loss can be substantial (after Bertram et al, 1999). **B:** Proportion of available energy potentially lost against release angle for ricochetal brachiation with a brief aerial phase. Available energy is calculated from velocity at bottom of first swing (when mechanical energy is in form of kinetic energy). A variety of release angles below 30° and above 60° would produce CoM trajectories that would not bring animal close enough to reach next handhold; these are indicated by solid gray trajectories in inset. **Inset:** Position of two handholds (dots) viewed laterally with CoM swing arc during support, with a fully extended arms shown as partial circles. Lines indicate realistic trajectories for kinetic energy state of animal. Minimal collision loss can be satisfied by both relatively shallow angles (solid curve on inset, and solid vertical line on plot) and steeper release angles (dashed curve on inset, and dashed vertical line on plot). Release angles between these minima (e.g., gray dashed curve) indicate that a large proportion of available energy can be lost to discontinuity in CoM trajectory. Collisional energy loss is calculated from a point-mass model, assuming no other loss reduction strategies. Shaded box on energy loss curve indicates release angles actually used at this handhold spacing. Illustrations after Usherwood and Bertram (2003).

lision loss minimization), there is also substantial variability. The low energy levels involved with the slow progression in continuous contact brachiation, combined with the fact that in the laboratory setting the animal had no particular goal to the motion, likely mean that any constraints for efficient (collision avoiding) motion were not important to the animal in many of these cases. Continuous contact

brachiation appears relatively unrestricted, although successful completion of the more vigorous ricochetal brachiation does appear to require satisfaction of the minimal loss criteria.

The correspondence between the collisionless model and gibbon brachiation was also analyzed by Usherwood and Bertram (2003). In this case, the kinetic energy possessed at the bottom of the preceding swing (when all mechanical energy existed in the kinetic form) was used to predict the options available for the following aerial phase (Fig. 4B). Since the aerial phase is ballistic and the path is determined by the initial conditions and the constant downward acceleration of gravity, the paths available depend on the CoM velocity (including direction) at release. The relationship between the trajectory path and the handhold determines whether the animal will be successful in reaching the handhold, and, given a successful contact, it will also determine the discontinuity of the CoM path at contact, and consequently the collisional energy loss.

Within the range of release points that result in successfully reaching the next handhold, potential energy losses vary from very little, when the transition satisfies the coincidence criteria, to substantial, on the order of 50% of the available energy, when the collision is maximal. For numerous ricochetal steps analyzed in this way, the release angle selected by the brachiating animal indicated that the perfect no-collision path was not precisely selected (Usherwood and Bertram, 2003). Rather, the animal always selected a release angle that took the CoM on a trajectory that was slightly longer than the minimal energy loss requirement, but one that approached the minimization, i.e., where energy loss was on the order of 10% (Fig. 4B). This overshoot is also indicated by the typically observed elbow flexure at the beginning of ricochetal contact (Fig. 1B), showing that during the initial stages of hand contact, the CoM of the animal passes within the circular arc defined by the fully extended supporting arm.

A variety of explanations are available for the observed small overshoot. It could be that collisional losses are of little consequence in brachiation, but the fact that the differences from the model are so slight suggests that this is not likely the case. Alternatively, it may be that the animal chooses a conservative solution to the problem of crossing between handholds. Under natural circumstances in which the animal brachiates within the high canopy, the consequences of missing a handhold can be rather large. Gittins (1983) reported that a family of agile gibbons (*Hylobates agilis*) in western Malaysia conducted the majority of their travel at heights over 25 m, and almost never traveled at heights less than 15 m. Evidence suggests that approximately 40% of wild gibbons sustain fall-related fractures (Schultz, 1944). It is possible that the small energy loss from overshooting occurs to ensure that the chances of extreme losses from missing the next contact are minimized.

The difference between prediction and observed behavior may also have to do with the properties of the artificial overhead supports the animal uses in the laboratory setting. In its natural environment, some flexibility would be expected from the supporting branches. Although the branch may deflect, it will eventually come into equilibrium with the load applied by the animal and then act to alter the path of the CoM (and have all the consequences of collisional energy loss described above). The deflection of the branch while resistive strain is being generated would alter its effective position, but it would then act like a stiff support at a slightly lower vertical position than existed in its unloaded state. It is therefore possible that the gibbon anticipates this, even though in the laboratory setting the handholds do not deflect in a natural manner. In any case, analyzed in this manner, the behavior selected by the animal appears to match, within limits, the expectations of the collision energy loss reduction.

SUBTLE MECHANICAL STRATEGIES IN BRACHIATION

It is likely that handholds evenly spaced at the optimum distance occur only in the laboratory. In a gibbon's natural environment, available handholds will be inhomogeneously distributed, and the animal will have to contend with whatever handhold spacing it is faced with. What options exist for the animal to deal with nonoptimally spaced handholds?

For handholds that are more closely spaced than the optimum for continuous contact brachiation, there are two basic strategies available for minimizing energy loss. One is to actively transfer the CoM from the natural trajectory of one handhold to the natural trajectory of the next handhold. Although this may sound like a discontinuity that should result in collisional energy loss, if done when speed is minimum, the potential losses are diminishingly small. This minimum collision transfer can be accomplished at the top of the swing, where active flexion of the previous contact arm moves the CoM horizontally to an appropriate location for the following extended arm swing (Usherwood and Bertram, 2003). By timing this adjustment to the top of the swing, when swing velocity is near zero and the animal is effectively in equilibrium with gravitational acceleration, only a very small amount of muscular effort is required. In this way, energy in excess of that needed to complete the current swing can be retained as available potential energy (indicated as the high swing that brings the animal too near its next handhold) and carried over to the following swing, in which it may be useful if the spacing is greater for the next available handhold. This results in a distinctive looping trajectory at the top of the continuous contact swing that is readily observed in gibbons brachiating under these circumstances. (This can be seen in the sequence in Fig. 1A, where the animal moves away from the handhold as the swing begins. Note that it was the previous

swing arc that brought the animal to its initially depicted position. The end of the previous swing arc and the beginning of the currently depicted swing combine to form a distinctive "loop" indicative of brachiation, when handholds are closer than the optimum for continuous contact brachiation.) Recent modeling analyses showed that even this apparently active shift in body position, as mediated by flexion and extension of contact limbs, could itself be the result of a passive, collision-free trajectory (Gomes and Ruina, personal communication). One set of collision-free passive brachiation solutions from this model suggests that the looping trajectory can simply be an unusual form of slow "ricochetal" brachiation. In this case, the reverse loop is essentially an aerial trajectory, but it does not appear so simply because the handholds are close enough for the animal to make hand contact, even if negligible contact forces are exerted. Presumably, placing the hands on the handhold provides some security even if loads are not carried by the arms. Whether actively mediated by minimal muscular activity or the result of passive motion, the CoM shift from the previous swing arc to one appropriate for the next swing on closely spaced handholds need not be mechanically costly. This is distinctly not the case if collision losses are not avoided.

Alternatively, the animal is able to adjust the position of the CoM by flexing limb joints during support rather than during the transition. For handholds that are closer than the natural, extended limb optima, there are two methods for adjusting the CoM relative to the handhold. These are 1) flexing or extending the supporting pectoral limb, and 2) flexing and extending the pelvic limbs so that their contribution to the total mass moves relative to the handhold. Flexing the pectoral limb can change the CoM distribution substantially, but also comes at a substantial cost. Muscles working to flex a proximal joint change the CoM position by moving almost the entire body mass, while muscle forces that act to lift a distal component such as the legs have only to support a portion of the body mass. To accomplish the same adjustment in CoM position, a greater flexion of the pelvic limbs is necessary, but Hylobatids appear adept at this maneuver. Although arm bend is commonly observed in brachiation, it is rare that the supporting pectoral limb is not fully extended at the bottom of the swing, when applied tension loads on the arm are greatest. As mentioned previously, some disagreement exists in the literature regarding the role of legs in brachiation (Fleagle, 1974; Jungers and Stern, 1984). Differences between such observations could result from differences in species, but are more likely due to differences in speed of travel or relative handhold spacing. It will not be until all available mechanical strategies are recognized that appropriately controlled experiments can be designed to verify the function of such limb-position adjustments.

The high energy levels, speeds, and aerial distances involved in ricochetal brachiation provide opportunities for some subtle but interesting movement strategies to adjust the animal's position or mitigate the energetic losses associated with not completely satisfying the no-collision criteria. These strategies can be divided into those occurring during the ballistic aerial phase, and those employed during the transition to full load-bearing in contact. In the aerial flight between contacts, the parabolic trajectory of the CoM is fixed, because in free-flight no appreciable forces can be applied to alter it. However, the position of the animal relative to its own CoM can be adjusted using leg flexion and extension. For instance, within the aerial phase of ricochetal brachiation, extension of the legs will cause a reactive shift of the trunk and pectoral limb in the opposite direction, so that the CoM trajectory remains unchanged in spite of the active extension of the legs. This means the position of the contact hand can be adjusted even within free flight, which might be particularly relevant when handholds are widely distributed. In this case, the animal assumes a nearly horizontal body position in midflight and at initial contact (Fig. 1B; Bertram and Chang, 2001). Therefore, extension of the legs can assist in reaching a handhold that would have otherwise been out of reach.

If the animal does overshoot the handhold slightly, as is commonly observed, there are strategies available to decrease the collisional energy loss. One of these may have to do with a key distinguishing morphology of the gibbon, the long pectoral limb proportions. The characteristically elongate pectoral limbs of Hylobatids cannot be explained by the point-mass model, which indicates that collision-free solutions to ricochetal brachiation are quite insensitive to arm length (Bertram et al., 1999). Usherwood and Bertram (2003) showed that for a given overshoot error, the longer the distance from the handhold to the CoM, the smaller the collision consequences. This is the same phenomenon that provides an advantage to a large wheeled over a small wheeled vehicle to contend with a given roadway irregularity. Compare, for instance, the consequence of hitting a small pothole on a bicycle vs. an inline skate. Considering the "irregularities" present in a gibbon's natural environment, this may represent one pressure that has contributed to the emphasis of this distinctive morphology among brachiators.

When the brachiator overshoots the handhold slightly, it does not necessarily mean that the collision losses have to be large. Rather than having a maximal collision when the CoM of the animal comes to the full extension of the supporting limb, it is observed that gibbons commonly use a posture that has the body axis aligned perpendicular to the CoM trajectory (Fig. 5, inset). In this case, when the contact limb begins to bear full load, the body becomes a double pendulum, where the arm pivots
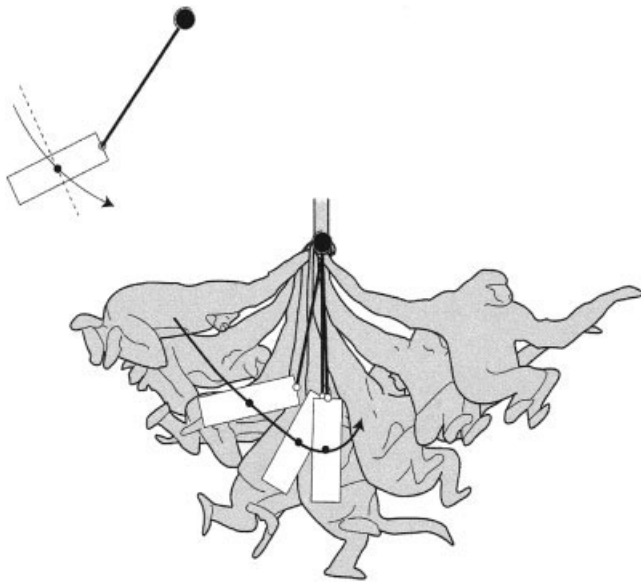
Fig. 5. Method of reducing collision energy loss in ricochetal brachiation. When trajectory of aerial phase of ricochetal stride takes CoM within extended arm arc of a smooth swing around next handhold, an energy-consuming collision can ensue. It is observed that prior to initial contact in this situation, gibbons routinely travel with body oriented perpendicular to trajectory of CoM. This is illustrated (**inset**) by dashed line running through model CoM. When arm comes to full extension, moment arm between axis of arm and position of CoM converts a large portion of energy that would be lost in a tension collision to rotational energy around shoulder joint. System then retains this energy and has some control over it via muscles stabilizing shoulder.

around the handhold and the body pivots around the shoulder (Fig. 5). This results in a unique whip-like motion that transfers some of the translational kinetic energy (kinetic energy involved with positional velocity) of the body to rotational kinetic energy (kinetic energy involved with rotational velocity) (Bertram and Chang, 2001), and reduces the total collisional energy loss of the system (Usherwood and Bertram, 2003). Although careful observation is needed to detect the details of this motion, it is commonly observed in fast-brachiating gibbons. This strategy also allows the large muscles of the shoulder girdle (pectoralis, latissimus, etc.) to control rotation of the body around the shoulder joint. Through this means, some acceleration or deceleration can be effected, as appropriate for the next aerial flight. Although it is possible for gibbons to generate torque about the handhold (Chang et al., 2000) and provide a similar degree of control directly to the handhold, the large moment arm between the handhold and body CoM makes this an ineffective strategy, particularly at high speeds (Usherwood et al., 2003). For rapid speeds and the consequent high energy and forces involved, it is far more logical for brachiators to rely on relatively massive trunk muscles to effect motion adjustments around the shoulder joint rather than directly to the handhold.

PASSIVE MOTION POSSIBILITIES IN BRACHIATION

Even though considerations of collisional energy loss change the basic perspective of brachiation mechanics, the initial impression of passively mediated motion in Hylobatid swinging need not be eliminated. In fact, it would appear that collision minimization works with the exploitation of the potential for passively driven motions as key factors determining the coordination dynamics of effective brachiation. Yamazaki (1990) explored passively driven motions in dynamical computer models of gibbon brachiation. He modeled brachiation as a two-dimensional system, with the gibbon composed of five jointed links. These links represented each pectoral limb as a single unjointed unit, the head and trunk as a single unit, both thighs operating as a single unit, and both shanks and feet acting as a synchronous unit. In the initial model, the size and mass distributions of these components matched those of an average-size gibbon. This model was able to demonstrate that purely passive motion, starting from a stationary double-contact and driven only by the acceleration of gravity, could effect a change of handholds, including the repositioning of the next contact arm.

Based on the similarity in action of the model with gibbon-like proportions and actual gibbon continuous contact brachiation, the model was adjusted for alternate limb lengths (individually for both pectoral and pelvic limbs) and mass distributions (pectoral, pelvic, and trunk masses) to investigate the effect of morphological features on brachiation. These simulations indicated that shorter pectoral limbs allowed successful passive brachiation, but had a substantial effect on the speed of progress. A similar conclusion was reached by Preuschoft and Demes (1984), using a simple pendulum model of swing dynamics. Longer limbs suggested that passive motion of the swing arm would not allow a successful grasp of the next contact. Although brachiation with longer arms would be possible through active (muscle-powered) motion of the swing limb, this would substantially increase the metabolic cost of brachiation. Other simulations suggested that the ratio of arm mass to body mass was important, and that the center of mass of the torso should be relatively high in the body, as was noted in gibbons (Preuschoft and Demes, 1984; Swartz, 1990).

The simulations by Yamazaki (1990) are interesting because they demonstrate the potential for much of the observed motion in brachiation to be determined by passive circumstances without direct active control. Unfortunately, the simulations do not include the main determinant of brachiation energy loss: collisional contact with the support. Instead, in the models of Yamazaki (1990), a torsional damping function is added at each joint which is responsible for all loss calculated in the simulations. Attempts were made to define joint function in a realistic

manner by making measurements on cadaveric material. It is not known either how well this function matched the properties of live gibbons (one would suspect that if it is to the advantage of gibbons to have minimal damping at their joints, this could be accomplished) or what influence collisional considerations would have had on the simulation outcomes.

Gomes and Ruina (personal communication) described an alternative simulation in which gibbon-like brachiation was used as a test case for a novel strategy for finding solutions to complex dynamic systems. The technique relies on locating solution sets for simple systems, and then tracking the solution space as single degrees of freedom are added to form more complex models. In this case, the process started with the simple point-mass model (Bertram et al., 1999), and worked through distributed mass forms with added links to finally arrive at a five-link model. This model is composed of two-component distributed-mass pectoral limbs, each with an intervening elbow joint, and these are attached to a distributed mass torso. Proportions and mass distributions of the model matched a median-size lar gibbon. Pelvic limbs as such are not included in this model, but their mass is included in the torso mass. Jungers and Stern (1984) reported a limited use of pelvic limbs in brachiation, and pointed out that Avis (1962) described the flexed leg posture as "giving the well-known impression of a furry ball hurtling through space." Provided the arms are also considered, this is an apt description of the model by Gomes and Ruina (personal communication). All joints of this model are completely freely moving and have no restriction on their range of motion. This means that motions in which the limbs spin freely around the joint in a decidedly unbiological manner are possible. In spite of the unrestricted limb motion, rotation of the arm at the shoulder "joint" occurs relative to the body, so the body remains facing in the direction of travel, as is the case for real gibbons.

The objective of the simulation is to locate periodic (repeating) solutions in which no collision occurs at the transition from one handhold to the next. Brachiation in the model of Gomes and Ruina (personal communication) is initiated by providing the system with a set of initial conditions that produce motions that satisfy these criteria. The solution-set tracking technique provides an effective means of determining what these initial conditions should be, based on the behavior of simpler systems.

This methodology was able to locate numerous continuous contact and ricochetal solutions for the five-link model. Note that these are not all paths that, if followed, describe brachiation motion. Rather, they are a set of conditions that, when initially met, will result in the spontaneous continuation of brachiation as a consequence of inertial and gravitational effects combined with passive joint influences without requiring added control or energy.

Due to the extreme mobility of the joints in this simulation, many of these mechanically possible solutions would not be available to a brachiating gibbon. However, a number of these solutions did correspond well to the observed gibbon behavior. These plausible solutions include ricochetal brachiation complete with a free-flight aerial phase between contacts. In this simulation, all arm motion occurs passively, including the repositioning of the next contact arm. The only feature that would have to be considered active is the gripping of the overhead support. Gripping is assumed to occur spontaneously when the hand contacts the support (and under the collision-free stipulation of the solution set, the hand will passively come to rest (vertical and horizontal velocity of zero) at this point).

Due to the passive periodicity of the model and the fact that the contacts are collisionless, the solution thus derived indicates an essentially cost-free mechanism of locomotion (Fig. 6). Given that such solutions are available, it would seem surprising indeed if the gibbon did not exploit these opportunities to some extent. One limitation, of course, is that the cost-free solutions depend on appropriately and evenly spaced level handholds, a condition the gibbon is not likely faced with in its natural environment. Although such cost-free solutions appear physically possible, it is observed that even under controlled laboratory conditions where even, level handholds are available, gibbon brachiation involves substantial muscular activity (Jungers and Stern, 1984). As will be discussed below, this is indicative of functional compromises that have been made to allow for an active control capacity necessary to deal with more complex (and commonly encountered) environments. This general, active capacity comes at the expense of the theoretical energy minimization potential (even when the environment for such is provided), but allows more realistic abilities within the environments the animal must be expected to naturally confront.

ACTIVE BRACHIATION MODELS

Brachiation has been an attractive problem from the robotics perspective because it entails the coordination problems of dynamic motion but does not require simultaneous balancing, i.e., the motion is self-stabilizing. Much like the value of projects in artificial intelligence for providing insights into how human intelligence operates, such robotics projects on brachiation can provide insights into the mechanical problems faced in the coordination of active brachiation.

Within dynamic control, two types of system are considered: underactuated, in which there are fewer actuators (motors) than degrees of freedom (jointed components), and overactuated, in which there are more actuators than degrees of freedom. The passive model of Gomes and Ruina (personal communication) described above is an extreme case of an underactuated system, and the real gibbon, with nu-
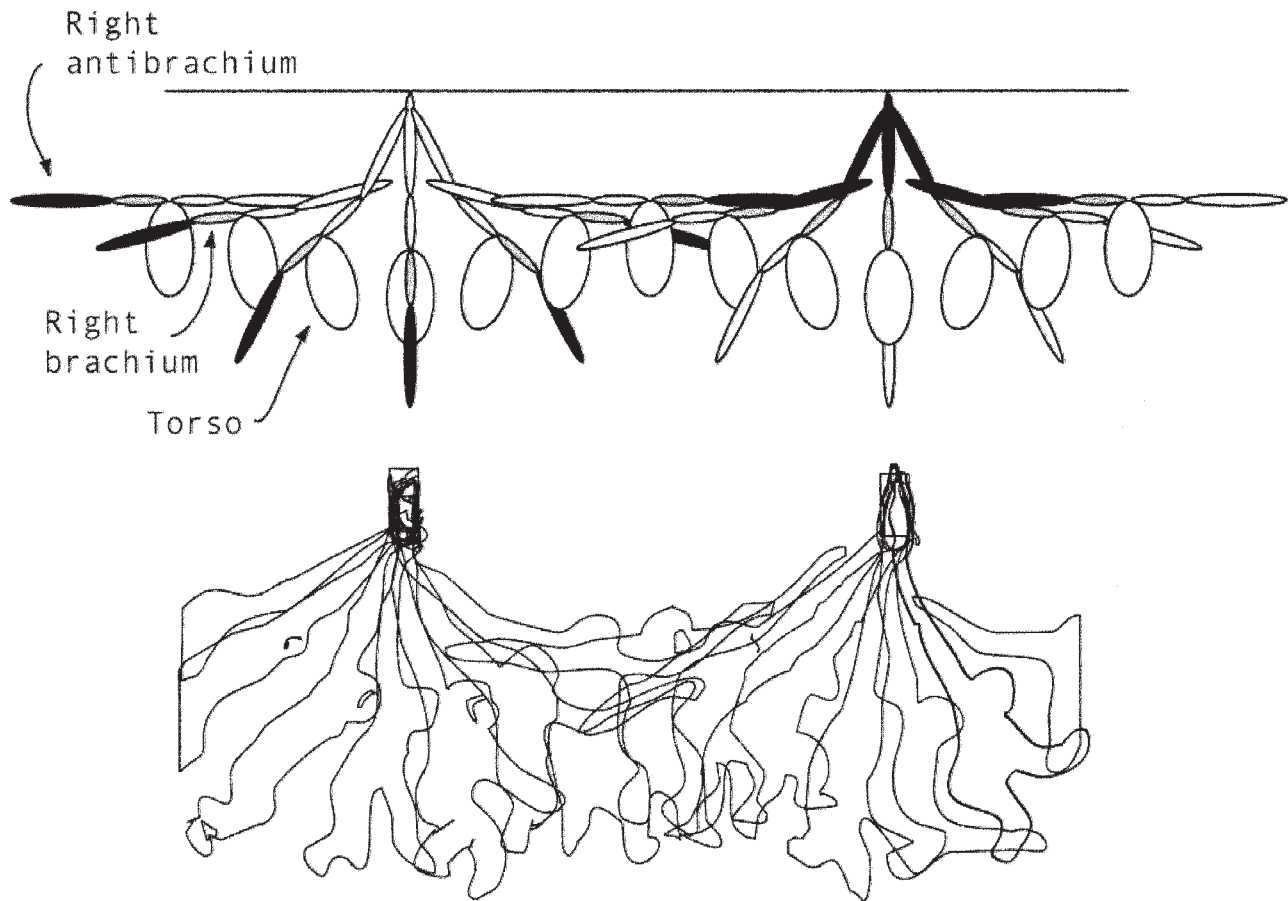
Fig. 6. Sketch of one ricochetal brachiation solution to five-link passive model of Gomes and Ruina (personal communication). In this model, all joints have complete freedom of movement, and all motions are generated passively as a result of inertial conditions determined at initiation combined with gravitational forces acting continuously throughout. "No-collision" condition is satisfied because next supporting arm swings up to superstrate as CoM descends. For appropriate initial conditions (horizontal velocity of CoM and rotational velocity of arms), "hand" reaches superstrate with zero velocity, and trajectory of CoM transitions smoothly from aerial to support phase. Below, a rough tracing (from video) of gibbon brachiating under similar circumstances is provided for comparison.

merous muscles crossing each joint, is a classic case of an overactuated system.

Fukuda et al. (1991); see also Saito et al., 1994) had success with a simple brachiating robot consisting of two rigid arms joined by a single rotating motor at the hinge. This machine is capable of moving continuously under a superstrate, and is also able to perform more complex movements as a result of its sophisticated adaptive control algorithm. The on-board controllers are capable of learning as the robot attempts to follow a target trajectory of the desired motion. The active control of the system adjusts effectively to gravitationally and inertially generated motions that may not have been anticipated in the original command set.

Saito and Fukuda (1997) extended this basic work on brachiation robotics and its dynamic control to create a three-dimensional robot with proportions that closely resemble a siamang. This system has 13 links and 12 degrees of freedom controlled by 14 motors, two of which are responsible only for grasping the superstrate (and cannot apply a controlling torque). This machine is able to initiate bra-

chiation from a stationary hanging position and continue moving beneath a horizontal series of ladder-like rungs. All brachiation in this system is of the type characterized as continuous contact.

Kajima et al. (2003) constructed an even more complex robot consisting of 19 links and 20 actuators. This highly complex machine, designated "Gorilla Robot II," was designed to be able to walk bipedally or quadrupedally and brachiate. It has the approximate proportions of a siamang and weighs 20 kg. Again using sophisticated motor learning algorithms, this machine was able to successfully achieve a full brachiation stride (two consecutive individual swings using alternating arms), and it spontaneously developed two different techniques to accomplish this: overhand and side-arm brachiation. In both cases, the machine employed substantial leg swinging to initiate the swing to the next handhold. The leg swing provides a means for the robot to generate initial position or motion conditions that make the mechanical solution of the brachiation motion more tractable. Such initial conditions to start the swing are an important part of the models

of both Yamazaki (1990) and Gomes and Ruina (personal communication). These initial motions indicate that the overactuated robotic model exploits inertial motion to assist its actively controlled brachiation swings. In Gorilla Robot II, actuated adjustments occur at each joint during motion (Kajima et al., 2003), but even for this system it is imperative that the passively generated motions be considered in the controlling strategy. This could only be avoided if the machine made a rigid contact to the overhead support, i.e., if rotation at the handhold or wrist was actively controlled.

Although impressive in its ability to accomplish even a limited degree of brachiation, Gorilla Robot II is rather ungainly in comparison to a real gibbon. Not reported in the descriptions of the systems' performance is the power requirement. Artificial machines, whether brachiator or walking machines, have the luxury of calling on whatever power requirements are necessary to accomplish the motion. It is likely that minimizing power requirements and total energetic cost are critical criteria in natural locomotion systems, including brachiation. Even with unlimited power availability, artificial systems do not perform ricochetal brachiation, although one two-link robot is capable of leaping between handholds (Nakanishi et al., 2000), which may be considered similar to a single ricochetal step. Missing from the actively controlled brachiation robots are the strategies that fully exploit the potential for passive motion and avoid unnecessary collisional losses.

BRACHIATION MECHANICS AND ECOLOGY

Modeling analyses could be interpreted as suggesting that Hylobatid evolution has stumbled onto a near perfect "perpetual motion machine" where muscle activity is not necessary and motion, once started, can continue without effort. But it is clear that as agile and acrobatic as these animals are, their locomotion requires substantial active investment. The key factor to recognize, however, is the environment in which Hylobatids operate in nature. The high canopy of the tropical forest is arguably the most three-dimensionally complex of any used by mammals. One factor that needs to be appreciated when evaluating Hylobatids and their brachiation is that every step that is taken differs from the previous one, sometimes quite substantially. This is not because of a lack of coordination on the gibbon's part, but because that is the nature of the opportunities for support provided by this unique environment. In their natural habitat, handholds will vary in horizontal and vertical distribution and resistance to applied load; this latter is a complex function of branch thickness (something that can be anticipated by the animal) and branch properties (a feature that may well come as a surprise when inadequate for the applied load). As is seen in the currently rudimentary motions of the robotic brachiators, the active component of the system allows adaptation to the support opportunities that are provided. It also allows for the muscularly mediated functions of acceleration and deceleration.

So after all this, what is the nature of gibbon locomotion? In a mechanical sense, a gibbon is a highly specialized locomotion system that is capable of exploiting low-cost opportunities for slow or fast brachiation, but that can actively modify its movement trajectory to match its imposed three-dimensionally complex environment. With an interest in recognizing what morphological features allow this function, and for the animal to exploit the canopy niche, we are now in a position to ask what key features or specific pressures could lead from a more generalist climbing/scrambling ancestor to the specialized gibbon and its capacity for dexterous brachiation? Size certainly is a critical factor, both in terms of the capacity to generate force internally and for the availability of suitable supporting structures externally (Jungers, 1984; Swartz, 1990). Longer pectoral limbs have a variety of advantages but they do not, in themselves, appear to be a determining feature of brachiation. Presumably, however, once brachiation was achieved, substantial pressure to increase the effectiveness of the system would result in elongate limbs. As was mentioned, this applies to both pectoral and pelvic limbs: even though the pelvic limbs are not employed for support in brachiation, their action can influence several aspects of brachiation motion. Yamazaki (1990) argued that specific distributions of mass and the balance between pectoral limb, pelvic limb, and trunk mass are determining characteristics for effective brachiation. Analysis of both simple (Bertram et al., 1999) and more complex (Gomes and Ruina, personal communication) simulations suggest that low-cost and effective brachiation is likely possible for a relatively wide range of mass distributions, but that each specific distribution will determine the options available within the repertoire of possible motions. Presumably as analysis progresses, the match between specific Hylobatid proportions and their environment will be explained. It was recognized, for instance, that sympatric populations of smaller lar gibbons and larger siamangs utilize different components of the canopy (Palombit, 1997).

If brachiation is so easy to accomplish and has such a high potential for low-cost movement, why has it been exploited by so few species? This locomotion mode is extremely well-suited to an environment composed of a network of overhead handholds, but this environment is relatively rare. It exists currently only in Southeast Asia, the Amazon basin of South America, and tropical Africa. The Hylobatids have exploited the niche in Southeast Asia and the Atelines in Amazonia. The African tropical canopy may have been disturbed by repeated climatic fluctuations, making it less than ideal to sustain an appropriate habitat. However, evidence exists that brachiating apes existed in this environment in the past (Andrews and Simons, 1977). When

the appropriate environment is available, it would appear that the advantages of this mode of locomotion are encouraging enough to stimulate its exploitation.

CONCLUSIONS

This review has attempted to provide a conceptual description of two features of brachiation mechanics that have gone largely neglected by anthropologists trying to understand brachiation: its function, and the morphological factors that allow for it. These features are collisional energy loss, identified as the major factor of mechanical cost in brachiation, and the potential for passively sustained spontaneous motion, even for apparently complex motions such as ricochetal brachiation. This review attempted to demonstrate the importance of these two factors in interpreting brachiation and the adaptations necessary (or not) to provide the basis for this unique style of locomotion. It did not focus on the substantial literature involving the documentation of muscle activity. Although numerous studies of this type exist, they are difficult to interpret within the context of the two mechanical factors that are the primary focus of this review, since this perspective was not available when the muscle activity studies (and their conclusions) were generated.

This review also attempted to describe brachiation mechanics within the context of the ecology and environment of the animals that utilize this style of locomotion. The ultimate goal of studies such as those described herein would be to fully understand the mechanical possibilities and constraints operating on brachiators and their morphology. As suspected by primate morphologists for some time, there exists a relationship between the form and the environment that brachiators operate within. Determining the details of this relationship, however, will depend on working from a firm understanding of the basis of brachiation mechanics; and it was to contribute to the foundation of such future investigations that this review was formulated.

ACKNOWLEDGMENTS

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