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Understanding brachiation: insight from a collisional perspective

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Summary

Gibbons are able to brachiate effectively through the forest canopy with a suspended swinging motion *via* contact with handholds. The swing phase is unlikely to be a cause of significant energy loss as pendulums are able to oscillate with only gradual mechanical energy dissipation. We consider the energetics associated with the transition of either a swing (during continuous-contact brachiation) or a ballistic flight (ricochetal brachiation) to a subsequent swing. In both styles of brachiation, kinematic data suggest that a gibbon overshoots the path that would allow a smooth transition into the swing phase. The sudden change in velocity due to such an overshoot is associated with a collision. Assuming neither the handhold nor the gibbon stores elastic strain energy, the energetic consequences of such overshoots can be calculated.

We suggest two reasons for overshooting smooth transition trajectories: in the case of continuous contact brachiation, excess mechanical energy can be maintained with a high amplitude swing, and an overshoot during ricochetal brachiation produces a safety margin.

The degree of energy loss with the transition to the swing phase is dependent both on the alignment of the pre- and post-transition paths, and on the kinetic energy at that instant. Active mechanisms reduce the effects of overshoots in both brachiation gaits. During continuous-contact brachiation, the path of the centre of mass can be controlled actively by flexion both of the trailing arm and the legs. During ricochetal brachiation, the length between the hand and the centre of mass (determining the subsequent swing path) can be controlled throughout the flight phase with leg flexion/extension. In addition, the elongated arms characteristic of gibbons improves the geometry of a collision for a given overshoot, and so may be viewed as a morphological adaptation reducing the energetic losses caused by overshooting for safety.

Key words: Gibbon, locomotion, collision, energy, pendulum, *Hylobates lar*.

Introduction

The gibbons and siamang are able to locomote quickly and effectively through the forest canopy by brachiation. Two distinct gaits of brachiation can be described, related to both speed and handhold spacing. Swinging beneath a series of handholds with a duty factor above 0.5 is termed 'continuous-contact' brachiation, and is characteristic of slow brachiation with close handhold spacing. Brachiation where periods without contact with the superstrate occur, resulting in a duty factor of less than 0.5, is termed 'ricochetal' brachiation. This gait is necessary for large handhold spacings, but may also be used for fast brachiation even with closely spaced handholds. Both brachiation gaits include a 'swing phase', when the body is connected to the superstrate by a single arm. Dividing the swing phases is either 'double-contact' (for the continuous-contact gait), during which handholds are gripped by both hands, or a 'flight' phase (for ricochetal brachiation), during which the body mass follows an approximately parabolic path.

Previous work on brachiation has largely focussed on the mechanics of the swing (Fleagle, 1974; Preuschoft and Demes, 1984; Swartz, 1989; Turnquist et al., 1999; Chang et al., 2000; Usherwood et al., 2003), occasionally including an intervening ballistic flight (Bertram et al., 1999). While the mechanics and equations governing pendulum-like swinging and ballistic flight are familiar, neither suggests significant sources of energetic loss.

This study highlights the mechanics and implications associated with connecting two swing phases (continuous contact) or a flight and a swing phase (ricochetal), focussing on the consequences of inelastic collision at contact with new handholds. Expressions are developed for energetic losses due to inelastic collision in brachiation for both point-mass and distributed-mass cases. Two point-mass models are presented that highlight the effects of missing 'ideal' contact conditions. Model 1 uses starting conditions derived from observed kinematics of gibbons brachiating under a range of controlled conditions described in previous studies (Chang et al., 1997; Bertram et al., 1999; Chang et al., 2000; Usherwood et al., 2003). Active trailing-arm flexion and leg-lifting (deviations from passive brachiation) are discussed as potential strategies for collision energy-loss reduction during brachiation. Model

2 presents a simple point-mass model for the energetic consequences of collision given a range of ‘overshoot’ distances, and mass to handhold length. It is used as a novel account for the pressure towards arm elongation in specialist brachiators: we suggest that the long arms characteristic of gibbons act to reduce collision losses associated with ‘safe’ brachiation. The principles of the jointed-body form of Model 2 provide a qualitative description of the benefits of the ‘double pendulum’ kinematics typical of fast ricochetal brachiation as a behaviour to reduce collisional energy loss resulting from an overshoot of the handhold.

Gibbons as pendulums

Previous analyses of brachiation have generally focussed on the pendulum-like behaviour of the gibbon body swinging beneath a handhold while supported by a passive, stiff, arm (Fleagle, 1974; Preuschoft and Demes, 1984; Swartz, 1989; Turnquist et al., 1999). Such studies show that the swing-phase of both continuous-contact and slow ricochetal brachiation acts mechanically as a simple pendulum. At higher velocities, with fast ricochetal brachiation, the arm and body acts more as a double or more complex pendulum (Bertram and Chang, 2001); during the swing phase, the arm and shoulder rotate about the handhold, while the hips and body rotate about the shoulder. Deviations from simple, or complex, *passive* pendulum behaviour can be informative about energy input to a ‘brachiating system’ (Usherwood et al., 2003). The energy losses from a pendulum-like gibbon cited by Jungers and Stern (1984) of aerodynamics or internal friction are slight (a gently swinging pendulum of 1 m length and 10 kg mass loses energy slowly, at less than 1% per swing cycle; our empirical observation), and the particulars of the pendulum (arm length, mass distribution etc.) are unlikely to increase such energy losses beyond the negligible. Mechanisms by which mechanical energy can be gained or lost are discussed in Usherwood et al. (2003). In addition, in brachiation, velocity is *not* constrained to zero at the beginning or end of the contact (swinging) phase. So, unlike clock-like pendulum behaviour, pendulum mechanics provides no limitations on locomotion speed.

Brachiation by analogy with terrestrial gaits

Continuous-contact brachiation can be considered mechanically as analogous to bipedal walking, where pendular exchange between potential and kinetic energies dominate (e.g. Cavagna and Keneko, 1977). Unlike bipedal running, however, high speed ricochetal brachiation does not appear to be dominated by spring-based mechanics. Instead, ricochetal brachiation typically involves complex motions, including rotation of the body about the shoulder joint. In such cases, the gibbon becomes a jointed pendulum, suspended from the handhold by an outstretched pectoral limb (Bertram and Chang, 2001). In this motion there is no indication of extensive elastic energy storage, although some use of the elastic characteristics of the branches used as a superstrate should not be completely discounted.

Based on our previous work (Chang et al., 2000; Bertram et al., 1999) and the absence of obvious elastic structures, ricochetal brachiation is not viewed here as the analogue of the bouncing gait of terrestrial running. Instead, brachiation is considered mechanically more analogous to the skipping of a stone across water, where the path of the stone is altered by interaction with the surface in a manner that resembles bouncing, but does not involve spring-like energy storage and recovery. Re-orientation of the velocity of the centre of mass (CoM) is achieved by inelastic collisions with non-deflecting handholds in much the same way as interaction with the water surface reorientates the travel of the skipping stone without removing all of its velocity.

Collision in brachiation

The role of inelastic collision in terrestrial walking is becoming increasingly recognised, both in terms of energy loss, and in loss reduction (McGeer, 1990; Garcia et al., 1998; Kuo, 2001; Donelan et al., 2002). The physics of inelastic collision also appear applicable to both continuous-contact brachiation and ricochetal brachiation, as neither gait involves extensive elastic energy storage. Dissipation of mechanical energy must be associated with a deflection in the same direction as an applied force (‘negative work’), both of which can be directly observable (an approach adopted by Usherwood et al., in press). An inelastic collision would result in such a force and deflection (whether in the handhold, or somewhere in the gibbon body, is not predicted), and this negative work may be spread over a finite time (see Donelan et al., 2002); energy loss due to collision, and the initiation of the swing phase, need not be instantaneous. Given that inelastic collision may not be the sole cause of mechanical energy dissipation – energy may be lost from a smoothly swinging pendulum if it is allowed to extend, or if a moment is applied opposing the direction of rotation – a direct assessment of energy losses due to collision is impossible, even from accurate force measurements at the handhold. However, the geometry and energetic consequences of collision, which we assume to be largely inelastic, can be inferred from the path of the gibbon mass at the initiation of a swing phase. We believe that the management of collisional energy loss during brachiation influences the mechanics of this animal, and must be considered in order to truly understand both the constraints of brachiation, and the opportunities that this hylobatid’s unique morphology and behaviour exploit. Below we describe simple expressions for point-mass energetic losses due to inelastic collision appropriate for brachiation.

Point mass description of collision losses in brachiation

The velocity (V') of a point centre of mass an instant after colliding with a rigid superstrate using an inextensible, inelastic arm, depends on the velocity the moment before (V), and the angle β subtended between the ballistic path and the support at that instant (Fig. 1):

$$\frac{V'}{V} = \sin(\beta)\,. \tag{1}$$

Thus, kinetic energy directly after collision (KE'), as a proportion of the available kinetic energy the instant before (KE), is given by:

$$\frac{KE'}{KE} = \left(\frac{V'}{V}\right)^2 = (\sin\beta)^2\,. \quad (2)$$

The proportion of the total initial (kinetic and potential) 'brachiation energy' E lost is thus:

$$\frac{\Delta KE}{E} = \frac{KE - KE(\sin\beta)^2}{E}\,. \quad (3)$$

This agrees with the point-mass model presented by Bertram et al. (1999), which describes ideal paths that avoid all losses due to collision: contact can be made with a new handhold without collision losses *only* if kinetic energy is zero, or if the paths are perfectly matched, and so β equals π/2. This description of inelastic tension-collision also accounts for the sudden jolt familiar to over-eager children playing on swings. If a child swings too high, allowing the swing rope to become loose, then the jerk as the rope becomes taught again is related to the changes in velocity described in Equation 1, and can cause some discomfort associated with the inevitable, and potentially substantial, dissipation of kinetic energy.

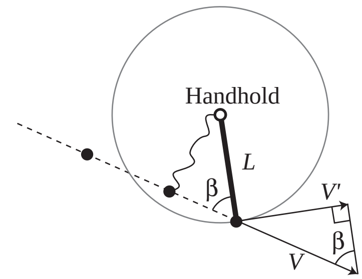


Fig. 1. The path of a point mass (filled circles) with a support able to oppose forces only in tension as it moves past a rigid handhold. The path of the mass prior to collision is indicated by the broken line; the straight, rigid mass-handhold connection at the moment of collision by the bold line; the velocity vectors relating to the velocity of the mass an instant before (V) and after (V') collision, by the straight arrows; and the arc described by the handhold-centre of mass length L about the handhold as a large circle.

The energetics of inelastic collision beyond the point-mass view

The above concept can be extended more generally, beyond a point-mass view of inelastic collision in ricochetal brachiation. The principles of inelastic collision result in conservation of momentum (both linear and angular, though see below) while allowing energy to be dissipated. The point-mass model supposes that the velocity vector of the point mass suddenly changes direction on contact, losing the entire component of velocity orientated along the arm (the velocity given to the Earth satisfies the conservation of linear momentum, but can be ignored). If no torque is applied about the handhold [supported by both gibbon anatomy (Jenkins, 1981) and direct measurements (Chang et al., 2000)], then the angular momentum of the gibbon about the handhold is maintained throughout the instant of collision. Thus, a second way of viewing the energetics of collision is in terms of angular and linear momentum, and their associated energies. Immediately after collision, angular momentum about the handhold is conserved (there being no torques about the handhold) but translational momentum is not (using this frame of reference – the slight increase in velocity of the massive Earth is not considered). Thus, ignoring (for the moment) gravity and any changes in gibbon shape at the instant of collision, the rotational kinetic energy associated with motion about (or past) the handhold is unaffected by collision. However, the component of kinetic energy associated with translation towards or away from the handhold prior to collision is lost. Thus, the energy loss due to collision is the difference between the total kinetic energy prior to collision, and the kinetic energy associated with motion about (past) the handhold prior (=post) collision. This can be used in a general method of stating the no-collision-loss conditions described by Bertram et al. (1999): no energy is lost if collision occurs at the instant of zero kinetic energy; and no collision loss occurs if the total kinetic energy equates to the rotational kinetic energy associated with motion about (equivalent, at that instant, to motion past) the new handhold (i.e. there is no motion towards, or away from, the handhold). Hence this represents a form of the path-matching criterion that extends beyond the point-mass view.

Error, safety and overshoot in ricochetal brachiation

Any movement towards a target is subject to a certain degree of error. Ricochetal brachiation is unusual in locomotion in that the consequences of an error in trajectory are highly dependent upon the direction of the error: a small overshoot results in an imperfect contact, and some collisional energy losses, whereas a small undershoot of the handhold results in a complete miss, a subsequent fall, and high likelihood of injury or death. We develop a simple point-mass model (Model 2) of energetic losses due to collision during ricochetal brachiation that allows for a degree of 'overshoot' e of the ideal contact path. This model is then used to quantify the energetic consequences of such an overshoot. The results suggest that this provides a previously unrecognised pressure towards arm elongation as an adaptation for collision reduction in ricochetal brachiation.

Models and methods

Two models were developed to demonstrate the potential energetic losses associated with inelastic collisions during brachiation. Both models were based on the expressions for collision losses of point-masses as described above. The behaviours and morphology that may be associated with amelioration of collision effects are examined below, based on the results of these simulations.

Parameters for Model 1 were derived from video observation of brachiation from slow, continuous-contact, to fast, richochetal brachiation (Table 1). For each case, the range of possible paths given the observed 'brachiation energy' state was calculated, where brachiation energy was defined as the mechanical energy available from the first of two brachiation

Table 1. *Parameters for Model 1*

Example Run	Figs	Style	Inter-handhold spacing *D* (m)	Mass *m* (kg)	Handhold-*CoM* length *L* (m)	Max. *PE* (J)	*KE* at max. *PE* (J)
A	4	cc	1.2	7.95	0.77	45.07	0
B	2,5	cc	1.2	7.95	*L*, 0.93; *L′*, 0.79	56.33	0
C	6	ric	1.93	7.95	0.71	38.79	21.87

CoM, centre of mass; *PE*, potential energy; *KE*, kinetic energy.

Style refers to brachiation technique: cc, continuous-contact brachiation; ric, ricochetal brachiation.

Example Run B shows parameters for two conditions: *L*, the *CoM* to handhold length observed for the first swing; *L′*, that observed at the bottom of the second.

'steps'. The energetic consequences of collision are presented for each potential path, and are related to release timing.

Model 2 is a development of the general case for point-mass brachiation collision losses for a range of 'overshoot' distances. The expressions include the handhold to centre of mass (CoM) length *L*, and suggest an energetic pressure towards arm elongation amongst specialist brachiators.

Model 1

Point-mass ballistic paths and their collision consequences due to release angle (timing): parameters derived from gibbon observation.

A captive, adult, female white-handed gibbon *Hylobates lar* L. was filmed brachiating freely in the animal facility of the Department of Anatomy, Stony Brook University, as reported in previous studies (Chang et al., 1997, 2000; Bertram et al., 1999; Usherwood et al., 2003). A series of aligned handholds at constant height were placed to encourage brachiation perpendicular to the plane of the video camera (Sony CCD/RGB). Handhold spacing (D) was altered between trials in order to induce a range of brachiation styles, from continuous-contact (D=1.2 m) to extreme ricochetal (D=1.93 m, the maximum spacing in which two handholds could be viewed with the camera). Video sequences were digitised of brachiation past two handholds. Every fifth field was traced using Adobe software, providing a constant interval between images of 0.083 s. Three example runs are presented here. Centres of body mass CoM were estimated from the tracings. With the support arm extended and the legs folded, the CoM was judged to lie just below the pectoral girdle, following the morphological observations of Preuschoft and Demes (1984), and the kinetics described by Chang and Bertram (Chang et al., 1997; Bertram and Chang, 2001). With the legs extended, the centre of mass was assumed to move distally, to halfway down the trunk (a reasonable approximation for use in this model to demonstrate the potential effects of leg extension; however, not a highly accurate quantitative assessment). The relevant length between contact handhold and estimated centre of mass (L) was then calculated for the bottom of the first swing (Fig. 2). In one instance (Example Run B) the distance between the second handhold and the estimated position of the centre of mass at the bottom of the second swing was also determined, providing a second value of L, L′, useful in demonstrating the effects of a 'leg-lift'.

The total initial 'brachiation energy' *E* was calculated from the sum of kinetic and potential energies measured at the end (top) of the first swing. The bottom point of the first swing was defined as zero potential energy, at which point all mechanical energy was assumed to be in the form of kinetic energy. This method of determining the energy state of the motion maximises accuracy, as the body moves slowest at the highest point in the cycle, thus centres of mass can be estimated most accurately. Relevant parameters for the three Example Runs are shown in Table 1.

Model 1 construction

For each of three Example Runs, the consequences of a range of potential release angles Θ (the angle between CoM, handhold, and vertical; see Fig. 2C) were calculated. If the swing phase was passive, then the empirically observed 'brachiation energy' for the highest position was also the kinetic energy at the bottom of the first swing. The range of ballistic flight paths available for each Example Run was calculated numerically (using *G* in LabVIEW 5.1, National Instruments, Austin, TX, USA). Release at Θ=0, when the support arm was vertical, resulted initially in a horizontal path of the point-CoM, which dropped immediately in a parabolic path, under the influence of gravity. The velocity V_θ at any angle θ (up to the 'potential release angle' Θ) was calculated from the remaining kinetic energy *KE*, as progressively more brachiation energy *E* became converted to potential energy *PE* during the swing:

$$KE = E - PE\,, \tag{4}$$

$$V_\theta = \sqrt{\frac{2[E - m\boldsymbol{g}L(1-\cos\theta)]}{m}}\,, \tag{5}$$

where *m* is the body mass, ***g*** is acceleration due to gravity, and *L* is the distance from the point centre of mass to the handhold. The kinetic energy, and so velocity, of the mass fell as the body swung upwards (increasing θ); a larger proportion of the brachiation energy became potential energy.

The direction of the velocity vector at each potential release

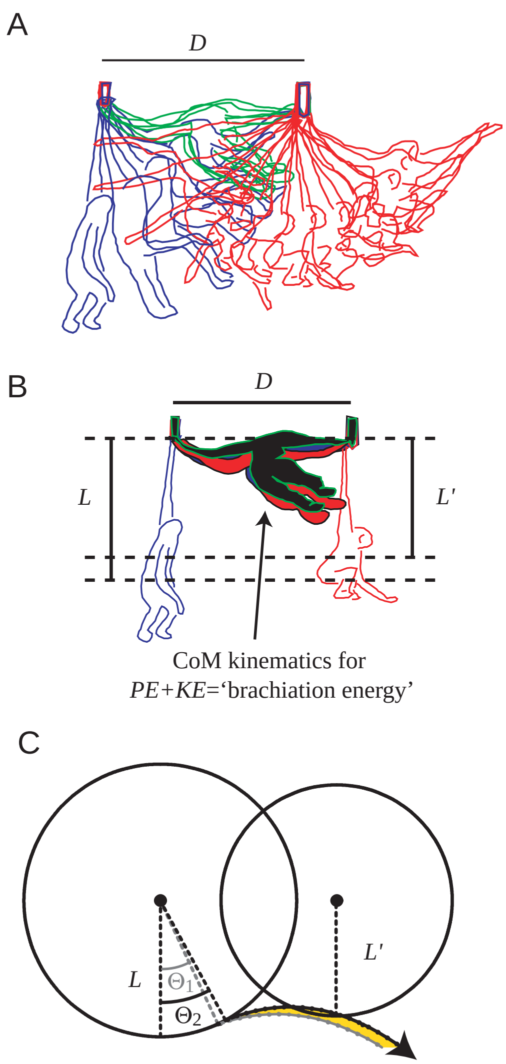


Fig. 2. Parameters required for Model 1 demonstrated using kinematics of Example Run B. The kinematics (A) show tracings of a brachiating gibbon derived from video recordings at 0.083 s intervals. Blue outlines indicate contact with the first handhold, green, contact with both handholds and red, contact with the second handhold. The centre of mass (CoM)-handhold distance L is taken from the bottom of the first swing (B). A second value of L relating to the CoM to handhold distance at the bottom of the second swing is shown as L', and its consequences are displayed in Fig. 5. (C) Two potential release angles, Θ_1 and Θ_2, and their resulting ballistic paths. The grey arc displays the result of release at the earlier, lower angle, Θ_1, which results in a narrow miss of the contact circle. At the later, higher release angle, Θ_2, the contact circle is overlapped. Between these two release angles, and their subsequent arcs, lies a strategy that results in 'ideal' contact, with path-matching resulting in zero collision loss. Such ideal paths are highlighted in yellow throughout.

position lay parallel to the arc described by the CoM-hand length L about the first handhold. Simple ballistic paths were calculated (assuming gravity to be 9.81 m s^{-1}, and neglecting aerodynamic forces), and used to provide the kinematics at overlap with an arc described by the appropriate length about the second handhold (in most cases taken to be the same value of L, but see below). Those paths that would result in a tension-collision with the second arm, along with the geometry of the second arc at that point, were used to determine the collision characteristics of the point-mass model as in Equations 1–3. Any energy levels or release angles that resulted in a total miss of the second handhold were excluded from consideration.

Each release angle Θ was also related to a release timing t_{rel}, as measured from the moment at which the centre of mass was directly beneath the first handhold:

$$t_{rel} = \int_{\theta=0}^{\theta=\Theta} \frac{L}{V_\theta} \, d\theta \,, \qquad (6)$$

where $d\theta$ is a small change in θ. Thus, the consequences of collision can be related to both the release angle and release timing.

Model 2
Consequences of arm length on collision with overshoot

The energetic consequences of some overshoot distance e of the 'ideal', no-loss ballistic path described by Bertram et al. (1999), whether attributed to error due to unpredictable environmental or biological variability, or a safety strategy, can be calculated for a point-mass brachiation collision. The geometry of collision (Equation 1) depends on both the magnitude of 'overshoot' and hand to CoM length L (Fig. 3):

$$\frac{V'}{V} = (\sin\beta) = \frac{L-e}{L} \,. \qquad (7)$$

Focussing specifically on the collision interaction, and ignoring gravity, Equations 2, 3 and 7 combine to give an expression for proportional energy loss due to an overshoot:

$$\frac{\Delta E}{E} = 1 - \left(\frac{L-e}{L}\right)^2 . \qquad (8)$$

Results and Discussion

Overview of Model 1 outcomes

Zero-collision-loss trajectories are not observed for either continuous-contact or ricochetal brachiation. Observed deviations from the passive case presented with Model 1 suggest active mechanisms (the trailing-arm-bend and leg-lift) that may act to limit the energy losses associated with brachiation, hypothesised as being constrained either by conservation of excess mechanical energy (continuous-contact), or by safety (ricochetal).

Excess energy in continuous-contact brachiation

In Example Runs A and B, displayed in Figs 4 and 5, the brachiation energy of the first swing is considerably greater than the minimum required to allow contact to be made with the second handhold. In both cases the first swing continues well past the intersection of the two arcs defined by L (see kinematics shown in Figs 2A and 4A); in both cases energy is

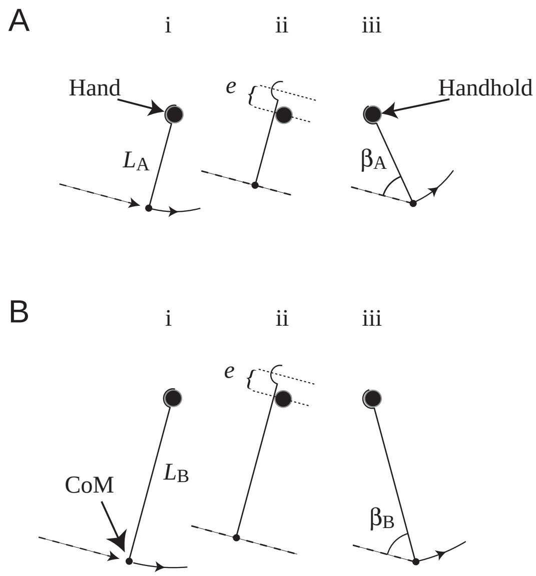


Fig. 3. Geometry for Model 2, a point-mass model for the energy loss due to collision for a range of overshoots *e* and handhold-centre of mass (CoM) lengths *L*. A point-CoM and an extended, rigid connection to the hand, are shown. The path prior to collision is indicated by a broken line. (i) The geometry of collision for short (A) and long (B) arms at ideal, no-loss contact, (ii) before collision but with an overshoot, and (iii) at the moment of collision, given an overshoot *e*. Collision angles (β) related to contact with shorter handhold-CoM lengths (both indicated with subscript A) are smaller than those related to contact with longer handhold-CoM lengths (subscript B).

clearly *not* lost deliberately to allow a zero-collision contact due to zero kinetic energy (Equation 3). This observation makes sense from the perspective of the brachiating animal: maintaining a high energy level resulting from previous actions, and suffering the consequences of higher collision losses, preserves more energy than 'dumping' the energy to achieve zero kinetic energy at contact.

In Fig. 4D the energetic consequences of a range of release angles for a passive system with constant *L* and appropriate initial brachiation energy are modelled. At release angles below 20° the ballistic path of the CoM is such that contact with the second handhold cannot be made, and would result in a fall with whatever negative consequences that would ensue. Release angles of 20–29° (an interval of approximately 40 ms), would allow completely passive brachiation with collision losses lower than those associated with any subsequent release. The fact that the time-window for this region is so small, and the cost of falling if release is too early is so large, may account for the usual decision (based on observations of the gibbons using the laboratory apparatus in this analysis) to extend the contact period, and overshoot the 'ideal' contact conditions slightly. However, it should be noted that ricochetal brachiation between even close handholds can be observed, so it would be unwise to suggest undue limitations on gibbon performance. Also, the energetic losses due to collision with delayed release may be overestimated. The model only calculates the losses for a passively brachiating system: in reality gibbons are active systems, and collision losses may be considerably reduced by a variety of active mechanisms. Some of these are discussed below.

Trailing-arm-bend in continuous-contact brachiation

Level, continuous-contact brachiation typically involves an arm-bend of the trailing arm while it remains in contact with the previous handhold, as shown in Example Runs A and B (Figs 2B, 4A,C). This trailing-arm-bend appears to be associated with active muscular forces (Usherwood et al., 2003), which act to pull the CoM backwards, towards the first handhold, and results in a characteristic looping path of the CoM. The action may reduce the energetic losses due to collision by two mechanisms. First, it may allow the path of the CoM to be connected to the arc described by the second *L* while the mass is moving slowly, with almost all energy converted to potential. It may also allow the path of the CoM to be actively adjusted to one with a more favourable angle when the tension connection is established with the second swing path. Thus a small amount of active muscular effort may help in the avoidance of large collision losses during continuous-contact brachiation. Using this strategy, excess mechanical energy from one swing can be carried to the next, and the deliberate loss of energy prior to a collision is unnecessary.

Leg-lift

A leg-lift can also affect collision energy losses (Example Run B; Fig. 5). While the trailing-arm-bend beneficially alters the path of the CoM to match that of the second arc, the leg-lift can also actively alter the relevant contact arc about the second handhold. This can result in improvements both in collision geometry, and a reduction in the amount of kinetic energy available to be lost, as a greater component of the brachiation energy is in the form of potential energy at the instant of collision. Together these account for the lower energy loss shown in Fig. 5D compared with Fig. 5B, the difference resulting from the shift in the CoM caused by the leg-bend, and the use of *L′* (0.79 m) instead of *L* (0.93 m) for the second arc in the model. This leg-bend can be achieved when the body approaches a horizontal orientation, and so energy is not deliberately put in to the 'brachiating system' *per se*, unlike the alternative case described by Fleagle (1974) for continuous-contact brachiation, and Usherwood et al. (2003) for the ricochetal gait. Instead, the leg-lift can simply provide a way of shortening the distance between CoM and hand.

The control of hand to CoM length could also be achieved with a flexion of the newly supporting arm. In a passive brachiating system, without mechanical energy input or removal, the CoM cannot move towards (implying an energy input) or away from (losing energy) the handhold while the arm is loaded (Usherwood et al., 2003). Passive brachiation while maintaining a knee-lift, or a flexed support arm, posture

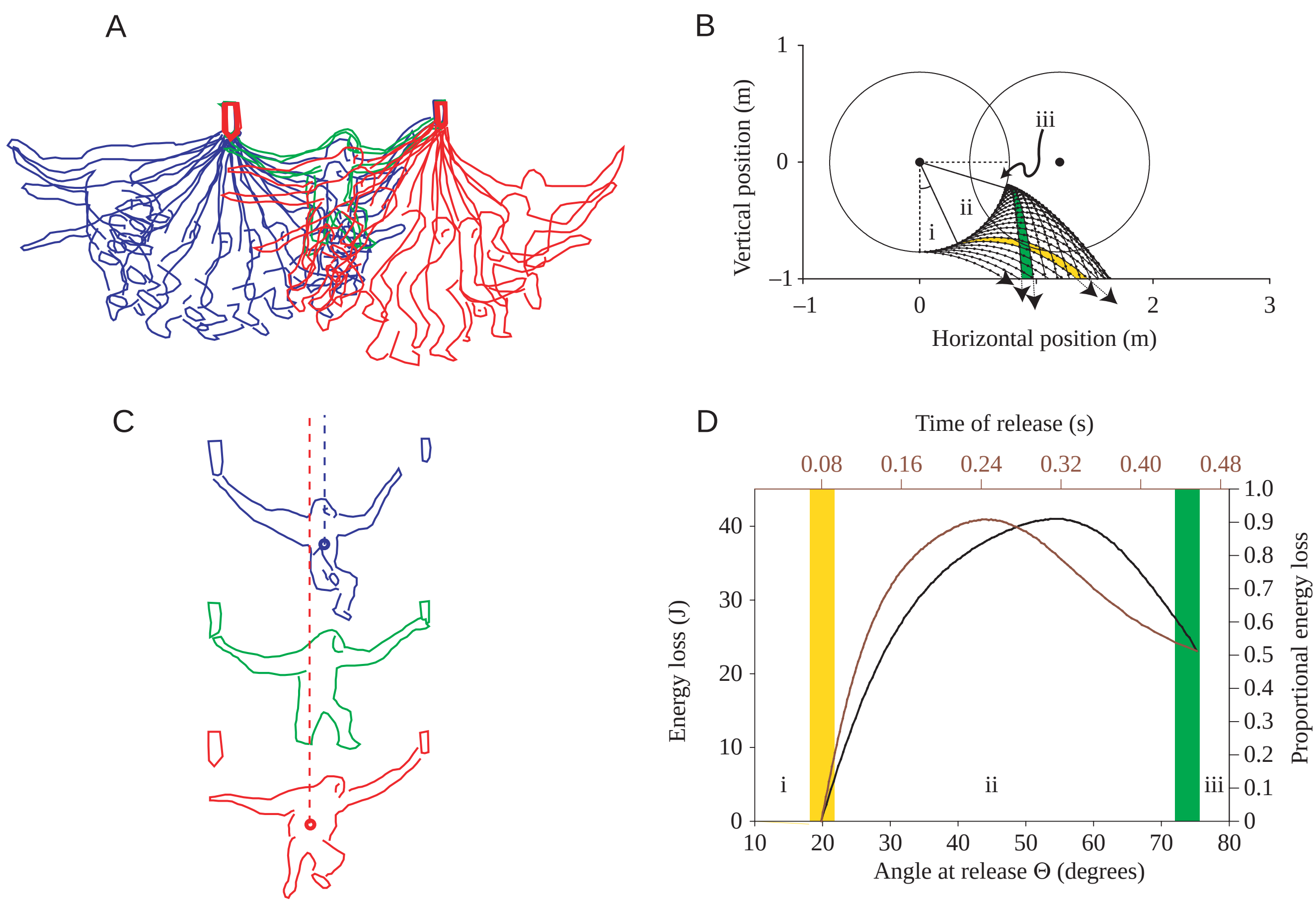


Fig. 4. Model 1 for simple continuous-contact brachiation with D=1.2 m. (A) Kinematics show tracings derived from video recordings at 0.083 s intervals. Blue outlines indicate contact with the first handhold, green, contact with both handholds, and red, contact with the second handhold. (B) The range of ballistic paths relating to Θ=0° to Θ=90°, given the observed brachiation energy. Each arc represents a separate trajectory due to differing angles of release: steeper arcs relate to later (higher release angle) releases, with lower release velocities due to the conversion of kinetic energy into potential through the swing. Arrows highlight the final direction of selected trajectories. The potential release angles can be put into three groups: (i) 'early release', leading to a path that does not intersect with an arc described by L about the second handhold (i.e. a fall); (ii) 'adequate release' resulting in ballistic paths that allow contact with the second handhold, albeit with some collision energy loss; and (iii) those angles that cannot be achieved because the required potential energy would be greater than the total mechanical energy of the gibbon. The underlying yellow regions (B,D) denotes the 'ideal', zero-collision-loss strategy. The underlying green shading (B,D) denotes the consequences of release at the maximum height possible for the observed energy. (C) Tracings before (blue), at (green) and beyond (red) double contact are aligned vertically to show the backwards movement of the centre of mass at the top of the swing. Broken lines indicate the approximate position of the centre of mass, and suggest a 'loop-the-loop' path due in part to the active flexion of the trailing arm. (D) The energetic consequences of collision are shown in alternative forms. The y-axes show energy loss in absolute terms, or proportional to 'brachiation energy', which relate directly. The x-axes show the release conditions, either in terms of release angle (bottom) or time of release (top). The x-axes, however, do not relate directly: there is a greater time difference between angles of release at higher angles, as the mass moves more slowly, due to conversion of kinetic to potential energy. Energy loss relating to 'angle at release' is shown in black, that relating to 'time of release' is indicated in dark red. Regions marked (i)–(iii) correspond in B and D.

throughout the swing would result in identical (zero) mechanical work. However, the metabolic costs of, or the absolute capability to perform, the two strategies may differ dramatically. The isometric forces associated with opposing tension throughout the swing are dependent on gravity, the angular velocity of the swing, and the mass distribution distal to the element under consideration. The tension force T_r experienced by any part of a swinging body of length R at a distance from the handhold r' (while maintaining a constant shape) and an angular velocity ω is given by:

$$T_r = \int_{r=r'}^{r=R} m_r(\boldsymbol{g}\cos\phi + \omega^2 r)\mathrm{d}r\,, \qquad (9)$$

where r is the distance of the element (of length dr and local mass per length element m_r) from the handhold, ϕ is the angle from the vertical and $\boldsymbol{g}$ the acceleration due to gravity. The terms $\boldsymbol{g}\cos\phi$ and $\omega^2 r$ show the components due to gravity and centripetal acceleration, respectively. Thus, the isometric muscle forces required to maintain a posture (and allow mechanically passive brachiation) would be greater about

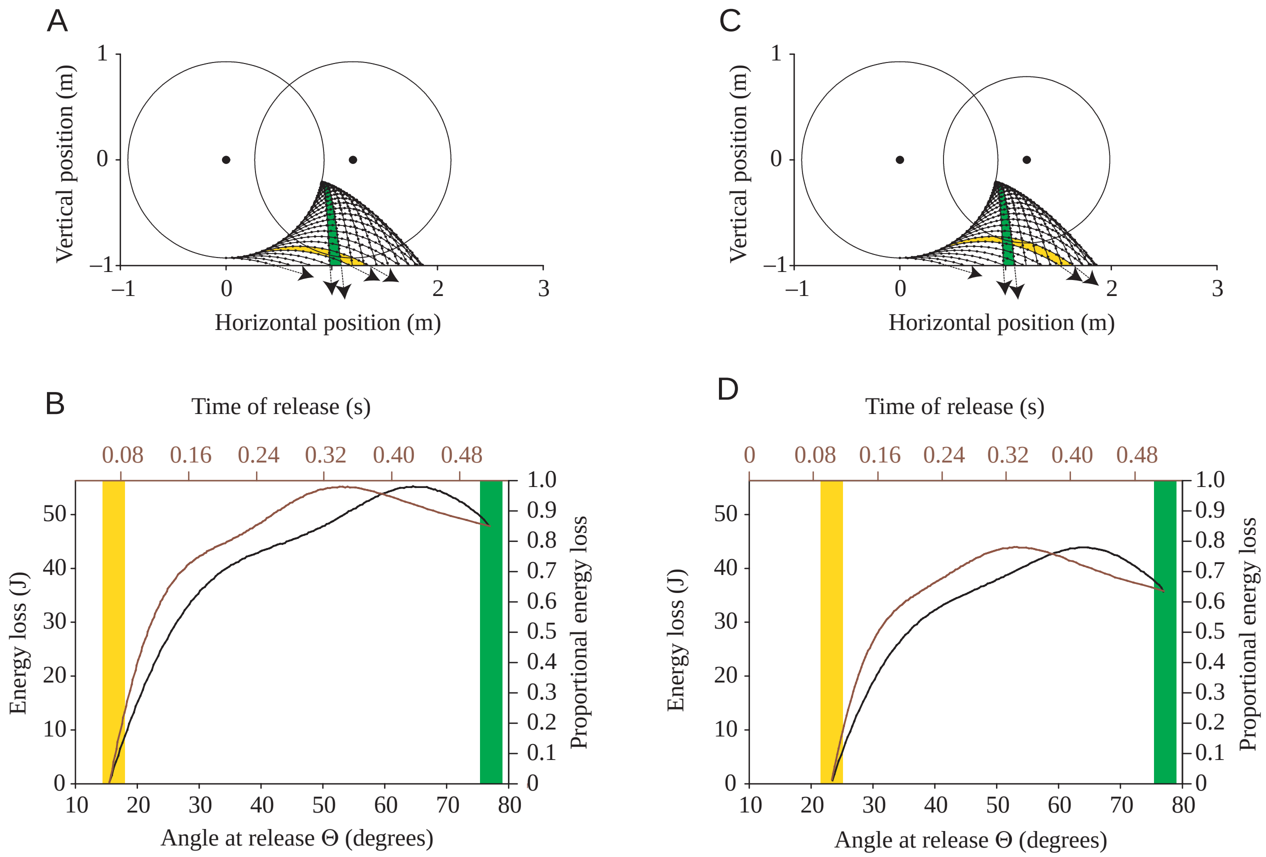


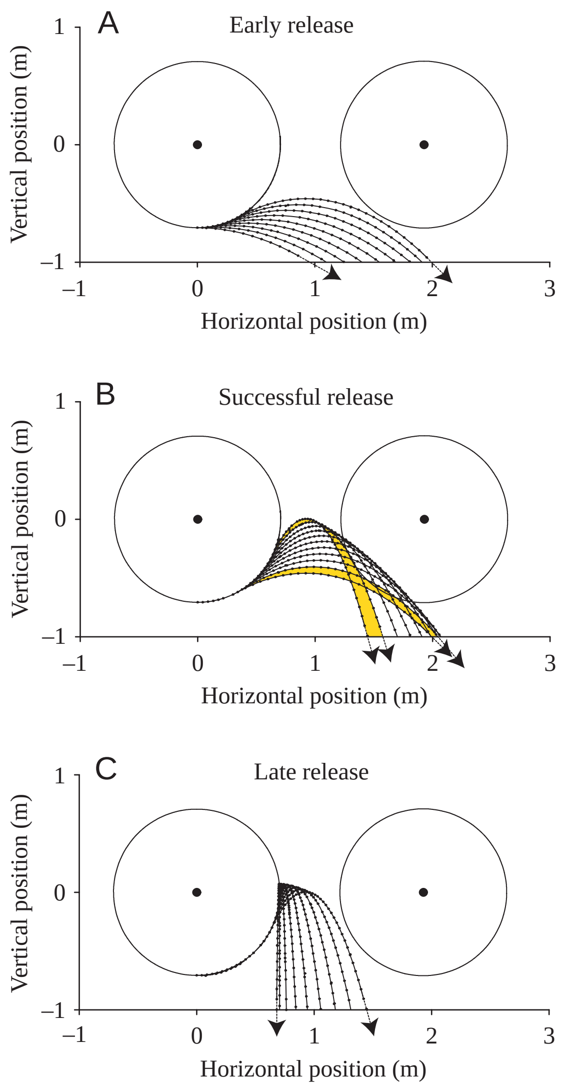
Fig. 5. Results of Model 1 for the kinematics shown in Fig. 2A (D=1.2 m), of continuous-contact brachiation, demonstrating the benefits of raising the centre of mass with a leg-lift. The potential ballistic paths are shown (A,C) and energetic consequences of collision (B,D) are derived from Model 1, with L' replacing L as the sole difference for plots C and D. Both potential ballistic paths and energetic consequences of collision are qualitatively similar to those described for Fig. 4. The leg-lift considerably reduces energetic collision losses. Axes and underlying highlights follow the notation in Fig. 4.

proximal joints (such as the elbow) than distal joints (the knee or hip). In addition to this, the mechanical advantages of the muscles about a slightly flexed elbow appear highly unfavourable. So, if it is beneficial to control L, the length between CoM and handhold, it appears favourable to do this with a knee-lift instead of an arm-bend.

Model 1 with ricochetal brachiation

In ricochetal brachiation, handhold contact is interrupted by periods of ballistic flight. The high velocities and requirement to change from parabolic (ballistic) flight to suspended (swing) paths make the animal susceptible to substantial collision loss. Fig. 6 shows the results for ricochetal brachiation. Two points are notable: (1) there is a limited total time window (120 ms) with which a release will result in a ballistic path that allows successful contact to be made with the second handhold; and (2) the energy losses may be high (up to 46%) due to collision, even when the second handhold is successfully attained, if the geometry of contact is not perfect. The exact paths of the CoM are uncertain even when calculated using directly measured force data, as the assumptions used for terrestrial force plate studies (Cavagna, 1975) are less valid for brachiation; an assumption that the CoM does not change in height over a complete cycle is highly unreliable. Some degree of overshoot, however, is readily apparent for fast ricochetal brachiation (Fig. 6F): the left arm flexes considerably after initial contact; and force records for typical double-pendulum brachiation (Chang et al., 2000) show that there is a delay between initial contact and loading of the handhold. During the interim between contact and full loading, the arm becomes partially flexed. Thus, the CoM appears to pass within the arc described by L, overshooting the path required for $\beta=\pi/2$ matching (see Fig. 1) of the parabolic flight and circular swing paths that determine a no-loss interaction between the animal and its support.

Given the considerable energetic consequences of a slight mistiming due to collision losses, and the potentially fatal consequences of a complete miss, strategies to allow some degree of overshoot while minimising collision energy losses may be expected. The trailing-arm-bend strategy described above, which adjusts the swing path in continuous-contact brachiation, is unavailable during ricochetal brachiation, as the trailing arm loses contact with the superstrate before path adjustments can be useful. Using a leg-lifting action to control



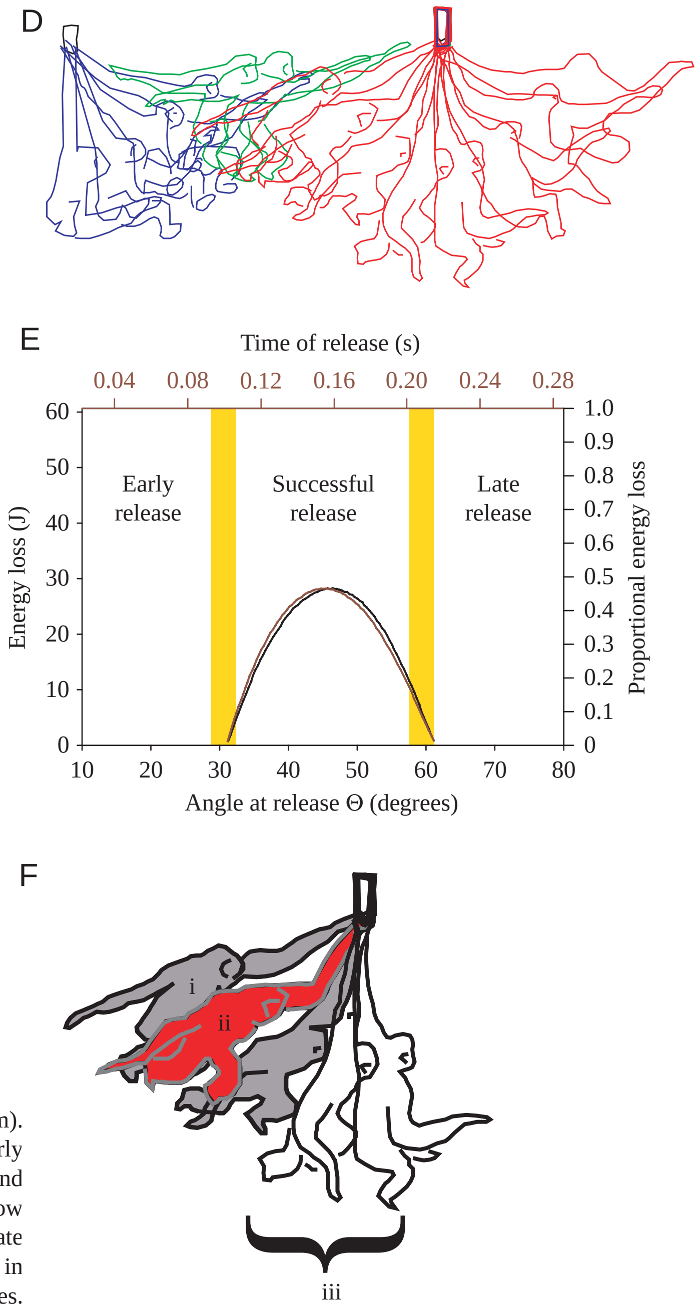


Fig. 6. Results of Model 1 for ricochetal brachiation (*D*=1.93 m). Potential ballistic paths (A–C) are separated into three groups: Early release (A), which would result in paths under-shooting the second CoM-handhold arc; Successful release (B), which would allow successful contact to be made to the second handhold; and Late release (C), showing an alternative range of paths that would result in a fall. Arrows highlight the direction of selected trajectories. Tracings in (D) are as described for Fig. 4A, except that green outlines relate to instances when neither hand is in contact with a handhold. The energetic consequences of collision (E) are presented as for Fig. 4D. The underlying yellow regions relate to the two potential paths entailing zero collision loss, also highlighted in B. Selected tracings of the second swing (F) emphasise: (i) initial contact; (ii) ‘overshoot’, with flexed support arm; and (iii) three tracings displaying the ‘double-pendulum’ action as the hips revolve about the shoulders prior to the bottom of the swing.

the distance between the catching hand and the centre of mass, however, can be advantageous in ricochetal brachiation. Such a behaviour may reduce collisional energy losses by both mechanisms: with a reduction in the proportion of mechanical energy as kinetic by control of the timing of collision, and by improvement in collision geometry, this time through alteration of the subsequent swing trajectory. Further, a slight undershoot of the ideal path may be compensated for with leg extension; movement of the leg mass distally lengthens the distance between the CoM and hand (while the CoM would continue on its ballistic path), thus permitting the avoidance of a catastrophic fall. Leg extension and retraction during flight is indeed frequently observed and, while unable to affect the ballistic path of the CoM, allows last-millisecond adjustment of the hand-CoM length, and thus the collision geometry.

Collision-reduction behaviours may save energy

While we suggest that both arm flexion and leg-lifting may be mechanisms to limit energy losses due to collision, they do not relate directly to the losses that would have been caused by inelastic collision without their actions. It is conceivable that these behaviours achieve a controlled movement of the centre of mass prior to collision, influence the timing (and so proportion of energy present as *KE*), or determine the subsequent swing trajectory, with relatively little energetic input. For the trailing-arm-bend, while some energetic input is presumably required to move the CoM, this is achieved when both support arms are relatively unloaded, at the top of the swing (Usherwood et al., 2003). In the case of the leg-lift during ricochetal brachiation, there are no net mechanical energy changes as the path of the CoM remains unaltered, though subsequent isometric muscle forces during the swing may incur some metabolic costs. Whatever the energetic investments required for these behaviours, they should not be considered as directly due to collision.

Model 2 and further collision-minimisation strategies for ricochetal brachiation

Arm elongation

Elongated arms may be viewed as beneficial to a brachiator for a variety of reasons (Preuschoft and Demes, 1984): increased reach can allow weight to be distributed among many branches, the chances of finding suitable support within grasping distance are increased, the number of handhold changes can be reduced, and feeding may be aided by increased reach. Previous attempts to relate the distinctive limb elongation observed in all specialist brachiators directly to advantages in the mechanics of brachiation have been unsatisfying. These explanations are usually based on pendular models of motion (e.g. Preuschoft and Demes, 1984). However, brachiation viewed as periods of pendular swinging interspersed with periods of ballistic flight, achieving ideal no-loss contacts, provides no pressures on arm length: energetic losses, even for relatively small pendulums, are trivial, and mean velocity is totally unconstrained by pendulum behaviour if the swing can begin and end at non-zero velocities.

The extension of the point-mass model into a method for calculating the collisional energy costs for imperfect handhold contacts, combined with a consideration of biological pressures in gibbon evolution, allows a novel account to be made for the elongated arms of specialist brachiators. If (1) release timing cannot be perfect, perhaps because of the brief availability of perfect release conditions, and (2) the cost of falling, either due to injury and subsequent repair (Schultz, 1944), or fatality, is high, then energetic losses due to collision are likely to be selectively important in the evolution of brachiators. Elongation of the arms not only results in a greater chance for *any* contact to be made with a subsequent handhold (by allowing a greater volume to be reachable for a given ballistic path), it also improves the collision geometry, and so reduces the energetic loss associated with an overshoot of the optimum contact path (see Equation 8).

While there need not be a constant relationship between mechanical energy cost and metabolic energy, it can be

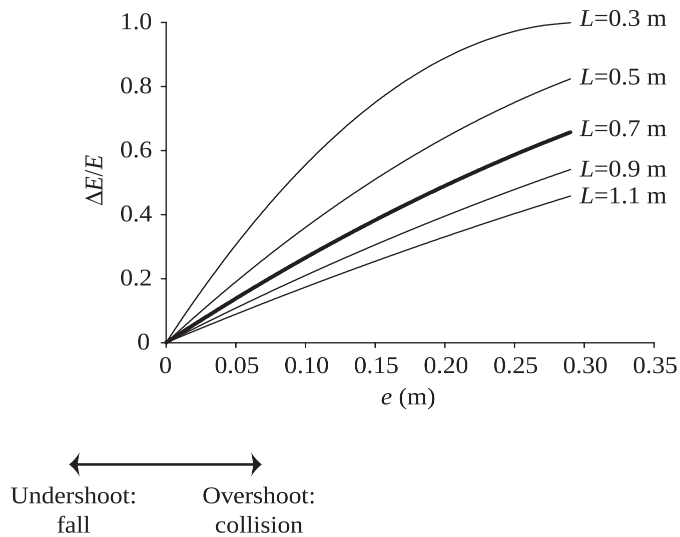


Fig. 7. Results of Model 2. Proportional energy loss due to collision with hand to centre of mass length *L* ranging from 0.3 to 1.1 m and overshoot *e* from 0 to 0.3 m. Negative *e* (undershoots) would result in missing the handhold, and a fall. The observed gibbon morphology relates most closely to *L*=0.7, indicated by the bold line.

assumed that mechanical energy costs do translate to metabolic losses. Equation 8 can be used to estimate the metabolic consequences of collision due to overshooting the 'ideal' path (Fig. 7). For a given absolute overshoot, long arms improve the collision geometry, and energetic savings may be considerable. Clearly, if overshoot is proportional to arm length, then arm length has no bearing on collision geometry. However, overshoot is more likely to be related to some degree of error, or safety factor, related to an absolute distance determined by the environmental conditions, such as the spacing of available handholds.

Brachiation energetics are influenced by tension-collision losses that may be unfamiliar to most readers. More familiar might be the compression-collision analogue of the tension-collision situation described here. The advantage of long arms for collision made with a small overshoot is the same as the advantage of large wheel size for operation over rough surfaces. While wheel size has relatively little bearing on energy losses for rolling on horizontal, smooth surfaces, increased wheel size does allow smaller loss on rough surfaces. 'Monster' trucks (e.g. Bigfoot) make use of large wheels to allow large obstacles (such as cars) to be driven over, while small-diameter rollerblade wheels fare poorly on a rough pavement. As an extreme case, a stiff, inelastic wheel colliding with an obstacle at the height of the axle loses all kinetic energy, just as a gibbon overshooting a handhold by length *L* suffers total kinetic energy loss.

The 'double pendulum' and collisional energy loss reduction

The above account for the benefits of arm elongation as an adaptation for limiting the energetic costs due to an overshoot may be extended beyond the point-mass case. In rapid

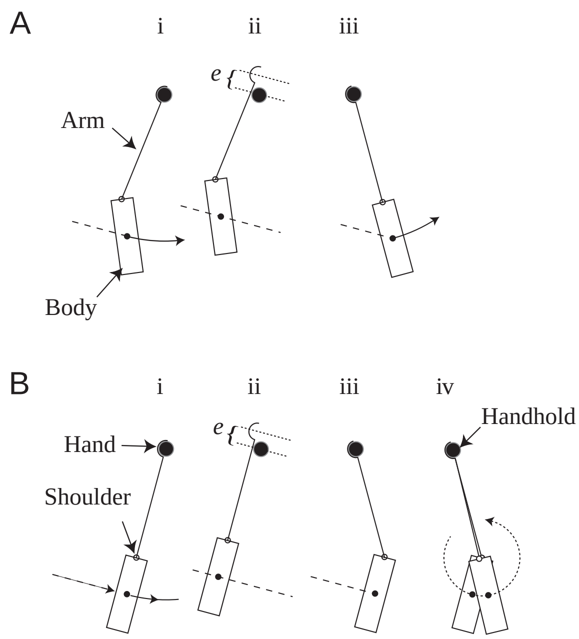


Fig. 8. Body posture without (A) and with (B) second moment of mass about the handhold maximised; a development from Fig. 3. The straight broken lines indicate the path prior to collision. With no overshoot (i), body orientation is unimportant and collision losses can be avoided. Given an overshoot *e* (ii, during which the handhold may be held lightly, and iii, the instant of collision), the posture with the body aligned perpendicular to the path (B) has a greater second moment of mass, and the overshoot results in smaller loss of energy due to collision. A consequence of aligning the body perpendicular to the path is the 'double pendulum' action (Biv), with rotation of the body about the shoulder (dotted line), which is commonly observed in ricochetal brachiation (see Fig. 6).

ricochetal brachiation between widely spaced handholds, gibbons do not swing with their body in line with their supporting arm (Bertram and Chang, 2001; see Fig. 6D,F). While distributed mass parameters are difficult to determine accurately and dynamically, the principles of inelastic collision may be extended beyond the point-mass model to provide a qualitative explanation for the body posture at the moment of collision. Energy loss due to collision is given by the difference between the total kinetic energy and the energy associated with motion about (past) the handhold. This difference is minimised for a given overshoot if the body is orientated to maximise the second moment of mass (moment of inertia) about the handhold at collision. So, just as for the point-mass model, an overshoot has a proportionally smaller effect on bodies with a distal mass distribution than proximal. This is achieved if the body is aligned perpendicular to the path of the CoM (Fig. 8). Combined with a slight overshoot, this results in a 'double pendulum' phenomenon. Thus, the double pendulum in itself may not be of direct importance in terms of control (compare Bertram and Chang, 2001); rather, it may be better viewed as an epiphenomenon, properly understood as a strategy in the context of collision energy loss minimisation.

Further biological implications of brachiation mechanics

The view of brachiation presented in this study, as locomotion utilising pendular and ballistic mechanics, but also substantially influenced by collision interactions with supporting structures, may have a bearing on many aspects of gibbon biology. The benefits of accurate release timing on minimisation of the costs of both collision and falling may have implications on the evolution and development of visual and mental abilities; these may limit the use of ricochetal brachiation to diurnal animals with well-developed brains and vision. Also, loss of energy due to collision, while avoiding tissue damage may affect both morphology and behaviour. For instance, the double-pendulum mechanism not only minimises collision losses, but can also allow large muscle groups (particularly the latissimus dorsi) to provide torques about the shoulder in a sense opposite to that of the rotation of the body. Thus the muscle can perform 'negative' work, and safely dissipate the 'internal' kinetic energy resulting from collision. This would allow the energy associated with collision, inevitable for each ricochetal 'step' if a margin for error is provided, to be lost without requiring a large jerk (rate of change of acceleration). Thus, contact can be made smoothly (although not avoiding the energetic consequences of collision), and damage to the arm or shoulder, or failure of the supporting tree limb, can be reduced.

List of symbols

CoM	centre of mass
D	inter-handhold distance
e	overshoot distance
E	total initial brachiation energy
$\boldsymbol{g}$	acceleration due to gravity (taken as 9.81 m s^{-2})
KE	kinetic energy
KE'	kinetic energy immediately after collision
L	length between handhold and centre of mass
L'	L for the second handhold in a selected instance
m	mass
m_r	mass per length dr of element at position r
PE	potential energy at highest point, with bottom of first swing as zero
r	distance from handhold
r'	distance of element from handhold
R	distance of most distal element from handhold
t_{rel}	time of release from θ=0
T_r	tension at element
V	velocity immediately before collision
V'	velocity immediately after collision
V_θ	velocity as a function of θ
β	angle between path and connection to handhold at collision
ϕ	angle of element to handhold from vertical
θ	angle of CoM to handhold from vertical
Θ	angle of CoM to handhold from vertical at instant of release
ω	angular velocity about the handhold

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