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ABSTRACT Hylobatidae (gibbons and siamangs) are known for their brachiation skills. The comparison of brachiation with a pendulum is made several times in the literature, and the costs and benefits of being pendulum-like are well described. However, the amount of energy exchange during brachiation of gibbons has rarely been determined. In this study, the amount of energy recovery (ER) during brachiation is assessed for three siamangs in a seminatural environment. The animals were recorded by four cameras while voluntarily brachiating on three different setups. The effects of locomotion speed, brachiation type, and setup on ER are determined. It is hypothesized that the amount of ER decreases with an increasing setup complexity while the external mechanical work increases. Additionally, we expect that support arm kinematics will be adjusted according to spatial complexity in order to maintain high recovery percentages. Our results show that ER is mainly determined by brachiation speed. Regardless of type of brachiation or setup, brachiation is done with a lower ER when brachiating faster. Within our limited range of setup variation, the expected effect of increasing complexity is not found. Although there is significant variation in support arm joint angles, no clear relation with speed, brachiation type, or setup is observed. Am J Phys Anthropol 145:581–591, 2011. © 2011 Wiley-Liss, Inc.

KEY WORDS Symphalangus syndactylus; energy recovery; biomechanics; gibbons

Brachiation is the primary mode of locomotion of hylobatids (gibbons and siamangs) (Fleagle, 1974, 1976; Andrews and Groves, 1976; Carpenter, 1976; Hollin, 1984; Preuschoft and Demes, 1984) and according to the definition of Hollin (1984), Hylobatidae are the only true brachiators. Other primates may use their forelimbs to propel themselves underneath overhead structures (e.g., suspensory locomotion of spider monkeys and langurs; Cant et al., 2003; Jones, 2008; Wright et al., 2008), but they are not able to do this for a substantial distance without the support of the hindlimbs or tail. During brachiation, a gibbon grasps a handhold (e.g., branch), swings its body below the handhold, and grasps the next handhold, which may result in an out-of-phase fluctuation of the body’s kinetic and potential energy creating the opportunity for energy exchange. Therefore, gibbon brachiation is described as highly pendulum-like numerous times (Fleagle, 1974, 1976; Andrews and Groves, 1976; Carpenter, 1976; Hollin, 1984; Preuschoft and Demes, 1984; Chang et al., 1997, 2000; Bertram et al., 1999; Bertram and Chang, 2001; Usherwood and Bertram, 2003; Usherwood et al., 2003). The amount of energy exchange between the animal’s kinetic and potential energy during brachiation, or the amount of energy recovery (ER), can be easily calculated. With a higher ER, the movement resembles a pendulum more closely and movements of the center of mass may be maintained through relatively passive mechanisms of energy exchange. This may in turn suggest that less external work is needed than would be necessary in a gait that operates less like pendulum, a condition that requires more active muscular input to accelerate and decelerate the center of mass. Therefore, if this is the case, the movements of the center of mass may be considered relatively more efficient, because it may require less external work at the expense of metabolic energy. To allow maximal ER, a gibbon should swing with a constant arm length about the handholds. However, a completely passive pendulum is not able to change direction or speed. Hylobatids live in tropical rainforests, consisting of a complex 3D array of compliant branches. Therefore, they have to be able to adjust each step they take to the available, flexible supports. Grabbing the next support is vital, because missing it induces a great risk of falling with grave injury or even death as a consequence. Because of this, we can assume that grabbing the next support likely prevails over efficiency and a lower ER can be expected when brachiating on or between unpredictable supports.

To brachiate from branch to branch, hylobatids use two distinct gait types (Fleagle, 1976; Bertram et al., 1999). During continuous contact brachiation, at least

Grant sponsor: Research Foundation Flanders (FWO Belgium).
Grant sponsor: Centre for Research and Conservation by the Flemish Government.

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Received 17 September 2010; accepted 21 March 2011
DOI 10.1002/ajpa.21539
Published online 3 May 2011 in Wiley Online Library (wileyonlinelibrary.com).
one hand is in contact with the superstratum at all times, and a period of double-hand contact occurs. In ricochetal brachiation, there is a flight phase without any hand contact between two consecutive handholds. Bertram et al. (1999) showed that, theoretically, gibbons can indeed brachiate in both modes without requiring any external work. To do this, not only perfect ER during the support phase is required, but also collisional losses should be avoided. A collision is defined, in mechanics, as a discontinuity in the body center of mass (bCOM) path (Chatterjee and Ruina, 1998; Bertram, 2004; Ruina et al., 2005). More specifically, a collisional loss can be described as a type of mechanical energy loss due to abrupt changes in the direction of motion that can, for example, occur when grasping a new support (see also Usherwood and Bertram, 2003; Bertram, 2004; Ruina et al., 2005). In brachiation, collisional losses can be avoided in two ways according to the two brachiation types: (1) when the change of supports happens at zero velocity, for example, in perfect continuous contact brachiation, the bCOM is at its highest when the next swing starts; or (2) when the trajectory of the bCOM at the end of the flight phase is coincident with the swing arc around the next handhold (Bertram, 2004).

Despite the importance of minimizing collisional losses in locomotion (Ruina et al., 2005), pendular dynamics determine the support phase of brachiation to a large extent, and maximizing mechanical energy conservation during swing remains an important concern. This conforms to former implicit assumptions that the optimization of ER is a strong selective force behind locomotor morphology in gibbons (e.g., Fleagle, 1974; Andrews and Groves, 1976; Preuschoft and Demes, 1984; Channon et al., 2010). Remarkably, hardly, any information regarding the actual ER can be found in the literature. To our knowledge, only Bertram and Chang (2001) have calculated the amount of energy exchange during brachiation for one white-handed gibbon moving along horizontally leveled transverse handholds. Despite these authors reporting recoveries as high as 90%, the variability was very high, and the values dropped rapidly with forward speed. The variability in forward speed was induced by increasing handhold spacing. The high variability in ER and the effect of handhold spacing may challenge the assumptions regarding optimization of energy exchange. However, the variability of the findings on recovery presented by Bertram and Chang (2001) may refer to the individual’s behavior and hence be less representative for gibbon brachiation in general. On the other hand, the uniformity of the setup (transverse and horizontal handholds) may have affected the reported recovery positively, resulting in pendular recoveries above those encountered on a more challenging course. In reality, gibbons move around in a highly complex habitat, living in the tropical rainforest tree tops. It is very likely that this habitat has shaped their locomotion mechanics over the course of evolution to develop them into the unique brachiators they are. Therefore, it would be interesting to investigate if the environment has any influence on the energy exchange during brachiation.

Considering the well-established interest in gibbon brachiation and the lack of knowledge about it in a natural habitat, a study investigating the influence of variability in environment on the general body mechanics seems to be an essential asset to gain insight in hylobatid brachiation. With the present study, we want to test the ER during brachiation of siamangs (Symphalangus syndactylus) performing on setups of different complexity. We hypothesize that the total external mechanical work will increase, and the ER will decrease with an increasing locomotor task complexity (in terms of speed and spatial complexity). Furthermore, we expect that support arm kinematics will be adjusted according to spatial complexity in order to maintain high-recovery percentages. We hypothesize that on-level brachiation, shoulder, and elbow joints will be kept fixed and extended to maximize pendular swing. However, it is expected that more angular variation will occur on the setup with handholds at different heights to keep the bCOM on the ideal track for maximum ER.

MATERIALS AND METHODS

Subjects

We recorded data of a family of three siamangs (Symphalangus syndactylus; Fam. Hylobatidae) during brachiation in their outdoor enclosure in Antwerp Zoo (Royal Zoological Society Antwerp, Belgium). Specimen data can be found in Table 1. All individuals were in excellent health and showed no obvious aberration in locomotion (e.g., use of both arms and no “limping”).

Setups

A steel beam of 7 m was installed in the outdoor animal enclosure. Handholds were placed below this beam, which were easy to adjust and allowed us to change the spatial organization of the setup. Three setups were used (see Fig. 1):

Setup 1. Eight handholds of 30 cm were placed parallel to the direction of movement at intervals of 80 cm and at equal height (step lengths possible between 50 cm and 120 cm).
Setup 2. Eight handholds placed perpendicular to the direction of movement, at intervals of 80 cm and at equal height (hence step lengths are fixed at 80 cm or a multiple thereof).

Setup 3. Eight handholds placed perpendicular to the direction of movement, at intervals of 80 cm but at varying heights (4, 6, 10, 14, or 20-cm height difference between consecutive handholds; step lengths are fixed at 80 cm or a multiple thereof).

Four cameras operating at 50 fields per second were installed around the setup (see Fig. 2) and recorded the movements of the siamangs simultaneously during sessions from four different angles. The four cameras were synchronized by means of a blackburst generator. Calibration was carried out by recording a calibration cube with sides of 50 cm. In the software package Kwon visual 3D (Visol), this calibration cube was digitized in all four views, and distances and coordinates in the three-dimensional space were entered. For each setup, there were three recording days spread over a period of 2 weeks on which the animals were recorded during 30-min sessions, three times a day. In total, 216 suitable brachiation sequences were recorded. A sequence was considered suitable when the animal made a continuous progress over the entire setup without using the feet for extra support.

Video analyses

The aim was to digitize at least two sequences for each brachiation type used by each individual on each setup (Table 2). In some cases, however, only one sequence was recorded for a specific situation, suggesting a strong preference from the individual for one brachiation type in that situation. These sequences were randomly selected from the different recording days and without a priori knowledge of speed. A total of 44 sequences were digitized on which further analysis was carried out. These sequences are representative for brachiation of the three siamang subjects and in the specific circumstances of this study.

Video images were loaded on the pc and digitized frame by frame for each camera view. As zoo policy does not allow any marking of the animals, digitization was performed manually using Kwon visual 3D. For each frame, 21 points were defined: crown, nose, chin, shoulders, elbows, wrists, metacarpals, fingertips, hips, knees, heels, and toes (right and left where possible). This resulted in a 3D 16-linked-segment body model consisting of the following segments: head, trunk, upper arm, lower arm, hand, fingers, upper leg, lower leg, and foot (left and right where possible). The raw positional data were filtered using a fourth-order Butterworth low-pass filter with a cut-off frequency based on the residual plot.

Body-segment parameters were collected during dissections on four adult siamang cadavers during 2007–2008 [for details on the included specimens, see Michielsen et al. (2009)]. The used body segment parameters include segment mass normalized to total body weight and segment center of mass and moments of inertia normalized to respective segment length (Table 3).
entering these relative parameters in Kwon 3D, combined with the known individual body mass and segment lengths of the subjects used in the current study, the instantaneous three-dimensional position of each segment center of mass was calculated. Subsequently, the instantaneous position of the entire bCOM was determined, and instantaneous velocity and acceleration of the bCOM were derived as well as the joint angles. From the position and velocity of the bCOM, respectively, the potential and kinetic energy of the body was calculated throughout the sequence.

\[ E_k = 0.5 \cdot m \cdot (v_x^2 + v_y^2 + v_z^2) \]

\[ E_p = mg \cdot h \]

where \( E_k \) is translational kinetic energy (J), \( E_p \) is gravitational potential energy (J), \( m \) is the mass of the individual (kg), \( v_x, v_y, \) and \( v_z \) are the lateral, forward, and vertical instantaneous velocities (m/s) and \( h \) is the height of the bCOM relative to the reference frame (m).

ER, external mechanical work and dimensionless speed

Percent mechanical energy recovery (ER) is a measure for the amount of the energy exchange between potential and kinetic energy of the bCOM (Cavagna et al., 1976; Full et al., 1991). The ER was determined as follows:

\[ ER = \left( \frac{\sum \Delta^+ E_p \cdot \sum \Delta^+ E_k - \sum \Delta^- E_{tot}}{\sum \Delta^+ E_p + \sum \Delta^- E_k} \right) \times 100 \]

where \( \Delta^+ \) is the sum of the positive increments of energy (i.e., the increases in energy over each time-step of 0.02s), \( E_p \) is gravitational potential energy (J), \( E_k \) is translational kinetic energy (J), and \( E_{tot} \) is the sum of \( E_p \) and \( E_k \), resulting in the total mechanical energy (J) (Bertram and Chang, 2001). In phase fluctuation of \( E_p \) and \( E_k \) will result in low ER (low energy exchange), whereas out-of-phase fluctuation of \( E_p \) and \( E_k \) will result in high ER (high energy exchange).

ER was calculated for each complete stride in each sequence. A stride was determined as the period from one hand contact until the same hand made contact with the support again. A sequence sometimes consisted of multiple strides, where the second step of the first stride is always the first step of the following stride. Because including multiples strides from one sequence would bias statistical analysis, only one stride from each sequence was included in the analysis. From each sequence, the stride with the highest ER was selected for further comparison, as this represents the maximal efficiency of the animals in that specific situation. For these strides (44, one from each digitized sequence), the total external mechanical work and dimensionless speed (\( v_d \)) were calculated.

Total external mechanical work (\( W_{ext} \)) is calculated to obtain an absolute measure for mechanical energy in brachiation in each situation. It allows us to assess the effect of setup and speed and allows comparison with other locomotor modes of gibbons and other animals. It is the amount of work performed to lift and accelerate the bCOM. The \( W_{ext} \) is the sum of each increase (over each time-step of 0.02 s) of the total energy during one stride. This means that, at each time interval, the sum of potential and kinetic energy is first taken, and each positive increment of this total mechanical energy is then added up. When there is energy exchange, kinetic energy will increase while potential energy decreases or vice versa. This will result in small increases in total mechanical energy. To allow comparison between animals, \( W_{ext} \) is divided by body mass and stride length resulting in the normalized external mechanical work, \( nW_{ext} \).

\[ nW_{ext} = \frac{\sum \Delta^+ E_{tot} / (m \cdot \Delta s)}{\sum \Delta^+ (E_p + E_k) / (m \cdot \Delta s)} \]

where \( m \) is the mass of the individual (kg) and \( \Delta s \) is the distance that the bCOM travelled during the stride (m).

To correct for differences in body size of the animals, the square root of Froude number was taken as dimensionless measure of locomotor speed (Vaughan and O’Malley, 2005). Dimensionless speed (\( v_d \)) was calculated as follows:

\[ v_d = \frac{<v>}{\sqrt{\left( l^2 \cdot g \right)}} \]

where \(<v>\) is the average forward velocity of the bCOM during one stride (m/s), \( l \) is a characteristic linear dimension of the animal (m), and \( g \) is the gravitational constant (m/s²). Anatomical arm length was used as the characteristic linear dimension and was individually calculated as the sum of upper arm, lower arm, and palm length based on five sequences (Table 1). With an extended arm, anatomical arm length corresponds approximately to the distance from shoulder to handhold (i.e., pivot point of movement), which can then be considered as the functional arm length.

Brachiation type

The distinction between continuous contact and ricochet brachiation was based on the number of frames
where double-hand contact or flight phase occurred. Strides with at least one frame of double-hand contact were considered continuous contact. All other strides were considered ricochet.

**Support arm joint angles**

Shoulder angles are calculated as the joint angle between trunk and upper arm and elbow angles as the joint angle between lower and upper arm. Joint angles are presented in degrees. Shoulder angles are considered 0° when the arms hang down, along the trunk and 180° when lifted entirely above the head. Elbow angles reach 0° when (theoretically) completely flexed and 180° when fully extended. Joint angles are only compared during support phase and are normalized to support duration. For each support phase, the variance of both shoulder and elbow angle was calculated. The amount of variance was further used to compare between setups and brachiation type. As the variability of the joint angles was fairly high, we decided to concentrate on two well-defined points in the brachiating cycle, namely contact (0%) and release (100%) of support arm.

**Statistics**

Using separate ANCOVA models, we tested whether brachiation type, setup, and dimensionless speed (including their two-way interactions) affected ER and $nW_{\text{ext}}$ as well as shoulder and elbow angles and their amount of variance. Individual was not added as a fixed factor, because assessing interindividual differences was not the aim of this study; but added as a repeated statement to account for any existing differences between the animals and to correct for variance among individuals that were measured repeatedly. The most suitable correlation structure was selected for each statistical model, based on the lowest BIC-value. Differences among brachiation types and setups were interpreted using post hoc tests. Furthermore, Pearson correlations among angles and $v_{g}$ or ER were calculated. All tests were executed in SAS 9.2 for Windows (SAS Institute, Cary, NC). Normality of the data and residuals was tested with Shapiro–Wilk test. All parameters demonstrated a W-value above 0.9 and were therefore, considered as normally distributed. For all results, $P$-values lower than 0.05 were considered significant.

**Results**

Of the 44 strides analyzed, 24 had a flight phase and 20 showed a double-handed contact phase (Table 2). Ricochet and continuous contact are considered two distinct brachiation types (Fleagle, 1976; Bertram et al., 1999) and are predefined as such, irrespective of any statistical difference.

**Energy recovery**

The average energy recovery (ER) during ricochet brachiation is 7–8% lower on each setup than the average ER during continuous contact brachiation (see Fig. 3). However, this difference is not significant ($P = 0.74$) when correcting for individuals and repeated measurements.

The different setups induce a small difference in average ER ($P = 0.05$). Ignoring the different brachiation types, average ERs are 58.8%, 67.4%, and 57.4%, respectively, for setups 1, 2, and 3. The average ER is highest on setup 2 with the handholds perpendicular to the direction of movement ($P = 0.04$ with setup 1 and $P = 0.02$ with setup 3). Setup 3, which has handholds at different heights, results in a similar ER as setup 1 with the handholds parallel and at the same height ($P = 0.66$).

However, it is primarily dimensionless speed that affects the ER (Fig. 4; slope $\approx -27$; $P < 0.01$). No interacting effects were found, indicating that a higher dimensionless speed results in a lower ER, regardless of brachiation type or setup used.

**Total external mechanical work**

The $nW_{\text{ext}}$ slightly increases with dimensionless speed, but the effect is not significant (slope $\approx 0.8$; $P = 0.06$). Also, the $nW_{\text{ext}}$ is the same for the different types of brachiation ($P = 0.95$).

The average $nW_{\text{ext}}$ of brachiating on setup 1, 2, or 3 is respectively 2.15, 1.53, and 2.18 J/kg·m. Although the overall effect of setup is not statistically significant ($P = 0.06$), setup 2 does result in a significantly lower $nW_{\text{ext}}$ than setups 1 and 3 ($P = 0.03$ and $P = 0.04$; see Fig. 5).

**Support arm joint angles**

Both shoulder and elbow angles show approximately the same amount of variation on the three setups (Fig. 6; $P = 0.09$ and $P = 0.5$).

In general, shoulder angles increase during the first half of support phase and decrease after that to a release angle that is smaller than the shoulder angle at contact. This seems to happen regardless of the setup. The elbow angles on the other hand stay constant or increase slightly (extension) during the start of the support phase after which the elbow flexes during the second half of the support phase. Near handhold release, the elbow can show an extension phase again, especially on setups 1 and 3 (see Fig. 6).

Regardless of setup, the shoulder angle at contact is correlated positively with the elbow angle at contact ($P < 0.01$) when using continuous contact brachiation. When, at the beginning of support phase, there is a large
shoulder angle, then the elbow angle will be larger too. During ricochet brachiation, however, no correlation is found between shoulder and elbow angle, which may indicate a different forelimb coordination pattern in ricochet brachiation. Dimensionless speed does not influence the shoulder angle at first contact, but the faster the animal moves, the more extended the elbow will be ($P < 0.005$) at first contact.

The shoulder angle at release is influenced by the interaction between setup and dimensionless speed (Fig. 7; $P = 0.01$). Shoulder release angle will be smaller when brachiating faster on setup 3; while it will be larger when brachiating faster on setup 1 and 2 (see Fig. 7).

Dimensionless speed also influences the elbow angle at release ($P = 0.01$). A faster moving animal will release the handhold with a more extended elbow.

**DISCUSSION**

*Do siamangs keep their ER high in any circumstance?*

**What affects ER?** Our data show that the dimensionless speed has a prominent effect on ER: a faster brachiating siamang exchanges less mechanical energy, resulting in a lower ER. This conforms to the results found by Bertram and Chang (2001). However, they found an optimal handhold spacing, related to an optimal speed at which the ER was maximal. An optimal speed inducing a maximal ER is also found in humans during walking (Cavagna et al., 1976). A lower or higher speed than optimal would then induce a lower ER, but during siamang brachiation, no optimal speed is found. Slower brachiation is always better for energy exchange, even when brachiating more slowly than determined by a theoretical passive pendulum. A passive pendulum has a constant pendulum length and swings freely. We measured the pendulum length of the siamang and the height of the bCOM upon first contact with the handhold for 10 random trials. With these two parameters, the velocity of the bCOM at the bottom of the swing can be calculated assuming a passive pendulum. It appeared that the animals can use both faster and slower speeds than the velocity of the passive pendulum.

*How do siamangs differ from a passive pendulum?*

In contrast to a passive pendulum, gibbons can change their pendulum length during support phase or between different sequences by flexing and extending elbow and shoulder joints. By doing this, the animals can actively brachiate more slowly, while apparently increasing the ER. But why would they invest muscle activity and thus energy to go slower? There are two possibilities: (1) obtain a higher ER and (2) reduce collisional losses.

First, a slower moving siamang may be more capable of changing the path of the center of mass to keep it on the ideal track for a high ER. However, support arm joint angles do not confirm this. Figure 6 clearly shows that siamangs do not keep a constant shoulder and
elbow angle during support phase and, as a result, the pendulum length (and moment of inertia) changes continuously. This may indicate that the animals use their variable pendulum length to affect speed and thereby ER. Exactly, how siamangs use a changing pendulum length to affect ER remains a difficult question to answer. The shoulder joint angle at contact is larger when siamangs brachiate faster. We would expect that elbow and shoulder angles are correlated at first contact as we expect some coordination of the movement. For example, in continuous contact brachiation, the elbow is more extended when the shoulder angle is bigger. Both joints may work together to keep the bCOM low for example and maximize ER. However, in ricochet brachiation, no correlation is found, indicating that there may be less coordination between the two joints in this gait type. Additionally, there is no difference in variance found for shoulder and elbow angles relating to speed. Shoulder and elbow angles change continuously during the support phase, regardless of speed, and there is no clear effect found on the ER. We can conclude that there is no clear pattern to indicate that changing support arm joint angles are used to increase ER. Instead, it may be that the legs are used to influence the path of the bCOM and thus the possible ER. Fleagle (1974) describes leg pumping as a way to minimize the loss of kinetic energy in the upswing. By flexing the legs in the upswing, the bCOM is moved closer to the center of rotation, and it can swing higher, resulting in a higher potential energy. The effect of pulling up the legs, however, would be

Fig. 6. Shoulder and elbow angles during one support phase of brachiation for the three different setups. Dark gray is continuous contact and light gray is ricochet.
smaller on the position of the bCOM than would the flexion of the support arm. Therefore, we mainly focused on the support arm joint angles in this study.

Second, a slower moving siamang may be more capable of changing the path of the center of mass to avoid collisions. When collisions can be avoided by adjusting the path of the bCOM or unavoidable collisions can be made smaller by going slower, less energy is lost.

Are there collisions in siamang brachiation? The path of the bCOM always shows a smooth transition between consecutive hand contacts (e.g., Fig. 8) and at no time did the kinetic energy suddenly drop to zero without any compensating rise in potential energy or velocity in a different direction. These findings are in agreement with Bertram et al. (1999), who declared that natural gibbon motion is even smoother than the smoothest motions predicted by their model. As has been noted in the literature (Bertram et al. 1999; Usherwood and Bertram, 2003; Ruina et al., 2005), collisions across step transitions may incur costs. Siamangs may make efforts to avoid those costs and create smooth transitions. Our data do not suggest that collision avoidance is an important factor driving limb length changes as no indications are found that the support arm is used to keep the bCOM on this ideal path. But it may be the case that other aspects of siamang gait do help avoid collisional losses. The data here cannot fully address those issues but point in important directions for future research.

Does the bCOM influence brachiation? Although bCOM movements are always smooth, a lot of variation was found. In Figure 8, two types of brachiation are shown: continuous contact and ricochet. Ricochet and continuous contact brachiation can clearly be distinguished by the path of their bCOM. During continuous contact, a distinction can be made based on the presence and type of loops. Three transition types were observed: no loop, a simple loop, and a reversed pendulum with a smaller pendulum length. However, no clear pattern could be determined. The reversed pendulum type only occurred in one animal (adult male), while the other patterns occurred in all three individuals, on all three setups, and at different speeds. Further comparison and especially support reaction forces during the double contact phases that result in loops would be very interesting to investigate. Chang et al. (1997) explain loops as a way of avoiding collisions during continuous contact brachiation when the handholds are too close together. However, we also find these loops with the smallest siamang (arm length smaller than step length), where it is doubtful that the handholds are placed too close for the animal. To date, the reversed pendulum has not been described in the literature. As we only see this in the adult male, this may be due to the fact that the handholds are positioned at a relatively close distance. It may be questioned, however, why the animal does not skip a handhold.

The variation in the path of the bCOM may offer an explanation for the effect of speed on ER if there is an underlying relation between the path of the bCOM and speed or ER. Unfortunately, a detailed comparison between these subtypes of brachiation is not possible with the present data. Therefore, we opted to present the rest of our data separately for the main two types of brachiation, that is, continuous contact and ricochet.

Do the different animals brachiate in the same way? The effects of different individuals and repeated measures are taken into account, but it was not our aim to investigate the causes of interindividual differences. Because the three animals are different in their developmental status (juvenile, subadult, and adult), the amount of experience may have affected the results. Of course, we expect the adult animal to use the most efficient brachiation and the youngest the most playful and energy-consuming locomotion. Indeed, the ER was found to be statistically higher for the adult male compared to the younger two individuals (which did not differ statistically). Fortunately, no interacting effects of individual
with speed, brachiation type, or setup were found, indicating that each animal’s capacity of exchanging mechanical energy was influenced in the same way by these parameters. But because age (and thus experience) goes together with growth (both mass and arm length) and because of the small sample size, it is not possible to allocate any difference to one of these specific factors either. Therefore, the analyses were corrected for individual, but no individual differences were discussed further.

Why is ER not influenced by brachiation type? Ricochet brachiation is used at higher speeds than continuous contact brachiation and higher speeds induce a lower ER. Nevertheless, brachiation type does not directly affect ER. One explanation may be that a high number of analyzed sequences were not extreme types of brachiation. Duty factor (i.e., percent time of support to stride duration) was often around 0.5, and, consequently, there was a large range of speeds where both ricochet and continuous contact occurred. For a significant number of the analyzed trials, only a few hundredths of a second made the difference between the two types of brachiation. This is an interesting finding, as it can be interpreted as an optimization by the animals: They go as fast as they can without losing contact with the handholds (with no or a very short flight phase), and therefore the risks of falling by missing a handhold are small. Brachiation with a duty factor around 0.5 may have to be considered as an extra brachiation type, which combines the benefits of both continuous contact (high ER and safe) and ricochet brachiation (fast).

Does the environment influence brachiation efficiency? Apart from the variation in speeds, we measured brachiation ER on setups of different complexity to induce variation. Yet, the different setups hardly affect the ER. It is not the most complex setup (i.e., setup 3 with handholds at different levels) that leads to the lowest ER (no difference between setup 1 and 3). In setup 1, the handholds are placed parallel to the direction of movement, which allows the animals to adapt their step length, whereas, in setup 2, the handholds are placed perpendicular to direction of movement, inducing a fixed step length. In setup 3, the handholds are placed perpen-

**Fig. 8.** Examples of different bCOM patterns (sagittal view). The horizontal bars show periods of hand contact.
dicular as well, but at different heights, yet no difference in ER is found between setups 1 and 3. This suggests that the orientation of the handholds (setup 1 vs. 2) may have an equal effect on the ER as the spatial complexity of the setup (setup 2 vs. 3). Alternatively, this may indicate that the variation in heights is too small to have an effect.

It seems that the presented limited variation in setups does not influence siamang brachiation in terms of ER and collision. The animals are able to keep the ER higher when brachiating slowly, but they use the same variety of handholds on each setup. Which mechanism is behind this effect remains unknown, but we have not found any indication that they use their support arm to adjust their movements.

How much does brachiation cost (mechanically)?

The $n_{\text{Wext}}$ is not influenced by type of brachiation or dimensionless speed. This is an interesting finding, as in legged locomotion the cost of locomotion usually increases with increasing speed (Willems et al., 1995). However, the average $n_{\text{Wext}}$ in other legged animals is distinctly smaller $(1.15 \pm 0.43 \text{ J/kg*m};$ Heglund et al., 1982; Full, 1989) than in siamang brachiation $(1.93 \pm 0.35 \text{ J/kg*m};$ over the three setups and two types of brachiation). Even more surprising is that the average $n_{\text{Wext}}$ of white-handed gibbons, walking bipedally, is even lower $(0.72 \pm 0.29 \text{ J/kg*m};$ Vereecke et al., 2006). So, although high ERs are possible, the $n_{\text{Wext}}$ of siamang brachiation is high compared to other (gibbon) locomotion types. This concurs with the findings of Parsons and Taylor (1977) who measured oxygen consumption during brachiation and walking of Ateles. They too found that brachiation is an energetically costly way of moving. Obviously, there are also benefits for brachiation, which can compensate for this high mechanical (and potentially high metabolic) cost, such as the unique niche they live in, the ability to escape from slower predators, and the ability to reach fruits at fine branches.

Interestingly, however, neither the setup nor the speed affects the $n_{\text{Wext}}$, which indicates that the work necessary to move the bCOM is not higher when handholds are offered at different heights or when siamangs brachiate faster. This is in contradiction with the findings of Parsons and Taylor (1977), who found a clear positive relationship between speed and oxygen consumption, which even increased when restrictions in stride length were imposed by using a ladder mill. Although, $n_{\text{Wext}}$ is no direct measurement for metabolic cost, it would be interesting to calculate the $n_{\text{Wext}}$ on more complex setups to investigate if it remains equal. If it does, this may suggest a very fascinating adaptation to the complex environment these animals live in.

CONCLUSION

It is clear that speed has a determining effect on brachiation. Brachiation type, ER, and shoulder release angle are all influenced by speed. When a siamang brachiates more quickly, the ability for ER will decrease, the gait will change to ricochetal brachiation, and the support will be released at a larger shoulder angle, unless handholds are placed at different heights. Except for the interacting effects of speed and setup for the shoulder release angle, increasing complexity of the environment does not influence brachiation kinematics as expected. The kinematics of the support arm do not appear to determine speed or the path of the bCOM.

Both Bertram et al. (1999) and Bertram and Chang (2001) argue that brachiation may be energetically costly because of the continuous adjusting of step lengths to the environment. We also found that the external mechanical work needed is high compared to other locomotion types. Nevertheless, we can conclude that the ER is kept high (over 50%) in all presented situations, except when brachiating faster (dimensionless speed $> 0.85$) and that the $n_{\text{Wext}}$ will remain equal. Exactly, how siamangs keep their $n_{\text{Wext}}$ constant remains a fascinating question. It seems that this is determined by a combination of factors, and a more detailed analysis of brachiation kinematics and kinetics is essential to fully understand brachiation. This study was supported by a research grant to the first author from the Research Foundation Flanders (FWO Belgium).

ACKNOWLEDGMENTS

I thank two master students (Anнемie Cardon and Benny Borremans) for their help with the digitizations and analyses and Arne Iserbyt for statistical help. A big thanks to Prof. Dr. Evie Vereecke as well, who helped with a lot of useful insights during the revision process. I also thank the Flemish Government for the structural support to the Centre for Research and Conservation (RZSA) and the Zoo keepers for making it possible for me to collect data whenever possible. I also thank Jan Scholliers for his help in developing the setup and Josie Meaney-Ward for English linguistic advice.

LITERATURE CITED


