Spring 5-3-2013

From Gibbons to Gymnasts: A Look at the Biomechanics and Neurophysiology of Brachiation in Gibbons and its Human Rediscovery

Emma ET Pennock
Clark University, pennock.emma6@gmail.com

Follow this and additional works at: https://commons.clarku.edu/studentworks

Part of the Biophysics Commons, Comparative and Evolutionary Physiology Commons, Evolution Commons, Exercise Physiology Commons, and the Other Neuroscience and Neurobiology Commons

Recommended Citation
Pennock, Emma ET, "From Gibbons to Gymnasts: A Look at the Biomechanics and Neurophysiology of Brachiation in Gibbons and its Human Rediscovery" (2013). Student Works. 2.
https://commons.clarku.edu/studentworks/2

This Conference Proceeding is brought to you for free and open access by the Scholarly Collections & Academic Work at Clark Digital Commons. It has been accepted for inclusion in Student Works by an authorized administrator of Clark Digital Commons. For more information, please contact mkrionis@clarku.edu, jodolan@clarku.edu.
ABSTRACT

This conference paper serves to examine the evolutionary linkages of a brachiating ancestor in humans, the biomechanical and neurophysiology of modern day brachiators, and the human rediscovery of this form of locomotion. Brachiation is arguably one of the most metabolically effective modes of travel by any organism and can be observed most meritoriously in Gibbons. The purpose of the research conducted for this paper was to encourage further exploration of the neurophysiological similarities and differences between humans and non-human primates. The hope is that in spurring more interest and research in this area, further possibilities for rehabilitating brain injury will be developed, or even theories on how to better train our athletes, using the biomechanics and neurophysiology of brachiation as a guide.

Keywords: Biomechanics, bipedalism, brachiation, brain trauma, evolution, Gibbons, neurophysiology, primates.
Introduction

There are many ways an animal might choose to move around its adaptive environment: aquatic species who have evolved fins and gills in order to swim and breathe underwater; aves who have developed hollow, bony appendages covered in feathers which allow them to soar high above the ground; humans who are unique hominids set apart by our upright posture and reliance on bipedal walking or running; and nonhuman primates, such as monkeys, who have learned to maneuver deftly in the treetops. All of these are examples of unique adaptation to a particular environment, which allows an individual of that species to easily traverse the space they inhabit.

Primates have adapted to deal with the challenges of traveling in complex environments that require the speed, agility, endurance and overall physical capability of the animal to be in peak condition (Cheyne, 2011). Different types of locomotor strategies have developed out of the need to negotiate specific environments and terrain. These strategies need to be cost effective energy-wise for the primate using them, while also allowing them to move through their environment with relative ease. Early anthropoids lived in trees and were exclusively quadrupedal, meaning no shoulder or upper-extremity modifications had yet been made that would allow suspended locomotion in trees. The advancements and changes in the shoulder girdle and chest wall that would allow for full brachiation are thought to have taken place in the mid or late Oligocene (around 33.9 to 23 million years ago) (Wilson, 1998). By the Miocene (around 24 mya), the anthropoids had branched into monkeys and apes. Monkeys and apes may have diverged as a result of size, as apes are markedly larger than their monkey counterparts. The apes’ larger mass could have posed difficulties for navigating the tops of trees where the food is plentiful but the branches are too weak to support heavier weight. The quadrupedal method of moving across branches was thus no longer effective when taking into account this larger center of gravity.

As the hominids evolved further into the Miocene and Pliocene eras, the major anatomical advancement that was critical to the development of brachiation as a more effective mode of transportation in an arboreal lifestyle was the freeing of the attachment of the ulna (the major forearm bone of the elbow that meets the wrist on the small-finger side). This allowed the twisting range of the arm below the elbow needed to
swing the body forward under the arm. This development also allowed the hand to tilt at the wrist, away from the thumb (Wilson, 1998).

This essay will serve as an informative analysis of the evolution of bipedalism from brachiating apes, as well as provide a concise understanding of the biomechanics of brachiation, using the biomechanics of bipedalism as a frame of reference. In addition, this analysis will include a comparison of the neurophysiology of gibbons, humans, gorillas and chimpanzees to provide a better understanding of the neuroscience behind certain types of locomotion and look at the human rediscovery of brachiation in the form of elite gymnasts and as a form of therapy for children suffering from brain injury. The purpose of this research is to focus on the development of bipedalism from brachiation and the neurophysiology of brachiating apes in the hopes of providing more relevant data that could be useful in various domains, from treating brain trauma to more effective training for gymnasts.

Evolution of Bipedalism

As evolved vertebrates, over the course of our ancestral lineage we have had to move from one type of environment to another, which held different selective pressures and anatomical expectations or constraints that lead to our adaptation and ultimate survival. Along the mammalian evolutionary trajectory, the development of lungs, limbs and the amniotic egg allowed for terrestrial life. The mammalian brain soon followed these evolutionary markers, becoming highly developed with connected cerebral hemispheres, thus making complex learning and thinking possible (Romer, 1971). When primates evolved, much of their time was spent living in the tree-tops, resulting in many of the anatomical adaptations we see in primates and humans that were tailored towards an arboreal lifestyle (See Figure 1).

![Figure 1: Skeletons of the gibbon, orangutan, chimpanzee, gorilla, and man, drawn from specimens in the Museum of the Royal College of Surgeons.](image-url)
This lifestyle demanded flexibility, agility and highly developed sensory organs in order to accommodate for the complex canopy systems and locomotor demands. Accurate vision is essential for safe travel through trees and it is found that in most primates, the eyes are turned forward so that the two fields of vision are not only identical, but intersect in the visual cortex, creating a panoramic view of the animal’s surroundings (Romer, 1971). Stereoscopic vision, depth perception and distance judgment are all developed through these highly sensitive optical organs. These adaptations have resulted in primates and humans having large brains with more developed grey matter of the cerebral cortex. When the arboreal lifestyle was finally abandoned by man in favor of bipedalism, they still retained the sensory and cerebral advancements that were necessitated by the tree-dwelling apes (Romer, 1971).

The direction of evolution is dominated by selection and resulting adaptations within (and to) a specific environment. The evolution of man can be seen as a development of certain kinds of behaviors that were beneficial to the species in regard to the environments that they began inhabiting in comparison to that of the apes. There are three different theories that dominate the evolution of man. First, that the ancestral populations which lead to man separating from the ancestral ape populations diverged more than 30 million years ago. This would mean that the ancestral form of man would have been a small quadrupedal primate of some kind (Washburn, 1971). The second theory argues a shared common ancestry between man and ape, which would not have become separate lineages until the Miocene (the critical part in this theory is whether or not the split occurred in the early Miocene era, dating the ancestry lineage pre-brachiating ancestor, or if it occurred in the late Miocene, during or post a brachiating ancestor). And third, the separation did not occur until the Pliocene, and man and the African apes are closely related (Washburn, 1971). Each of these theories argue a very different idea of how behaviors and locomotor structures evolved and from what ancestral lineages. In the case of the first theory, this line of thought would imply that not much can be known about the evolution of man for the first 30 million years and only by viewing the evolution of man and ape as a parallel trajectory can we account for any similarities betwixt the two species. The second way of thinking would argue that the similarities between men and apes can be accounted for by a common ancestry and a
common way of life. The third theory would suggest that both man and ape share a common arboreal, quadruped lifestyle, which evolved into brachiation. Some apes and men continued to share ground-living, knuckle-walking lifestyles (as opposed to living solely in arboreal contexts) where humans began to adapt and develop as bipedal locomotors (Washburn, 1971).

Even in modern day primates, we can see anatomical evidence supporting this evolutionary trajectory. Gibbons are “true” brachiators, relying on this as their dominant form of locomotion. Gorillas are much too big to navigate through delicate canopies and so remain on the ground as knuckle-walkers. Humans are solely bipedal locomotors, using an upright position and traveling by either walking or running on the hind limbs. Chimpanzees show evidence of a bridge of sorts between these three methods as they are mainly knuckle walkers, but can also climb and swing under branches (brachiating) and can even walk bipedally for short periods. However, even given all of this evidence, it is still difficult to argue evolutionary sequence or put to use any typological thinking since there are no living prebrachiators with which we might compare fossils (and no brachiators fossils to begin with). Further, there is little reason to believe that any ancestral forms are identical to the living versions. There is so much variability in each of the species and their corresponding habitats that many evolutionary lineages evolved, some diverging and some remaining parallel. If these fundamentals are kept in mind, it would be reasonable to suggest that the evolutionary sequence could have followed a quadruped ➔ prebrachiators ➔ brachiators ➔ knuckle-walker ➔ biped trajectory (Washburn, 1971). The anatomically evidence that supports this evolutionary trajectory is compelling. Primarily, the trunk and arms of living species seemed to have evolved ahead of the pelvis and pelvic limbs (with the exception of the foot, which reached the “final” human form before the hand). The length of the arm, breadth of the trunk and shortness of the lumbar region all speak to the quantitative anatomical similarities between ape and man (Washburn, 1971). However, the most important anatomical similarities between ape and man that argue evolution from brachiating ancestors can be found in the hand and wrist, suggesting more of a shared adaptation with brachiators than with knuckle-walkers. Along with the development of the flexion of the wrist, wrist form, and loss of sesamoid bones (bones that are embedded with a tendon that pass over a joint), the structure of the human trunk and
arms is strikingly representative of ape-like anatomy (Washburn, 1971).

Neurophysiologically speaking, we see how humans rely so heavily on coordination and dexterity of the hands and feet since bipedal locomotion and our ability to use tools requires a certain degree of balance in response to the high center of mass that comes with upright posture. The human cerebellum is three times the size of an ape’s and the part that is enlarged is associated with learned hand movements (in a monkey, the areas of the cortex controlling hand and foot movements are about equal in size). It is important to note that the brain tends to follow the trajectory which natural selection, and subsequently evolution sets in motion. The locomotor characteristics evolve first, and the brain adapts to the new anatomical patterns afterwards. In regard to our evolutionary trajectory, we see how natural selection acts on a species to fuel the evolution from arboreal locomotion necessary for high canopies and forested environments when there was a move from those environments in our ancestral lineage to the savannah-type environment requiring bipedalism as the most effective mode of transportation (Washburn, 1971).

**Biomechanics of Bipedalism**

A description of the biomechanics of bipedal locomotion in useful in order to understand the biomechanics of brachiation. In order to understand something seemingly so simple as placing one foot in front of the other in a motion we have come to term “walking” or “running” should that placement reach higher speeds, it is necessary to understand the functional relationship between the biomechanical and neurophysiological elements related to postural control in both standing and walking based on “movement efficiency” (Sousa et. al., 2012). A person’s ability to stand or walk safely is entirely dependent on the underlying mechanisms that interact with the environment which allow for safe and efficient locomotion. Postural equilibrium involves the coordination of sensorimotor strategies to stabilize the body’s center of mass (hereinafter “CoM”) during “self-initiated and externally triggered postural stability” (Sousa et. al., 2012). “Postural stability” can be defined as the ability to control the CoM in relation to the base support; the postural control system is what adjusts based on the goal of the organism in a particular circumstance (for example, deciding between walking, running, and
standing still or even maintaining balance on uneven or unusual terrain) (Sousa et. al., 2012). Biomechanically speaking, postural control is achieved when the CoM is within the base of support and aligned with the center of pressure (hereinafter “CoP”). Any sudden external or internal event that alters this delicate relationship between the CoM, base of support, and CoP could lead to a complete change in postural stability (hence why we lose our balance, stumble to catch ourselves when pushed suddenly or met with uneven terrain without warning). In conditions of high instability, the central nervous system (CNS) may suppress anticipatory postural adjustments (APA), which act to stabilize posture and equilibrium prior to a voluntary movement. APAs can have destabilizing effects in these conditions of “high instability” (for example, walking over marbles or ice) and in overriding this mechanism, the CNS takes over the responsibility of ensuring postural control and stability (Sousa et. al., 2012). The main sensory systems involved in postural control are proprioception, from Latin proprius meaning “one’s own” perception, or the sense of the relative position of neighboring parts of the body and strength of effort being employed in movement. The vestibular system, located in the temporal bone near the cochlea (the auditory sensory organ), contributes to balance in most mammals and to the sense of spatial orientation. The vestibular system contain two types of sensory organs, the two otolith organs (the saccule and utricle) which are in charge of sensing linear acceleration, and the three semicircular canals, which sense angular acceleration in three planes (See Figure 2). These signals are then translated and sent to the brain via neural circuits, which control eye movement, posture, and balance (Cullen & Sadeghi, 2008). Vision, and all related pathways within the CNS, such as the primary and sensorimotor cortex, spinal cord, brain, stem, cerebellum, and midbrain are all

Figure 2: The Vestibular System
leading contributors to movement and sense of balance as well.

Human gait is influenced by a multifactorial interaction that results from neural and mechanical interplay. This includes musculoskeletal dynamics, a central pattern generator (CGP) which are a network of neural connections which produce rhythmic patterned outputs without any sensory feedback and peripheral and supraspinal inputs (such as the cerebellum and brain stem). The upright stance is an unstable position, as it requires that the CoM never deviate from the base support (think of leaning too far over a precipice, or someone shoving you so that your torso is propelled too far away from your base, causing you to lose balance and fall). The vestibular system acts as an adjuster in body weight support and plays a major role in the antigravity function (ostensibly what keeps us standing upright against the force of gravity). This in turn activates lateral and ipsilateral extensor motor neurons and associated gamma neurons which affect APA production as it is a receptor for input from all the sensory systems and also from the pre-motor cortex and supplementary motor cortex (Sousa et al., 2012). In order for human gait to function smoothly and effectively, it is necessary that the proper mechanisms controlling muscle tone and locomotor interaction all work as a cohesive unit to drive the person forward in a bipedal gait (See Figure 3).

**Figure 3:** A conceptual illustration of the main structures involved in postural control in both standing and walking.
Neurologically, during bipedalism, there is a net inhibition from the basal ganglia (located at the base of the forebrain, these tightly knit nuclei have strong connections to the cerebral cortex and thalamus and are involved in a variety of functions including voluntary motor control) and net excitation from the motor cortex. Using the cortico-ponto-cerebellar pathway (arguably the most important connection by which the cerebral cortex can influence the cerebellar cortex) which connects the cortex with the nucleus of the brain stem and cerebellum, these excitatory signals are able to travel from the motor cortex to the appropriate muscle fibers which stimulate the postural transition from upright stance to bipedal gait (Sousa et. al., 2012).

During bipedal gait, there is a feedback loop that adapts through a reciprocal response system of the CPG to environmental requirements. During this response, muscle activation sequences are stimulated, and there is a reinforcement of any ongoing motor activity (particularly for load-bearing muscles such as the legs) while the body transitions from one phase of movement to another. The “swing” which propels the leg forward occurs when one leg is “extended,” using the stretch flexor muscles and “unloaded,” causing reduced force in extensor muscles. The trajectory depicted by the CoM in the bipedal gait is a sinusoidal curve that moves vertically twice during one cycle and laterally in the horizontal plane, and biomechanically, most of the work during gait is performed by a passive mechanism of exchange between gravitational potential and kinetic energies. The change in the velocities of the legs and the CoM are caused by a low energy recovery, which occurs in the double support phase (standing upright, both feet on the ground) in relation to the interruption of the energy-conserving motion of single support (one leg is unloaded) by the collision of the swing leg with the ground (See Figure 4).

![Figure 4: Illustration of stance phase vs. swing phase in bipedal locomotion.](image-url)
Basically, as we step one foot in front of the other to propel ourselves forward, the muscles in the ankle and hip (including the gluteus maximus and the hamstrings) work to restore the energy to the body with each swing of the leg and collision of the foot with the ground (again using that translation of potential to kinetic energy). In trying to visualize the biomechanics of bipedal gait, it helps to use an inverted pendulum as a model. The ankle plantar flexors work together with minimal metabolic energy expenditure to hinder progression before “midstance” (the ball and heel of the foot are flat on the substrate) and maintain body support and the forward motion of the trunk and leg during “midstance.” The biarticular hip extensors (such as the hamstrings) generate forward propulsion while the uniarticular quadriceps muscles and uniarticular hip extensors (such as the gluteus maximus) decelerate the body mass center and provide support and balance (Sousa et al., 2012).

From a neurophysiological standpoint, there is a specific neural output that would be necessary to create an action potential, which by navigating along the appropriate circuitry would determine the correct limbs and muscles to stimulate in order to achieve proper kinematic patterns. The subsequent muscle response and redundancy allow the movement (in this case bipedal gait) to be carried out in different combinations depending on the external circumstances under which the action is performed. This allows us to choose appropriate gait speed and stride length depending on the surface we are traversing or how fast we would like to go. All in all, the major function of muscle gait is to absorb energy. The human body has an innate capacity to transfer energy between its joint segments (such as the ankles, knees, and elbows) and can store and recover that energy in the passive elastic tissues found in our tendons and muscles. Due to this capacity to store and recover energy in walking patterns, the CNS has developed a method of creating motor patterns that conserve as much energy as possible in the earlier generated gait cycle (Sousa et al., 2012). This allows humans to simultaneously store and recover energy that is converted both externally from gravitational potential energies to kinetic energies and internally from the foods we eat which fuel our muscles and cells to keep them functioning.
In order to understand Gibbons as “true” brachiators, it necessary to know a bit about them as a species. Part of the Hylobatidae family, there are 12 classified species of Gibbon and all are qualified as “lesser apes” due to their smaller size. Defining characteristics include an enlarged brain, flat face, stereoscopic vision, grasping hands and feet, opposable digits, lack of a tail, upright posture and, of course, the ability to brachiate which is made possible by their broad chest, full shoulder rotation and over-developed pectoral limbs. Unusually long arms, hands and fingers aid them in their dominant mode of transportation - swinging through the high canopies in a form of locomotion called brachiation. Gibbons are found primarily in different parts of Southeast Asia, such as the countries of Burma, China, Indonesia, Malaysia, North Sumatra and Thailand, in old growth tropical rainforests, semi-deciduous monsoon forests and tropical evergreen forests. They prefer the covered closed canopy but will climb to the crowns of trees when feeding (mainly on high sugar fruits like figs, but are also omnivorous and will eat plant-life, seeds, insects and even small birds) or venture to the clumps of bamboo and bushes on the forest floor for water. While brachiating, the gibbon will use four fingers (excluding the thumb) on their hand as a hook and are also able to “walk” bipedally along branches (or on the ground on the rare occasion that they descend to the forest floor) for short distances, using their arms extended for balance and support (not unlike a tightrope walker). However, brachiation still comprises about 90% of all gibbon locomotor activity. Their agility, speed, impressive hand-eye coordination, keen eyesight, dexterity and arboreal lifestyle make an adult Gibbon challenging prey to catch (Zoological Wildlife Foundation, 2013).

In its functionality and basic form, brachiation is most simply locomotion using the pectoral limbs. However, this leaves something to be desired because if we were to use this as the basis for defining brachiators, bats would be lumped in with gibbons since they travel solely with their pectoral “limbs” as well. To ensure the absence of any confusion or doubt, the definition of brachiation must be amended to include the degree to which pectoral limb locomotion is used and how those animals
that have greater dominance on the pectoral limbs versus pelvic limbs also travel beneath substrate as opposed to over it, often in below-branch suspension of some kind. Thus, brachiation can be 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 a tail or hind limbs and the interruption of climbing (Bertram, 2004).

Primates that are best at brachiation possess certain anatomical characteristics similar to those of humans and the great apes, such as a dorsoventrally flattened thorax, upright posture, and wrist specializations. Brachiators have a unique ability to move below their support as opposed to over it (as we do in bipedalism or gorillas do in knuckle-walking). Gibbons are, therefore, considered to be the only “true brachiators” as they are uniquely specialized for this type of locomotion. On flat surfaces, terrestrial organisms are able to choose where to place their feet, decide where they want to step next, the suitable speed for that particular step and the frequency and length of stride. For a brachiator, however, their ability to locomote is dependent on the distance between handholds and available overhead support. Brachiators interact with their stratum in a remarkably different way than humans or other bipedal locomotors who rely on surface friction to maintain their foothold with the ground. Gibbons can brachiate either by using totally active (musculature in use) or totally passive (pendulum-effect) mechanisms. This allows for both metabolic energy preservation and adaptation to the gibbon’s variable living environment (Bertram, 2004). In brachiation, there is a substantial amount of rotation around the long axis of the support limb, an enhanced mobility made possible by the unique ball and socket joint in the wrist (similar to what we see in humans at the shoulder). This development allows the gibbon to rotate its body nearly 180 degrees about the vertical axis with each handhold grasp (Chang et. al., 2000). The forward velocity of the swing will increase in direct correlation with the spacing distance between handholds and in this regard, a gibbon will rely on two different types of gait depending on the distance that needs to be covered between handholds. At distances of less than 1.20 meters, gibbons will often use a continuous contact gait (can be closely compared to bipedal walking). At distances of greater than 1.60 meters, a moderate to fast velocity gait would often be used, also known as ricochetal brachiation (akin to bipedal running). A brachiating gibbon
usually produces a positive horizontal force (propulsion) during the first half of limb support and then a negative force (braking) during the second half for both continuous contact and ricochetal brachiation. The time of connection between limb and handhold decreases as stride length and gait increases and brachiation is an incredibly effective mode of transportation as it allows the gibbon to minimize its metabolic expenditure while keeping stride parameters virtually unrestricted (Chang et. al., 2000). Once handhold contact is made, gravity works to propel the gibbon forward until mid-support, where it then decelerates the gibbon after the fact. Conversely, bipeds (as were previously discussed) are decelerated by gravity immediately after ground contact and then accelerated forward by gravity during the second half of the step. Human gaits can be described by an inverted pendulum (bipedal walking) or a spring-mass system (See Figure 5), which is applicable to bipedal running.

In the inverted pendulum model of walking, higher levels of potential energy at midstance are converted to kinetic energy as the following foot contacts the substrate; this kinetic energy is converted back to potential energy as the CoM is lifted as it hits midstance once again. At higher speeds, the inverted pendulum-exchange is no longer an efficient model so the gait is switched to running, more akin to a spring-mass system that describes the bounce-like behavior with an exchange of both potential and kinetic energy with strain potential energy of the limb muscles and connective tissues (Bertram, 2004). The model most useful in understanding the physics of brachiation is a regular pendulum. In this model, the pendulum swings from an initial height and is accelerated by gravity until it reaches its lowest point, where gravity works to decelerate it. Gravity will decelerate the pendulum when its maximum height is achieved and then accelerate it forward again. This model is most useful in understanding how brachiation is so energy efficient for the gibbon, especially considering that unlike terrestrial mammals that employ a bouncing spring-mass mechanism, gibbons do not possess long slender elastic tendons that can act as

![Spring-mass model](image)

*Figure 5: Spring-mass model used to describe bipedal running.*
effective strain energy storage and recovery. This is particularly important to keep in mind since gibbons spend 50% of their day in “traveling behavior,” 80% of that traveling being done by brachiating. Both continuous contact brachiation and ricochetal can be executed passively without muscle power, making brachiation and the pendulum model mechanism the least strenuous method in terms of metabolic output (Bertram, 2004).

**Continuous-Contact Brachiation**

In order for brachiation to remain an effective and efficient mode of transportation, it must allow the gibbon to travel along a smooth trajectory with the least amount of energy loss and expenditure possible. The most effective swing period is determined by the geometry of the mass distribution around the swing pivot (for example, the handhold or wrist). Active gibbons in an adequate brachiation environment appear quite unrestricted in both “step” length and speed of propulsion and are able to redistribute their weight during brachiation in order to convert their angular momentum in such a way that increases their angular velocity. In continuous-contact brachiation, this will occur if the end of the previous swing intersects with the arc of the following swing. For this type of gait, it is best if the handholds are spaced apart slightly less than the full arm spread of the gibbon, making it so that the CoM is slightly lower than the handholds, but both handholds can be reached simultaneously if the gibbon reaches both arms out (around a 1.2 meter arm span) (See Figure 6).

![Figure 6: A typical stride of continuous contact brachiation showing support and swing phases for one limb. Shaded limb shows alternation between support phase (A-C) and swing phase (C-E).](image)

In this regard, the pendular action of the animal is maximized, resulting in an overall minimization of potential energy loss. Generally, even for distances of twice the animal’s arm length, so long as the gibbon executes the swing smoothly into the transition of the next contact, the animal is not restricted in the path that it selects to make that transition (Bertram, 2004).

However, the optimum brachiation gait for closely spaced handholds is continuous contact. In this gait, there are two basic strategies for minimizing energy loss. First, actively transferring the CoM from its natural trajectory of one handhold to the next. This
would be executed most effectively at the top of the swing, where the arm actively flexes from the previous to the subsequent swing, moving the CoM horizontally to the desired appropriate location. If this transition is done properly, the velocity at the top of the swing is near zero and the animal effectively reaches equilibrium with the gravitational acceleration acting on the swing. This (start to finish) would only require a very small amount of metabolic expenditure on the gibbon’s part. The second strategy is using any excess energy from the first swing and immediately storing it so it may be used as potential energy for the next swing (Bertram, 2004). This is an especially effective way to make sure that the animal has enough energy to make the second swing in the first place and, if the second handhold happens to be a bit further away, the excess energy will provide the gibbon with enough propulsion for it to bridge the gap to avoid falling (which can result in severe injury or death).

During continuous-contact brachiation, it is common that gibbons will actually “overshoot” the target handhold, which allows the excess mechanical energy to be maintained with a high amplitude swing (Usherwood, 2003). Other mechanical techniques used by the gibbon to ensure the completion and energy efficiency of the swing are the trailing-arm bend and leg lifting. The trailing-arm bend (with the arm not actively gripping the superstrate) during continuous-contact brachiation serves as an active muscular mechanism, which pulls the CoM backwards towards the first handhold and creates a looping path of the CoM. It is thought that this action serves to reduce energetic loss due to collision by two mechanisms, since excess mechanical energy in this strategy can be carried from one swing to the next as almost all energy is converted to potential. In this case, the CoM uses only a small amount of active muscular effort to help in the avoidance of large collision energy losses. Leg lifting can assist much in the same way as the trailing-arm except functions to alter the relevant arc after contact has been made with the second handhold resulting in improvements to collision geometry and a reduction in kinetic energy loss (Bertram, 2004).

Ricochetal Brachiation

For handholds that are beyond a distance where continuous-contact brachiation is comfortable and reliable, or a higher speed gait is necessary, gibbons will switch to a gait with a ballistic aerial phase known as ricochetal brachiation. Often, the
ballistic flight paths that require high-speed (ricochetatal) brachiation, distance between handholds can exceed four times the arm length of the animal. The greater the distance between the first handhold and the second, the greater kinetic energy content that will be necessitated to be converted to vertical velocity. A rapidly brachiating gibbon therefore needs more kinetic energy than potential energy in order to have adequate available kinetic energy that can be used to cross an extended distance between two handholds (Bertram, 2004). In ricochetal brachiation, the trajectory of the CoM at the end of the ballistic aerial phase must intersect with the swing arc around the handhold as the grip is transferred to that handhold (See Figure 7).

The transition from continuous contact to ricochetal brachiation can often be compared to the transition from bipedal walking to running. However, unlike the spring-mass system that we see in bipedal running, ricochetal brachiation more resembles the skipping of a stone across water. In this case, the trajectory of the CoM is evenly diverted from a downward fall to an upward propulsion (Bertram, 2004). This does not use the same energy storage and recovery system that we see with the spring-mass model or the inverted pendulum, instead the energy during ricochetal brachiation is available for use not because it has been stored and returned, but because it was never lost in the first place. Therefore, the energy that will be required for the subsequent swing will be available to the gibbon, provided the initial swing is smooth and the CoM follows the ideal flight path, which does not use much energy. The contact between the superstrate and the arm of the gibbon causes the same change in direction for the CoM as the water causes for the stone. For a ricochetally brachiating gibbon, as long as the transition from the aerial phase to contact is smooth, there will be no energy loss. Ricochetal brachiation with long aerial components termed, “bimanual saltatation,” is an important means

Figure 7: (A) depicting the continuous contact brachiation pendulum where velocity is zero at double contact, (B) depicting the ricochetal brachiation pendulum with a ballistic aerial phase.
for crossing large gaps, almost akin to “skipping” through the canopy. However, ricochetal is not entirely no-collision, and therefore is not entirely meet a no-energy-loss criteria. This is because during high velocities, there is a requirement to change from parabolic (ballistic) flight to suspended (swing) paths, which make the gibbon vulnerable to collision loss (Usherwood, 2003). In order to cope with the higher speeds and brief aerial phases necessitated by larger handhold spacing, the gibbon will subtly alter its CoM to compensate for the ballistic flight and subsequent collision with the second handhold. During the aerial phase, the CoM will follow a parabolic trajectory, during which no appreciable outside forces are able to act on it and its fixed path. The gibbon, however, is able to adjust its CoM in relation to “itself” by a series of pelvic limb extensions and trailing arm flexions. In this case, there will be a shift in the trunk in reaction to a leg extension or flexion, or bending or flexing of the trailing arm, resulting in the ability of the contact hand (hand which will collide with the handhold) to be properly adjusted without changing the position or trajectory of the CoM (Bertram, 2004). This will result in a nearly horizontal body position midflight and at initial contact. Should the gibbon overshoot the handhold, its overdeveloped, long pectoral limbs are particularly equipped to deal with preventing excess energy loss due to the collision. Gibbons in this case will respond to the overshoot and subsequent collision by posturing itself in such a way that it creates a perpendicular axis between the body and the CoM trajectory. This in turn creates a “double pendulum” where the arm pivots around the handhold (usually at the wrist and shoulder which are controlled by the large pectoralis and latissimus around the shoulder joint). The body itself will pivot around the shoulder, and the collision energy loss is therefore reduced since the translational kinetic energy of the body is slightly transferred over to the rotational kinetic energy. A gibbon overshooting during ricochetal brachiation may mean an imperfect contact with the target handhold and some collisional energy loss, but when a small undershoot could mean a complete miss and a fall from such great heights, the energy loss is a small price to pay considering the potential serious injury or death. However, should there be a slight undershoot, leg lifting and flexion can assist in rectifying a faulty pathway by lengthening the distance between the CoM and the hand. The CoM will remain on the same ballistic path while the extension of the leg can help
to drive forward propulsion and prevent a potentially disastrous miss.

The environment in which we see the most brachiation (high forest canopies in tropical and sub-tropical climates) are some of the most intricate and complex habitats on planet earth. These forests are three-dimensional in regard to the abilities that are necessitated by the gibbon in order to transverse it using “limb-contacts” and, because of brachiation, the gibbon is able to respond quite effectively to the handholds that might vary from one contact swing to the next (Bertram, 2004). This means that the ideal paths that avoid all losses due to collision are the ones where contact can be made with a new handhold only if kinetic energy is zero, or if the paths are perfectly matched, and so the angle between the handholds would prevent excessive inelastic tension collision. An angle too great between handholds or where the kinetic energy exceeds what contact can be made with no energy loss could best be comparable to a child on a swing. If the child swings too high and the swing ropes become loose, there is a sudden jerk as the swing and child plummet back down to earth and the swing comes to a sudden halt due to the change in velocity, angle and dissipation of kinetic energy. Since the gibbon applies no torque around the handholds, the angular momentum of the gibbon about the superstrate is maintained through the instant of collision, allowing momentum (both angular and linear) to be conserved and the associated rotational kinetic energy associated with motion about (or past) the handhold to remain unaffected. However, this does not mean that there is zero energy dissipation during the collision. The kinetic energy associated with the gibbon and the chosen handhold that translates towards or away from the handhold just prior to collision is lost and that energy loss is due to the collision having a difference between the total kinetic energy prior to collision and the kinetic energy associated with motion about the handhold post collision. However, no energy will be lost if the 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 the new handhold (Usherwood, 2003). The brachiation energy seen in the first swing is markedly greater than the minimum required to allow contact to be made with the second handhold. This allows the gibbon to maintain 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 summation, the gibbon’s elongated arms allow even weight distribution among branches, and improve chances of finding handholds and suitable support during brachiation, concurrently decreasing the number of necessary handhold changes. Those anatomical features combined with the pendulum-type mechanics seen in brachiation make it almost limitless in terms of locomotion speed, as well as extremely efficient in terms of low energy expenditure for both high or low speed gaits. These factors prevent the gibbon from ever having to descend to the forest floor, all while evading predation, having ample access to food and plenty of space and ability for social interaction (Usherwood, 2003).

**Brain Physiology**

While looking at the biomechanics of brachiation is certainly necessary in order to gain a better understanding of this mode of travel, it is only a small part of the picture. The neurophysiology of both the gibbon and the human play an important role in understanding not only brachiation, but how we have adapted as bipedal locomotors. This section seeks to inspire more interest in comparative neurological studies between humans and nonhuman primates in the hopes that it might shed some light on not only our development as a species, but how we might become better athletes, or even rehabilitate those suffering from brain injury. Locomotion requires the motor cortex and corticospinal outflow to be actively engaged when the appropriate limb is needed. This requires visuomotor coordination, which neurologically can be achieved by a connection between the motor cortex and interconnected parietal and cerebellar areas (Georgopoulos & Grillner, 1989). The motor cortex is involved when the gibbon reaches out to grasp a branch in preparation for a swing, or collision and the hind and forelimbs work together to propel the animal during locomotion and maintain its equilibrium. In contrast, humans are unique in that their forelimbs have been freed entirely from any role in locomotion (outside of when we first learn to move ourselves around by crawling and grasping on to things or if someone utilizes crutches due to an injury of the hind limbs), leaving that responsibility to the hind limbs. The forelimbs have thus developed to be geared more towards precision work and dexterity (Georgopoulos & Grillner, 1989).
In humans, the cerebellum is the second largest region of the brain (See Figures 8 and 9).

![Figure 8: Major areas of the human brain.](image)

![Figure 9: Human cerebellum.](image)

It coordinates motor output, measures body position and balance and comprises about 11% of the total brain. Comparatively, the cerebellum makes up 14% of the total brain in bonobos, 16% in gorillas, and 13% in gibbons. The lateral cerebellum expanded substantially in the ancestors of apes and humans. Given the importance of the cerebellum in both the planning and execution of motor tasks, visual-spatial skills and learning, this cerebellar expansion may underlie some of the greater cognitive abilities of apes and humans. To provide a bit of context when considering our ancestral lineage and the human brain, in early hominids, the cerebral hemispheres increased in size while the cerebellum remained relatively small. However, Neanderthals and Cro-Magnon “1” possess the largest cerebrum to cerebellum size ratio known in primates. When looking at more recent humans in comparison, the cerebellum as compared to the rest of the brain has increased and the relative size of the cerebrum has decreased. The cerebrum comprises a large portion of the brain and lies in front or on top of the brain stem. It is composed of the cerebral cortex, basal ganglia and the limbic system, which the cerebrum surrounds. The cerebrum codes for higher, more complex functioning in humans.
such as language, speech, thought, judgment, learning and working memory. The cerebellum’s intrinsic function in the motor capabilities in humans can be seen in the adverse effects of brain damage in that area due to trauma or disease. For example, a rare condition called “disequilibrium syndrome” caused by abnormal development of the cerebellum and abnormalities in the cerebrum cause the individual to be capable of complex coordinated movements, but incapable of bipedal walking (“The Cerebellum”, 2013).

Interestingly, the human cerebellum is in fact smaller than expected for an “ape brain” of human size. It is suggested that the cerebellum increased less than the cerebrum after the split of the human lineage from the African ancestral hominoid “stock” (Semendeferi & Damasio, 2000). Gibbons have a relatively smaller frontal lobe than the rest of the hominids and, in fact, the human frontal lobe is not drastically bigger than that of other nonhuman primates. This may suggest that the overall size of the frontal lobe as a whole has not changed drastically over the course of hominid evolution (See Figure 10). Overall, humans have the largest brains followed by the great apes (such as gorillas) and then the small-bodied gibbons. Among the great apes, orangutans have the largest brain (being counted as the two hemispheres and the cerebellum together) followed by gorillas, bonobos and chimpanzees. With respect to cerebellum size, gorillas show the largest, followed by orangutans, bonobos and then chimpanzees. Among the apes, orangutans have the largest frontal lobe followed by the

Figure 10: Comparison of brains of referenced living hominids.
gorilla, the bonobo and the chimpanzee. These comparisons go to show how little we know about what relative brain size might mean for capability in complex thinking or tasks (See Appendix A, figures 11-14 for comparative neuroanatomy). It is interesting how the frontal lobe is smallest in the chimpanzee, when we might initially think the chimpanzee to be the most capable in terms of task performing and short-term memory; even the gorilla who is thought to be capable of learning sign language has a frontal lobe smaller than that of the orangutan. So, does size have anything to do with cognitive capability? Or is it instead the wiring that dominates in terms of capacity for complex thought processes and motor function? The frontal lobes make up 35-38% of the hemispheres in humans, 36% in the orangutan, 35% in the gorilla and 34% in the chimpanzee. The gibbon has the smallest frontal lobe, which makes up 27-2% of the hemispheres. But the most compelling contrast is in both the parieto-occipital regions of the brain, which is in charge of integrating sensory information from somatosensory and visual input. In this case, it is the gibbon (along with the gorilla) that is on the higher end of the size range with 39% of the brain being taken up by parieto-occipital lobe function. Humans fall on the lowest end with orangutans, with 36% and 35% (respectively) of the brain designated to parieto-occipital lobe activity (Semendeferi & Damasio, 2000). It is noteworthy that gibbons rely so heavily on somatosensory and visual input in the closed tree canopies where they dwell; while they are small bodied apes with smaller brains relative to great apes and humans, a much larger percentage of their brain space is allotted to integrating that sensory input. Interestingly enough, however, the largest cerebellum was in fact not found in arboreal species such as the gibbon (it was initially predicted this small agile creature who relies so heavily on fine motor capabilities would have the largest cerebellum) but instead in the larger terrestrial species such as the gorilla (Semendeferi & Damasio, 2000). However, it must be taken into account that very little research has been done in this area, and it is entirely possible that the larger cerebellum is correlated more so the brain being large as a whole, or potential outlier effects.

Overall, it is not the size of the frontal lobe as whole that distinguishes the human brain amongst the hominids, as it is not necessarily larger than expected for an ape brain of human size. The compelling difference lies more in humans having a relatively larger prefrontal sector, which
deals mainly with emotions, personality expression, moderating social behavior, and decision-making (including the processing of risk and fear). This expansion of these prefrontal projections could explain the evolution of higher cognitive functioning in humans compared to primates. Ostensibly, this enlargement of the prefrontal cortex is what makes us human. Furthermore, humans have enlarged prefrontal grey matter compared to nonhuman primates, including the expansion of white matter in the prefrontal cortex. This provides supporting evidence for the argument of tandem development in the brain between segments that share reciprocal connections. This theory is called “concerted” evolution and suggests that evolutionary pressures cause development of the brain as a whole functional unit, as opposed to the evolution of individual brain segments (Balsters et. al., 2009). Remarkably, studies have found that the lobules that form the motor loop in humans (the cerebellar cortex has connections with both the prefrontal cortex and motor cortex forming reciprocal pathways with each) are significantly larger than those found in other primates such as chimpanzees and capuchin. The lobules related to motor and prefrontal cortex function together occupied 83.7% in humans and 67.1% in chimpanzees, showing a greater proportion of these lobules in the cerebellum in humans than in other nonhuman primates (Balsters et. al., 2009). Expansions seen in the cerebellar cortex from an evolutionary standpoint seem to correspond approximately to expansions observed in the prefrontal cortex, arguing the evolution of the brain as an interconnected entity. One part cannot evolve and develop further without other reciprocal areas following suit. So while it could be argued that chimpanzees have better balance, precision grip strength and agility than humans, the human brain has evolved further than nonhuman primate’s when it comes to cognitive ability; therefore, other reciprocal areas of the brain have become larger and more developed in tandem. However, in keeping with this recognition of nonhuman primate’s innate locomotor capabilities, where we see an increase in size in the prefrontal cortex in humans, there is also a proportional decrease in the size of the motor cortex (even though it is still larger than that of chimpanzees, the chimp motor and prefrontal cortex are much closer in size). This discrepancy in size could be a result of positive selection in the species’ recent past. For nonhuman primates, it could have been more beneficial to have a brain that
developed the prefrontal cortex and motor cortex to take up similarly sized cerebellar components whereas in the human brain, the prefrontal cortex is proportionately larger than the motor cortex, and larger than that found in nonhuman primates.

**Human Rediscovery of Brachiation**

While we can hardly argue humans have the physical capability to take on brachiation as a reasonable form of locomotion, or the social structure to accommodate such a monumental change from substrate dependence to superstrate, humans have “rediscovered” brachiation in other ways. First, in a way that is most obvious, there has been much research done in the brain injury sector, especially in regard to children, surrounding how to best treat and rehabilitate young children that have suffered some type of trauma or have a debilitating neurological disorder such as cerebral palsy. All babies are born with a branch-holding reflex; in fact, infants are pound-for-pound incredibly strong, and are capable of holding themselves suspended by grasping a finger or bar. “Brachiation ladders” have been built and used for treatment of children as young as infants who suffer from cerebral palsy, autism and brain injuries. Brachiation exercises the neomammalian brain along with the scapulohumeral muscles, including the deltid, teres major, coracobrachialis, and the four muscles that make up the rotator cuff (“Brachiation”, 2013). The reason the brachiation ladders have become such a monumental development in the rehabilitation techniques for children with brain injury is because not only does it stimulate and challenge the child’s body physically, brachiation exercises each hemisphere of the brain independently as the child swings from left to right by alternating hands with each swing and collision (“Brachiation Kits for Cerebral Palsy”, 2013). This neurological stimulation creates and strengthens new synaptic connections that would either not have been made in the first place, or would have become weakened and died from lack of excitation. It is possible that through these brachiatory exercises, certain pathways in the brain that were damaged by injury or disease could be strengthened or even fixed.

From an athletic standpoint, gymnasts who utilize the uneven bars are ostensibly brachiating. The grips and swings that are used in order to move from one bar to the next often include some continuous-contact gaits and gaits that require a brief ballistic aerial phase (not unlike brachiation). The
grips gymnasts use also hold striking similarities to those employed by a brachiating gibbon and it is notable that a gymnast leaping from one bar to the next will utilize a slight overshoot in order to ensure the collision with the bar, or risk a fall most likely resulting in injury and definitely resulting in point deduction (“Uneven Bars Skills Terminology”, 2013).

Conclusion

Understanding how species navigate and locomote through their particular environments can shed light on how selective pressures act on certain communities of organisms. While it is clear that humans have developed away from brachiation being a useful form of transportation considering our reliance on bipedalism and traveling over substrate, as opposed to underneath it, much can be learned of our ancestral lineages in looking at brachiating apes as a major player in our evolutionary trajectory. Furthermore, based on the foregoing, it is readily apparent that studying the biomechanics and neurophysiology of brachiation not only provides the psychological and scientific community with useful information that can better our understanding of human ancestral lineages, but can also teach us how to better train our athletes or perhaps more effectively rehabilitate or even treat brain injury.
References Cited


Appendix A

Figure 11: Human Brain.
Figure 12: Gibbon Brain.
Figure 13: Gorilla Brain.
Figure 14: Chimpanzee Brain.