ANTHR 1-L: Biological Anthropology Lab **Name**____
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BUILDING BODIES
Primate Bipedalism: Understanding Standing Up

THE BIG IDEA: Bipedalism, walking on two legs, is one of the major biological innovations of the human lineage. Combined with other characteristics, it makes us unique. Members of the human lineage developed this locomotive pattern perhaps as long ago as 6 million years, nearly four million years before evidence for increased brain size and the regular use of stone tools. The Laetoli trackway, dated at 3.6 million years old, provides one of the most powerful and persuasive bits of early hominid behavior and anatomy. These tracks confirm and extend other fossil evidence that indicates changes in locomotion were among the earliest human characteristics to appear in our ancient forebears.

BACKGROUND: There's little doubt that the great apes, especially chimpanzees, have a great deal in common with humans. Their anatomy, DNA, and even their behavior come so remarkably close to our own that we find ourselves captivated by them. Some have seen them as models of our ancient relatives, creatures in many ways nearly human, but not quite. These distant cousins may indeed give us hints into the lives of our early hominid ancestors who emerged in Africa. Remarkably, even Charles Darwin had correctly predicted in the 1870s in his *Descent of Man* that the ancient ancestors of modern humans had their origins in Africa.

A century ago there was little direct fossil evidence to show the sequence of events in human evolution. One popular expectation was that increases in brain size, and thus cranial capacity, preceded other changes in the human lineage. Human intelligence was thought by many to be a key characteristic in human origins. Changes in posture, locomotion, diet, behavior, jaws and teeth, etc., were expected to come later.

Ultimately, the fossil evidence, thousands of specimens of early human and prehuman hominids to date, showed that this brain-first scenario was not correct. An extensive fossil record has since then provided definitive evidence for a sequence of events that began with human ancestors first walking upright, but developing bigger brains, tool use and manufacture, and a rich and varied material culture much later, over the course of several million years of evolution.

Human bipedalism is one of the most unusual forms of locomotion to have evolved in the animal kingdom. The biomechanical difficulties associated with moving the body forward and balancing it above two limbs have led to a number of anatomically unique specializations (Tattersall, et. al, p. 394). Despite obvious disadvantages to our hominid forebears like the greater difficulty of young learning to walk, humans have successfully capitalized on these newfound abilities to the extent that the evolution of bipedalism is arguably the most important adaptation in the early part of human evolution.

Although chimpanzees are capable of upright walking for short periods, it is less energetically efficient than human bipedalism. By comparing the skeletal and muscular anatomy of humans and chimpanzees we can speculate what changes in anatomy were necessary for accomplishing this transition to upright walking in our hominid ancestors. Bipedality, the definitive characteristic of the human lineage among primates, is just the first in a series of anatomical modifications that have shaped our destiny as a species.

SELF CHECK: Based on your reading of the previous Background Information, check your understanding at this point by answering the following questions.

1. Fossil and other evidence indicates that the first major innovation in hominid evolution was:

a) increased brain size
b) tool making
c) material culture
d) bipedal locomotion

2. Current evidence indicates that hominids first emerged in:

a) Africa
b) North America
c) Asia
d) Indonesia

PART 1: Modern Clues to Bipedality: Comparing Anatomy of Humans and Chimpanzees

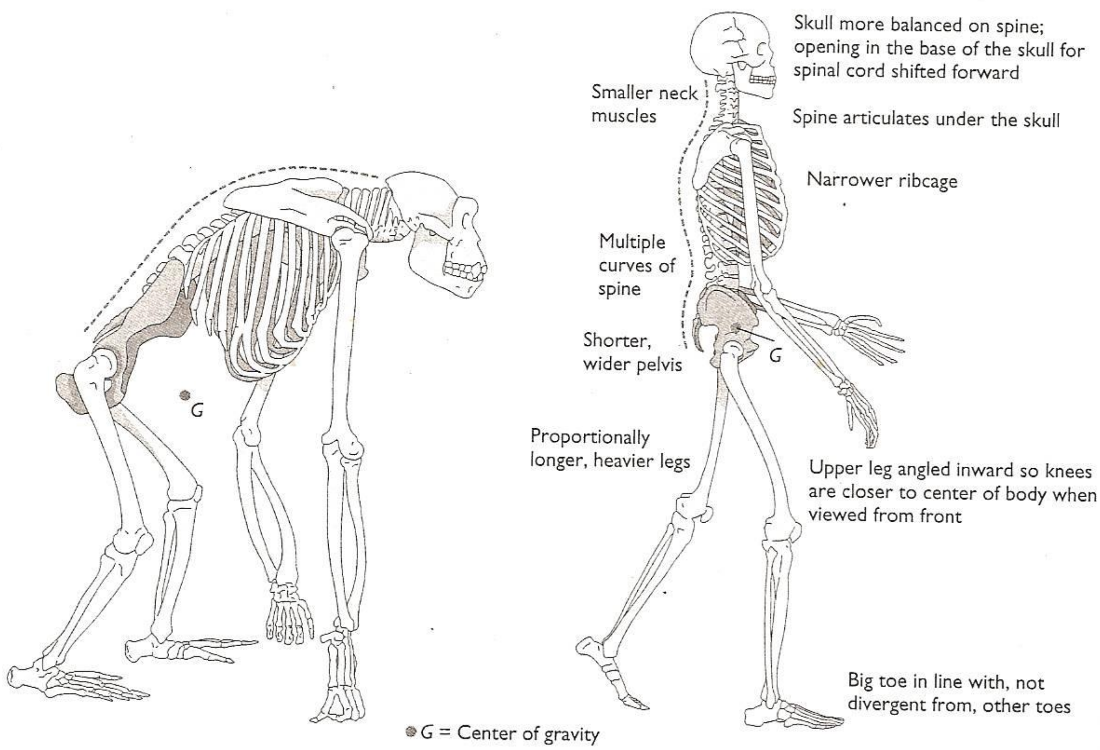
Fortunately for us, an ancient ancestor of modern chimpanzees also left descendants that eventually developed upright walking, tool making and bigger brains. We are the result of these changes in an evolutionary history spanning 6-8 million years. As important and profound a change as it may have been, the transformation from walking on all fours to walking upright on two legs among primates is not as drastic a transition as it might first appear. Unlike the quadrupedal locomotion typical of dogs or horses, many four-legged primates regularly stand upright and some can even walk upright (for short distances and duration). These observations lead some scientists to view human upright posture not as a unique trait of human evolution, but as a primate evolutionary trend.

So why don't apes walk upright like us? With so much already in common with humans, what prevents apes from habitual bipedal locomotion? Though apes can walk upright for short periods, it is less energetically efficient. Anatomical differences which among other things produce a higher center of gravity, result in a stooping upright posture that requires the use of the hands to periodically prop up the chimpanzees and gorillas. Unlike a human's fluid gait, a chimpanzee attempting to walk upright show a noticeable side to side rocking as each step is taken forward in order to keep the body balanced over widely spaced legs. The more graceful human motion results from modifications of the pelvis, legs, and foot which have produced shifts in the center of gravity and noticeable improvements in the ability to balance on each leg as a stride is taken. Also, changes in the positioning of the skull on the spine insure a natural angle for carrying the head and being able to look forward while walking.

Anatomy of Bipedalism

Note the anatomical differences between the quadrupedal ape and the bipedal human skeletons in the illustration on the following page. The features pointed out in the illustration represent the physical evidence associated with bipedalism in the human primate. Compare the human features with corresponding ones in the quadrupedal ape. *G* represents the center of gravity when standing bipedally. The ape expends much more energy to keep from falling forward.

Figure 1: Anatomical evidence for bipedalism



CHECK QUESTIONS: Using the figure above as a reference:

1. Compared to chimpanzees, humans show relative shortening of the arms and lengthening of the legs.
a) True
b) False

2. The center of gravity while walking is different for a quadruped (ape) as compared to a biped (human).
a) True
b) False

3. The human pelvis is long and narrow providing little support for internal organs, and little surface area for the attachment of large buttock muscles in standing and walking upright.
a) True
b) False

4. The human foot has a divergent big toe, giving the foot a strong and efficient grip.
a) True
b) False

PART 2: Interpreting Ancient Hominid Tracks
Most scholars have concluded that early human ancestors never did pass through a dedicated knuckle-walking phase, but became bipedal hominids soon after leaving the trees. In fact, recent studies of orangutan locomotive behavior suggests that bipedalism may have emerged in the trees, thus, giving the earliest hominids a "pre-adaptation" for terrestrial bipedal locomotion. But actual evidence of how early human ancestors may have walked seemed remote and unlikely to be found until, in 1976, a team led by Mary Leakey discovered the fossilized footprints of human ancestors at Laetoli, Tanzania. Dated at 3.6 million years, these tracks provide a direct record of early hominid locomotion that can help us understand their anatomy and behavior. The trackways were made when a few individuals walked across an African plain recently covered by ash and rain from a volcanic eruption. The wet ash hardened like cement and then was covered by more ash and sediments. The tracks are as unmistakable as they are remarkable. An early hominid had developed upright posture and was, several million years ago, already walking capably on two legs across Africa, the continent of human origins.

Recall from Part 1 that chimps have a strongly divergent big toe. A modern human foot has an arch and strong heel strike, and so did the individuals that left their footprints in the Laetoli trackway. This seems to suggest that these early hominids were strong walkers. Yet, without actual bony fossil evidence, conclusions about their anatomy can be difficult.

Depending on how the known bony fossil evidence has been interpreted, early hominids may have had a slightly bent, bow legged, and bent-kneed gait similar to that of a chimpanzee attempting to walk on two legs, or a longer striding gait similar to modern people. But these tracks, which provide distinctive evidence of a strong heel strike, distinct arch, and non-divergent big toe support the latter conclusion. Very likely able to forage over long distances, these creatures were walking like us nearly four million years ago.

PART 3: Fossil Evidence and Mosaic Evolution of Hominids.
To date, the bones of thousands of fossil hominids have been unearthed, representing a number of distinct taxonomic groups dating back to about 6 million years ago. Most such fossils are fairly fragmentary, often just a single bone. However, sometimes several bones from a single individual are found together. On rare occasions, a large portion of an entire skeleton may be preserved. These more complete remains allow scientists to reconstruct body size, shape, and proportions with some confidence.

One particular discovery that had a profound impact on our understanding of human evolution occurred in 1974. In that year, a team led by Donald Johanson discovered the now famous "Lucy" fossil at Hadar, Ethiopia. This partial skeleton, along with hundreds of additional fragmentary fossils of *Australopithecus afarensis* is close to 3 million years old. Not only was this the oldest so-complete hominid ancestor ever discovered up to then, but it also possessed a range of characteristics that confirmed that fully capable bipedalism started very early in the evolution of the hominid line. These and other finds of *Australopithecus afarensis*, show that early human ancestors had already developed a host of physical traits to make efficient bipedal locomotion possible.

Though small relative to humans, Lucy and her kin were relatively human like from the neck down, but remained much more apelike from the neck up. Increases in cranial capacity did not occur for almost another million years. Here then was a mosaic pattern of evolution. Our ancestors continued to evolve above the neck after most of the rest of the body had essentially reached a modern form capable of walking upright.

Later discoveries of hominid species pre-dating *Australopithecus afarensis (*Lucy's species*)*, would provide further confirmation of the bipedal adaptive pattern in the earliest hominids. These fossils belong to a new genus & species of hominid known as *Ardipithecus ramidus.* Like Lucy, in the 1970's, "Ardi," as this species has come to be nicknamed, is an extraordinary find due to the completeness of the skeletal material. But unlike *Aus. afarensis*, Ardi evolved in a much more arboreal context. This key discovery has overturned a long standing scientific hypothesis associated with bipedalism; that our ancestors only became bipedal once the forests began to decline and the grasslands (savannas) begin to open up, creating distance between trees (the Savanna Hypothesis) due to selective pressures associated with major changes in climate and thus, the landscape.

Ardipithecus ramidus, however, exhibits very clear skeletal adaptations for bipedalism including: a slightly less elongated pelvis with a broader pelvic opening, and a femur slanted towards the knees. These features, however, are accompanied by some arboreal adaptations in the skeleton including: elongated finger and toe bones (to enhance grasping ability), a divergent and grasping big toe (unique among all known bipedal hominids to date) and extremely long upper limbs. While longer upper limbs are generally associated with the knuckle-walking great apes (chimps, gorillas, and orangutans when terrestrial), Ardi's wrist bones do not exhibit the knuckle-walking adaptions of the great ape species. Given the dense forest habitat in which Ardi's remains have been uncovered, the arboreal adaptations seen in Ardi's skeleton suggest that these locomotive patterns remained advantageous in such a context, although bipedalism provided additional selective advantages. This is why recent research into the origins of bipedalism is now shifting towards the one great ape species that is the MOST arboreal (and interestingly, most genetically distant from humans): Orangutans. Understanding how Orangutans have developed their acute sense of balance and upright posturing in the trees may provide clues as to how these behaviors served as "pre-adaptations" for our earliest bipedal ancestors.

The unique combination of features exhibited by *Ardipithecus ramidus*, combined with its age range of 5.8 – 4.4 mya, warranted its assignment to a new genus and species. As the oldest ***confirmed/established***, biped in the hominid lineage, "Ardi" pushes the origin of bipedalism back even further than Lucy's species. Moreover, Ardi's features remind us that although bipedalism was an important evolutionary turning point, other more human-like features would not be selected for until much later in time. Only modern genetic analysis and the discovery of additional fossil material will eventually help us to piece together and understand the selective pressures operating in hominid populations in the past.

CHECK QUESTION

1. Fossil evidence from specimens of *Australopithecus afarensis* and *Ardipithecus ramidus* indicate that:

a) All anatomical traits of hominids evolved together at the same rate and time
b) Some traits, like those that make bipedalism possible, evolved first, with other traits like a bigger brain, evolving later
c) No pattern is discernible in the fossil record since modern humans and their ancient relatives remain unchanged throughout their history.

PART 4: Walking Upright: Consequences, Benefits, and Causes.

Certainly one of the greatest challenges to paleoanthropologists who study human evolution is to understand why early human ancestors stood up. Though the fossil record of apes remains sparse between 4-12 million years ago, it appears that successful and expanding monkey populations in the trees, during a global climate that had become much cooler and drier, increased competition for food in the forests. Current evidence supports the conclusion that early apelike ancestors became bipedal while still in this familiar forest environment.

A large number of hypotheses have been offered for the evolution of bipedalism including: energy efficiency, temperature regulation, food gathering, and predator avoidance & threatening displays. But these are largely secondary causes that leave little, if any, clues in the fossil record. Many anthropologists concede that scientists may never know with certainty why hominids stood up and began walking on two feet. But certainly the evidence leads us to conclude that the events that happened so early in the hominid line had profound effects on our anatomy and evolution. It seems in some ways ironic that common ailments such as low back pain, herniated vertebral discs, fragile knee and ankle joints, and flat feet are all a reflection of imperfections in the structures that evolved to allow biomechanically efficient bipedal locomotion.

CHECK QUESTION

1. Human anatomy which evolved to facilitate bipedal locomotion can best be described as:

a) A functional compromise of workable, though rarely perfect, physical adaptations limited by modification of existing structures inherited from ancient quadrupedal primate ancestors.
b) A complete collection of perfect adaptations that allow us to move faster and more efficiently than any other mammal.
c) Unchanged and no different from modern ape anatomy.

Part 5: The Hallmark of Humanity
Bipedalism is indeed a hallmark of humanity. Human bipedalism is also unique in its striding gait. Although most of us walk every day, we rarely think about the "mechanics" as we are doing so. In bipedalism, the walking cycle has two phases:

1. **<u>The Stance Phase</u>** – In the stance phase, the foot is in contact with the ground and supports the weight of the body. This phase has three parts: the heel strike, the flat foot (or midstance), and the toe-off (leaving the ground for the next step.

2. **<u>The Swing Phase</u>** – In the swing phase, the foot comes off the ground and is being repositioned for the next stance phase. Here, the leg comes forward and around toward the center (called *adduction*). In humans, some of the gluteal muscles are positioned on the side so we don't fall over to the side when one foot is off the ground. Our legs come in at the knees so the center of gravity doesn't have to be shifted laterally back and forth much when walking.

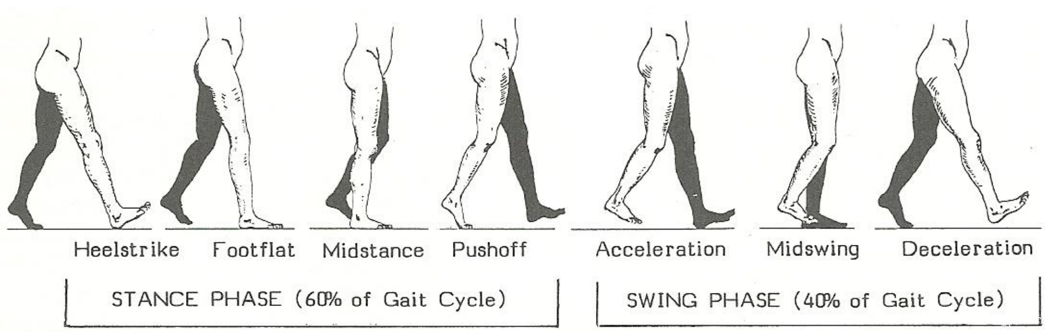


Figure 4.19. The complete gait cycle: stance and swing. Walking is a purposeful disturbance in body equilibrium during which alternating leg displacement sustains body weight.

Compared to most other animals, humans are “unbalanced” in locomotion. Think about it: We are balancing all of our weight on just one leg about half the time we are walking! This causes balance problems that are dealt with by our having redistributed (during our evolutionary past) the orientation and function of various muscles and their associated skeletal supporting structures.

Three main aspects of our locomotion are:

1. *Propulsion* (push-off),
2. *Stabilization* (so we don’t fall over trying to balance on one leg), and
3. *Adduction* (our leg swings around to the center with each step).

Certain muscle groups allow each of these actions, and we will see the differences in the hip and leg bones in humans versus apes resulting from this difference in muscle function.

CONCLUSIONS

In future years, it is certain that paleoanthropologists will continue to unearth fossil evidence which helps us to better understand the events and physical changes that define the evolution of our species in the process of becoming human. Though it remains uncertain whether physical evidence can be found to help us understand what *specific* selection pressures may have contributed to our development as a biped, a number of hypotheses remain intriguing. The greatest advantage of bipedalism was most likely the *adaptive flexibility* this allowed early hominids who found themselves in ever changing environments and habitats.