Bipedalism

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Bipedalism, or locomotion on two legs, is one of several characteristics of humans that is unique among the primates. Bipedalism, in the human context, is the condition of standing or moving on two legs, compared to the four that most other terrestrial animals use, although it should not be forgotten that bipedalism in trees and shallow water is also possible. *Homo sapiens* is said to be an obligate biped, in the sense that people have little other option as a mode of locomotion. Chimpanzees and gorillas, by contrast, are said to sometimes exhibit facultative bipedalism, in that they can move bipedally when they choose but usually decide not to.

Some believe that the earliest hominins were facultative bipeds. One of the key challenges for paleoanthropology is to understand how early, apelike, facultative bipedalism evolved into our current obligate form.

Phylogeny of bipedalism

Bipedal locomotion has evolved several times in land-dwelling vertebrates (termed "tetrapods"). Some exhibit forms of obligate bipedalism but none of these forms are like our own. The earliest evidence of bipedalism is a long-extinct reptile, *Eudibamus cursoris*, dated to approximately 290 million years ago (Ma), although better-known examples are found among the theropods, a major clade of the dinosaurs, such as *Tyrannosaurus rex*. They lived in the Jurassic and Cretaceous eras (ca. 200–65 Ma).

Extant lizards, such as the genus *Basiliscus* of Central America, have been observed "running" bipedally on the surface of water and, of course, almost all birds are bipedal when they are not flying. The clade *Palaeognathae*, comprising cassowaries, emus, kiwis, ostriches, and rheas, is flightless, so its members are even more strictly obligate bipeds than humans.

There are also several notable examples of bipedalism in the Mammalian class. Perhaps the most important are the macropods (kangaroos and wallabies), mainly native to Australasia and New Guinea. They are characterized, primarily, by having a lengthened and narrowed hind foot—hence "macropod"—and often a large tail that can act as a third foot. Kangaroos, when moving slowly, tend to do so pentapedally, using all four limbs and their tails. Kangaroo rats and kangaroo mice (Heteromyidae), like macropods, also have large hind limbs, which appear to be adapted to a peculiar form of leaping bipedalism.

Relatively infrequent incidents of facultative bipedalism have also been noted in the Mammalian order Artiodactyla, the even-toed ungulates. For example, gerenuk

(*Litocranius walleri*) are well known to stand on their hind legs to reach foliage from branches in trees that they would not otherwise be able to access.

In the order Carnivora, too, examples of infrequent facultative bipedalism can be found. One cat-like carnivore genus is *Suricata* (the meerkats), which feed mainly on insects and small animals such as lizards. Meerkats move quadrupedally almost all the time but they are noted for a peculiar type of sentinel behavior where they adopt a bipedal posture and stand still while they seem to be on the lookout for predators or prey.

Among the dog-like carnivores are the bears, which also move almost exclusively quadrupedally. However, they are also known to adopt bipedal postures, and even use bipedal locomotion, from time to time. Scenarios include threat display and sentinel behavior, such as looking out for prey. This has sometimes been observed in water—for example, when brown bears hunt salmon.

The order in which humans are embedded is, of course, Primates, which comprises some 200 species. Most primates are arboreal, especially the smaller species. Small primates are able to move along the tops of branches by scrambling along quadrupedally but larger primates naturally find this more difficult and their locomotor repertoire usually includes below-branch brachiation (swinging) and vertical trunk climbing. This size increase also appears to provide a propensity to upright posture and bipedalism, evidenced by various examples.

The lemurs, uniquely isolated in Madagascar for at least 20 million years, have experienced an adaptive radiation, where their common ancestor evolved into a variety of related species, each adapted to different niches. Some have become larger, some smaller. Genera such as the sifaka, which has a body weight of between three and seven kilograms, are large enough to require a more vertical posture in trees and appear to have evolved a locomotor specialism for leaping from tree to tree using their powerful hind limbs. Sifakas are also notable for their mode of locomotion on the ground, using bipedal leaping, throwing their arms above their heads for balance. Similarly, in South America, among the five major families of New World monkeys (Platyrrhini) is the Atelidae, which contain some of the largest animals living on that continent. The spider monkey (*Ateles geoffroyi*) is well known for its characteristic prehensile tail, which it can use to hold on to and swing from branches in trees. Spider monkeys are almost totally arboreal and are very adept climbers and brachiators, but they are known to adopt a rather humanlike form of bipedalism when on the ground. With their long tails held erect, they walk upright with bent hips and knees.

Even larger, and more adept in trees, than spider monkeys is a genus of tailless primates, called *Hylobates*, including the lesser apes, gibbons, and siamangs. They inhabit Southeast Asia and much of the Indonesian archipelago. They are certainly the most adept brachiators of all the primates. Like the spider monkey, they rarely come down to the ground, but when they do they adopt a similarly bipedal posture and mode of locomotion. Their propensity to bipedal locomotion led some early anthropologists to suggest that human bipedalism evolved from such forms.

Larger still are the three major genera of great ape: *Pongo* (orangutans), *Gorilla*, and *Pan* (bonobos and chimpanzees). They are less adept at brachiation than Hylobates, although *Pongo* does spend much of its time moving in trees suspended below branches.

Due to their large size, they have a propensity to adopt an upright posture when in trees, as their size precludes them from the smaller horizontal branches. Upright climbing is a major component in their locomotor repertoire and, according to Hunt (1994), postural feeding in trees is also strongly correlated with their occasional (approximately 2–3 percent) bipedalism. On land, great apes are most likely to move quadrupedally. Orangutans tend to move quadramously (on four hands), while chimpanzees, bonobos, and gorillas exhibit a peculiar form of quadrupedal locomotion called knuckle walking.

Apes have been observed moving bipedally while carrying things, although they can also do so tripodally. They can carry objects in their mouths or, in the case of infants, on their backs, while moving quadrupedally. Another scenario where great apes are sometimes bipedal is during threat displays. In particular, gorillas are well known for their exhibitions of chest beating. Finally, it should be noted that, although the great apes are rarely seen moving through water, when observed doing so in depths around their waists, they appear almost obligated to move bipedally.

Early development of the capacity for human bipedalism

Human infants are born unable to locomote (move from one place to another) on their own. Only after about a year do they start to exhibit obligate bipedalism. The development of this ability is innate but also requires learning and support at key stages. The earliest trace of a future locomotion capability in the human embryo begins with the development of limb buds when the embryo is about four weeks old. These buds form four standard pentadactyl limbs that, in the adult, will comprise thirty bones each, in three sections: one bone closest to the trunk, two intermediate and the rest most distal. By the eighth week of gestation, the arms have rotated medially and the legs laterally, so that the elbows flex toward the front while the knees flex toward the back. The digits of the hands and feet become separated around this time too. Muscles and innervation form during these phases and limbs begin to move almost immediately. The limbs continue to grow in size throughout pregnancy and by the third trimester the fetus starts to exhibit complex movements in utero.

After birth, it takes six to nine months before infants are able to locomote on their own. At first they move quadrupedally, crawling on their hands and knees. A relatively easy and stable form of locomotion is thus learned, with a diagonal interlimb support pattern (left hand and right knee followed by right hand and left knee) being commonly adopted. As infants develop limb strength and muscular coordination, they gradually learn to pull themselves up and stand on their two hind limbs. With parental encouragement and support, the first steps are usually made between nine and twelve months, and by eighteen months most infants have already selected bipedalism as their usual mode of locomotion. Walking is remarkably difficult to do, as evidenced by the sophistication needed to simulate it in robots, but human infants are able to acquire the skills and muscular coordination to do so with little help, through a combination of innate psychomotor instinct and basic trial and error.

Kinetics of walking

Although humans are bipedal when standing and running, walking is by far the most common mode of locomotion for our species and therefore it is the aspect of bipedalism that perhaps needs the most attention. It is a unique form of bipedalism in the animal world, characterized by a vertical body and long, extended limbs. While striding, the body propels itself forward through momentum, with little muscular work. It is known as an "inverted pendulum" gait and it is energetically efficient, at slow walking speeds on flat ground, compared to other modes of locomotion in other animals.

The human gait is cyclical, but it is said to start with a "heel strike," the moment the foot touches the ground. This marks the start of the "stance phase" of that (extended) limb, which takes up approximately 60 percent of the gait cycle. At this point, the other limb is still in contact with the ground too, although it is just about to start its own "swing phase." By the middle of the stance phase, the whole body is supported on one leg, with the abductor muscles at the hip acting to counter the effect of gravity on the body. The walker continues to move forward largely through his or her own momentum. The stance phase ends with "toe off," when the limb finally leaves the ground. Arches in the foot provide a spring-like force at this point, adding to the energy efficiency of walking. As the leg is lifted, it becomes slightly flexed, using some muscular action, to ensure the foot does not drag on the ground during the swing phase.

During walking (but not running), toe off can only occur once the other limb has begun its own stance phase with its own heel strike, and so the two phases overlap. Some muscular action guides the swinging limb to its next point of contact with the ground, rotating it medially, closer to the body's center of mass. Muscle action also fully extends the limb again just before the next heel strike, and just after it, to prevent the leg jack-knifing. The symmetrical gait cycle continues from here with the semblance of banality but with the underlying reality that at every stage it teeters on the edge of collapse.

Skeletal adaptations for bipedalism and evidence for them in the fossil record

The human body appears to be well adapted to the striding gait described in the previous section. Many related traits are skeletal, providing the potential for fossilization and their evolution being recorded for posterity. Luckily, thousands of fossils have now been found that can be placed into paleospecies thought to be closely related to *Homo sapiens*. Often this placement is based on what is seen as evidence for their bipedalism.

Skeletal markers for bipedalism may be broadly grouped into two types: those indicative of upright posture and some kind of early (facultative) bipedalism, and those indicative of a more modern, striding, humanlike gait.

Upright posture, as seen in humans, is characterized by the head being carefully balanced on top of the spine. Through the base of the skull, the brain connects to the spinal cord via a large hole, called the foramen magnum. In largely quadrupedal chimpanzees and gorillas, it is found toward the back of the head. A more anterior position is seen as an adaptation to help balance the head when the body is upright. The first fossil reported

with this trait was from *Australopithecus africanus* ("Taung Child"), dated to around 2.5 Ma (Dart 1925). The skull of a *Sahelanthropus tchadensis* has also been found, dated to around 7 Ma, and this also had a more centrally positioned foramen magnum (Brunet 2002). Related cranial traits include the presence or absence of features indicative of muscular support of the skull, such as the nuchal crest in the skulls of quadrupedal apes.

Postcranial skeletal markers tend to be indicative of weight bearing and increased stability when in an upright posture. Knee, hip, and lower vertebrae in the spine and their articular surfaces are generally broader and more robust compared to those of quadrupedal great apes. Some features of the femur, such as a relatively long femoral neck, are also thought to be markers of upright posture and bipedal locomotion. Although there is still little consensus, some anthropologists deem the fossil remains of *Orrorin tugenensis*, found in Kenya and dated at around 6 Ma, to show this kind of evidence (Pickford et al. 2002).

The shape of the pelvis is also very much a key indicator. In most primates, it is elongated from top to bottom and relatively narrow from side to side. In fossils where this ratio appears to be reversed, it is taken as adaptation for greater stability when upright. The large, thin, bony plates on the pelvis are called the ilia. In most primates they are flat. In humans and hominins thought to have been bipedal, they are "laterally flared," meaning that the bony plates appear to be bent around to face the sides, forming more of a bowl shape. This helps the muscles to perform abduction—pulling the leg away from the center line—which is important for stability during the stance phase. *Australopithecus afarensis* (AL 288-1, "Lucy"), for example, despite being small in stature, has a sacrum that is broader and a body (the surface articulating with the last lumbar vertebra) that is larger than that of chimpanzees. It also has relatively flared ilia. The fossilized pelvis of *Ardipithecus ramidus*, dated earlier, to around 4.4 Ma, was very fragmented and distorted; however, using methods such as high-resolution tomography, it has been reconstructed to show traits consistent with a greater degree of bipedalism than modern African great apes (Lovejoy et al. 2009).

Another key postcranial skeletal trait indicative of bipedalism is an adducted hallux (big toe). An opposable big toe, capable of grasping branches, is indicative of an arboreal way of life. Humans have lost this ability and the toe has become specialized for walking and other aspects of upright posture. Similarly, curved phalanges of the hands and longer digits on the feet are indicative of branch grasping, and the absence of such traits indicates a more terrestrial lifestyle in hominins. *Australopithecus afarensis* and *Ardipithecus ramidus* show a mosaic set of features here, indicating that they were somewhat arboreal while also exhibiting some form of upright posture and locomotion.

More modern fossils, with traits providing evidence of more humanlike forms of bipedalism, have been found in the thousands. For example, the knee joint has characteristics that appear to be adaptive to the striding gait described earlier. The two condyles of the femur, which articulate with the tibia at the knee, form an angle with the vertical when placed on a flat surface. This "bicondylar angle" helps the knee to be placed very close to the body's center of mass during the stance phase, adding to the stability and hence efficiency of walking. Furthermore, when viewing the condyles from the side, they appear more oval in humans, compared to being more circular in great

apes. Again, this is seen as a weight-bearing trait that helps the knee to "lock" when fully extended to allow the inverted pendulum gait.

The earliest fossil evidence (dated at around 4.2 to 3.9 Ma) that has been found to be consistent with some of these traits is attributed to *Australopithecus anamensis*, from Lake Turkana, Ethiopia. However, Nariokotome (or Turkana) boy, attributed to *Homo erectus* (dated much later to around 1.5 Ma but found close by), provides even clearer and more unequivocal early evidence of modern humanlike, striding bipedalism.

Famously, supplementing the many fossilized skeletal samples, ancient remains of footprints have been found at Laetoli in Tanzania, indicating that two individuals walked, with an apparently humanlike gait, across a muddy field of volcanic ash approximately 3.7 Ma.

Evolution of human bipedalism

The seemingly mundane human activity of walking about in our daily lives becomes remarkable when one considers what is involved from a physiological and developmental point of view. It is even more striking when we consider the numerous disadvantages of bipedalism, such as susceptibility to injury, and poor speed and stability. Indeed, the fact that no other animal walks about like us today, and the paucity of evidence for anything similar in the fossil record until approximately 4 Ma, mean it is reasonable to wonder how human bipedalism ever evolved at all.

It is a question that has remained central to physical anthropology for over a hundred years as evidence has gradually accumulated in the fossil record. Charles Darwin's original idea on this subject, before any such evidence was available, can be characterized as "freeing the hands." It had been widely imagined that human intelligence preceded, and hence drove, bipedalism. That concept was first contradicted by hard fossil evidence with the discovery of the Taung Child in 1925. However, doubts about the specimen meant that it was a couple of decades before it became established that human bipedalism had preceded encephalization.

For most of the time since, the most popular context for human evolution may be characterized as some variant of the ideas put forward in Yves Coppens's "East Side Story" (1994). According to this line of thinking, our last common ancestor with the great apes was quadrupedal and lived in dense tropical woodland. Climate change, due to rifting, gave way to savannas in East Africa and our ancestors living there came down from the trees and began to move out onto the open plains bipedally while the ancestors of chimpanzees and gorillas did not.

As the decades passed by and evidence from hominin paleohabitats accumulated, this paradigm began to be challenged in a number of ways. There are perhaps as many as forty distinct published accounts as to how human bipedalism may have evolved, although most overlap with each other in some way or other. Whether this is "an embarrassment of riches, or just embarrassment" (Hunt 2001) is a debated point, as is how to classify them. Some of the models are based on advantages of human bipedalism today and attempt to work backward, looking for scenarios where bipedalism could have been adaptive in our ancestors. Others look for behavioral contexts of upright

posture or bipedal movement in extant animals that might have been advantageous to early hominins in their putative paleohabitat.

Following is a brief selection of hypotheses, grouped according to their proposed mode of selection (after Rose 1991). They are organized chronologically so as to give an indication of how the savanna paradigm became established and, more recently, challenged.

Darwin's notion of "freeing of the hands" was probably the first attempt to explain human bipedalism in evolutionary terms. The idea had to be reinterpreted after the discovery of *Australopithecus africanus* showed that bipedalism preceded encephalization, and others have followed in Darwin's footsteps in the decades since with more specific suggestions of forelimb preemption (or "carrying"), usually in a savanna context, including of carcasses from open grassland to gallery forest bases and of infants, tools, and weapons.

Perhaps the next published idea was Arthur Keith's (1923) "Hylobatian" model, which seems to have been inspired by the remarkable propensity to bipedalism in gibbons when on the ground. The idea received support until molecular evidence began to emerge placing humans closer phylogenetically to great apes. However, later findings (e.g., Brunet 2002; Pickford et al. 2002) suggesting bipedalism evolved earlier than previously thought have given the idea fresh impetus. If the last common ancestor of gorillas, chimpanzees, and humans was already somewhat bipedal, it is reasonable to consider whether this was in an arboreal context, as brachiation, below-branch suspension, and climbing vertical branches all encourage upright posture.

Another scenario that not only encourages upright posture in great apes but also almost guarantees their unsupported bipedal locomotion is wading in shallow water. Although evidence of such behavior in extant apes has only been published recently (e.g., Myers Thompson 2002), the concept that wading in shallow water might have been a factor in the evolution of human bipedalism is actually very old. Max Westenhöfer and, independently, Alister Hardy had both published their ideas that humans may have originated in "more aquatic" habitats by 1960. The idea was largely ignored, at first presumably because it was so at odds with the prevailing savanna-based paradigm. Later, it appears to have become tainted by its association with the "aquatic ape hypothesis" of Elaine Morgan (1997), and few anthropologists invested much time in anything to do with it until the late twentieth century. Carsten Niemitz's (2002) "Amphibische Generalistentheorie" ("Amphibian generalist theory") is based upon the wading arguments of Westenhöfer, Hardy, and Morgan minus any notions of swimming and diving. *Ardipithecus ramidus*, possibly the earliest good evidence of an early hominin biped, has been placed in a specific gallery forest habitat adjacent to a significant river system (Gani and Gani 2011). Seasonally flooded riparian habitats certainly offer plausible scenarios for early hominin bipedalism.

Most of the published models are, of course, somewhat complementary to the others and none are offered in an entirely exclusive way. Indeed some anthropologists, such as Michael Day, John Napier, Michael Rose, and Becky Sigmon, have emphasized that a combination of these ideas is likely to be important (see, e.g., Rose 1991).

In the early 1960s, inter- and intraspecific threat displays, such as the chest beating of gorillas, appear to have been the inspiration for a set of published models of human

bipedalism based on social behavior. Most overlap with and complement carrying models. Today these ideas are championed by Nina Jablonski and George Chaplin (2000). Other ideas invoking changes in social behavior that induce more bipedalism include meerkat-like vigilance, phallic display, and a kind of fashion or behavioral meme.

Food procurement is another mode of selection that has understandably attracted much support. Clifford Jolly's (1970) "seed-eating hypothesis," based on observations of baboons, suggests that early humans may have foraged grass seeds—again assuming they lived in open habitats—requiring a kind of squatting type of bipedalism. Jonathon Kingdon's book *Lowly Origins* (2003) was written around a similar "squat-feeding" idea in "ground apes" (the meaning of *Ardipithecus*). However, in accordance with the paleohabitat evidence of that species, Kingdon's apes were gathering fallen foods in East African gallery forests, not on the open savanna. Kevin Hunt's (1994) "postural feeding hypothesis" was based on empirical observational data from extant chimpanzees. Hunt found that 80 percent of recorded incidents of bipedalism were in the context of feeding. However, almost all of them were in trees, standing upright, stretching for food with one hand while supporting the body with the other.

As we have seen, modern human walking is undoubtedly an efficient form of locomotion. It is therefore perhaps surprising that it was not until 1980 that it was first suggested that an increase in the energy efficiency of locomotion may have driven its evolution. Rodman and McHenry (1980) showed that, although humans are relatively inefficient compared to other mammals when running, they are more efficient when walking. It was thus postulated that slow, long-distance foraging could have provided a scenario where bipedalism would have been adaptive. One variation of this theme is Bramble and Lieberman's (2004) "endurance running hypothesis," which postulates long-distance running as a key driver in the evolution of human bipedalism.

Owen Lovejoy's (1981) "provisioning model," like the earliest ideas, proposes carrying as a mode of selection driving early bipedalism, but crucially the model envisages it in the context of monogamous-pair relationships. The idea is based on demographics. The low rate of reproduction in apes and the pressure on females to obtain sufficient food to sustain their child rearing was a critical factor in ape survival. It is proposed that females that procured males as a dependable resource to bring them food gained a significant survival advantage.

A novel idea to explain human bipedalism was put forward by Peter Wheeler (1984) in the 1980s, still in a savanna context. It suggests that bipedalism was a thermoregulatory adaptation in hot, dry habitats. Standing upright reduces the profile of solar radiation on the body at noon compared to being quadrupedal, and standing upright in grassland exposes the upper body to breezes, which help with evaporative sweat cooling.

Whatever drove the evolution of human bipedalism, it was undoubtedly accompanied by genetic change resulting from random mutation. Most models propose that behavior changed first—probably driven by habitat change—and then that traits which aided that behavior were selected for to improve fitness. However, Filler (2007) has promoted an alternative view, that key mutations came first. The proposal is that a genetic mutation affecting the development of the vertebral column, causing a sudden change in the orientation of the backbone and, consequently, the preferred mode of locomotion of our ancestors.

Problems and future directions

Considering that Darwin published his *Descent of Man* in 1871, it is perhaps remarkable how little consensus there is today on this most fundamental aspect of the human condition. With so many models published, it is fair to ask which ones are considered to be the best. Any attempt at an answer should be based upon a rational evaluation of the models' strengths and weaknesses. An ideal model should offer an explanation for the evolution of human bipedalism that includes a significant selective advantage for bipedal locomotion over quadrupedalism, in a plausible scenario that the evidence suggests existed at the right time and place. It should account for the risk of predation and should work for both sexes and all age groups. It should do this throughout the course of the proposed evolutionary pathway and not just propose a circular, anthropocentric "positive feedback loop" based on known current advantages of bipedalism at the end of the human lineage. Perhaps most of all, it should be backed by simple, repeatable contexts that reliably induce bipedalism in extant apes.

The savanna-based paradigm described earlier has been challenged by findings that have pushed back the estimated date for the first bipedal hominins (e.g., Brunet 2002; Pickford et al. 2002) to the point that they may even predate the last common ancestor of humans, chimpanzees, and gorillas and into paleohabitats that were not simply open plains but wooded and relatively wet, at least locally. If new evidence continues to support this idea in the future, any model of human bipedal origins will need to be sophisticated enough to explain not only why a clade of great apes started moving bipedally but also why some of them then stopped doing so. Any explanation of human bipedality would need to include two adaptive shifts: the first to some kind of early facultative type of bipedalism, shared with the ancestors of the other great apes, and then, through the genus *Homo*, the evolution of our own obligate type. Although models for the later of these two phases would seem to be well grounded on the evidence of the energy efficiency of the human striding gait and adaptive scenarios surrounding it, the first adaptive shift still appears to be poorly understood.

SEE ALSO: Anatomy, Evolution of Human; Childbirth and Brain Size, Evolutionary Constraints of; Dubois, Eugène (1858–1940); Hominins, Early; *Homo*: Evolution of the Genus; Meat Eating in Apes and Early Hominins; Walking

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