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"The taller the better" or the origins of human bipedalism

As we may remember, being tall helps on many accounts both in human and animal life. Taller kids are less likely to be bullied at school, taller presidential candidates are more likely to win the election, taller sales personnel are better at convincing potential buyers into buying their stuff and taller boys and girls often get more attention. On the animal side of the things, taller and bigger animals are less likely to be attacked by predators than smaller animals, and taller and bigger animals are more likely to be successful in their bid to intimidate rivals and obtain territories and mates. We must remember that no trait has only positive sides, and on the negative flip-side for many species (both predators and prey), taller animals find it more difficult to stay unnoticed. Another negative aspect to being big is that predators will sometimes prefer to attack larger prey animals simply because they will 'provide' more food. Overall however, the positive aspects of distinct visual traits outweigh the negatives.

In the next few sections I will argue that human (and hominid) morphology is the direct result of our perennial evolutionary strive to become taller.

We will start our discussion with bipedalism, a trait widely accepted as arguably the first and most important step on the long evolutionary road between our primate ancestors and modern humans. The origin of bipedalism has been one of the most prominent topics of human evolution since Charles Darwin proposed his theories to explain our animal descent. After more than 140 years since the appearance of Darwin's work, the origin of bipedalism is still largely shrouded in mystery. On one hand, the skeletal adaptation to bipedalism is well documented throughout the evolution of hominids, but on the other hand scholars are still arguing on the exact reasons that could have led to this walking style (which is extremely unusual for mammals).

When discussing the origins of bipedalism, we should be aware that bipedal locomotion had (and still has) both positive and negative effects. On the positive side, for example, bipedalism frees up the hands and allows the bipedal creature to see its surroundings better. On the negative side of the coin, bipedalism uses twice the energy as mammalian quadrupedalism, and bipedalism and associated skeletal changes created several problems for our ancestors, some of which are still visible

today. For example, tree climbing became more difficult, our running speed drastically declined, hiding from predators became more difficult, and human lower back and knee joints have since become plagued by osteological problems, predominantly because in bipedal posture these joints support much more weight than in the "normal" quadrupedal walking gait.

Of course we hardly require tree climbing in our contemporary life anymore, and 99% of the time we do not care if we are easily seen while walking in tall grass, but the lower back pain that many readers of this book may have experienced (and some are possibly even experiencing as they read these words) also comes from our constant bipedal posture. In this context I would like to remind readers that traces of osteological problems are apparent in the discovered skeletal remains of prehistoric hunter-gatherers (Koella & Stearns, 2008).

We have discussed how bipedalism has both positive and negative sides, but for a new locomotion model (as for any other morphological or behavioural trait) to be successful, the benefits must outweigh the disadvantages. Several million years of relentless everyday struggle for survival will eliminate an unwanted morphological or behavioural element. With this strict evolutionary rule in mind, let us remember that none of the other terrestrial mammalian species opted to shift to constant bipedal locomotion, therefore our ancestors must have had very worthy reasons to shift to this style of locomotion, which was and is so unpopular among other terrestrial animals.

From the moment our ancestors started walking upright habitually more than 4 million years ago, the long process of transformation towards becoming a modern-day human had begun. It is universally agreed that bipedalism evolved well before the enlargement of brain and the development of stone tools. To understand what was behind this crucial change is to understand the main forces at play during the very beginning of the human evolution process - this is why bipedalism is universally accepted as one of the most important behavioural and morphological changes in the evolution of our species. It is no wonder that hardly any other topic of human evolution has received as much attention as bipedalism has.

There had been plenty of hypotheses, ideas and models to explain why and how bipedalism started and consequently established in human evolution. The different hypotheses are not necessarily mutually exclusive, as different selective forces could have acted in conjunction to lead to hominid bipedalism. Here are some of the best known ideas on the origins of human bipedalism, presented in chronological order:

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List of ideas on human bipedalism

- 1871. Charles Darwin suggested that our ancestors were forced to shift to bipedalism after they became terrestrial, in order to have free hands to carry weapons and meat. The idea of bipedalism freeing hands was later used by many other scholars, but also with many varying functions for the free hands (to carry food, to carry weapons, to throw weapons, to carry children – see below).
- 1923. Arthur Keith, based on the fact that gibbons use bipedalism when on the ground, proposed that human bipedalism had a connection to the gibbons' locomotion pattern.
- 1925. Raymond Dart suggested that standing upright in open habitats would be adaptive to help our hominin ancestors to scan the surroundings in order to see their prey and avoid predators.
- 1936. John de la Marrett came up with a diet-oriented hypothesis, according to which bipedalism was caused by the lack of iodine in early hominid environment.
- 1942. Max Westenhofer suggested that human morphology and behaviour (including bipedal locomotion) evolved in a marine environment. Marine biologist Alister Hardy came to a similar conclusion in 1930, although he published his ideas a staggering 30 years later. The name coined for this hypothesis, "Aquatic Ape", belongs to Desmond Morris. The idea was later popularized in several books written by Elaine Morgan.
- 1953. George Bartholomew and Joseph Birdsell argued that carrying tools and weapons was the key factor for the origin of bipedal locomotion.
- 1954. William Etkins (and later Tanner, 1981) suggested that infant carrying by mothers was the key factor for adopting bipedal posture and locomotion.
- 1954. Kenneth Oakley supported the idea that the need to look over tall grass was the initial motivating factor for hominid bipedalism.
- 1959. Raymond Dart suggested that intra and inter-species conflict and violence was one of the key factors for the adoption of bipedal posture.
- 1959. Raymond Dart and Craig Dennis also supported the idea that looking over the terrain was an important element in establishing bipedalism.
- 1959. Wolfgang Köhler, observing primate behaviour, proposed that moving on muddy and cold substrate (for example, snow) could lead to bipedal locomotion.
- 1960. Alister Hardy, and later also Helen Morgan in several books, suggested that human ancestors went through a long period of living in a coastal area, spending most of their time in the water.

- 1961. Gordon Hewes suggested that the principal reason for hominid bipedalism was freeing hands in order to transport food.
- 1962. Frank Livingston (and later Roger Wescott in 1967, and Nina Jablonski and George Chaplin in 1993) suggested that as plenty of animal species use bipedal threat displays to look taller in order to intimidate antagonists, bipedal threat displays could have been the initial behaviour that led hominids to adopt permanent bipedal posture.
- 1962. Lloyd Du Brul, and later Wrangham (1980) and Rose (1977) suggested that bipedalism was a result of early hominid feeding and gathering activities on the ground.
- 1970. Clifford Jolly suggested that foraging and eating seeds from savannah grasses led to bipedalism.
- 1975. Russell Tuttle suggested an updated version of the gibbon hypothesis, suggesting that human bipedalism evolved from gibbon-like tree climbing abilities.
- 1978. Glynn Isaac suggested that, as a result of scavenging for carcasses on the savannah, hominids had to carry scavenged food back to the group base, and that hominids adopted bipedal locomotion in order to use their arms to hold the food.
- 1978. Valerius Geist proposed that human ancestors started bipedal locomotion while still in the trees, before their move to the ground. According to Geist, our distant ancestors were carnivorous and were obtaining food by stalking silently and killing tree-dwelling species with hand-held rocks.
- 1980. Jack Prost suggested that quadrupedal vertical climbing, used by apes, was the ancestor of human bipedalism.
- 1980. Peter Rodman and Henry McHenry proposed that bipedalism evolved as an energy-efficient way of walking long distances, albeit at slow speeds.
- 1980. Adriaan Kortlandt conducted field experiments with lions and proposed that hominid bipedalism was initially used as inter-species intimidating displays, standing upright and using thorny branches to defend themselves from large predators.
- 1981 C. Owen Lovejoy suggested that the origins of bipedalism were linked to monogamy and the male provisioning his family with food, thus improving the survivorship of the offspring and increasing the pair's reproductive rate. The same year Lovejoy suggested another similar hypothesis, but this time based more on a sexual selection model and without suggesting monogamy among early hominids.
- 1981. Nancy Tanner suggested a new version of the sexual selection model, suggesting that the male phallic display could have been the initial incentive for bipedal posture.

- 1983. Matt Cartmill (soon followed by Carrier in 1984 and by Bramble & Lieberman two decades later) suggested that our hominid ancestors were hunters and hunted prey using long-distance endurance hunting, which led to bipedal locomotion.
- 1984. Peter Wheeler proposed that, as bipedal posture raises the body away from the hot ground, it helps to keep the human body temperature lower.
- 1985. Vernon Reynolds suggested that bipedal locomotion started with moving from tree to tree.
- 1986. A.R.E. Sinclair and Pat Shipman virtually simultaneously proposed that hunting, scavenging, and then bringing the meat back to the base camp was the major factor in the gradual acquisition of bipedalism.
- 1987. Felix Fifer (and later Holly Dunsworth, John H, Challis, and Alan Walker in 2003) suggested that the defensive throwing of objects (especially missiles as weapons) was the key driver of hominin bipedalism.
- 1987. Barbara Isaac also wrote about the importance of throwing in human evolution; however she did not concentrate on the role throwing had in the evolution of human bipedalism.
- 1988. Renate Eickhoff proposed that human ancestors got used to bipedalism while still living on the tree branches, that they were carnivorous, and that their method of hunting was to sit and wait for the prey to approach and then grab them using their upper limbs.
- 1988. Liza J. Shapiro and William L. Jungers suggested that the acquisition of habitual bipedalism in humans probably involved not so much a major change in back muscle action or function, but rather an improvement in the mechanical advantages and architecture of these muscles.
- 1991. Derek Ellis proposed a version of the early "aquatic ape" hypothesis, suggesting that bipedal locomotion could have started after human ancestors spent arid periods of the year in the wetlands.
- 1991. Peter Wheeler suggested that the increased cooling, reduced heat gain, and reduced water requirements in a hot, tropical climate was the driving factor for bipedal posture.
- 1996. Kevin Hunt suggested that human ancestors were initially bipedal only when they ate. According to Hunt, bipedal feeding posture may have been a pre-adaptation for habitual bipedalism which appeared later, only in Homo erectus.
- 1996. Lynne Isbell and Truman Young proposed that the mixture of savannah and scattered forests led to increased terrestrial travel by proto-humans between clusters of trees, and that bipedalism offered greater efficiency for long-distance travel between these clusters than quadrupedalism.

- 1996, 1998. Richard Potts suggested in his publications that different environmental conditions were chiefly responsible for human ancestors starting bipedal locomotion.
- 2002. Algis Kuliukas proposed a hypothesis dubbed the "wading hypothesis", where humans were living in an environment of seasonally-flooding rivers, requiring them to resort to bipedal locomotion to avoid drowning, and that during the dry season they maintained this bipedal posture.
- 2002. Mark Verhaegen, Stephen Munro and Pierre-Francoise Puech suggested the idea of an "aqua-arboreal" phase in human evolution, which came from the Hardy and Morgan idea of "aquatic ape" although in this model our ancestors were also still living in the trees as well as spending plenty of time in the water.
- 2003. According to Jonathan Kingdon, bipedalism arose through adaptations in 'ground apes' whilst feeding on fallen foods on the floor of gallery forests.
- 2004. Richard Dawkins has argued that bipedalism could have begun as a kind of fashion that just caught on and then escalated through sexual selection.
- 2004. Holger Preuschoft suggested that transporting heavy loads was the primal reason for human bipedalism.
- 2004. Weijie Wang and Robin Crompton also suggested that load-carrying was the central reason for human bipedalism, albeit only for establishing the later Homo body proportions.
- 2005, 2009. Donna Hart and Robert Sussman suggested that defence from predators was the key issue in hominid evolution, although according to them none of the adaptive reasons was important for adoption of bipedal posture. Instead, as a part of ape locomotion, it was "given" to hominids and only proved to be advantageous for several purposes after bipedalism had already been adopted as a standard of locomotion.
- 2006. Adam Sylvester suggested that bipedalism was an adaptation in order to maintain the mobility of hominid shoulders.
- 2007. Aaron Filler proposed that bipedalism was a result of a genetic mutation, and according to him human ancestors of some 20 million years ago already had the genes for bipedal locomotion.
- 2007. Susannah Thorpe, Roger Holder and Robin Crompton suggested that Orangutans using an upright posture in thin branches was the precursor to human bipedalism.
- 2009. Herman Pontzer, with David Raichlen and Michael Sockol, suggested that bipedalism was primarily a successful locomotion model because of the lower metabolic cost of walking.
- 2010. Stephanie Braccini, Susan Lambeth, Steve Schapiro, and Tecumseh Fitch researched the relationship between chimpanzee tool use and the ensuing

effects on lateralization and posture, and suggested that tool use may have pushed our nearest ancestors upright.

- 2010. Carsten Niemitz supported the so called 'Amphibian Generalist Theory', a version of the wading theory, and suggested that though the earliest of ancestors would have needed hands and arms for many reasons (self-defence, food gathering, infant carrying), it was living in woodlands and thus close to the rivers that was crucial for bipedalism.
- 2011. Kirsty Robertson synthesized earlier suggestions by Wheeler (cooling heat) and Shipman (freeing hands) and came to a conclusion that bipedalism emerged as the need to be energetically efficient for subsistence strategies, such as scavenging.
- 2011. David Carrier proposed that sexual selection via male combat was the decisive factor for the origins of bipedal locomotion, and that bipedal posture was primarily a means to deliver a more powerful punch to rival males.
- 2012. Graeme Ruxton and David Wilkinson suggested that it was only after early humans began walking upright that they began to lose their fur coats, and that these two processes were closely connected in human evolution.

As we can see, the list of hypotheses and suggestions on the reason of bipedalism goes on and on. Hardly any other human morphological or behavioural trait has received as much attention from scholars as bipedalism has. Despite the large number of hypotheses as seen above, I must remind readers that this list still does not cover every single expressed idea about the origins of human bipedalism – it is merely a somewhat brief overview. Also, it is easy to notice that a number of existing hypotheses use similar reasons for the adoption of bipedalism as others, but sometimes with minor differences. Many scholars and authors tend to group different suggestions on the origins of bipedalism into several general frameworks, such as the "walking hypothesis", "postural feeding hypothesis", "ecology hypothesis", "thermoregulation hypothesis", "enhanced vision hypotheses", "wading hypothesis" and "provisional hypothesis."

Most evolutionary hypotheses constructed to account for the appearance of bipedalism have serious shortfalls. For example, the hypotheses that connect the transition to bipedalism to a shift in environment to the savannah habitat cannot be correct as bipedalism started before this environmental shift. Bipedalism also started long before hominids started using tools. The male "provisional" hypothesis is based on a monogamous relationship between sexes which, in the light of available evidence, is unlikely to be true for our hominid ancestors. In the case of hominids needing to travel long distance, it is not clear why would they choose such an energy-consuming and slow mode of locomotion to use such as bidepalism. Supporters of the "wading" model fail to notice the fact that the areas in proximity to the river banks are the most predation-prone both from terrestrial predators (lions) and water predators (crocodiles). The more recent hypotheses for bipedalism which focus on male aggressiveness and the advantage in fist fighting also fail to explain

why our ancestors were gradually becoming physically weaker if the selection was favouring stronger and more aggressive males.

My own suggestion for the origins of bipedalism is that bipedalism was merely one of the many parts of a grand survival strategy for early hominids known as **aposematism**. Although aposematism is mostly known among scholars as "warning colouration", it is much more than a simple colouration, and also contains audio, olfactory and behavioural signals. I prefer to use a more complex and more precise term: "Audio-Visual-Olfactory Intimidating Display". As the strategic aim of an aposematic display is generally to avoid unnecessary physical violence, the acronym which is produced by the above term, "AVOID", seems almost too much of a coincidence to take seriously.

The model of aposematism is so integral to this book that I was considering to title this book "Aposematic Model of Human Evolution." After some careful consideration I decided to acknowledge the importance that big cats played in our evolution, instead of merely acknowledging the strategy that helped our ancestors deal with the mighty ancestors of big cats and other predators.

Therefore, I believe that the origins of bipedalism must be explained through the principles of warning display (aposematism). Standing on hind legs, as we can remember from our previous evaluations of other aposematic species, is one of the most widely used means to rapidly increase body size in an aposematic display, and there is a vast amount of animals which utilise this form of warning display in tense confrontations.

The idea that human bipedalism could have originated from animal threat display is not new. We may remember from the list of ideas on human bipedalism that it has been postulated by a number of scholars during the last 50 years: Frank Livingston wrote about this in 1962, as did Roger Wescott in 1967 and Nina Jablonski and George Chaplin in 1993. Furthermore, according to Adriaan Kortlandt (1980) bipedalism was initially used for inter-species intimidating displays as well as standing upright and using thorny branches to defend themselves from large predators.

The largest issue that is pointed out by the critics of this scenario is that, in the animal world, the bipedal threat displays are only used for a few seconds – therefore how could this posture, maintained only for few second in emergency situations, eventually become the constant mode of locomotion? Bears can actually make a few bipedal steps, but they never became constantly bipedal, right? This is absolutely correct. In order to distinguish between bear bipedal steps and hominid bipedal locomotion, we need to remember that aposematic signals can be of two different categories: **(1) temporary**, used in critical situations only, and **(2) constant**, or displayed by the animal at all times. Temporary warning signals can be (and are) used by virtually all animal species (bears included), but constant warning signals are as a general rule used by aposematic animals only, i.e. those who try to constantly advertise their presence in various modalities. What our ancestors did

was they turned a temporary warning/intimidating display into a constant aposematic feature. This was a revolutionary change, going from a temporary warning posture into a constant mode of locomotion, and one that indicates that our ancestors were finding the warning display a lifesaving strategy. Bears are not aposematic creatures - humans are.

For all animal species that are able to make several bipedal steps (from bears to African apes), maintaining this upright posture is quite difficult. Shifting to bipedal posture and maintaining this constantly was no doubt equally difficult for our primate ancestors as well. There must have been much stronger pressure for such a behavioural change to qualify through natural selection.

It might seem extraordinary to say this, but the original pressure that led our ancestors towards bipedal locomotion, that critical pressure from predators, is still present today. Do you want proof of this strange proposition?

If you search the internet for survival manuals on how to behave if you suddenly find yourself facing any big and dangerous animals (like a tiger, lion, bear, or a wolf), the most constant and important advice in the list of tips is to stay tall. Bending down, even for a few seconds, may cost your life. When I visited the Corbett National Park in January 2011, forest officials were hunting a man-eating tiger that had, by that point in time, killed two women. Both women, at the time of attack, were not standing erect. One of them was cutting grass and another one was answering the call of nature. Facts proving the importance of maintaining a tall bipedal posture for staying safe in the jungles come from many sources. From documental writings of Jim Corbett, Kenneth Anderson and their peers, who hunted man eating tigers and leopards, we know that Indian villagers were mostly attacked when they were cutting grass, collecting firewood, going to the toilet, or doing some kind of other activity which requires bending down and generally results in temporary loss of bipedal posture. Staying tall is still a potent aposematic signal, saving human lives in countless encounters with various dangerous animals.

On February 18th 1975 a terrible tragedy took place during a safari at the Namibia-Angola border. As a few cars full of tourists were viewing a pack of lions, against of all safety precautions a tourist came out of his car and walked up very close to the lions in order to film them from a closer range. It is difficult to understand where exactly the tourist's common sense had escaped to when he left a car with his wife and two small children in it. There is graphic video footage on YouTube, filmed from another car, showing the tragic scene where the man is eaten alive in full view of his wife and two children. For several seconds the intrusion of the man in the midst of the lion pride is left unpunished, but the last straw that essentially provokes the attack is when the man crouches down. The man with the camera had crouched down to film the snarling male lion at a more effective angle - as soon as he went down to his knees, an unsighted lioness jumped on his crouched figure from behind.

I do not know whether staying tall would have saved the life of the tourist, but I am certain that when he bended down he severed all chances of survival. So remember, if you see a dangerous animal and cannot get to safety quickly, stay tall

and you will have a much better chance of survival! If you do not look tall you are in danger – Because of this children are particularly vulnerable in the presence of big cats and it is advised to keep them in your arms. I am very grateful to Mr Soulemenn Kalee, a professional hunter from South Africa, who provided me (with the help of our common friend Kristof Kotecha) important information on why it is very dangerous for children to be next to big cats. Kalee has great experience in dealing with lion attacks on humans, and has also assisted Hajee Mackumboro, the chief ranger of the Selous park in Tanzania, in the hunt for arguably the worst man-eater of the 21st century, the lion pack headed by the notorious male man-eater "Osama". According to Kalee, a child's smaller stature (when the height is less than 140cm) ignites a lion's hunting instinct, and even hand-reared, disciplined lions can become dangerous when they encounter children.

From the evidence above it is obvious that predators would have provided strong evolutionary pressure for the establishment of bipedalism. Early hominids must have noticed that they were being attacked much less when they were staying tall, or more correctly those of our ancestors who were spending more time erect on two legs were attacked less and naturally outlived those who were moving around half crouched, similar to the evolution of other apes. In one way or another, staying tall and bipedal locomotion became a life-saving strategy for our distant ancestors. Staying tall still remains an effective strategy in encounters with dangerous predators to this day, and will remain so in the future.

According to ethnographers and contemporary ethologists (Schaller, 1972; Bertrand, 1972; Marshall, 2001), lions flee when they see even an unarmed human on foot. Brian Bertrand, who studied lions in the Serengeti the same time as George Schaller, wrote directly on this subject: "All my observations were made from a Land Rover, not for the reasons one might think but because lions in the wild are afraid of humans on foot" (Bertram, 1972:33), and also "If I had got out of my Land Rover and shouted out and waived my arms, the lions would have run off, for almost all wild lions are still afraid of humans on foot" (pg. 43). But it is a different story if a human crouches and loses the bipedal posture in the presence of lions and other dangerous predators. During a field experiment where two scholars, George Schaller and Gordon Lawther, covered on foot about 160 kilometres in the Serengeti, they encountered a number of lions, and "All the seven lion groups that we encountered while we were on foot fled when we were at distances of 80 to 300 meters" (Schaller & Lowther, 1969:328).

The gradual shift to bipedalism must have taken hundreds of thousands, even millions of years, and also very importantly, the establishment of bipedalism must have eventuated while our distant ancestors were still living in the woodlands, well before they moved out into open grasslands. Bipedalism was **not** the *result* of our distant ancestors moving from the woodlands to the open savannah (as some theories of bipedalism suggest), but on the contrary **bipedalism was the necessary condition that allowed early hominids to move to open grasslands**. Our distant ancestors left the safety of the trees because bipedalism (and a number of other

aposematic strategies which we will be discussing in the following pages) provided adequate security in a new environment where trees were not around to be climbed up in critical moments. Early models of human evolution were using the open African savannah as the only theoretical environment for early human evolution. We now know that all of the sites discovered in relation to early hominids (before 3 million years ago) seem to have been partially or fully wooded. No early hominids have been discovered to have been living in the open African savannah. The morphology of these early hominids shows adaptations for climbing as well.

Bipedalism was by no means the only new morphologic-behavioural means to look taller. I am sure that contemporary human morphology has several other important evolutionary developments that have made our ancestors taller and more visually impressive over time. Let us discus these evolutionary developments.