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Chapter One

The Evolution of Bipedality

The process of walking around on two legs is an inherently unstable form of transportation. Watch any toddler attempt a few steps and it is easy to appreciate the complexity of the task. It is also an unusual way to get around: of the more than 4,000 species of mammals on earth today, only one is upright when walking (1). Even Plato commented on the curious nature of our preferred form of transportation by referring to humans as the only "featherless bipeds."

In 1871, Charles Darwin claimed that bipedality was the defining feature separating humans apart from our ape ancestors (2). Darwin theorized that the conversion to bipedal gait freed the hands to allow for tool use, which in turn created an environment that favored rapid brain expansion. This line of reasoning is consistent with that of modern anthropologists such as Mary Leakey (3), who states that bipedality "freed the hands for myriad possibilities: carrying, toolmaking, intricate manipulation... this new freedom of the forelimbs posed a challenge. The brain expanded to meet it. And mankind was formed."

According to the classic theory of bipedal evolution, approximately 2.5 million years ago a seismic shifting of tectonic plates caused a rapid global cooling that quickly converted the once dense forests of eastern Africa into the open grasslands of the savanna. Because food sources became more spread out, our early quadruped ancestors were forced to stand up and walk. This new form of transportation theoretically allowed the early hominids to see over the tall savanna grasses and cover larger distances in search of food.

The problem with the savanna hypothesis is that recent discoveries show that the timing is all wrong. In 2001, a team of French and Kenyan paleontologists announced the discovery of multiple specimens of a 6-million-year-old hominid they named *Orrorin tugenensis* (4). Discovered in the Tugin hills of Kenya, the femur of this early hominid was remarkably humanlike, as it even possessed a groove on the back of the femoral neck for the obturator externus muscle. This groove is only present in bipeds and confirmed that *Orrorin* most definitely walked upright (Fig. 1.1). In 2002, a team of paleontologists led by Michael Brunet (5) unveiled a newly discovered skull from a 7-million-year-old hominid they called *Sahelanthropus tchadensis* (named after the region in Africa where the fossil remnants were discovered). Although no other remains have been found, the skull of this hominid possessed a centrally located

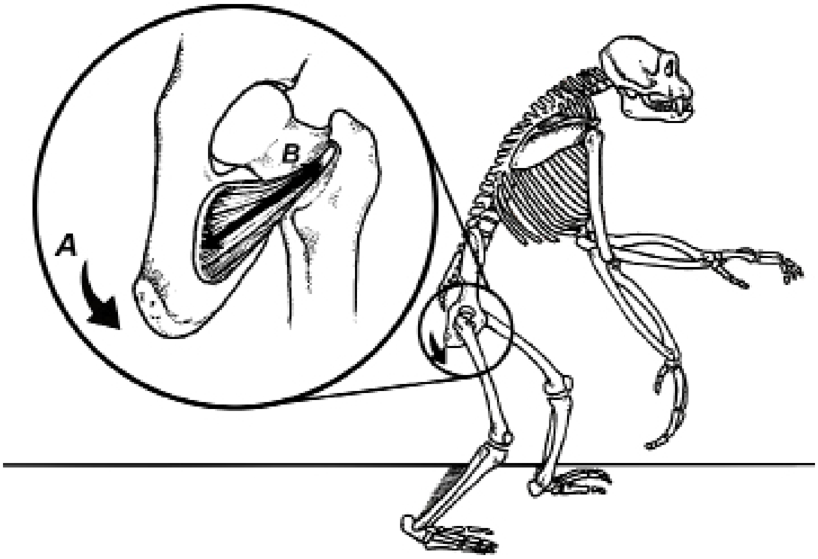

Figure 1.1. In contrast to quadrupedal locomotion, bipedal gait forces the ischium to move down and forward (arrow A), which significantly increases tensile strain placed on the obturator externus tendon where it passes along the posterior aspect of the femoral neck (B).

foramen magnum, strongly suggesting *Sahelanthropus* was a dedicated biped; i.e., because bipeds walk with their heads balanced over their upright cervical spines, they possess centrally located foramen magnums. This contrasts with almost all quadrupeds, who walk with their heads down and typically possess posteriorly displaced foramen magnums. The discovery of *Sahelanthropus tchadensis* in Africa pushes back the origins of bipedality from 4 million years ago to a minimum of 7 million years ago. This means the early hominids were bipeds approximately 4 million years before the formation of the savanna grasslands, 5 million years before our freed hands were manipulating tools, and at least 6 million years before significant brain expansion. These recent findings raise significant questions concerning the reasons why we began to walk upright.

Obviously the transition to bipedal gait has served us well, but why did those early hominids stand up and take the first few steps? The most current theories are summarized as follows:

1) Freeing of the hands*:* Bipedality freed the hands so the early hominids could more efficiently carry food and/or offspring. This reduced the metabolic cost of foraging, as larger amounts of food could be carried longer distances. While this became extremely important when day ranges for foraging increased after the formation of the savanna grasslands, it would have provided little advantage to the 7-million-year-old *Sahelanthropus,* who lived in dense forests where day ranges for foraging were so small.

2) Improved vision: Standing upright improves visual range allowing for improved foraging and/or observation of predators. Again, this would have been important after the appearance of the savanna grasslands, but not 7 million years ago as *Toumai* and *Orrorin* inhabited heavily forested jungles.

3) Aquatic theory: Originally described by Alister Hardy and later popularized by Elaine Morgan (6) this theory maintains that the early hominids became bipeds in the relatively weightless environment of water. They support this theory with the observations that unlike most mammals, humans are hairless and possess a thick layer of subcutaneous fat that is necessary for buoyancy and insulation in an aquatic environment. They also note that during childbirth, only human offspring present headfirst in the vaginal canal making land-births hazardous. Despite still being presented as valid in the popular press, virtually all aspects of the aquatic theory have been dismissed (7).

4) Threat display theory: In 1974, R. Guthrie suggested that the earliest male hominids used their newly exposed penises as a "threat display organ" to intimidate rival males (8). Although this may have occurred with some of the earliest hominids, the concept seems far-fetched and few paleontologists consider this theory valid.

5) Temperature regulation: Walking upright lessens solar skin exposure thereby allowing for increased foraging distances in the mid-day tropical sun. While this provided no benefit to the earliest hominids (approximately 7 million years ago), beginning 5 million years ago, it most likely provided a significant advantage over the quadruped apes.

6) Improved efficiency: This theory proposes the transition from quadruped to biped gait was associated with a decreased cost of locomotion that saved precious calories and improved foraging ranges. Even a slight decrease in the metabolic cost of locomotion would have provided a considerable benefit to the early hominids since the saved calories could have been used for improved growth and/or reproduction. Of all the proposed theories, improved efficiency has been the most intensively studied and surprisingly, the early research was inconclusive.

In 1973, Taylor and Rowntree (9) evaluated the metabolic efficiency of trained juvenile chimpanzees as they ambulated with biped and quadruped gaits. Because the metabolic costs of locomotion between the two gait patterns were the same, the authors stated that improved biomechanical efficiency could not be a factor in the development of bipedality. In 1996, Steudel (10) reviewed the literature concerning the metabolic efficiency controversy and concluded that because of the shape of a chimpanzee's pelvis, their center of masses are displaced anteriorly, which forces them to walk in a stooped position with exaggerated hip and knee flexion (Fig. 1.2). This is extremely inefficient, since the chimp is forced to apply propulsive period forces in front of the hip joint instead of behind the extended hip, as in humans. Because of dramatic differences in skeletal alignment between chimps and modern humans, Steudel (10) argues the early hominids would have faced similar challenges and that energetic efficiency should not be considered when discussing the origins of bipedality, since "it is not possible

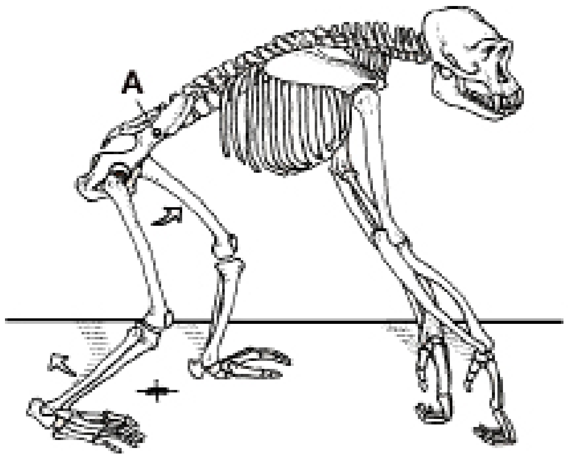

Figure 1.2. Unlike *Homo sapiens*, the chimpanzee's longer pelvis displaces the center of mass forward (circle A), causing them to walk with both hips and knees flexed (white arrows).

to compare such structurally different creatures as the early hominids and modern humans." The findings by Taylor and Rowntree (9) and Steudel (10) have been supported by more recent research by Nakatsukasa et al. (11), who calculated metabolic efficiency in a wide range of primates and demonstrated that bipedalism was metabolically more expensive than quadrupedal locomotion in every situation.

Arguing in favor of improved efficiency with bipedality, Sockol et al. (12) note the research by Taylor and Rowntree (9) was flawed as they only studied juvenile chimps (who are often less efficient than their adult counterparts) and the authors failed to include a complete biomechanical analysis of the metabolic expense of biped and quadruped locomotion. In an extremely detailed study, Sockol et al. (12) evaluated the cost of locomotion (COL) of 5 adult chimpanzees (ages 6 through 33 years) after they spent 4 months training the chimps to walk with both biped and quadruped gaits on a treadmill. The chimps wore masks so their oxygen consumption could be measured and high-speed video analysis was performed with kinematic data calculated by evaluating motion between markers placed on each chimp's shoulder, elbow, wrist, knee and ankle. By extrapolating information from this data, joint moments were evaluated and the volume of muscle activated for each step was then calculated and compared to total contact times during biped and quadruped locomotion.

By using research on efficiency from other studies, Sockol et al. (12) determined that when averaged out between the 5 chimps, bipedal walking was slightly more costly than quadrupedal walking. However, a more detailed analysis comparing biped and quadruped locomotion among individual chimpanzees revealed that for 3 of the chimps, bipedalism was more expensive, in 2 of the chimps, the cost of locomotion was similar, and in one specific chimp (a 33-year-old female), the cost of bipedal locomotion was significantly lower than quadrupedal locomotion. In fact, this particularly efficient chimp consumed only .16 ml of oxygen per kilogram per meter when walking biped compared to .29 ml of oxygen when walking as a quadruped. The authors conclude that even if our early ancestors walked with a "bent knee, bent hip form of bipedalism" the results of this study suggest that even the earliest transitional forms of hominids could have reaped some energy savings with the conversion to bipedal gait. This in turn would have provided critical selection pressure favoring bipedality.

The controversy regarding metabolic efficiency continued until October of 2009, when the journal *Science* published the results of a 15-year analysis of the 4.4-million-year-old hominid *Ardipithecus ramidus* (nicknamed *"Ardi"*). This important hominid predated Lucy by more than 1 million years and biomechanical analysis of her surprisingly complete skeleton confirmed that *Ardi* could easily stand upright and was in fact a dedicated biped (Fig. 1.3). This finding was unexpected since scientists assumed that 4.4 million years ago, upright walking might have occasionally occurred in our hominid ancestors, but that it would not be the primary form of transportation. The fact that *Ardi* walked upright as a habitual biped forced scientists to change the way they viewed our last common ancestor in that prior to *Ardi*, experts assumed that the farther back you went in the evolutionary tree, the more chimpanzee-like our ancestors became. The discovery of *Ardi* changed that, because her skeleton possessed an unanticipated amount of modern human traits. For example, the bones of her hands revealed surprisingly short thumbs, short metacarpals and exceptionally mobile wrists confirming that she was not a terrestrial knuckle-walker. The feet of *Ardipithecus* were also unexpected as they were chimp-like in appearance but her lesser metatarsals were humanlike in function as they were short and extremely strong, allowing her to walk with her hips slightly extended during the push-off phase of gait.

The most surprising skeletal discovery as related to bipedality was that *Ardi's* lumbar spine was so mobile that she could arch her back into a lordosis, effectively balancing the weight of her upper body over her pelvis. The ability to create a lordotic lumbar spine was essential

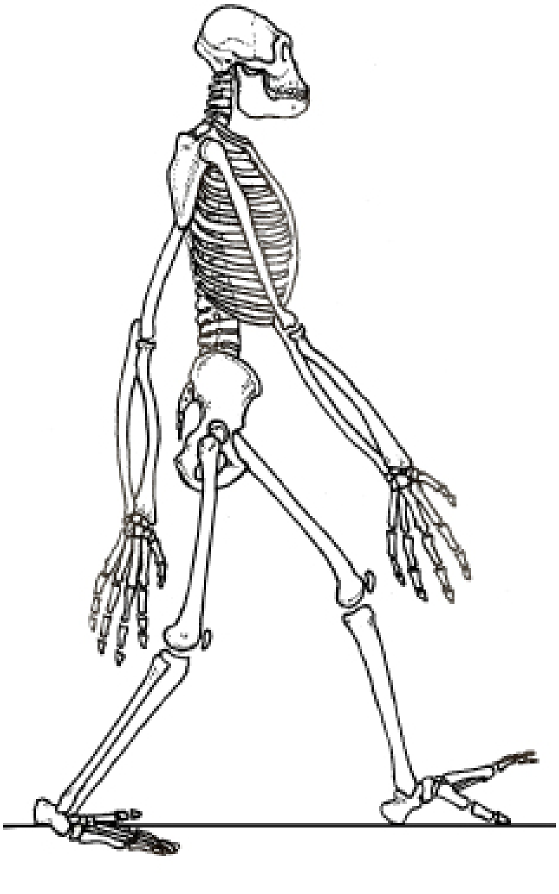

Figure 1.3. ***Ardipithecus ramidus.*** Modified and redrawn from an illustration by J. H. Matternes in *Science*. 2009;326:101.

for improved metabolic efficiency since balancing the upper body over the pelvis markedly reduces extensor moments in the back, hip and thigh musculature, which in turn significantly reduces the cost of locomotion (Fig. 1.4). Because chimpanzees have such rigid lumbar spines (that provide invaluable protection against spinal shear forces associated with twisting between branches) they are unable to balance effectively in an upright position and can only walk as bipeds by excessively flexing their knees, hips and spine.

The shape of *Ardi's* upper pelvis was also unexpected as her ilia angled forward allowing the hip abductors to support weight more effectively during single-limb support. This is in contrast to the chimpanzee ilia that rest flat against the back and project up towards the ribs (Fig. 1.5). Because the chimpanzee ilia are positioned posteriorly, gluteus medius behaves more as a hip extensor and is unable to stabilize the pelvis in the frontal plane during single-limb stance (i.e., a chimpanzee cannot stand upright on one leg).

All of these findings confirm that our last common ancestor was not similar in shape to a modern chimp but more closely resembled a blend between chimpanzees and humans. *Ardi* confirmed what in hindsight seems obvious: while modern humans have spent the last 7 million years evolving into our present form, chimpanzees and apes have also evolved considerably, perhaps even more so, developing features making them more efficient at suspending themselves from branches and moving about in high trees.

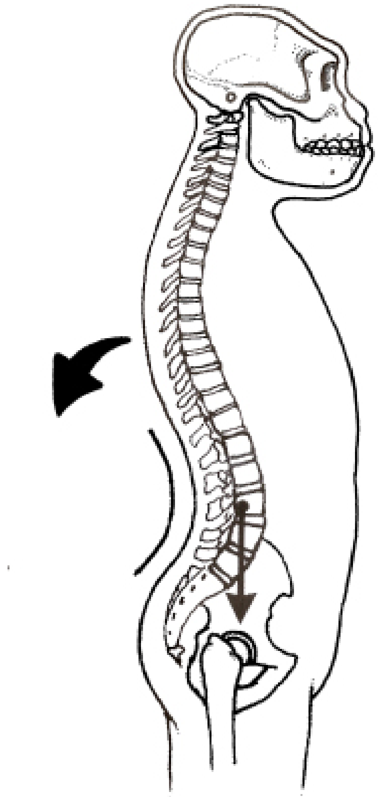

Figure 1.4. By extending the lumbar spine into a lordotic position (arrow), *Ardipithecus* could balance the upper body over the pelvis thereby minimizing stress on the hip and back musculature.

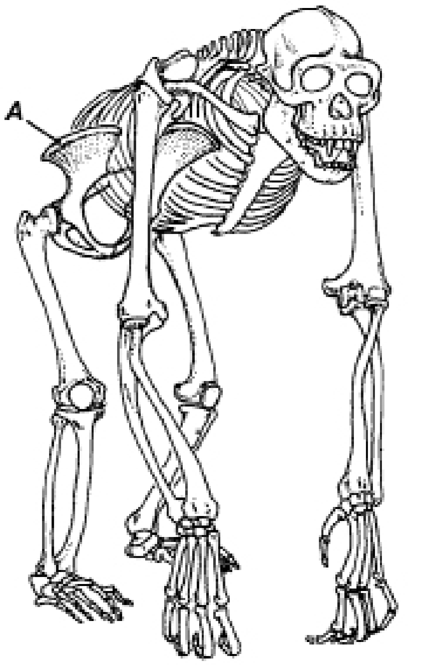

Figure 1.5. The chimpanzee ilia (A) are positioned in the frontal plane, which makes it impossible for the hip abductors to stabilize the pelvis effectively during single-limb support.

Because our last common ancestor possessed a mobile lumbar spine and an upper pelvis that angled slightly forward, the transition to bipedality would have been much easier than previously believed using the chimpanzee-centric model. This transition would have provided the transitional hominids a slight increase in metabolic efficiency for terrestrial locomotion while also allowing them to use their hands, possibly supplying food to pregnant females thereby ensuring that natural selection would heavily favor bipedality (13). After meticulously analyzing every detail of *Ardi's* skeleton and comparing it to past and present hominids, Lovejoy et al. (14) claim the last common ancestor was not skilled at prolonged suspension or climbing high branches and most likely spent most of its time in the lower canopy, and may have even been partially terrestrial. They suggest that the hindlimb of the last common ancestor "remained dominant for body mass support during bridging and arboreal climbing" allowing for an easier transition to walking upright on two legs. Lovejoy et al. (14) make the interesting statement that if the early hominids could have adapted to climbing as

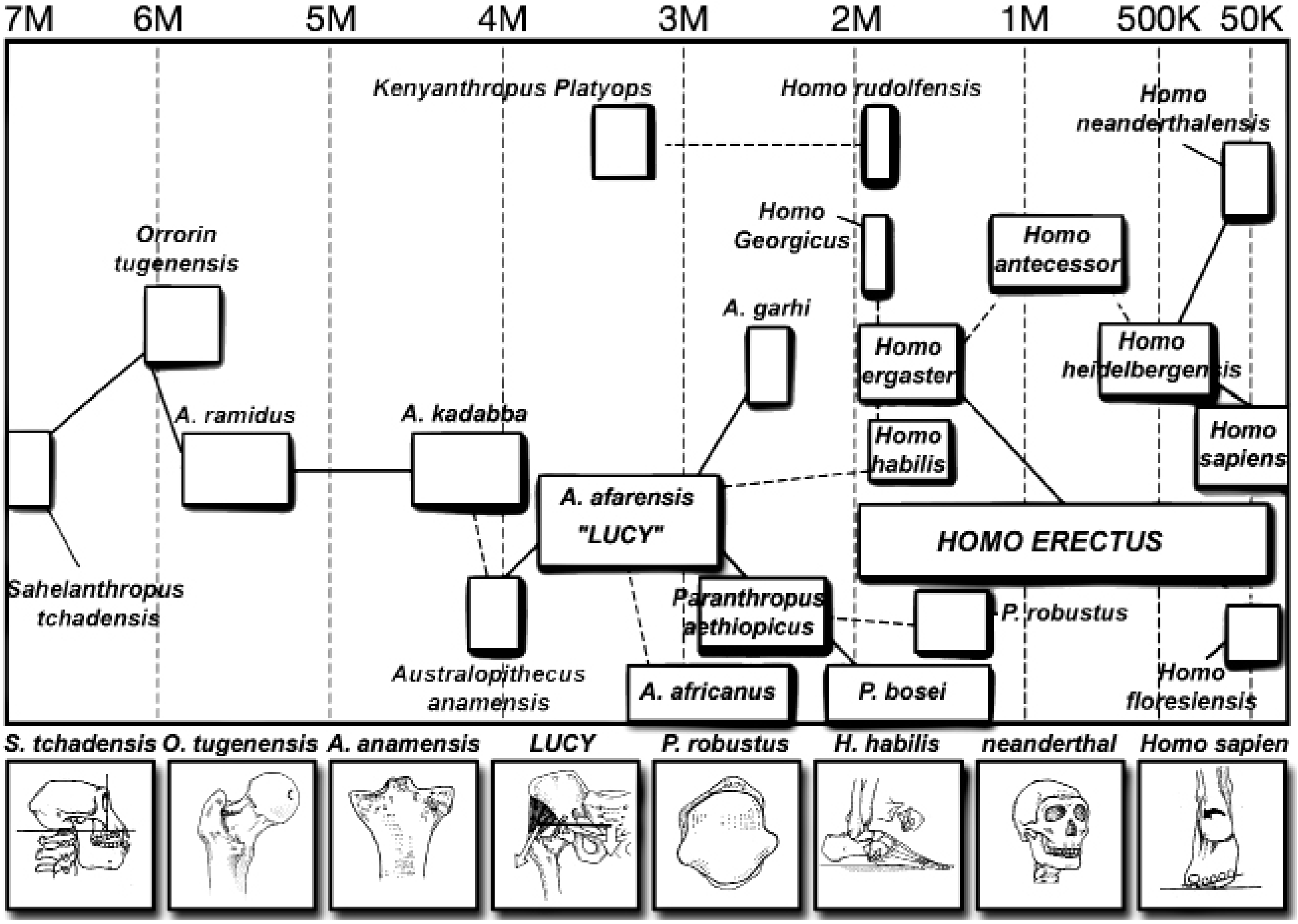

Figure 1.6. Time line of our hominid ancestors. Solid lines represent well-supported relationships while the dashed lines represent suspected but not confirmed relationships. Based on information from Wong K. The human pedigree. *Scientific American*. January 2009:60-63.

well as apes and chimps, "neither bipedality nor its social correlates would likely have evolved."

By piecing together the ever-increasing supply of skeletal remains of our hominid ancestors, researchers have been able to assemble a family tree that chronicles the 7 million year transition towards efficient bipedalism (Fig. 1.6). The following section reviews the anatomical changes in each of our hominid ancestors and relates this information to how these changes improved efficiency during upright walking and running.

Sahelanthropus tchadensis

The genus name *Sahelanthropus* translates into "Man from Sahel" and refers to the African region near the Sahara where this hominid was first found. The species name refers to Chad where the majority of fossil specimens have been recovered. The nickname for this early ancestor is *Toumai* for "Hope of Life," which is the name local villagers frequently use for human children born just before the dry season (15).

The only skeletal remains are a single crushed skull, a few jaw fragments and a few teeth. Dating back 7 million years, *Toumai's* skull possessed a cranial base similar to both *Ardipithecus* and Lucy, confirming that *Sahelanthropus* was definitely a hominid, not an extinct ape (16). The reconstructed skull had a centrally located foramen magnum, which is a strong indicator of bipedality as it both balances the upright head on top of the cervical spine and allows for a perpendicular angle between the orbits of the eye and the base of the skull (Fig. 1.7). This angle is essential for vision with bipedal walking and is not seen in quadrupeds. Unfortunately, without additional bony fragments it is impossible to verify the extent to which *Sahelanthropus* walked upright.

Orrorin tugenensis

Orrorin translates into "Original Man" in the Tugen language and *tugenensis* refers to the hills in Kenya where this hominid was first discovered. Bony fragments date back from 5.7 to 6.2 million years ago and include

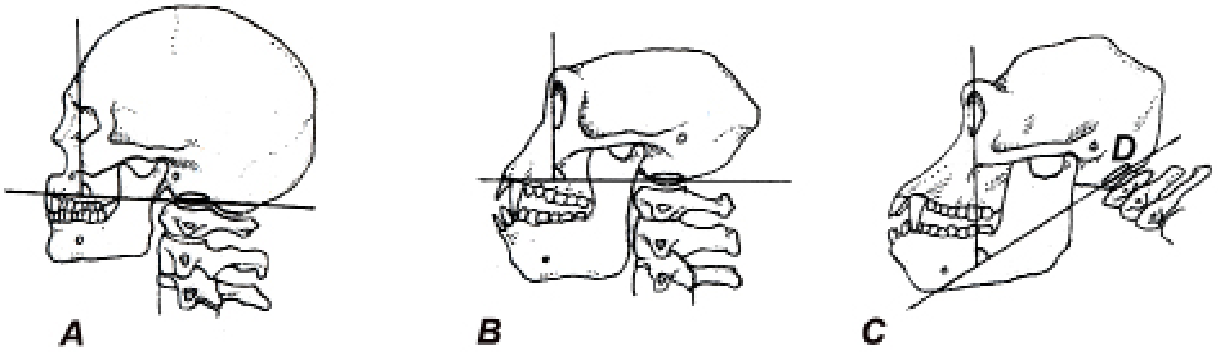

Figure 1.7. In modern humans (A) and *Sahelanthropus tchadensis* (B), the lines bisecting the foramen magnum and the anterior rim of the eye sockets form a nearly perpendicular angle. In chimpanzees (**C**), the intersecting lines form a more acute angle making it difficult for them to maintain a horizontal gaze without prolonged hyperextension of the cervical spine. Because they spend so much time looking down, the foramen magnum is positioned posteriorly in the chimpanzee (**D**).

jaw fragments, a few molars, a finger phalanx, and most importantly, the upper two thirds of a left femur. According to Sawyer et al. (15), the femur was "remarkably humanlike" in that it had a long femoral neck and a groove for the obturator externus muscle. This bony groove would only have formed if *Orrorin* walked upright on a regular basis. Arguing against significant bipedality, CT evaluations of *Orrorin's* femoral neck revealed a chimp-like distribution of cortical bone; i.e., because of the higher bending forces on the chimpanzee femoral neck, a chimp possesses a greater percentage of cortical bone on both the superior and inferior surfaces. Because of this, Lovejoy (17) states that *Orrorin* was "frequently, but not habitually upright, and most likely spent a significant amount of time in the trees."

Ardipithecus ramidus

Discovered in the Awash river valley in Ethiopia, *Ardi* translates into "ground floor" while *ramid* means "root." These names pay tribute to the Afar people who have "strong roots" in the Awash River area of Ethiopia (15). Until recently, all that was known about *Ardi* was that the glenohumeral joints were elliptical, the wrists were wide, and the proximal phalanx of the hallux tilted backwardly suggesting that *Ardipithecus* was occasionally bipedal but most likely behaved more like a ground-moving ape than a tree climber (15).

This all changed in 2009 when the journal *Science* published 11 papers detailing findings from a 15-year evaluation of dozens of bony fragments, including the nearly complete skeleton of a female recovered from an erosional degradation. By carefully analyzing thousands of samples of vertebrate, invertebrate, and plant fossils found at the site, researchers were able to determine that *Ardipithecus* lived from 4 to 6 million years ago and spent most of its time in woodland areas surrounded by small patches of hackberry, fig and palm trees. Surviving on a diet made mostly of ripe fruit, there was little evidence that *Ardipithecus* consumed open-environment resources, confirming that inhabitation of the grasslands was not a driving force for the development of bipedality (18).

Because their canine teeth were so small and because males and females were similar in size (averaging 4 feet tall, weighing 110 pounds), social aggression must have been minimal and females may have chosen their mates not based on physical prowess, but by their foraging efficiency (13).

As previously mentioned, the spine and upper pelvis of *Ardipithecus* were remarkably humanlike in that her lumbar spine could form a lordosis and the ilia flared forward, becoming vertically shorter and horizontally wider. The ability of the lumbar spine to extend enabled *Ardi* to balance the upper body over the pelvis while the forwardly angled ilia allowed gluteus medius to more effectively stabilize the pelvis when standing on one leg. The changes in the lumbar spine and ilia represent the most fundamental adaptations necessary for efficient bipedality.

Because *Ardipithecus* was habitually bipedal, the anterior aspect of the pelvis was forced to remodel as the constant tensile strain produced by the rectus femoris muscle pulled on the anterior ilium, causing the formation of the anterior inferior iliac spine (AIIS) (Fig. 1.8). Analysis of her skeleton revealed the AIIS was exceptionally strong and formed from a separate ossification center (19).

While *Ardi's* upper pelvis was designed for bipedality, her lower pelvis was not as it retained an ape-like shape in that the ischial tuberosities projected downwardly, not posteriorly, as they do in modern humans and even Lucy (Fig. 1.9). This downward slope would have allowed *Ardi* to climb trees more effectively but it would have significantly limited the ability of the hamstring musculature to decelerate the forward swing

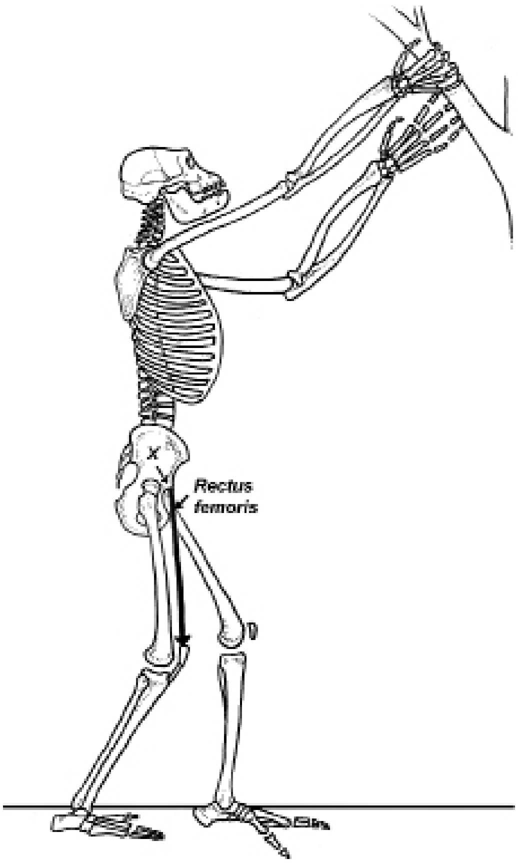

Figure 1.8. Prolonged upright postures increase tensile forces placed on the origin of the rectus femoris muscle (one of the 4 quadriceps muscles) eventually resulting in the formation of a bony exostosis (**x**) known as the anterior inferior iliac spine (AIIS).

of the leg during upright walking. This in turn would have markedly reduced *Ardi's* ability to walk quickly as it alters the length/tension relationship in the hamstrings: In *Ardipithecus*, the hamstrings generate peak torque when the hip is flexed towards the chest (as when climbing a tree) but the downward slope of the ischial tuberosities places the hamstring musculature in a shortened position when standing upright, which significantly reduces force output.

The upper extremity of *Ardipithecus* provided crucial evidence that we were not descendents of knuckle-walking apes, as *Ardi's* wrists were extremely mobile and the metacarpals remained primitively short and lacked the cortical thickenings and adaptations typical of knuckle-walking (20). The midcarpal joint was capable of such extreme ranges of motion that it is assumed that *Ardi's* wrists were used for "advanced arboreal palmigrady," in which she could maintain her grip on a tree branch by extending her wrist as her body progressed beyond the branch.

The fact that we did not descend from knuckle-walking apes was also confirmed by a biomechanical analysis of the wrists of great apes by Kivell and Schmitt (21). These researchers evaluated the carpal bones of modern apes and determined that contrary to all published literature, the wrists of modern apes do not possess bony locking mechanisms (in fact, their wrists were extremely mobile) and stability is achieved through a vertical stacking of their carpal bones in a manner similar to the legs of an elephant (Fig. 1.10). This vertical stacking is accomplished in part by a centralized head of the capitate bone that possesses a slight narrowing in the midsection. The capitate of *Ardipithecus* more closely resembled that

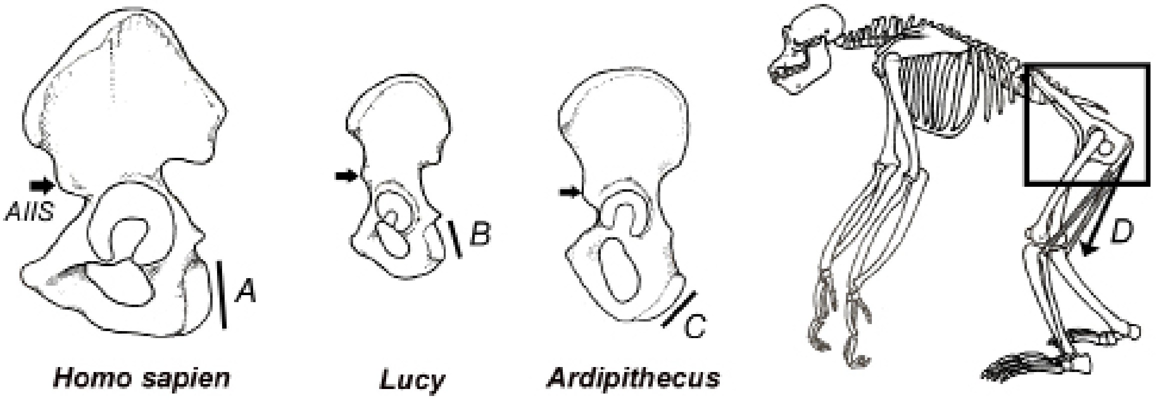

Figure 1.9. The ischial tuberosity in humans and Lucy (A and B) project posteriorly, allowing the hamstrings to remain under tension during upright postures. Because the ischial tuberosity in *Ardipithecus* **(C)** and chimpanzees (**D**) angle downwardly, the hamstrings play a more important role in stabilizing the pelvis during quadrupedal locomotion and while climbing (arrow in **D**). Notice the well-developed AIIS in humans, Lucy, and *Ardipithecus* (small arrows). Partially adapted from Lovejoy O, Suwa G, Spurlock L. The pelvis and femur of *Ardipithecus ramidus*: the emergence of upright walking. *Science.* 2009;326:71.

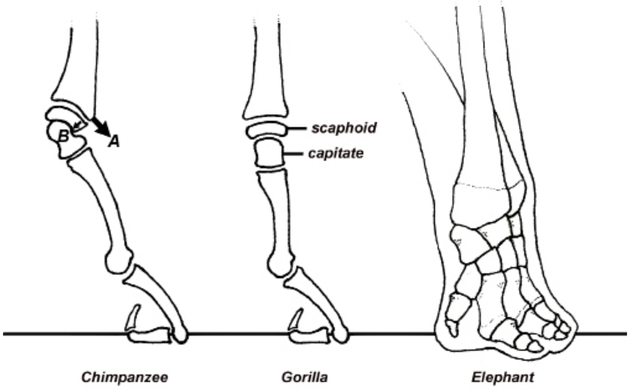

Figure 1.10. As chimpanzees knuckle-walk, the radius displaces forwardly (A) causing the scaphoid and lunate to compress into the central portion of the capitate (B). In apes and elephants, the bones of the wrists stack neatly on top of each other, thereby minimizing impingement of the central capitate. Partially adapted from: Kivell T, Schmitt D. Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. PNAS August 25, 2009;106:14241-14246.

of a chimpanzee with palmar displacement of its head (20). These findings confirm that our last common ancestor was not a knuckle-walker, because this trait developed much later in the large-bodied apes as a generalized adaptation allowing them to remain highly arboreal while also effectively moving about on the ground (21).

The foot of *Ardipithecus* was perhaps the strangest finding as it retained an extremely primitive appearance in which the first metatarsal and great toe were displaced medially (giving the appearance of a hand-like foot), while the lesser metatarsals were more modern as they were relatively short, extremely strong, and possessed an upward cant at the proximal phalanges. The upwardly canted lesser metatarsals would only be present if the leg was allowed to extend beneath the pelvis during the push-off phase of bipedal locomotion (Fig. 1.11). *Ardi's* foot represents a true evolutionary mosaic, as her opposable great toe that remained fully functional for arboreal climbing while her lesser metatarsals were structurally reinforced so they could tolerate the accelerational forces associated with the propulsive period of walking. This unusual arrangement completely disappears in later hominids as the first metatarsal moves into a centralized position and becomes significantly wider and stronger, supporting the majority of weight during the propulsive period of walking. In fact, a recent cadaveric study by Jacobs et al. (22) confirmed that during the push-off phase of modern human locomotion, the first metatarsal head supports 119% of body weight (this includes accelerational forces) while the second metatarsal head supports only 28% of body weight. The *Ardipithecus* foot represents the proverbial "missing link" in evolution, as it retains qualities common to modern humans and chimps and has a design that seems to be choosing between climbing and walking.

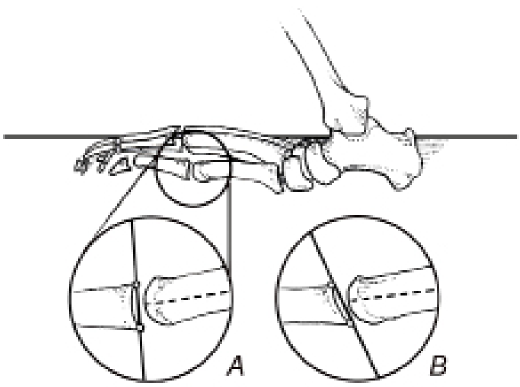

Figure 1.11. While the proximal phalanx of the chimpanzee (A) project slightly downward relative to the bisection of the first metatarsal shaft, the proximal phalanx of *Australopithecus ardipithecus* (B) has an upward cant that allows for an increased range of first metatarsophalangeal joint dorsiflexion during bipedal gait.

Australopithecus anamensis

Australopithecus refers to "Southern Ape" while *anamensis* translates from the Turkana language into "lake" and was chosen because all of the specimens have been found near lakes. Bony fragments from a tibia dating back 4 million years clearly shows that *Australopithecus anamensis* routinely moved about on two legs while changes in the distal humerus revealed that *anamensis* had lost the ability to knuckle-walk efficiently (Fig. 1.12). The distal aspect of the tibia was also consistent with a dedicated biped as the long axis of the tibia is perpendicular to the articular surface of the ankle joint. Oddly, the lower extremity features of *Australopithecus anamensis* reveal significant changes associated with the transition into efficient bipeds, but the skull and facial features remain primitive and more closely resemble orangutans.

Australopithecus afarensis

Better known by her nickname Lucy (after the Beatle's song that frequently played at the archeological site), *Australopithecus afarensis* actually translates into "Southern Ape from Afar", as she was discovered in the Afar region of Northeast Ethiopia. While fragments of *Australopithecus afarensis* were found as early as 1935, the discovery of Lucy by Donald Johanson in 1973 was significant as it included pieces of her pelvis, femur, and tibia. In 2000, only 4 km from where Lucy was discovered, paleoanthropologists unearthed a significant portion of the skeletal remains of a 3-year-old *Australopithecus afarensis* that became known as Lucy's baby (which is ironic as carbon dating revealed the child was more than

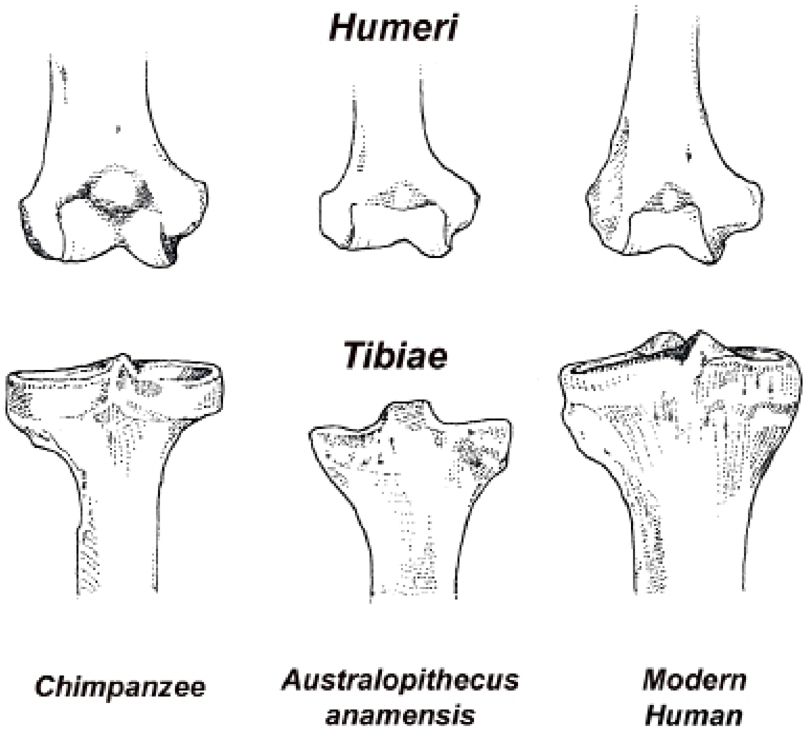

Figure 1.12. Posterior views of the left distal humeri and proximal tibiae in different species. Note the deeper olecranon fossa in the chimpanzee humerus that allows the ulna to lock in place during knuckle-walking. Because the chimpanzee's proximal tibia is T-shaped, it is unable to effectively bear weight during bipedal locomotion. In *Australopithecus anamensis* and *Homo sapiens*, the proximal tibial metaphysis flares out providing an increased quantity of cancellous bone that significantly improves the ability to absorb shock. Partially adapted from photographs in Leakey M, Walker A. Early hominid fossils from Africa. *Scientific American.* 2003;13:14-19.

100,000 years older than Lucy). Originally nicknamed the Dikka Child after the region in Ethiopia in which she was discovered, she was later renamed Selam, which means peace in several Ethiopian languages.

The 3-year-old Selam, who was most likely buried shortly after death by a flood, was discovered with a remarkably intact skeleton possessing the complete skull and mandible, the entire torso and significant segments of both upper and lower extremities including the patellae. By piecing together bony fragments from Lucy and Selam, it becomes clear that *Australopithecus afarensis* was most likely an accomplished biped. Although Lucy's lumbar vertebrae suggested occasional support from her forearms during bipedal gait, changes in her pelvis and lower extremity revealed that she was a very efficient walker (15). By meticulously casting and rebuilding Lucy's innominate (which had been crushed and fused into a single mass of matrix stone with about 40 separate pieces of the innominate inside), Lovejoy (17) was able to recreate the pelvis of our 3.1-million-year-old ancestor. Compared with *Ardipithecus*, the most obvious change in Lucy's pelvis was in the angle of her ischial tuberosities. Because they angled posteriorly in a manner similar to modern humans, the ability of the hamstring musculature to decelerate the forward swing of the leg significantly improved. This simple change would have provided Lucy with a significant metabolic advantage over her predecessors, particularly for long distance foraging and walking at faster speeds. To emphasize the importance of even small increases in efficiency as the day ranges for foraging increased, Leonard and Robertson (23) evaluated every aspect of Lucy's skeleton and created a model to determine energy savings as Lucy walked as a biped and a quadruped. By calculating Lucy's assumed speed as a biped (believed to be 2.3 miles per hour [14]) the authors considered total daily expenditures for male and female *afarenses* over a variety of day ranges and concluded that the metabolic savings associated with bipedality would have been relatively small over the shorter day ranges but were substantially larger as day ranges increased. Because Lucy existed 3 million years ago when food sources were becoming more spread out, and because modern hunter-gatherers have day ranges for foraging of approximately 8 miles per day, Leonard and Robertson (23) calculated that the energy savings for the larger day ranges could result in as much as an 8% reduction in energy expenditure per day. This significant caloric savings could have provided considerable benefit favoring bipedal locomotion as the saved calories could have been used for improved growth and reproduction.

Lovejoy's (17) analysis of Lucy's pelvis also revealed that her sacrum was becoming wider and her ilia became more dish-shaped (Fig. 1.13, A and B), flaring laterally even farther than *Ardipithecus's* ilia (20). This significantly improves bipedal efficiency by increasing the mechanical advantage afforded the gluteus medius muscle for resisting vertical forces associated with single-limb stance (Fig. 1.13, C). By having the ilia flare farther laterally, Lucy was able to use her gluteus medius to stabilize the vertical upper body during single-limb support, and walking suddenly became an efficient form of transportation.

Lovejoy (17) supports the theory that the newly flared ilia improves stability by comparing CT scans from chimpanzee and modern human femoral necks with a scan from Lucy. Because the chimpanzee's femoral neck lacks the stability provided by the lower gluteus medius and piriformis muscles, the femoral neck is subjected to a "greenstick effect," in which the superior surface is exposed to tensile strains (Fig. 1.14, A). As a result, as is consistent with Wolff's law, there is greater cortical bone formation present in the superior aspect of the chimpanzee femoral neck as it remodels to provide support at the site of tension. In contrast, modern humans have a significant decrease in tensile strains placed on the femoral neck

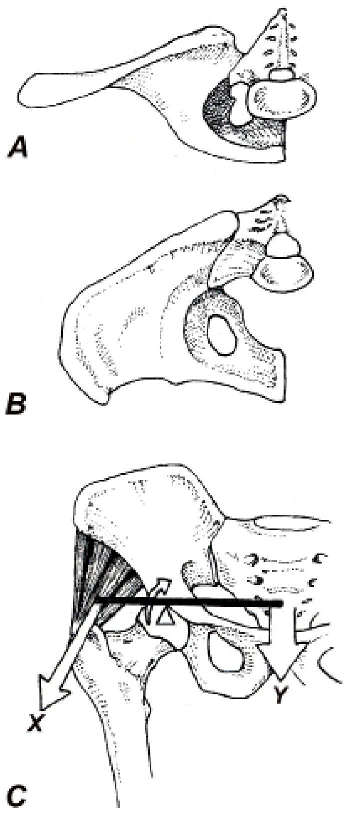

Figure 1.13. Superior views of a chimpanzee pelvis (A) and Lucy's pelvis (B and C). The outward flare of Lucy's pelvis allows gluteus medius (arrow **X**) to resist the downward motion of the weight-bearing torso (arrow **Y**). This represents a class one lever comparable to a playground seesaw in which the fulcrum is the hip and forces on the opposing sides are body weight and the pull of gluteus medius. The length of the femoral neck determines the lever arm afforded gluteus medius (think of one person on a seesaw moving farther away from the fulcrum). Interestingly, Lucy's femoral neck was longer than a modern human's femoral neck. Modified from Lovejoy O. Evolution of human walking. *Scientific American.* November 1988: 118-125.

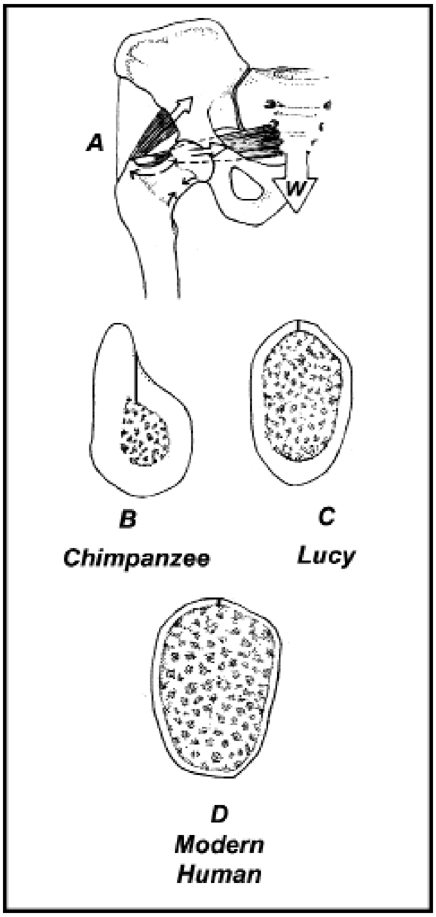

Figure 1.14. The weight of the torso during single-leg stance (W), creates a bending force on the femoral neck in which the upper and lower portions are exposed to significant tensile and compressive loads, respectively (small black arrows in A). In Lucy and in modern humans, the piriformis and lower gluteus medius muscles (small white arrows in **A**) create a powerful compressive force that reduces the femoral neck bending moments. The ability of these muscles to lessen bending strains is evidenced by the reduced quantity of cortical bone in the upper femoral neck (compare the dark lines in **B-D**). Modified from Lovejoy O. Evolution of human walking. *Scientific American*. November 1988:118-125.

because the lower fibers of gluteus medius and piriformis create a stabilizing compressive force that lessens the need for added support from dense cortical bone. Upon analyzing Lucy's femoral neck, Lovejoy noted a pattern of cortical bone formation similar to modern humans, which strongly supports the theory that Lucy was an efficient biped (see Fig. 1.14, B-D).

Also supporting Lucy's status as a dedicated biped are the famous Laetolli footprints. Discovered in Tanzania by Mary Leakey and her team of archeologists (24), these 3.2-million-year-old footprints were formed as 3 *Australopithecus afarensis* walked along a steep slope of volcanic ash. Despite a significant incline, there was no evidence of hand contact with the ground confirming that these hominids were indeed bipedal. The only consistent finding with these footprints was that all 3 *afarenses* walked with significant toe-out gait patterns. Also, while the Laetolli footprints lacked the detail necessary to evaluate shape of the medial longitudinal arch, recent research suggests that *Australopithecus afarensis,* like modern humans, exhibited variation in arch structure: some *afarenses* possessed well-developed arches, while others were flat-footed (45).

In addition to the occasional well-formed arch, Lucy's skull and lower extremities possess a number of changes consistent with frequent bipedality. Her foramen magnum is centrally located and the orbits of her eyes parallel her line of vision. The metaphysis of her proximal tibia flares out allowing improved dissipation of ground-reactive forces through the knee during upright walking. In the foot and ankle, the calcaneus was becoming wider and a deep groove was forming in the posterior fibular malleolus and in the trochlea of the calcaneus for the peroneal tendons. Latimer and Lovejoy (25) claim that these bony changes are consistent with a greater percentage of ankle plantarflexion force coming from the peroneal musculature rather than the Achilles tendon.

One of the most significant anatomical clues suggesting that Lucy was a biped is the distinct groove for tibialis anterior located on the distal aspect of her medial cuneiform. According to Latimer and Lovejoy (25), the distal location of this groove is essential for bipedality, because it allows tibialis anterior to physically block migration of the first metatarsal. The authors note that in less efficient bipeds such as chimps and apes, the groove for tibialis anterior is positioned proximally, making the first metatarsal unstable (Fig. 1.15). This would allow the first metatarsal to shift when exposed to the forces of propulsion.

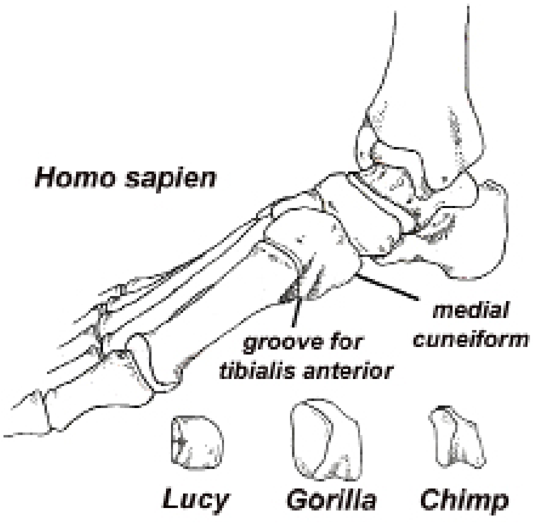

Figure 1.15. In modern humans and Lucy, a bony groove for the tibialis anterior tendon is located distally, while in gorillas and chimpanzees, the groove is positioned proximally. Partially modified from photographs in Latimer B, Lovejoy O. Am J Phys Anthropol 1990:125-133.

Although the distal articular surface of the medial cuneiform has a convexity midway between humans and chimpanzees, the proximal aspect of the first metatarsal possesses a double concavity with an invagination of the articular surface that limits axial rotation of the first metatarsal shaft (Fig. 1.16). This is an extremely important

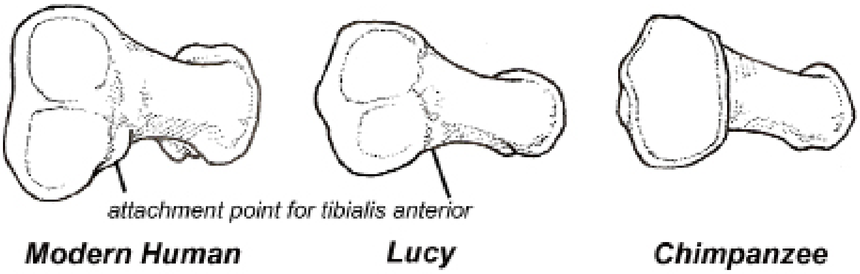

Figure 1.16. Posterior view of the left first metatarsal. Compared to the chimpanzee first metatarsal, both Lucy and modern humans possess a bony ridge that serves to lessen axial rotation. Note the distal attachment of the tibialis anterior tendon to the plantar medial aspect of the proximal first metatarsal in both Lucy and modern humans. Modified from Latimer B, Lovejoy O. Hallucal tarsometatarsal joint in *Australopithecus afarensis. Am J Anthropol.* 1990:125-133.

change as it stabilizes the medial forefoot and creates a bony block that lessens muscular strain during the propulsive period. The changes present in Lucy's feet suggest that she is giving up her opposable great toe in exchange for improved efficiency during bipedal locomotion. Because Lucy's hip could not extend as far back as modern humans, she was unable to create a significant force during push-off and her gait pattern most likely resembled something between modern humans and chimps. Her thick radial shaft cross-sections confirm that despite the lack of handprints present in the Laetolli footprints, Lucy frequently used her forearms for support (15). Because of her blend of anatomical features allowing support from both upper and lower extremity, Lucy serves as an excellent example of "mosaic evolution" in that she is exchanging the grasping skills of the foot (which *Ardipithecus* found so invaluable) in favor of improved stability necessary for bipedality (Fig. 1.17).

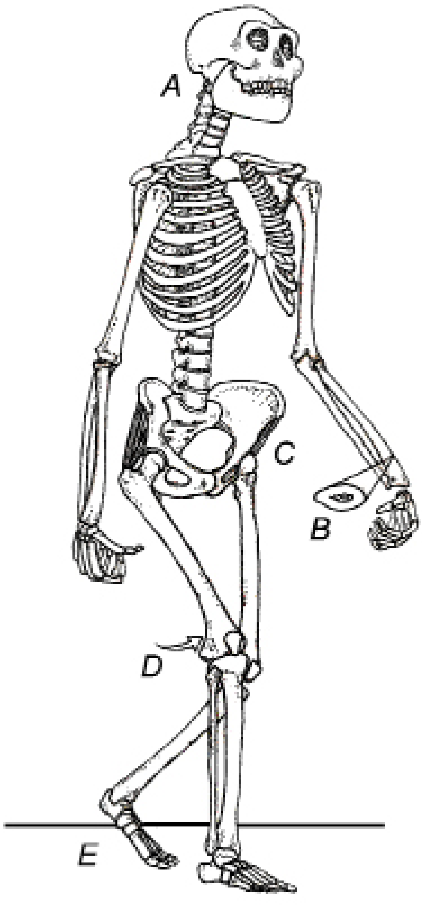

Figure 1.17. **Lucy walking.** With her centralized foramen magnum (**A**) Lucy maintains a horizontal gaze while walking. Her thick radial cortex (**B**) confirms that she frequently used her forearms for support while her elongated and curved fingers confirms that she spent a significant amount of time grasping branches and climbing. Compared to modern humans, her limited range of hip extension (**C**) would have shortened her stride length and she most likely would have walked with exaggerated knee flexion during initial ground contact (**D**). Because her talar neck was everted, the joints of the mid and forefoot may have been able to tolerate the forces of propulsion without buckling (**E**).

Australopithecus garhi

Because paleontologists were searching for an *Australopithecus afarensis* when they discovered the bony fragments of this hominid, they named the species *garhi* from the Afar language meaning "surprise." Although only a few skeletal fragments have been discovered, the length ratios of the upper and lower limbs are more humanlike than Lucy. The midshaft diameter of the radius suggests that *garhi* spent less time knuckle-walking than Lucy and fragments from the tibia and foot are close in size and shape to *Australopithecus afarensis* so it is assumed that *garhi* moved mostly upright and was habitually bipedal.

Australopithecus africanus

In 1924 a South African miner working in the Taung quarry near Johannesburg stumbled upon the skull of a new species of hominid. *Australopithecus africanus* literally translates into "The Southern Ape from Africa." Nicknamed the Taung child by the paleontologist Raymond Dart, the skull belonged to a young child and consisted of almost a complete face, a few teeth and a section of the braincase. Subsequent discoveries include another nearly complete skull, which was remarkably humanlike with its reduced jaw length and fairly vertical face. The ratio of upper extremity length to lower extremity length was .85, which is about halfway between modern humans (.76) and pygmy chimpanzees (.92). The tibiae are shorter than the femurs and various foot bones suggest that *Australopithecus africanus* had a very mobile foot with an abducted first metatarsal and no significant presence of a medial longitudinal arch (15). Analysis of the lumbar spine revealed small articular cross-sectional areas with a flattening of the lumbar lordosis suggesting limited upright walking. When compared to Lucy, *Australopithecus africanus* had limited hip extension and thicker cortical bone in the forearms, strongly suggesting that this species was not habitually bipedal and most likely stood upright primarily when feeding.

Paranthropus robustus

Accidentally discovered by a South African schoolboy in the 1930s, this hominid was named *Paranthropus* because it is from a side branch of human lineage, and *robustus* because of its robust teeth, skull, and jaw. *Paranthropus* stands out among early hominids because bone tools were found at various archeological sites containing skeletal remains of this hominid. Because of heavy wear patterns along the tips and scratches along the shafts, it is theorized that these early bone tools were used to dig for tubers and/or possibly termites (15). The most important finding relating to bipedality was the discovery in 1981 of a complete, undistorted first metatarsal (26). The morphology of this bone was remarkably humanlike in that it had a groove for the tibialis anterior tendon, a prominent tubercle for peroneus longus and a small area along the lateral aspect of its base that served as a contact point for the second metatarsal. The proximal portion of the base also possessed separate articular surfaces that limited mobility and the shaft was short and stout: strongly indicative of bipedal gait. When viewed distally, the lower section was appreciably flatter than a chimpanzee's first metatarsal head (compare X and Y in Fig. 1.18). Susman and Brain (26) argue that the inferior aspect of the first metatarsal head flattened in response to the increase in first metatarsophalangeal compressive forces associated with more frequent upright locomotion; i.e., when the heel leaves the ground while walking, the distal first metatarsal head is pushed into the proximal phalanx, which is maintained in a fixed position by the plantar ligaments, including the plantar fascia. The authors state that over time, the repeated intrinsic joint compression flattened the metatarsal head. Susman and Brain (26) state that flattening of the first metatarsal head represents the first sign of a functional metatarsophalangeal joint with the presence of a windlass mechanism described by Hicks (27).

The most important factor arguing against significant efficiency during bipedal locomotion is the relative dorsal narrowing of the superior distal aspect of the first metatarsal head (compare B and C in Fig. 1.18). This dorsal narrowing suggests the first metatarsophalangeal joint would be unstable when the hallux reached its full range of dorsiflexion, which would significantly limit this hominid's ability to apply force during the final moments of the propulsive period. In humans, the wider distal surface allows for a locking mechanism in which the metatarsophalangeal joint maintains stability as forces peak during propulsion. This finding alone would indicate that *Paranthropus robustus* most likely did not have an effective terminal push-off and the limited articular joint surface area present in the lumbar spine along with a relatively unstable hip joint suggests that *Paranthropus* was not a particularly efficient biped and frequently walked on all fours (15).

Homo rudolfensis

Named after Lake Rudolf in Western Kenya where this hominid was first discovered, *Homo rudolfensis* possessed such a large braincase that it was the first of our ancestors to be classified as *Homo* (which is Greek for "same"). Skeletal remains of the pelvis and lower extremity suggest that *Homo rudolfensis* spent almost all of its time walking on two legs. The lumbar facet and hips have increased surface areas capable of supporting body weight for long periods without assistance from the arms. The femoral neck angle, thickness, and shape of the femoral diaphysis (more teardrop-shaped with a greater anterior to posterior thickness) and improved alignment between the femur and tibia all provide significant advantages for efficient bipedality. The patellae face forward when the hip is extended and there is a humanlike ankle that is aligned in the transverse plane so the foot moves forward in the same plane as the lower extremity; i.e., unlike Lucy who walked with a significant toe-out, *Homo rudolfensis* walked with knees and feet moving forward in the sagittal plane.

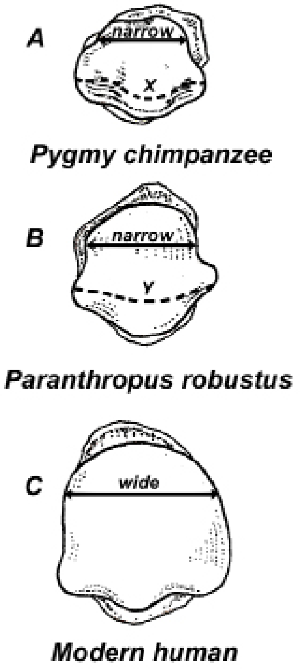

Figure 1.18. Distal view of the first metatarsal head in pygmy chimpanzee, *Paranthropus robustus,* and modern human. Dotted lines represent transverse plane bisections. While the inferior aspect of the *Paranthropus robustus's* first metatarsal head is relatively flat (compare **X** and **Y**), the superior aspect remains narrow compared to modern humans (double arrows). Redrawn from photographs in Susman R, Brain T. *Am J Phys Anthropol.* 1988;77:7-15.

An extremely important by-product of *Homo rudolfensis's* habitual bipedality is that it decoupled the process of breathing from locomotion. As noted by Carrier (28), running quadrupeds time their respiration with their strides: when their legs extend forward they inhale and when they hit the ground and their muscles contract to absorb shock, they exhale. This coupled pattern locks the breathing cycle during quadrupedal locomotion to the stride rate. In a full-time biped, breathing is no longer coupled with locomotion, which is essential for the development of speech as it allows for an adjustable rate of airflow. Whether or not our hominid ancestors began talking 50,000 years ago or 5 million years ago is the subject of

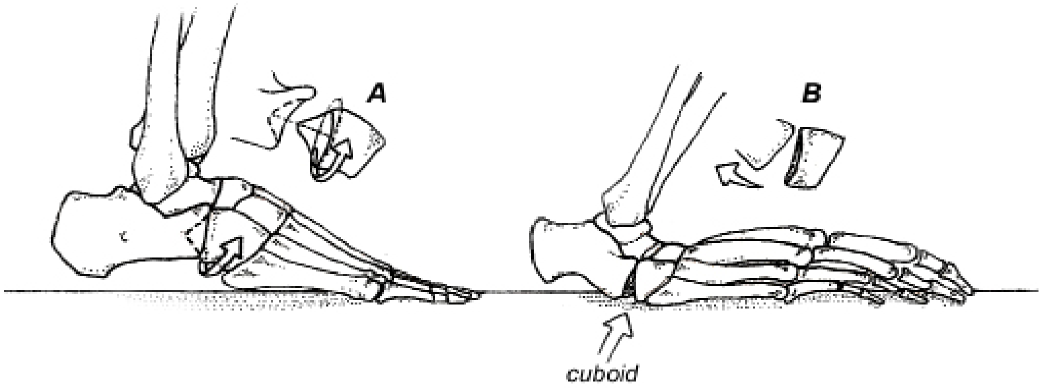

Figure 1.19. In modern humans (A), heel lift occurs with the cuboid pivoting about the calcanean process until its dorsal border contacts the overhanging calcaneus. This action essentially locks the midfoot during the propulsive period and allows for an efficient transfer of force from rearfoot to forefoot during propulsion. In a chimpanzee (**B**), the first stage of heel lift occurs with the cuboid maintaining ground contact (arrow): the calcaneocuboid joint fails to lock and the midfoot buckles under the forces of propulsion. The second stage of heel lift occurs when the cuboid leaves the ground transferring body weight to the forefoot through a collapsed and buckled arch.

debate but it is clear that the process of walking on two legs was responsible for the eventual development of language.

Homo habilis

"The Handyman" was named by Raymond Dart because it was the first hominid to routinely use tools and its increased brain size suggested that this hominid was "mentally skillful": *habilis* is Latin for "able, handy, mentally vigorous." Discovered in Tanzania in 1959, *Homo habilis* is somewhat controversial because it has many characteristics of *Australopithecus afarensis* (e.g., Lucy), causing some paleontologists to argue whether it should be classified as a *Homo* or if it would be more appropriately named *Australopithecus habilis* (15). For example, its hand is wide and humanlike but its fingers possess a chimp-like curvature with the thumb rotated in a manner similar to a great ape. The midshaft diameter of the radius is thick confirming that *Homo habilis* was not a full-time biped. In addition, the lower tibia and ankle internally rotate in the transverse plane, which would have forced *Homo habilis* to walk with a significant toe-in gait pattern. In fact, Sawyer et al. (15) note that modern humans that are as pigeon-toed as one particular specimen of *Homo habilis* are unable to maintain balance while walking. Other skeletal remains of *Homo habilis* are consistent with a more humanlike form: a centrally located foramen magnum with a slight indentation in the posterior skull for the nuchal ligament, suggesting that this hominid frequently walked upright with a balanced head.

An almost complete *Homo habilis* foot discovered in 1960 has been extensively studied and it possesses many humanlike qualities. The calcaneocuboid joint was remodeled so the cuboid possessed a medial plantar prominence that projects proximally into the calcaneus and serves as a locking mechanism for the lateral column (Fig. 1.19, A). Unlike chimpanzees who have a double push-off where the calcaneus initially leaves the ground followed shortly thereafter by the cuboid, human heel lift occurs as a single event with the calcaneocuboid joint locking so the midfoot does not contact the ground during propulsion (Fig. 1.19, B). As described by Bojsen-Moller (29), the calcaneocuboid joint locking mechanism provides significant stability as the cuboid pivots about its medial plantar prominence until its dorsal surface collides with the overhanging calcaneus, thus providing a bony locking that lessens muscular strain. Kidd et al. (30) demonstrate that the calcaneocuboid joint locking mechanism in *Homo habilis* was even better developed than in modern humans, perhaps because the toe-in gait placed greater stress on the lateral column.

Morphological evaluation of a *Homo habilis* foot revealed an orangutan-like talus with an ape-like navicular (30). The first metatarsal was remarkably humanlike as the hallux aligned with the lesser metatarsals and the dorsal surface of the first metatarsal head significantly widened, which would have allowed the first metatarsophalangeal joint to be stable through a full range of motion during the propulsive period. Whether or not *Homo habilis* should be classified as an *Australopithecus* or *Homo* may be the subject of debate, but the development of a stable first ray, a calcaneocuboid joint locking mechanism that allowed for a single-phase push-off, along with a dorsally widened first metatarsophalangeal joint that could provide stability during terminal propulsion are all extremely important advances in the process of becoming efficient bipeds.

Homo ergaster

Named from the Greek word meaning "workman" (numerous tools have been found at various archeological sites) this hominid should have more appropriately been named "the traveler" as it was one of the first hominids to leave Africa (31). Evaluation of a 1.5-million-year-old skeleton of a 12-year-old boy revealed that *Homo ergaster* was surprisingly humanlike in appearance. Unlike *habilis, ergaster* had limb proportions comparable to modern humans. In fact, the tibiae of *Homo ergaster* were actually longer than ours, which could have allowed for more efficient bipedality. Because the growth plates of the young boy had not closed, it was impossible to ascertain adult articular ranges of motion but the transverse plane alignment of the lower extremity was similar to *Homo rudolfensis* in that the foot and leg moved together in the same transverse plane; i.e., unlike Lucy with her toe-out gait and *habilis* with the extreme toe-in, *ergaster* walked with a straight gait pattern and was most likely a very efficient biped.

Homo georgicus

Discovered in volcanic deposits in the medieval town of Dmanisi in southeastern Georgia, *Georgicus* is the first hominid discovered outside of Africa. Although recent findings include a femur, patella, lower leg and various foot bones, these bony fragments have yet to be studied in detail. The prior discovery of a 1.8-million-year-old *Homo georgicus* third metatarsal was significant, as it was small but stocky and possessed a large tubercle at its base. This may have been associated with the development of an early medial longitudinal arch (15).

Homo erectus

Named *erectus* because of its upright stature and narrow frame, this hominid had a remarkably long species lifespan with fossil remnants dating from 1.9 million years ago to as recently as 27,000 years ago. In a beautifully written article detailing specific evolutionary traits associated with the development of bipedal locomotion, Bramble and Lieberman (32) argue that *Homo erectus* was the first hominid capable of endurance running. This is important as no primates other than humans are capable of endurance running and the ability to jog long distances would have provided significant advantages when scavenging for food. The authors support their hypothesis by noting that the skull of *Homo erectus* has a significant ridge along the base of the occiput where the nuchal ligament attaches. They suggest that this ridge would only be present if *Homo erectus* was capable of endurance running, because running results in a slight but rapid deceleration of the body following heel strike that causes the skull to pitch forward abruptly with each stride. The increased forward head pitch coupled with the oscillations present at heel strike would significantly stress the nuchal ligament insertion, eventually producing a thickening of the ridge (the nuchal ridge is absent both in chimpanzees and *Australopithecus afarensis*). To support their case, the authors note that a computerized tomographic evaluation of a *Homo erectus* skull revealed a dramatic increase in the size of the semicircular canals (33). Because running often lacks a double-limb support phase in which both feet are on the ground (i.e., the airborne phase is followed by a precarious single-limb support phase), the improved balance provided by the large semicircular canals is essential for stability. Other authors have noted that chimpanzees lack a well-developed semicircular canal, which partially explains why they are incapable of balancing on one leg during static stance. This would also have been true for *Australopithecus afarensis,* as computerized tomographic evaluations of Lucy's skull revealed poorly developed semicircular canals (32).

Besides changes in skull shape and the inner ear, the upper extremities in *Homo erectus* also revealed significant changes consistent with endurance running, as there was a 50% reduction in the mass of the forearms relative to body mass and the scapulae were less cranially oriented (32). These changes would have made *Homo erectus* less skilled at climbing but would have been invaluable for running, since the wider shoulders and shorter arms would have allowed for independent counter rotation of the upper extremity and pelvis while also reducing weight of the upper extremity: both of which are important with endurance running.

The spine and pelvis of *Homo erectus* had also undergone significant changes compared with prior hominids, as the ratio of articular surface area to body mass significantly increased in the lumbar spine, sacroiliac joint, femoral head and tibiofemoral joints. These changes would have been essential in order to handle the increased ground-reactive forces associated with running. The femur of *Homo erectus* is particularly interesting as it is identical to that of modern humans: e.g., the femoral neck angle is 120° with approximately 10° of anteversion (which allows the patellae to face forward when the hip is extended), while the midshaft cross section is teardrop-shaped and the posterior aspect of the greater trochanter possesses thickened ridging at the attachment points for the gluteal muscles.

Compared to *Australopithecus afarensis,* there was a reduction in the length of the femoral neck (which decreased metabolic efficiency while walking because it lessened the lever arm afforded gluteus medius) but the shorter femoral neck was essential for running since it decreased the bending moments on the neck during single-limb support, thereby reducing the risk of femoral neck stress fracture. Interestingly, the tibiae of the *Homo erectus* were identical to modern humans except for the fact that they were more robust. Although there are no skeletal remains of *Homo erectus* feet, the recent discovery of 1.5-million-year-old *Homo erectus* footprints in Ileret, Kenya, revealed well-defined medial longitudinal arches and a modern humanlike angle of abduction of the hallux: the angle between the hallux and shaft of the first metatarsal in the *Homo erectus* footprints averaged 14°, which is comparable to the modern human angle of 8° (34). In contrast, the abduction angle of the hallux in the *Australopithecus afarensis* footprints discovered in Laetoli averaged 27° (34). Additionally, the path of the prints paralleled the direction of travel and a detailed optical laser analysis of pressure patterns revealed a greater depth of print beneath the medial forefoot, suggesting a medial weight transfer before the push-off phase of walking (34). These findings are consistent with a long, modern, humanlike stride with push-off occurring over extended lower limbs and stable first metatarsophalangeal joints.

Typically standing 5 feet 2 inches tall and weighing only 110 lbs, *Homo erectus* developed a narrow, elongated form that lessened solar exposure and increased heat dissipation while running. The skull possessed accessory "vaults and expansions" that would have allowed for improved venous cooling in the face and scalp. By combining all of these features, Bramble and Lieberman (32) make a very strong case arguing that *Homo erectus* was indeed an efficient endurance runner and was the first "fully terrestrial hominoid."

Homo erectus's proficiency at endurance running may have also been indirectly responsible for brain expansion, since the improved scavenging skills provided by endurance running would have allowed *Homo erectus* to outperform other hominid and primate competitors: although non-human primates can sprint, they are not capable of long distance running (35). Because numerous early *Homo erectus* archeological sites show an increase in the presence of animal bones, it is suggested that for the first time in hominid evolution, meat was now part of the diet. Leonard (36) states that because the brain consumes 16 times the calories of an equivalent mass of muscle, and because resting brain metabolism in humans consumes approximately 25% of the total caloric intake (in most mammals the brain consumes 3 to 5%), the addition of meat into the diet would be essential to provide the calories necessary for brain expansion; e.g., meat provides up to 4 times the calories of an equal sized serving of fruit (36). In addition to incorporating meat, *Homo erectus* was the first hominid to utilize fire to heat food. Cooking played an important role in brain expansion because it allowed for a greater percentage of nutrients to be metabolized by the body: 100% of cooked food is metabolized while only 30-40% of the nutrients present in raw food can be digested. The combination of improved foraging skills associated with running and the increased nutritional gains associated with cooking enabled *Homo erectus* to double its brain size in just 600,000 years.

Homo floresiensis

Discovered in 2003 on the remote Indonesian island of Flores (hence the name *Homo floresiensis*), this enigmatic hominid stood only 3 feet 6 inches tall and possessed such a small brain case that it was initially incorrectly suggested that the skull belonged to a microcephalic *Homo sapien* (Fig. 1.20). Because *Homo floresiensis* lacked the bony characteristics typically seen in pygmies and pituitary dwarfs (both of which have small bodies and large brains), researchers determined that *Homo floresiensis* was not related to *Homo sapiens* and must have descended from a prior hominid. It was assumed that this hominid managed to drift to the remote island at least 800,000 years ago (which is significant since there is no evidence of boat building until 50,000 years ago) and, after being marooned for several hundred thousand years, evolved into the dwarf species *Homo floresiensis*.

The process of dwarfing with isolation seems implausible but it has been repeatedly demonstrated that when animals are isolated with limited predation and/or competition for food, large animals become small and small animals become large. The reason for this is that small creatures such as rabbits and rats survive in conventional environments by becoming smaller and producing so many offspring that despite predation, they survive because of their population density. Conversely, large animals such as elephants and rhinos have a greater chance for survival if they become so big that predators will no longer attack. The only problem with this hypothesis is that the brain of *Homo floresiensis* was so exceedingly small that it was disproportionate to all known scaling relationships associated with isolation dwarfing.

The mystery of *Homo floresiensis*'s tiny brain was recently solved by researchers from the Natural History Museum in London. By analyzing fossils from hippopotamuses that had been isolated on the island of Madagascar, Weston and Lister (37) demonstrated that compared with conventional isolation dwarfing, island isolation results in significantly greater reductions in

Figure 1.20. The microcephalic skull of *Homo floresiensis*.

brain versus body size, explaining how a large-brained hominid could have evolved into the microcephalic *Homo floresiensis*.

The only question that remained was figuring out which hominid evolved into *Homo floresiensis*. Early research suggested that *Homo erectus* was the most likely predecessor, mainly because it was assumed that only a biomechanically efficient hominid could travel all the way to Asia. Recent fossil evidence questions this view since analysis of multiple *Homo floresiensis* skeletons makes it clear that this mysterious hominid bore a much stronger resemblance to Lucy and other australopithecines than to *Homo erectus*. Evaluation of skeletal remains from 14 different individuals revealed that this tiny hominid had a pelvic structure similar to Lucy's (confirming that *Homo floresiensis* did indeed walk upright), with an appendicular skeleton that more closely resembled the early australopithecines (e.g., an ape-like wrist with short femurs and tibiae).

Perhaps the strangest feature of the *Homo floresiensis* skeleton was the foot. Despite a hallux that aligned with the first metatarsal, the rest of the foot was extremely primitive and bore a much stronger resemblance to the foot of a Bonobos chimpanzee in that it completely lacked a medial longitudinal arch and possessed long, curled toes that would have been useful for grasping (38). By far, the most unusual characteristic of the *Homo floresiensis* foot was its length: while modern humans typically have a foot measuring 55% the length of their femur, the *Homo floresiensis* foot measured 70% the length of the femur (38). Such an extremely long foot would have forced *Homo floresiensis* to walk with a steppage gait in which the hips flexed excessively in order to allow the toes to clear the ground during midswing (comparable to walking while wearing swim fins). Although they may have been able to run, it would have been for extremely short distances and only in emergencies.

In an attempt to determine the hominid predecessor of *Homo floresiensis*, Argue et al. (39) used a technique called cladistics, in which a wide range of shared physical traits are evaluated to establish relationships between organisms. Using this technique, researchers determined that *Homo floresiensis* most likely evolved sometime between *Homo rudolfensis* and *Homo habilis* and found no connection between the tiny hominid and *Homo erectus*. The results of their findings are significant because it proves that relatives of this large-footed, small-brained hominid somehow managed to leave Africa almost 2 million years ago, eventually making its way to this remote Indonesian island. To confirm this theory, paleoanthropologists are searching for *Homo floresiensis* skeletons at other sites in Asia.

Because *Homo floresiensis* survived until 17,000 years ago, and because skeletal remains of *Homo sapiens* have been found on Flores dating back to 55,000 years ago, it is known that *Homo floresiensis* and *Homo sapiens* coexisted for at least 28,000 years. It is unclear whether *Homo floresiensis* was simply absorbed into the *Homo sapien* population or if they became extinct because of disease or an inadequate ability to compete for food. Despite a brain volume comparable to a modern chimpanzee, *Homo floresiensis* used remarkably sophisticated stone tools, such as blades, awls, punches and even micro-blades for big game hunting, which made some researchers question the connection between brain size and intelligence. This paradoxical relationship was made clear when virtual reconstructions of skull fragments revealed that despite its small skull, *Homo floresiensis* possessed an enlarged Brodmann's area 10, a section of the frontal lobe associated with complex cognitive function (40).

Homo antecessor

While cutting a railroad path in Northeast Spain, workers unearthed skeletal remains that included an upper jaw and a few teeth (the fragments were carbon-dated to approximately 800,000 years ago). In 1997 it was determined that these fragments belonged to a new species of hominids named *Homo antecessor* (from the Spanish word for ancestor), since this *Homo* was initially believed to be the ancestor of all modern Europeans. Although little is known about the joint surface areas and upper vs. lower extremity length ratios, skeletal remains from the hands and feet suggest that *Homo antecessor* was an efficient biped, comparable to modern humans (with the exception that the patellae were significantly smaller) (15).

Homo heidelbergensis

The jawbone *Homo heidelbergensis* was unearthed in 1903 in a quarry near Heidelberg, Germany. Evaluation of scratch marks on the teeth suggests that this hominid used stone tools to cut objects held in its mouth. Oddly, the teeth also revealed wear patterns consistent with toothpick use (15). Standing nearly 5 feet 8 inches tall with a species lifespan from 700,000 until 200,000 years ago, *Homo heidelbergensis* was the common ancestor to both *Homo neanderthalensis* and *Homo sapiens*. Despite its relationship to modern humans, *Homo heidelbergensis* was almost identical in appearance to *neanderthalensis* and skeletal remains revealed an extremely wide pelvis with the lower extremity bones being shorter and stockier than modern humans.

The skeletal proportions of *Homo heidelbergensis* were most likely the by-product of its environment, because 500,000 years of living in a cold climate eventually allows natural selection to favor a skeletal shape in which the torso gets larger and the extremities get shorter as this lessens the surface area to volume ratio. This in turn favors reduced heat dissipation because the smaller the surface area, the less body heat lost to the environment through convection.

Homo neanderthalensis

The prototypical caveman, almost all skeletal remains of *Homo neanderthalensis* have been recovered from cave and rock shelters found throughout Europe and Asia. Although a Neanderthal infant was discovered in Belgium in 1829, the first adult skeletal remains were found by miners in the Neander Valley of northern Germany (*tal* is old German for valley while *thal* replaced *tal* in the early 1900s as the German word for valley). Skull fragments revealed a particularly short forehead with independent bony thickenings over the orbits of each eye giving *Homo neanderthalensis* the characteristic caveman appearance often depicted in cartoons and the media. Although originally considered a primitive brute (skeletal remains revealed routine cannibalism), it is now known that Neanderthals buried their dead with rituals that included specific positioning, the use of markers and perhaps even the incorporation of flowers with the deceased. Sawyer et al. (15) note that *Homo neanderthalensis* was often blue-eyed and frequently possessed blond and/or reddish hair and were most likely capable of speech.

The species lifespan for *Homo neanderthalensis* was from 175,000 to as recently as 27,000 years ago. Expanding glaciers throughout Europe and Asia during that time suggest that *neanderthalensis* was exposed to snow almost year-round. As with *Homo heidelbergensis*, consistent exposure to cold for tens of thousands of years allowed natural selection to favor a skeletal shape that lessened heat loss: the extremities (particularly the fingers, forearms and legs) were significantly shorter than modern humans while the torso was long, wide and barrel-chested. These combined features make *Homo neanderthalensis* a little shorter than modern humans but about the same weight. Because of their short tibiae and stocky femurs (which had reduced femoral neck angles), it was originally assumed that *Homo neanderthalensis* walked with a stooped, bent knee gait. However, the recent discovery of osteoarthritis in the weight-bearing joints of a particularly old Neanderthal confirms that they most likely walked upright in a manner similar to modern humans (although their shorter lower extremities resulted in reduced stride lengths making for a fairly inefficient gait) (Fig. 1.21).

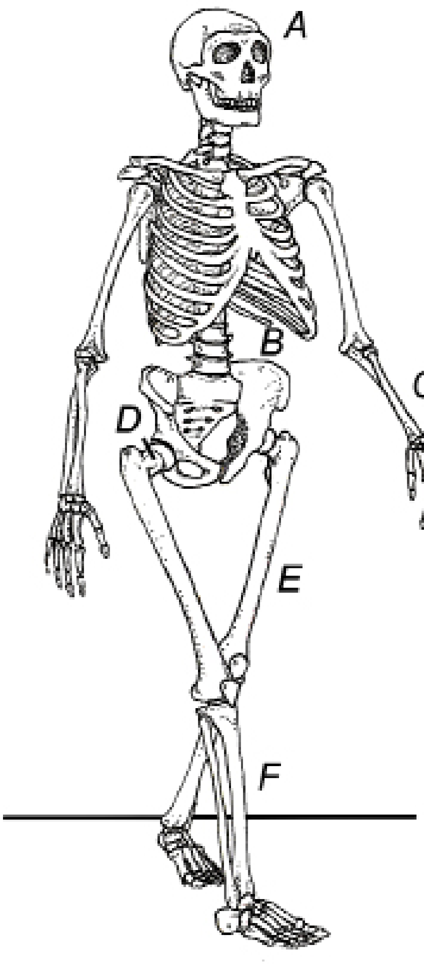

Figure 1.21. *Homo neanderthalensis* walked with an upright posture similar to modern humans. The primary difference in skeletal structure relates to the bulging brow ridge (**A**), widened rib cage (**B**), short forearms (**C**), reduced femoral neck angle (**D**), stocky femurs (**E**) and shortened tibiae (**F**). The shorter legs and excessive muscle mass significantly increased the metabolic cost of locomotion.

Because *Homo neanderthalensis* and modern humans inhabited the same geographic location for thousands of years, it was always suspected that occasional interbreeding between *Homo sapiens* and *Homo neanderthalensis* might have occurred. Although early DNA research suggested otherwise, a team of researchers from the Max Planck Institute for Evolutionary Anthropology in Leipzig Germany evaluated 4 billion nucleotides from Neanderthal bone fragments found in a cave in Croatia and conclusively demonstrated that interbreeding did occur (45). In fact, between 1 and 4% of modern human DNA comes directly from Neanderthals, including genes coding for cognitive function and skeletal development. By comparing the Neanderthal genetic code to modern humans throughout the world, the authors concluded that interbreeding most likely took place between 50,000 and 80,000 years ago, somewhere in the Middle East. The offspring of Neanderthals and humans quickly spread: people from Papua New Guinea (where Neanderthals never lived) have just as much Neanderthal DNA as people from France. The only modern humans devoid of Neanderthal DNA are from Africa, since interbreeding occurred after our ancestors crossed into Eurasia.

Despite occasional interbreeding, the Neanderthal population slowly dwindled, becoming extinct approximately 30,000 years ago. While it was originally assumed that Homo sapiens unwittingly caused the extinction of *Homo neanderthalensis* through competition for food and/or by the spread of disease, more recent research suggests that metabolic inefficiency may have played an important role in their demise. In a detailed study of the energetic cost of locomotion as related to lower limb length, Steudel-Numbers and Tilkens (42) prove that the Neanderthal's shorter tibiae would have increased the metabolic cost of locomotion by at least 30%. Froehle and Churchill (43) went on to calculate the daily energy expenditure of Neanderthals versus modern humans and determined that because of their stockier frames and increased muscularity, *Homo neanderthalensis* had to spend anywhere from 100 to 350 kcal/day more than their *Homo sapien* relatives. While the Neanderthal's greater body mass and increased muscularity significantly improved thermoregulation and made them effective big game hunters, their inability to survive on non-meat food sources (meat was becoming increasingly sparse as rapid changes in climate reduced the number of large mammalian prey) coupled with their higher cost of locomotion may have created an environment where they were spending more calories on transportation then they were able to consume. As noted by Froehle and Churchill (43), the biomechanically more efficient modern humans "may have been able to convert their energetic savings into a slight reproductive advantage" thereby ensuring their survival.

Homo sapiens

"The Knowing Man" (*sapiens* translates from the Latin "to know") represents us: the remarkably successful species of modern humans (Fig. 1.22). DNA evidence coupled with carbon dating of skeletal remains suggests that the first *Homo sapiens* emerged from Africa about 200,000 years ago. These early humans were remarkably adept at locomotion as they were quick to cover the planet. With a small band of modern humans leaving Africa about 100,000 years ago (estimated to be between 50 and 100 individuals [1]), skeletal remains have been dated in the Middle East at 90,000 years ago, China 67,000, Australia 30,000, and the Americas starting at 11,000 years ago. Within 1,000 years, our early ancestors spread from the steppes of Russia to the lower tip of South America.

The skeletal factors that allowed for such efficient long distance travel included a widening of the dorsal first metatarsal head (that stabilizes the hallux throughout the propulsive period), an effective calcaneocuboid joint locking mechanism (that decreases muscular strain and prevents buckling of the midfoot after heel lift occurs), a centralized first metatarsal with a powerful peroneus longus muscle wrapping around its base (providing improved medial stability during push-off) and an increased mass in the distal tibia and fibula that allowed for a larger and more stable ankle joint complex. Also, in order to provide variable gearing depending on the terrain and/or the desired speed, the distal metatarsal heads formed a parabolic curve that enabled the early *Homo sapiens* to rapidly change the length of the forefoot lever arm depending upon the locomotor requirements; e.g., walking up a steep hill is more efficient when pushing off the lateral forefoot (low gear), while rapid sprinting is best accomplished by pushing off the medial forefoot (high gear) (Fig. 1.23).

Compared with our ancestors, the tibiae became longer, the toes became shorter (which reduced weight as we no longer needed them for grasping) and the patellae became wider, allowing for improved stability of the knee in the sagittal plane. The femoral neck angles increased to an average of 130°, which reduced bending strains on the neck and improved efficiency of the gluteus medius muscle during single-leg stance. A slightly adducted femoral shaft (coxa varum) positioned the femur directly over the perpendicular tibia effectively converting the lower extremity into a stable vertical column thereby lessening

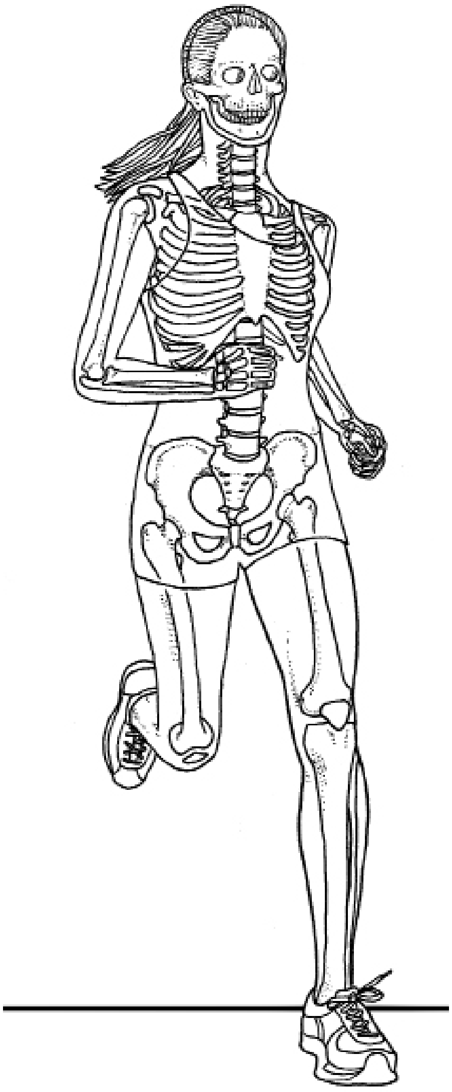

Figure 1.22. The modern human.

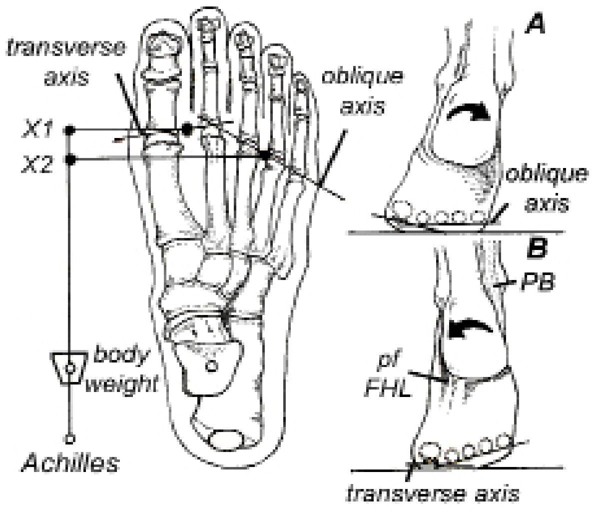

Figure 1.23. Because the second metatarsal is longer than the remaining metatarsals, it serves as a pivot point allowing the human foot to choose between 2 different push-off options. When the rearfoot supinates (**A**), push-off occurs through the oblique axis which has a shorter lever arm to the ankle joint (compare X1 and X2). This lessens strain on the Achilles and is often used when running uphill. Because of the shorter lever arm, use of the oblique axis allows for what Bojsen-Moller (44) refers to as a low gear push-off. When greater force is needed (e.g., sprinting) the peroneus brevis muscle (PB in **B**) everts the rearfoot thereby forcing the foot onto the transverse axis (**B**). Because of the longer lever arm, use of the transverse axis is referred to as a high gear push-off and this axis is used when faster speeds are required. Notice in figure B that the plantar fascia (pf) and flexor hallucis longus muscle (FHL) tense to stabilize the medial forefoot against the greater forces associated with use of the transverse axis. The transition from low to high gear push-off results in a brief period in which body weight is supported solely by the second metatarsal. Despite its narrow width, the second metatarsal shaft possesses a greater percentage of cortical bone allowing it to tolerate the significant bending forces associated with this brief but frequent transition phase.

bending strains. The articular surface areas increased in size relative to bone length (which allowed for an improved distribution of joint pressure) and the spine developed 3 curves that provided larger ranges of motion while more evenly distributing pressure between the discs and facets. There was a continued progressive increase in vertebral girth moving from the cervical spine to the lumbar spine that provided protection against the large ground-reactive forces associated with our upright posture. The sacrum's 5 vertebrae fused and our tail (coccyx) shriveled in size.

Unlike Lucy, the pelvis became wider and the birth canal size increased in females, allowing for the delivery of our big-brained babies. Soft tissue changes occurred in which the tendons responsible for the storage of energy (e.g., the Achilles and the plantar fascia) became broader and stronger so they could both absorb and return energy during the gait cycle (getting farther on fewer calories is the ultimate goal of efficient bipedality). Muscle attachment sites became thicker and left clear marks on our skeletons (particularly in males). According to Sawyer et al. (15), these unique skeletal features all serve to increase the efficiency of our two-legged movements. These authors go on to explain why the world's most successful long distance runners are from sub-Saharan Africa (notably Kenya and Ethiopia). They suggest that since the original *Homo sapiens* were from eastern Africa, they have had the longest time to allow natural selection to produce a skeletal shape that could accommodate heat dissipation so essential in a tropical environment. Just as the early *Homo sapiens* living in cold environments for thousands of years eventually developed wide, long torsos with short extremities that favored heat retention (e.g., Inuit, Mongolians and even the early European cave dwelling Cro Magnons), the earliest *Homo sapiens* that remained in sub-Saharan Africa eventually developed reduced trunk volume and longer extremity lengths that increased the surface area to volume ratio thereby providing for improved heat dissipation. As is consistent with natural selection, the greater the time period, the more pronounced the changes: the Inuit, with only a few thousand years in a cold environment do not have the same torso extremity length ratios as the Mongolians, who have been exposed to cold climates for tens of thousands of years. Sawyer et al. (15) claim that after 200,000 years of adapting to extreme heat, the increased lower limb lengths relative to torso volume make sub-Saharan African runners the most efficient endurance runners on earth. Given the small populations of Kenya and Ethiopia compared to the world population, and the number of world records held by these two countries in the 10 km and marathon distances, this theory seems more than plausible.

It took a long time but by standing upright and taking those first few steps 7 million years ago, *Sahelanthropus tchadensis* set into motion a series of events that would eventually convert a tree-dwelling ape into the most successful species the world has ever seen. Bipedality freed the hands for a variety of actions from tool use to creating music and art. It uncoupled respiration and locomotion (which turned out to be essential for the development of speech) and improved our long distance foraging skills, so crucial in providing the calorie dense diet our expanding brains required. In 100,000 years, *Homo sapiens* have grown from a small band of adventurous (and probably hungry) modern humans taking those first few steps out of Africa, into a world population exceeding 7 billion and growing rapidly. Although unaware of the causes and timing of specific events, Darwin was right: bipedality was the defining feature that made us human.

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Chapter Three

Ideal Motions during the Gait Cycle

The fundamental component of human locomotion is the gait cycle. One complete gait cycle consists of the anatomical interactions occurring from the moment the foot first contacts the ground, until that same foot again makes ground contact with the next step. The human gait cycle consists of two phases: stance phase, in which the lower extremity is contacting the ground; and swing phase, in which the lower extremity is swinging through the air preparing for the next impact (Fig. 3.1). When a person is walking, the gait cycle lasts approximately one second (1). As a result, stance phase occurs in 0.6 seconds and swing phase in 0.4 seconds. Because the distal end of the kinetic chain is fixed by ground-reactive forces during stance phase, motions during this portion of the gait cycle are referred to as closed-chain motions. In contrast, swing phase motions are referred to as open-chain motions since the distal end of the kinetic chain is freely mobile. Because of the complexity of stance phase motions, this portion of the gait cycle has been subdivided into contact, midstance, and propulsive periods (Fig. 3.2).

When walking, the contact period represents the first 27% of stance phase, beginning at touchdown and ending when the entire forefoot makes ground contact. Midstance occupies 27-67% of stance, representing the period in which the body's center of mass is "vaulting" over the stance phase foot. The propulsive period occupies the final 33% of stance phase, beginning the moment the heel leaves the ground and ending when the tips of the phalanges no longer make ground contact. Although running is also divided into the same 3 periods, the increased speed and the need for a more forceful propulsive period changes the timing of the events, as the contact and midstance periods are slightly shorter (occurring in the initial 0-20% and 20-45% of stance phase, respectively), while the propulsive period is extended, occupying the final 55% of stance phase (2). With more than 5,000 cycles performed daily, the gait cycle is one of the most repetitive events in our lives.

The neurological mechanisms necessary to complete a gait cycle are unusual in that swing phase motions are reflexive and present at birth (e.g., an unbalanced toddler will immediately swing the lower extremity into a protected position), while movements associated with stance phase represent a learned process (3). Scott (4) supports this statement with the clinical observation that children born without sight make no spontaneous attempts to stand up and walk on their own, and will only do so when physically guided. With or without sight, once upright and moving about, children immediately begin experimenting with a wide range of walking and running patterns, subconsciously analyzing the metabolic expense associated with each variation in gait. This is a time-consuming process and perfecting the musculoskeletal interactions necessary to

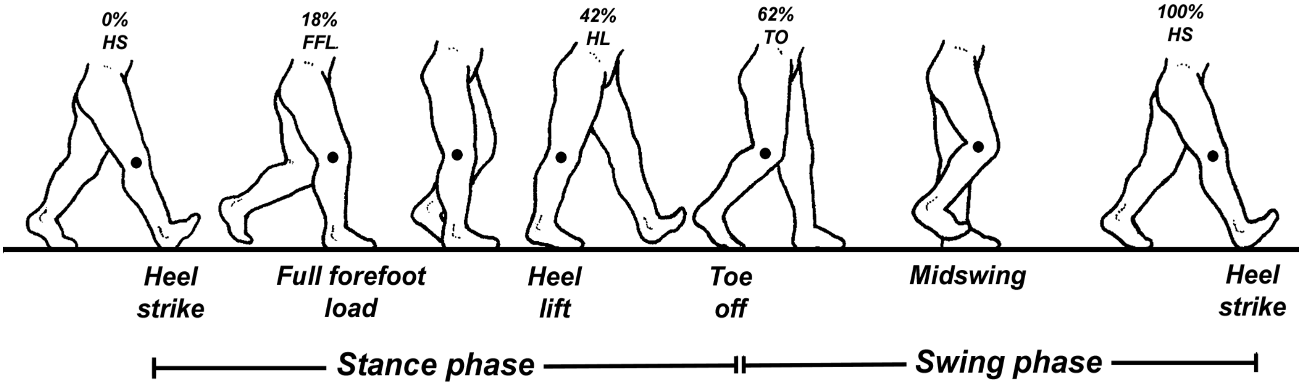


Figure 3.1. Gait cycle of the right leg. Stance phase begins at heel strike (HS) and ends when the great toe leaves the ground. Swing phase continues until the heel again strikes the ground. The length of stride, which refers to the distance between successive ipsilateral heel strikes, is approximately 0.8 times a person's body height and the average cadence is 115 steps/minute. Because size affects stride length and cadence, there is much individual variation in the gait cycle as women typically have slightly shorter stride lengths and a more frequent cadence. Children have particularly high cadences as the average 7 year old takes approximately 143 steps per minute. Because of the prolonged airborne phase, stride lengths while running significantly increase and it is not uncommon for world-class runners to possess stride lengths exceeding 3.5 meters (11 feet 6 inches), which is more than one meter longer than a comparably sized running quadruped (13).

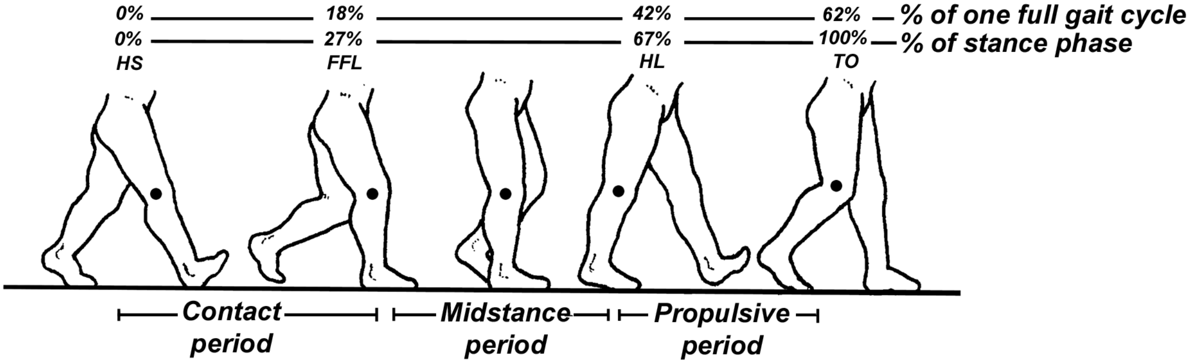


Figure 3.2. The various periods of stance phase. HS, heel strike; FFL, full forefoot load; HL, heel lift; TO, toe off.

become metabolically efficient can take up to a decade to master. Even when considering size differences, the average 3 year old consumes 33% more oxygen when traveling at a fixed speed compared to an adult (5). By the age of 6, children continue to have significantly higher ratios of energy costs versus work performed (6). Fortunately, by age 10, mechanical efficiency has improved and the cost/work ratios of 10 year olds and adults are about equal (6): after almost a decade of practice, children are finally efficient at bipedal locomotion.

In order to create a metabolically efficient gait, Saunders et al. (7) claim that individuals must learn to "translate their center of mass through space along a path requiring the least expenditure of energy." This is accomplished by modifying joint positions in the lower extremity and pelvis in such a way that the pathway of the center of mass through space is flattened. For example, if an individual were to walk with knees locked and the pelvis stiff, the body's center of mass would move through a series of abruptly intersecting arcs (Fig. 3.3A) that would greatly increase the metabolic cost of locomotion because muscles must tense to accommodate the exaggerated angular displacements. Further strain would be placed on the supporting muscles since they would initially absorb, and then accelerate these forces as the curves reverse direction. To lessen the metabolic cost of locomotion, each person incorporates a specific series of articular interactions that effectively decrease angular displacement of the body's center of mass. These actions, or determinants, are listed as follows: pelvic rotation; pelvic tilt; knee flexion/extension during stance phase; hip-knee-ankle interactions; and lateral pelvic displacement. The following illustrations, which were adapted from Saunders et al. (7), demonstrate how each determinant affects translation of the center of mass through space (Figs. 3.3-3.8).

Although the determinants described by Saunders et

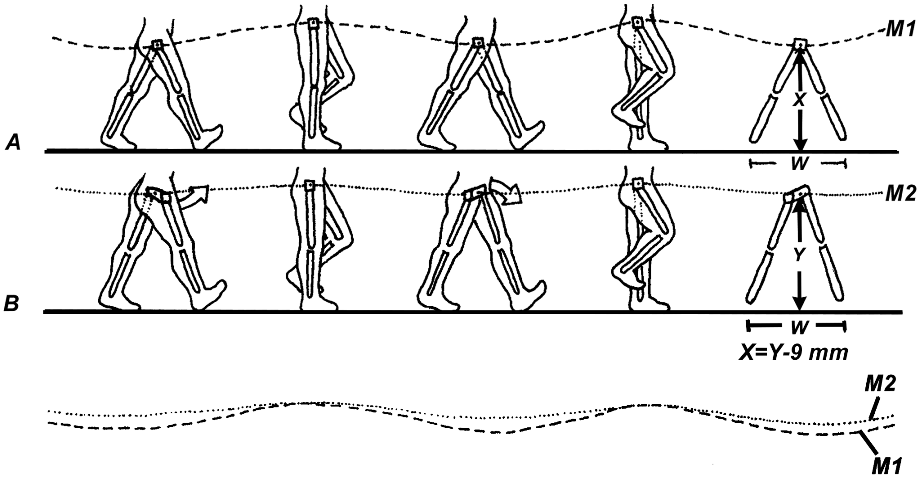


Figure 3.3. Determinants of gait: pelvic rotation. Panel A represents a lateral view of the gait cycle with the knees and hips locked. Notice how the pathway of the center of mass creates an exaggerated sine wave (**M1**), which is metabolically expensive because the hip abductors must raise and lower the center of mass through the exaggerated ranges. By incorporating pelvic rotation (arrows in panel **B**), the pathway of the center of mass is flattened slightly as rotation of the pelvis decreases the amount of hip flexion/extension necessary to achieve the same stride length (**W**). This decreases vertical drop during double-limb support by approximately 9 mm (the difference between the ground and the center of mass in **X** and **Y**), flattening the pathway for the center of mass (compare **M2** and **M1**).

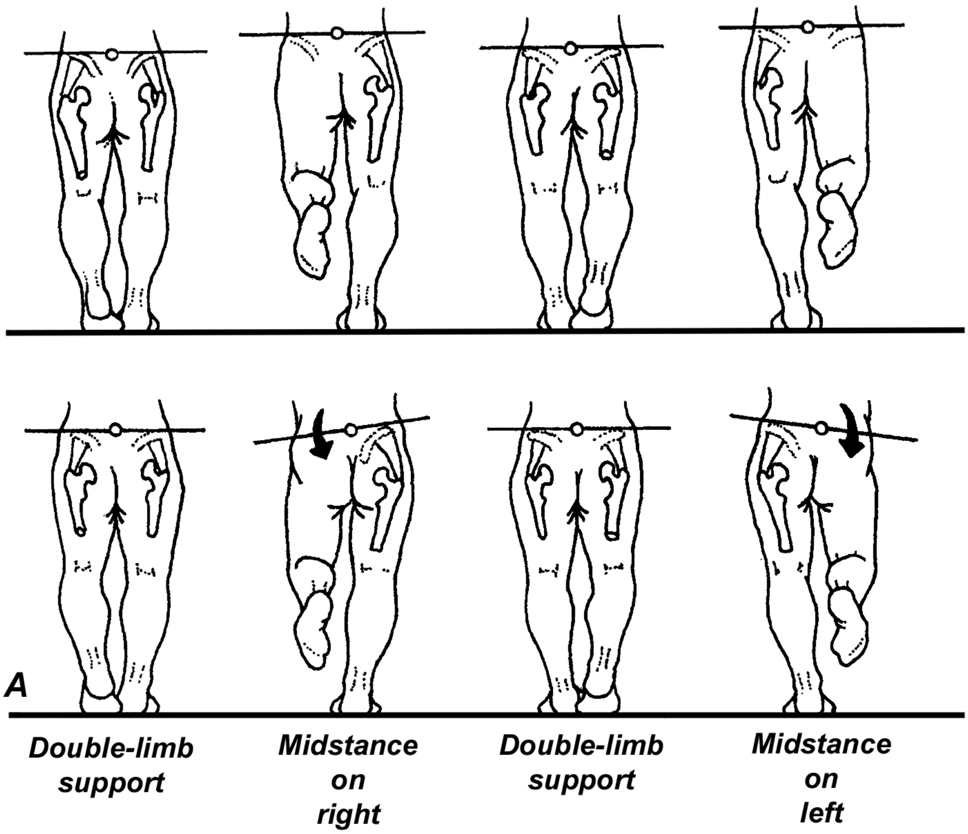


Figure 3.4. Pelvic tilt. Eccentric contraction of the hip abductors during midstance lowers the pelvis on the side of the swing leg (arrows in **B**). This decreases vertical displacement of the center of mass by approximately 3 mm.

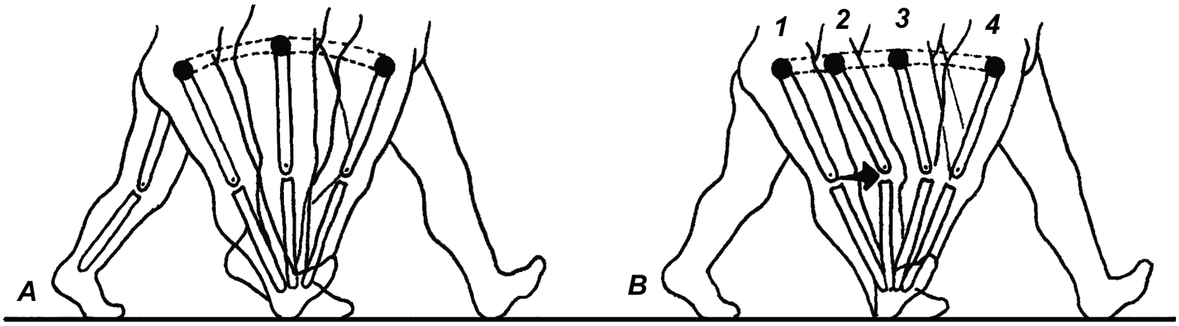


Figure 3.5. Knee flexion/extension during stance phase. Part **A** represents stance phase lower extremity motion without knee flexion while Part **B** represents the same leg with knee flexion/extension. Notice that when the lower extremity is straightened throughout stance phase, the center of mass describes a path along the arc of a circle, with the length of the lower extremity being the radius. This arc is effectively flattened by knee flexion during early stance phase and knee extension during late stance phase.

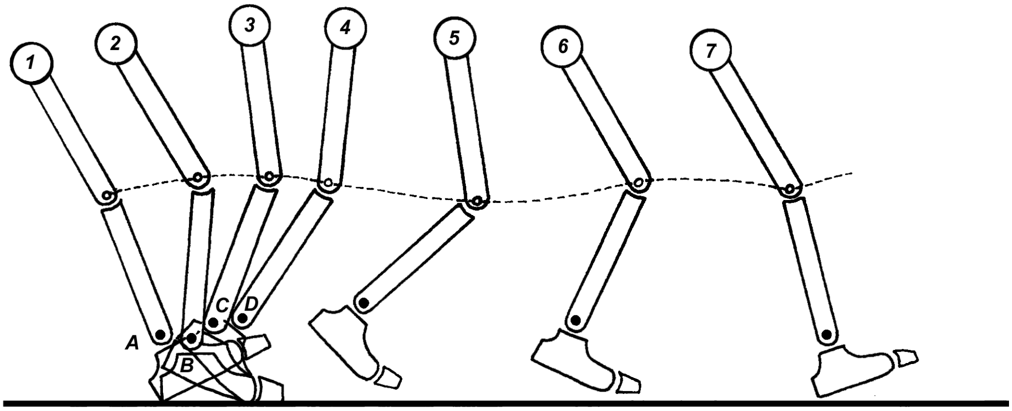


Figure 3.6. Hip, knee, and ankle interactions. As heel strike occurs, the anterior compartment muscles eccentrically contract to slowly lower the stance leg to the ground (**A** and **B**). This action, coupled with simultaneous knee flexion, maintains a smoother course for the center of mass during the contact period. Forceful ankle plantarflexion during propulsion markedly elevates the leg (**B**-**D**) and is responsible for the maintenance of an almost straight pathway for the center of mass during late stance phase (3-4). Flexion of the knee and hip during swing phase (5-7) allows for sufficient ground clearance despite lowering of the pelvis that is normally occurring on the swing leg side. If the knee and hip were unable to move through adequate ranges of motion, the individual would most likely compensate by circumducting the swing leg. This action greatly distorts movement of the center of mass and is metabolically very expensive.

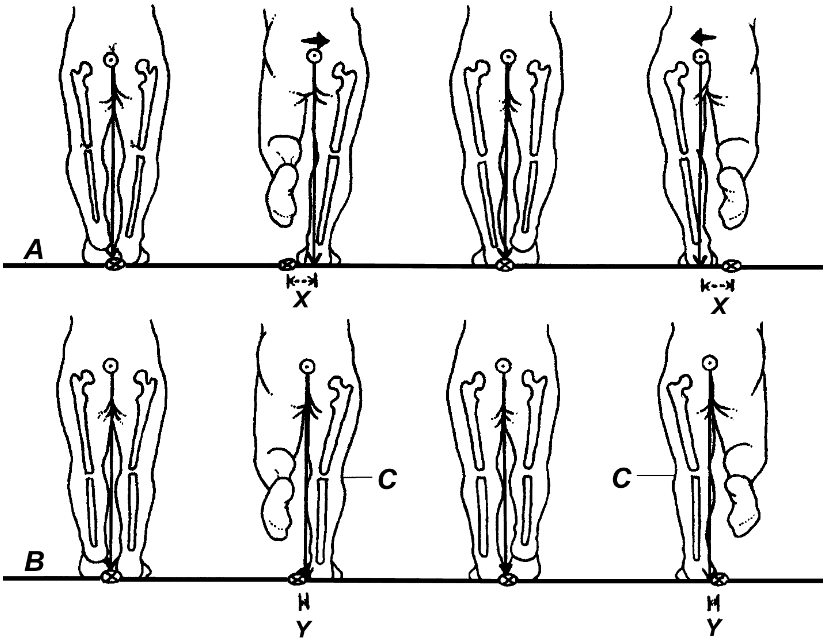


Figure 3.7. Lateral pelvic displacement. To maintain balance during the gait cycle, the weight-bearing leg adducts, and the swing leg abducts. This allows the center of mass to be displaced laterally over the supporting leg (Panel **A**, **X**). If the lower extremity were perfectly straight (as in panel **A**), the degree of lateral deviation necessary to maintain balance is significant. This markedly increases strain on the hip abductors and peroneals when these muscles accelerate the center of mass medially during late midstance and early propulsion. Fortunately, most people possess a slight degree of genu valgum (**C**) that reduces the degree of lateral displacement by allowing for a more approximated base of gait (**Y**). A mild genu valgum also allows the tibia to move through the gait cycle in a near vertical position (Panel **B**).

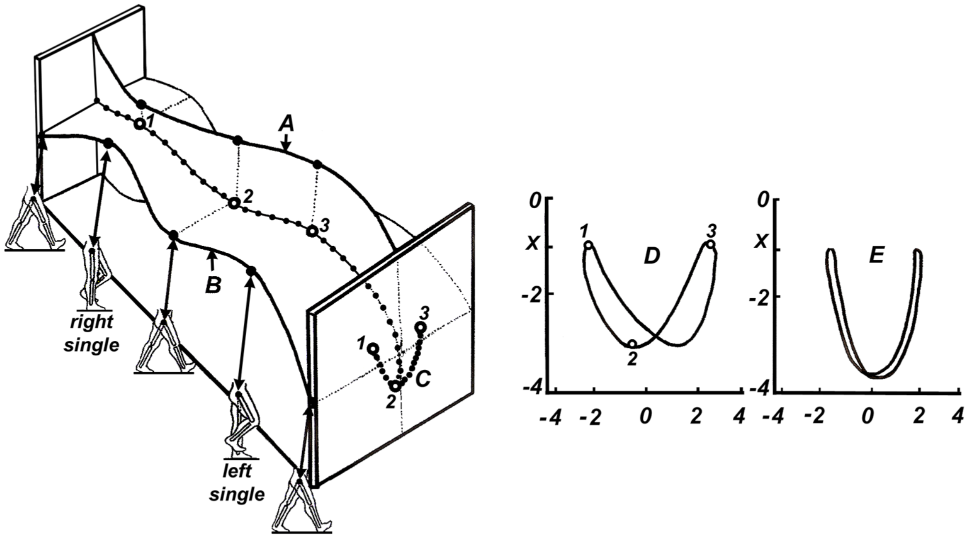


Figure 3.8. Final translation of the center of mass during a single stride. Lateral and vertical displacements are represented by **A** and **B**, respectively. Notice that these displacements form sine waves, with the frequency of vertical displacement being exactly twice that of the lateral displacement. **C** represents the projection of these displacements (which have been exaggerated) onto a plane perpendicular to the body's line of progression. Points 1, 2, and 3 represent the location of the center of mass during successive single, double and single-limb stance points, respectively. Because peak vertical displacements are reached slightly before peak lateral displacements, this curve represents a slightly distorted "lazy 8" (**D**). At higher speeds of walking, the amplitude of lateral displacement is decreased, and the lateral and vertical displacements peak at the same time. As a result, the perpendicular displacement of the center of mass more closely resembles a "U" (**E**). Note that even at maximal vertical displacement (**X**), the center of mass never reaches the level it would assume during static stance (which is represented by **0**). When walking, forward acceleration of the center of mass, at both high and low speeds, is greatest at the low points of vertical displacement (i.e., during double-limb support) and least at the high points (i.e., during midstance period). Another way of saying this is that kinetic energy is greatest at the low points whereas potential energy is greatest at the high points. This is comparable to rolling an egg end over end: the egg is moving rapidly at the low point in the cycle and gradually decelerates, so that it is barely moving by the time it reaches the high point in the cycle.

al. (7) improve efficiency by flattening the progression of the center of mass through space, it is possible to flatten the pathway so much that the resultant gait pattern becomes metabolically inefficient. To demonstrate this concept on yourself, try walking in a manner similar to the comedian Groucho Marx. Although hyperflexion of the knees and hips associated with this style of gait will flatten the pathway of the center of mass, it is metabolically expensive because the caloric cost associated with exaggerated knee flexion is high. In fact, McMahon et al. (8) found that walking with a "Groucho gait" resulted in a 50% increase in oxygen consumption. Excessive flattening of the pathway of the center of mass accomplished by flexing the extremities explains why small mammals are so inefficient compared to large mammals; e.g., on a gram per gram basis, a mouse consumes 20 times more energy than a pony (9). It also explains why elephants, despite their enormous size, are one of the most metabolically efficient animals on the planet: unlike rodents that are forced to hyperflex their extremities with each step, elephants keep their extremities locked during stance phase thereby lessening the muscular cost of locomotion.

An important consideration is that the determinants described by Saunders et al. (7) must be modified depending upon the speed of locomotion. For example, at low speeds we are most efficient when the lower extremities are stiff and inflexible but at higher speeds we must increase the degree of knee and hip flexion in order to improve shock absorption. To determine exactly which gait pattern is most efficient at a specific speed of locomotion, Srinivasan and Ruina (10) created a computerized mathematical model to evaluate metabolic efficiency associated with every possible type of gait (including odd patterns such as the Groucho gait). As expected, at low speeds of locomotion, walking was most efficient with an inverted pendulum gait while at higher speeds, a "bouncing" or "impulsive running" style of gait was most efficient (Fig. 3.9). These findings correlate with the clinical observation that walking feels more comfortable when moving slowly, while running is more comfortable as speeds increase.

Notice in these illustrations that the defining difference between walking and running is the center of mass is at a low point during midstance when running, and a high point during midstance when walking. This is

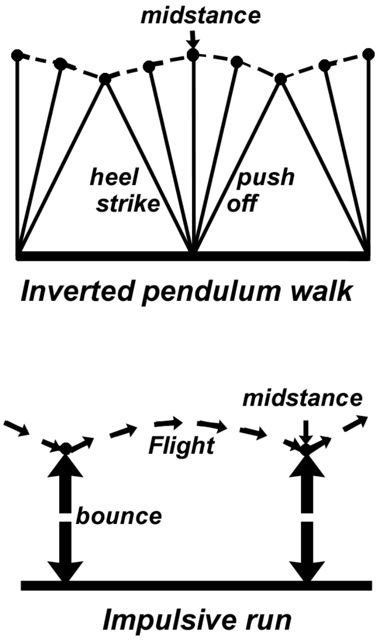


Figure 3.9. Computerized model simulating gait confirms that at slow speeds, the inverted pendulum gait is most efficient, as the lower extremity remains relatively straight, minimizing the metabolic cost of locomotion. When higher speeds are necessary, the body launches into an impulsive run in which the lower extremities collapse in a spring-like manner in order to allow for the storage and return energy necessary for the prolonged flight phase (although fast, propelling the body into flight is metabolically very expensive). Notice the length of stride is significantly longer with impulsive running.

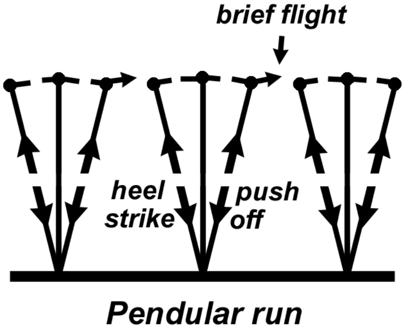


Figure 3.10. Pendular running. This gait pattern represents a hybrid gait containing characteristics of both inverted pendulum walking and impulsive running. At slower speeds of locomotion, pendular running more closely resembles walking in that the lower extremity stiffens and the flight phase is reduced. In contrast, when walking speed increases, pendular running more closely resembles impulsive running because the legs become more compliant and the flight phase is increased. Notice the center of mass fluctuates less with pendular running than in either inverted pendulum walking or impulsive running, creating two small peaks during midstance and swing.

important because the presence of an airborne phase has historically been used to differentiate walking from running. McMahon (11) notes that using an airborne phase to define running is inadequate since slow running often occurs with a double-limb support followed by a single-limb stance; i.e., there is no airborne phase. The author suggests that a more accurate indicator of the transition from walking to running occurs when the center of mass switches from a high to a low point during midstance. McMahon (11) supports this statement with the observation that Groucho running lacks an airborne phase and the center of mass is at its lowest point during midstance.

The most important result of the computerized model by Srinivasan and Ruina (10) was that walking and running were only used at the extremes of speed: walking at low-speed and running at high-speed. For all in-between speeds, the computer model suggested that people would choose a hybrid gait referred to as "pendular running" (Fig. 3.10). In this gait pattern, the stride length is significantly shortened, there is a marked reduction in airtime, and the lower extremities behave as inverted pendulums for brief periods during stance phase. Surprisingly, except for occasional references to "Groucho running" and "double-limb support slow running," options other than conventional walking and running are rarely discussed in the literature. Because it has only a brief airborne phase and a shorter stride length, the hybrid pendular running is metabolically more efficient than impulsive running and may even have been the preferred gait used by *Homo erectus*, as Biewener et al. (12) claim that impulsive running was too expensive to allow for survival of this hominid ancestor. By comparing muscular forces associated with different speeds of locomotion, these authors determined the transition from walking to running resulted in a 68% decrease in the mechanical advantage at the knee, along with a 5-fold increase in ground-reactive forces. These combined factors resulted in a 5.2-fold increase in the quadriceps muscle impulse, which would have made it difficult for this hominid to gather the calories necessary to fuel such an inefficient form of transportation. Because of the inflated metabolic expense associated with conventional running, Biewener et al. (12) claim that running efficiency was "unlikely a key selective factor favoring the evolution of erect bipedalism in humans." Although this was an extremely detailed study, a flaw with this research is the authors assumed that these early hominids were forced to choose between the highly efficient inverted pendulum walking and the metabolically expensive impulsive style of running. It is much more likely that these early hominids, like most recreational joggers, developed a transitional hybrid gait, which would have been significantly more efficient and allowed for the improved foraging skills described by Bramble and Lieberman (13).

The various types of gait available during locomotion are made apparent by stepping onto a motorized treadmill and gradually increasing your speed. At first, inverted pendulum walking is comfortable but as you press the acceleration button to increase speed, you are unable to match the speed of the treadmill so you quickly respond by increasing cadence (each person has a preferred stride length so it is usually more comfortable to increase turnover rate rather than lengthen the stride). This only works for a short time because the metabolic cost of rapidly accelerating and decelerating the lower extremities is too high, so you respond by increasing your stride length. While professional racewalkers are capable of greatly increasing stride lengths by hyperextending their knees and exaggerating pelvic and ankle motions (often achieving walking speeds of 6 minutes/mile), the average person quickly reaches a length of stride that becomes difficult to maintain. At this point, most people transition into a hybrid slow run (either a double-limb support slow run or a pendular run). The precise point at which the transition to slow running occurs varies as each person has his or her own unique transition speed (which tends to occur somewhere around 2 meters/second). The reason each person has a preferred transition speed (PTS) has been the subject of debate as some studies suggest that people switch from walking to running to improve efficiency, while other studies have shown the switch to running always occurs before a metabolically optimal walking speed is achieved.

The controversy regarding the walk-run transition was resolved in a clever paper by Neptune and Sasaki (14). By comparing ground-reactive forces beneath the forefoot with EMG activity of the ankle plantarflexors, these authors determined that the preferred transition speed occurs when the degree of ankle dorsiflexion becomes so great that the gastrocnemius and soleus muscles can no longer generate the force necessary for propulsion because their length-tension relationship has been compromised; i.e., the Weber paradox states that when a muscle is fully stretched or shortened, contact between the muscle filaments is diminished and the muscle is weakened. The presence of the Weber paradox is readily apparent to anyone attempting a pull-up: at first, it feels impossible to lift yourself but once you move past the first few inches, the pull-up seems easier until you are almost at the bar, when it again seems difficult. The reason for this is that when a muscle is close to a midline position (neither stretched nor shortened), a greater percentage of contractile filaments are in contact with one another so greater forces can be generated.

By measuring force output beneath the forefoot, Neptune and Sasaki (14) confirmed that as walking speed increased, the range of ankle dorsiflexion increased and the Weber paradox made it difficult for the gastrocnemius and soleus to generate the force necessary to initiate propulsion. The transition to running improved the length-tension relationship of the ankle plantarflexors and the force generated by these muscles nearly doubled after the transition occurred. The authors relate the sudden increase in force to the "improved contractile conditions" associated with a more midline position of the ankle plantarflexors. Interestingly, the EMG output for the ankle plantarflexors did not appreciably change despite the significant drop in force output, confirming that electrical activity of a muscle has little to do with the force being generated by the muscle since it does not take into account the length-tension relationship.

When the highest speeds of locomotion are necessary (e.g., sprinting), you launch into impulsive running. As the speed of impulsive running increases, the pathway of the center of mass flattens slightly. Although metabolically expensive, impulsive running allows you to increase your speed simply by increasing stride length (15). By analyzing all methods of increasing the speed of impulsive running (e.g., increasing cadence and/or shortening the time the swing phase leg is airborne), Weyand et al. (16) conclude that success with sprinting is determined by the amount of force produced during stance phase: greater force generated while making ground contact translates into longer stride lengths, greater aerial time and faster speeds.

Because the increased aerial phase associated with impulsive running results in a 5-fold increase in ground-reactive force, the body must immediately choose from several different biomechanical options in order to dissipate these amplified forces. For example, the increased ground-reactive forces can be dampened by making initial ground contact with the forefoot, exaggerating frontal plane pelvic motions, and/or by hyperflexing the knee and hip. The exact combination of biomechanical options chosen is highly variable as each person has significant differences in strength, bony architecture, and flexibility. Even prior injury may influence which determinants are incorporated. By experimenting with every biomechanical option, people select a specific running pattern that is metabolically most efficient for them. This explains why runners, unlike walkers, present with such a wide range of running styles. It also explains why any attempt to modify a runner's self-selected stride length will result in a metabolically less efficient gait (17). According to Anderson (18), runners are able to critically evaluate all factors associated with "perceived exertion to arrive at a stride length which minimizes energy cost."

Despite differences in timing, stride lengths, energetic criteria and the degree of joint excursions, the articular interactions associated with walking and running are remarkably similar. The following section reviews in detail the various kinetic/kinematic events occurring during the different phases of the gait cycle. When applicable, differences between walking and running will be discussed.

Gait Cycle Summary: Static Stance

The simple task of initiating the gait cycle requires intricate interactions between the proprioceptive and motor systems necessary for fine-tuning postural adjustments, and the motor commands necessary to produce volitional movement. This is complex because the motor circuits governing these two activities function independently, which is clinically evidenced by the fact that people with Parkinson's disease have trouble initiating the gait cycle, but once started, can walk without difficulty.

In order to take the first step, the central nervous system incorporates a stereotyped pattern of motor recruitment known as the gait-initiation motor control program, in which a series of imperceptible postural adjustments shift the center of pressure posteriorly, first towards the foot that is about to become the swing leg, and then back towards the soon-to-be stance leg (Fig. 3.11, A). Because the posterior migration of the center of pressure occurs before any noticeable movement of the center of mass, the forward component of the ground-reactive force increases (arrow X in Fig. 3.11, B). At this time, the soleus/gastrocnemius muscles relax, followed shortly thereafter by activation of the bilateral tibialis anterior muscles. The sudden relaxation of the gastrocnemius/soleus muscles initiates a smooth free-fall in the desired direction of travel, while the delayed contraction of tibialis anterior pulls the center of mass forward on the stance side and begins dorsiflexing the ankle to improve ground clearance on the swing side.

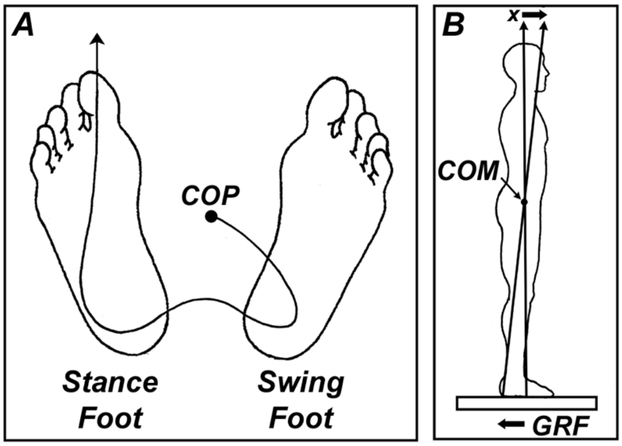


Figure 3.11. To initiate the gait cycle, the calf and hip abductor musculature shift the center of pressure (COP) laterally and posteriorly, first to the swing foot and then to the stance foot (A). Because the posterior displacement of the COP occurs without perceptible motion of the center of mass (COM), the body tilts slightly forward, pivoting about the center of mass (**B**). See text. Redrawn from Polcyn et al. (130).

In young adults, the timing between soleus inhibition and tibialis anterior activation is consistent with little variation. This is not the same for healthy older adults, because age-related changes in the motor cortex make it difficult to inhibit the gastrocsoleus complex prior to stimulating tibialis anterior, explaining the frequent prevalence of gait initiation falls in the elderly (130).

Immediately upon the initiation of the gait cycle, the abdominal core muscles tense to lock the torso and pelvis, providing a stable foundation for the hip flexors, which are beginning to swing the lower extremity forward in preparation for ground contact.

Stance Phase Motions: Contact Period

The initial choice to be made during the contact period is deciding which part of the foot should make ground contact first. While walking and hybrid running almost always begin with initial ground contact occurring at the back of the heel, runners often vary their initial point of impact, striking the ground at either the rearfoot, midfoot, or forefoot. In an analysis of foot strike patterns in 415 runners participating in an elite-level half marathon, Hasegawa et al. (19) determined that 75% of the runners made initial ground contact at the rearfoot, 23.7% at the midfoot, and only 1.4% made initial ground contact at the forefoot. The authors went on to evaluate foot strike patterns of the fastest 50 runners, many of whom were Olympians, and noted that the percentage of midfoot strike patterns present in the fastest runners increased from 23.7 to 36%. The researchers also noted the fastest runners had a tendency to strike the ground with the foot inverted, which the authors suggested might somehow improve metabolic efficiency.

Despite the fact that one third of the world's fastest runners make initial ground contact at the midfoot, little is known about the biomechanics associated with this strike pattern. In contrast, a significant body of information exists on the relatively rare forefoot strike pattern; i.e., only 1.4% of elite runners made initial ground contact at the forefoot (19). In one of the first studies comparing different strike patterns, Cavanaugh and LaFortune (20) measured vertical forces as subjects switched from rearfoot to forefoot strike patterns and noted the forefoot strike reduced vertical forces by more than 50%. This large reduction in vertical force was attributed to the posterior calf musculature absorbing impact forces that would otherwise have traveled through the lower extremity.

In a detailed evaluation of the differences between forefoot and rearfoot strike patterns, McClay and Manal (21,22) compared the biomechanics of 10 rearfoot and 10 forefoot strikers and noted that the forefoot strikers made initial ground contact with greater degrees of ankle plantarflexion and rearfoot inversion, which resulted in increased eversion excursions and eversion velocities during the contact period. Like Cavanaugh and LaFortune (20), McClay and Manal (21,22) noted 50% reductions in vertical loading rates, which they suggest may play a role in lessening the potential for tibial stress fracture. They also suggest that, because knee flexion excursions and velocities were significantly reduced with the forefoot strike pattern, rates of knee injuries might also be lessened. However, the greater work performed by the ankle plantarflexors coupled with the higher ankle dorsiflexion velocities would predispose the Achilles and posterior calf musculature to injury: The forefoot strike pattern reduces the risk of knee injury while increasing the risk of Achilles and forefoot injury.

In one of the few studies evaluating the biomechanical effects of midfoot strike patterns, Altman and Davis (23) used tibial accelerometers to measure vertical loading rates as 5 subjects ran with rearfoot, midfoot or forefoot strike patterns. As expected, the forefoot strike resulted in significant decreases in vertical loading (at the expense of the posterior calf musculature), while the midfoot strike pattern produced loading rates about halfway between those occurring in forefoot and rearfoot strike patterns. The authors suggest that midfoot strike patterns may provide "a compromise between these two extremes" and may reduce the risk of injury. They support this statement with the clinical observations that barefoot runners attempt to lessen impact loads by switching to midfoot strike patterns (24), and that barefoot runners anecdotally report fewer injuries.

Despite anecdotal reports, midfoot strike patterns have never been proven to lessen the rate of injury (25), and may even increase the rate of forefoot injuries because ground contact forces beneath the forefoot are prolonged (increasing the risk for sesamoiditis and metatarsalgia). Furthermore, claims that midfoot strike patterns are more efficient than rearfoot strike patterns are unfounded, since eccentric contraction of the ankle plantarflexors during early stance phase is metabolically expensive. The inability of mid/forefoot strike patterns to improve metabolic efficiency was confirmed by Cunningham et al. (26). By calculating joint torque, mechanical work performed and muscle activity associated with altering initial contact points at various speeds of locomotion, the authors determined that running with a mid/forefoot contact provided no clear metabolic advantage over a heel-first strike pattern, because the costs of transport when using the different contact points was about the same. The only biomechanical difference was that runners making initial ground contact with the mid/forefoot tended to have increased stride frequencies and decreased stride lengths.

In contrast to running, Cunningham et al. (26) confirmed that walking with a heel-first strike pattern reduced the metabolic cost of transport by a surprising 53%. The authors demonstrate that the rearfoot strike pattern was metabolically more efficient for several reasons: It improved pendular exchange of kinetic and potential energy; decreased mechanical work performed by the limbs; decreased the ground-reactive force moment at the ankle; and it decreased muscular activity in the extensors of the ankle, knee, hip and back. All of these factors greatly influence efficiency and explains why more than 99% of walkers make initial ground contact with the heel. Given the huge advantage associated with heel-first strike while walking, it is likely that the slow pendular style of running described by Srinivasan and Ruina (10) is also significantly more efficient with a rearfoot strike since it closely resembles walking. This is clinically supported by the fact that although one third of elite runners make ground contact at the midfoot (19), slower marathoners almost always make ground contact with the heel.

The preference for rearfoot strike patterns dates back millions of years, as laser analysis of the 1.5 million-year-old *Homo erectus* footprints found in Ileret, Kenya, revealed that our most efficient hominid ancestor made initial ground contact at the heel (27). The reason for this is simple: 7 million years of evolution has molded the calcaneus into a shape that is perfectly suited for absorbing the forces associated with heel strike. One of the most important factors making the calcaneus effective at stress dissipation is its size: the average 100-pound human female has a larger calcaneus than a 350-pound gorilla. The increased size provides more space for pressure distribution through the thin but complex trabecular network.

Another factor improving its ability to absorb shock is the somewhat incongruous finding that the calcaneus, despite being exposed to large vertical forces during contact, possesses extremely thin cortical bone and sparse trabeculae. This combination creates an essentially hollow structure in which the calcaneus functions like an overblown cushion at heel strike; i.e., the well-developed vascular supply maintains an elevated intraosseous pressure that reinforces the slender cortical bone, allowing it to bend in and out with the application of ground-reactive forces. Like the end plates of the lumbar vertebral bodies (refer back to Fig. 2.91), the walls of the calcaneus bulge slightly during heel strike and the trabeculae, with their abundant blood supply, quickly repair the microfractures associated with repeat impacts. The thin cortical walls are helpful when differentially diagnosing a possible calcaneal stress fracture: because the cortical walls are so thin, lightly squeezing the medial and lateral walls elicits discomfort when a stress fracture is present.

The final factor making the calcaneus effective at stress dissipation is that it is protected by an incredibly well-designed fat pad. Averaging 18 mm thick in the typical adult male, the calcaneal fat pad is comprised of spiral chambers of sealed fat surrounded by whorls of fibroelastic tissue (28) (Fig. 3.12). These fibroelastic chambers form a honeycomb pattern and are completely isolated as injections

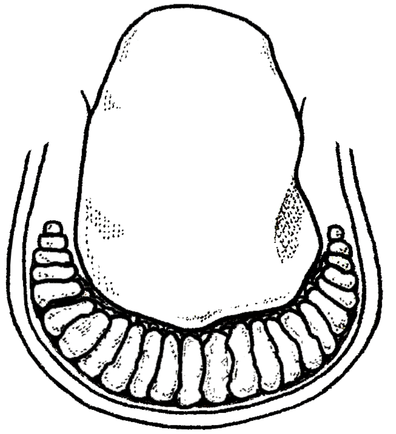


Figure 3.12. The calcaneal fat pad. Modified from Jahss et al. (28).

of India ink into the individual chambers confirms there is no leakage: these compartments behave as closed-cell chambers that deform and return to their original shape as they absorb shock (29). Ultrasonography reveals the fat pad is divided into a deep, thick, highly deformable macrochamber, and a thin, superficial, nondeformable microchamber (30). Because it maintains its shape upon compression, the microchamber functions as a protective cup that serves to contain the macrochamber layer beneath the calcaneus, while the macrochamber layer functions as the major shock absorber, quickly deforming and rebounding with the application of force (Fig. 3.13).

To prevent slippage and maintain its position beneath the calcaneus, the fat pad is anchored by numerous fibrous reinforcements to the skin and heel. Snow and Bohne (31) determined the heel pad's strongest attachment to the calcaneus occurred through a previously unidentified fibrous band they named the "medial calcaneal retinaculum." This structure is made from large retinacular fibers that branch into the fibrous stroma of the heel pad, essentially tethering the heel pad to the calcaneal tuberosity. The authors claim that this medial retinaculum, present in 9 out of 10 heels, plays an important role in "counteracting the valgus shear force on the fat pad at the time of heel strike."

During static stance, the heel pad lessens peak contact pressure points beneath the heel by distributing pressure evenly over the entire surface of the calcaneus. Because plantar pressures are highest in the center of the heel, the chambers in this region are tightly packed, narrower and positioned in a vertical manner. These densely packed vertical chambers more effectively distribute ground-reactive forces away from the center of the calcaneus (32).

Besides distributing pressure during static stance, the heel pad may also play an important role in reducing heat loss to the environment. Irving (33) notes that mammalian heel pads fall to temperatures close to freezing when standing on snow, providing insulation and reducing heat loss from the body to the ground. Bennett and Ker (34) evaluated the viscoelastic properties of the cadaveric human heel pads throughout a range of temperatures and noted that even at 0°C, the human fat pad retains almost all of its shock absorbing properties. The ability of the heel pad to function in cold environments may in part be due to the higher percentage of polyunsaturated fatty acids: Unlike conventional adipose tissue with a polyunsaturated to saturated fat ratio of 2.5:1, the healthy human heel pad contains 4.5 times more polyunsaturated fatty acids (35). The increased prevalence of polyunsaturated fat might improve function because it lessens heel pad viscosity and is more stable at lower temperatures.

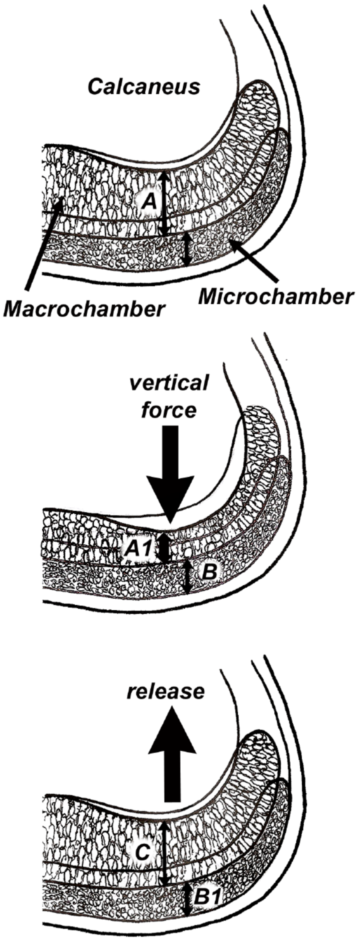


Figure 3.13. The normal heel fat pad is composed of a deep macrochamber and a superficial microchamber. When exposed to vertical force, the macrochamber compresses significantly (compare **A** and **A1**) while the microchamber remains unchanged (compare **B** and **B1**). Once vertical forces are removed, the macrochamber springs back to its original shape (**C**). Drawn from ultrasonography images in Hsu et al. (30).

Using radiographic fluoroscopy with an optical pressure display, Gefen et al. (36) evaluated the *in vivo* biomechanical behavior of the fat pad and determined that when walking, the fat pad compressed very rapidly to a deformation of about 40%, dissipating 17-19% of the forces associated with heel strike. The deformation occurred during the first 150 ms of stance phase and was initially rapid, with a slower period of compression that continued into early midstance, when an unloading phase was initiated. In a study of the viscoelastic properties of the human fat pad, Jorgenson and Bojsen-Moller (37) note that a healthy pad absorbs shock 2.1 times better than sorbothane (considered one of the best synthetic shock absorbers) and possesses an open plexus of veins that allows it to enhance the countergravitational return of blood. The venous plexus enhances shock absorption as the contained blood acts as a cushion.

Although effective at dampening forces associated with static stance and walking, the 3- to 5-fold increase in vertical forces associated with heel strike while running produces a jarring impact capable of damaging the walls of the heel pad chambers. In an *in vivo* cineradiographic study of the heel pad in barefoot and shod running, De Clerq et al. (38) demonstrate that barefoot running produces a 60% deformation of the heel pad, compared to the 35% reduction when running shod. This contrasts with the 40% deformation associated with walking barefoot (36). Over time, the repeated application of 60% deformation could cause the heel pad to bottom out, limiting its ability to distribute pressure and absorb shock. To avoid damaging the fat pad when running, barefoot runners intuitively switch to a midfoot strike pattern (24). This strike pattern protects the heel pad from the exaggerated vertical forces as the initial point of contact is displaced forward, away from the heel pad, allowing the posterior calf musculature to absorb the increased ground-reactive forces.

The ability to dampen impact is important since typical ground-reactive forces when walking average 110%, 15%, and 10% in the vertical, forward, and medial directions, respectively (39). This may not seem like much but when multiplied by the 5,000 foot strikes taken each day, it translates into nearly 640 tons of pressure the average person must absorb daily (10). To compound the problem, these forces travel through the body at speeds exceeding 200 mph (40).

In order to prepare itself for the sudden application of ground-reactive force associated with contacting the ground, the body aligns itself during swing phase so every joint is in an ideal position to dampen these forces. At the moment heel strike occurs, the spine is in a neutral position; the hip is flexed 30°; the knee is almost fully extended; the ankle is slightly dorsiflexed; the subtalar joint is slightly supinated; and the midtarsal joint is fully pronated about its oblique axis and supinated (inverted) about its longitudinal axis (Fig. 3.14). The muscles stabilizing these joints are in their midline positions (maximizing their length/tension relationships) and many of them are pretensed in anticipation of impact forces. In fact, switching from soft to hard surfaces produces immediate increases in anticipatory muscle activity prior to heel strike as preactivation improves the ability to absorb shock (41). Animal studies confirm that variation in surface hardness is accommodated with altered muscle function and joint excursions within a single stride length (42).

In an interesting study of ground-reactive forces in horses, Wilson et al. (43) determined that when a galloping horse's leg strikes the ground, the impact causes the horse's leg to vibrate at a rate of 30-40 Hz, and these potentially dangerous vibrations have to be dampened in order to avoid fatigue failure in tendons and bones. The authors demonstrate that these impact vibrations are dampened by the digital flexor muscles, which had been previously believed to be vestigial in horses, since its muscle fibers are too short to produce motion. Although useless for creating joint movement, the digital flexor muscles are ideal for dampening bony vibrations, as their angled origins allow for lateral force transmission of bony vibrations through their "complex 3-dimensional architecture."

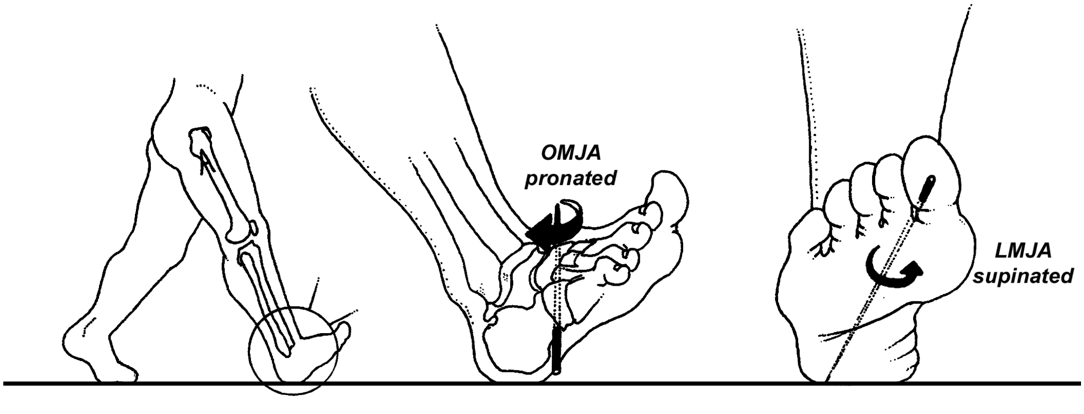


Figure 3.14. Ideal joint positions present at heel strike. OMJA, oblique midtarsal joint axis; LMJA, longitudinal midtarsal joint axis.

Because impact vibrations occur in the first 100 ms following ground contact, reflex muscular activation is too slow to provide protection and the vibration dampening muscles, to be effective, must be preactivated prior to ground contact. In humans, barefoot running has been shown to produce similar vibrations as accelerometer and kinematic data recorded from human tibiae during barefoot running revealed horizontal oscillations between 40-50 Hz, which continued for 100 ms following impact (44). According to Wakeling and Nigg (45), tension created in antagonistic muscles preceding ground contact serves to stiffen the leg in anticipation of these bony oscillations. This preactivation may be used to "increase the resonant frequencies of the soft tissues of the leg and optimally tune the system to minimize vibrations" (45). In a separate *in vivo* study of human walking, Wakeling et al. (41) measured force transmission and muscle activity associated with landing on hard and soft materials and determined the lateral head of the gastrocnemius and the bicep femoris muscle were the major contributors to dampening lower extremity vibrations associated with heel strike.

Following the initial impact, a combination of ground-reactive forces (which are typically applied to the posterolateral heel) and inertial forces (the pelvis and lower extremity continue their internal rotation, which began during early swing phase) cause the ankle to plantarflex and the subtalar joint to pronate. Plantarflexion of the ankle is resisted by the eccentric contraction of the anterior compartment musculature. These muscles play an important role in absorbing shock as they smoothly lower the forefoot to the ground, thereby reducing trauma to the plantar soft tissues. Radin and Paul (46) state that joint motion controlled by muscles lengthening under tension is the primary kinematic process responsible for shock absorption. Tibialis anterior is particularly well-suited for decelerating ankle plantarflexion since its muscle architecture is arranged in such a way that it is almost impossible to damage with repeated eccentric contractions (47). The ankle continues to plantarflex during the first 70% of the contact period, reaching a maximally plantarflexed position of 10° (Fig. 3.15). At that time, ground-reactive forces beneath the forefoot cause the ankle to dorsiflex slightly (although the ankle is still plantarflexed 5° by the end of the contact period).

Plantarflexion of the ankle also serves to decelerate the braking phase associated with heel strike; i.e., frictional forces immediately pin the heel to the ground and the body's forward progression comes to an abrupt halt. To demonstrate the braking phase on yourself, walk across a room while holding a full bowl of soup: Every time heel strike occurs, the soup has a tendency to spill forward as progression of the center of mass is temporarily halted by frictional forces associated with heel strike. Pandy and Berme (48) evaluated the various determinants of gait and concluded that transverse plane pelvic motion plays the greatest role in limiting the magnitude of the braking phase in that posterior rotation of the pelvis during initial ground contact smoothly absorbs the temporary reduction in speed associated with braking.

When initial ground contact is made with heel, the anterior compartment muscles also play a role in reducing braking because ankle plantarflexion allows the ankle to continue to roll forward, providing a more gradual deceleration of the lower extremity (refer back to figure 3.6). Because midfoot and forefoot strike patterns negate the ankle's ability to accommodate the braking phase with a forward role of the ankle, the body is forced to rely more heavily on transverse plane pelvic motions. The negative influence of forefoot strike patterns on braking is made obvious by running downhill while alternating between rearfoot and forefoot strike patterns: the moment ground contact is made with the forefoot you feel the lower extremity come to an abrupt halt, while a rearfoot strike pattern produces a smoother braking phase as the ankle rolls downward and forward.

In addition to sagittal plane motions at the ankle, frontal plane motion of the subtalar joint also plays a role in shock absorption when tibialis posterior eccentrically contracts to resist calcaneal eversion. This muscle is well-designed for shock absorption, because it has the longest lever arm for controlling subtalar pronation and prior to inserting beneath the arch, its tendon rotates approximately 45° in order to store and return energy (49,50) (Fig. 3.16). In many ways, tibialis posterior is the frontal plane equivalent of the Achilles tendon. The ability of tibialis posterior to absorb shock is enhanced when heel strike occurs with the rearfoot inverted, since this allows the subtalar joint to move through a larger range of motion

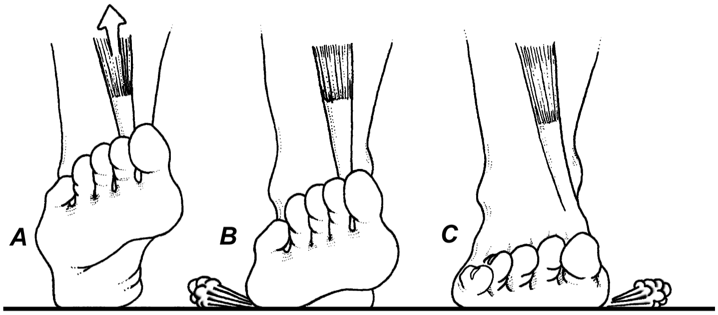


Figure 3.15. Ankle plantarflexion during early and midcontact period is resisted by eccentric contraction of the anterior compartment muscles (arrow in A). Roughly 40% of the way through contact period (**B**), the fifth metatarsal head strikes the ground. The forefoot is then smoothly loaded from lateral to medial with the entire forefoot making ground contact approximately 70% of the way through the contact period (**C**).

with tibialis posterior eccentrically contracting to absorb shock. Perhaps this explains why runners who make initial ground contact with the rearfoot inverted are less prone to injury (132).

Throughout the contact period, the talus continues to slide medially down the calcaneus, adducting and plantarflexing over the calcaneal facets. Because no muscles attach to the talus, this motion is controlled by bony and ligamentous restraining mechanisms (particularly the anterior talofibular and the sinus tarsi ligaments). In addition to improving surface accommodation by creating a parallelism of the shared midtarsal joint axes (Fig. 3.17), plantarflexion of the talus also produces a cushioning effect during heel strike by gradually lowering the ankle mortise towards the ground (Fig. 3.18).

While motions in the subtalar joint are frequently likened to a mitered hinge in which frontal plane motion of the rearfoot is converted into transverse plane motion of the shank, recent research reveals that this model is inaccurate because only 66% of frontal plane rearfoot motion is converted into tibial rotation (52). The clinical implication of this is that the subtalar joint plays a more important role in dissipating torsion between the rearfoot and leg than previously believed.

Even though some of its motion is dissipated, pronation of the subtalar joint continues to convert frontal plane motion into tibial rotation by forcing the talus to adduct, which in turn causes the tibia to internally rotate. The resultant internal tibial rotation causes the lateral tibial plateau to glide anteriorly beneath the lateral femoral condyle, which unlocks the ligamentous restraining mechanisms and allows the knee to flex (i.e., the knee is not a ginglymus joint as the tibia must internally rotate for the knee to flex properly).

Knee flexion resisted by eccentric contraction of the quadriceps muscle is by far the body's most effective shock absorbing system. Because ground-reactive forces associated with walking are comparatively low, the knee flexes through a range of only 20° to 25°. In many situations, individuals move through the contact and midstance periods

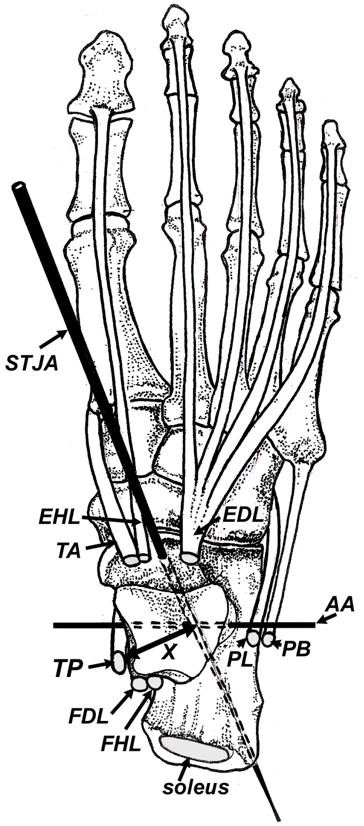


Figure 3.16. Relative lever arms to the subtalar joint axis (STJA). Cadaveric analysis of lever arm lengths by Hinterman et al. (49) confirms that tibialis posterior (**TP**) has the longest lever arm for controlling subtalar motion (**X**). By giving tibialis posterior's lever arm a reference value of 1.00, these authors calculated comparative lever arm lengths for the remaining muscles responsible for stabilizing the subtalar joint, which are listed as follows: flexor digitorum longus (**FDL**) .75, flexor hallucis longus (**FHL**) .62, tibialis anterior (**TA**) .59, soleus .24, extension digitorum longus (**EDL**) -.26, peroneus longus (**PL**) -.82, peroneus brevis (**PB**) -.85. **AA** refers to the ankle axis of motion while positive and negative numbers are used to describe muscles that either supinate or pronate the subtalar joint, respectively.

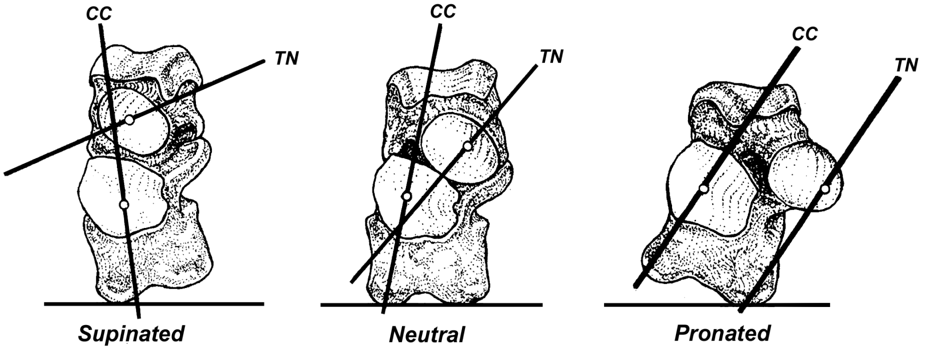


Figure 3.17. Anterior view of the right talus and calcaneus. Note the parallelism of the talonavicular (**TN**) and calcaneocuboid (**CC**) axes as the subtalar joint pronates.

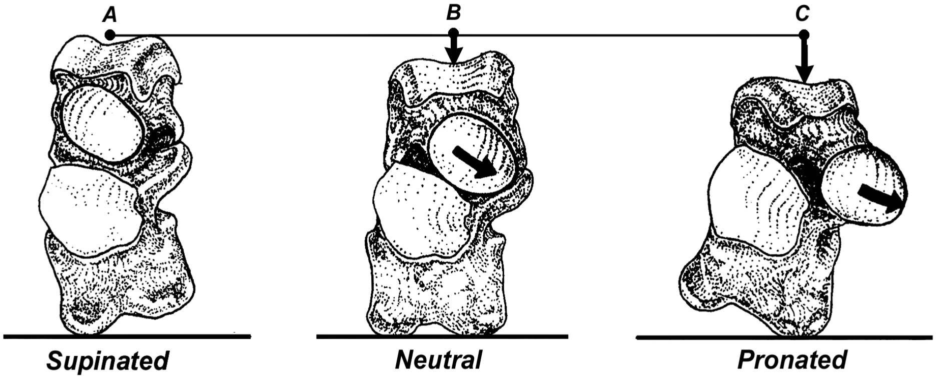


Figure 3.18. Anterior view of the right talus and calcaneus. Notice the talus is lowering as the subtalar joint pronates (compare **A**, **B**, and **C**).

with their knees fully extended, producing a walking pattern that more closely resembles the classic inverted pendulum gait. While a stiff knee gait is metabolically efficient because it lessens strain on the quadriceps, it significantly increases stress on the gluteus medius muscle, which eccentrically fires to lower the contralateral pelvis. The gluteus medius muscle, however, has a limited ability to absorb impact force and as shock absorption requirements increase with the transition to running, the degree of knee flexion increases in a linear manner; i.e., slower speeds of running have lower knee flexion angles while faster speeds have proportionately higher degrees of knee flexion. As knee flexion increases, the patellar tendon drags the patella downward over the femoral condyles and patellofemoral contact points increase, providing improved distribution of pressure (refer back to figure 2.48). Fortunately, the patella is well-equipped to handle these forces because it possesses the thickest cartilage in the body and is stabilized by the powerful retinacular ligaments.

To evaluate the 3-dimensional motions in the knee associated with walking, Komistek et al. (53) used fluoroscopy and computerized tomography to measure *in vivo* tibiofemoral motion as subjects walked in a specially designed apparatus. They confirmed the tibia internally rotates about a vertical axis projecting through the medial femoral condyle with the lateral tibial plateau moving 8.4 mm anteriorly while the medial joint remained stationary (Fig. 3.19). This refutes prior research suggesting rotation occurred about an axis though the center of the cruciate ligaments and explains why osteochondral fragments frequently form at the medial femoral condyle. In an *in vivo* analysis of sagittal plane tibiofemoral motion, van den Bogert et al. (54) plotted the shifting location of the tibiofemoral axis as subjects ran through a functional MRI machine and determined the axis was frequently found close to the intersection of the cruciate ligaments and, more importantly, it moved posteriorly as the knee flexed. They also made the interesting observation that when the knee transitioned from flexion into extension (which occurred during midstance when the knee was flexed approximately 40°), there was a consistent and unexpected 10 mm posterior shifting of the tibiofemoral joint's axis of motion, which improved the mechanical efficiency of the quadriceps muscle by temporarily increasing the length of its lever arm (Fig. 3.20). The authors theorized the abrupt shifting of the axis allowed the bony architecture of the tibiofemoral joint to automatically compensate for the temporary loss in force that occurs when the quadriceps muscle switches from eccentric to concentric contraction (i.e., the transition produces a temporary weakening of the muscle secondary to the "intrinsic force-velocity relationship of muscle strength"). The unexpected posterior shifting of the axis is extremely useful because it improves metabolic efficiency and provides significant stability against knee buckling by briefly increasing the lever arm afforded the quadriceps muscle at a time when the muscle is temporarily weakened as it transitions from eccentric to concentric contraction.

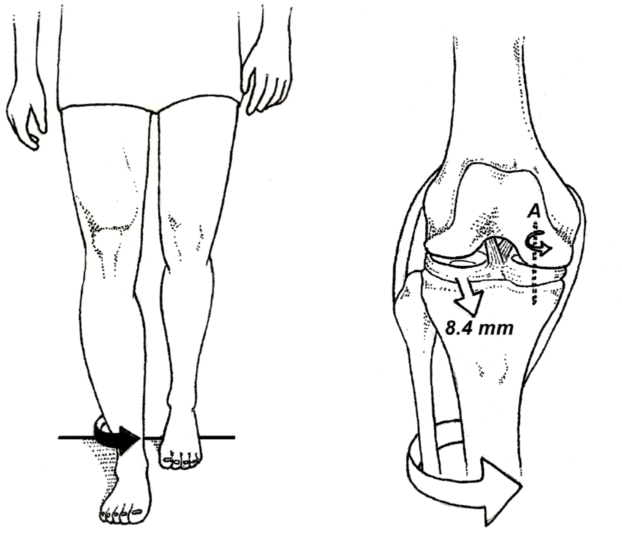


Figure 3.19. Vertical axis of the right knee joint (A). The medial tibiofemoral joint behaves as a ball and socket, while the lateral side of the joint moves with a gliding motion as the tibia moves anteriorly relative to the femoral condyle.

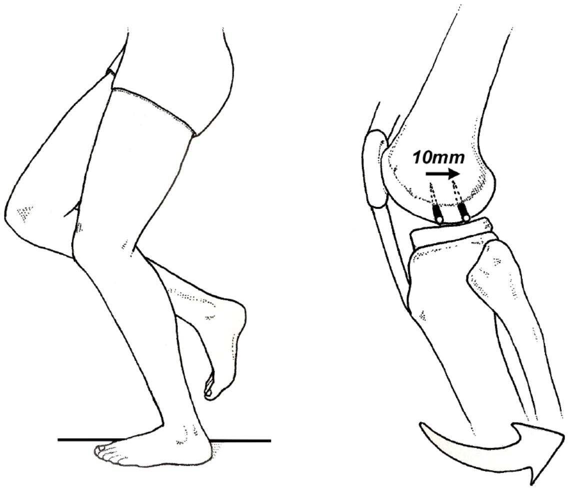


Figure 3.20. Posterior shifting of the sagittal plane axis as the knee transitions from flexion to extension.

While knee flexion resisted by the eccentric contraction of the quadriceps muscle is the body's most important shock absorber, the hip, with its powerful muscular support and significant surface area, also contributes appreciably to the dissipation of ground-reactive forces. At heel strike when walking, the hip is flexed 30° allowing for greater distribution of pressure as contact areas in the hip increase when the hip is flexed. As mentioned, because the forces associated with walking are relatively small, the gluteus medius muscle effectively dampens these forces by eccentrically contracting to lower the contralateral pelvis.

As speeds of locomotion increase, gluteus medius is unable to resist the exaggerated forces associated with impulsive running and the gluteus maximus muscle vigorously tenses to stabilize the hip. Because it possesses significant lever arms for controlling transverse, sagittal, and frontal plane motion (Fig. 3.21), the gluteus maximus muscle very effectively dampens triplanar forces at the hip. In addition, the piriformis and obturator internus muscles play an important role during early stance by decelerating internal rotation of the femur and protecting the femoral neck from the bending forces associated with single-limb stance (Fig. 3.22). Because of its fibrous slips traversing over the sacrum (refer back to figure 2.81), the piriformis is also an important stabilizer of the sacroiliac joint; i.e., internal rotation of the femur during the contact period creates a tensile strain in this muscle that is transferred directly into the soft tissues covering the posterior sacroiliac joint.

Perhaps the most interesting series of biomechanical events necessary for stability occur at the pelvis. Following heel strike, deceleration of the lower extremity associated with the braking phase of ground contact creates significant pressure in the femoroacetabular joint as the

Figure 3.21. The upper fibers of gluteus maximus possess a significant lever arm for controlling frontal plane motion (A), while the lower fibers effectively control sagittal (B) and transverse plane motions (C).

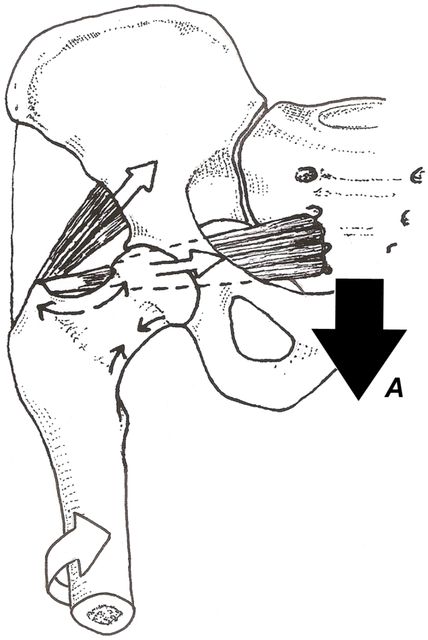


Figure 3.22. During single-leg stance, body weight (A) creates tensile and compressive strains on the femoral neck (small black arrows), which are resisted by the compressive force created by the piriformis, obturator internus and lower gluteus medius muscles (white arrows).

torso continues to move downward and forward, creating a pivot at the hip (particularly when the knee is straight). During normal walking, these forces are directed into a relatively small area in the anterosuperior quadrant of the acetabulum (55). Even though hip joint forces vary considerably while walking (with ranges from 200 to 2200 N), the gluteal muscles function to distribute pressure over a larger surface area while maintaining femoroacetabular joint forces at a constant level.

Because the weight of the torso is applied posteromedially to the acetabulum, the ipsilateral ilium tilts upward and extends while the sacrum nutates forward (Fig. 3.23). The innominate easily manages the transfer of forces associated with ground contact, as the cortical shell of the pelvic bone is thickest along a line connecting the acetabulum and sacroiliac joint. Using data obtained from a telemetrized hip prosthesis, Dalstra and Huiskes (56) created a detailed *in vivo* model in which they evaluated external loading of the hip, including the effect of 22 muscles on hip joint forces during normal walking. These authors confirm that hip joint forces increase rapidly during the contact period and are initially resisted by both gluteus maximus and gluteus medius. By midstance, gluteus medius supports the vast majority of force at the hip. The authors created a computer image to demonstrate stress intensity distribution in the cortical shell of the pelvic bone during the different phases of gait (Fig. 3.24). Notice that the preponderance of load transfer occurs from the superior acetabulum, through the posterior iliac pillars, into the interosseous region of the sacroiliac joint.

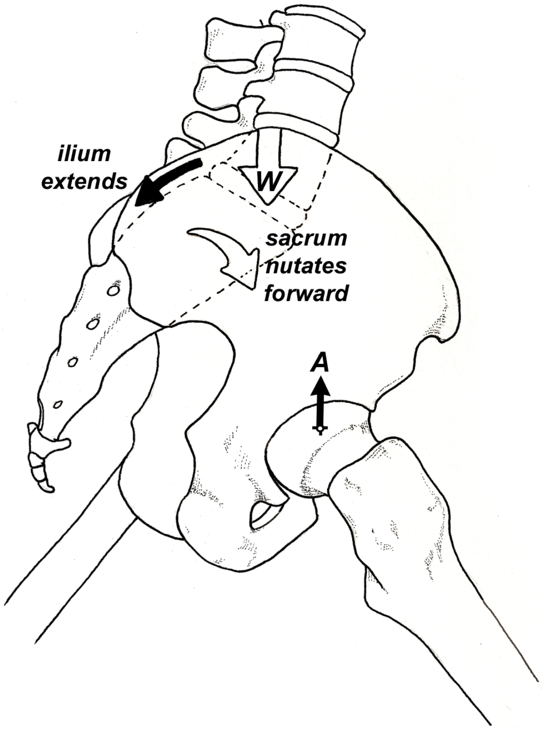


Figure 3.23. Because body weight (W) is applied posteromedially to the point of support in the acetabulum (A), the sacrum is forced to nutate forward while the ilium extends (white and black arrows, respectively).

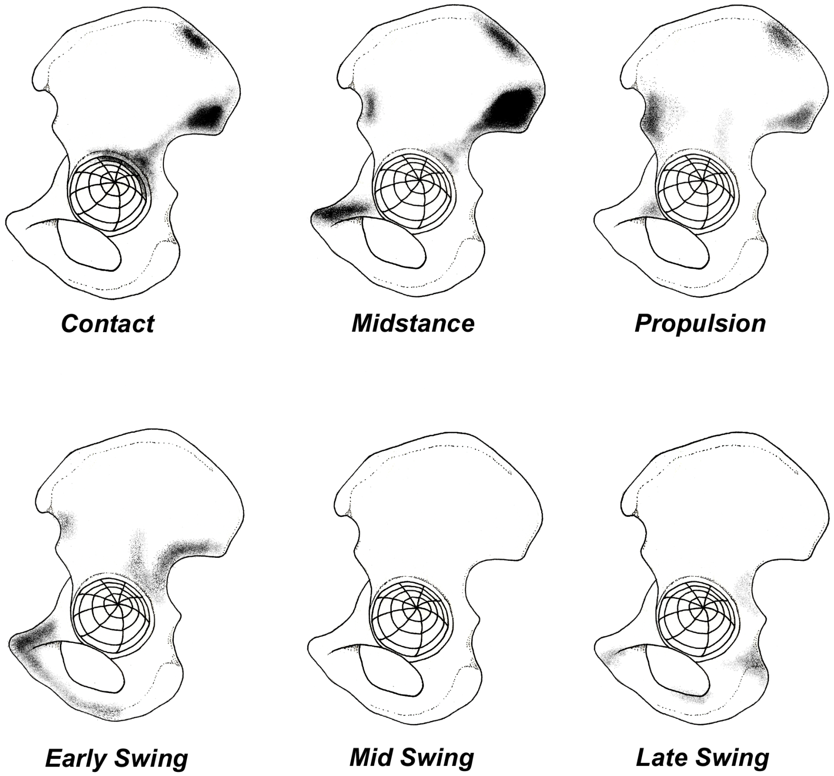


Figure 3.24. Stress distribution through the cortical shell of the left innominate during stance phase of gait. The dark shading represents increased areas of stress distribution. Redrawn from Dalstra and Huiskes (56).

As noted by Vleeming et al. (125), a self-locking mechanism occurs to protect the sacroiliac joint when pretension in the bicep femoris, which is activated during late swing phase to decelerate forward motion of the leg, increases tension in the spiral fibers of the sacrotuberous ligament. This increased tension (most of which is stored in the form of elastic recoil) serves to decelerate forward nutation of the sacrum, when forces are transferred through the sacrotuberous ligament into the deep fibers of the multifidi muscles, crossing the sacrum into the contralateral erector spinae and latissimus dorsi muscles (Fig. 3.25). While Vleeming et al. (125) claim the self-locking mechanism is enhanced by downward motion of the fibula occurring during heel strike (Fig. 3.26), recent *in vivo* research reveals there is negligible motion of the fibula during early stance and the concept of a muscle-tendon-fascial sling being pulled by a dropping fibula needs to be reevaluated (57,58).

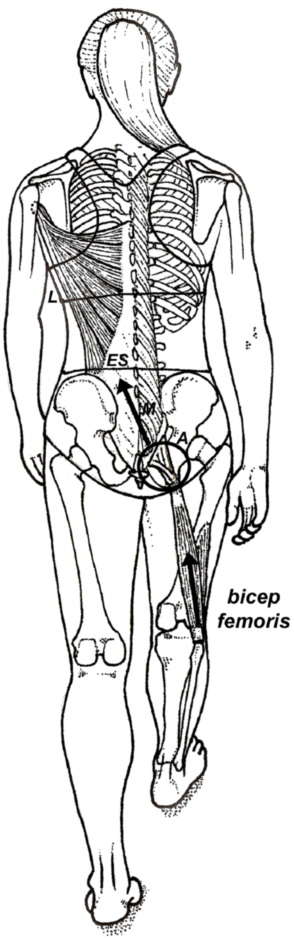


Figure 3.25. Tension created in the long head of the bicep femoris muscle passes through the spiral fibers of the sacrotuberous ligament (A) into the deep fibers of the ipsilateral multifidus (M). These forces are then transferred into the contralateral erector spinae (**ES**) and into the latissimus dorsi muscle (**L**).

Fortunately, tension associated with eccentric contraction of the bicep femoris muscle is more than enough to stabilize the sacrotuberous ligament because the distal aspect of this muscle has a lower point of attachment compared with the other hamstrings. This lower attachment allows forward motion of the swing phase leg to produce greater tensile strain in the long head of the bicep femoris (see Fig. 3.49 at the end of this chapter). Because the late swing/early contact period tension in bicep femoris increases as ground-reactive forces increase, this muscle is able to provide variable stability depending upon the degree of impact force. As previously mentioned, Wakeling et al. (41) demonstrate that when forces present at heel strike

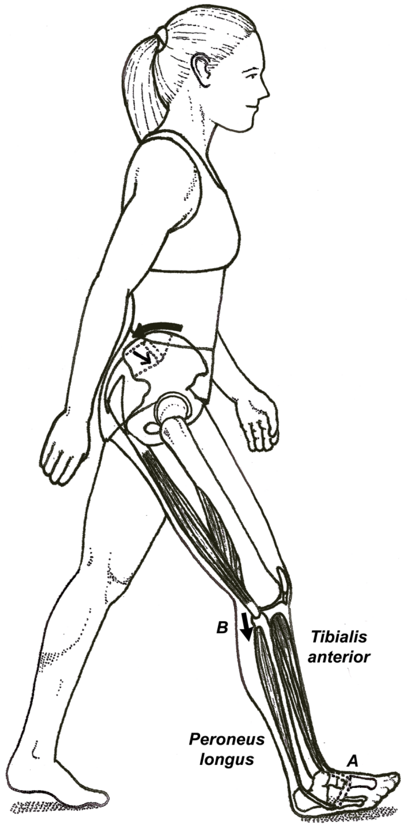


Figure 3.26. According to Vleeming et al. (125), tension created in the tibialis anterior muscle during the contact period is transferred into the fascia of the peroneus longus muscle (dotted lines near A), where it is then transferred through connecting fascia into the bicep femoris tendon (B). Vleeming et al. (125) claim the load transfer into the bicep femoris muscle is enhanced by downward motion of the fibula, which early research by Weinert et al. (126) suggested occurred during early stance phase. Unfortunately, the belief that the fibula drops downward during the contact period has been refuted by several high-quality 3-dimensional *in vivo* studies (57,58). As a result, the concept that fibular motion somehow stabilizes the sacroiliac joint is most likely invalid.

increase (e.g., landing on concrete), the bicep femoris and lateral gastrocnemius muscles pretense during late swing phase in anticipation of these forces. This anticipatory pretension in the bicep femoris enhances sacroiliac stability as the muscle tenses more vigorously when ground-reactive forces increase, providing the sacroiliac with variable degrees of reinforcement depending upon the amplitude of the impact force.

Keep in mind that despite the protection provided by the bicep femoris, the sacroiliac joint remains a relatively unimportant shock absorber because it possesses such a limited range of motion that its contribution to dampening impact force is at best limited, especially in older adults. Furthermore, the finger-sized bony bridge that traverses the interosseous section of the sacroiliac joint, which is present in 60% of 50 year olds and 100% of 60 year olds, would completely block nutation of the sacrum, and once formed, would force vertical forces to transfer directly into the lumbar spine. Of note, even without sacroiliac involvement, the sacrum, by itself, functions as a shock absorber because its thin cortical shell allows it to bulge in and out with the application of vertical force in a manner similar to the calcaneus following heel strike.

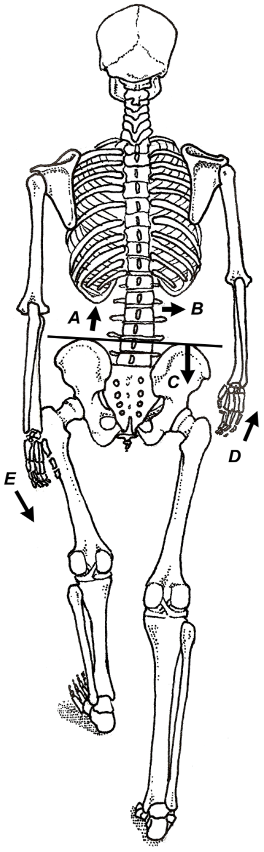


Figure 3.27. Spinal motion. As the left foot strikes the ground, the lumbar spine is rotated 3° and laterally flexed 1° to the right (**A** and **B**, respectively). Immediately following heel strike, the contralateral pelvis drops 4° (**C**) and the lumbar vertebrae flex forward to assist with shock absorption (60). Because the arms are swinging in the opposite direction of the pelvis (**D** and **E**), the upper thoracic spine rotates in the opposite direction of the lumbar spine. The transition from right rotation of the lumbar spine to left rotation of the upper thoracic spine typically occurs at the eighth thoracic vertebra. Shortly after heel strike, the lumbar spine reverses directions in all planes in order to dampen movement of the pelvis.

Forces not dampened at the pelvis travel into the spine (Fig. 3.27). In the transverse plane, the lumbar spine rotates approximately 3° in each direction and these forces are dampened by the spinal rotators. In the frontal plane, the contralateral pelvis drops approximately 4° while the spine laterally flexes less than 1° in each direction. Lateral flexion of the spine is resisted by the contralateral internal/external obliques and by the quadratus lumborum muscle. Because of its 110 mm lever arm to the spine, the external oblique muscle is particularly well-suited for minimizing frontal plane displacement of the pelvis. While early research suggested that contralateral lateral flexion of the spine following heel strike produced ipsilateral spinal rotation (i.e., Fryette'e law), recent research confirms that the coupling of spinal lateral flexion and rotation is extremely variable and there are no preset rules defining the coupling of lateral flexion and rotation.

Sagittal plane spinal motions also contribute to shock absorption. Following heel strike, the braking action associated with initial ground contact causes the torso to displace forward rapidly. The powerful iliolumbar ligament plays an invaluable role at this time by reducing forward glide of the fourth and fifth lumbar vertebrae on the sacrum, significantly reducing the risk of injury to these very mobile vertebrae (Fig. 3.28). Flexion of the lumbar spine following heel strike is resisted by eccentric contraction of the erector spinae muscles. Because they

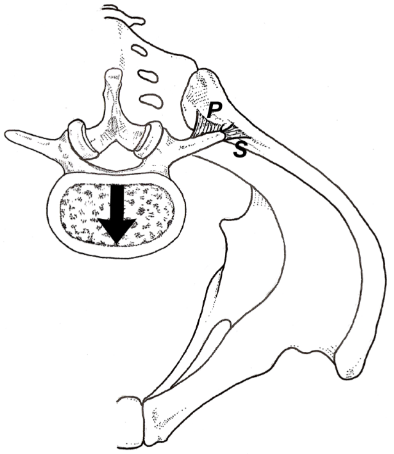


Figure 3.28. The posterior (P) and superior (S) bands of the iliolumbar ligament protect the fourth and fifth lumbar vertebrae from the excessive anterior translation associated with the braking phase following heel strike (arrow).

possess 4 inch lever arms for controlling spinal flexion and attach to the lower 6 ribs, the longissimus thoracis pars lumborum and iliocostalis lumborum pars lumborum very effectively decelerate forward motion of not just the lumbar spine, but the entire torso.

Callaghan et al. (59) evaluated spinal motions at different speeds of walking and noted that when the speed of walking increased, the degree of forward flexion present during the contact period also increased, while the ranges of rotation and lateral flexion remained relatively unchanged (emphasizing the role of spinal flexion in shock absorption). McGill (60) notes that arm motions associated with fast walking may serve to lessen strain associated with the amplified spinal motions, since swinging of the arms was shown to reduce spinal torque, muscle activity, and spinal loading by up to 10%. McGill (60) confirms that slow walking is associated with reduced spinal movement, resulting in a prolonged static load of the lumbar ligaments and muscles. Apparently, swinging the arms while fast walking "facilitates efficient storage and recovery of elastic energy," lessening the need for muscle stabilization with each step. This explains why Nutter (61) recommends incorporating fast walking into exercise protocols prescribed to manage various low back disorders. It also explains why slow walking (such as walking in a mall) is uncomfortable to individuals suffering from low back pain. Despite significant individual variation in upper extremity motions during the gait cycle (some individuals move their wrists asymmetrically across the body while others symmetrically move their hands up and down in a rhythmic manner), arm motions play an important role in reducing spinal torque immediately following heel strike.

In addition to absorbing shock through muscular activity, the vertebral bodies, like the calcanei and sacrum, possess extremely thin cortical bone (i.e. less than 0.6 mm thick) that bulge in and out with the application of vertical forces (refer back to figure 2.91). Reinforced by well-nourished trabeculae, the bulging end plates are capable of rapid self-repair and play an important role in shock absorption. According to McGill (60), the intervertebral discs play only a limited role in dampening vertical forces as they function to distribute stress evenly over the end plates (improving the ability of the end plates to absorb shock) and separate the vertebrae, allowing for increased ranges of vertebral motion. Adams, in a personal communication with McGill (60), suggests the elevated hydrostatic disc pressures associated with upright postures serves to prevent the ingrowth of nerves, lessening the potential for chronic spinal pain.

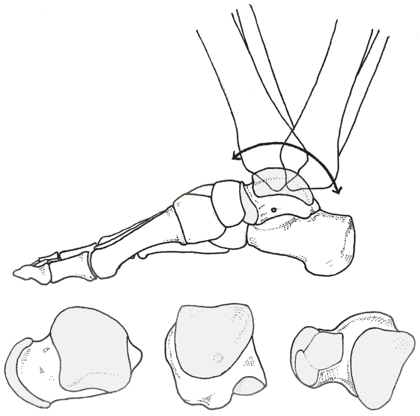
Although some research suggests that a vertical spine at heel strike is most efficient because it requires less effort to maintain postural equilibrium (62), Wlliam and Cavanagh (63) evaluated efficiency in runners and determined the most economical runners made ground contact with the spine flexed forward 5.9°, while the least efficient runners made ground contact with the spine almost vertical. Perhaps the slightly flexed spine lessens angular kinematics following ground contact thereby reducing the metabolic cost of locomotion. The end result of the various spinal movements present during the contact period is that the head remains relatively stationary despite significant spinal oscillations. In an interesting evaluation of head motions associated with walking on varied terrain, Menz et al. (64) demonstrate that although accelerations of the pelvis increase when walking on irregular surfaces, head accelerations remain unchanged. The authors state that "one of the primary objectives of the postural control system when walking on irregular surfaces is head control, and that subjects adapt their stepping pattern on irregular surfaces to ensure that the head remains stable." They suggest elderly people might be more prone to falling because of an inability to maintain smooth head motions while walking.

Midstance Period

Midstance period begins at full forefoot load and ends at heel lift. When walking, it is the longest period, occupying 40% of stance phase and lasting approximately 0.24 seconds (3). While running, midstance is significantly shorter, occupying only 25% of the gait cycle. Because the energetic criteria during walking and running are reversed, the lower extremity joint interactions are significantly different. During running, the knee and hip continue to flex throughout midstance, bringing the center of mass to a low point by the middle of stance phase. Conversely, while walking, the hip and knee remain relatively straight, returning the center of mass to its highest position by the middle of the midstance period.

To get the center of mass to its high point while walking, the lower extremity remains in a nearly straightened position while the entire lower extremity pivots up and over the talus. The talus is well-designed to function as a pivot point during midstance, since more than 70% of its body is covered with cartilage. This interesting bone essentially functions as an almost frictionless ball bearing while the stiffened lower extremity pivots over it (Fig. 3.29). The stiffening of the lower extremity necessary to propel the center of mass upwardly during midstance is accomplished primarily by maintaining the knee in a fully extended position: During the contact period while walking, the knee flexes through the relatively small range of 10° to 20°. This essentially allows the lower extremity to behave as a pole vault, gradually elevating the center of mass until it reaches its high point during the middle of midstance.

During the contact period when walking and the midstance period when running, tension in the iliotibial band decreases the metabolic costs of locomotion by assisting gluteus medius in preventing the contralateral pelvis from dropping. Throughout midstance, tension in the iliotibial



3.29. Because 70% of the talus is covered with cartilage (shaded areas), it functions like a frictionless ball bearing, allowing the lower leg to glide over its superior surface (arrow).

band is enhanced by expansion of the contracting vastus lateralis muscle, which displaces the center of the iliotibial band laterally creating a bowstring effect that increases tension in this important structure. Because the iliotibial band is connected through the lateral intermuscular septum to the entire posterior femur, it acts as a powerful brace that lessens bending strain on the femur during early and mid stance phase (65).

Contrary to popular belief, the iliotibial band does not "roll over" the lateral femoral epicondyle, compressing a bursa as it shifts back and forth over this bony prominence. Detailed cadaveric analysis coupled with MRI evaluations of individuals with and without iliotibial band friction syndrome confirms that the band never snaps over the epicondyle, because the distal aspect of the band is anchored too firmly to the femur by strong fibrous bands. As demonstrated by Fairclough et al. (65), the progressive increase in the degree of knee flexion during early stance phase shifts tension from the anterior to the posterior fibers of the iliotibial band depending on the degree of knee flexion, creating the illusion of movement (Fig. 3.30). In no cadaver, volunteer, or patient was a bursa ever found, as the subsurface of the iliotibial band was protected by a deep layer of fat. Because tension was greatest in the anterior fibers of the iliotibial band at low angles of knee flexion and in the posterior band at higher angles, it is possible the anterior portion provides stability when walking (through tension in the tensor fasciae latae) while the posterior fibers provide greater support when running as the ranges of knee flexion increase and the gluteus maximus muscle tenses more vigorously.

Throughout the midstance period while walking, the knee gradually straightens so it is fully extended by the time heel lift occurs. In contrast, knee flexion associated with running continues until the middle of the midstance

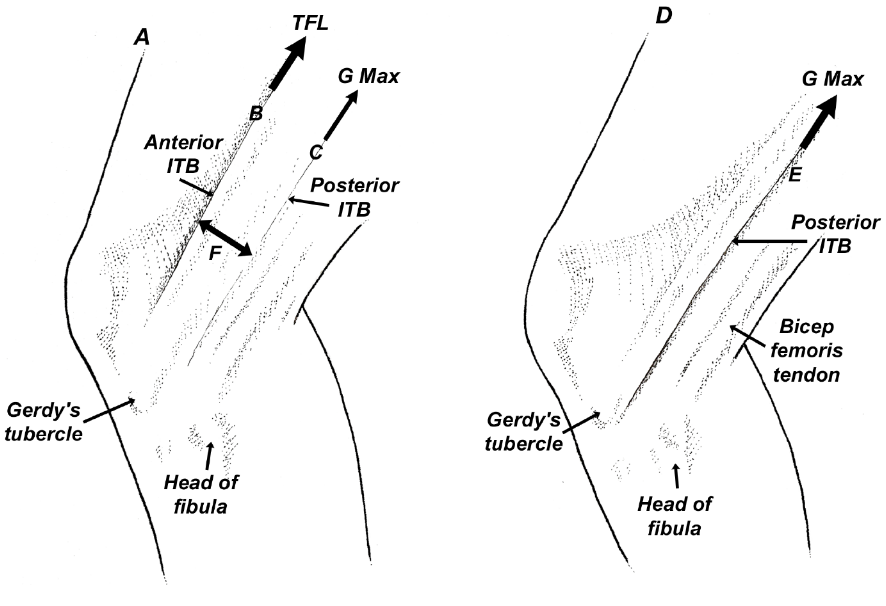


Figure 3.30. The iliotibial band (ITB). When the knee is flexed slightly (**A**), the tensor fasciae latae muscle (**TFL**) pulls with more force than the gluteus maximus muscle (**G Max**) causing the anterior aspect of the ITB to become more prominent (compare **B** and **C**). As the degree of knee flexion increases (**D**), greater tension is created in the gluteus maximus muscle and the posterior aspect of the iliotibial band becomes more prominent (**E**). The shifting of tension from the anterior to the posterior fibers of the ITB (**F**) creates the illusion that the band is displacing forward and backward. This can be demonstrated on yourself by placing your index and middle fingers on the anterior and posterior aspects of the iliotibial band as you flex your knee through a 40° range of motion. Notice that when the leg is straight the anterior aspect of the band is more prominent and tension gradually transitions to the posterior band when the knee flexes past 30°. Drawn from photographs in Fairclough et al. (65).

period, reaching a range of more than 40°. The increased range of knee flexion allows the center of mass to drop significantly while running, reaching a low point during the middle of midstance. At this time, the center of mass reverses direction and the body springs up and forward.

Even though knee and hip kinematics differ significantly between walking and running, foot motions are very similar in that the midstance period represents a time for continued surface accommodation and, more importantly, energy storage. During the majority of the midstance period, the subtalar joint continues to pronate while the talus drops inferomedially. This motion continues until shortly before heel lift, when subtalar joint pronation is stopped by, in order of importance, the congenital placement of the axes of the subtalar and midtarsal joints, the geometry of their articulating surfaces, and by the connecting ligaments (66). Throughout its range of motion, the talus is sliding medially down the calcaneal facets, pivoting about the posterior band of the interosseus talocalcaneal ligament; coming to a halt when the talar head drops into the superomedial calcaneonavicular ligament and the inferior calcaneonavicular ligament (Fig. 3.31).

To be efficient during this process, the body must absorb as much force as it can during early stance so it can return it during the latter half of stance phase. Cavagna et al. (67) demonstrate that the metabolic cost of running would be 30-40% higher were it not for the storage and eventual return of energy. Energy return is accomplished primarily by structural differences in muscle architecture between proximal and distal muscles of the lower extremity. As demonstrated by Biewener and Daley (68), the proximal muscles of the hip and knee tend to have long parallel fascicles with little tendon elasticity, while the distal muscles of the foot and leg tend to have short, pennate fascicles with long, flexible tendons.

The short fibers present in the distal muscles allows them to generate force extremely economically by contracting either isometrically or with low shortening velocities: energy is stored in their stretched tendons with little work being done by their short pennate fibers. This contrasts with the proximal muscles, which are recruited in complex patterns, producing force by altering the length of their muscle fibers. This finding is consistent with prior research by Ker et al. (69), who demonstrate that energy-saving tendons have small cross-sectional areas that allow them to stretch through large ranges, storing and returning energy like rubber bands. Although counterintuitive, muscle fiber lengths present during midstance remain relatively unchanged while their corresponding tendons stretch and rebound back through significant ranges, comparable to the spring on a pogo-stick. This relationship allows tendon elasticity to perform most of the work while muscle action occurs isometrically. In detailed biomechanical studies of turkeys and kangaroos, Alexander (70) confirms that even though the joints of these animals move through large excursions when they run, there is little change in muscle fiber length, since the tendons store and return energy with no help from the muscles (which saves precious calories). In fact, certain tendons are so efficient they are able to return 93% of the work performed when stretching them (71). Because 7% of the work done while stretching is dissipated as heat, repeat use over time causes the tendon's temperature to rise gradually, potentially producing thermal injury. If the tendon was less resilient (which is consistent with prior models of muscle function in which the muscles performed the work and the tendons passively transmitted force), a greater percentage of the stretch force would be converted into heat, making prolonged locomotion impossible since the tendon would fail when exposed to elevated temperatures. A study of juvenile pigs confirms that elasticity is reduced in immature tendons (possibly explaining the metabolic inefficiency present in children), and the capacity of tendons to store and return energy lessens with age (i.e., running economy is significantly

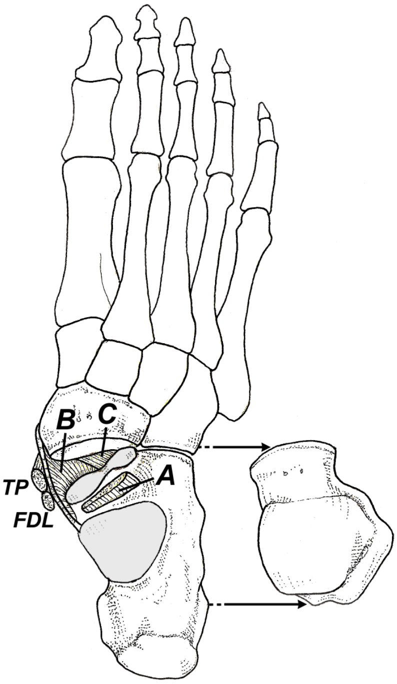


Figure 3.31. Superior view of the right foot with the talus removed. During early stance phase, the talus slides medially down the calcaneal facets (shaded areas), pivoting about the posterior band of the interosseus talocalcaneal ligament (**A**). Motion of the talus continues until the talar head rests in the superomedial calcaneonavicular ligament (**B**) and the inferior calcaneonavicular ligament (**C**). As suggested by Davis et al. (127), because the calcaneonavicular ligament contains very few elastic fibers, it should be renamed the "sling ligament," rather than the "spring ligament," since it functions like a sling to stabilize the talar head. Notice the tendons of tibialis posterior (**TP**) and flexor digitorum longus (**FDL**) pass just medial to the head and neck of the talus.

reduced in older adults because the muscular system is unable to compensate for the diminished tendon elasticity) (72).

In order for tendons to store energy effectively, they must be stretched through very specific ranges, since excessive stretching could produce injury while too small a range would limit energy storage; e.g., a rubber band stretched through a small a range of motion would not return significant energy and an overstretched rubber band would break. To provide the range of motion necessary for the proper degree of stretching, joints of the foot and ankle have been designed to move through precise ranges of motion. In an *in vivo* study of the degree of arch lowering associated with running, Ker et al. (73) determined the average vertical deflection of the medial longitudinal arch is 7 to 10 mm.

In a separate study of the effect of surface stiffness on energy efficiency, McMahon and Greene (74) demonstrate that this exact distance provides the perfect degree of tendon stretch to maximize the return of energy. By having subjects run over experimental tracks made of varying stiffness, the authors confirmed that overly flexible surfaces absorb too much energy while rigid surfaces absorb too little, causing running speeds to be diminished in both situations. McMahon and Greene (74) prove that the perfect track deflects vertically 7-8 mm and it returns more than 90% of the elastic energy stored following heel strike, resulting in significantly faster running speeds. Because this distance is identical to the degree of *in vivo* deflection noted by Ker et al. (71), McMahon (75) suggests that this may be the perfect degree necessary for ideal storage of energy. The author specifically states that tendons in the arch of the foot can return 17% of the energy absorbed during a single step.

Although difficulties in quantifying energy storage make it impossible to determine exactly which tissues are responsible for specific amounts of energy storage, it is possible the flexor digitorum brevis plays a significant role, since this muscle is important in maintaining arch height (increasing tone though barefoot exercise results in an elevated arch as measured on weight bearing X-rays [76]). Also, the of role flexor digitorum brevis in force transmission is clinically evidenced by the fact that calcaneal heel spurs form at the origin of this muscle, not the origin of the plantar fascia (77). Because both actomyosin cross-bridges and tendons are capable of storing and returning energy (78), this muscle, in addition to the long digital flexors, is in an ideal position to store and return energy. By increasing tone in response to stress, flexor digitorum brevis may behave as a variable length spring that functions as a secondary restraint to vertical lowering of the arch.

While early research emphasized the importance of the subtalar joint in dampening ground-reactive forces, Kitaoka et al. (79) suggest that the subtalar joint possesses too small a range of motion to allow it to play a significant role in dampening ground-reactive forces. By evaluating the effect of physiological loading on cadaveric joints of the foot and ankle, the authors determined the greatest degree of motion occurs in the talonavicular joint (9.4°), while the least amount of motion occurs in the subtalar joints (4.4°). In a recent series of important *in vivo* motion studies, Lundgren et al. (58) and Arndt et al. (57) inserted self-drilling intracortical pins into 9 bones of the foot and ankle to evaluate motion of the rear, mid, and forefoot as 6 male subjects walked and ran slowly over level terrain. Subsequent 3-dimensional analysis confirmed motion in the talonavicular joint was significantly greater than subtalar motion and in some situations, transverse and frontal plane talonavicular motions were twice as much as subtalar motions occurring in the same planes. The authors state that the curvature of the talar head and its corresponding navicular facet enables this joint to function with little osseous constraint, allowing for a considerable range of triplanar motion that makes it highly adaptable to the functional demands of the gait cycle.

Motion between the medial cuneiform and the navicular joint was much larger than expected, moving up to 10° in the frontal and sagittal planes (Fig. 3.32). The authors claim that this degree of motion is likely to have a significant effect on foot function, since the joints of the midfoot dorsiflexed through a larger range than the ankle in 4 of 5 subjects tested. There was also an unexpected amount of motion between the calcaneus and cuboid and between the fifth metatarsal and cuboid, confirming that the lateral arch of the foot has some capacity for accommodating surface irregularities and dampening motion. These two studies represent for the first time, a comprehensive description of *in vivo* kinematics during walking and slow

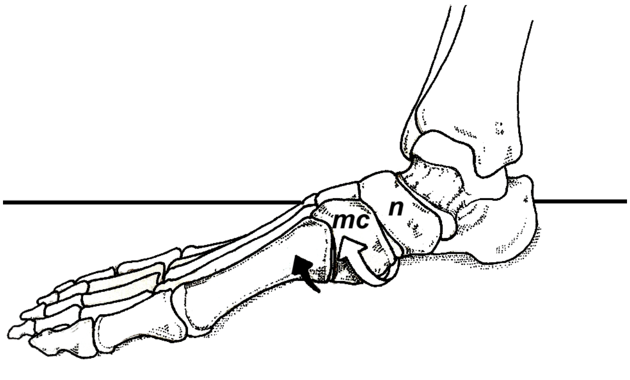


Figure 3.32. During stance phase, the medial cuneiform (mc) was shown to dorsiflex and invert up to 10° relative to the navicular (n) (white arrow). Movement between the medial cuneiform and the first metatarsal was inconsistent and approximately half that of the medial cuneiform and the navicular (black arrow).

running, emphasizing that *in vivo* motions in the foot and ankle are more complicated than previously believed, and that subtalar joint mobility is limited compared with the talonavicular, first metatarsal-cuneiform and even cuboid-fifth metatarsal joint motion. Interestingly, in all 3 planes, the ranges of motion in the joints of the feet were greater while walking than during slow running. The clinical implication of this is that slow running is easier on the joints of the foot and patients with various mechanical foot disorders should not be discouraged from running slowly.

During the latter half of midstance, ground-reactive forces centered beneath the heel begin to lessen, and the subtalar joint begins to supinate, causing the foot to stiffen in anticipation of the accelerational forces associated with the propulsive period. Subtalar supination is accomplished in part by taking advantage of the forward motion in the contralateral lower extremity: the forward momentum of the swing phase leg externally rotates the pelvis (white arrow in Fig. 3.33), which then externally rotates the weight-bearing leg (black arrow in Fig. 3.33). Since the leg and talus behave as a closed kinetic chain during midstance, external rotation of the weight-bearing leg causes the talus to abduct, which in turn supinates the subtalar joint. This motion help stabilize the tarsal by decreasing parallelism of the midtarsal joint axes.

Supination of the subtalar and midtarsal joints during late midstance is assisted by the return of elastic energy stored in the muscles of the arch, by concentric contraction of tibialis posterior, and most importantly, by the return of energy stored in the Achilles tendon. Because the fibers of this tendon rotate approximately 90° before attaching to the posterior calcaneus (Fig. 3.34), the Achilles tendon is the most important energy storing tendon in the body. As demonstrated by Ker (73), this tendon is capable of returning 35% of the energy used to stretch it. Despite its short lever arm to the subtalar joint, the Achilles tendon generates the vast majority of the inversion torque necessary to supinate the subtalar joint. Subtalar supination during late midstance creates a malalignment of the midtarsal joint axes (thereby locking the midfoot), and displaces the progression of the center of mass laterally, allowing the cuboid to begin dorsiflexing into the overhanging calcaneus. Dorsiflexion of the cuboid relative to the calcaneus was demonstrated in the *in vivo* studies performed by Lundgren et al. (58) and Arndt et al. (57), when the cuboid was shown to dorsiflex on the calcaneus during late midstance while walking and propulsion while slow running. Malalignment of the midtarsal joint axes and locking of the calcaneocuboid joint are necessary prerequisites for efficient propulsion.

Throughout late midstance, the hip and knee are extending and externally rotating, allowing the knee to lock (through twisting of the cruciate ligaments), while also allowing the hip to assist in the storage of energy: rotation of the hip's capsular ligaments provides a soft tissue locking mechanism that decelerates hip extension

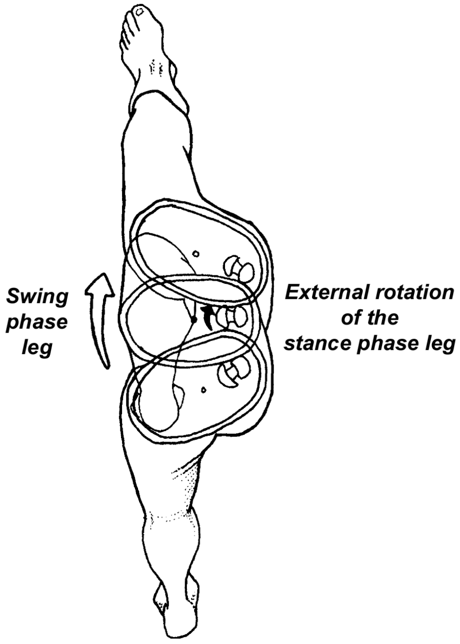


Figure 3.33. Forward motion of the swing phase leg externally rotates the stance leg, which in turn supinates the subtalar joint. Mann (66) emphasizes the role the adductors play in producing external rotation of the stance leg by noting their firm attachment to the anterior pelvis and posterior femur allows these muscles to act as effective lever arms capable of translating forward momentum of the swing leg into external rotation of the stance leg femur.

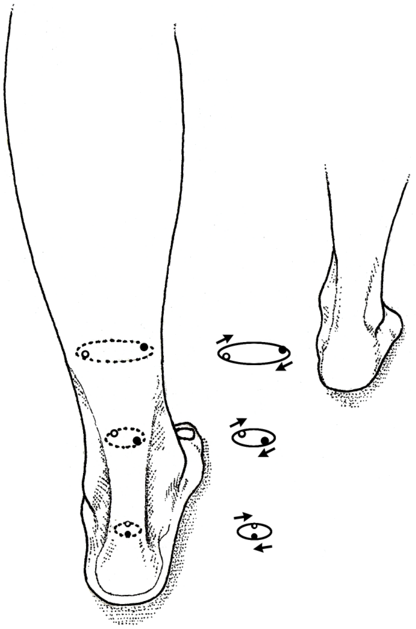


Figure 3.34. Rotation of the Achilles tendon. When moving proximal to distal, the medial fibers move posteriorly (black dots) while the lateral fibers move anteriorly (white dots) This results in a 90° twisting of the tendon (131).

while also storing and eventually returning energy in the twisted fibers (refer back to figure 2.65). Perhaps more importantly, the rectus femoris muscle, like the Achilles tendon, also possesses a natural twist that allows this muscle to store energy in a spring-like manner. As demonstrated by Hasselman et al. (80), the indirect head of the rectus femoris muscle rotates near its proximal muscle tendon junction, twisting 90° before attaching to the superior acetabular rim (Fig. 3.35). Although the exact percentage of energy stored and returned is unknown, twisting of these fibers suggests the rectus femoris muscle plays a role in lessening the metabolic cost associated with flexing the hip by storing and returning energy.

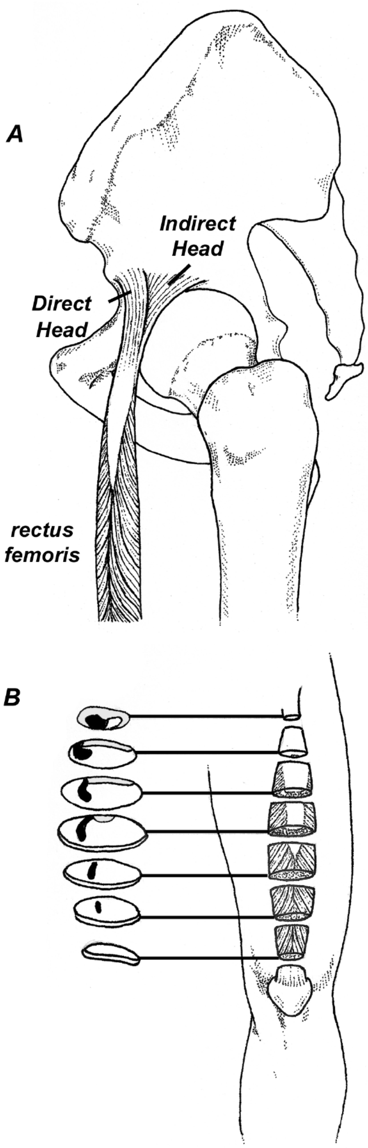


Figure 3.35. Twisting of the indirect head of the rectus femoris muscle. Notice in the transverse sections (**B**), that the indirect head of the rectus femoris (black) rotates nearly 90° before attaching to the superior acetabular rim. Redrawn from Hasselman et al. (80).

By the end of the midstance period, the ankle is dorsiflexed 10° (forward momentum of the body coupled with simultaneous knee extension throughout midstance allows ground-reactive forces applied beneath the forefoot to dorsiflex the ankle), the subtalar joint is moving towards its neutral position, and the midtarsal joint is fully pronated about both axes; i.e., the midtarsal joint has remained fully pronated about its oblique axis throughout midstance although its available range of motion has significantly decreased due to subtalar supination. Because ankle dorsiflexion displaces the naturally wider anterior talus upwardly (creating a bony block that stabilizes the ankle), the distal tibiofibular articulation gaps anteriorly while the fibula moves posteriorly during late midstance. Stance phase functions of the fibula are reviewed in figure 3.36.

Propulsive Period

The propulsive period begins the moment heel lift occurs and ends with toe off. This period occupies the final 33% of stance phase while walking and lasts approximately 0.2 seconds. When running, propulsion is the longest period, occupying 55% of stance phase, with forces on the Achilles tendon, tibia, and the plantar forefoot averaging 7, 9, and 2.7 times body weight, respectively. Although it appears to be a simple process, there are numerous biomechanical factors responsible for producing heel lift. First, forward momentum of the torso displaces the center of mass directly over the forefoot, reducing the vertical forces responsible for maintaining ground contact at the heel (Fig. 3.37A). At that time, continued contraction of the soleus and deep posterior compartment muscles acts to limit the range of ankle dorsiflexion by decelerating the forward motion of the proximal tibia. By limiting ankle dorsiflexion, these muscles create a new pivot point at the forefoot that allows forward momentum of the center of mass to be applied directly towards lifting the heel (Fig. 3.37B).

The biarticular gastrocnemius muscle also plays an important role in initiating heel lift by flexing the knee while simultaneously plantarflexing the ankle. These combined actions serve to lift the knee upward and forward, providing a significant force to assist with flexing the hip (Fig. 3.37C). Because it flexes the knee and hip, gastrocnemius indirectly allows for improved ground clearance during swing phase. In fact, Neptune et al. (81) claim that by itself, the gastrocnemius muscle is the most important muscle responsible for initiating swing phase. These separate actions confirm that despite their shared insertions into the Achilles tendon, the uniarticular soleus and biarticular gastrocnemius behave very differently during gait.

To improve muscular efficiency, the gastrocnemius fires almost isometrically during the latter half of stance phase, allowing the Achilles tendon to store and return energy. To prove this, Roberts et al. (82) surgically

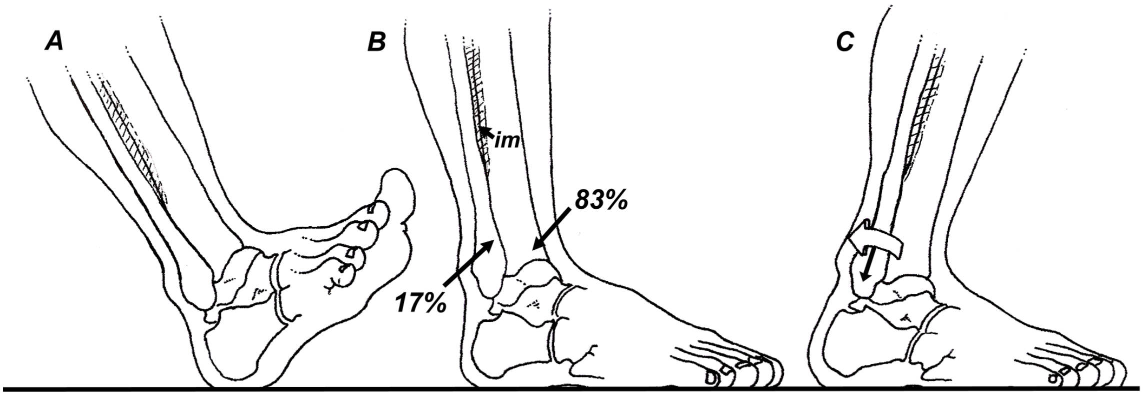


Figure 3.36. Summary of stance phase fibular motion. During the contact period (**A**), the fibula remains relatively immobile as ankle plantarflexion and rearfoot eversion limit downward motion of the fibula. As demonstrated in a cadaveric study by Wang et al. (128), eversion of the rearfoot tilts the lateral aspect of the talar dome superiorly, creating a physical block that limits downward migration of the fibula. By midstance, the fibula supports 17% of the total load borne by the lower leg and the interosseous membrane (**im**) plays a significant role in distributing force evenly throughout the entire fibula (128). As vertical forces peak shortly before the push-off (**C**), the upward migration of the anterior talar dome associated with ankle dorsiflexion forces the fibula to glide posteriorly approximately 1 mm (129), which serves to increase ankle stability by setting the talus firmly in the ankle mortise. This close-packed position increases the percentage of weight borne by the fibula from 17-30% (128). Although *in vivo* studies show inconsistent fibular motions during the latter half of stance phase (56,57), cadaveric research suggests the fibula drops inferiorly during propulsion (black arrow in **C**), thereby improving stability by deepening the ankle mortise (128). Theoretically, downward migration of the fibula at this time is facilitated by contraction of soleus, flexor hallucis longus, and peroneus longus/brevis, all of which originate from the fibula and are actively tensing during late stance phase. As with coupled motions in the spine, there is much individual variation in fibular movement patterns and there are no preset rules defining motion.

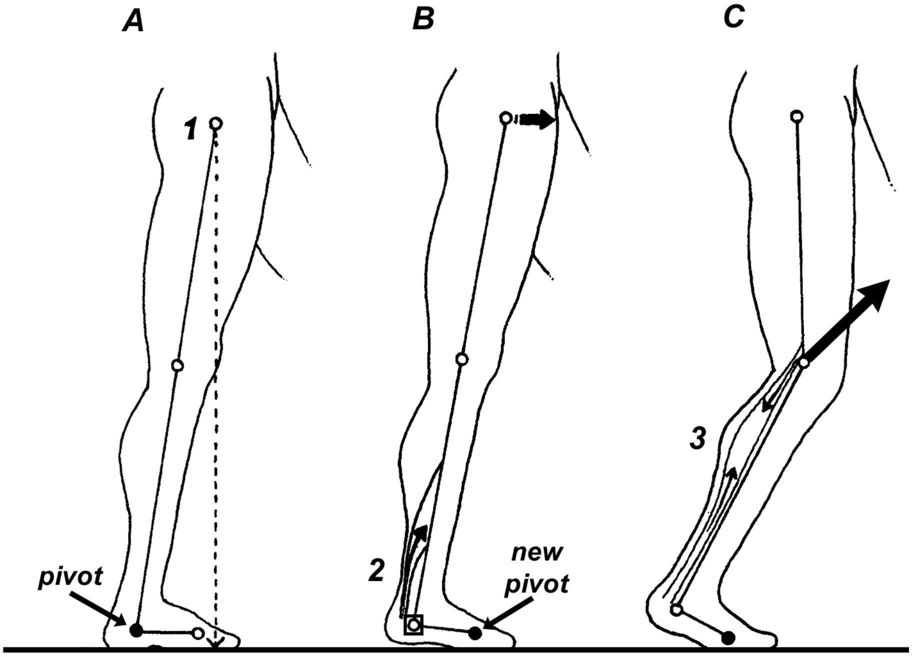


Figure 3.37. Heel lift results from the combined actions of the forward momentum of body mass (1), muscular deceleration of ankle dorsiflexion (2), and active flexion of the knee produced by gastrocnemius contraction (3). Note that in panel **A**, the pivot point for motion is the ankle joint while soleus contraction in panel **B** locks the ankle (square) and creates a new pivot point at the forefoot (black circle in **B** and **C**).

implanted special crystals and strain gauges into gastrocnemius muscles and Achilles tendons of turkeys and forced them to run on treadmills. By having the turkeys run at progressively faster speeds, these researchers confirmed that there was little change in gastrocnemius length (approximately 7% change with each stride) and the muscle generated just enough force to keep the Achilles stretched, thereby allowing the tendon to store gravitational energy. By calculating muscle activity and force production, Roberts et al. (82) demonstrated that storing and recovering energy in the stretched Achilles tendon was responsible for more than 60% of the work performed by the muscle-tendon complex.

This study confirms the spring-like action of the Achilles tendon appreciably lessens the metabolic cost of locomotion by reducing the workload on the muscular support system. According to Taylor (83), it is metabolically expensive for muscles to generate force when tensing either concentrically or eccentrically and isometric contractions are significantly more efficient because they produce large forces with little metabolic expense. By converting the gradual eccentric contraction present during midstance into an "isometric impulse" that allows the Achilles tendon to store and return energy at just the right moment, isometric contraction of the gastrocnemius allows the body to take advantage of the "free elastic energy" associated with stretching this large, well-designed tendon. According to Anderson (18), optimizing the storage and return of energy requires considerable practice as it is a learned process, involving precise timing of numerous kinetic and kinematic variables. Eccentric contraction followed by near isometric contraction (allowing for the storage of energy) is not unique to the gastrocnemius/soleus, since it occurs in almost every other shock absorbing muscle in the body (e.g., tibialis anterior and vastus lateralis).

Once the heel has left the ground, a considerable amount of stress is transferred directly into the forefoot. To protect the forefoot from the extreme ground-reactive forces associated with propulsion, stimulation of cutaneous receptors in the skin (e.g., Meissner's corpuscles) cause the digital flexors to tense reflexively, producing a strong plantarflexion force at the toes that significantly reduces pressure beneath the metatarsal heads.

The exact degree of protection provided by the digital flexors was determined in an interesting study by Ferris et al. (84). By mounting cadaveric feet in a heel rise position on a specially designed apparatus, these authors measured plantar contact pressures in the forefeet before and after sequentially applying tension to a series of tendons clamped to pneumatic actuators. The authors also embedded strain gauges into the second metatarsal shafts in order to measure bending forces present in the bone with and without simulated muscle contraction (Fig. 3.38). Using this elaborate technique, Ferris et al. (84) concluded that in the absence of the digital flexors, pressure beneath the hallux and second toe decreased 27% and 80%, respectively. More importantly, the authors confirmed the reduced pressure beneath the toes produced a corresponding increase in pressure beneath the metatarsal heads, resulting in large bending strains being placed on the metatarsal shafts. Apparently, a primary role of the digital flexors is to create a compressive force along the plantar metatarsal shafts that counteracts the bending moments associated with propulsion. The authors emphasize that although the toe flexors are relatively weak compared to the gastrocnemius and soleus muscles, weakness of the long digital flexors can have a profound effect on regional forefoot pressures. They go on to suggest that fatigue of these muscles would result in elevated metatarsal shaft bending moments, predisposing to stress reactions. Flexor hallucis longus is particularly important, since the loss of function at the hallux results in a transfer of load to the lateral forefoot that may increase bending strains placed on the lesser metatarsal shafts.

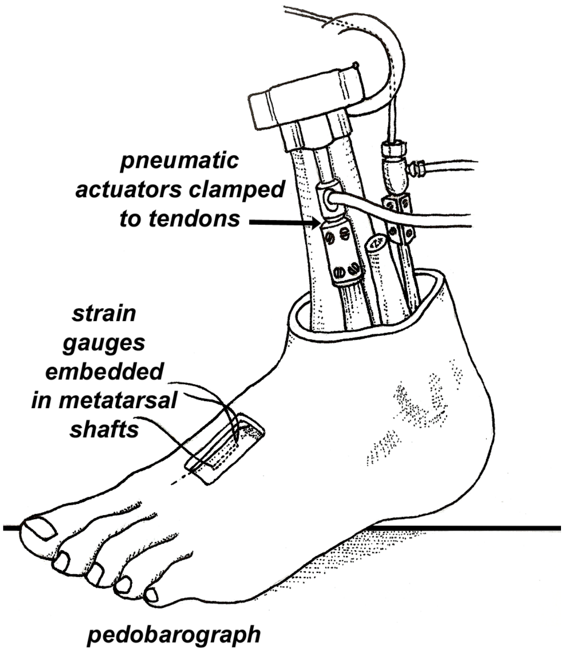


Figure 3.38. Cadaveric model evaluating plantar pressures and metatarsal bending strains present during heel lift. Redrawn from Ferris et al. (84).

In a separate study of forces acting on the foot during propulsion, Jacob (85) determined that flexor hallucis longus and brevis exert forces of 52% and 36% body weight, respectively, while flexor digitorum longus and brevis exert forces of 9% and 13% body weight, respectively. Besides distributing pressure and reducing metatarsal bending strains, these muscles play an important role in postural stability. In a study of balance in the elderly, Menz et al. (86) determined that decreased plantar tactile sensation and weakness of the digital flexors were independent predictors of impaired balance and may be associated with an increased risk of falls. By muscularly controlling anterior displacement of the center of mass during propulsion, the digital flexors increase the size of the fall envelope. After evaluating age and gender strength differences in the digital flexors, Menz et al. (87) determined that older individuals, on average, possess 32% less plantarflexion strength in the hallux and 27% less plantarflexion strength of the lesser toes; and women possess 42% less hallux plantarflexion strength than men. According to the authors, improving strength in the digital flexors will theoretically improve balance and may reduce the risk of falling.

In addition to the support provided by the digital flexors, the joints of the midfoot must be architecturally stable in order to tolerate the accelerational forces associated with early propulsion. The primary factor responsible for stabilizing the midfoot is supination of the midtarsal joint. This important action locks the talonavicular and calcaneocuboid joints, preventing the chimp-like buckling that would otherwise occur (refer back to figure 1.19). In order to efficiently supinate the midfoot, the body takes advantage of the external shank rotation supplied by the forward momentum of the opposite swing phase leg. Because the closed kinetic chain ends at the metatarsal heads after heel lift occurs, continued external leg rotation supinates the subtalar joint beyond its neutral position (ground-reactive forces no longer maintain the calcaneus in a fixed position so it is free to move with the rotating talus), while markedly supinating the forefoot about the oblique midtarsal joint axis: The entire rearfoot pivots medially as it abducts and dorsiflexes about the OMJA (Fig. 3.39). Notice in this illustration how external rotation of the leg creates a screw-like motion at the midfoot that greatly increases arch height, essentially converting the foot into a rigid lever.

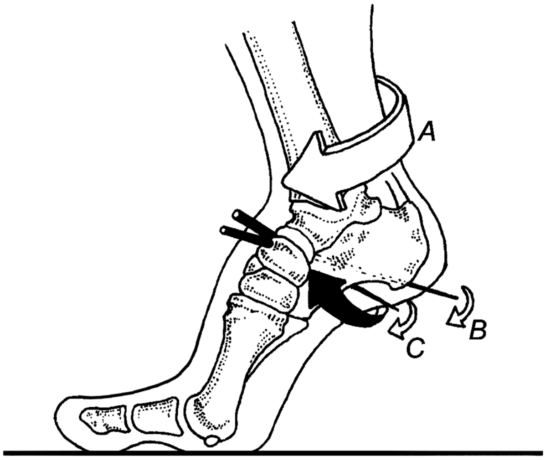


Figure 3.39. External leg rotation (A) acts to supinate the subtalar joint (B) while simultaneously supinating forefoot about the oblique midtarsal joint axis (C). These motions increase arch height (black arrow), thereby stabilizing the various articulations of the midfoot during propulsion.

Supination about the oblique axis of the midtarsal joint is aided by contraction of the intrinsic muscles originating from the medial calcaneus (particularly abductor hallucis) and by what is known as the windlass effect of the plantar fascia: dorsiflexion of the toes after heel lift draws the plantar fascia around the metatarsal heads, pulling the anterior and posterior pillars of the longitudinal arch together (Fig. 3.40). This approximation of the rearfoot and forefoot allows for continued supination about the oblique midtarsal joint axis, with its associated increase in arch height.

Using fiberoptic cables embedded in cadaveric plantar fascias during simulated walking, Erdemer et al. (88) demonstrate that force in the plantar fascia gradually increases during contact and midstance, peaking at 96% body weight during propulsion. These researchers conclude that because there is a strong correlation between Achilles tendon and plantar fascial stress, the plantar fascia serves as an intermediary, transmitting force from the Achilles tendon into the forefoot during propulsion. In an *in vivo* study of plantar fascial mechanics, Wearing et al. (89) determined the long and short digital flexors protect the plantar fascia by decelerating the range of metatarsophalangeal joint dorsiflexion during propulsion, thereby lessening tensile strain in the plantar fascia as these muscles absorb force that would otherwise go into the stretching plantar fascia.

While considerable stability is afforded by elevation of the arch associated with the windlass effect of the plantar fascia, the foot could not be considered a rigid lever were it not for the continued forefoot pronation about the longitudinal midtarsal joint axis. During early propulsion, the calcaneocuboid locking mechanism is maintained by forceful contraction of the soleus muscle, which simultaneously plantarflexes the ankle while inverting the subtalar joint. Despite its short lever arm, this muscle possesses 5 times the mass of any other deep posterior compartment muscle and is therefore an effective supinator of the subtalar joint (90). While ankle plantarflexion allows for a forward acceleration of body mass, subtalar joint inversion allows ground-reactive forces to dorsiflex the fourth and fifth metatarsals, locking the lateral column.

The effectiveness of the soleus muscle in maintaining the midtarsal locking mechanism is only temporary, since early in propulsion the range of ankle plantarflexion places soleus in such a shortened position that it is unable to generate sufficient force to invert the calcaneus. At this time, the continued forceful contraction of peroneus longus (which passes beneath the cuboid in the peroneal groove) acts to dorsiflex and evert the cuboid, thereby maintaining the close-packed position of the

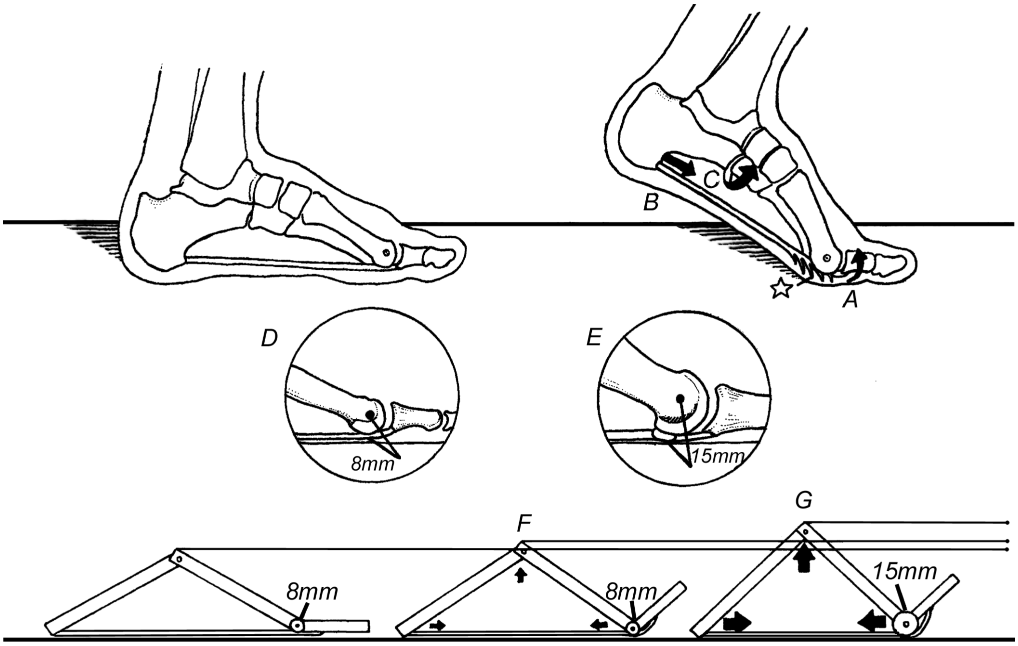


Figure 3.40. The windlass effect of the plantar fascia. During the propulsive period, ground-reactive forces dorsiflex the toes, which pulls the plantar fascia around the metatarsal heads (**A**). This action results in the approximation of the rearfoot and forefoot (**B**) and allows for the increased arch height necessary for stability (**C**). The amount of pull generated by the plantar fascia is directly related to the distance between the transverse axis of the metatarsophalangeal joint and the passage of the plantar fascia: the greater the distance, the greater the pull placed upon the plantar fascia while the digit dorsiflexes. For example, the average lesser metatarsal has an average of 8 mm between its transverse axis and the passage of the plantar fascia (**D**) while the first metatarsal, with its larger head and the presence of sesamoid bones (which the plantar fascia invest) has a distance of nearly 15 mm between the transverse axis and the plantar fascia (**E**) (91). As a result, dorsiflexion of the first digit produces a much greater tractioning effect on the plantar fascia than any of the lesser digits (compare **F** and **G**). In order to resist the greater tensile load, the plantar fascia has its strongest attachment distal to the first metatarsal head. The plantar fascia also has strong attachments to the skin beneath the metatarsal heads (star), which prevents sliding on the skin as posterior shear forces are applied during the propulsive period (91). The short digital flexors play an important role in reducing strain placed on the plantar fascia because they reinforce the arch and stabilize the metatarsophalangeal joints, essentially behaving as a variable length buttress to lessen load borne by the plantar fascia.

calcaneocuboid joint (Fig. 3.41). Furthermore, because the fourth and fifth metatarsals are shorter than the remaining metatarsals, the lateral column is unable to maintain ground contact during mid and late propulsion and is therefore unable to assist with the forward acceleration of body mass. Locking of the calcaneocuboid joint at this time continues to serve a purpose, because it affords peroneus longus and brevis an effective lever arm as they now function to direct body weight medially towards the opposite foot by everting the entire lateral column (Fig. 3.42).

By lifting the lateral column and transferring weight medially, peroneus brevis plays an important role in improving speed by transferring force to the medial forefoot. This medial shift of body weight is necessary to maintain a straight gait pattern and to allow the final transfer of vertical forces to occur off the medial forefoot, which is better equipped to handle these forces since the first metatarsal is twice as wide and 4 times as strong as the remaining lesser metatarsals (21). In a cadaveric study of forefoot pressures associated with the propulsive period of walking, Jacob (85) demonstrates that the first metatarsal head supports a force of 119% body weight while the second metatarsal head supports only 28%. Because of the force difference, Jacob (85) states that if the first metatarsal were unable to bear weight, the second metatarsal would fail, since it could not tolerate the transfer of forces.

Because of its passage under the cuboid and eventual insertion into the base of the first metatarsal and medial cuneiform, peroneus longus has the interesting ability to transfer body weight medially while simultaneously stabilizing the medial forefoot so it may better tolerate these forces. This stabilizing action is related to the improved angle of approach afforded the peroneal longus tendon as the subtalar joint is supinating (Fig. 3.43).

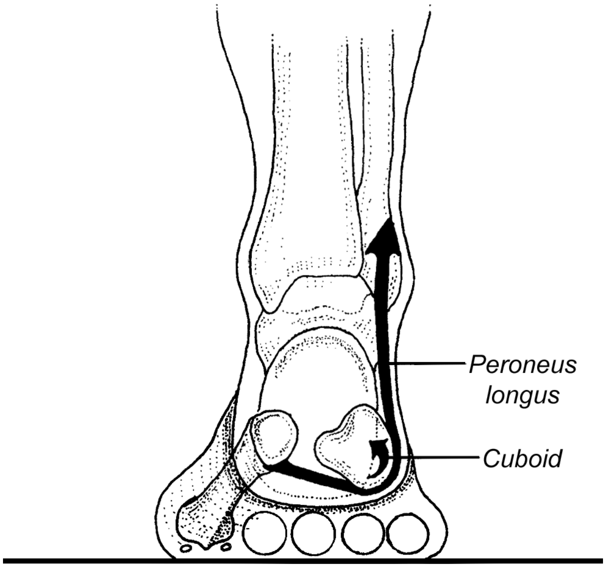


Figure 3.41. Concentric contraction of peroneus longus during early and mid propulsion serves to lift (dorsiflex and evert) the cuboid, thereby locking the midtarsal joint.

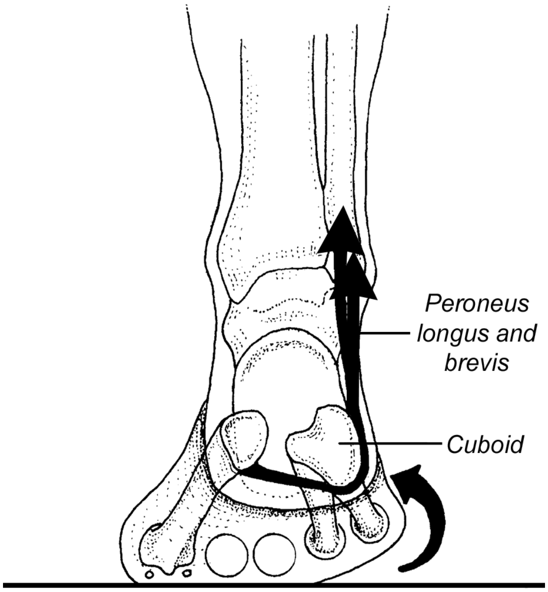


Figure 3.42. Because they are so short, the fifth metatarsal leaves the ground approximately 33% of the way through the propulsive period, with the fourth metatarsal leaving shortly thereafter. At that time, continued contraction of the lateral compartment musculature serves to shift body weight medially towards the opposite foot (arrow), which is just beginning its contact period.

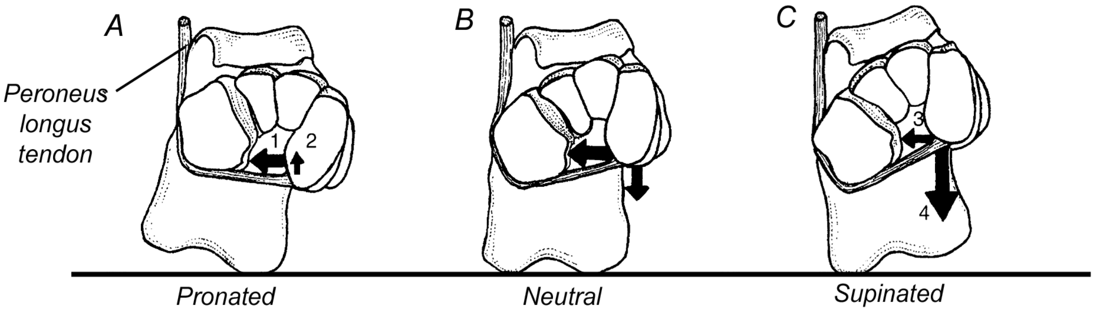


Figure 3.43. The effect of subtalar positioning on peroneus longus function. When the subtalar joint is pronated (**A**), the nearly horizontal angle of approach afforded peroneus longus allows for the production of a strong posterolateral compressive force (**1**) and a mild dorsiflectory force about the first ray axis (**2**). As the subtalar joint moves into a progressively more supinated position (**B** and **C**), the posterolateral compressive force is lessened (**3**), and the more vertical approach of the peroneus longus tendon allows for the development of a strong plantarflectory force about the first ray axis (**4**).

The improved ability of peroneus longus to function as a first ray plantarflexor is extremely important during the propulsive period, because the increased height of the medial longitudinal arch coupled with the normal parabolic curve of the metatarsal heads (i.e., the first metatarsal is normally shorter than the second metatarsal) necessitates the first ray actively plantarflex in order to maintain ground contact. Besides the obvious importance of maintaining ground contact to resist ground-reactive forces, active plantarflexion of the first metatarsal allows for the dorsal-posterior shifting of the first metatarsophalangeal joint's transverse axis needed for the hallux to reach its required range of dorsiflexion (Fig. 3.44).

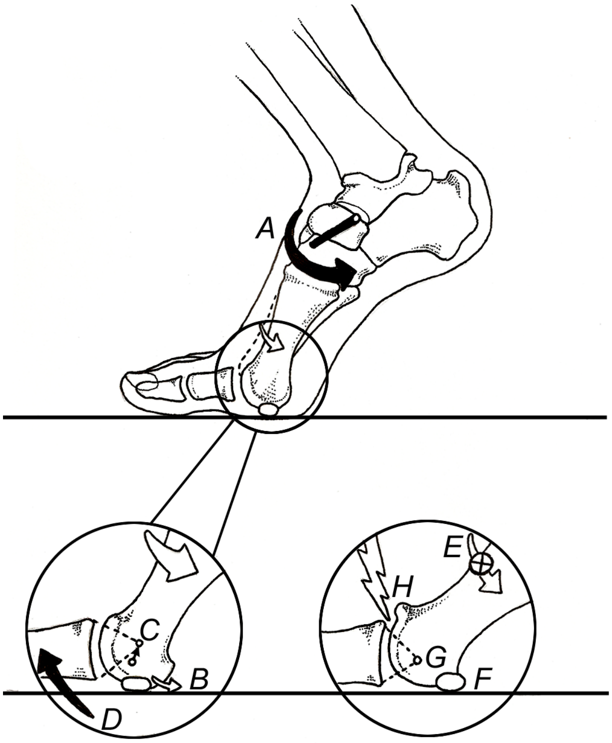


Figure 3.44. Because the first metatarsal is normally shorter than the second metatarsal, it actively plantarflexes to maintain ground contact during the propulsive period (A). As the first metatarsal plantarflexes, the metatarsal head glides posteriorly along the sesamoids (**B**), which allows for a dorsal-posterior shift of the transverse axis of the first metatarsophalangeal joint (**C**). This new axis allows for an unrestrained range of hallux dorsiflexion (**D**). Failure of the first metatarsal to plantarflex during propulsion (**E**) inhibits the posterior glide of the metatarsal head on its sesamoid (**F**), which in turn prevents the dorsal-posterior shift of the transverse axis. The hallux is now forced to dorsiflex about the original axis (**G**). This results in a "jamming" of the dorsal cartilage (**H**) with its characteristic resorption of subchondral bone and dorsal lipping of the first metatarsal head.

The combined actions of peroneus longus as an evertor of the lateral column and a plantarflexor of the first ray allow for what Bojsen-Moller (91) refers to as a high gear push-off. By everting the lateral column, the peroneals allow the final transfer of body weight to occur through the transverse axis of the metatarsal heads (Fig. 3.45). Use of the transverse axis supplies the ankle plantarflexors with a longer, more effective lever arm for accelerating body mass forward. Failure of the peroneals to evert the lateral column would allow for continued supination of the subtalar joint with the final push-off occurring as a rolling action through the oblique axis of the metatarsal heads. Because the oblique axis has a shorter lever arm to the ankle axis (the oblique axis is 15-20% closer to the ankle axis than the transverse axis), it allows for a less efficient propulsion referred to as a low gear push-off. It is clinically interesting that transitions to faster speeds of running are associated with significant increases in peroneus brevis activity, with little change in activity of the gastrocnemius and soleus muscles (92). According to Bojsen-Moller (91) use of the transverse axis by means of peroneus longus/brevis contraction represents the final evolutionary change in the process of producing a fast, efficient propulsion.

During the final portion of the propulsive period, the foot will ideally be supinated about the oblique midtarsal and subtalar joint axes. In addition, the forefoot will remain fully pronated about the longitudinal midtarsal joint axis. This axis is maintained in a pronated position during late propulsion as extensor digitorum

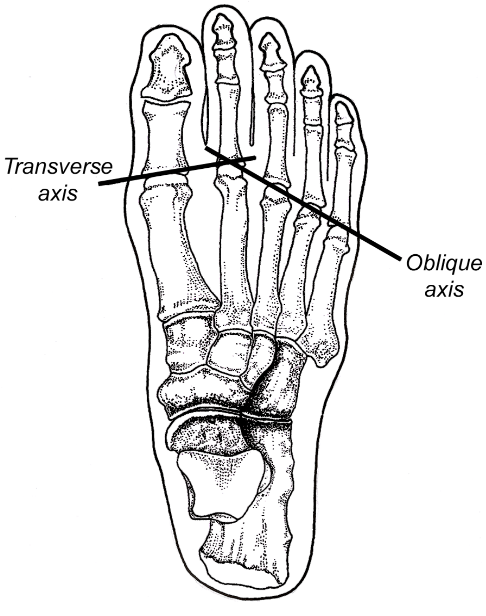


Figure 3.45. The transverse and oblique axes of the metatarsal heads.

longus and peroneus tertius are vigorously contracting in preparation for the swing phase of gait. The final transfer of forces should occur through the hallux, which has been stabilized throughout the propulsive period by vigorous contraction of flexor hallucis longus. The propulsive period ends when the hallux leaves the ground.

Swing Phase Motions

The swing phase begins at toe off and ends at heel strike, occupying 38% of the gait cycle and lasting approximately 0.4 seconds (1). The primary kinematic actions during this phase are to provide ground clearance of the forefoot by midswing and to position the articulations in such a way that the supporting muscles are prepared to dampen impact forces as the next heel strike occurs. Because the typical lower extremity weighs 15% of body mass, and each leg moves through a full cycle 2,500 times each day, the average 160-pound person must accelerate and decelerate 56,000 pounds of force per leg, per day. The late stance phase activity of the gastrocnemius muscle has already played an important role in lessening the metabolic cost associated with initiating swing phase by storing energy in the Achilles during late midstance, and returning it during propulsion to drive the knee and hip up and forward. This markedly reduces strain on the iliopsoas, rectus femoris and hamstring musculature, which, were it not for the energy returned from the Achilles, would have fired with significantly more force to swing the lower extremity forward.

Even though the total workload performed by the iliopsoas muscle is reduced by the highly efficient gastrocnemius/Achilles tendon complex, contraction of these muscles during the initiation of swing phase imposes substantial compression on the lumbar vertebrae as the psoas extends the lumbar spine while the iliacus tilts the pelvis anteriorly. To lessen strain and protect the spine and pelvis from the elevated shear force associated with combined iliopsoas activity, the multifidus, erector spinae, rectus abdominus, abdominal obliques and latissimus dorsi muscles actively contract during propulsion, with peak forces occurring at the initiation of swing phase (60).These muscular actions lessen strain by preventing spinal and pelvic hyperextension, locking the spine and pelvis while the lower extremity is being pulled forward (Fig. 3.46).

Gracovetsky (93) proves that activity in the lumbar spinal musculature also plays an important role in initiating swing phase by demonstrating that individuals born without legs are capable of walking with extremely efficient gait patterns by pivoting on their ischial tuberosities. Kinematic analysis of these individuals reveals that they maintain their lumbar spines in lordotic positions, converting lateral bending moments of the spine into an axial rotation that drives the pelvis forward. Referred to as the spinal engine, electromyography of their torsos confirms that although the amplitude of spinal motions vary, abdominal muscle function is similar when walking with and without legs and the abdominal muscles, without contribution from the iliopsoas and lower extremities, are capable of producing a very smooth gait. This model of muscle function suggests that the iliopsoas functions in a manner similar to the plantar fascia during heel lift, in that it transfers force generated in a proximal area into a distal area. Of course, the iliopsoas can add to these forces by concentrically contracting while the plantar fascia provides a more passive transfer of force.

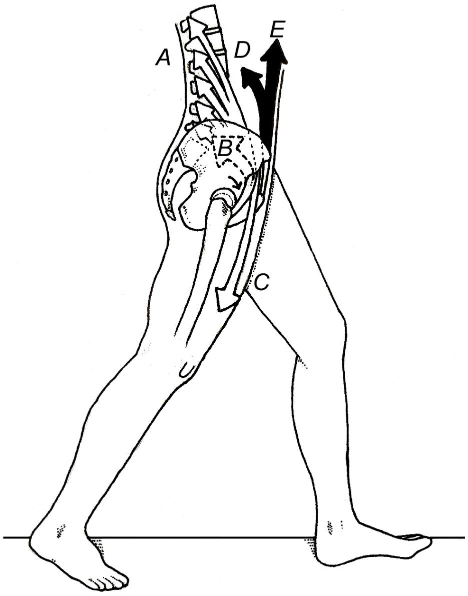


Figure 3.46. During the late propulsive period, tension created in the psoas (A), iliacus (B) and rectus femoris (C) extend the lumbar spine and tilt the pelvis forward (black arrow above acetabulum). To protect against these potentially injurious motions, the external obliques (**D**) and rectus abdominus (**E**) pull the anterior pelvis upwardly, counteracting forces created by the hip flexors, allowing the spine and pelvis to function as a stable anchor.

Because the ankle reaches its maximally plantarflexed position shortly after toe off, the anterior compartment muscles have less than 0.2 seconds to overcome inertial forces and dorsiflex the forefoot into a safe position by midswing. Since extensor digitorum longus and peroneus tertius are the first anterior compartment muscles to contract (94), the foot, in addition to dorsiflexing at the ankle, will immediately pronate about the oblique midtarsal and subtalar joint axes. (These muscles possess significant lever arms for pronating these axes.) The dorsiflectory components of these pronatory motions allow for improved ground clearance.

Almost immediately after extensor digitorum longus and peroneus tertius contract, tibialis anterior and extensor hallucis longus begin contracting, markedly increasing the dorsiflectory movement created at the ankle. Root et al. (94) claim that extensor hallucis longus is the strongest ankle dorsiflexor during early swing phase. Tibialis anterior, by virtue of its insertion on the first metatarsal and medial cuneiform, also acts to improve ground clearance by dorsiflexing the first ray during early swing phase (Fig. 3.47). Notice in this illustration how the forefoot is maintained in an everted position about the longitudinal midtarsal joint axis during early and midswing phase by the continued contraction of extensor digitorum longus and peroneus tertius. The dorsiflectory motion of the first ray, besides improving ground clearance, also serves to enhance the efficiency of extensor hallucis longus as an ankle dorsiflexor, since it results in an anterior/inferior shift of the first metatarsophalangeal joint's transverse axis (Fig. 3.48).

By far, the most important kinematic factor responsible for producing ground clearance is flexion of the knee. In fact, if for any reason the knee is unable to adequately flex during midswing, the metabolic cost of locomotion skyrockets, because the individual is forced to circumduct the stiff swing phase lower extremity by excessively abducting both the stance and swing phase hips. By the time midswing has occurred, the hip and knee are flexed 30° and 50°, respectively; the ankle is dorsiflexed to a near neutral position; the subtalar and midtarsal joints are pronated (the midtarsal joint is pronated about both axes); and the first ray is dorsiflexed and inverted. In an attempt to reduce the metabolic cost of locomotion, the large hip and thigh muscles contract with only enough force to allow the foot to barely clear the ground; i.e., the typical foot clears the ground by only 1.29 cm (95). Although this occasionally causes the individual to trip on an unseen object, clearing the ground by such a small margin lessens the metabolic cost of locomotion by decreasing strain on the hip, knee and ankle musculature.

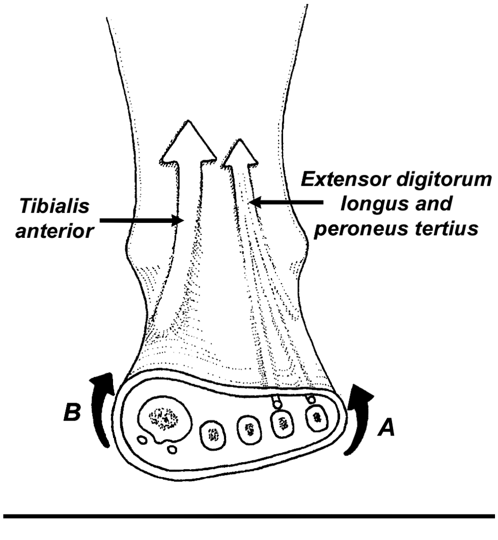


Figure 3.47. During early swing phase, the lateral branches of extensor digitorum longus and peroneus tertius actively pronate the forefoot (A) while tibialis anterior, in addition to dorsiflexing the ankle, actively dorsiflexes and inverts the first ray (B), thereby allowing for improved ground clearance.

Shortly after the forefoot has cleared the ground, muscles of the swing leg have a relatively quiet period when motion is maintained by inertial forces generated during propulsion and early swing (96). At this time, the vacuum phenomena present in the hip decreases the metabolic cost of locomotion by temporarily supporting the weight of the lower extremity (97). As discussed in Chapter 2, the hip labrum creates such a tight seal around the periphery of the acetabulum that even when all of the hip's supporting muscles and ligaments are cut, the weight of the entire lower extremity can be supported solely by the negative intraarticular hip pressure generated by the dangling lower extremity. This negative pressure provides stability and decreases the metabolic cost of locomotion by reducing the muscular effort necessary to maintain the femur in the acetabulum during the middle of swing phase.

Following the midswing quiet period, the hamstrings begin eccentrically contracting to decelerate forward motion of the swinging leg. The bicep femoris is the most efficient decelerator of the swinging leg, since its more distal insertion provides a longer lever arm for decelerating the swinging leg (Fig. 3.49). Although prior researchers suggested that the dual innervation of this muscle was responsible for its high rate of injury while running (98), Thelen et al. (99) confirm the lower attachment of the bicep femoris produces greater tensile strains in this muscle during late swing phase, explaining the higher injury rate. The authors demonstrate that compared with upright postures, the bicep femoris lengthens 9.5% during late swing phase, while semitendinosus and semimembranosus lengthen 8.1% and 7.4%, respectively. As is consistent with muscles responsible for dampening vibration, the bicep femoris muscle has short muscle fibers and long tendons, allowing it to dampen vibration very effectively. In a separate study of the long head of the bicep femoris during sprinting, Thelen et al. (100) determined that following the onset of muscle activity during late swing phase, stretching of the muscular component of the bicep femoris slowed considerably while the tendon lengthened and stored elastic energy. The authors emphasize that a more compliant tendon reduces peak muscle stretch and negative muscle work, potentially lessening the risk of injury.

Just before making ground contact, the anterior compartment muscles simultaneously contract in anticipation of dampening the impact forces associated with the contact period. Because of their relationships with the various axes, tibialis anterior and extensor digitorum longus produce mild dorsiflexion at the ankle, with tibialis anterior markedly inverting the forefoot while extensor digitorum longus and peroneus tertius assist with ankle dorsiflexion and pronation of the forefoot about the oblique

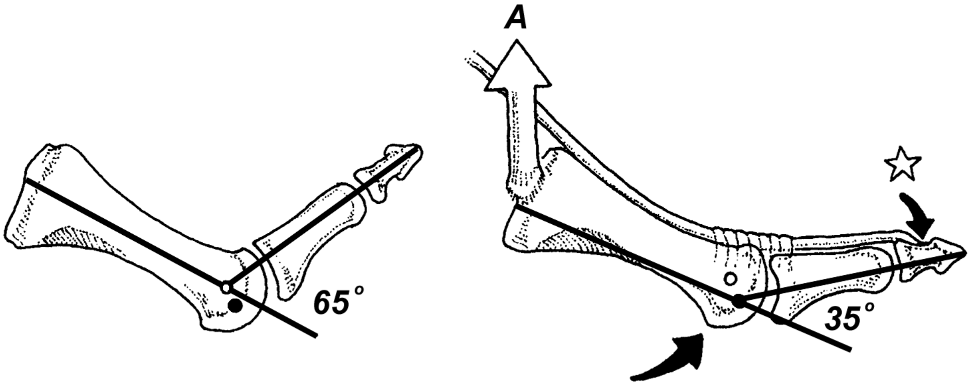


Figure 3.48. Dorsiflexion of the first ray by tibialis anterior (A) shifts the first metatarsophalangeal joint's transverse axis back to its original position (black dot), thereby limiting the range of hallux dorsiflexion possible. The plantarflectory motion of the hallux improves the efficiency of extensor hallucis longus as an ankle dorsiflexor by stabilizing its insertion on the distal phalanx (star).

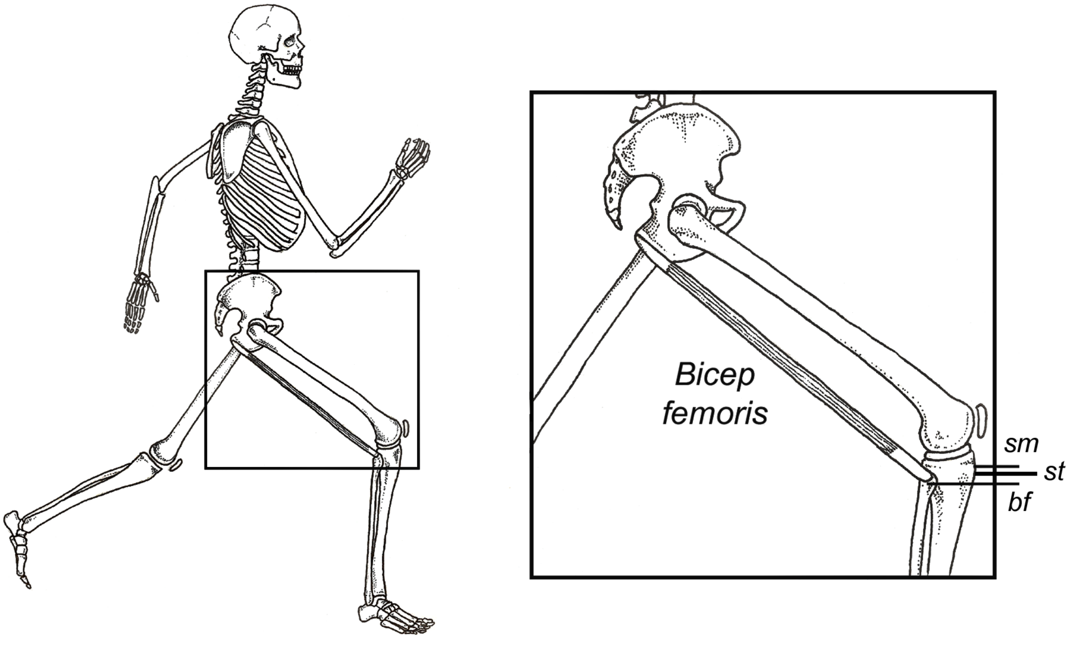


Figure 3.49. Because the distal bicep femoris has a lower point of attachment than the semitendinosus (st) and semimembranosus (sm), forward motion of the leg during swing phase creates a greater tensile strain in the bicep femoris muscle. Modified and redrawn from Thelen et al. (99).

midtarsal joint axis. Basmajian and Deluca (51) state that tibialis anterior acts as an ankle dorsiflexor during early swing phase and an inverter of the forefoot during late swing phase. By positioning the foot with the ankle dorsiflexed, the forefoot inverted, and the subtalar joint slightly supinated, the pretensed muscles of the foot and leg are now prepared to dampen ground-reactive forces associated with stance phase. It is interesting that with sprint running and anticipated falls, other shock-absorbing muscles (lateral gastrocnemius, vastus lateralis, gluteus maximus, bicep femoris, etc.) become hyperactive prior to heel strike when they pretense in an effort to more effectively dampen the perceived increase in ground-reactive forces (101,41).

Summary of Gait Cycle Muscle Function: Gluteus Maximus

This muscle contracts during late swing and early stance phase to decelerate flexion and initiate extension at the hip (although it may also mildly assist with abduction of the hip). Basmajian and Deluca (51) demonstrate that during terminal stance (toe off), the middle fibers of gluteus maximus display a brief burst of activity. Contraction at this time possibly allows these fibers to assist gluteus medius with abducting the swing phase leg. Lyons et al. (102) note that the angles of approach afforded the various sections of this muscle allow its lower portion to act as a hip extensor while the upper portion acts as a hip abductor. Cadaveric studies confirm gluteus maximus has the greatest capacity for controlling internal rotation of the hip.

In an important *in vivo* analysis of gluteus maximus function during walking, Preece et al. (103) demonstrate that this muscle places large external torques on the femur, ultimately leading to rapid deceleration of the tibia during early stance phase. Although the common belief is that rotation of the lower leg is controlled by pronation of the subtalar joint (i.e., talar adduction associated with subtalar pronation maintains the lower extremity in an internally rotated position), these authors confirm that gluteus maximus plays a significant role in controlling transverse plane motions of the lower leg, overcoming the influence of subtalar pronation. This is consistent with research by Bellchamber and van den Bogert (104), who demonstrate that during the late stance phase of gait, the hip musculature plays a more important role in controlling rotation of the lower extremity than the foot and ankle. Because the largest portion of gluteus maximus inserts into the posterior fibers of the iliotibial band, the gluteus maximus muscle provides significant stability to the hip and knee during contact and midstance, particularly while running as knee flexion angles increase.

Erector Spinae

Because iliocostalis is the most lateral of the erector spinae musculature, it is able to assist in maintaining frontal plane stability of the pelvis during transitions from double-limb support to single-limb support. Peak activity is seen during the early and midpropulsive periods (51), when the erector spinae tense to maintain frontal plane alignment of the pelvis. Waters and Morris (105) note a brief burst of activity during the latter half of swing phase, when this muscle possibly contracts to assist the weakening contralateral gluteus medius in raising the pelvis in preparation for heel strike. As noted by McGill (60), longissimus thoracis pars lumborum and iliocostalis lumborum pars lumborum limit forward motion of the lumbar spine following heel strike, dampening impact forces on individual vertebra while the spine flexes forward. Because longissimus thoracis and iliocostalis lumborum attach to the lower 6 ribs, they function to decelerate forward motion of the torso.

Gluteus Medius

Gluteus medius is the primary frontal plane stabilizer of the pelvis. It begins contracting during late swing and continues throughout midstance and into propulsion. Peak activity occurs during early midstance when this muscle vigorously contracts to prevent excessive lowering of the contralateral pelvis (which is entering its swing phase). Basmajian and Deluca (51) note a brief burst of activity in the anterior fibers of gluteus medius during toe off; possibly to assist with abducting and internally rotating the femur during early swing phase. Because the lower fibers of the gluteus medius muscle parallel the femoral neck, contraction of these fibers lessens bending forces at this site. Gluteus medius also plays a role in distributing pressure throughout the femoroacetabular joint during stance phase (55), functioning in a manner similar to the rotator cuff musculature of the glenohumeral joint.

Gluteus Minimus

This muscle functions agonistically with gluteus medius during early stance phase. The brief burst of activity during midswing most likely allows for continued internal rotation of the femur. Like the gluteus medius, this muscle also functions to maintain femoroacetabular joint pressures at a steady level during stance phase.

Tensor Fasciae Latae

Because of its insertion into the anteroproximal iliotibial band, contraction of tensor fasciae latae during the contact period acts to balance the force placed on the iliotibial band by the simultaneous contraction of gluteus maximus. Contraction of tensor fasciae latae during early stance increases tension in the anterior aspect of the band, providing stability while walking. The tensor fasciae latae also contracts with significant force during late propulsion and early swing, when it assists iliopsoas with flexing the hip.

Iliopsoas

The iliopsoas muscle demonstrates peak activity during terminal stance and early swing phase, when it assists the adductors, tensor fasciae latae, rectus femoris and sartorius with flexing the hip. Momentum gained by rapid thigh flexion during early swing phase plays an important role in forward acceleration of the center of mass during late swing phase (66). Although occasionally referred to as a spinal stabilizer, EMG analysis confirms the psoas muscle functions primarily as a hip flexor (60,106). Because contraction of the iliacus muscle tilts the pelvis anteriorly, extending the lumbar spine, the psoas muscle counters these motions by anchoring the lumbar spine to the hip, allowing the iliacus to act as a hip flexor. Despite its ability to externally rotate the hip, an EMG evaluation by Juker et al. (106) revealed only slight activity of the psoas during hip rotation tasks. As mentioned, because of their different origins and functions, McGill (60) feels the iliopsoas should be referred to as two separate muscles.

Sartorius

Sartorius is active only during swing phase with peak activity shortly after toe off. Because of its origin on the anterior superior iliac spine (ASIS) and insertion on the proximal anteromedial tibia, this muscle is able to assist with flexion of the knee and hip while simultaneously internally rotating the tibia during the first half of swing phase.

Adductors

The adductors, as a group, demonstrate peak activity during toe off, when they flex the hip and possibly assist with internally rotating the swing phase femur. These muscles again contract during late swing as they pretense in anticipation of ground-reactive forces. Although there is much individual variation in the behavior of the adductors (1), Basmajian and Deluca (51) note that with the exception of a brief quiet period at midswing, adductor magnus fires constantly throughout the gait cycle. Also, it is possible that the more horizontal sections of the adductors assist the contralateral swing phase pelvis with externally rotating the femur during the ipsilateral midstance period (66).

Hamstrings

The hamstrings demonstrate peak activity during the terminal portion of swing phase, when they eccentrically contract to decelerate forward motion of the rapidly extending leg. These muscles continue to contract through the majority of the contact period, at which time they assist the gluteus maximus with decelerating flexion and initiating extension of the hip joint. Interestingly, Hollinshead and Jenkins (107) note that because the distal semimembranosus sends fibrous attachments to the posterior horn of the medial meniscus, it is able to prevent impingement by drawing the medial meniscus posteriorly while the knee flexes. During propulsion, semitendinosus demonstrates a mild burst of activity (51), when it may assist gastrocnemius with flexing the knee. Elliot and Blanksby (108) note that with running, all of the hamstring muscles maintain high levels of activity during the propulsive period, when they function as powerful knee flexors and moderate hip extensors. Throughout late swing phase, the more distal attachment of bicep femoris results in an increased stretching of this muscle compared to the other hamstrings (99), allowing it to stabilize the sacroiliac joint through tension transferred into the sacrotuberous ligament. Pretensing of the bicep femoris may also play an important role in dampening bony and soft tissue vibrations associated with foot strike (41). Because of its multiple attachments on the posterior oblique ligament and the medial collateral ligament, the semimembranosus muscle plays an important role in resisting valgus strains at the knee.

Quadriceps

The quadriceps pretense during late swing phase and demonstrate peak activity during the early contact period, when they eccentrically contract to decelerate knee flexion. These muscles continue to contract until the center of mass passes in front of the knee (1). A brief and less forceful burst of activity is seen during late stance and early swing phase as rectus femoris assists with hip flexion (particularly at faster speeds) and the quadriceps function as a group to decelerate the range of knee flexion associated with early swing. The quadriceps muscles are by far the body's most important shock absorbers, and activity in these muscles increases as the degree of knee flexion increases. While the vastus medialis obliquus stabilizes the medial patella, the lower fibers of vastus lateralis and fibrous slips from the iliotibial band stabilize the lateral patella, preventing displacement while the knee flexes and extends.

Popliteus

The popliteus muscle is a stance phase muscle that has a slight peak in activity during heel strike with another more sustained peak through midstance and propulsion. During the contact period, popliteus concentrically contracts to assist the posterior cruciate ligament in preventing excessive forward glide of the femur on the tibia, while simultaneously assisting the subtalar joint with internally rotating the tibia. Because this latter action is necessary to unlock the cruciate and collateral ligaments, popliteus is often referred to as "the key to the knee." Throughout midstance, popliteus eccentrically contracts to aid gastrocnemius with decelerating extension at the knee. During propulsion, popliteus again concentrically contracts, producing external rotation of the femur. This action is necessary for knee flexion to occur because it restores the normal coupled motions present in the knee;

i.e., throughout the propulsive period, the knee is flexing while the tibia is externally rotating (elevation of the arch abducts the talus, which externally rotates the tibia). Because these motions conflict with the normal coupled motions associated with knee flexion (the tibia should be internally rotating as the knee flexes), the femur must externally rotate farther than the tibia for knee flexion to occur. The greater range of external femoral rotation allows the normal coupled motions to occur, as even though the tibia continues to externally rotate, it remains internally rotated relative to the more externally rotated femur.

Tibialis Anterior, Extensor Hallicus Longus, Extensor Digitorum Longus, and Peroneus Tertius

The anterior compartment musculature demonstrates peak activity immediately after heel strike. During the contact period, these muscles decelerate ankle plantarflexion, with tibialis anterior maintaining the forefoot in an inverted position about the longitudinal midtarsal joint axis during the early and midcontact periods. (Ground-reactive forces maintain this inverted position during the late contact period.) When walking, these muscles are normally inactive during midstance and again contract during terminal stance. When running, the anterior compartment muscles remain active during midstance, during which time they function to accelerate the body by pulling the proximal tibia over the fixed foot (66)

Because extensor digitorum longus and peroneus tertius are the first anterior compartment muscles to contract during the propulsive period (94), they are able to dorsiflex the ankle while simultaneously maintaining the forefoot in a pronated position about the oblique midtarsal joint axis. (Extensor digitorum longus also acts to maintain a compressive force on the lesser metatarsophalangeal and interphalangeal joints, which prevents clawing of the digits.) During terminal stance, the early swing phase contraction of tibialis anterior also assists with ankle dorsiflexion, but its insertion on the medial cuneiform and first metatarsal allows it to produce simultaneous dorsiflexion and inversion of the first ray. The extensor hallucis longus muscle acts to maintain tension on the hallux during late stance and early swing, when it behaves as the strongest ankle dorsiflexor.

The anterior compartment muscles usually demonstrate a brief period of inactivity shortly after midswing, which is followed by simultaneous contraction of all of these muscles during terminal swing (51). This simultaneous late swing phase activity allows for mild dorsiflexion of the ankle and metatarsophalangeal joints with extensor digitorum longus and peroneus tertius reestablishing the forefoot in a pronated position about the oblique midtarsal joint axis. The late swing phase activity of tibialis anterior produces marked inversion of the forefoot about the longitudinal midtarsal joint axis.

Tibialis Posterior, Flexor Digitorum Longus, and Flexor Hallucis Longus

Tibialis posterior functions during early stance phase as the body's most important decelerator of subtalar pronation. It is also important during the latter half of stance phase, when it assists the gastrocsoleus complex and the Achilles tendon with plantarflexing and inverting the foot to allow for an efficient propulsive period.

The long digital flexors play important roles during terminal midstance, as they assist with heel lift by decelerating the forward momentum of the proximal tibia (see Fig. 3.37). The digital flexors continue contracting throughout most of the propulsive period, forcefully maintaining the digits against the ground and assisting abductor hallucis with supinating the foot about the oblique midtarsal joint axis. Because of its attachment to the flexor digitorum longus tendons, the quadratus plantae muscle significantly increases forces transferred through this tendon. In fact, EMG analysis confirms the quadratus plantae muscle may act as a primary flexor of the lesser toes, being preferentially recruited over the flexor digitorum longus (109).

Gastrocnemius and Soleus

Both soleus and gastrocnemius demonstrate peak activity during terminal midstance, when they function to produce heel lift. Soleus prevents forward motion of the proximal tibia (decelerating ankle dorsiflexion) while gastrocnemius flexes the knee and plantarflexes the ankle (initiating heel lift). The femoral origin of gastrocnemius allows this muscle to maintain a constant flexion tension on the knee throughout midstance, lessening the risk of hyperextension injury.

During the contact period, soleus decelerates internal rotation of the tibia while gastrocnemius decelerates internal rotation of the femur. These dual actions reduce the buildup of torsional strains at the knee during the early stance. Soleus continues to contract through midstance and into early propulsion, when it supinates the subtalar joint, externally rotates the tibia, and stabilizes the lateral forefoot against the ground (thereby locking the lateral column). Gastrocnemius continues to contract throughout midstance and into propulsion, when it assists with subtalar joint supination and external femoral rotation. Of course, in addition to assisting with heel lift, one of the most important actions of the gastrocnemius muscle during late propulsion is to drive the knee up and forward, thereby lessening strain on the hip flexors and indirectly assisting with producing ground clearance by midswing.

Peroneus Longus and Brevis

Just prior to heel strike, the peroneal musculature plays an important role in limiting excessive rearfoot inversion, providing invaluable protection against inversion ankle sprain (133,134). The preparatory activation of the peroneal musculature is enhanced in individuals with a prior history of inversion ankle sprain (134). During the midstance period, peroneus longus and brevis create a pronatory force at the subtalar joint (brevis more so than longus) that partially resists the supinatory forces generated by the superficial and deep posterior compartment musculature. This antagonistic action decelerates the speed of subtalar joint supination and allows the subtalar joint to return smoothly to its neutral position by early propulsion. Contraction of peroneus longus also acts to stabilize articulations of the midfoot as this muscle works synergistically with tibialis posterior to create a compressive force on the tarsals: peroneus longus applies an abductory and posterior force at its insertion while tibialis posterior applies an adductory and posterior force at its insertion. These forces are resolved into a straight compressive force that prevents splaying of the tarsals during late midstance and early propulsion.

The peroneus brevis muscle is also able to create an important compressive force as it pulls the fifth metatarsal into the cuboid and the cuboid into the calcaneus, thereby stabilizing the lateral column. The peroneals continue to contract throughout the majority of the propulsive period, when peroneus longus plantarflexes the first ray (improving ground contact and allowing for the dorsal-posterior shift of the first metatarsophalangeal joint's transverse axis) while peroneus longus and brevis act together to evert the locked lateral column (thereby transferring body weight medially and allowing for a high gear push-off). Because the peroneals have such short lever arms to the ankle axis, they only slightly assist with ankle plantarflexion during propulsion.

Abductor and Adductor Hallucis

The abductor and adductor hallucis muscles function during the propulsive period to stabilize the proximal phalanx of the hallux against the ground. (They maintain a plantarflectory tension on the first metatarsophalangeal joint.) These muscles are also responsible for transverse plane stabilization of the hallux, since they act to create equal and opposite rotational components of force on the proximal phalanx (which resolve into pure compressive force). Because of its origin on the proximal phalanx of the hallux and insertion into the distal metatarsal heads (refer back to figure 2.116), the transverse head of adductor hallucis (transverse pedis) prevents splaying of the metatarsals as it pulls medially on the metatarsal heads from its stable anchor on the proximal phalanx. Failure of abductor and adductor hallucis (oblique head) to compress/stabilize the first metatarsophalangeal joint during the propulsive period makes it impossible for the transverse pedis muscle to prevent splaying of the metatarsals, since its unstable origin is set into motion.

Because abductor hallucis has a significant lever arm and angle of approach to both the first ray and oblique midtarsal joint axes, it functions as an important plantarflexor of the first ray (it assists peroneus longus in this action) and supinator about the oblique midtarsal joint axis (it is assisted in this action by flexor hallucis longus, flexor digitorum longus, flexor digitorum brevis, and quadratus plantae).

Flexor Hallucis Brevis and Flexor Digitorum Brevis

By virtue of its tendinous investment of the sesamoids, flexor hallucis brevis is a powerful stabilizer of the proximal phalanx. This muscle functions with flexor hallucis longus to create a compressive force at the first metatarsophalangeal joint and to maintain the hallux against the ground during propulsion. Flexor digitorum brevis has a similar role in that it functions with flexor digitorum longus to compress the metatarsophalangeal joints of the second through fifth rays and allows the lesser digits to maintain effective ground contact during the propulsive period. Unlike flexor hallucis brevis, flexor digitorum brevis assists in producing a strong supinatory force about the oblique midtarsal joint axis during propulsion. Because it lessens the velocity in which the toes dorsiflex during the propulsive period, flexor digitorum brevis protects the plantar fascia from high tensile strains by acting as a muscular synergist to the plantar fascia.

Interossei and the Lumbricals

The interossei function during late midstance and propulsion to maintain transverse plane stability at the second through fifth metatarsophalangeal joints and to compress the proximal phalanx against the metatarsal heads. The lumbricals have the interesting ability to compress the intermediate and distal interphalangeal joints while also maintaining the lesser digits against the ground by creating a plantarflectory force about the metatarsophalangeal joints (94). Because the lumbrical tendons pass medially to the metatarsophalangeal joints, they are also able to generate a mild adductory force to resist the abductory shear force associated with ground contact. Since the tendons of the interossei pass below the transverse axis of the metatarsophalangeal joints, they act as plantarflexors of the proximal phalanx and, in conjunction with the lumbricals, play an important role in maintaining extensor rigidity of the digits during midstance and propulsion.

Graphic Summary of the Gait Cycle while Walking

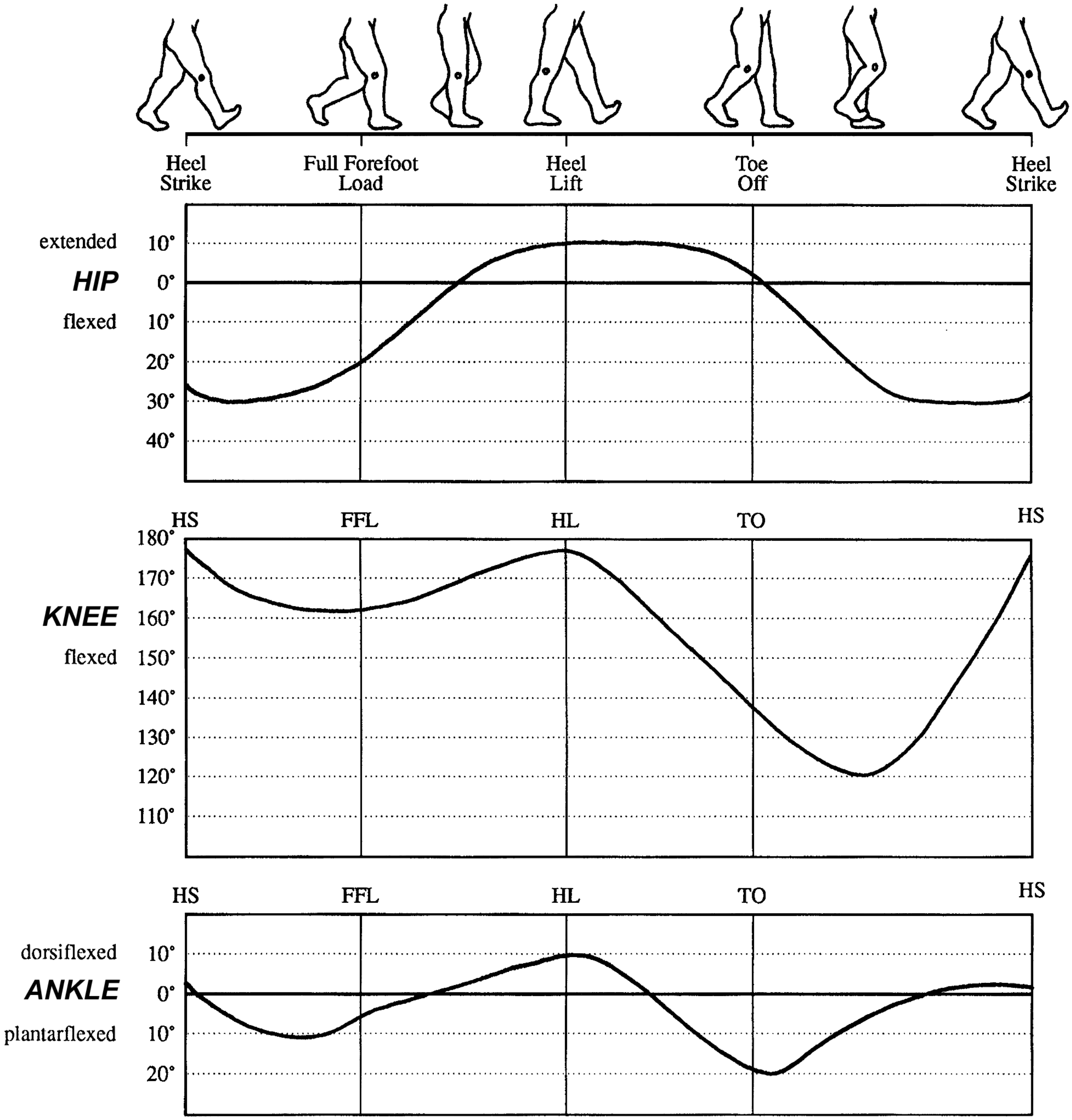


Figure 3.50. Sagittal plane motions.

Graphic Summary of the Gait Cycle while Walking

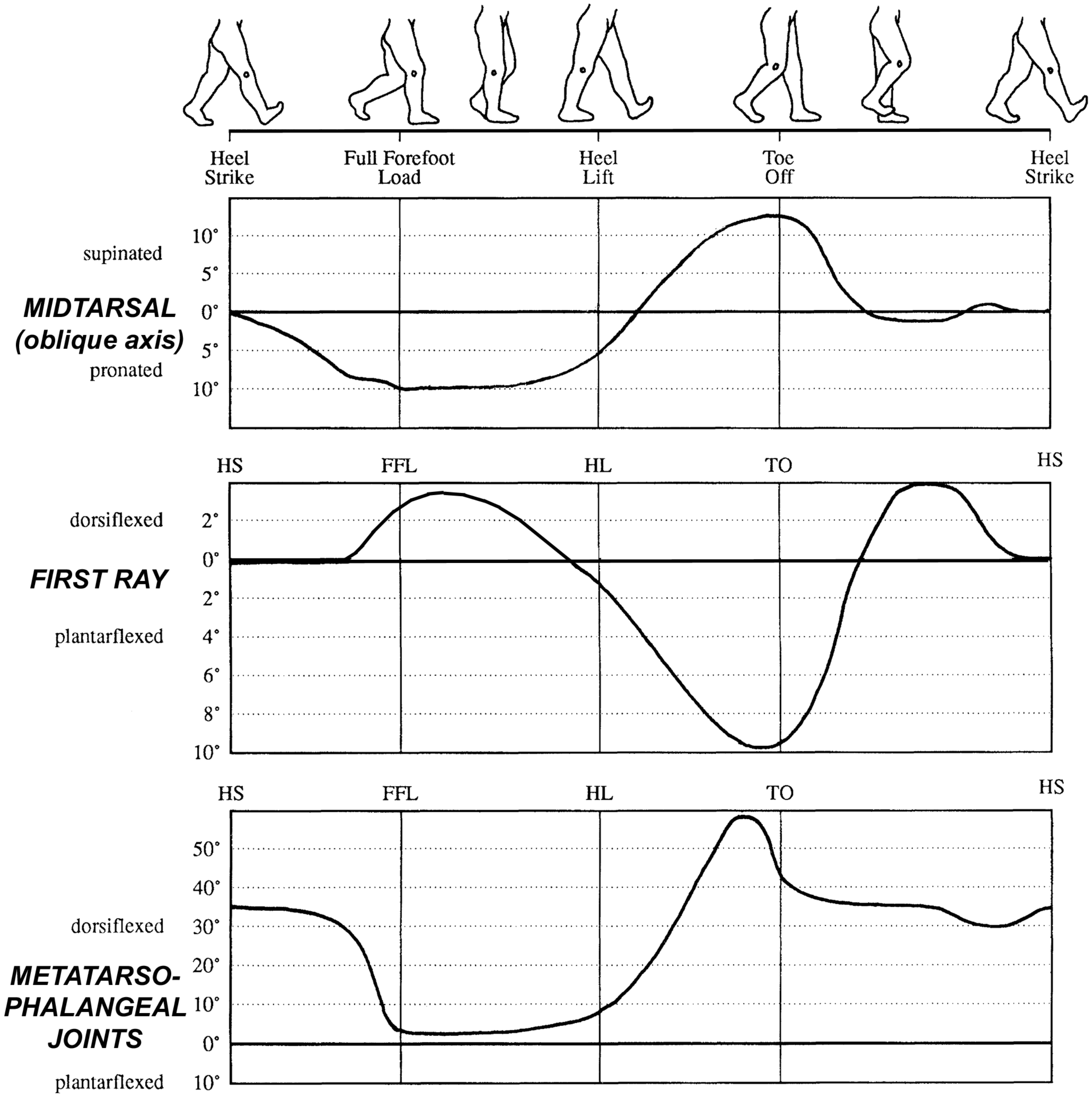


Figure 3.50. Sagittal plane motions, cont.

Graphic Summary of the Gait Cycle while Walking

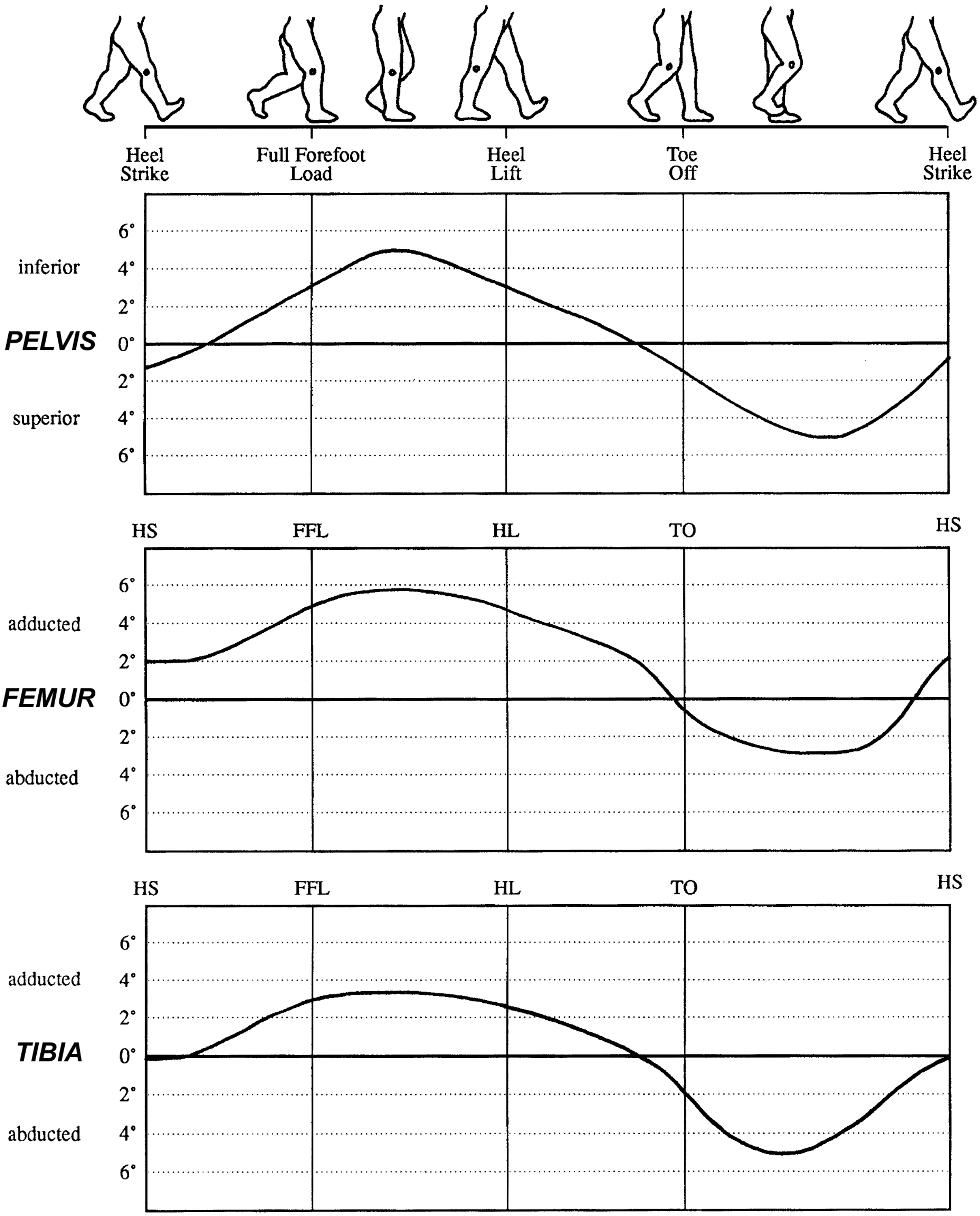


Figure 3.51. Frontal plane motions.

Graphic Summary of the Gait Cycle while Walking

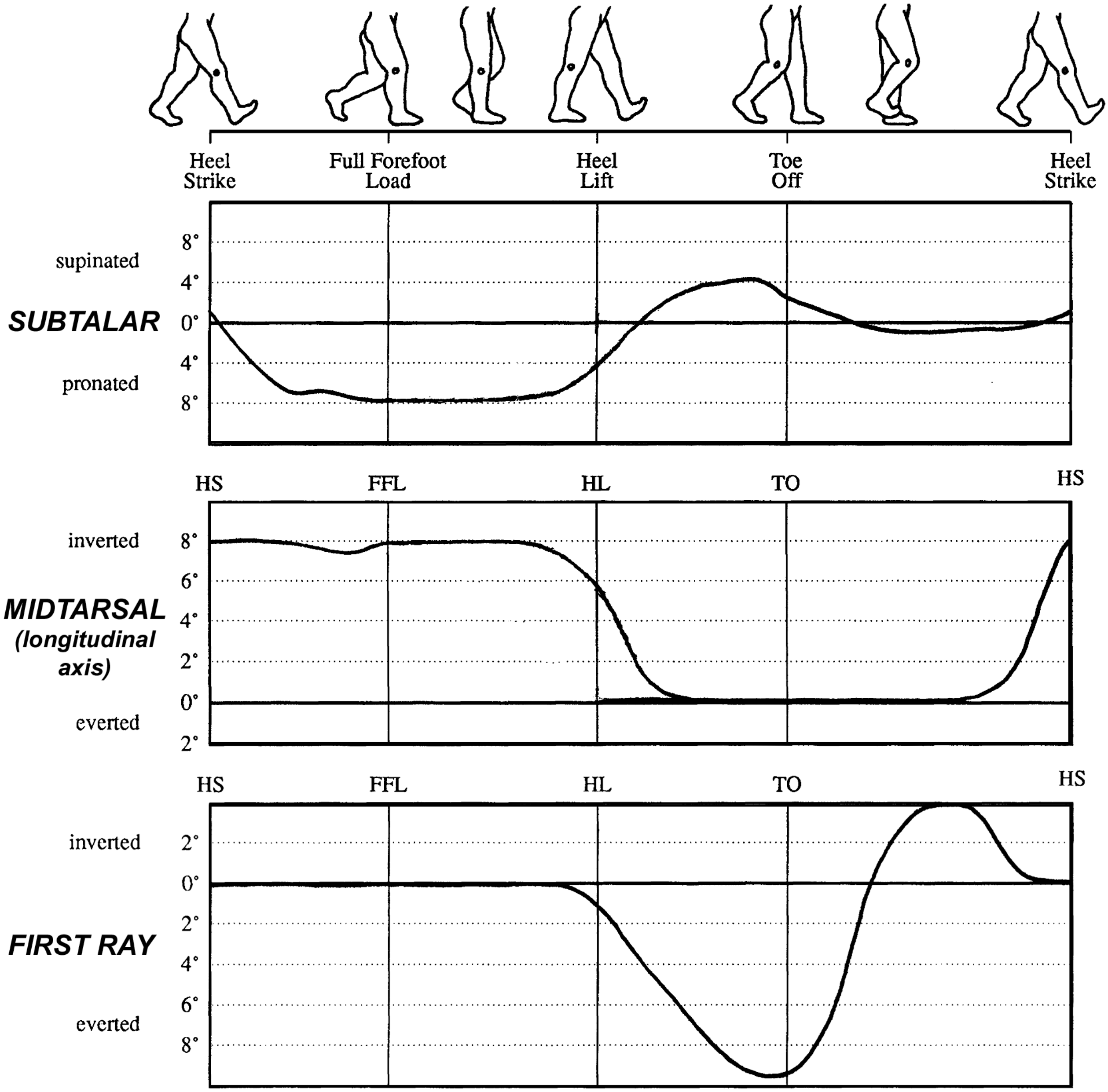


Figure 3.51. Frontal plane motions, cont.

Graphic Summary of the Gait Cycle while Walking

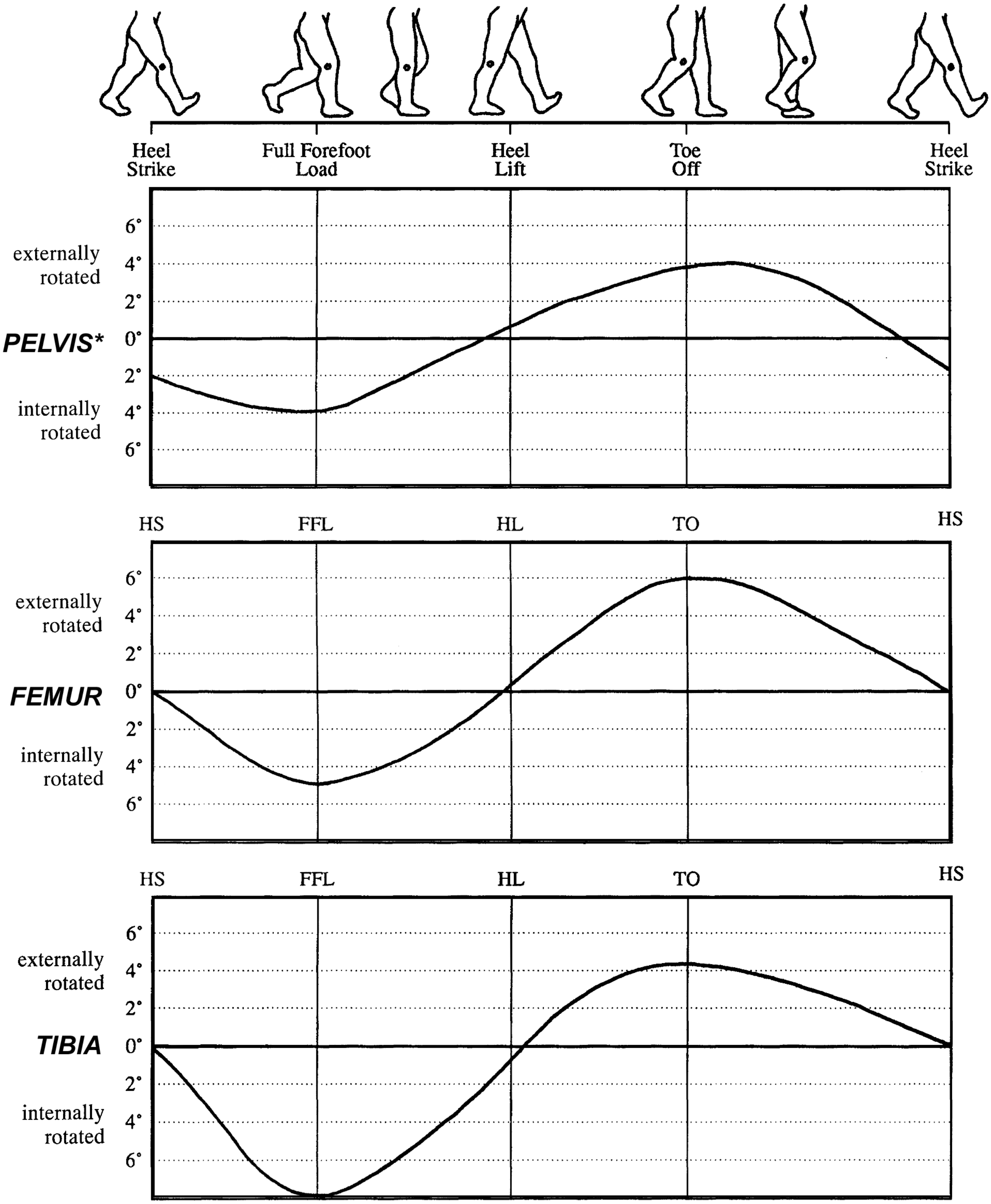


Figure 3.52. Transverse plane motions. *Although the pelvis in this graph is internally rotated only 2° at heel strike, at higher speeds of locomotion, the pelvis is often maximally internally rotated at heel strike, which allows for a significant increase in length of stride.

Graphic Summary of the Gait Cycle while Walking

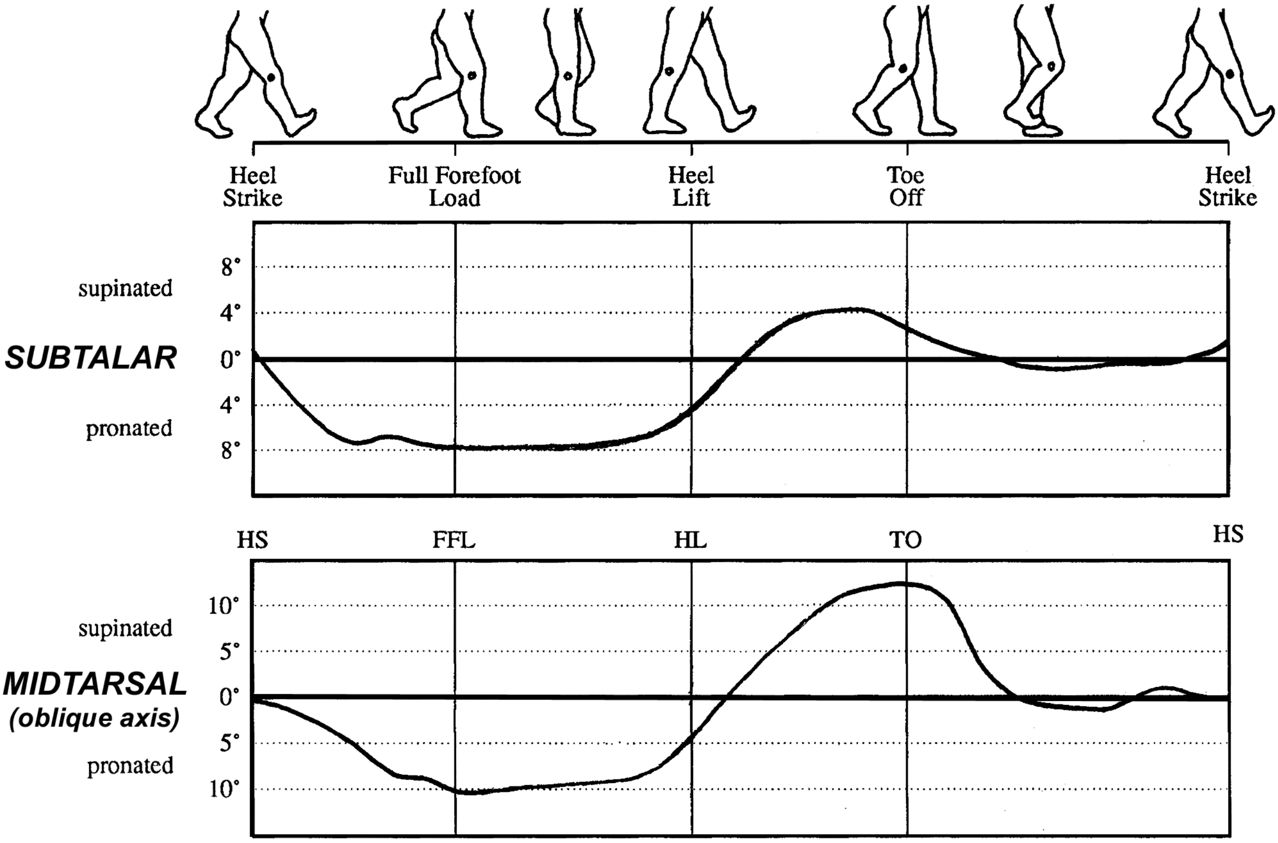


Figure 3.52. Transverse plane motions, cont.

Summary of Muscle Function during the Gait Cycle:

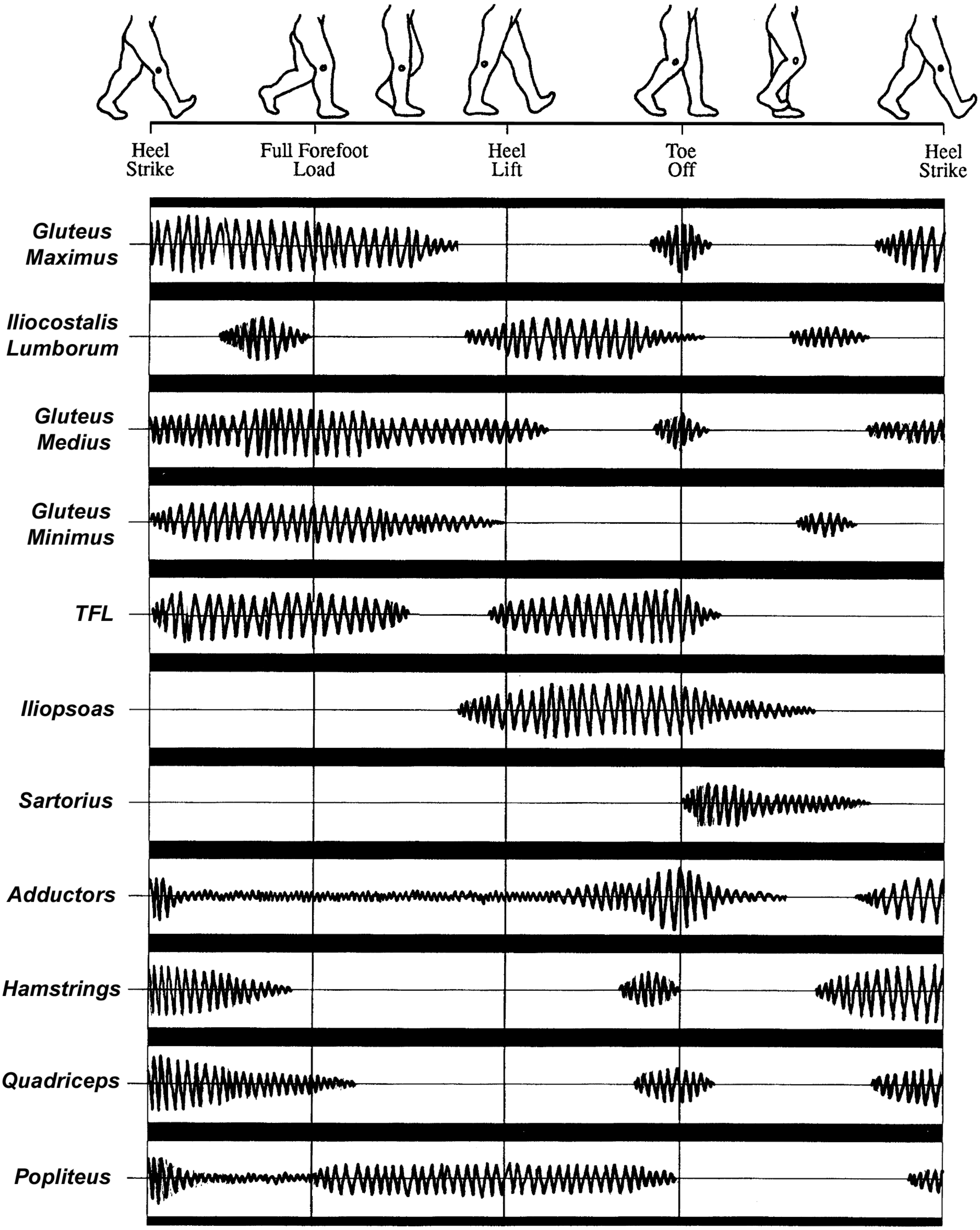


Figure 3.53. Muscle function. TFL= tensor fasciae latae.

Summary of Muscle Function during the Gait Cycle:

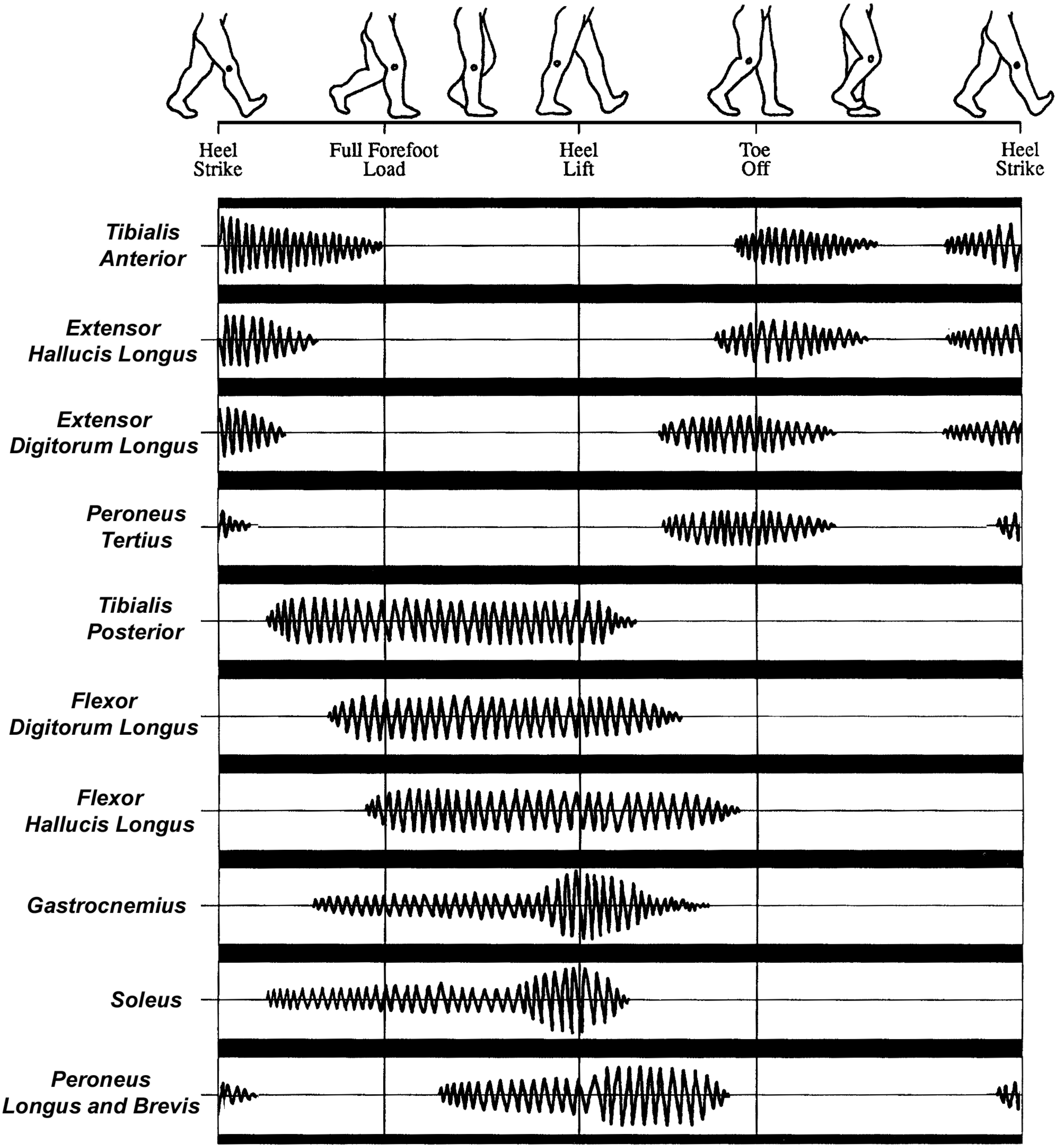


Figure 3.53. Muscle function, cont.

Summary of Muscle Function during the Gait Cycle:

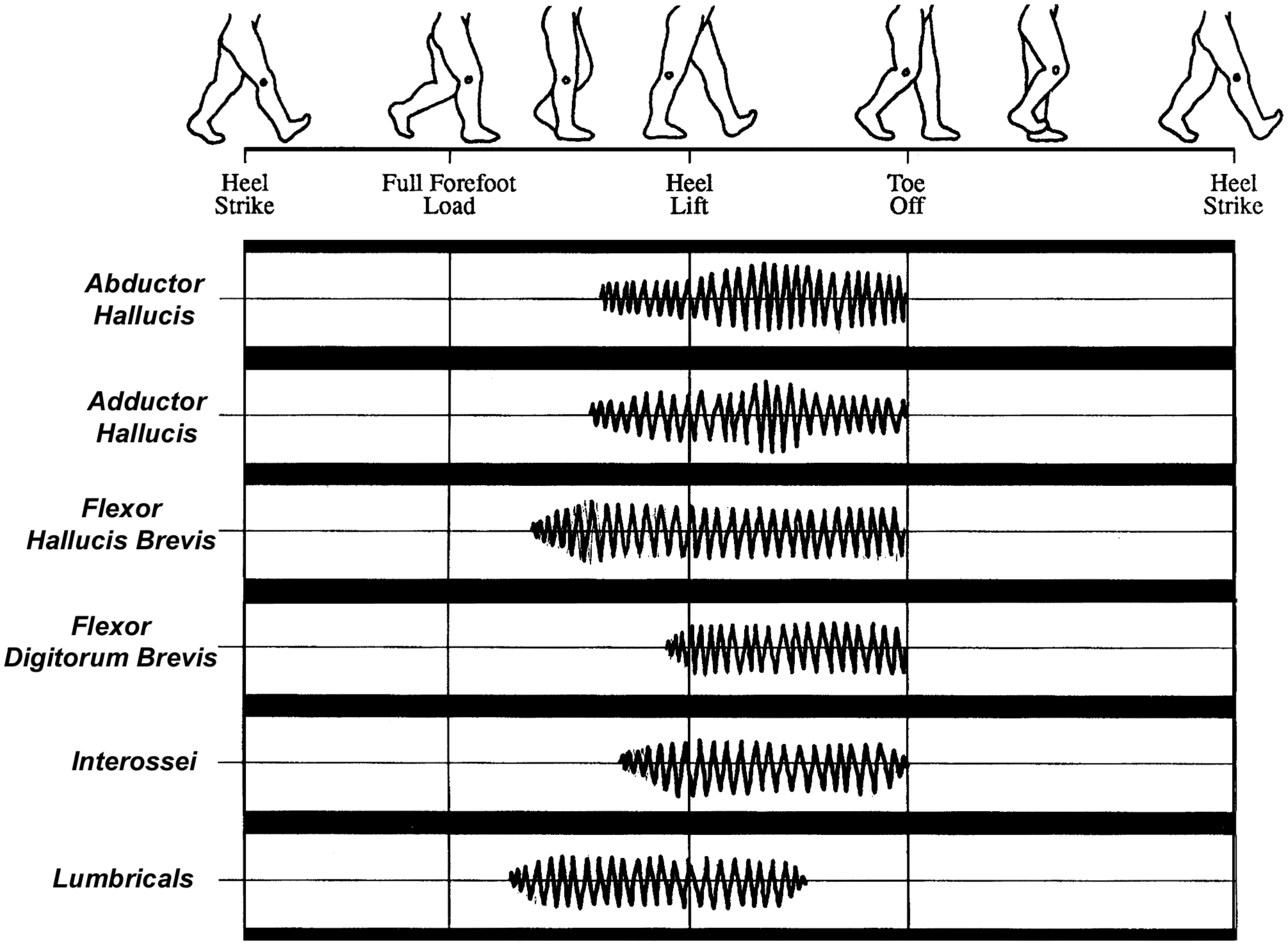


Figure 3.53. Muscle function, cont.

Summary of Biomechanical Factors Associated with Improved Running Economy:

In closing this chapter on ideal motions during the gait cycle, it seems fitting to discuss the various biomechanical factors responsible for maximizing speed and metabolic efficiency (which are often mutually exclusive since sprinters make terrible long distance runners, and long distance runners are often terrible sprinters). Even though natural selection has relentlessly modified each person's musculoskeletal system for over 7 million years, there is significant individual variation in running skill: some people are fast and tire easily while others are slow but can run extremely long distances without fatiguing. Because there are dozens of anthropomorphic and movement variables capable of affecting performance, the following section reviews kinetic/kinematic traits responsible for success in endurance running, followed by a list of factors associated with successful sprinting.

Endurance Running

1) According to Anderson (18), the best male long distance runners tend to be slightly shorter than average while females tend to be slightly taller than average. Females tend to be ectomorphic while males tend to be ectomesomorphic. Both males and females present with lower percentages of body fat. Sawyer et al. (110) note that sub-Saharan Africans (e.g., Kenyans and Ethiopians) possess increased limb lengths relative to torso volume, which markedly improves efficiency because a smaller torso is easier to move long distances. Although longer limbs relative to torso volume improve efficiency while running, the benefits associated with longer tibiae are less clear. Despite the fact that walking efficiency improves with longer legs (111), anthropomorphic evaluation of tibial lengths in runners provides conflicting results: a study of Olympic level male runners revealed that long distance runners were short-legged, middle distance runners were long-legged and sprinters were short-legged (112). In a detailed study comparing metabolic efficiency in runners of different abilities, Williams and Cavanagh (63) found no connection between leg length and efficiency when running.

2) The best long distance runners possess leg morphology that distributes mass closer to the hip joint. Runners possessing muscular hips with relatively thin lower legs are more efficient because accelerating and decelerating the distal segments contributes greatly to the metabolic cost of locomotion. Since the distal segments have long levers to the proximal muscles, even a slight increase in weight applied to the foot will greatly reduce efficiency. To prove this, Martin et al. (113) measured oxygen consumption before and after adding weights to either the foot or thigh of recreational runners. These authors determined that adding weight to the feet more than doubled the metabolic costs of locomotion. Additional studies have confirmed that increasing shoe weight by only 2 ounces increases the metabolic cost of running approximately 1% (114,115). These findings explain why endurance runners with small feet are more efficient than their large-footed rivals (63).

3) Running efficiency is associated with low vertical oscillation of the body's center of mass. In an interesting study of efficiency in middle and long distance runners competing in a 5 km race, Miayashita et al. (116) determined that the center of mass in the best runners moved with a vertical displacement of only 6 cm, while the less efficient runners averaged vertical displacements of 10 cm. The length of stride between fast and slow runners was also different in that the average stride length for a good runner was 1.77 m compared to 1.60 m for the less skilled runners. The authors determined that the good runners ran 5,000 meters in 2,825 steps while the poor runners required 3,125 steps. The added work associated with lifting the center of mass the additional 4 cm with each stride produced an increased workload roughly the equivalent to the cost of running up a 50-story building. While this seems impressive, the notion that increasing stride length will automatically improve efficiency may be flawed. Because the less skilled runners generated less force with their shorter strides, the metabolic expense associated with long versus short strides is difficult to compare. Remember that every runner selects a stride length that maximizes efficiency and any attempt to modify an individual's freely chosen stride length invariably increases the metabolic cost of locomotion (17).

4) Efficient runners plantarflex their ankles through a smaller range during propulsion (117) and this reduced movement occurs at a faster velocity (18). While studying kinematic differences during propulsion, Cavanagh et al. (117) determined that efficient runners plantarflex their ankles 10° less than inefficient runners. In a separate study, Williams and Cavanagh (63) evaluated 3 groups of runners based on economy and determined that the best runners again plantarflex their ankles through a smaller range of motion during propulsion. The decreased range of motion present in the ankle coupled with the increased angular excursion velocity noted by Anderson (18) may represent a kinematic marker associated with improved storage and return of energy, as isometric contractions produce smaller changes in movement with more rapid joint excursions.

5) Running efficiency is associated with reduced angular excursions of the arms and wrists. Williams and Cavanagh (63) correlated running efficiency with decreased wrist excursions while Anderson and Tseh (119) confirm that the most economical runners present with the smallest arm movements. Although arm motions lessen strain on the back musculature (60), exaggerated movements require muscular effort to initiate and dampen, and are therefore associated with reduced metabolic efficiency.

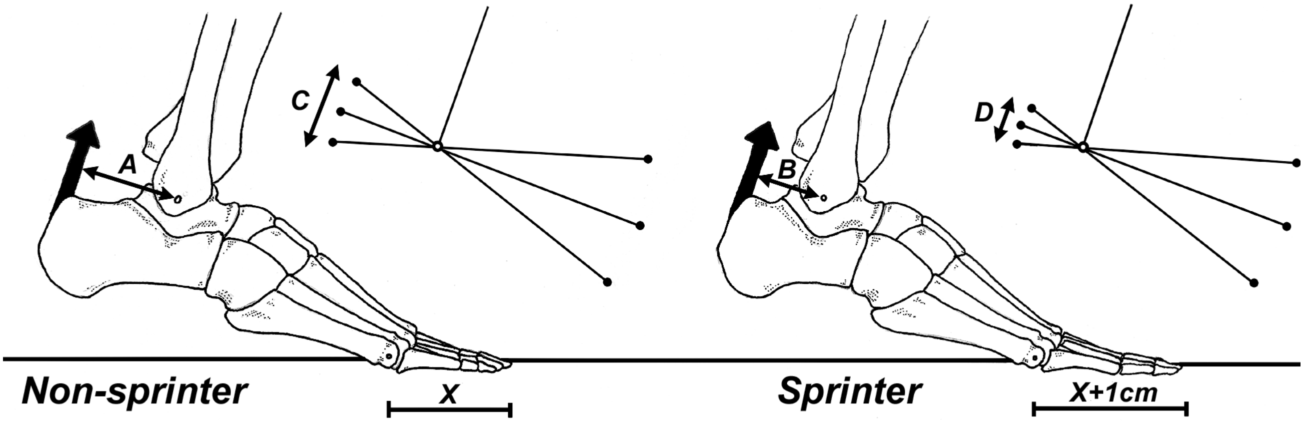
Sprinting

1) Several studies (120,121) reveal that sprinters have significantly longer fascicles in their gastrocnemius muscles compared with non-sprinters. The longer fibers allow the calf muscle to operate more efficiently through a larger a range of motion, improving the force-velocity ratio. Another possibility is that longer fascicles are more efficient at storing and returning energy in the actomyosin cross-bridges because they can stretch farther than shorter muscle fibers. The longer fascicles may be inherited but more likely result from training as muscles rapidly adapt to high intensity training by increasing fascicle length (122).

2) Although peroneus brevis is important with sprinting because it everts the rearfoot allowing for a high gear push-off, EMG analysis of a wide range of muscles utilized while running confirms that the majority of force associated with forward propulsion is produced by hip flexion and knee extension (123). This is consistent with research demonstrating the distal muscles act as springs to store and return energy while the proximal muscles act as force generators, muscularly accelerating and decelerating the lower extremity with each step (68).

3) In an interesting study of foot morphology in sprinters, Piazza (124) determined the distance from the posterior calcaneus to the center the ankle is 25% shorter in elite sprinters compared with the non-sprinter controls. Conversely, sprinters possess toes that are almost 1 cm longer than non-sprinter controls. While counterintuitive, the 25% shorter lever arm allows the Achilles to effectively plantarflex the ankle with little change in length occurring in the gastrocnemius and soleus (Fig. 3.54). The reduced lever arm may decrease mechanical efficiency of the Achilles tendon, but it allows the gastrocnemius and soleus to move the ankle with a nearly isometric contraction.

On the opposite side of the fulcrum, the longer toes allow for greater force production in the forefoot because the increased toe lengths provide the digital flexors with significantly longer lever arms that allow for a more powerful push-off. Even though the added metabolic cost of accelerating and decelerating the longer, heavier toes would lessen efficiency while walking and running long distances (which is why evolution has favored shorter toe lengths), the longer toes provide increased force production during propulsion, thereby allowing the elite sprinter to run at the fastest speed possible. The combination of a short Achilles lever arm coupled with long toes is also found in nature; e.g., cheetahs, which are capable of sprint speeds exceeding 70 mph, have shorter posterior calcanei and longer toes than lions. Although it takes millions of years, natural selection eventually matches form to function with the simplest possible design.



3.54. Because the distance from the Achilles tendon is 25% longer in non-sprinters (compare A and B), the gastrocnemius and soleus must move through larger ranges of motion to plantarflex the ankle (compare C and D). Notice the toes of sprinters are 1 cm longer than non-sprinters.

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