# Gracilization of the Modern Human Skeleton

## *The latent strength in our slender bones teaches lessons about human lives, current and past*

Christopher B. Ruff

People often think of the human skeleton as a symbol of death. In one sense this is true: Bone resists decomposition better than flesh, so it has a greater chance of being preserved after death. However, bone is also a living tissue. The skeleton is remarkably dynamic during life—even in adults—and it responds to metabolic needs and mechanical requirements. When muscles grow stronger, the underlying bone adapts by changing its physical shape to bear the increased stress. Likewise, atrophied muscles lead to weakened bones. In this way, our bones tell the story of our lives long after we're gone.

Because most of the archaeological and paleontological record consists of bones, skeletal remains form the basis for most of what we know about human ancestors and our evolution. My colleagues and I read the stories of these ancient peoples through the bones they've left behind. This work builds on a record of controlled laboratory experiments that help connect the specific geometry of a bone to a certain pattern of behavior (and vice versa).

One of the conclusions we've reached is that the skeletons of human beings have changed over the past 2 million years, becoming less robust, or more gracile. Our explanation for this phenomenon provides new insight into the modern problem of osteoporosis and confirms that our bones retain their ancient capacity to grow strong.

### Sticks and Stones and Sidewalks

Vertebrate skeletons must be both rigid and strong, but animals have to balance these needs against the cost of producing, maintaining and maneuvering a heavier skeleton. Consequently, skeletal size tends to match mechanical requirements closely. There are disadvantages to having grossly under- or overbuilt bones.

Engineers use a similar concept of building a structure to meet a specific need. This so-called *factor of safety* is the ratio of actual strength to required strength under maximum load. Biomechanical engineers such as R. McNeill Alexander at the University of Leeds estimate that factors of safety for vertebrate limb bones generally range from two to four. Indeed, limb-bone fractures are relatively rare. Scientists estimate that an individual bone has a one to three percent lifetime risk of fracture, based on data from a variety of species.

There is one condition, however, that leads to far higher rates of bone failure: osteoporosis, in which bone becomes more porous and brittle. This condition is particularly prevalent among older women. In the United States, the estimated lifetime risk of osteoporotic hip fracture is 17 percent among white women and 6 percent among white men. The great majority of these fractures occur in adults over 50 and result from minimal to moderate trauma—usually a fall from standing height or less. Broken vertebrae and wrists are also common in this age group.

The risk of fracture among the elderly isn't uniformly high in every population, however. Northern Europeans and people of European ancestry in other parts of the world (North America, Australia, New Zealand and South Africa) have higher rates than African, African-American and some Asian and Pacific groups. During the second half of the 20th century, the fracture rates among high-risk European populations grew even higher, but this increase was modest compared with the spike in fractures among residents of Hong Kong, Singapore and other rapidly urbanizing populations in Southeast Asia. In these areas, the low incidence of hip fracture in the 1960s quickly gave way to a rate similar to that of Europeans by the 1980s.

Older people suffer more broken bones because the mass and strength of bone decrease with age. There is no single reason why this occurs, or why some individuals and populations are more vulnerable than others. Like other complex traits, age-related changes in bone result from interactions between environmental and genetic factors. Scientists have linked changes in bone strength to variations in physical activity, the levels of dietary calcium and vitamin D, and alcohol and tobacco use. However, among these, physical activity is the variable most likely to account for the geographic heterogeneity in the incidence of

*Christopher B. Ruff is a professor and director of the Center for Functional Anatomy and Evolution at the Johns Hopkins University School of Medicine in Baltimore, Maryland. He received his Ph.D. in biological anthropology at the University of Pennsylvania in 1981 and carried out postdoctoral work in the Orthopaedic Biomechanics Laboratory at Beth Israel Hospital and Harvard Medical School. Ruff joined the faculty of Johns Hopkins in 1983. His major research interest is the relation between mechanical forces and bone structure in living and fossil animals. Most recently he has been studying the effects of changes in subsistence strategy on skeletal form in Holocene Europe and Western Asia. Address: Center for Functional Anatomy and Evolution, Johns Hopkins University School of Medicine, 1830 E. Monument Street, Baltimore, MD 21205. Internet: cbruff@jhmi.edu*

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**Figure 1. The bones of anatomically modern humans are, on average, more slender and less strong than those of our ancestors. Although this trend of gracilization has been progressing for more than a million years, the pace of skeletal weakening has accelerated over the past few millennia. However, individuals who perform rigorous exercise develop much more rigid bones, nearly equal in strength to the skeletons of our ancestors. This computer-generated artwork is based on individual x-ray images.**

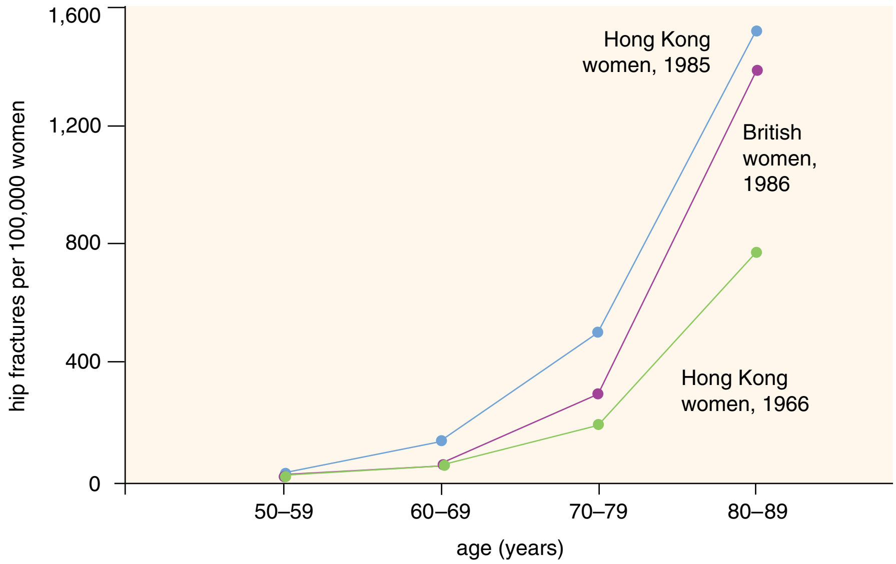

**Figure 2. The rate of hip fractures among Hong Kong women grew dramatically between 1966 and 1985, a period of increasing industrialization. The incidence now equals or exceeds the fracture rate found in some high-risk European populations. Bone fractures among Hong Kong men show a similar trend. A decrease in physical activity, coupled with traditionally low calcium intakes, probably explains the elevated risk. (Adapted from Lau *et al.* 1990.)**

fractures. In Hong Kong, for example, increasing urbanization and mechanization have led to a reduction in weight-bearing activities. Together with a low-calcium diet, this shift to a more sedentary lifestyle is the most likely explanation for the recent increase in fracture rates. John Chalmers and K. C. Ho at the Universities of Edinburgh and Hong Kong, who authored the 1970 paper on this subject, actually predicted this trend.

From an evolutionary perspective, the high incidence of broken bones late in life is a recent development for *Homo sapiens*. Elderly members of our ancestral populations had many fewer hip fractures than senior citizens do today, even after controlling for their shorter life spans. In fact, out of many thousands of excavated archaeological specimens, only a handful of hip fractures have ever been described. Yet the same specimens do show age-related loss of bone mass or density—and at a frequency and severity similar to modern levels. How can these seemingly contradictory observations be reconciled? The answer comes from basic principles of engineering.

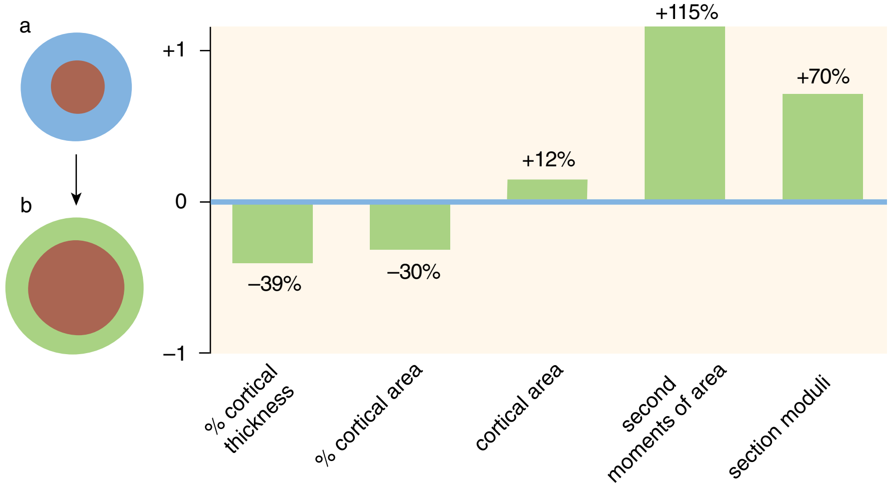

**Figure 3. The thickness of the dense outer cortex is not the best index of bone strength. Some physicians diagnose osteoporosis when the bone cortex gets thinner. This conclusion may not be correct if the bone's diameter increases, a change that can accompany aging. This cartoon compares two hypothetical cross sections of bone: baseline *(a)* and increased-diameter *(b)*. Compared with the blue cortex of *a*, the green cortex of *b* makes up a smaller fraction of its cross section (expressed as percent cortical thickness or percent cortical area). However, the bone with the expanded cross section *(b)* would be more rigid (second moments of area) and stronger (section moduli).**

### Predicting Bone Strength

When an engineer analyzes a structure to see how strong it is, he or she takes into account not only the design, but also the properties of the construction materials and the size of the structure. This analysis is a little simpler for bone biomechanics because the material properties of bone—at least the kind found in most parts of the skeleton—are fairly constant within and between species. On this basis it appears that bone tissue evolved only once. From giant whales to tiny shrews, the many skeletons that have existed during vertebrate history are largely made of the same substance. As a result, those of us who study old bones can compare samples that have been buried for millennia. The material properties of these bones may change with time, becoming friable or fossilized, but their size and shape are generally well preserved.

Because the bones themselves aren't suitable for testing, we use their dimensions in a computer simulation, or model, to predict their original strength. We can represent the long bones of the limbs fairly precisely using the same type of model that an engineer would use to judge the strength of a structural beam. The most important properties in this simulation are quantities that describe its cross-sectional size and shape. The *cross-sectional area* of bone determines its axial rigidity (in other words, how resistant the bone is to deformation under compression or tension). Other properties are called the *second moments of area* and *section moduli*, which measure the bone's resistance to bending in different planes as well as to torsion (twisting). These last two variables depend on the amount of material in the cross section, but they depend even more on how far from the center of the cross section that material is distributed. Section moduli vary as a product of the third power of the distance from the central axis, and second moments of area vary as a product of the fourth power.

The vast majority of bone-aging studies, including those of archaeological samples, have concentrated on the bone's mass, volume, density or a combination of these. However, these parameters yield an incomplete picture of skeletal biomechanics. Based on engineering principles, animal models and human observations, the architectural properties described above are probably more important in determining overall strength and the likelihood of fracture.

In fact, without an engineering perspective, some commonly evaluated measurements can easily be misinterpreted. For example, the cortex—the dense outer shell that makes up the shaft and ends of long bones—gets thinner with age in nearly everyone. This change is most often expressed as a decrease in percent cortical thickness, and most clinicians view it as a sign of increasing fragility. However, this interpretation is only valid if the outer diameter of the bone stays the same. If the bone itself gets wider with age—a documented phenomenon—then its strength and rigidity can increase even as the cortex gets to be a smaller percentage of the diameter. Some scientists hypothesize that the age-related widening of long bones compensates for the loss of overall bone mass, although the effect seems to vary between human populations. Anthropologists rarely consider this factor in their studies of human skeletal remains.

### More Brain, Less Brawn

Biomechanical analysis can tell us much about past human populations and skeletal changes over time. With my colleagues Erik Trinkaus at Washington University in St. Louis and Brigitte Holt at the University of Massachusetts, Amherst, I have investigated the changes in relative bone strength among modern humans and their ancestors from the past several million years. I refer to "relative" bone strength because we find that it is critical to control for variation in body size: Larger bodies have longer, stronger bones—a rule that is particularly true for weight-bearing bones. This relation applies to adults within and between hominid species, and also to individuals as they grow.

Although we can easily measure the length of an archaeological or fossil bone specimen, body mass is more difficult to calculate. Our methods for doing so are based on the size of the femoral head (the ball that fits into the hip socket), and estimates of the individual's original total body height and breadth (from long bone lengths and pelvic width, usually). We avoid the possibility of circular reasoning because the femoral head shows patterns of growth that are largely independent of the shaft, where biomechanical properties are measured.

In one set of experiments, we obtained optical cross sections from the long bones of more than 100 human specimens that were 5,000 to 1.9 million years old. All were members of the genus *Homo*, either direct ancestors or close relatives of modern humans. The remains came from all over Africa and Eurasia, although the earliest specimens (older than 600,000 years) were African, and most of the later ones were European. We took a few of the measurements from photographs of broken fossils, but most of the data came from x-ray scans combined with detailed molds of the originals. (Computed tomography would have been preferable, but this technology was unavailable at most of the museums that housed these remains.) Because of differences in the condition of the samples, the best data came from the *diaphysis*, or middle region of the femur (about mid-thigh). To control for differences in body size, we normalized the section modulus at this site by dividing by the product of estimated body mass and femoral length.

In a plot of these relative strengths versus sample age, the best fit is an exponential decrease, that is, a decline

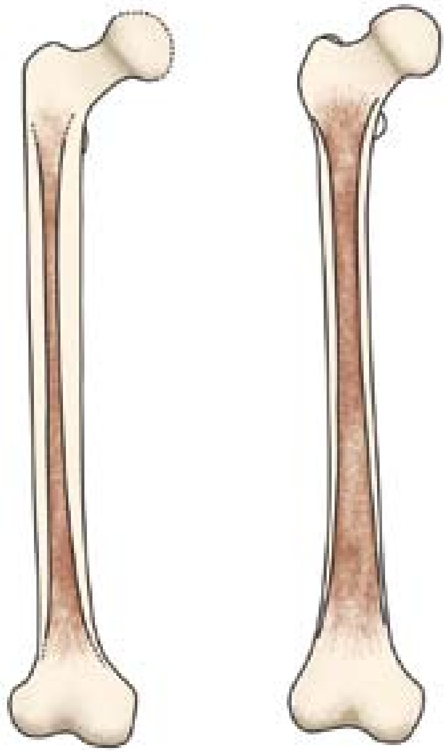

**Figure 4. Outwardly similar to its modern counterpart *(right)*, the femur of a 1.9-million-year-old *Homo* species *(left)* has a much thicker cortex. (Adapted from Ruff *et al.* 1993.)**

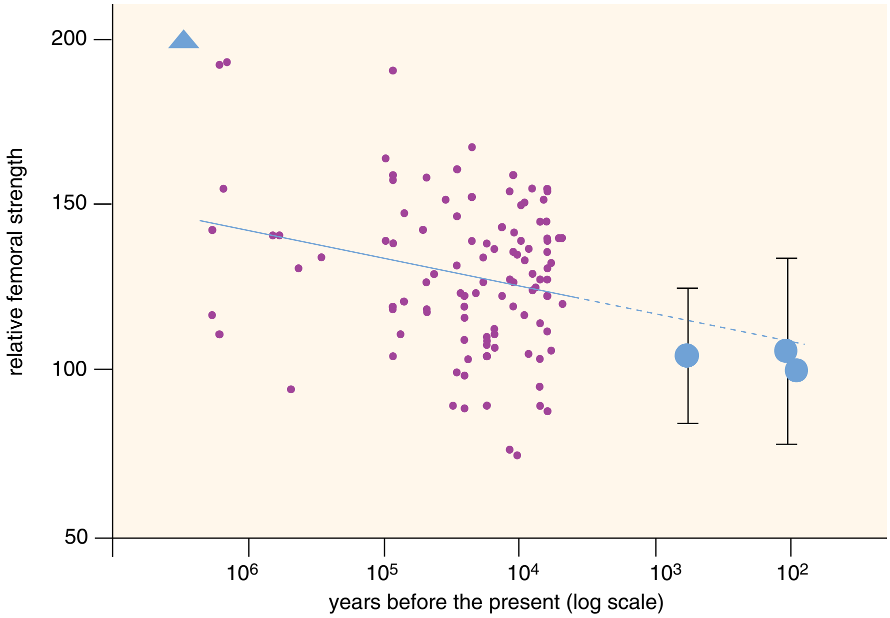

**Figure 5. The average bone strength of human beings and human ancestors has fallen during the past 2 million to 3 million years. This graph shows temporal changes in the strength (section moduli) of the femur relative to body size. Time is expressed in logarithmic units because the relation is exponential. The solid line shows a regression drawn through 104 individual fossils *(purple circles)* attributed to the genus *Homo*; the dotted line is the theoretical extension of this line to the near-present. The blue triangle is "Lucy," an earlier human relation (australopithecine) not included in the regression. The blue circles indicate mean values for three populations of anatomically modern humans: an archaeological sample of Native Americans from the American Southwest who lived about 900 years ago, and East Africans and U.S. whites from the early to mid-20th century. The error bars indicate plus or minus two standard deviations for the Native Americans and East Africans; individual body-size data were unavailable for U.S. whites. (Adapted from Ruff 2005.)**

that gets progressively steeper. There is a lot of scatter in the data, but the trend is statistically significant. From roughly 2 million years ago to about 5,000 years ago, human bones became almost 15 percent weaker.

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**Figure 6.** ***Australopithecus afarensis*** **was one of the earliest bipedal hominids and probably an ancestor of the genus *Homo*. This specimen, "Lucy," is unusually complete for a 3.1 million-year-old skeleton, which enables an accurate estimate of overall body size (she stood about 1.1 meter or 3 feet, 8 inches tall). Taking body size into account, Lucy's femur is considerably stronger than those of more recent human ancestors, despite the fact that her species spent less time walking than did their descendants.**

We also compared these values to more recent human remains from less than 1,000 years ago, using three diverse populations from North America and East Africa. The bones from all of these specimens were, on average, 15 percent weaker than those from 5,000 years ago—in fact, they lay below the extended regression line from the main data set. Thus, relative bone strength decreased even faster during the past 5,000 years than it did over the previous 2 million years.

## The Penalty for Tool Use

Because the remains are seldom complete, it becomes more difficult to reconstruct body size for fossils of human ancestors older than 2 million years. The exception is "Lucy," the famous 3.1 million-year-old skeleton from Ethiopia, which is complete enough that we can estimate her original body size with a fair degree of confidence. Judging by our calculation of Lucy's relative femoral strength, her bones were even stronger than those of the early *Homo* specimens and almost twice as strong as an average human from several hundred years ago.

Lucy was an australopithecine—a member of a very early group on or near the lineage leading to modern humans. Although Lucy and her relatives walked bipedally, they most likely kept to the trees more than later *Homo* and probably weren't long-distance travelers. The arm bones from other members of this group appear to be very strong, which may reflect this behavior. (Cross sections from Lucy's arm bones were unfortunately not available for study.) If true, this hypothesis makes Lucy's relative femoral strength even more remarkable, since she probably walked less than do many modern humans.

We see similar results among modern nonhuman primates, such as chimpanzees, gorillas and baboons. Relative to body size, their arm and leg bones are much stronger than those of humans. (The difference is greater for the arm than the leg, of course, since these species locomote using both sets of limbs.) Not surprisingly, nonhuman primates also appear to have much stronger muscles than humans relative to their size. Thus, the bone strength results make sense: Stronger muscles generate greater force, greater force increases the mechanical stress on the bones, and this stress induces the bone to adapt over time by becoming more rigid.

**Figure 7. Adult chimpanzees in the wild weigh between 30 and 60 kilograms (between 66 and 132 pounds), yet primatologists estimate that chimps are more than twice as strong as human beings, on average. The musculature that generates such force is especially visible on Cinder, a female chimpanzee at the Saint Louis Zoo who lacks body hair as a result of the disease *alopecia areata*. Remarkably, Cinder is somewhat small compared with other members of her species. The bones of chimpanzees, like their muscles, are much stronger than those of modern humans. (Photograph courtesy of Carol Weerts, Saint Louis Zoo.)**

The bone-strength results also imply that earlier human ancestors had stronger muscles, a hypothesis consistent with the large muscle-insertion scars that anthropologists see on many of the specimens. (The scar observations, however, are far from definitive, as the bones of some modern nonhuman primates don't carry such marks.) If early humans were indeed more muscular than you or I, they probably got that way (at least in part) because they were more active and vigorous. This, in turn, is probably related to tool use: The rise of technology that has accompanied human evolution has, in effect, progressively shielded the human body from its environment.

Scientists have never found tools from Lucy's time period, and in terms of technology, her kin probably interacted with the natural world much as modern chimpanzees and gorillas do. This absence of technology predicts a very high relative bone strength. Early *Homo* had simple stone tools, and their bones were not quite as strong as Lucy's, but still much more rigid than the average modern human's. The comparatively weak bones of recent humans are an inevitable consequence of a sedentary lifestyle and ubiquitous, sophisticated tools that make physical strength much less relevant to survival. For perhaps the same reason, human bodies as a whole have gotten smaller on average during the past 50,000 years, despite very recent increases that are probably tied to better nutrition and health care.

**Tennis, Anyone?**

Many animal studies have demonstrated that bones become stronger with exercise. For example, the femurs of young pigs that ran an hour every day for a year were 24 percent stronger than those of sedentary controls. The increase was purely a product of geometric changes—primarily a thickening of the bone cortex—with no effect on bone material properties. Other studies have noted similar findings, further supporting the practice of using a bone's geometry to estimate past mechanical loadings.

The human upper limb presents a "natural experiment" of this sort because almost everyone favors one hand or the other for most tasks. Thus, scientists can compare bone adaptations in dominant and nondominant arms of people with differing activity levels. Unlike most animals, human beings don't use their arms for locomotion, leaving them freer to reflect asymmetrical usage and structure. In fact, human forelimbs show more left-right asymmetry than those of any other mammal. In the normal population, right-handers and left-handers have similar magnitudes—but opposite directions—of bilateral asymmetry in the strength of the second metacarpal (a hand bone). Righties are stronger on the right, lefties on the left. One of the advantages of this comparison is that it inherently controls for nonbehavioral factors such as overall body size, nutrition and hormonal influences, which affect both sides equally.

In the 1970s, Henry H. Jones (who was one of my undergraduate advisors), James D. Priest and their coworkers at Stanford University x rayed the arms of professional tennis players. They focused on the bone in the upper arm called the humerus and compared the dimensions of the bone cortex in the playing and nonplaying arms. In the dominant arm, the outer surface of the cortex had gotten bigger and the inner surface had gotten smaller.

Almost 20 years later, we were able to get Jones's original measurements and calculate geometric section properties. By our calculations, playing-side humeri were more than 40 percent stronger on average than non-playing-side humeri. By contrast, in nonprofessional athletes the average left-right asymmetry in bone strength is about 5 to 10 percent. The tennis players in the study were between 14 and 39 years old and had played for at least 5 years. All started playing between ages 5 and 19. Interestingly, these changes were more pronounced among subjects who began playing earlier in life. Since we published our data, other studies have also noted that bone adaptation is partly age-dependent. Adult skeletons remain responsive to increased exercise, but they respond more slowly and less completely than those of children.

Unlike the cross sections from the humeral shaft, the sizes of the right and left elbow joints were more similar in the tennis players. In animal studies, too, the size of the articular surface and the length of the bone (which depends on articular growth) are less affected by mechanical loadings than are diaphyseal cross sections. The cortex of the shaft of long bones appears to be particularly "plastic," or responsive to changes in mechanical loadings during life, so it's helpful for reconstructing the behaviors of past populations. The restrained growth and remodeling of the ends of the bones may help to avoid incongruity at the joint surface that predisposes it to problems such as arthritis.

We also examined the humeri of Neandertals (50,000 to 100,000 years old) and anatomically modern humans (10,000 to 30,000 years old) for which

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**Figure 8. Vigorous exercise can lead to large increases in bone strength. This diagram shows the average difference in cross-sectional dimensions of the humerus between nonplaying *(blue)* and playing *(blue plus green)* arms of professional tennis players measured by Henry Jones and coworkers at Stanford University. The author and his colleagues re-analyzed the data and calculated average increases in bone rigidity and strength of 62 percent and 45 percent, respectively, in the playing arms. The changes were most pronounced in players who began training at an early age, such as Amelie Mauresmo, currently ranked among the top female professionals in the world. Based on data from Ruff *et al.*, 1994.**

both arms had been preserved. (Such fossils are somewhat rare.) Our ancestors showed bilateral asymmetry in shaft strength almost as great as that of the modern professional tennis players. Based on experimental studies using human volunteers, Daniel Schmitt and Steven E. Churchill at Duke University have suggested that this asymmetry reflects the use of weapons or tools that loaded one arm more than the other. Interestingly, all five Neandertals and 19 of the 24 early modern humans have stronger right humeri, indicating right-handedness. In the larger group of early modern humans, the frequency at which we found stronger arm bones on the right side—about 80 percent—is similar to the rate of right-arm-bone asymmetry in a wide range of recent human populations. Not surprisingly, it's also similar to the frequency at which people favor their right hand. (Many sources state that 90 percent of the population is right-handed, but they're usually referring to writing preference, which can be biased by various cultural factors. In cross-cultural studies, the frequency of right-arm preference is a little lower for activities such as throwing and hammering.)

### The Leg Bone Connected to the …

It is clear that limb bones, at least, respond to increased mechanical force by changing their geometry, adding bone material to strengthen the outer cortex. The bilateral asymmetry found in pro tennis players and pre-agrarian humans suggests that bone strength can increase by 40 percent or more under the proper conditions. Conversely, reduced mechanical loads lead to the loss of bone. For example, after six months in space under zero-gravity conditions, the leg bones of astronauts aboard the International Space Station were 20 percent weaker on average than before, based on section moduli derived from bone mineral scans of the femoral neck. Paralyzed patients experience even greater losses over longer time periods.

These examples may represent extremes, but they demonstrate the potential for bone to adapt when circumstances change. In a few years, the strength of a person's bone structure can change as much as the total average change over the past 2 million years of human evolution. Although some of this evolutionary change may reflect nonmechanical factors, including genetic changes, the most parsimonious explanation is that the human skeleton has simply adapted to a lesser workload. The gracilization of the modern human skeleton is probably a direct result of our consistently advancing technology.

This conclusion has implications for understanding the etiology of osteoporotic fractures. As noted above, broken hips are more common in urbanized, less physically active populations. The significant increase in skeletal strength that is gained through physical exercise, if maintained throughout a person's lifespan, may help to prevent such fractures.

The bones of our ancestors show that the human skeleton was once stronger than it is today. Studies of modern athletes, however, demonstrate that we are still able to achieve such strength. The skeletons in our evolutionary closet can teach us some valuable lessons about modern lifestyles and their consequences.

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