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Evolutionary Aspects of Exercise

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As a species, human work (exercise) capacities and limitations are a result of our species-specific anatomical and physiological characteristics, which in turn are defined by our genetic constitution. Similar to all other organisms, the human genome was shaped by environmental selective pressures over eons of evolutionary experience. As hominids evolved and became separate from pongids between 6.3 and 7.7 million years ago (MYA), in response to selective pressures, they developed specific structural and functional characteristics which allowed them to exploit environmental niches which were previously unavailable to their pongid ancestors. Consequently, the selective pressures of the ecological niche which hominids occupied were responsible for shaping those genetic characteristics which are unique to our species (including anatomical and physiological parameters influencing our exercise capacities, limitations and requirements). Examination of both the hominid fossil record and structural and functional differences between modern humans and primates provides insight into the evolutionary changes which occurred in human anatomy and physiology which directly influenced the exercise capacities of contemporary men and women. Further, by studying modern-day hunter-gatherer societies, it is possible to not only develop models of optimal exercise patterns for fitness, but to evaluate how the discordance between the activity patterns of modern sedentary societies and hunter-gatherer societies is implicated in a wide variety of chronic degenerative diseases which plague contemporary man.

Table 1. The main events of human evolution [adapted from ref. 1]

Years ago	Epoch	Development
7,500.000		hominid-pongid divergence
	late Miocene	
4,200.000	Pliocene	bipedal *Australopithecus anamensis* present
3,900.000		*Australopithecus afarensis* present
		Australopithecine divergence
2,000.000		*Homo habilis* present
1,700.000	early Pleistocene	*Homo erectus* present
400.000		archaic *Homo sapiens* appears
230.000		*Homo sapiens neanderthalensis* appears
	late Pleistocene	
45.000		*Homo sapiens sapiens* (anatomically modern) appears
	latest Pleistocene	
10.000		agricultural revolution
	Holocene	
200		industrial revolution

Changes in Hominid Anatomy/Physiology Impacting Exercise Capacities

The evolution of the human species can ultimately be traced to the origin of life itself. However, the distinctive structural and functional features which characterize our species have occurred following the evolutionary split between pongids (apes) and hominids (upright, bipedal primates) 6.3–7.7 MYA (table 1) [1]. Evolutionary changes in hominid anatomy/physiology which have had the greatest impact upon our present day exercise capacities include the development of an upright bipedal gait; increases in cranial capacity and body size associated with changes in dietary quality; the attenuation of body hair and the subsequent development of a highly efficient sweat gland system. In conjunction with these basic anatomical and functional alterations were changes in behavioral complexity which led to increased tool use which in turn is associated with a decreased upper and lower limb robustness [2] (fig. 1).

Bipedalism

The first hominids to walk fully upright (*Australopithecus anamensis*) appear in the fossil record between 3.9 and 4.2 MYA [3] in East Africa coincident with climatic changes in which large areas of the tropical rain forest

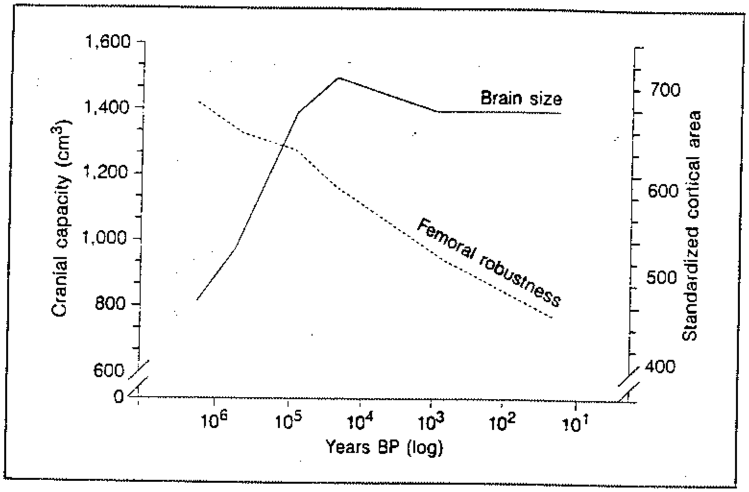

Fig. 1. Changes in percent femoral cortical area [(cortical area/periosteal area) × 100] relative to changes in cranial volume over the course of the evolution of the genus Homo. Adapted from Ruff et al. [2].

were replaced by a more open woodland [4]. *A. anamenis* perhaps represents the ancestral species of the better known Australopithecine, *Australopithecus afarensis* (table 1). *A. afarensis* exhibited sexual dimorphism (weight: 30–70 kg, height 1–1.5 m) and had a cranial capacity of 400–500 ml [5]. *A. afarensis* did not make stone tools and because they maintained a more ape-like body with relatively longer arms and shorter legs than contemporary men, these hominids may have been well adapted to both arboreal and terrestrial environments [6]. Analysis of both fossil footprints and pelvic/leg bone structure indicate that *A. afarensis* walked/ran with a mechanical efficiency similar or superior to modern humans [7].

Although it is not entirely clear which specific environmental pressures were ultimately responsible for the evolution of bipedal locomotion, a number of potential advantages have been identified. An upright, bipedal gait raises the level of the head and provides for a greater visual field for location of food, water and predators in a more open woodland environment [8]. Additionally, bipedalism frees the hands to carry food and other objects during locomotion [7].

More importantly, from an exercise standpoint, bipedalism may be more energy efficient than a comparable quadrupedal posture for standing/walking but not for running. Whereas the oxygen cost of running in man (0.212 ml/g/km) is approximately twice that of other mammals [9], the oxygen cost of human walking is at least as economical as the walking of typical mammalian quadrupeds [10, 11]. Moreover, the difference in energy expenditure for adult humans between their erect and resting (supine) postures is less than that for a quadrupedal animal [12]. Collectively, these data suggest that bipedalism for the most frequent hominid posture (standing/walking) resulted in an energy savings which may have produced a slight but meaningful selective advantage.

Thermoregulation

An upright posture would have had selective advantage for an exercising, diurnal hominid in a hot, sunny woodland or savanna environment because it would reduce the surface area of the body exposed to the sun and thereby reduce the thermal load [13]. Because *A. afarensis* was a biomechanically efficient walker and runner [7] and because their daily range increased substantially with the evolution of bipedalism [14], it has been argued that they may have begun to evolve a more complex eccrine sweat gland system which would have allowed them to run considerable distances under a hot tropical sun without overheating [15]. Further, the evolution of a 'naked' skin (attenuation of body hair size) would have increased the rate at which sweat could be evaporated from the surface of the skin and therefore would have increased the evaporative cooling efficiency of the cutaneous sweat glands [15].

The adaptive value of man's elaborate eccrine system has been largely attributed to its facilitation of heat dissipation during running [16]. The ability to rapidly run considerable distances without overheating would have had obvious survival advantages for bipedal hominids during locomotion in more open woodland and savanna environments. Escape from predators and location and transport of food, infants and other objects would have been facilitated by an efficient evaporative cooling system.

Cranial Capacity and Body Enlargement

The first hominids likely to have made stone tools, *Homo habilis*, had body dimensions similar to *A. afarensis*, but a slightly larger cranial capacity (~750 ml). Increasingly, it has been recognized that in order for a larger, more metabolically active brain to have evolved, an increase in dietary quality (caloric density) had to occur [17–19].

Throughout evolutionary history, carnivorous mammals have always maintained a proportionately larger brain size relative to body size when compared to their herbivorous prey [20]. Because proportionately larger brains are more metabolically active, in order to fuel their increased energetic demands they either require an increase in dietary quality, a reduction in the size and metabolic rate of another tissue, or both [17]. Carnivores have evolved their

Table 2. Metabolic parameters in primates [adapted from ref. 21]

Species	Sex	Weight kg	RMR kcal	TEE kcal	Ratio (TEE/RMR)	PA-EE kcal	Day range km
Nonhuman primate							
Pan troglodytes	M	39.5	1,036	1,510	1.46	474	4.8
	F	29.8	839	1,144	1.36	305	3.0
Fossil hominids							
Australopithecus afarensis		37.1	1,149	1,824	1.59	675	
Homo habilis		48.0	1,404	2,387	1.70	983	
Homo erectus		53.0	1,517	2,731	1.80	1,214	
Homo sapiens (early)		57.0	1,605	2,889	1.80	1,284	
Modern hunters-gatherers							
Kung	M	46.0	1,275	2,178	1.71	903	14.9
	F	41.0	1,170	1,770	1.51	600	9.1
Ache	M	59.6	1,549	3,327	2.15	1,778	19.2
Acculturated modern humans							
Homo sapiens (office worker)[1]	M	70.0	1,694	2,000	1.18	306	0
	F	55.0	1,448	1,679	1.16	231	0
Homo sapiens (runner)[2]	M	70.0	1,694	2,888	1.70	1,194	12.1

RMR = Resting metabolic rate; TEE = total energy expenditure; PA-EE = energy expenditure attributed to physical activity.
[1] Sedentary office worker [22].
[2] Runner running 12.1 km/h [22].

larger, more metabolically active brains at the expense of a smaller gut. This adaptation can occur because less digestive energy is required to extract food energy from the nutrient dense lipids and proteins in animal foods than from plant foods of low digestibility.

As hominids increasingly included animal foods in their diet, there was a relative increase in brain size and a reduction in their gut size [17] similar to carnivores. These changes were associated with increased behavioral complexity which in turn led to an increased daily range and an increased total energy expenditure (TEE) (table 2). By 1.7 MYA, *H. habilis* was succeeded by *Homo erectus* who stood as tall as contemporary humans [23, 24] and based upon cortical bone thicknesses and diameters [2] was quite heavily muscled and therefore was likely stronger than most modern humans.

Besides being powerfully muscled, *H. erectus* likely had aerobic capacities similar to modern men. Pongids and Australopithecines have rib cages which narrow as they move upward in order to accommodate the extremely powerful muscle groups of the pectoral girdle which are used during arboreal locomotion [17]. Therefore, ventilation of the lungs was probably mainly dependent upon the movements of the diaphragm and would have been less effective than in *H. erectus*, in which the upper part of the rib could have been raised to enlarge the thorax during inspiration [17].

With the appearance of *H. erectus*, hominids not only became taller, but there was a relative decrease in maximal pelvic breadth relative to stature [24]. This relative increase in body linearity would have allowed the (surface area/body mass) ratio to remain favorable for heat dissipation during aerobic activities such as running even though absolute body size had increased from earlier hominids. A relative increase in body linearity may have also facilitated a greater stride length [16] for greater efficiency during running. Regardless of the mechanisms involved, it is clear that the wider rib cages of *H. erectus* and their tall slender physiques facilitated high level aerobic activities in hot climates.

H. erectus (the Kenyan version is sometimes referred to as *H. ergaster*) walked out of Africa by at least 1 MYA or perhaps earlier and colonized eastern Asia but not Europe. Archaic *Homo sapiens (Homo heidelbergensis)* inhabited Europe by 400,000–500,000 thousand years ago or perhaps even much earlier [25] and probably represents ancestors of the well-known Neanderthals (*Homo sapiens neanderthalensis*) [26]. Anatomically, modern human beings first appear in the fossil record 90,000–100,000 years ago in the Near East and Africa, and the first truly modern humans, complete with art, culture and sophisticated tools are recognizable 40,000 years ago. Until the agricultural revolution 10,000 years ago, all hominids occupied the hunter-gatherer niche, and regular daily activity utilizing both endurance and strength pathways was essential for all but the most infirm individuals. Consequently, by studying living groups of hunters-gatherers, it is possible to examine the physical activity patterns to which we are genetically adapted so that insight can be gained in determining optimal exercise levels for modern, sedentary societies.

Metabolic Considerations in Primates, Hunters-Gatherers and Contemporary Humans

Activity Patterns in Primates, Hominids and Modern Hunters-Gatherers

Table 2 contrasts the metabolic rates and activity patterns of primates, fossil hominids, modern hunters-gatherers, sedentary office workers and a modern runner. It can be seen that as body weight increases, resting metabolic rate (RMR) increases proportionately. This relationship is well established across mammalian species such that RMR scales to the 3/4th power of body weight [27]. As hominids evolved, they became larger; consequently RMR increased [21]. Additionally, as the tropical forest gave way to more open woodland and savanna environments, caused by prolonged drying periods [4, 28], food resources became less abundant and more dispersed [29]. Therefore, it is probable that early members of the genus *Homo* would have had to increase their daily range [14] and thereby increase the physical activity component (PA-EE) of their total daily energy expenditure (TEE). Since human body size has remained essentially constant since the first appearance of *H. erectus* [24], then the ratio of TEE/RMR in table 2 reflects (ignoring the small thermic effect of food ~5–10% TEE) changes in activity levels which have occurred during the evolution of hominids. The mean estimated (TEE/RMR) ratio (1.87) for hominids since the appearance of full-sized humans *(H. erectus)* represents the activity level for which our species is genetically adapted. The TEE/RMR ratio of sedentary office workers (1.18) denotes activity levels which have previously not been encountered in our species and which are clearly discordant with our genetic requirements.

From table 2, it can be seen that hunter-gatherer males typically spend between 19.6–24.7 kcal/kg/day in physical activity whereas the sedentary office worker would expend only 4.4 kcal/kg/day. Even if a 3.0-mile walk (minimal health benefits suggested by the American College of Sports Medicine [30]) were added to the office workers activities, the resulting value of 8.7 kcal/kg/day would be significantly lower than that which would be normal for our pre-agricultural ancestors. Only when higher level activities are engaged in (say running 12.1 km/h for 60 min) do modern sedentary workers simulate the energy expenditures of our stone age ancestors.

'Primitive' Physical Fitness and Acculturation

Previous studies of modern hunters-gatherers have been compiled by Eaton et al. [31], and mean estimates of maximal oxygen consumption (VO_{2max}) in young men (52 ml/kg/min) would place them in either the excellent to superior fitness classifications as established by Cooper [32] for modern industrialized populations, whereas comparably aged modern men would only have 'fair' fitness levels ($Vo_{2\,max}$=40.8 ml/kg/min) [31]. Clearly, the normal day-to-day activities of hunters-gatherers, even without the benefit of specific exercises designed to improve cardiorespiratory fitness, produce high levels of endurance.

Rode and Shepherd [33] recently completed a 20-year study (1970–1990) of an Inuit community and were able to document the changes in fitness levels as these hunters-gatherers adopted a more modern, sedentary existence. Not only did activity levels decrease substantially with the adoption of mechanized tools and equipment, but the native diet changed so that it approximated the typical diet of industrialized populations [34]. Associated with these lifestyle changes were increases in body fat, a loss of muscular strength and a decrease in aerobic fitness levels. This native Inuit community is now threatened with 'diseases of civilization' (such as hypertension, cardiovascular disease, and diabetes mellitus) which have been rare until recently [33].

Evolutionary Insights into Exercise, Health and Disease

With the exception of *H. sapiens*, mammals have to work in order to eat: food procurement depends directly upon energy expenditure. Because technological achievement and social organization have disrupted this basic relationship for contemporary humans, low levels of physical exertion have become unprecedentedly common in western, industrialized societies. This departure from exercise patterns which prevailed throughout our evolutionary history has been implicated in the etiology of many chronic degenerative diseases which plague modern-man including diseases of insulin resistance (obesity, non-insulin-dependent diabetes mellitus (NIDDM), hypertension and coronary artery disease) and bone demineralization and fractures.

Diseases of Insulin Resistance

Increasingly it is being recognized that insulin resistance/hyperinsulinemia may be a primary factor in the development of three major diseases (hypertension, NIDDM, coronary artery disease – collectively referred to as 'syndrome X') as well as obesity [35, 36]. These diseases are so epidemic in modern, industrialized societies as to be designated 'diseases of civilizations', since they are rare to nonexistent in less-acculturated societies [31]. The extent to which environmental and genetic factors play in disposing people to these diseases is not clear, however both dietary [37] and exercise [38] patterns seem to play an essential role in the development of syndrome X via their long-term influence upon insulin metabolism.

Acute exercise bouts, either aerobic [39] or strength [40] enhance glucose uptake by skeletal muscle, whereas chronic training is associated with increased skeletal muscle insulin sensitivity and reduced plasma insulin levels [39]. The net effect of an increased insulin sensitivity in conjunction with the increased metabolism of exercise serves to beneficially influence body composition (loss of fat), blood pressure and glucose (lower BP, glucose) and lipid metabolism thereby reducing many of the risk factors for syndrome X.

Relative to activity levels and body composition, trained individuals are similar to our hunter-gatherer ancestors. In response to a glucose load, they secrete less insulin and have lower peak plasma glucose levels than do nonathletes [41]. Twentieth century hunters-gatherers (African San and Efe) and isolated horticulturists (Venezuelan Yanomamo) have insulin sensitivity which is exceptional when compared to that which is considered 'normal' for westernized, affluent individuals [42–44]. When a group of urbanized Australian Aborigines temporarily reverted to a foraging lifestyle, their serum insulin and glucose levels were markedly reduced [45]. For Paleolithic humans, obesity was rare and physical exertion the norm [31]. Accordingly, syndrome X and diseases of hyperinsulinemia would have also been rare.

Bone Demineralization and Fractures

Osteoporosis, a major orthopedic disease (primarily in postmenopausal women), is marked by a decalcification of bone which results in a loss of bone tensile strength that can ultimately lead to fractures. Even though many factors (diet, smoking, genetic and metabolic diseases) including physical activity levels have been suggested as causes of osteoporosis [46], it is likely that the etiology of the disease is multifaceted and no single factor is entirely responsible for its onset [47].

Although there are numerous cross-sectional studies showing that active men and women have a higher bone mineral density (BMD) than those who are sedentary, prospective studies have generally indicated that exercise has a minimal influence upon the postmenopausal decline in BMD [47]. Additionally, studies of BMD using dual-energy X-ray absorptiometers in archaeological skeletons from the Bronze Age [48] and Medieval times [49], during which there was less mechanization and humans presumably were more active, have shown the range of BMD to be similar to modern populations.

Although the most commonly recognized index of bone integrity is BMD, bone structural geometry may be equally, if not more important, in determining a bone's intrinsic strength and ability to resist mechanical stresses [2]. Since BMD is a function of both cortical mass and volume, it is possible to have bones of identical densities but with considerably differing volumes. The greater long bone robustness exhibited by all pre-industrialized humans appears to

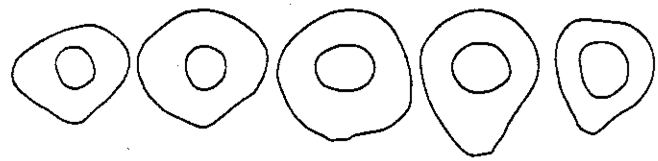

Fig. 2. Reduction in femoral mid-shaft cross-sectional cortical area from early to recent members of the genus Homo. % CA = [(cortical area/periosteal area) × 100]. Adapted from Ruff et al. [2].

have occurred from relative increases in cortical volume (fig. 2) elicited by greater activity levels [2]. Consequently, the regular loading of skeletal tissue experienced by our pre-industrialized ancestors produced robust, fracture-resistant bones via changes in structural geometry which may have counterbalanced deficiencies in bone mineral content.

Conclusions

Because of the sedentary nature of industrialized societies, exercise is usually viewed as an activity (jogging, walking, swimming, bicycle riding, aerobics, weight lifting, etc.) separate from daily activities, done during leisure time to improve fitness or strength. In contrast, in living hunters-gatherers, exercise results from the daily muscular activity needed to adequately function within the hunter-gatherer niche. Food and water procurement, social interaction, escape from predators, and homeostatic maintenance evoke obligatory movements, and these movements needed to carry out life's functions represent the genetically established exercise patterns of man prior to the agricultural revolution of 10,000 years ago. Although human lifestyles have changed almost inconceivably since the advent of the agricultural revolution and the more recent industrial revolution, our exercise capacities, limitations and requirements remain the same as those selected by natural selection for our stone age ancestors. Deviation from these intrinsic exercise patterns established long ago inevitably results in dysfunction and disease.

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