Is Exercise Really Medicine? An Evolutionary Perspective

Daniel E. Lieberman, PhD

Abstract

An evolutionary perspective helps evaluate the extent to which exercise is medicine and to explain the exercise paradox: why people tend to avoid exercise despite its benefits. Many lines of evidence indicate that humans evolved to be adapted for regular, moderate amounts of endurance physical activity into late age. However, because energy from food was limited, humans also were selected to avoid unnecessary exertion, and most anatomical and physiological systems evolved to require stimuli from physical activity to adjust capacity to demand. Consequently, selection never operated to cope with the long-term effects of chronic inactivity. However, because all adaptations involve trade-offs, there is no evolutionary-determined dose or type of physical activity that will optimize health. Furthermore, because humans evolved to be active for play or necessity, efforts to promote exercise will require altering environments in ways that nudge or even compel people to be active and to make exercise fun.

Introduction

If you are reading this article, you almost certainly know the compelling evidence that physical activity is a vital means of preventing morbidity and mortality. You also are well aware of the scale of the obesity and physical inactivity epidemics in developed nations such as the United States and their rapid increase through much of the developing world. Also, you know that decades of efforts to encourage the public to undertake the modicum of physical activity prescribed as a minimum by the American College of Sports Medicine and the Surgeon General — just 150 min·wk⁻¹ have had only modest effects (29). Too many people indulge their instincts to take it easy whenever possible and to eat a surfeit of highly processed, obesogenic foods. These tendencies, in conjunction with recent technologies that make it possible for billions of people to actually eat and act as they wish, have led to a worldwide rise in avoidable, chronic

Department of Human Evolutionary Biology, Harvard University, Cambridge, MA

Address for correspondence: Daniel E. Lieberman, PhD, Department of Human Evolutionary Biology, Harvard University, 11 Divinity Avenue, Cambridge, MA 02138; E-mail: danlieb@fas.harvard.edu.

1537-890X/1404/313–319

Current Sports Medicine Reports

Copyright © 2015 by the American College of Sports Medicine

noninfectious diseases that have become the dominant causes of morbidity and mortality in the developed world (30).

But why? Why do so many people fail to act in their own best self-interest, at least in terms of promoting good health? Why is exercise actually necessary for health? And what explains the exercise paradox: most people avoid exercise even though physical activity is vital for health?

As Theodosius Dobzhansky famously wrote more than 40 years ago (9), "nothing in biology makes sense except in the light of evolution." By this, Dobzhansky meant that although fields such as genetics, molecular biology, and physiology are necessary to explain the proximate mechanisms ("how" questions) that are

immediately responsible for biological phenomena, only evolutionary theory and data can explain the ultimate mechanisms ("why" questions) that provide deeper explanations of a phenomenon's true underlying causes. Simply put, since all living things evolved rather than were designed, it is necessary to consider an organism's evolutionary history to understand why it is the way it is. Evolution thus provides the only scientific explanation for why humans have teeth and big brains and walk on two legs. I therefore would add a corollary to Dobzhansky's famous sentence to state that "nothing in biology *including the obesity and inactivity epidemics* makes sense except in the light of evolution."

This article therefore uses an evolutionary perspective to ask three questions about the exercise paradox. First, "how much and what kinds of physical activity are humans adapted for?" Second, "to what extent are humans also adapted to be physically inactive?" And third, "how is information on the evolution of human physical activity and inactivity relevant to addressing the exercise paradox?" My argument is that although evolutionary history specially adapted humans to be endurance athletes, we are just as adapted to be physically inactive. Furthermore, because natural selection acts only on reproductive success by favoring adaptations that trade off energy between activity and reproduction, there is no evolutionary-determined dose or type of physical activity that will optimize health. To make this argument, I begin with a brief review of how to apply

evolutionary data and theory to problems of health and disease, focusing on the thorny concept of adaptation. I then review the evidence for human physical activity and inactivity and conclude with thoughts about how an evolutionary perspective applies to ameliorating the inactivity epidemic.

Evolution and Health

Doctors and patients rarely consider evolutionary biology relevant to medicine, and, sadly, the most common perceptions of how to apply evolution to issues of health and disease are the "Paleo" diet and fitness movements. These movements encompass diverse opinions and practices, but their essential underlying logic is that since we evolved to live and eat in Stone Age conditions, then living and eating like a hunter-gatherer is likely to promote good health (11). Although there is a kernel of truth to this argument, many medical professionals and patients are justifiably skeptical of superficial claims that eating and acting like a huntergatherer is the key to lowering morbidity and mortality. Such simplistic prescriptions are contradicted not only by evolutionary theory but also by evolutionary data (44). Most importantly, it is wrong to assume that adaptations promote health. As discussed in the following section, adaptations evolve only if they increase reproductive success (the number of offspring that survive and reproduce). Therefore, even if humans are adapted to Paleolithic lifestyles, it does not follow that foods and behaviors that are ancient (e.g., raw meat and hunting mammoths) necessarily promote health or those that are modern (e.g., yogurt and cycling) are unhealthy. Second, Paleolithic lifestyles were highly varied (20), making it impossible to define a single Paleolithic diet or behavior to follow. Finally, evolution did not stop in the Paleolithic, but actually intensified during the farming era and continues to the present day (13,40).

That said, there is much useful information to be gleaned about health from evolutionary history and theory, which has given rise to the nascent field of evolutionary medicine. One of the first thinkers to relate evolution to health was actually Charles Darwin's grandfather, the physician Erasmus Darwin, whose 1794 book Zoonomia (8) endeavored to relate an evolutionary view of comparative anatomy and physiology to disease and influenced his grandson's theory of natural selection. Charles Darwin, however, did not extend his theory to medicine, and it was not until Nesse and Williams' groundbreaking 1995 book Why We Get Sick that the medical implications of evolutionary biology really took off (32). Since then, a growing number of researchers have been applying evolutionary theory and data to many different aspects of health and disease, often with surprising implications (12,24,39).

At the heart of almost all efforts to apply evolutionary theory and data to health issues such as the exercise paradox is the theory of natural selection and the concept of adaptation. To briefly review, natural selection derives from the following three uncontroversial phenomena: 1) all organisms vary, 2) some of these variations are genetically heritable, and 3) organisms compete for resources, leading to differential reproductive success. As Darwin, Wallace, and others have since shown, the emergent outcome of these three phenomena is a special kind of change over time,

natural selection, in which heritable features that increase or decrease an organism's chance of having more offspring become either more or less common between succeeding generations (7). Among the many concepts that derive from this profound insight, the most important is adaptation, defined formally as a novel feature, shaped by natural selection, which improves an organism's ability to survive and reproduce. Natural selection favors the evolution of adaptations and selects against features that are maladaptive. However, over a century of research has shown that the concept of adaptation is actually complex and hard to test. Although adaptations are important and abundant, not all features are adaptations; they are often highly context dependent (e.g., features may be adaptive in some environments but not in others), they often conflict with each other, and adaptations promote health only to the extent that health promotes reproductive success (36).

To apply and test the concept of adaptation to the exercise paradox, it is first necessary to consider what kinds of physical activity and inactivity humans are actually adapted for.

What Kinds of Physical Activities are Humans Adapted For?

All animals are adapted to be physically active, especially to acquire resources and mates as well as to avoid becoming prey, and humans are no exception. However, there are several lines of evidence that humans evolved to be unique among primates and somewhat unusual among mammals in being especially well adapted for plentiful physical activity dominated by endurance as opposed to power. A comparative perspective indicates that humans also evolved to be adapted for a wide range of unusual and sometimes unique physical activities such as long-distance walking and running in the heat, digging, carrying, and throwing projectiles both fast and hard.

To trace the origins of the unique nature of human athleticism, a good place to start is with the divergence of the human lineage from its last common ancestor (LCA) with chimpanzees, which occurred approximately five to eight million years ago (17). Although the exact nature of the LCA is not entirely known, this species must have been a treeclimbing, quadrupedal ape that inhabited rainforests in Africa. Like all great apes, other primates, and the vast majority of mammals, the LCA must have been adapted more for power rather than endurance. Chimpanzees, for example, are more than twice as strong as the strongest humans; they typically walk less than 3-5 km·d⁻¹, they rarely sprint and only for short distances, and they climb less than 100 m·d⁻¹ (34). In addition, chimp leg muscles are dominated by fast-twitch fibers, they cannot cool effectively through sweating, and they spend approximately four times as much energy per unit body mass to walk compared with most mammals (25,31,38).

The first transition toward a more endurance-based phenotype likely began with the origins of bipedalism among early hominins. Although the first hominins walked differently than modern humans, bipedalism was probably favored by natural selection because it helped hominins travel and feed more effectively in more open, nonforested habitats that were becoming more common then in Africa (24). The chief cost of bipedalism, however, was loss of speed and stability. But the trade-off must have been worth it because over the

course of the next several million years, a diverse radiation of bipedal hominin species evolved, collectively known as the australopiths. Fossil evidence suggests that these highly variable species were effective bipeds, but they also retained many features for climbing trees (1).

The next major shift in hominin physical activity probably started around three million years ago, when further climate change expanded open habitats in Africa, spurring the origins of the genus Homo between three and two million years ago. Although the earliest species of Homo are poorly known, one particularly important species, H. erectus, evolved by two million years ago. H. erectus was different from earlier hominins in having a larger brain combined with smaller teeth and a generally human-like body with relatively long legs, short arms, and modern feet. Abundant evidence indicates that species of early Homo, especially *H. erectus*, evolved to be the first hunter-gatherers (1,24). Hunting and gathering is a subsistence system that combines foraging and hunting with the use of tools to acquire, extract, and process foods as well as high levels of cooperation including food sharing and division of labor.

From the perspective of exercise, the evolution of the hunter-gatherer way of life was a monumental shift because this subsistence system requires a broad range of novel and intensified physical activities that are especially dependent on endurance. The most important is long-distance walking (trekking). Modern hunter-gatherers of similar body mass to *H. erectus* and who inhabit similar arid, tropical African environments walk an average of 9 to 15 km (5 to 10 miles) per day to forage for enough food (28). It is almost certain that H. erectus would have needed to walk similar distances per day to forage enough food, which helps explain the evidence that the genus Homo, especially H. erectus, has many novel adaptations for long-distance trekking such as long legs, a more modern pelvis, and relatively large joints (1,24). In addition, hunter-gatherers have to carry food and babies across long distances, they occasionally have to throw projectiles and climb trees, and tropical huntergatherers typically spend 2 to 3 h·d⁻¹ using sticks to dig up

Finally, there is good reason to infer that endurance running was especially important in the genus *Homo*. Although modern hunter-gatherers in Africa acquire about 30% of their calories from hunted meat, the technologies they use to hunt including the bow and arrow, dogs, and nets are probably less than 100,000 years old, and stone-tipped spears were invented less than 500,000 years ago (26,27). Thus, it is probable that for nearly two million years, a major way to acquire meat was through persistence hunting. Although now rare, this kind of hunting takes advantage of the fact that humans can run long distances at speeds that require quadrupedal mammals to gallop and that whereas other mammals cool by panting, humans primarily cool by sweating. Since quadrupedal mammals cannot pant while galloping, they can overheat when they are chased for lengthy periods and must eventually stop to cool down. Running hunters can thus effectively and safely hunt large animals through a combination of chasing while running and tracking while walking. In the Kalahari, persistence hunts average 31 km (19 miles), with hunters running only about half that distance, usually at a moderate pace (23). Two major lines of evidence support the hypothesis that endurance running was practiced by the early *Homo*. First, fossils of *H. erectus* include many adaptations for running that are unrelated to walking such as an expanded gluteus maximus, short toes, and enhanced abilities to stabilize the head against pitching forces (4). In addition, there is strong evidence that by two million years ago, hominins were able to hunt large prime-aged adult males in the absence of tipped projectiles or other lethal weapons (5,10).

In short, the demands of hunting and gathering account for a wide range of novel adaptations, many of which require endurance rather than power or speed. Because of the intrinsic trade-off between endurance and power, we can infer that the transition from an ape-like physiology dominated by power to a more modern human-like physiology dominated by endurance was selected for strongly in early *Homo*, especially *H. erectus*. Although walking was certainly the dominant physical activity, running also must have been important, along with carrying, digging, climbing, and more.

What Kinds of Physical Inactivity are Humans Adapted For?

Humans were selected to be endurance athletes, but it is uncontroversial to state that humans also are adapted to rest whenever possible. Hunter-gatherers in camp usually sit on the ground (they have no chairs), do chores, take care of children, and engage in other activities that require little exertion. For example, Kalahari Bushmen spend only 4 to 6 h·d⁻¹ doing demanding work (21). Although it is possible to misinterpret such modest working hours as evidence that hunter-gatherers have it easy (37), energy allocation theory indicates that minimizing effort is actually adaptive in conditions with limited food. It is axiomatic that organisms can use energy either for reproduction, growth, or maintenance (which includes activity). Since natural selection favors only adaptations that increase reproductive success, it follows that organisms are selected to divert energy toward reproduction whenever possible and that excess energy spent on functions that do not lead to increased numbers of surviving offspring are maladaptive.

In this context, it is hardly surprising that energetic data collected from a wide range of habitats indicate that huntergatherers rest whenever possible because they struggle to stay in energy balance. Average total energy expenditures (TEE) of hunter-gatherers are approximately 2,600 to 3,000 kcal·d⁻¹ for males and 2,000 to 2,600 kcal·d⁻¹ for females, but females typically require approximately 1,000 to 2,000 additional kcal·d⁻¹ because they are almost always pregnant or nursing and they also need to supply food to both infants and children who are unable to forage on their own (18,19). However, acquiring this much energy is a challenge, especially for mothers who can reliably gather only about 2,000 kcal·d⁻¹ and thus need to be provisioned by others including husbands and grandmothers (13,18). Although hunter-gatherers are usually able to stay close to energy balance, they undergo periodic stress, gaining and losing several kilograms between seasons of abundance and scarcity, and complaints of hunger are common (19).

www.acsm-csmr.org Current Sports Medicine Reports 315

Studies of hunter-gatherer energy budgets further elucidate why it is reasonable to infer that humans were selected to avoid excess activity. Physical activity levels (calculated as TEE divided by resting metabolic rate) average 1.9 and 1.8 for male and female hunter-gatherers, respectively (range, 1.6 to 2.2), slightly lower than those for subsistence farmers, which average 2.1 for males and 1.9 for females (range, 1.6 to 2.4), but considerably higher than that for postindustrial Americans, which average 1.6 (15,22,33). These data have been used to argue that changes in diet, not physical activity, have been the dominant cause of recent energy surpluses, hence obesity in contemporary postindustrial humans (33). However, it is important to note that huntergatherers tend to have much smaller body masses than people in developed nations, so estimates of their active energy expenditure (TEE-RMR) relative to body mass indicate that they expend on average 30 kcal·kg⁻¹·d⁻¹, almost twice that of Americans, which is 17 kcal·kg⁻¹·d⁻¹ (24). In other words, hunter-gatherers who are very physically active for only 4 to 6 h·d⁻¹ are still nearly twice as active as people in postindustrial economies, which explains why they are under such strong selection to be inactive as much as possible. I know of no behavioral studies on inactivity among hunter-gatherers but predict that they are just as keen to avoid physical activity. The one important exception to this rule is play, a voluntary form of exercise unrelated to subsistence. Play is clearly an ancient adaptation, hardly unique to humans, that helps mostly nonadults learn athletic skills and develop appropriate physical capacities.

In short, available data on energy budgets indicate that since hunter-gatherers are often close to the margin of energy balance (sometimes above, sometimes below), extraneous physical activity of the sort often considered exercise today (such as going for a jog) is usually maladaptive. In addition, the evidence suggests that humans, especially females, evolved to be specially adapted to store as much fat as possible to have sufficient energy reserves to reliably and consistently afford several unusually costly aspects of human biology such as large brains and bodies, rapid rates of reproduction, delayed development, and the need for mothers to feed not only infants but also other dependent children. Like most mammals, other species of primates have only about 5% to 8% body fat, but lean hunter-gatherer males have 10% to 15% and females have 15% to 25% (3). Even so, the body mass index of hunter-gatherers is always below 23 kg·m⁻ (16). Altogether, there was strong selection for humans to be relatively fat compared with other primates but regularly catabolize those stores as well as to engage in more physical activity than other primates but also to rest whenever possible.

Why and to What Extent Did Exercise Evolve to Be a Form of Medicine?

According to my dictionary, a "medicine" is something used to treat or prevent disease and "exercise" is an activity requiring physical effort carried out especially to sustain or improve health and fitness. By any standards, exercise is clearly one of the most potent medicines there is. But why does our history as relatively fat endurance athletes who take it easy whenever possible make exercise medicine? And

to what extent does this evolutionary history also limit the extent to which exercise functions as a kind of medicine?

In addressing these questions, one must keep in mind that since humans until recently never had the chance to avoid being physically active on a regular basis, there was never strong selection to prevent persistent and extreme physical inactivity. (By the same logic, there never was selection to prevent obesity.) To go a step further, because selection ultimately acts on reproductive success and because energy is a limited resource, one predicts that selection rarely, if ever, acted to cope with the negative effects of physical inactivity. Such a lack of selection should be especially marked for energetically expensive physiological systems that require physical activity as a stimulus to adjust capacity to demand. Because costly excess capacity wastes limited energy that could otherwise be spent on reproduction, natural selection will favor dose-response curves that adjust capacity to demand economically to reserve as much energy as possible for reproduction (42). Put differently, since natural selection acts on reproductive success and since organisms must trade off limited energy resources, natural selection will always favor mechanisms that trade off energy in ways that favor reproduction. As a result, the body's physiology and anatomy are adapted to respond to the stresses generated by physical activity to generate enough but not too much capacity.

A well-studied example of this kind of predicted trade-off between capacity and demand is the dose-response relationship between physical activity and muscle tissue. Since muscles consume about 40% of a body's resting metabolic rate, individual muscles thus hypertrophy primarily upon demand and degenerate under conditions of disuse. Similar reaction norms in response to varying levels of physical activity apply to almost every system in the body including the circulatory system, the skeletal system, and metabolism. In the circulatory system, for example, vigorous activity stimulates expansion of peripheral circulation, causes ventricular enlargement to increase cardiac output, and increases arterial elasticity. Individuals who avoid moderate physical activity thus develop low cardiovascular capacity, predisposing them to many kinds of disease that used to be rare (see the following section). Walking, running, and other forms of physical activity also generate mechanical stresses in the skeleton that are necessary to stimulate bone deposition and repair mechanisms. As a result, persistent inactivity leads to weak bones that increase the risk of osteoporosis and other previously uncommon diseases (see the following section). Physical activity even acts on the nervous system to increase neuronal function, helping explain why physical inactivity is correlated with diminished mental health and some forms of dementia (43).

It is worth emphasizing that the many mechanisms by which physical inactivity increases the risk of chronic, noninfectious diseases do not occur because physical activity evolved as an adaptation to prevent ill health, but instead, they evolved as adaptations to prevent excess capacity in individuals who were already active but energy limited. For example, the protective effects of exercise against osteoporosis are likely a byproduct of selection to prevent costly overbuilding of the skeleton. Seen in this light, the fact that exercise helps prevent osteoporosis is

primarily a consequence of the skeletal system — like every other system — requiring physical activity to adjust capacity to demand and thus failing to develop normal capacity in the absence of normal demand. Exercise did not evolve as a form of medicine.

The argument that exercise did not evolve as medicine because people until recently were rarely, if ever, able to be regularly physically inactive leads to one of the most important concepts in evolutionary medicine: mismatch. Mismatch conditions are defined as diseases that are more prevalent or more severe today than in the past because the body is inadequately or insufficiently adapted to modern environmental conditions (24). Just as cavities, which used to be rare, are now common because teeth are poorly adapted to the effects of diets rich in sugar and starch on our oral microbiome, many chronic, noninfectious diseases have become more common and severe because humans never evolved to be almost always physically inactive. Two kinds of data are needed to test hypotheses of mismatch. First, since all diseases result from gene-environment interactions, mismatch diseases are predicted to be caused by recent changes in environments not genes. Second, mismatch diseases are predicted to be rare or less severe among hunter-gatherers and other populations for which the environmental variable in question remains similar to the ancestral condition.

In terms of the first line of evidence — that a disease is primarily caused by recent environmental changes that interact with ancestral genes — we know enough about the etiology of some common diseases (e.g., type 2 diabetes, heart disease, osteoporosis) to state confidently that recent changes in physical activity play an important causal role in their increased prevalence. However, the etiology of many other complex diseases for which physical inactivity is a major risk factor (e.g., certain cancers, Alzheimer's) is not well enough understood to diagnose them as mismatch diseases or to be sure of what factors cause the mismatch. Lack of data is even more problematic for testing the extent to which hypothesized mismatches are rare in huntergatherers and other physically active populations. There have been several efforts to collect data on health and disease among such populations (reviewed in Lieberman, 2013) but sample sizes are small, modern diagnostic tools are often unavailable, and they often necessarily rely on anecdotal information. Despite these and other concerns, the evidence overwhelmingly indicates that many if not most of the diseases for which physical inactivity is a major risk factor are considerably less prevalent in hunter-gatherers and many populations of subsistence farmers. As an example, comprehensive medical evaluations of Kalahari Bushmen from the 1960s and 1970s found no evidence for coronary heart disease, hypertension, diabetes, dyslipidemia, hearing loss, and more (41). In fact, contrary to common belief, these and other studies indicate that life in the Paleolithic was not always nasty, brutish, and short. Although infant mortality is high among hunter-gatherers, studies of numerous foraging populations indicate that individuals who survive the first few years of life can expect to live to their 70s or older (2). Furthermore, these individuals continue to be highly physically active as they age (18). As a result, it is reasonable to hypothesize that there was probably little selection to prevent mismatch diseases caused by physical inactivity even in old age.

What about the effects of recent selection? Natural selection did not cease with the end of the Paleolithic and in some respects may have been accelerated by farming, which drastically altered the environment and increased population sizes, hence the number of available mutations (17). For most of the farming era, people still had to work very hard, making physical inactivity rare for all but a few privileged individuals prior to the postindustrial era. In addition, mismatch diseases that are caused by physical inactivity tend not to affect people until they are postreproductive. Since grandparents are no longer needed to forage for their grandchildren, it is unlikely that there is strong selection for mutations (if they exist) that protect against the effects of physical inactivity.

Finally, while natural selection is still ongoing, cultural evolution is now a much stronger and more rapid force (35). The result is that we have set in motion and new dynamic, which I term dysevolution, in which we get sick from mismatch diseases caused by novel environmental conditions such as physical inactivity and then devise cultural solutions to cope with their effects (24). Because the causes remain prevalent and we are able to buffer their negative effects, we create a positive feedback loop in which the diseases remain prevalent or become more common and severe. Dysevolution is not a form of biological evolution but instead is a form of cultural evolution that results from the interaction between biology and culture. In the case of exercise, physical inactivity is causing growing numbers of people in the developed and developing world to develop coronary heart disease, hypertension, type 2 diabetes, osteoporosis, and more. Although these diseases cause considerable misery not to mention great expense, they are an example of dysevolution because we have devised technologies and support systems to effectively treat and cope with the symptoms of these diseases for extended periods. Although we can and must continue to treat those who become sick, by promoting more exercise, especially among children, we could break this pernicious positive feedback loop by preventing the diseases from occurring in the first place.

Conclusion: Is There an Evolutionary-Based Prescription For Exercise?

In short, while physical activity is unquestionably a potent medicine, it never evolved for that role. Instead, humans' evolutionary legacy as physically active endurance athletes on the margin of energy balance has resulted in a myriad of adaptive dose-response relationships in which the body uses stimuli from physical activity to adjust capacity to demand in order to maximize reproductive success. In addition, a chronic absence of moderate physical activity was so rare until recently that, from an evolutionary perspective, such levels of inactivity are not only abnormal but also cause pathology. Given these conclusions, does an evolutionary perspective suggest alternative ways to think about the role of exercise as medicine? And how does the lens of evolution help solve the urgent challenge of how to help people overcome their inertial tendencies to avoid exercise?

These are big questions, but one evolutionary-based prediction is that we are not adapted for any particular dose or kind of exercise. Instead, like everything else, different types, intensities, and doses of exercise involve multiple tradeoffs with complex effects on health. Thus, while exercise is an effective prescription to promote health, there is no minimum dose, no optimal dose, and no dose without risks or negative consequences. For example, while exercise has many benefits for cardiovascular function, it does not prevent all forms of heart disease and may actually be harmful in certain doses. Put differently, an evolutionary perspective predicts that while an absence of physical inactivity almost certainly increases the chances of morbidity and mortality, exercise is not a guarantee of good health and inevitably involves trade-offs. For example, people who exercise to lose weight have to cope with increased hunger and metabolic shifts, presumably because these reactions are adaptations to regain energy balance (6).

A second major conclusion is that while humans are adapted to be physically active endurance athletes, we are just as adapted to be inactive whenever possible. It is natural and normal to be physically lazy. No one has ever done the experiment, but I predict that hunter-gatherers in the Kalahari or the Amazon are just as likely as 21st century Americans to instinctually avoid unnecessary exertion. Although a small percentage of people today exercise as a form of medicine, doing their prescribed dose, the vast majority of people today behave just as their ancestors by exercising only when it is fun (as a form of play) or when necessary. An evolutionary perspective therefore predicts that the most effective ways to promote exercise will be in these two contexts. It follows that we have two urgent challenges, which are appropriately the focus of many worthy initiatives. The first is to devise ways to make physical activity more enjoyable in schools, workplaces, and other environments. The second is to restructure our environments to require more physical activity. The bottom line is that just as cultural innovations are causing the physical activity epidemic, new cultural measures are needed to restore the need to move in our environments. Until we do so effectively, we can expect to remain trapped in a pernicious vicious circle in which, by treating the symptoms rather than the causes of diseases that are caused by physical inactivity, we will permit the exercise paradox to persist and worsen.

Acknowledgments

The author thanks Aaron Baggish and Frank Marino for comments. Daniel E. Lieberman received no funding for this research.

The author declares that the results of the present study do not constitute endorsement by the American College of Sports Medicine.

References

- 1. Aiello LM, Dean MC. Human Evolutionary Anatomy. New York (NY): Academic Press, 1990, p. 595.
- Blurton Jones NG, Smith LC, O'Connell JF, et al. Demography of the Hadza, an increasing and high density population of Savanna foragers. Am. J. Phys. Anthropol. 1992;89:159–81.
- Bogin B. Patterns of Human Growth. 2nd ed. Cambridge (United Kingdom): Cambridge University Press, 2001, p. 267.
- 4. Bramble DM, Lieberman DE. Endurance running and the evolution of *Homo*. *Nature*. 2004;432:345–52.

- Braun DR, Harris JW, Levin NE, et al. Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. Proc. Natl. Acad. Sci. U. S. A. 2010;107:10002–7.
- Cook CM, Schoeller DA. Physical activity and weight control: conflicting findings. Curr. Opin. Clin. Nutr. Metab. Care. 2011;14:419–24.
- Darwin C. On the Origin of Species. London (United Kingdom): John Murray, 1859, p. 513.
- Darwin E. Zoonomia; or the Laws of Organic Life. London (United Kingdom): J. Johnson, 1794, p. 620.
- Dobzhansky T. Nothing in biology makes sense except in the light of evolution. Am. B. Teacher. 1973;35:125–9.
- Dominguez-Rodrigo M. Hunting and scavenging by early humans: the state of the debate. J. World Prehist. 2002;16:1–54.
- Durant J. The Paleo Manifesto: Ancient Wisdom for Lifelong Health. New York (NY): New York Harmony Books, 2013, p. 359.
- Gluckman P, Beedle A, Hanson M. Principles of Evolutionary Medicine. Oxford (United Kingdom): Oxford University Press, 2011, p. 296.
- Hawkes K, O'Connell JF, Jones NG, et al. Grandmothering, menopause, and the evolution of human life histories. Proc. Natl. Acad. Sci. U. S. A. 1998;95:1336–9.
- 14. Hawks J, Wang ET, Cochran GM, et al. Recent acceleration of human adaptive evolution. Proc. Natl. Acad. Sci. U. S. A. 2007;104:20753–8.
- James WPT, Schofield EC. Human Energy Requirements. Oxford (United Kingdom): Oxford University Press, 1990, p. 182.
- Jenike MR. Nutritional ecology: diet, physical activity and body size. In: Panter-Brick C, Layton RH, Rowley-Conwy P, editors. *Hunter-gatherers*. An Interdisciplinary Perspective. Cambridge (United Kingdom): Cambridge University Press; 2001. pp. 205–38.
- Jensen-Seaman MI, Hooper-Boyd KA. Molecular clocks: determining the age of the human-chimpanzee divergence. In: Encyclopedia of Life Science. Chichester (United Kingdom): Wiley, 2013.
- Kaplan HS, Hill KR, Lancaster JB, Hurtado AM. A theory of human life history evolution: diet, intelligence, and longevity. *Evol. Anthropol.* 2000;9:156–85.
- 19. Kelly RL. The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways. Clinton Corners (NY): Percheron Press, 2007, p. 446.
- Kramer KL, Ellison PT. Pooled energy budgets: resituating human energy allocation trade-offs. Evol. Anthropol. 2010;19:136–47.
- 21. Lee RB. The !Kung San: Men, Women and Work in a Foraging Society. Cambridge and New York: Cambridge University Press, 1979, p. 556.
- Leonard WR. Human nutritional evolution. In: Stinson S, Bogin B, O'Rourke D, editors. Human Nutritional Evolution Human Biology: an Evolutionary and Biocultural Perspective, Second Edition. New York (NY): Wiley; 2012, pp. 251–324.
- Liebenberg L. Persistence hunting by modern hunter-gatherers. Curr. Anthropol. 2006;47:1017–26.
- 24. Lieberman DE. The Story of the Human Body: Evolution, Health and Disease. New York (NY): Pantheon, 2013, p. 460.
- Lieberman DE. Human locomotion and heat loss: an evolutionary perspective. Compr. Physiol. 2015;5:99–117.
- Lieberman DE, Bramble DM, Raichlen DA, Shea JJ. The evolution of endurance running and the tyranny of ethnography: a reply to Pickering and Bunn (2007). J. Hum. Evol. 2007;53:439–42.
- 27. Lieberman DE, Bramble DM, Raichlen DA, Shea JJ. Brains, brawn and the evolution of human endurance running capabilities. In: Grine FE, Fleagle JG, Leakey RE, eds. The First Humans: Origin and Early Evolution of the Genus Homo. New York (NY): Springer, 2009, pp. 77-98.
- 28. Marlowe FW. *The Hadza: Hunter-Gatherers of Tanzania*. Berkeley (CA): University of California Press, 2010, p. 325.
- Matheson GO, Klügl M, Engebretsen L, et al. Prevention and management of non-communicable disease: the IOC consensus statement, Lausanne 2013. Sports Med. 2013;43:1075–88.
- 30. Mokdad AH, Marks JS, Stroup DF, Gerberding JL. Actual causes of death in the United States, 2000. *JAMA*. 2004;291:1238–45.
- Myatt JP, Schilling N, Thorpe SK. Distribution patterns of fibre types in the triceps surae muscle group of chimpanzees and orangutans. *J. Anat.* 2011;218:402–12.
- Nesse R, Williams GC. Why We Get Sick: the New Science of Darwinian Medicine. New York (NY): New York Times Books, 1995, p. 290.
- 33. Pontzer H, Raichlen DA, Wood BM, et al. Hunter-gatherer energetics and human obesity. PLoS One. 2012;7:e40503.

- 34. Pontzer HD, Wrangham RW. The ontogeny of ranging in wild chimpanzees. *Int. J. Primatol.* 2006;27:295–309.
- 35. Richerson PJ, Boyd R. Not By Genes Alone: How Culture Transformed Human Evolution. Chicago (IL): University Chicago Press, 2008, p. 342.
- 36. Rose MG, Lauder GV. Adaptation. San Diego (CA): Academic Press, 1996, p. 511.
- 37. Sahlins MH. Stone Age Economics. Chicago (IL): Aldine, 1972, p. 348.
- Sockol MD, Raichlen D, Pontzer HD. Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc. Natl. Acad. Sci. U. S. A.* 2007; 104:12265–9.
- Stearns SC, Koella JC. Evolution in Health and Disease. 2nd ed, Oxford (United Kingdom): Oxford University Press, 2008, p. 374.

- Stearns SC, Byars SG, Govindaraju DR, Ewbank D. Measuring selection in contemporary human populations. Nat. Rev. Genet. 2010; 11:611-22.
- Truswell AS, Hansen JDL. Medical research among the !Kung. In: Lee RB, DeVore I, eds. *Kalahari Hunter-Gatherers*. Cambridge (MA): Harvard University Press, 1976, pp. 167–94.
- Weibel ER, Taylor CR, Hoppeler H. The concept of symmorphosis: a testable hypothesis of structure-function relationship. *Proc. Natl. Acad. Sci. U. S. A.* 1991;88:10357–61.
- Zschucke E, Gaudlitz K, Ströhle A. Exercise and physical activity in mental disorders: clinical and experimental evidence. J. Prev. Med. Public Health. 2013;46:S12–21.
- 44. Zuk M. Paleofantasy: What Evolution Really Tells Us about Sex, Diet and How We Live. New York (NY): WW Norton, 2013, p. 336.

www.acsm-csmr.org Current Sports Medicine Reports 319