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Review

An evolutionary perspective on human physical activity: implications for health☆

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Abstract

At present, human genes and human lives are incongruent, especially in affluent Western nations. When our current genome was originally selected, daily physical exertion was obligatory; our biochemistry and physiology are designed to function optimally in such circumstances. However, today's mechanized, technologically oriented conditions allow and even promote an unprecedentedly sedentary lifestyle. Many important health problems are affected by this imbalance, including atherosclerosis, obesity, age-related fractures and diabetes, among others. Most physicians recognize that regular exercise is a critical component of effective health promotion regimens, but there is substantial disagreement about details, most importantly volume: how much daily caloric expenditure, as physical activity, is desirable. Because epidemiology-based recommendations vary, often confusing and alienating the health-conscious public, an independent estimate, arising from a separate scientific discipline, is desirable, at least for purposes of triangulation. The retrojected level of ancestral physical activity might meet this need. The best available such reconstruction suggests that the World Health Organization's recommendation, a physical activity level of 1.75 (∼2.1 MJ (490 kcal)/d), most closely approximates the Paleolithic standard, that for which our genetic makeup was originally selected.

Keywords: Human evolution; Physical activity; Exercise recommendations; Exercise and health; Evolutionary health promotion

1. Introduction

Before the domestication of draft animals and the development of mills powered by wind or water, the activities of human ancestors, like those of all other free-living organisms, were entirely dependent on individual physical exertion. There was an obligatory and natural linkage between caloric acquisition, as food energy, and caloric expenditure, as physical activity. This relationship existed throughout the long course of human and pre-human evolution, exerting ongoing adaptive pressure that affected selection of genes related to the cardio-respiratory and musculoskeletal systems as well as the internal metabolism of our progenitors.

The circumstances of human existence in the 21st century are far different from those that obtained during the remote past. Physical activity is no longer a requirement for daily living; the

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relationship between eating and physical work has been abrogated. However, genetic evolution has been wholly unable to match the rapidity of cultural change and our genes remain adapted for conditions that existed during their selection by Darwinian mechanisms (Gould, 1980; Wilson, 1998; Klein, 1999). This discordance or mismatch between our contemporary lives and our genetic makeup has important pathophysiological implications: coronary atherosclerosis, age-related fractures, obesity and 'syndrome x' disorders related to insulin resistance are all promoted by physical inactivity (United States Department of Health and Human Services, 1996).

In evolutionary perspective, contemporary exercise requirements for health promotion might logically be expected to reprise the exertional circumstances or, better, the anatomical and physiological end results of preagricultural ancestral experience. Accordingly, an understanding of physical activity levels (PALs) in the Stone Age is of more than theoretical interest. The exertional patterns of our ancestors[1] might well be considered targets for disease prevention and improved life quality in the present.

2. Physical activity in the Stone Age

Retrojecting ancestral physical activity depends primarily on painstaking evaluation of human skeletal remains (e.g. Larsen, 1997) and on methodical study of recent hunter-gatherers, who are considered the best available, if imperfect, surrogates for late Paleolithic humans (e.g. Jenike, 2001). Both lines of investigation have obvious, frustrating limitations, but by dint of continuing multidisciplinary efforts a defensible and increasingly reliable picture of physical activity during the period from 50 000 to 20 000 years ago has emerged. Naturally, levels and types of activity in the Stone Age varied. In some areas, seasonal fluctuations were prominent due to shifts in game animal and plant food availability. While most Paleolithic Stone Agers were nomadic, some in especially favored locations lived a relatively settled existence. Activities in the subarctic, along seacoasts, and in savanna locations necessarily differed—but in terms of physical energy expenditure the experiences of Stone Agers were probably more uniform than are those of contemporary Americans whose propensities range from exercise fanaticism to near total sedentism.

A major difficulty is that recent hunter-gatherers have generally been much smaller than were their (and our) late Paleolithic ancestors (Walker and Leakey, 1993)—presumably reflecting the nutritional stress of foraging in the marginal environments to which they have been relegated (Lambert, 1993; Larsen, 1997; Eaton et al., 2002). This necessitates correction for differences in size—a source of potential error.

These difficulties having been noted, the best available estimates of energy expenditure as physical activity for humans (males and females averaged) living in the late Paleolithic, say 25 000 years ago, center approximately 5.4 MJ (1240 kcal)/d or near 91.3 kJ (21.8 kcal)/kg for a 57-kg composite individual[2] (Eaton et al., 1988a; Cordain et al., 1997, 1998). These values contrast with an estimated 2.3 MJ (555 kcal)/d or 36.4 kJ (8.7 kcal)/kg for a hypothetical 64-kg male/female contemporary American. It should be emphasized that the level of ancestral physical activity is actually in line with, or less than, what is normal for non-industrial, more active contemporary human populations (Ruff et al., 1993; Heini et al., 1996). The average PALs in current industrialized nations are those biologically out of step.

Stone Age exertional activities covered a broad spectrum: walking while gathering, during hunting trips and on visits to neighboring campsites; running after wounded prey; carrying children, game meat, gathered plant foods or firewood; erecting shelters; flint knapping and making composite tools; digging for roots or tubers; butchering and cleaning game animal carcasses; shelling nuts; breaking open crania and long bones for brains and marrow; dancing for simple recreation or as part of religious ceremonies; vigorous play and so forth. Paleolithic physical exertion patterns likely resembled cross-training, not the more focused regimens of pure runners or weight-lifters (Ruff, 2000); activities analogous to both aerobic conditioning and strength training were thus integral

[1] The lives of Stone Age (during 1.5 million years) and agricultural (during 10 000 years) human ancestors differed in many ways, particularly their nutritional, psychosocial and infectious disease experience. However, their daily energy expenditure, as physical activity, appears to have been reasonably equivalent (Larsen, 1997).

[2] This value and others like it throughout the review are obviously over-specific. They should be regarded as approximate mid-points for ancestral ranges—to be modified towards increased precision as more data become available.

components of their typical routine. Although each day's ordinary tasks required at least some muscular effort and stamina, recently studied hunter-gatherers tended to space their more vigorous exertion. Men commonly hunted from 2 to 4 non-consecutive days a week, while women usually gathered every 2–3 days. This spacing of the more physically demanding aspects of forager life has been termed a 'Paleolithic work rhythm' (Eaton et al., 1988b).

Formal studies of recent hunter-gatherers and members of other non-mechanized traditional societies reveal that aerobic power for such people (7 groups) averages approximately 50% greater than that for age-matched affluent Westerners ($V\mathrm{O}_2$ max = 57.2 ml/kg/min vs. 37.2 ml/kg/min; males 20–49 years old) (Cordain et al., 1998). More limited studies of muscular force (leg extension) suggest that foragers are approximately 20% stronger than comparable (age- and weight-matched) Westerners (Shephard, 1980).

3. Health implications

3.1. Skeletal

The ability of bones to resist mechanical stresses depends largely upon their mineral density and structural geometry. Strenuous physicality in early life promotes formation of dense, well-mineralized bones (Burr et al., 1990; American College of Sports Medicine, 1995; United States Department of Health and Human Services, 1996), while regular exercise during maturity (especially after menopause) retards the bone mineral loss that occurs to some extent in all aging human populations (Nelson et al., 1994; American College of Sports Medicine, 1995; United States Department of Health and Human Services, 1996).

In addition to its beneficial effects on bone mineral density, high-level physical activity, especially during childhood, adolescence and early adulthood, exerts a powerful influence on bone structural geometry (Larsen, 1997). Mechanical engineers have long recognized that any structural element's stress-resisting capacity is heavily dependent on its overall size and its cross-sectional configuration (Larsen, 1997). Physical anthropologists liken the bony remains of behaviorly modern, late Paleolithic humans to those of contemporary elite athletes such as Olympians (Ruff et al., 1998; Trinkaus and Rhoads, 1999; Ruff, 2000). Skeletal robusticity of this degree reduces age-related fracture risk because the bones have larger overall cross-sectional area relative to their length and because their cross-sectional shape is slightly oval compared with the more rounded cross-sectional outline that tends to characterize the bones of sedentary individuals. Other factors being equal, semi-oval bones are more resistant to potential fracture-producing stresses than are bones with relatively circular cross-sections (Larsen, 1997).

3.2. Cardiovascular

Multiple investigations have established the existence of a strong, graded, inverse relationship between aerobic power and risk of subsequent cardiac events such as non-fatal arrhythmia, myocardial infarction, incident angina pectoris and sudden cardiac death (Myers et al., 2002; Balady, 2002). With progressively increasing aerobic fitness, the likelihood of such disorders decreases stepwise. There are numerous physiological mechanisms that, acting collectively, presumably explain why individuals with greater endurance should be protected. Aerobic exercise elevates blood levels of 'good' high density cholesterol, lowers blood pressure and resting heart rate, decreases platelet aggregability as well as the tendency for vasoconstriction, and enhances endothelial health as determined by post-ischemic brachial artery vasodilatation (Froelicher and Myers, 2000).

Also there is growing evidence that, like endurance exercise, strength training enhances heart health (Hurley et al., 1988; Winnett and Carpinelli, 2001). Resistance exercise lowers blood pressure (Kelley and Kelley, 2000) and beneficially influences serum lipids (Staron et al., 2000). Positive effects on body composition and insulin sensitivity may also be contributing factors (Flucky et al., 1994; Winnett and Carpinelli, 2001).

3.3. Obesity

In 1970, American males were 8.7 kg (22 lbs) heavier than were age- and height-matched men in 1863 (Hathaway and Foard, 1960; Kuczmarski et al., 1994). During much of this period, from 1909 to 1970, food disappearance data indicate that energy available in the food supply remained constant (National Research Council, 1989), while in its later stages, per capita caloric intake actually appears to have declined (National Research Council, 1989), a phenomenon also observed in Britain (Ministry of Agriculture, Fisheries and Food, 1995) and Japan (Shimamoto et al., 1989). These seemingly contradictory trends might be reconciled if caloric expenditure has declined disproportionately. That soldiers in today's United States Army perform poorly relative to test scores achieved on the same physical fitness test administered to their predecessors in 1946 (Thomas, 2000) tends to support this likely possibility, but more rigorous investigative data are scarce. However, a rational explanation for secular decrease in physical activity is readily apparent. Ever-increasing reliance on labor-saving machinery at home, for travel, and in the workplace was a salient feature of late 20th century life, and one that shows every sign of continuing. Likewise, recreational pursuits have become more sedentary with the introduction of video games, internet browsing and greater promotion of spectator, as opposed to participant, sports enjoyment. The change from ancestral experience could hardly be more profound. One of its many implications concerns basal, or resting, metabolic rate (BMR)—responsible for much of the total energy expenditure (TEE) on any given day. Individuals with greater lean body mass (especially skeletal muscle) tend to have a higher BMR than do otherwise comparable individuals whose body composition includes a greater proportion of adipose tissue (Tataranni and Ravussin, 1995). Other factors being equal, a higher BMR means less ingested food energy will be available for storage as fat. The best available study suggests that semitraditional, still relatively lean, Inuit as surrogates for hunter-gatherers generally (and, by implication, ancestral humans) had BMRs averaging 15% greater than those of typical sedentary affluent Westerners (Shephard and Rode, 1996).

Since approximately 1980, obesity prevalence in the United States (and elsewhere) has increased precipitously (Mokdad et al., 1999; Lewis et al., 2000), while PALs have altered little if at all (Neiman, 1999). Food industry changes such as an increased supply of lower cost, high energy ingredients (e.g. palm oil, soybean oil and high-fructose corn sweeteners), effective marketing strategies (e.g. supersizing, value meals) and ever wider availability of calorie-dense convenience foods may be the important factors accelerating recent body mass index increases. They are superimposed on the preexisting, unnaturally low PALs that have accompanied industrialization. The additive effect further distances contemporary subsistence efficacy from the ancestral pattern (Section 4).

3.4. Body composition and insulin resistance

Consistent with their habitual high levels of physical activity, hunter-gatherers studied in the past century have invariably been lean, with skinfold thicknesses only a fraction of those characterizing typical individuals in affluent nations (Eaton et al., 1988a). Similarly, forager body mass indices have generally been in the low normal range as established for Westerners (Jenike, 2001). Moreover, like all other free-living mammals excepting those species that accumulate adipose tissue for hibernation or thermal insulation, recent hunter-gatherers have had a high proportion of skeletal muscle relative to their fat mass (Shephard and Rode, 1996), a body-compositional pattern that presumably characterized ancestral humans as well (Trinkaus, 1997; Ruff, 2000).

Adipose tissue and skeletal muscle differ strikingly with regard to their participation in carbohydrate metabolism. Given equivalent insulin stimulation, a gram of muscle can remove from the blood far more glucose than a gram of fat can remove (De Fronzo, 1997). The differential is accentuated by exercise conditioning: fit muscle has more capacity for blood glucose extraction than does unconditioned muscle (Goodyear et al., 1990; Flucky et al., 1994). This pattern is analogous to that for fatty acid metabolism. Skeletal muscle can oxidize more ingested fatty acid than can an equal mass of adipose tissue (Bessesen et al., 2000) and the discrepancy is increased by exercise (Smith et al., 2000; Herd et al., 2001).

These factors help explain why excess adiposity predisposes to insulin resistance. A disproportionate amount of adipose tissue relative to skeletal muscle reduces the blood-glucose-lowering effect of a given pancreatic insulin secretory pulse so that additional insulin secretion is necessary to achieve appropriate blood glucose levels; i.e. insulin sensitivity is reduced (Eaton and Eaton, 1999; Eaton et al., 2002). Furthermore, another body-compositional consideration intensifies this pathophysiology. Affluent Westerners are not only over-fat, they are also under-muscled, sarcopenic, in comparison with ancestral standards. The elite athletes whom physical anthropologists consider to reprise typical Stone Agers have far more muscle tissue than do otherwise matched sedentary non-exercisers (Ruff, 2000), a discrepancy readily apparent to radiologists who frequently interpret magnetic resonance images.

Three separate, but interrelated and interactive influences on insulin sensitivity and/or resistance are thus linked to contemporary divergence from ancestral experience. These can be expressed:

$$\text{Insulin sensitivity} \sim \frac{(\text{skeletal muscle mass}) \times (\text{skeletal muscle metabolic activity})}{(\text{fat mass})}$$

For each factor, the lifestyle and consequent body composition/metabolic activity of Stone Age humans acted to promote insulin sensitivity, while that of contemporary Westerners fosters insulin resistance. The enviable carbohydrate metabolism of hunter-gatherers tested in the past century supports this contention (Joffe et al., 1971; Kuroshima et al., 1972; Merimee et al., 1972; Spielmann et al., 1982; Lindeberg et al., 1999).

4. Discussion

Evolution occurs through differential reproductive success that, in large measure, reflects subsistence efficiency: how much food energy can be acquired for a given amount of physical exertion. During nearly all human (and pre-human) evolutionary experience, energy acquisition and expenditure have been inextricably linked, but economic growth accompanying the industrial revolution disrupted this ancient and basic relationship. Over the past two centuries, adjusted per capita income, a correlate or measure of subsistence efficiency, has increased 12-fold in Western nations (Landes, 1998).

The average daily energy expenditure, as physical activity, of Stone Age humans is estimated at approximately 5.2 MJ (1240 kcal) and their total caloric intake at approximately 12.1 MJ (2900 kcal) (Cordain et al., 1998). Their subsistence efficiency was thus approximately 2.25 kJ (kcal) acquired for each kilojoule (kilocalorie) expended in physical activity. In contrast, sedentary humans in contemporary affluent societies commonly consume perhaps 8.5 MJ (2030 kcal)/d with expenditure, as physical activity, of approximately 2.3 MJ (555 kcal)/d (Cordain et al., 1998), a subsistence efficiency of 3.66 to 1. This improved efficiency of food energy acquisition, a 50% increase, represents a fundamental triumph of human achievement, but not one without real, albeit potentially correctable, drawbacks. Most of the benefits and disadvantages might be predicted by considering an energy utilization equation:

$$\text{Food Energy Acquired} \sim \begin{array}{l} \text{Physical Exertion} \\ + \\ \text{Resting Metabolic Activity} \\ \text{Specific Dynamic Action} \\ + \\ \text{Host Resistance} \\ \text{Growth} \\ \text{Reproduction} \\ + \\ \text{Energy Storage} \end{array}$$

These include greater longevity as a result of improved host resistance (augmented by public health measures and medical care); earlier menarche and greater height as energy availability maximizes genetic potential; less bone and skeletal muscle, a consequence of reduced physical exertion; hyperadiposity due to greater energy storage and altered metabolism as the integral of all these factors—each differing from those for which our genome was originally selected.

While life expectancy doubled during the past century, the recent efforts of health promotion have been frustratingly ineffective. The United States Surgeon General's *Healthy People 2000* Project met only 15% of its goals, while for 19% of the targeted objectives, there was actual regression from the 1990 baseline (National Center for Health Statistics, 1999). The prevalence of exercise-related conditions, such as obesity and type 2 diabetes, has skyrocketed in recent decades. One of the proposed reasons for health promotion's limited success is that contradictory recommendations are advanced by expert panels, thus confusing and alienating the health-conscious public (Angell and Kassirer, 1994). Physical activity goals are no exception: the United States Surgeon General's recommendation translates into roughly 628–837 kJ (150–200 kcal)/d, depending on body weight (United States Department of Health and Human

Services, 1996), while the World Health Organization's target (WHO, 1998) can be interpreted as approximately 2.1 MJ (490 kcal)/d.

Although the ideal of evidence-based health promotion holds intuitive appeal, the reality of conflicting data (and differing interpretations by reputable authorities) makes an independent standard, derived from a non-epidemiological perspective, highly desirable, if only for triangulation. For this purpose, the experience of ancestral humans, whose lifeways influenced selection of the contemporary human genome, seems an ideal resource.

Physicians and scientists interested in the linkage between exercise and health commonly employ the concept of PAL. This term designates the ratio between basal or resting metabolism (BMR) and TEE. For typical sedentary Americans, PAL approximates 1.4 (BMR of 6.1 MJ (1450 kcal), TEE of 8.5 MJ (2030) kcal)). If, like hunter-gatherers who were studied in the last century, Stone Age human BMR was approximately 15% greater than that of sedentary Americans, its value would have been approximately 7 MJ (1665 kcal). If their daily TEE was 12.1 MJ (2900 kcal), then their PAL would have been 1.74. While this result must be in part fortuitous, it does almost exactly match the WHO recommendation of 1.75, while exceeding the US Surgeon General's recommendation, which is equivalent to a PAL of from 1.5 to 1.55.

In practical terms the US Surgeon General's and WHO's recommendations differ substantially: 30 min of exercise on most, preferably all, days vs. 60 min. Inconsistencies of this, or greater, magnitude are disturbingly common in health promotion, an apparently unavoidable, inherent consequence of the discipline's dependence on epidemiological evidence. Evolutionary insight's independent support for WHO's position in this specific instance—physical activity prescription for disease prevention—might be an indicator of its potential value for public health research and recommendations generally.

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