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Influence of lower limb configuration on walking cost in Late Pleistocene humans

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ABSTRACT

It has been proposed that Neandertals had about 30% higher gross cost of transport than anatomically modern humans (AMH) and that such difference implies higher daily energy demands and reduced foraging ranges in Neandertals. Thus, reduced walking economy could be among the factors contributing to the Neandertals' loss in competition with their anatomically modern successors. Previously, Neandertal walking cost had been estimated from just two parameters and based upon a pooled-sex sample. In the present study, we estimate sex-specific walking cost of Neandertals using a model accounting for body mass, lower limb length, lower limb proportions, and other features of lower limb configuration. Our results suggest that Neandertals needed more energy to walk a given distance than did AMH but the difference was less than half of that previously estimated in males and even far less pronounced in females. In contrast, comparison of the estimated walking cost adjusted to body mass indicates that Neandertals spent less energy per kilogram of body mass than AMH thanks to their lower limb configuration, males having 1–5% lower and females 1–3% lower mass-specific net cost of transport than AMH of the same sex. The primary cause of high cost of transport in Neandertal males is thus their great body mass, possibly a consequence of adaptation to cold, which was not fully offset by their cost-moderating lower limb configuration. The estimated differences in absolute energy spent for locomotion between Neandertal and AMH males would account for about 1% of previously estimated daily energy expenditure of Neandertal or AMH males.

Introduction

It has been proposed that Neandertals had 30% greater gross cost of transport than did contemporary anatomically modern humans (AMH) (Steudel-Numbers and Tilkens, 2004). That would imply greater energy cost of foraging (Weaver and Steudel-Numbers, 2005), reduced effective foraging radius (Verpoorte, 2006; Anwar et al., 2007; MacDonald et al., 2009), and greater daily energy expenditure or at least higher proportion of energy spent on locomotion relative to other activities (MacDonald et al., 2009). These proposed consequences of such high walking cost would have disadvantaged Neandertals in their struggle for survival and in possible competition with AMH (Churchill, 2007; MacDonald et al., 2009). Estimation of Neandertal walking cost is thus important for understanding the life and extinction of Neandertals and the expansion of AMH to Eurasia during the Late Pleistocene.

While previous estimation of Neandertal gross cost of transport (Steudel-Numbers and Tilkens, 2004) was based on a pooled-sex sample, sex-specific estimation of walking cost would be beneficial for drawing inferences about sexual division of labor in this taxon. Furthermore sex-specific analysis avoids biases related to potential differences in male to female proportion in the compared samples. Steudel-Number and Tilkens (2004) estimated gross cost of transport for Neandertals from just two morphological features: body mass and lower limb length; but other features of lower limb configuration also affect walking cost (Pontzer et al., 2009).

Abbreviations: a, ankle; AMH, anatomically modern humans; BMR, basal metabolic rate; COM_{trunk}, trunk's center of mass; COP, center of pressure; EMA, effective mechanical advantage; EUP, early Upper Paleolithic Europeans; g, gravitational acceleration; GRF, ground reaction force; grossCOT, gross or total cost of transport (cost to travel a given distance including basal metabolic cost and postural cost); h, hip; k, knee; l, muscle fascicle length; L_{step}, step length; mass-specific netCOT, mass-specific net cost of transport; MIS, marine isotope stage; MPMH, Middle Paleolithic modern humans; netCOT, net cost of transport (cost to travel a given distance excluding basal metabolic cost and postural cost, energy used exclusively for locomotion); PAR, physical activity ratio; r, muscle moment arm; R, moment arm of the ground reaction force; v, walking speed; V_{musc}, mass-specific volume of muscles activated per distance traveled; σ, constant relating tension to muscle cross-sectional area.

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Although most features of lower limb configuration are very likely intercorrelated in homogenous populations or species and could thus usually be effectively omitted from models linking walking cost to general anatomical variables in such populations (e.g., Steudel-Numbers and Tilkens, 2004), caution should be maintained when extrapolating results of such models to specimens deviating from the lower limb configuration of an initial sample (Kramer and Sylvester, 2009; Pontzer et al., 2009).

Neandertal postcranial morphology is characterized by a wide and relatively high trunk, which results in a great body mass, and by short limbs (Ruff, 1994; Ruff et al., 1997; Holliday, 1997a, 1999). Both the wide voluminous trunk and short limbs have been proposed to reflect structural adaptation to cold environment, as anticipated by Bergmann's and Allen's ecogeographic rules (Ruff, 1994; Holliday, 1997b, 1999). However, the same characteristics (with the exception of upper limb length in humans) also affect walking cost (e.g., Taylor et al., 1982; Pontzer, 2005). The great body mass resulting from a voluminous trunk would impose a heavy load onto Neandertals' lower limbs, which would need to be withstood by bones and overcome by muscles during locomotion. Since most of the energy spent for locomotion is consumed by muscles that oppose gravity (i.e., body weight Griffin et al., 2003), it is reasonable to expect that Neandertals, with their great body mass, would have had high walking cost (at least when expressed as non-adjusted to body mass). In addition, short lower limbs of Neandertals would correspond to short steps. As a result, more steps would be required to cover a given distance and thus Neandertal would expend even more energy for locomotion.

In addition to body mass and lower limb length, however, walking cost is influenced also by other features of the lower limb configuration, among the most important being effective mechanical advantage (EMA) of the limb joints (defined as the ratio of muscle moment arm to moment arm of the ground reaction force) and muscle fascicle length of limb extensors (Biewener, 1989; Roberts et al., 1998; Sockol et al., 2007; Pontzer et al., 2009). Neandertals are reported to have differed considerably from AMH in parameters determining EMA at the knee and ankle (Trinkaus, 1975, 1983; Miller and Gross, 1998; Schmitt, 1998; Trinkaus and Rhoads, 1999). At the knee, Neandertals are expected to have had both parameters determining EMA modified in a direction to maximize knee EMA. The moment arm of the knee extensor, quadriceps femoris, is long due to posteriorly displaced tibial condyles and a thick patella (Trinkaus, 1983, 1986). The moment arm of the ground reaction force at the knee is expected to be short in Neandertals as a consequence of their lower limb proportions (i.e., short tibia relatively to femur) or due to absolutely short lower limbs (Polk, 2004; Gruss, 2007). At the ankle, Neandertals are expected to have had a prolonged muscle moment arm due to a long calcaneus (particularly from the midtalar trochlea to the posterior margin of the calcaneal tuberosity; Trinkaus, 1981, 1983, 1986). A longer calcaneus would have increased the mechanical advantage of ankle plantar flexors through power arm enlargement (Trinkaus, 1983, 1986). It is also to be expected that Neandertals differed from AMH in muscle fascicle lengths, as these seem to reflect the longitudinal characteristics of the limb segments (Griffin et al., 2003) in which Neandertals and AMH clearly differed (Trinkaus, 1981; Holliday, 1999). As a whole, the characteristic lower limb configuration of Neandertals could constitute an effective cost-saving mechanism selected to moderate the impact of their great body mass upon their walking cost. Thus, walking cost estimation accounting for lower limb configuration is desirable for evaluating the possible walking cost differences between Neandertals and AMH.

The goal of this study is to estimate the sex-specific walking cost of Neandertals while accounting for their lower limb configuration in comparison with that of other Late Pleistocene humans. Further, we aim to evaluate the influence of particular features of the Neandertal lower limb configuration on walking cost. We also evaluate the possible influence of the walking cost difference between Neandertals and AMH upon their daily energy expenditure for walking.

Materials and methods

Sample

The compared Late Pleistocene sample consists of 50 individuals (35 males; 15 females; see Supplementary Online Material [SOM] Table S1 for specimens and data sources) divided into three groups: Neandertals (MIS [marine isotope stage] 5–3), Middle Paleolithic modern humans (MPMH; MIS 5), and early Upper Paleolithic Europeans (EUP; MIS 3–2 with an upper limit of 18,000 years BP [before present]). The comparative Holocene sample consists of 21 individuals (15 males; six females) from the Opava-Pivovar burial site, Czech Republic (sixteenth to eighteenth century). The MPMH, EUP and Holocene samples we also refer to as anatomically modern humans (AMH). Due to fragmentation of the Pleistocene material, a single average sex-specific representative of each comparative group was computed from the individual data and further processed in our analyses.

Measurements

We used six measurements defined by Martin (Bräuer, 1988): bipelvic breadth (Pel 2), femoral bicondylar length (Fe 2), femoral head superoinferior diameter (Fe 18), tibial maximum length (Ti 1a), talar articular height (Tal 3b), and calcaneal height (Cal 4). An additional four measurements were also used: skeletal trunk height (Franciscus and Holliday, 1992), tibial condylar displacement (anteroposterior distance, perpendicular to the diaphyseal axis, from the anterior surface of the tibial tuberosity to the line between the anteroposterior centers of the tibial condyles; Trinkaus, 1983; Trinkaus and Rhoads, 1999), subtalar length (distance between the posterior edge of calcaneal tuberosity and the anterior edge of first metatarsal head measured parallel to the basal plane of the subtalar skeleton on the articulated pedal skeleton; Trinkaus, 1975), and posterior pedal moment arm (distance between the posterior edge of the calcaneal tuberosity and the middle of the medial talar trochlear arc measured parallel to the basal plane of the subtalar skeleton on the articulated pedal skeleton; Trinkaus, 1975).

Walking cost estimates

Walking cost can be expressed in various ways, and researchers are far from a consensus about terminology. In the present study, we follow the definitions of Steudel-Numbers et al. (2007) for terms used to discuss the absolute amount of energy spent on walking not adjusted to body mass. In addition, an estimate of cost adjusted to body mass is used here. Thus, we will use three estimates of walking cost: 1) gross cost of transport (grossCOT), which is the cost to travel a given distance and including the costs of keeping a vertical body position and of general metabolism during locomotion; 2) net cost of transport (netCOT), which is the cost to travel a given distance but excluding basal metabolic cost and postural cost, thus representing energy used exclusively for locomotion; and 3) mass-specific net cost of transport (mass-specific netCOT), which is netCOT adjusted by body mass and is ordinarily used for interspecies comparisons.

GrossCOT estimation The gross cost of transport (grossCOT; ml O_2 m^{-1}) was calculated as: