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## Calcaneus length determines running economy: Implications for endurance running performance in modern humans and Neandertals

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## ABSTRACT

The endurance running (ER) hypothesis suggests that distance running played an important role in the evolution of the genus *Homo*. Most researchers have focused on ER performance in modern humans, or on reconstructing ER performance in *Homo erectus*, however, few studies have examined ER capabilities in other members of the genus *Homo*. Here, we examine skeletal correlates of ER performance in modern humans in order to evaluate the energetics of running in Neandertals and early *Homo sapiens*. Recent research suggests that running economy (the energy cost of running at a given speed) is strongly related to the length of the Achilles tendon moment arm. Shorter moment arms allow for greater storage and release of elastic strain energy, reducing energy costs. Here, we show that a skeletal correlate of Achilles tendon moment arm length, the length of the calcaneal tuber, does not correlate with walking economy, but correlates significantly with running economy and explains a high proportion of the variance (80%) in cost between individuals. Neandertals had relatively longer calcaneal tubers than modern humans, which would have increased their energy costs of running. Calcaneal tuber lengths in early *H. sapiens* do not significantly differ from those of extant modern humans, suggesting Neandertal ER economy was reduced relative to contemporaneous anatomically modern humans. Endurance running is generally thought to be beneficial for gaining access to meat in hot environments, where hominins could have used pursuit hunting to run prey taxa into hyperthermia. We hypothesize that ER performance may have been reduced in Neandertals because they lived in cold climates.

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## Introduction

The endurance running (ER) hypothesis, first proposed by Carrier (1984) and further refined by Bramble and Lieberman (2004), suggests that selection for ER capabilities played an important role in the evolution of the genus *Homo*. This hypothesis is supported by multiple lines of anatomical evidence (see Carrier, 1984; Spoor et al., 1994, 2003; Bramble and Lieberman, 2004; Lieberman et al., 2006, 2007, 2009), although various aspects of the hypothesis have been challenged (see comments in Carrier, 1984; Larson et al., 2007; Pickering and Bunn, 2007; Simpson et al., 2008; Larson, 2009). Speculations on the selection pressures that led to increased ER capacity in *Homo* center on the use of persistence hunting (PH) in hot, arid, and partly open habitats (Carrier, 1984; Bramble and Lieberman, 2004; Lieberman, 2006; Lieberman et al., 2007, 2009). During persistence hunting, hominins run at speeds that force animals to gallop, thus preventing them from thermoregulating by

panting, and driving them into hyperthermia. If PH was a key selector for ER performance, then one predicts selection for ER capabilities to vary based on climatic or geographical differences that may limit the use of persistence hunting. Because the genus *Homo* spans a wide geographic range with diverse habitats and climates, inter-specific differences in ER capacity may help us better understand how climate and habitat impacted selection pressures for ER performance.

Neandertals offer an interesting test case for examining climate-related differences in ER performance since they generally inhabited colder climates than other members of the genus *Homo* (Gamble, 1986; Stringer and Gamble, 1993; Steegman et al., 2002; Lieberman et al., 2009), and several researchers have noted possible locomotor differences between Neandertals and modern humans, including potentially reduced ER performance (e.g., Holliday and Falsetti, 1995; Spoor et al., 2003; Finlayson, 2004; Weaver and Steudel-Numbers, 2005; Steudel-Numbers et al., 2007; Weaver, 2009). However, it remains unclear whether or not Neandertal ER performance differed from other hominin taxa. Here, we make use of recent data from both biomechanical modeling and experimental studies that tie lower limb anatomy to the energy costs of ER in

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humans. Using these links, we test the hypothesis that ER performance differed between modern humans and Neandertals. Support for this hypothesis would be consistent with suggested links between climate and ER (e.g., Lieberman et al., 2009).

#### Anatomy and ER performance in humans

Human ER capabilities overlap with even the best mammalian cursors when compared over long distances (Carrier, 1984; Bramble and Lieberman, 2004). Within humans, however, running performance varies greatly. Running economy (the mass-specific energy cost of running at a given speed; ml O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>) is an important example of intra-specific variation in ER performance, and even at the highest levels of human performance, running economy can vary by up to 20–30% (di Prampero et al., 1986; Heise and Martin, 2001; Saunders et al., 2004; Scholz et al., 2008). Further, there is some evidence that running economy is not strongly affected by training (Bailey and Pate, 1991; Lake and Cavanagh, 1996; Franch et al., 1998; Midgley et al., 2007), and is more likely a function of anatomical differences (Scholz et al., 2008). Thus, explaining differences in running economy using skeletal variables may help clarify variations in running energetics and ER performance in the fossil record.

Several decades of research have shown that inter-specific differences in mammalian running economy are mainly consequences of variation in the amount of muscle force required to support body weight (see Taylor et al., 1980; Taylor, 1985; Kram and Taylor, 1990; Roberts et al., 1998; Pontzer, 2007; Sockol et al., 2007; Pontzer et al., 2009). However, intra-specific variation in energy costs of locomotion is more difficult to explain (e.g., Scholz et al., 2008). One likely and major source of intra-specific energy cost variation in humans is the energy recovered from elastic stretching of tendons (Scholz et al., 2008). During running, tendons act like springs, stretching during early stance phase as the springs are loaded, and recoiling and returning energy to the limb during the latter portion of stance phase (Cavagna et al., 1964). The amount of energy that is stored in a tendon is a function of tendon mechanical properties (notably stiffness) as well as the force that stretches the tendon (Scholz et al., 2008). The spring-like function of a tendon is expressed as:

$$F = ku^n \quad (1)$$

where  $F$  is tendon force,  $k$  is the spring constant,  $u$  is the change in tendon length and  $n$  is the order of the spring (linear, quadratic, etc.). The magnitude of  $F$  is determined by the moment arm ( $r$ ) of the tendon (the perpendicular distance of the line of action of the tendon to the joint center of rotation) and the moment at the joint ( $M_j$ ):

$$F = \frac{M_j}{r} \quad (2)$$

Based on these equations, Scholz et al. (2008) developed a simple model to estimate tendon energy ( $E$ ):

$$E = \left( \frac{1}{n+1} \right) M_j^{\left( \frac{n+1}{n} \right)} r^{-\left( \frac{n+1}{n} \right)} k^{-\left( \frac{1}{n} \right)} \quad (3)$$

Since  $k$  is generally calculated based on the maximal isometric muscle force ( $F_{\max}$ ), the resting length of the series elastic element ( $l_{se0}$ ) and the elongation of the tendon at  $F_{\max}$  ( $u_{\max}$ ) (Scholz et al., 2008), Eq. (3) was re-written as:

$$E = \left( \frac{1}{n+1} \right) M_j^{\left( \frac{n+1}{n} \right)} r^{-\left( \frac{n+1}{n} \right)} F_{\max}^{-\left( \frac{1}{n} \right)} l_{se0} u_{\max} \quad (4)$$

Based on these equations, when  $M_j$  is held constant, a smaller moment arm should lead to an increase in tendon energy (Scholz et al., 2008). Scholz et al. (2008) noted from these equations that the length of the moment arm plays a more important role in determining tendon energy storage than the tendon mechanical properties. Using empirical data, Scholz et al. (2008) supported this model and showed that running economy in humans was indeed inversely related to Achilles tendon moment arm length (measured externally from the lateral malleolus to the Achilles tendon). Therefore, because the Achilles tendon moment arm is correlated with the length of the calcaneus (e.g., Miller and Gross, 1998), and because tendon mechanical properties play a much smaller role in determining tendon energy, we can use skeletal anatomy to reconstruct ER performance in the fossil record.

#### Achilles tendon and the evolution of running economy in humans

Bramble and Lieberman (2004) noted that humans have much longer Achilles tendons than the African great apes, which lead to improved elastic energy storage capabilities and therefore improved running economy (see also Lieberman et al., 2009). It is not possible to determine tendon lengths from fossils, but based on the ape-like size of the insertion of the Achilles tendon on the calcaneus of australopiths, one can hypothesize that a well developed Achilles tendon did not evolve until at least the origins of the genus *Homo* (Bramble and Lieberman, 2004).

Unfortunately, the calcaneus is not well represented in fossils of early *Homo* and *Homo erectus*, making it impossible to determine whether or not the calcaneus was under selection for running economy with the origins of the genus *Homo*. However, there are a number of calcanei attributed to Neandertals and to early *Homo sapiens* (EHS) (Trinkaus, 1975, 1983a,b; Schmitt, 1998). Several researchers have pointed out that the Neandertal calcaneus is relatively long compared to modern humans, both overall (Trinkaus, 1975, 1983b; Miller and Gross, 1998; Schmitt, 1998) and in terms of the length of the calcaneal tuber (distance from the talocalcaneal joint surface to the attachment point of the Achilles tendon) (~8% longer; Trinkaus, 1975). Because calcaneal tuber length (CTL) is a better proxy for Achilles tendon moment arm length than overall calcaneus length, the longer calcaneal tuber of Neandertals suggests they may have had increased energy expenditures during ER compared to modern humans. However, this hypothesis is not testable using the Scholz et al. (2008) model since they used an external measurement of Achilles tendon moment arm length that cannot be easily related to skeletal measurements on isolated calcanei. Thus, an accurate reconstruction of ER performance in Neandertals requires tying running economy directly to skeletal variables.

#### Linking ER performance and climate: predictions for Neandertals

Reconstructing ER performance in Neandertals may play an important role in unraveling the links between climate and the evolution of ER, as suggested by Carrier (1984) and Bramble and Lieberman (2004). One key element of the ER hypothesis is that the adoption of this behavior improved foraging success by aiding hominins in PH, and since this technique relies on forcing prey taxa into hyperthermia, its success is constrained by climate. The links between PH success and climate are fundamentally based on exercise physiology in bipeds and quadrupeds. According to the ER hypothesis, hominins used ER to cause animals to gallop over long distances. Since quadrupeds cannot simultaneously pant and gallop (Bramble and Jenkins, 1993), forcing prey animals to gallop for long periods of time in hot environments drives them to hyperthermia. Additionally, heat generation increases with positive allometry

relative to body size (Schmidt-Nielsen, 1997), making PH more effective on larger animals. Since humans can run long distances at speeds above the trot gallop transition of most mammals (Bramble and Lieberman, 2004), and humans lose heat by sweating rather than panting, PH can permit hunters to get close to large mammals after they are immobilized due to heat exhaustion. In particular, when chased, quadrupeds generally gallop away from a predator and then stop to hide and to pant (Carrier, 1984; Liebenberg, 2006; Lieberman et al., 2009). If a human hunter can track the prey and chase it again at a gallop before the animal has restored its normal core body temperature, then the prey's body temperature will continue to rise. Eventually (often within hours), the prey will develop hyperthermia.

It is important to note that ambient temperature greatly affects the time needed to drive an animal into hyperthermia (Lieberman et al., 2009). Studies of environmental temperature on exercise in quadrupeds show that low ambient temperatures do not lead to large exercise-induced changes in body temperature. Entin et al. (1998) showed that in a warm room (mean ambient temperature of 22.4°C), 30 minutes of high intensity exercise (70% of  $\text{VO}_2$  Max) increased core body temperature in sheep to over 41°C. This value is near the range of lethal body temperatures for mammals (42–44°C; Adolph, 1947). However, when running at the same intensity in a cold room (~12°C), core temperatures of these sheep remained within the range of resting temperatures, failing to rise above 39.1°C in any subjects. Ethnographic evidence of PH supports this link to climate. Kalahari Bushmen are known to do most persistence hunts in the hottest times of the day, when ambient temperatures range from 39°C to 42°C (Liebenberg, 2006; Lieberman et al., 2009). Therefore, PH is hypothesized to have increased hunting success rates in hot, arid climates (Lieberman et al., 2009). Since most researchers agree that Neandertals lived in much colder climates than EHS and earlier members of the genus *Homo* (Gamble, 1986; Stringer and Gamble, 1993; Steegman et al., 2002; Lieberman et al., 2009), we predict their ER performance would have been lower than that of modern humans.

To test this prediction, this study attempts to link one aspect of skeletal anatomy, CTL, to running economy in order to evaluate whether or not Neandertals may have had higher energy costs of running compared to modern humans. We first test a model of the relationship between CTL and the energy cost of running in modern humans. Specifically, we hypothesize that CTL will be strongly correlated with mass-specific energy costs in running but not walking. We then apply these data to CTLs in late Pleistocene fossils to make inferences about variation in hominin ER performance. Although this inevitably involves extrapolations from intra-specific data to another taxon, the biomechanical model we test applies equally to Neandertals and humans and should hold constant unless they differed substantially in the use of spring mechanics during ER. Further, there are no other animal models with which to test this hypothesis because of substantial anatomical differences between humans and quadrupeds (in this case, calcaneal morphology is not comparable to other quadrupedal cursors; see Lieberman et al. [2006] and Steudel-Numbers et al. [2007] for similar approaches that use human variation to model ER performance in hominins). We conclude by considering how these differences might relate to environmental and behavioral variation among these taxa.

## Methods

We recruited eight highly trained endurance runners for this research. All subjects gave their informed consent to participate in the project and all procedures were approved by the University of Arizona IRB. Subjects were male, between the ages of 18 and 22, and were all competitive runners with 10K personal bests of less than 36 minutes.

Mean body mass for the sample was  $69.93 \pm 6.14$  kg. We chose trained runners as our sample because, while economy is mainly determined by anatomy (Scholz et al., 2008), training can have a small effect on performance (Franch et al., 1998). Using this population ensures that we remove possible confounding variance in economy arising from low levels of physical fitness and should provide the clearest test of anatomical influences on running performance for use with the fossil record. Although sample sizes were small, the variance in CTL and running economy were substantial within the sample, yielding statistically significant results.

## Running economy

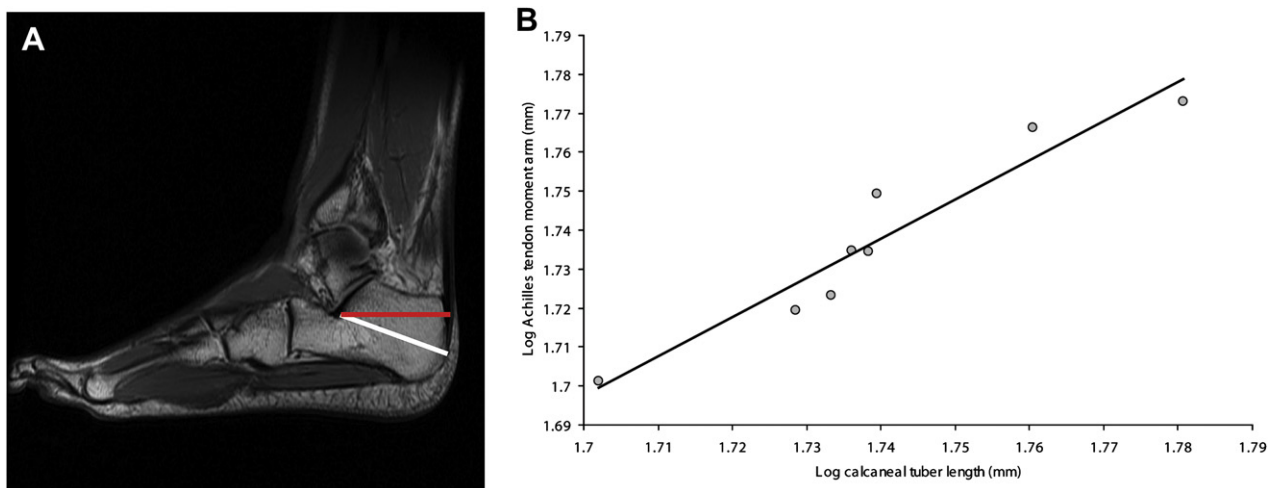
Methods for measuring running economy followed those of Scholz et al. (2008). Oxygen consumption was measured using the open-flow technique (Fedak et al., 1981). Subjects warmed up on a treadmill for 10 minutes. Following the warm-up, treadmill speed was gradually increased to 16 km/hr (Froude number =  $2.27 \pm 0.12$ ). Subjects ran for 10 minutes at this speed. On a second day, subjects returned to the lab to complete a walking trial (with a short warm-up) at 5.4 km/hr, which is approximately preferred human walking speed for this sample (Froude number =  $0.26 \pm 0.01$ ). During locomotor trials, subjects wore a loose-fitting mask, and expired air was collected and analyzed using a Sable Systems firefox oxygen and carbon dioxide analyzer (Sable Systems, Las Vegas, NV, USA). Air was pulled through the mask at  $450 \text{ l min}^{-1}$ . This air was sub-sampled continuously at  $200 \text{ ml min}^{-1}$ , scrubbed of water vapor, and carbon dioxide and oxygen concentrations were analyzed. Data were monitored in real time and recorded at 30 Hz via Vicon Nexus software. Oxygen and carbon dioxide concentrations during the final two minutes of each trial were used to calculate the rate of oxygen consumption ( $\text{ml O}_2 \text{ min}^{-1}$ ) following Lighton (2008). Prior to each locomotor trial, resting rates of oxygen consumption were measured while the subjects stood quietly for 15 minutes. Trials were analyzed only when oxygen consumption visibly reached a plateau (plateaus were identified as less than 10% change in oxygen consumption over the last two minutes of the trial). The net rate of oxygen consumption during walking or running was calculated by subtracting the resting rate of oxygen consumption from the rate of oxygen consumption measured during treadmill trials. The net cost was then divided by body mass to give the mass-specific cost of locomotion at walking and running speeds ( $\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ ).

## Measuring the calcaneus

On a separate day, subjects underwent an MRI scan of their right foot and ankle at the University of Arizona MRI research laboratory. MRI scans were conducted using a GE Excite 3T94 (3.0 Tesla) MRI scanner (repetition time [TR] = 1600; echo time [TE] = 25; slice thickness = 4.0 mm; field of view = 16 cm × 16 cm). Subjects had their ankles placed in a device that immobilized the joint at a 90° angle during the scan. Because of the multiplanar orientation of the compound subtalar joint, this alignment helped ensure that CTL length could be measured in the parasagittal plane.

Calcaneal tuber length was measured using Image J software (Fig. 1), defining CTL as the maximum distance between the posterior edge of the calcaneal tuberosity and the anterior edge of the posterior talocalcaneal surface. Although this measurement is not the exact moment arm of the Achilles tendon (the perpendicular distance from the ankle joint center of rotation to the line of action of the Achilles tendon), it does provide a very similar measurement that can be reproduced on isolated skeletal elements without requiring an articulated foot or soft tissue. We also measured the moment arm of the Achilles tendon (Fig. 1A) to determine how well CTL predicts the actual tendon moment arm.





**Figure 1.** CTL and moment arm measurements. A) Sagittal MRI of foot and ankle. The white line is an approximation of the measurement for CTL and the red line is the actual Achilles tendon moment arm. See text for further details. B) Relationship between CTL and Achilles tendon moment arm measurements. The correlation is significant ( $r = 0.95$ ;  $p = 0.0002$ ). The following ordinary least-squares regression line may be used to determine actual moment arm lengths from isolated calcanei (slope [95% CI] = 1.00 [0.31]; intercept [95% CI] = -0.01 [0.54];  $r^2 = 0.91$ ).

Neandertal ( $n = 7$ ) and fossil EHS ( $n = 13$ ) CTLs were taken from the literature (Trinkaus, 1975, 2000, unpublished data; Baba and Endo, 1982; Schmitt, 1998; Sladek et al., 2000). We used only specimens identified as male (Ruff et al., 1997; Trinkaus, pers. comm.) in the analysis, since our living human sample was restricted to male runners. When both left and right calcanei were available, mean values were used in the analysis. If more than one measurement was available for a single specimen, mean values of all measurements were used in the analysis. Estimates of Neandertal and EHS body masses were taken from Ruff et al. (1997, 2005) for each specimen and a ratio of CTL to the cube root of body mass was calculated to control for size differences in the sample (following Christiansen, 2002). Specimens used and calcaneus dimensions are presented in Table 1.

#### Statistical analyses

We examined the relationship between CTL, Achilles tendon moment arm, and running economy in two ways. Most biomechanical analyses use the mass-specific energy costs of running at a given speed ( $\text{ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ ) as their primary measure of economy (e.g., Scholz et al., 2008). We calculated a Pearson moment correlation between economy and the anatomical variable of interest (CTL and true Achilles tendon moment arm length) and determined the relationship between these variables using a quadratic function of the form  $y = ax^{-2} + c$ , following Scholz et al. (2008). This quadratic function is used because it corresponds to the model of spring mechanics (assuming a linear spring where  $n = 1$ ) previously shown to predict running economy in humans (Scholz et al., 2008). As an alternative size correction for running economy, we calculated residuals from the least-squares regression line describing the relationship between body mass and energy cost of running ( $\text{ml O}_2 \text{ min}^{-1}$ ) in log space. These residuals are then used in linear regression analyses with anatomical variables. Due to the small sample size, we conducted a post-hoc power analysis using G\*Power 3 software (see Faul et al., 2007) to assess the chance that we incorrectly rejected the null hypothesis (in this case, that there is no correlation between anatomy and economy and that any slope describing this relationship will not significantly differ from zero). We used data from Scholz et al. (2008) to generate an appropriate effect size for both the correlation analysis and for a linear regression of the variables. For comparisons of anatomy

between modern humans and Neandertals, we used one-tailed t-tests with a Bonferroni adjustment for multiple comparisons to account for the possibility of Type I error.

#### Results

Calcaneal tuber length and Achilles tendon moment arm length are highly correlated ( $r = 0.96$ ;  $p = 0.0002$ ; Fig. 1B), indicating measurements on isolated calcanei can be used to estimate moment arm lengths. The relationship between Achilles tendon moment arm length and running economy at 16 km/hr is highly significant ( $p < 0.005$ ) and Achilles tendon moment arm length explains 64% of the variation in mass-specific energy costs of running at this speed in our human sample (Fig. 2A). The coefficients of the nonlinear best-fit equation match those found by Scholz et al. (2008) (Table 2). The relationship between CTL and running economy at 16 km/hr is also highly significant ( $p < 0.005$ ) and CTL explains 80% of the variation in mass-specific energy costs of running at this speed in our human sample (Fig. 2B). As predicted, CTL and Achilles tendon moment arm length are not significantly correlated with walking economy ( $p = 0.13$  and  $p = 0.12$ , respectively). Further, other anatomical variables (body mass, height, lower leg length, hind limb length) were not correlated with walking or running economy (Table 3).

In addition to examining mass-specific energy costs, we controlled for the effects of body size on running economy by calculating residuals of running economy ( $\text{ml O}_2 \text{ min}^{-1}$ ) from body mass using a least-squares regression in log space. The correlation between Achilles tendon moment arm length and residual running economy is very strong ( $r = 0.79$ ;  $p = 0.02$ ; Fig. 2C), as is the correlation between CTL and residual running economy ( $r = 0.88$ ,  $p = 0.004$ ; Fig. 2D).

Given the small sample size of modern humans used here, we took an additional step to rule out the possibility of Type II errors. Following Faul et al. (2007), we performed a post-hoc power analysis of our correlation and regression analyses. A post-hoc power test shows that our results have high power (87% and 86% for correlation and regression models, respectively), providing us with a robust analysis to examine fossil calcanei in this context.

To explore the evolutionary implications of these results, we first examined the possibility that body mass could confound a comparison of CTLs in the fossil record. CTL is not significantly correlated with body mass in the human sample ( $r = 0.10$ ;  $p = 0.81$ ), the

**Table 1**  
Subject data from human participants, fossil EHS, and Neandertals.

Sample	Subject	Side	Body mass (kg)	Achilles tendon moment arm length (mm)	Calcaneus body length (mm)	Size-corrected CTL <sup>a</sup>	Walk VO <sub>2</sub> (ml kg <sup>-1</sup> min <sup>-1</sup> )	Run VO <sub>2</sub> (ml kg <sup>-1</sup> min <sup>-1</sup> )	Lower prediction interval	Upper prediction interval
Modern humans (this study)	1	Right	77.30	59.30	60.35	14.17	12.09	55.47		
	2	Right	68.80	52.87	54.12	13.21	10.41	51.14		
	3	Right	70.90	52.40	53.52	12.93	10.90	52.74		
	4	Right	73.60	56.14	54.88	13.10	10.55	51.35		
	5	Right	62.30	58.40	57.61	14.53	12.92	53.57		
	6	Right	76.30	54.30	54.47	12.84	9.90	48.85		
	7	Right	60.20	54.26	54.75	13.97	10.17	51.33		
	8	Right	70.00	50.26	50.35	12.22	11.00	44.91		
		Mean		69.93	54.74	55.00	13.37	10.99	51.17	
	Standard deviation		6.14	3.06	2.94	0.78	1.02	3.19		
Fossil EHS	Skhul 4	Left <sup>1</sup>	74.40		60.00	14.27		55.67	51.03	60.31
	Predmostí III	Average <sup>2</sup>	73.00		62.50	14.95		57.44	52.30	62.58
	Predmostí XIV	Average <sup>2</sup>	64.20		60.50	15.11		56.04	51.31	60.78
	Chancelade	Left <sup>2</sup>	64.50		61.00	15.21		56.40	51.57	61.24
	Oberkassel 1	Right <sup>2</sup>	72.40		61.00	14.64		56.40	51.57	61.24
	Qafzeh 8	Left <sup>2</sup>	77.40		59.00	13.84		54.89	50.43	59.35
	Dolní Věstonice 13	Left <sup>3</sup>	68.00		54.00	13.23		50.36	46.29	54.42
	Dolní Věstonice 16	Left <sup>3</sup>	71.00		57.90	13.98		54.00	49.71	58.28
	Ohalo 2	Average <sup>3</sup>	73.50		55.00	13.13		51.36	47.32	55.41
	Minatogawa 1	Left <sup>3</sup>	60.30		45.00	11.48		38.06	30.29	45.83
	Paviland	Average <sup>3</sup>	74.80		57.00	13.53		53.22	49.05	57.40
	Dolní Věstonice 15	Average <sup>3</sup>			53.85			50.25	46.18	54.32
	Sungir 1	Average <sup>3</sup>			57.20			53.40	49.20	57.59
		Mean		70.32		57.23	13.94		52.88	48.17
	Standard deviation		5.35		4.61	1.10		5.04	5.74	4.44
Neandertals	La Chapelle 1	Left <sup>1</sup>	75.80		58.70	13.87		54.65	50.24	59.06
	La Ferrassie 1	Left <sup>4</sup>	85.00		65.83	14.97		59.48	53.65	65.32
	Kiik-Koba 1	Average <sup>4</sup>	78.10		64.48	15.08		58.72	53.16	64.28
	Regourdou 2	Right <sup>4</sup>	72.10		57.70	13.86		53.83	49.57	58.09
	Spy 2	Right <sup>4</sup>	83.60		58.60	13.40		54.57	50.18	58.97
	Shanidar 1	Average <sup>5</sup>	80.50		65.55	15.18		59.37	53.58	65.16
	Amud 1	Left <sup>2</sup>	70.30		63.00	15.26		57.77	52.53	63.02
		Mean		77.91		61.98	14.52		56.91	51.84
	Standard deviation		5.56		3.54	0.78		2.47	1.78	3.17

Notes: <sup>a</sup>Size-corrected CTL is tuber length divided by the cube root of body mass.

Tuber lengths are from: <sup>1</sup>Trinkaus (1975), <sup>2</sup>Schmitt (1998), <sup>3</sup>Trinkaus (unpublished data), <sup>4</sup>average of data from Trinkaus (1975) and Schmitt (1998), and <sup>5</sup>Trinkaus (1983a). All body mass estimates for Neandertals and fossil EHS are from Ruff et al. (1997: supplementary data) with the following exceptions: body masses for Skhul 4, Predmostí III, Predmostí XIV, Paviland, and La Chapelle 1 are from Ruff et al. (2005). Estimates of running economy for fossil hominins calculated using the CTL vs. mass-specific running economy equation in Table 2.

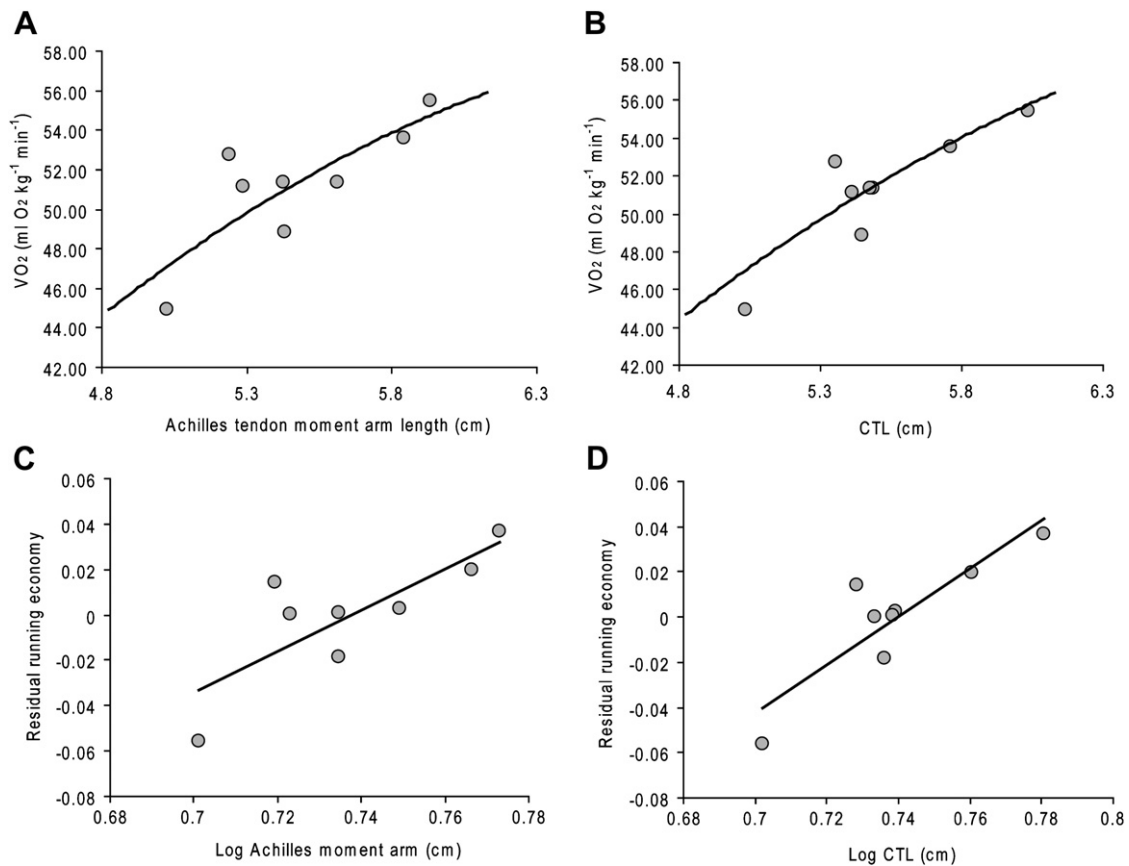
Neandertal sample ( $r = 0.31$ ;  $p = 0.50$ ), or the fossil EHS sample ( $r = 0.50$ ;  $p = 0.12$ ).

Mean CTL measured from MRI scans in this study (mean  $\pm$  SD =  $55.00 \pm 2.94$ ) is similar to values collected from caliper measurements from larger samples of modern human calcanei by Trinkaus (1975; mean  $\pm$  SD for Libben sample [ $n = 40$ ] =  $53.9 \pm 3.6$ ; mean for Keneh sample [ $n = 25$ ] =  $54.5 \pm 4.3$ ) and by Latimer and Lovejoy for the Hamann–Todd collection (1989; mean  $\pm$  SD [ $n = 20$ ] =  $53.8 \pm 3.19$ ). This similarity indicates that, even though our living sample is composed of trained runners, their CTLs do not reflect a bias toward small tuber length. CTLs in fossil EHS do not significantly differ from those of humans in this study (Table 4). Absolute tuber length is significantly longer in Neandertals compared to both modern humans in this study and fossil EHS (Table 4). Differences found remain significant after using a Bonferroni adjustment to account for multiple comparisons (Table 4).

When CTL is corrected for body mass (tuber length/[body mass<sup>1/3</sup>]), the difference between Neandertals and modern humans remains significant (Fig. 3B; Table 5). However, relative to body mass, fossil EHS falls in between extant modern humans and Neandertals. T-tests show no significant difference between EHS and extant modern humans and no significant difference between fossil EHS and Neandertals (Table 5).

Differences found remain significant after using a Bonferroni adjustment to account for multiple comparisons (Table 5).

If we assume that running biomechanics of Neandertals and *H. sapiens* are roughly similar in that both use similar spring mechanics, we can estimate the energy costs of running in Neandertals and fossil EHS using the human regression describing the relationship between CTL and mass-specific running economy (Table 2). We calculated Neandertal and fossil EHS estimated energy costs of running using both the quadratic regression line (mass-specific running economy vs. CTL) and upper and lower 95% prediction intervals of this regression line. These estimates must be taken with caution since the Neandertal data fall outside of the range of the human dataset and prediction intervals in this range are very wide. On average, Neandertal energy costs of running were 11.4% (SD = 2.47) higher than modern humans (mean upper and lower prediction intervals are both higher than mean running economy in modern humans; Table 1). EHS energy costs would have been, on average 6.88% (SD = 5.04) higher than the extant sample of modern humans, however, the 95% prediction intervals encompass the modern human mean (see Table 1). Although the calcaneal data suggest higher energy costs in Neandertals, one must use these estimated energy costs with much caution, since values estimated



**Figure 2.** Relationship between anatomical variables and locomotor energetics. A) The energy cost of running (ml O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>) at 16 km/hr regressed on Achilles tendon moment arm length. B) The energy cost of running (ml O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>) at 16 km/hr regressed on calcaneus tuber length. C) Residuals of running economy (ml O<sub>2</sub> min<sup>-1</sup>) from body mass regressed on Achilles tendon moment arm length. D) Residuals of running economy (ml O<sub>2</sub> min<sup>-1</sup>) from body mass regressed on calcaneus tuber length. See Table 2 for regression statistics.

outside of the range of the regression sample are subject to large amounts of error.

**Discussion**

The strong correlation between CTL and running economy supports the hypothesis that storage and release of elastic strain energy in the Achilles tendon plays an important role in reducing the energy costs of human running (i.e., Scholz et al., 2008). This spring-like action of the Achilles tendon during running means that individuals with short calcaneal tubers stretch their Achilles tendons to a greater degree and therefore convert a higher percentage of kinetic energy into elastic energy, which is then returned leading to lower energy costs. Importantly, calcaneal length is not correlated with the energy costs of walking, providing a powerful argument for using CTL as a performance marker for solely ER.

Although we compared calcaneal tuberosity lengths across taxa both before and after controlling for differences in body mass, there is reason to think that raw calcaneal tuberosity measures are most relevant here. Absolute CTLs will determine the moment arm of the

Achilles tendon and will therefore determine how much stretching occurs. Additionally, body masses of fossil taxa are estimates and comparisons of size-corrected CTLs are therefore less reliable. The high correlation between calcaneal tuberosity length and the energy costs of ER means that one can tentatively assess running economy in fossil humans from skeletal measurements. Based on absolute values of calcaneal tuberosity lengths, our data suggest that *H. sapiens*, both fossil and extant, would have had lower energy costs of running compared to Neandertals.

*Is a short calcaneus an adaptation for ER?*

There are two problems that impede testing the hypothesis that a short calcaneus is an adaptation for improved running economy in the genus *Homo*. First, without calcanei attributed to early *Homo*, we cannot assess running economy in these species using this method. Second, we lack the definitive evidence necessary to test whether or not the Achilles tendon was elongated in australopiths (Bramble and Lieberman, 2004; Lieberman et al., 2009). Absolute calcaneus tuber length in *Australopithecus afarensis* is intermediate

**Table 2**  
Regression coefficients for relationships between anatomy and running economy.

Relationship	Regression model	a (95% CI)	c (95% CI)	r <sup>2</sup>	p
Moment arm vs. mass-specific economy	y = ax <sup>-2</sup> + c	-685.10 (513.8)	74.22 (17.38)	0.64	0.02
CTL vs. mass-specific economy	y = ax <sup>-2</sup> + c	-815.2 (412.4)	78.31 (13.79)	0.80	0.005
Moment arm vs. residual economy	y = ax + c	0.91 (0.70)	-0.67 (0.52)	0.62	<0.0001
CTL vs. residual economy	y = ax + c	1.06 (0.58)	-0.78 (0.43)	0.77	0.0003

Note: p-values are for Pearson moment correlations.

**Table 3**

Correlation statistics for anthropometric variables with running and walking economy.

Variable	r (running)	p-value (running)	r (walking)	p-value (walking)
Body mass	0.03	0.94	0.26	0.53
Limb length	0.44	0.28	0.36	0.38
Height	0.50	0.21	0.07	0.87
Foot length	0.02	0.96	0.10	0.81

between *Pan troglodytes* and *H. sapiens* (Latimer and Lovejoy, 1989), however, we lack body size estimates for these specimens, making it difficult to compare them directly with modern human or Neandertal calcanei. Because *A. afarensis* was likely smaller in body mass than modern humans and Neandertals (McHenry, 1992), it is reasonable to hypothesize that there was no major reduction in the length of the calcaneal tuber with the transition from *Australopithecus* to *Homo*. Calcanei from individuals with associated body mass estimates are needed to test this hypothesis.

Without more fossil data, we are left with the problem of a two-taxon analysis (Garland and Adolph, 1994). Garland and Adolph (1994) argued convincingly that, for the most part, two taxon comparisons cannot allow us to test hypotheses of adaptation. Thus, we must be cautious about interpreting these differences in CTL as the result of selection. That said, basing our comparative analysis on an explicit prediction from a biomechanical model increases our confidence in these results (i.e., Spencer and Demes, 1993) and differences in CTL length should permit accurate assessments of the relative differences in cost unless the biomechanics of energy storage by the Achilles tendon was different in these closely related species. Further, despite the lack of data available for early *Homo*, data from EHS do allow us to hypothesize that a reduction in CTL is not a recent feature. Short calcaneal tubers compared to Neandertals are evident in fossil EHS including those that overlap in time with Neandertals (e.g., Qafzeh: >80 ka; Stringer et al., 1989). Although CTLs relative to body mass in EHS fall intermediate between extant modern humans and Neandertals, it is the absolute tuber length that determines mass-specific energy costs of running (Fig. 2). Thus, EHS would have had relatively lower energy costs of ER compared to Neandertals, with the caveat that adaptive inferences will require a larger sample of calcanei from more species.

#### Implications for endurance running performance in Neandertals

Previous research by Trinkaus (1975, 1983a,b), and Schmitt (1998) showed that Pleistocene hominins exhibit considerable calcaneus size variation, with Neandertals having relatively large calcanei compared to modern humans and earlier specimens of EHS. Our results support these conclusions and further show that the large calcanei of Neandertals compared to extant humans are not due simply to increased body mass.

As previously noted, the relatively long Achilles tendon moment arms in Neandertals would have increased the mechanical advantage of the plantar flexors and thus provided an advantage in torque

**Table 4**

Significance of t-tests comparing mean CTLs in humans from this study, fossil EHS, and Neandertals. Values given are one-tailed p-values (p-value after Bonferroni adjustment).

Sample	This study	Fossil EHS	Neandertal
This study	x	0.12 (0.36)	<b>0.0005 (0.002)</b>
Fossil EHS	x	x	<b>0.0146 (0.04)</b>
Neandertal	x	x	x

Note: Bold values are significant following a Bonferroni adjustment to account for multiple comparisons.

generation capabilities, which may have improved locomotor performance when walking on irregular or uneven terrain (Trinkaus, 1986; Miller and Gross, 1998). This interpretation is correct in the sense that Neandertal ankle plantar flexors could produce larger moments with the same muscle force when compared with modern humans. Alternatively, large Achilles tendon moment arms would have required less muscle force in Neandertals than modern humans to produce a given ankle moment. However, results presented above indicate that increased plantar flexion efficiency comes at the cost of larger moment arms that would have increased energy costs during ER.

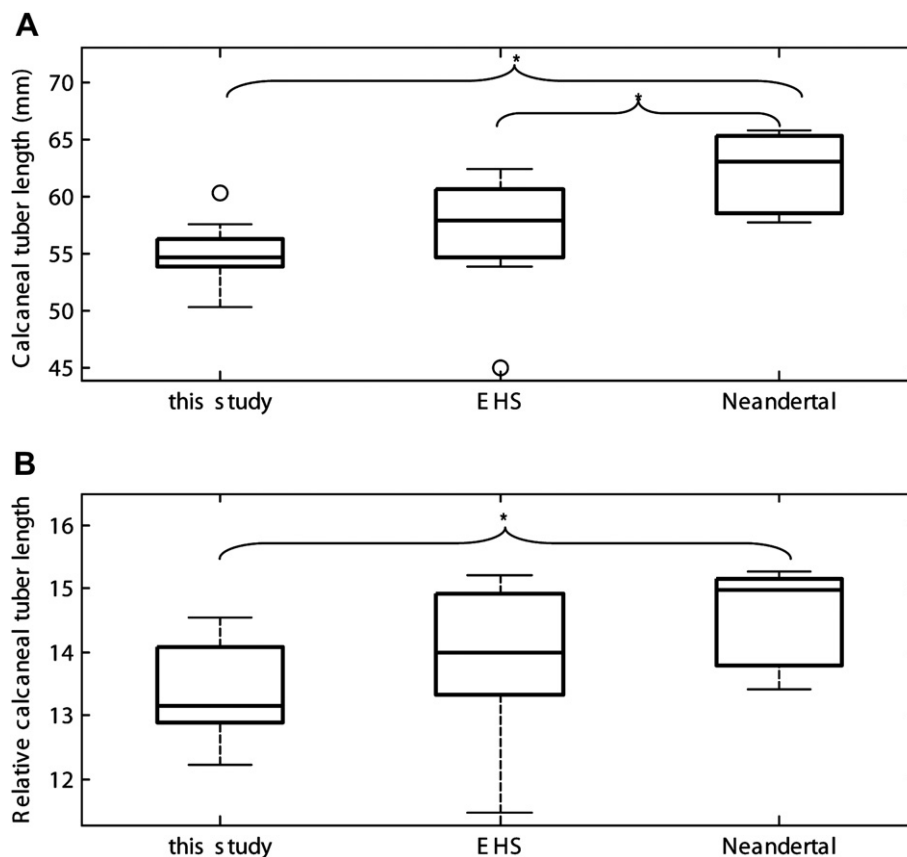
These results are consistent with a few other lines of evidence suggesting reduced ER capabilities in Neandertals. For example, Spoor et al. (2003) noted that Neandertal semicircular canal morphology differs significantly from both modern humans and from *H. erectus*. The semicircular canal system senses angular rotations of the head and plays a major role in coordinating head, eye, and body movements (Spoor and Zonneveld, 1998). The diameter of the canals is tuned to the frequency spectrum of head movements experienced by a particular taxon, with relatively larger canal dimensions strongly associated with animals that engage in faster, more agile locomotor behaviors that cause higher angular accelerations of the head (Spoor and Zonneveld, 1998; Spoor et al., 2007). Humans have relatively larger anterior and posterior semicircular canals compared to great apes and australopiths (Spoor et al., 1994, 1996). Since these canals sense head pitching, Spoor et al. (1994, 1996) suggested that enlargement of these canals were adaptations for agile behavior, and possibly for running. Anterior and posterior semicircular canal enlargement is present in *H. erectus* (Spoor et al., 1994), however, there is a decrease in the diameter of these canals relative to body mass in Neandertals (Spoor et al., 2003). This reduction in size suggests that Neandertals were engaging in less rapid locomotion, leading Spoor et al. (2003) to infer that their morphology was more consistent with endurance walking (trekking) rather than endurance running. Other features of Neandertals also imply they did not engage in regular ER (Spoor et al., 2003). For example, their relatively short limbs and increased body mass are not consistent with selection for increased ER performance (Spoor et al., 2003; see also Pontzer, 2005, 2007; Steudel-Numbers et al., 2007).

Our results from the calcaneus provide an independent line of evidence to support Spoor et al.'s (2003) interpretations of Neandertal locomotor performance. In both absolute and relative terms, Neandertal calcanei are larger than those of modern humans. Based on the strong positive correlation between calcaneus tuber length and the energy costs of running, these results suggest that Neandertals were not economical runners compared to modern humans. This does not mean Neandertals could not have engaged in ER, but rather that they did so less frequently and/or it was less important for their subsistence strategy.

#### Climate and ER performance in Neandertals

The results of this study allow us to further explore the possible links between ER performance and climate. There are two main hypothesized selection pressures for ER (Carrier, 1984; Bramble and Lieberman, 2004), both of which may be relevant to the higher estimated energy costs of ER in Neandertals. Each of these hypotheses focuses on improved access to animal protein during diurnal hot and arid conditions. First, it is possible that ER evolved to improve scavenging success (Bramble and Lieberman, 2004; Lieberman et al., 2009). Under this scenario, ER would allow hominins to gain access to distant carcasses faster than other carnivores (Bramble and Lieberman, 2004; Lieberman et al., 2009). Alternatively, or additionally, ER may have been selected to improve hunting performance





**Figure 3.** CTL in humans and Neandertals. Asterisk indicates significant difference between two samples ( $p < 0.05$ ; see Tables 4 and 5). A) Absolute values of the length of the calcaneal tubers in Neandertals, modern humans, and fossil EHS. Difference between Neandertal and modern human samples is significant. Difference between humans and fossil EHS is not significant. Difference between fossil EHS and Neandertals is significant. B) Size-corrected values of the CTLs in Neandertals and modern humans. Size correction is CTL divided by the cube root of body mass. Difference between Neandertal and modern human samples is significant. Difference between humans and fossil EHS is not significant. Difference between fossil EHS and Neandertals is not significant.

prior to the invention of projectile weapon technology (Carrier, 1984; Bramble and Lieberman, 2004; Lieberman et al., 2009). PH is particularly relevant for the discussion of Neandertal ER capabilities since Neandertals hunted medium- to large-sized game (Chase, 1986; Stiner, 1994, 2002; Kuhn and Stiner, 2006) in relatively cold, temperate climates and habitats. In cold conditions, PH would probably not produce the necessary change in prey body temperature to effectively immobilize an animal (e.g., Entin et al., 1998). Thus, PH in cold climates would not likely produce a hyperthermic response, even if predators kept prey taxa running at very high intensities.

These climatic constraints on PH likely reduced the need to effectively use ER in Neandertals because previous research strongly suggests that Neandertals lived in very cold habitats (Stringer and Gamble, 1993; Steegman et al., 2002). Many aspects of Neandertal anatomy seem related to cold-climate living (Coon, 1962; Trinkaus, 1981; Holliday, 1995, 1997; Steegman et al., 2002).

**Table 5**

Significance of t-tests comparing CTLs relative to the cube root of body mass in humans from this study, fossil EHS, and Neandertals. Values given are one-tailed  $p$ -values ( $p$ -value after Bonferroni adjustment).

Sample	This study	Fossil EHS	Neandertal
This study	x	0.11 (0.34)	<b>0.007 (0.02)</b>
Fossil EHS	x	x	0.12 (0.37)
Neandertal	x	x	x

Note: Bold values are significant following a Bonferroni adjustment to account for multiple comparisons.

For example, increased body mass relative to height is thought to reflect “Bergmann’s rule,” reducing skin surface area relative to body mass to increase heat retention (Holliday, 1997). Low brachial and crural indices in Neandertals are thought to reflect “Allen’s rule,” again reducing skin surface area of extremities to increase heat retention (Holliday, 1997). Comparing crural and brachial indices across human populations living in a variety of climates, Holliday (1995) showed that Neandertal intra-limb proportions are consistent with mean annual temperatures of between 2.4°C and –1.7°C. These anatomically-based predictions coincide with paleoclimatic reconstructions. At most Neandertal sites, mean annual paleotemperatures average between 0°C and –15°C over the entire range of Neandertal occupation dates (250–30 ka) (Steggman et al., 2002). Mean summer paleotemperatures are reconstructed between 5°C and 15°C (Steggman et al., 2002). These temperatures place Neandertals in cold temperate to sub-arctic conditions over long time periods (Gamble, 1986; Stringer and Gamble, 1993; Steegman et al., 2002), which would limit, if not prohibit, the possibility of using ER to run animals into hyperthermia for much of the year.

Paleopathological and archaeological evidence are also consistent with the hypothesis that Neandertals did not regularly engage in PH. Although Neandertals hunted medium- and large-sized game (Chase, 1986; Stiner, 1994, 2002; Kuhn and Stiner, 2006), they likely did so at close range and without the advantages of immobilization due to hyperthermia. Weapons available to Neandertals were more suited to close range use (e.g., thrusting) (Berger and Trinkaus, 1995), and Neandertal upper limb morphology does not

suggest the ability for high performance throwing (Churchill and Trinkaus, 1990). Thus, Neandertals must have engaged in hunting methods that required close range use of their weapons. As described above, in hot climates, PH allows hunters to use thrusting weapons at close range with very little risk of injury. Without immobilizing their prey through hyperthermia, Neandertals would have been subject to increased injury risk from prey that were either not immobilized prior to attack, or immobilized by less effective means (e.g., in marshes, traps, etc.). This inference accords with evidence that Neandertals experienced trauma, especially in the upper limbs, at rates higher than all but one population of modern hunter-gatherers (Underdown, 2006), and the patterns of skeletal trauma in Neandertals are consistent with injury due to close contact with large mammals (Berger and Trinkaus, 1995; but see Underdown, 2006). Thus, the available evidence suggests that Neandertals often dispatched their prey at close distances and that their prey were not always effectively immobilized.

#### Implications of increased ankle extensor moment arms for Neandertals

An interesting problem generated by this project concerns why Neandertals had relatively longer calcaneal tubers. One possibility is that the last common ancestor of Neandertals and modern humans had long calcanei, and short calcanei are a derived feature of *H. sapiens*. Another possibility is selection for relatively long calcaneal tubers in Neandertals compared to other members of the genus *Homo*. Since CTL is not correlated with walking economy, increased moment production capabilities do not reduce the energy costs of walking at a given speed. However, increased CTL may have improved performance in other activities that require large amounts of moment production in the ankle planter flexors. For example, walking uphill significantly increases ankle moment production (McIntosh et al., 2006), while running uphill has no significant effect on moment production at the ankle (Roberts and Belliveau, 2005). Thus, the relatively long calcaneal tubers of Neandertals may have improved walking performance over uneven or mountainous terrain. In addition to uphill walking, jumping requires extremely large ankle moments (e.g., Thorpe et al., 1998). Neandertals would have had reduced muscle forces for a given ankle moment during jumping compared to modern humans. Thus, it appears that Neandertal calcanei and force production capabilities are well suited for performance in more varied movements, while calcanei of modern humans permit more economical running.

The possibility that selection acted to increase Neandertal calcaneal tubers relative to other members of the genus *Homo* raises the question of whether relatively short calcanei are, in fact, a response to selection for increased ER economy in *Homo*. Although fossil data suggest that *H. erectus* has some adaptations for ER (e.g., Bramble and Lieberman, 2004; Lieberman et al., 2009), there are no calcaneus specimens attributed to this species. Since fossil calcanei from EHS are short compared to Neandertals, it is possible that either relatively short calcanei evolved with the origins of the genus *Homo*, or with the origins of modern humans. Until remains of calcanei are found for *H. erectus*, it is not currently possible to determine which of these two possibilities is correct.

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#### References

- Adolph, E.F., 1947. Tolerance to heat and dehydration in several species of mammals. *Am. J. Physiol.* 151, 564–575.
- Baba, H., Endo, B., 1982. Postcranial skeleton of the Minatogawa man. In: Suzuki, H., Hanihara, K. (Eds.), *The Minatogawa Man: The Upper Pleistocene Man from the Island of Okinawa*. Bulletin of the University Museum, University of Tokyo, Tokyo, pp. 61–195.
- Bailey, S.P., Pate, R.R., 1991. Feasibility of improving running economy. *Sports. Med.* 12, 228–236.
- Berger, T.D., Trinkaus, E., 1995. Patterns of trauma among the Neandertals. *J. Archaeol. Sci.* 22, 841–852.
- Bramble, D.M., Jenkins, F.A., 1993. Mammalian locomotor-respiratory integration: implications for diaphragmatic and pulmonary design. *Science* 262, 235–240.
- Bramble, D.M., Lieberman, D.E., 2004. Endurance running and the evolution of *Homo*. *Nature* 432, 345–352.
- Carrier, D.R., 1984. The energetic paradox of human running and hominid evolution. *Curr. Anthropol.* 25, 483–495.
- Cavagna, G.A., Saibene, F.P., Margaria, R., 1964. Mechanical work in running. *J. Appl. Physiol.* 19, 249–256.
- Chase, P.G., 1986. The Hunters of the Combe Grenal: Approaches to Middle Paleolithic Subsistence in Europe. BAR Intl. Series 286.
- Christiansen, P., 2002. Locomotion in terrestrial mammals: the influence of body mass, limb length and bone proportions on speed. *Zool. J. Linn. Soc.* 136, 685–714.
- Churchill, S.E., Trinkaus, E., 1990. Neanderthal scapular glenoid morphology. *Am. J. Phys. Anthropol.* 83, 147–160.
- Coon, C.S., 1962. *The Origin of Races*. Alfred A. Knopf, New York.
- di Prampero, P.E., Atchou, G., Brueckner, J.C., Moia, C., 1986. The energetics of endurance running. *Eur. J. Appl. Physiol.* 55, 259–266.
- Entin, P.L., Robertshaw, D., Rawson, R.E., 1998. Thermal drive contributes to hyperventilation during exercise in sheep. *J. Appl. Physiol.* 85, 318–325.
- Faul, F., Erdfelder, E., Lang, A., Buchner, A., 2007. G\*Power 3: a flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behav. Res. Meth.* 39, 175–191.
- Fedak, M.A., Rome, L., Seeherman, H.J., 1981. One-step N2-dilution technique for calibrating open-circuit VO2 measuring systems. *J. Appl. Physiol.* 51, 772–776.
- Finlayson, C., 2004. *Neanderthals and Modern Humans: An Ecological and Evolutionary Perspective*. Cambridge University Press, Cambridge.
- Franch, J., Madsen, K., Djurhuus, M.S., Pedersen, P.K., 1998. Improved running economy following intensified training correlated with reduced ventilatory demands. *Med. Sci. Sports. Exerc.* 30, 1250–1256.
- Gamble, C., 1986. *The Paleolithic Settlement of Europe*. Cambridge University Press, Cambridge.
- Garland Jr., T., Adolph, S.C., 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiol. Zool.* 67, 797–828.
- Heise, G.D., Martin, P.E., 2001. Are variations in running economy in humans associated with ground reaction force characteristics? *Eur. J. Appl. Physiol.* 84, 438–442.
- Holliday, T.W., 1995. *Body size and proportions in the Late Pleistocene western old world and the origins of modern humans*. Ph.D. Dissertation, University of New Mexico.
- Holliday, T.W., 1997. Postcranial evidence of cold adaptation in European Neandertals. *Am. J. Phys. Anthropol.* 104, 245–258.
- Holliday, T.W., Falsetti, A.B., 1995. Lower limb length of European early modern humans in relation to mobility and climate. *J. Hum. Evol.* 29, 141–153.
- Kram, R., Taylor, C.R., 1990. Energetics of running: a new perspective. *Nature* 346, 265–267.
- Kuhn, S.L., Stiner, M.C., 2006. What's a mother to do? The division of labor among Neandertals and modern humans in Eurasia. *Curr. Anthropol.* 47, 953–980.
- Lake, M.J., Cavanagh, P.R., 1996. Six weeks of training does not change running mechanics or improve running economy. *Med. Sci. Sports. Exerc.* 28, 860–869.
- Larson, S.G., 2009. Evolution of the hominin shoulder: Early *Homo*. In: Grine, F.E., Fleagle, J.G., Leakey, R.E. (Eds.), *The First Humans: Origin and Early Evolution of the Genus Homo*. Springer, New York, pp. 65–76.
- Larson, S.G., Jungers, W.L., Morwood, M.J., Jatmiko, Sutikna, T., Saptomo, E.W., Rokus Awe Due, Djubiantono, T., 2007. *Homo floresiensis* and the evolution of the hominin shoulder. *J. Hum. Evol.* 53, 718–731.
- Latimer, B., Lovejoy, C.O., 1989. The calcaneus of *Australopithecus afarensis* and its implications for the evolution of bipedality. *Am. J. Phys. Anthropol.* 78, 369–386.
- Liebenberg, L., 2006. Persistence hunting by modern hunter-gatherers. *Curr. Anthropol.* 47, 1017–1026.
- Lieberman, D.E., Bramble, D., Raichlen, D.A., Shea, J.J., 2007. Endurance running and the tyranny of ethnography: a reply to Pickering and Bunn. *J. Hum. Evol.* 53, 434–437.
- Lieberman, D.E., Bramble, D.M., Raichlen, D.A., Shea, J.J., 2009. Brains, brawn, and the evolution of human endurance running capabilities. In: Grine, F.E.,

- Fleagle, J.G., Leakey, R.E. (Eds.), *The First Humans: Origins and Early Evolution of the Genus Homo*. Springer, New York, pp. 77–92.
- Lieberman, D.E., Raichlen, D.A., Pontzer, H., Bramble, D., Cutright-Smith, E., 2006. The human gluteus maximus and its role in running. *J. Exp. Biol.* 209, 2143–2155.
- Lighton, J.R.B., 2008. *Measuring Metabolic Rates: A Manual for Scientists*. Oxford University Press, New York.
- McHenry, H.M., 1992. Body size and proportions in early hominids. *Am. J. Phys. Anthropol.* 87, 407–431.
- McIntosh, A.S., Beatty, K.T., Dwan, L.N., Vickers, D.R., 2006. Gait dynamics on an inclined walkway. *J. Biomech.* 39, 2491–2502.
- Midgley, A.W., McNaughton, L.R., Jones, A.M., 2007. Training to enhance the physiological determinants of long-distance running performance: can valid recommendations be given to runners and coaches based on current scientific knowledge? *Sports. Med.* 37, 857–880.
- Miller, J.A., Gross, M.M., 1998. Locomotor advantages of Neandertal skeletal morphology at the knee and ankle. *J. Biomech.* 31, 355–361.
- Pickering, T.R., Bunn, H.T., 2007. The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *J. Hum. Evol.* 53, 438–442.
- Pontzer, H., 2005. A new model predicting locomotor cost from limb length via force production. *J. Exp. Biol.* 208, 1513–1524.
- Pontzer, H., 2007. Predicting the cost of locomotion in terrestrial mammals: a test of the LiMb model in humans and quadrupeds. *J. Exp. Biol.* 210, 484–494.
- Pontzer, H., Raichlen, D., Sockol, M.D., 2009. The metabolic cost of walking in humans, chimpanzees and early hominins. *J. Hum. Evol.* 56, 43–54.
- Roberts, T.J., Belliveau, R.A., 2005. Sources of mechanical power for uphill running in humans. *J. Exp. Biol.* 208, 1963–1970.
- Roberts, T.J., Chen, M.S., Taylor, C.R., 1998. Energetics of bipedal running II. Limb design and running mechanics. *J. Exp. Biol.* 201, 2753–2762.
- Ruff, C.B., Niskanen, M., Junno, J.A., Jamison, P., 2005. Body mass prediction from stature and bi-iliac breadth in two high latitude populations, with application to earlier higher latitude humans. *J. Hum. Evol.* 48, 381–392.
- Ruff, C.B., Trinkaus, E., Holliday, T.W., 1997. Body mass and encephalization in Pleistocene *Homo*. *Nature* 387, 173–176.
- Saunders, P.U., Pyne, D.B., Telford, R.D., Hawley, J.A., 2004. Factors affecting running economy in trained distance runners. *Sports. Med.* 34, 465–485.
- Schmidt-Nielsen, K., 1997. *Animal Physiology*, fifth ed. Cambridge University Press, Cambridge.
- Schmitt, A., 1998. Approche de la variabilité du calcanéus néandertalien. Comparaison avec l'homme moderne. *Bull. Mem. Soc. Anthropol. Paris*. 10, 273–292.
- Scholz, M.N., Bobbert, M.F., van Soest, A.J., Clark, J.R., van Heerden, J., 2008. Running biomechanics: shorter heels, better economy. *J. Exp. Biol.* 211, 3266–3271.
- Simpson, S.W., Quade, J., Levin, N.E., Butler, R., Dupont-Nivet, G., Everett, M., Semaw, S., 2008. A female *Homo erectus* pelvis from Gona, Ethiopia. *Science* 322, 1089–1092.
- Sladek, V., Trinkaus, E., Hillson, S.W., Holliday, T.W., 2000. The People of the Pavlovian: Skeletal Catalogue and Osteometrics of the Gravettian Fossil Hominids from Dolní Věstonice and Pavlov. *Dolní Věstonice Studies* 5. Akademie věd České republiky, Brno.
- Sockol, M.D., Raichlen, D.A., Pontzer, H., 2007. Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc. Natl. Acad. Sci.* 134, 12265–12269.
- Spencer, M.A., Demes, B., 1993. Biomechanical analysis of masticatory system configuration in Neandertals and Inuits. *Am. J. Phys. Anthropol.* 91, 1–20.
- Spoor, F., Zonneveld, F., 1998. Comparative review of the human bony labyrinth. *Yrbk. Phys. Anthropol.* 41, 211–251.
- Spoor, F., Garland Jr., T., Krovitz, G., Ryan, T.M., Silcox, M.T., Walker, A., 2007. The primate semicircular canal system and locomotion. *Proc. Natl. Acad. Sci. U.S.A.* 104, 10808–10812.
- Spoor, F., Hublin, J.-J., Braun, M., Zonneveld, F., 2003. The bony labyrinth of Neandertals. *J. Hum. Evol.* 44, 141–165.
- Spoor, F., Wood, B., Zonneveld, F., 1994. Implications of early hominid labyrinthine morphology for the evolution of human bipedal locomotion. *Nature* 369, 645–648.
- Spoor, F., Wood, B., Zonneveld, F., 1996. Evidence for a link between human semicircular canal size and bipedal behaviour. *J. Hum. Evol.* 30, 183–187.
- Stegman Jr., A.T., Cerny, F.J., Holliday, T.W., 2002. Neandertal cold adaptation: physiological and energetic factors. *Am. J. Human Biol.* 14, 566–583.
- Studel-Numbers, K.L., Weaver, T.D., Wall-Scheffler, C.M., 2007. The evolution of human running: effects of changes in lower-limb length on locomotor economy. *J. Hum. Evol.* 53, 191–196.
- Stiner, M.C., 1994. *Honor Among Thieves: A Zooarchaeological Study of Neandertal Ecology*. Princeton University Press, Princeton.
- Stiner, M.C., 2002. Carnivory, coevolution, and the geographic spread of the genus *Homo*. *J. Arch. Res.* 10, 1–63.
- Stringer, C., Gamble, C., 1993. *In search of the Neandertals*. Hudson, New York.
- Stringer, C.B., Grun, R., Schwarcz, H.P., Goldberg, P., 1989. ESR dates for the hominid burial site of Es Skhul in Israel. *Nature* 338, 756–758.
- Taylor, C.R., 1985. Force development during sustained locomotion: a determinant of gait, speed, and metabolic power. *J. Exp. Biol.* 115, 253–262.
- Taylor, C.R., Heglund, N.C., McMahon, T.A., Looney, T.R., 1980. Energetic cost of generating muscular force during running: a comparison of large and small animals. *J. Exp. Biol.* 86, 9–18.
- Thorpe, S.K.S., Li, Y., Crompton, R.H., Alexander, R.M., 1998. Stresses in human leg muscles in running and jumping determined by force plate analysis and from published magnetic resonance images. *J. Exp. Biol.* 201, 63–70.
- Trinkaus, E., 1975. A functional analysis of the Neandertal foot. Ph.D. Dissertation, University of Pennsylvania.
- Trinkaus, E., 1981. Neandertal limb proportions and cold adaptation. In: Stringer, C.B. (Ed.), *Aspects of Human Evolution*. Lord and Francis, London, pp. 21–53.
- Trinkaus, E., 1983a. The Shanidar Neandertals. Academic Press, New York.
- Trinkaus, E., 1983b. Functional aspects of Neandertal pedal remains. *Foot. Ankle*. 3, 377–390.
- Trinkaus, E., 1986. The Neandertals and modern human origins. *Ann. Rev. Anthropol.* 15, 193–218.
- Trinkaus, E., 2000. The human remains from Paviland Cave: Late Pleistocene and Holocene human remains from Paviland Cave. In: Aldhouse-Green, S.H.R. (Ed.), *Paviland Cave and the 'Red Lady': A Definitive Report*. Western Academic and Specialist Press Ltd., Bristol, pp. 141–199.
- Underdown, S., 2006. A comparative approach to understanding Neandertal trauma. *Period. Biol.* 108, 485–493.
- Weaver, T.D., 2009. The meaning of Neandertal skeletal morphology. *Proc. Natl. Acad. Sci. U.S.A.* 106, 16028–16033.
- Weaver, T.D., Studel-Numbers, K., 2005. Does climate or mobility explain the differences in body proportions between Neandertals and their upper Paleolithic successors? *Evol. Anthropol.* 14, 218–223.