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The effects of body proportions on thermoregulation: an experimental assessment of Allen's rule

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Abstract

Numerous studies have discussed the influence of thermoregulation on hominin body shape concluding, in accordance with Allen's rule, that the presence of relatively short limbs on both extant as well as extinct hominin populations offers an advantage for survival in cold climates by reducing the limb's surface area to volume ratio. Moreover, it has been suggested that shortening the distal limb segment compared to the proximal limb segment may play a larger role in thermoregulation due to a greater relative surface area of the shank. If longer limbs result in greater heat dissipation, we should see higher resting metabolic rates (RMR) in longer-limbed individuals when temperature conditions fall, since the resting rate will need to replace the lost heat. We collected resting oxygen consumption on volunteer human subjects to assess the correlation between RMR and lower limb length in human subjects, as well as to reexamine the prediction that shortening the distal segment would have a larger effect on heat loss and, thus, RMR than the shortening of the proximal segment. Total lower limb length exhibits a statistically significant relationship with resting metabolic rate ($p < 0.001$; $R^2 = 0.794$). While this supports the hypothesis that as limb length increases, resting metabolic rate increases, it also appears that thigh length, rather than the length of the shank, drives this relationship. The results of the present study confirm the widely-held expectation of Allen's rule, that short limbs reduce the metabolic cost of maintaining body temperature, while long limbs result in greater heat dissipation regardless of the effect of mass. The present results suggest that the shorter limbs of Neandertals, despite being energetically disadvantageous while walking, would indeed have been advantageous for thermoregulation.
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Introduction

Numerous studies have discussed the influence of cold adaptation on hominin body shape (e.g., Roberts, 1978; Trinkaus, 1981; Beals et al., 1984; Franciscus and Trinkaus, 1988; Holliday and Trinkaus, 1991; Ruff, 1991, 1993, 1994). It is widely believed that numerous physical features, including relatively short limbs, offer an advantage for survival in glacial climates (Coon, 1962; Badoux, 1965; Roberts, 1978). Such advantages of shorter limbs include reducing the surface area to volume ratio (Coon, 1962; Trinkaus, 1981; Wolpoff, 1989; Frayer et al., 1993) in compliance with Allen's rule, an ecogeographical pattern in which individuals from higher latitudes exhibit shorter appendages than individuals of the same species living closer to the equator (Allen, 1877). Because the body dissipates heat through the skin, an organism's surface area is directly proportional to the amount of heat lost. A homeothermic animal is better able to retain body heat in cold temperatures when its relative surface area is reduced, while an organism living in a warm environment would be better adapted to dissipate heat if the relative surface area of the body is increased.

Both extinct and extant hominin populations have been shown to exhibit body proportions which conform to Allen's expectations. Holliday (1997a) has characterized the European

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Neandertal postcranial morphology as hyper-polar; that is, their short limbs and broad trunks are similar to those of modern humans living in Arctic environments. However, anatomically modern human (AMH) populations living in arctic conditions (Hrdlicka, 1930; Newman, 1953; Coon, 1962; Auger et al., 1980; Holliday and Trinkaus, 1991; Holliday, 1997b) have somewhat less pronounced body proportions than Neandertals, at least when considered in a multivariate manner, despite the harsher conditions of the Holocene Arctic (Holliday, 1997a).

Additionally, Holliday and Trinkaus (1991) demonstrated that, while the European Neandertals possess both shortened proximal and distal limb segments relative to trunk height, the shortening is much more pronounced in the distal limb segment. As a result, hyper-polarization is most conspicuously expressed in the extreme shortening of the distal segments of both the upper and lower limbs. When Trinkaus (1981) regressed the length of the radius on the humerus and the length of the tibia on the femur, the European Neandertals fell markedly below the regression line for recent humans. Holliday (1999) hypothesized that the reduction in the distal lower limb segment among Neandertals might improve their ability to thermoregulate in the cold because the smaller diameter in the distal lower limb segment suggests any change in length would have a dramatic effect on relative surface area—more so than a change in the length of the proximal segment. Holliday's (1999) investigation into limb segment changes in early to late Upper Paleolithic anatomically modern humans, however, reported a decrease in total leg length with no concurrent change in the ratio of distal to proximal segment lengths.

Despite some disagreement regarding the theoretical framework of Allen's rule (Scholander, 1955; Irving, 1957), the fact remains that the majority of workers accept the validity of this trend. Nonetheless, Allen's rule is a generalization that rests solely on the dependability of the empirical pattern (Mayr, 1956). While the expected theoretical basis of Allen's rule (thermoregulation) seems very plausible, observed patterns do not necessarily have the causal basis that we might expect (Taylor et al., 1974; Heglund et al., 1982).

The question, however, is amenable to direct experimental testing. Numerous experiments have investigated the relationship between human morphology and climate in both heat (Robinson, 1942; Wyndham et al., 1970; Epstein et al., 1983) and cold conditions (Sloan and Keatinge, 1973; McArdle et al., 1984; Toner and McArdle, 1988; Stocks et al., 2004); several studies reporting human responses to cold conditions report a reduction in heat loss with a reduction in the surface area to volume ratio, consistent with Allen's rule (Sloan and Keatinge, 1973; Kollias et al., 1974; McArdle et al., 1984). Experiments focusing on human reactions to cold adaptations generally use water immersion techniques—a procedure not employed in the current study. Additionally, several reoccurring problems in these studies, such as small sample sizes, unbalanced participant sex ratios, and unnatural test conditions, have been discussed in previous reviews (Steegman, 1975; Hanna et al., 1989; Ruff, 1994). The current study investigates the physiological response to cold while correcting for these methodological issues.

If, in fact, longer limbs result in greater heat dissipation, we should see higher resting metabolic rates (RMR) in longer limbed individuals when temperature conditions fall substantially below that of body temperature, since RMR will need to replace the lost heat. The present study tests this hypothesis by assessing the correlation between RMR and lower limb length in human subjects. Further, we reexamine Holliday's (1999) theoretical prediction that shortening the distal segment will have a larger effect on heat loss and, consequently, RMR than would shortening the proximal segment.

Methods

Resting metabolic rates for the current study were quantified by determining the average oxygen consumption over a four-minute period after the subject had been sitting for at least eight minutes, allowing the values to represent steady-state aerobic respiration solely. Previous work from our laboratory (Steudel-Numbers and Tilkens, 2004) has found that the total of twelve minutes is an adequate length of time to achieve steady-state conditions. We make no claim to be measuring basal metabolic rate, which indeed would require a much more specialized experimental design. Here we are simply determining whether extremity length is correlated with short-term resting metabolic rate in a cool environment.

All 20 subjects included in the study participated in multiple sessions, each taking place on separate days (to avoid same day changes in VO_2 values). The data reported were collected from at least three separate sessions for each subject and the results averaged.

Oxygen consumption was measured using a SensorMedics Vmax 29 c respiratory gas analysis system. The temperature in the laboratory was controlled and monitored before and after each individual session took place. The average temperature was 21.9 °C (s.d. = 0.99). Since average human body temperature hovers around 37 °C, [humans usually die if their body temperature deviates from about 35 to 40 °C (Kormondy and Brown, 1998)] this gives a discrepancy of approximately 15 °C. This serves as cold enough to activate a response, but not so cold that vasoconstriction would be a factor (McArdle et al., 2001). Each subject wore a tee shirt, running shorts, and running shoes, thus exposing the appendages to the room air temperature. During each trial, the subjects sat comfortably in a bean bag chair with their knees bent loosely at an obtuse angle, exposing them to the air. All subjects were healthy and between the ages of 18 and 35. The Human Subject Committee of the University of Wisconsin approved the experimental procedures. Volunteers for this study completed a written informed consent form after the nature, purpose, and possible risks were carefully explained and prior to the beginning of each subject's first session.

Anthropometric measurements (mass, height, thigh length, and shank length) were measured during each subject's first session in the lab. Thigh length was obtained by measuring the distance between the proximal portion of the greater trochanter to the lateral midpoint of the knee (equal distance between the femoral epicondyles and the tibial plateau), while the