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

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Received 30 January 2006; accepted 6 April 2007

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; R² = 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.

Published by Elsevier Ltd.

Keywords: Resting metabolic rate; Climate; Hominin evolution

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
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 (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 VO2 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
measurements of the shank included the distance between the lateral midpoint of the knee to the most lateral portion of the lateral malleolus. Together, thigh length and shank length constituted the total length of the lower limb. All lower limb measurements were collected using calipers. At the conclusion of all trials, lean body mass and percent fat mass were determined at the University of Wisconsin Clinics using dual-energy X-ray absorptiometry (DEXA). This method utilizes low-energy X-ray beams to penetrate body tissues, reconstructing the bone mineral content, lean mass, and fat mass from the attenuation of the X-rays as they scan the entire body. This method is quickly becoming the gold standard in body composition analysis (Kohrt, 1995; Prior et al., 1997).

P-values, as well as coefficient of determination values, were determined from regressions between RMR and height, mass, thigh length, shank length, lean mass, and percent fat, as well as total lower limb length (thigh length + shank length). In addition, because both RMR and limb length are highly correlated with lean mass, we examined the correlation between RMR and lower limb length while controlling for lean mass. Statistical investigations for changes in distal and proximal portions of the lower limb were conducted with unpaired t tests; p-values and the coefficient of determination for both the shank and the thigh were calculated.

Results

Anthropometric measurements of our 20 volunteer subjects are listed in Table 1. Subjects ranged from 50—95 kg with total lower limb lengths from 71 to nearly 99 cm. Pearson correlations as well as significance levels between resting metabolic rate and the collected anthropometric variables (mass, height, total lower limb length, thigh length, shank length, lean mass, and percent fat) are presented in Table 2. As expected, total mass (p = 0.002) as well as lean mass (p < 0.001) are both highly correlated with resting metabolic rate.

Total lower limb length exhibits a statistically significant relationship with resting metabolic rate (p < 0.001; R² = 0.794). While this strongly supports the hypothesis that as limb length increases, resting metabolic rate increases (Fig. 1), it also appears that this relationship is driven primarily by the length of the thigh, rather than the length of the shank (Table 2). When both lean mass and percent fat are controlled for, shank

### Table 1
Body dimensions and resting metabolic rates for volunteer subjects

<table>
<thead>
<tr>
<th>Sex</th>
<th>Mean (VO²RMR)</th>
<th>Mass</th>
<th>Average thigh length</th>
<th>Average shank length</th>
</tr>
</thead>
<tbody>
<tr>
<td>M</td>
<td>0.25</td>
<td>70.59</td>
<td>45.20</td>
<td>47.20</td>
</tr>
<tr>
<td>M</td>
<td>0.18</td>
<td>61.09</td>
<td>42.90</td>
<td>45.10</td>
</tr>
<tr>
<td>M</td>
<td>0.18</td>
<td>71.49</td>
<td>41.45</td>
<td>38.40</td>
</tr>
<tr>
<td>M</td>
<td>0.17</td>
<td>73.30</td>
<td>38.95</td>
<td>39.40</td>
</tr>
<tr>
<td>M</td>
<td>0.18</td>
<td>69.68</td>
<td>39.55</td>
<td>39.90</td>
</tr>
<tr>
<td>M</td>
<td>0.26</td>
<td>81.90</td>
<td>48.80</td>
<td>44.90</td>
</tr>
<tr>
<td>M</td>
<td>0.28</td>
<td>70.59</td>
<td>43.85</td>
<td>46.00</td>
</tr>
<tr>
<td>M</td>
<td>0.29</td>
<td>82.58</td>
<td>43.30</td>
<td>43.15</td>
</tr>
<tr>
<td>M</td>
<td>0.25</td>
<td>95.45</td>
<td>47.35</td>
<td>51.60</td>
</tr>
<tr>
<td>M</td>
<td>0.18</td>
<td>62.26</td>
<td>36.65</td>
<td>41.60</td>
</tr>
<tr>
<td>M</td>
<td>0.23</td>
<td>90.45</td>
<td>43.73</td>
<td>51.27</td>
</tr>
<tr>
<td>Male mean</td>
<td>0.22</td>
<td>75.39</td>
<td>42.88</td>
<td>44.41</td>
</tr>
<tr>
<td>s.d.</td>
<td>0.05</td>
<td>10.95</td>
<td>3.60</td>
<td>4.48</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sex</th>
<th>Mean (VO²RMR)</th>
<th>Mass</th>
<th>Average thigh length</th>
<th>Average shank length</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td>0.14</td>
<td>50.23</td>
<td>36.70</td>
<td>36.80</td>
</tr>
<tr>
<td>F</td>
<td>0.17</td>
<td>65.45</td>
<td>40.05</td>
<td>38.90</td>
</tr>
<tr>
<td>F</td>
<td>0.22</td>
<td>63.57</td>
<td>42.97</td>
<td>41.07</td>
</tr>
<tr>
<td>F</td>
<td>0.21</td>
<td>61.54</td>
<td>42.05</td>
<td>43.10</td>
</tr>
<tr>
<td>F</td>
<td>0.14</td>
<td>59.50</td>
<td>38.80</td>
<td>36.45</td>
</tr>
<tr>
<td>F</td>
<td>0.17</td>
<td>65.91</td>
<td>41.50</td>
<td>41.50</td>
</tr>
<tr>
<td>F</td>
<td>0.16</td>
<td>66.82</td>
<td>38.70</td>
<td>45.60</td>
</tr>
<tr>
<td>F</td>
<td>0.15</td>
<td>95.45</td>
<td>35.35</td>
<td>36.30</td>
</tr>
<tr>
<td>F</td>
<td>0.17</td>
<td>52.73</td>
<td>38.13</td>
<td>36.90</td>
</tr>
<tr>
<td>Female mean</td>
<td>0.17</td>
<td>64.58</td>
<td>39.36</td>
<td>39.62</td>
</tr>
<tr>
<td>s.d.</td>
<td>0.03</td>
<td>12.96</td>
<td>2.52</td>
<td>3.36</td>
</tr>
<tr>
<td>Total mean</td>
<td>0.20</td>
<td>70.53</td>
<td>41.30</td>
<td>42.26</td>
</tr>
<tr>
<td>Total s.d.</td>
<td>0.05</td>
<td>11.6</td>
<td>3.57</td>
<td>4.62</td>
</tr>
</tbody>
</table>

Conversions of external to skeletal measures (Porter, 1996) suggest that external thigh measures are ~2% shorter than skeletal and that shank are ~8% longer than skeletal.

1 Mean and standard deviation values for resting metabolic rates, mass, and thigh and shank lengths between the sexes. Reported thigh and shank lengths are external segment measures, not bone (femur and tibia, respectively) measurements.
length has no significant correlation with RMR, while thigh length remains highly correlated (see Table 3).

To determine whether the correlation between RMR and lower limb length might be simply a result of their mutual correlation with lean mass, we calculated the standardized residuals of the regression of lower limb length on lean mass and the residuals of the regression of RMR on lean mass. Residual limb length retained a significant relationship with residual RMR ($p = 0.018$, $R^2 = 0.274$). This significance level, lower than for the original variables, is primarily a consequence of a single subject who has a Cook's value (i.e., the calculation of a data point's degree of influence on the regression; Cook and Weisberg, 1999) substantially above all other subjects (nearly 0.5 while others are less than 0.01). This individual has a relatively high metabolic rate and relatively short limb length (filled circle in Fig. 2). When this individual is removed, the significance ($p = 0.001$) as well as the correlation (0.711) are comparable to those of the untransformed variables.

Because females generally have higher fat mass and lower lean mass than males, one might predict a gender difference in the effect of lower limb length on RMR due to the greater insulation in females. In our sample, females had roughly twice the percent body fat of males (22% to 11% on average) and two-thirds the lean mass (42 kg to 62 kg). Nonetheless, females have higher significance levels and correlation values than do males (males: $p = 0.023$, $R = 0.673$; females: $p = 0.016$, $R = 0.764$).

**Discussion**

Thus, the results of the present study confirm the widely held expectation of Allen’s rule for cold-adapted populations (Schreider, 1950, 1964, 1975; Trinkaus, 1981; Ruff, 1991, 1994): that short limbs reduce the metabolic cost of maintaining body temperature, while long limbs result in greater heat dissipation. As mentioned previously, the collection periods of VO$_2$ values differ between investigations, with some collections continuing for several hours. Extending our collection time may, in fact, help to clarify the relationship between RMR and lower limb length. Regardless, it should be noted that despite the shorter, yet physiological relevant, collection of twelve minutes for resting metabolic rates, we still report a statistically strong relationship between RMR and limb length. Therefore, collection of twelve minutes for resting metabolic rates, we still report a statistically strong relationship between RMR and limb length. Regardless, it should be noted that despite the shorter, yet physiological relevant, collection of twelve minutes for resting metabolic rates, we still report a statistically strong relationship between RMR and limb length, thus suggesting that the relationship can be seen with as little as twelve minutes of collection.

The present results do not reveal any thermal advantage in changing the length of the shank segment in particular. When the effects of lean mass are removed, shank length has no correlation at all with RMR, whereas thigh length retains a high significance level when variation due to lean mass and percent fat are accounted for.

<table>
<thead>
<tr>
<th>RMR</th>
<th>Limb length (cm)</th>
<th>Femur length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower limb length (cm)</td>
<td>0.524*</td>
<td></td>
</tr>
<tr>
<td>Thigh length (cm)</td>
<td>0.626**</td>
<td>0.871**</td>
</tr>
<tr>
<td>Shank length (cm)</td>
<td>0.313</td>
<td>0.891**</td>
</tr>
</tbody>
</table>

* Correlation is significant at the 0.05 level.
** Correlation is significant at the 0.01 level.
relationship \( R = 0.625 \), higher even than total lower limb length. While it remains possible this extreme result is a function of the variation between external and skeletal measures (Porter, 1996), the results do seem to suggest that the particular shortening of the distal limb segments in Neandertals may not be a consequence of cold thermal considerations.

The shorter overall limbs of Neandertals, despite being disadvantageous while walking (Weaver and Steudel-Numbers, 2005), would indeed have been advantageous for thermoregulation. In contrast, the early Upper Paleolithic modern human successors of the Neandertals in Europe retained body proportions that would have been disadvantageous for a substantial period of time.

Acknowledgements

We would like to thank Randall Clark for conducting the DEXA scans as well as the L.S.B. Leakey Foundation for financial support.

References


