Locomotor advantages of Neandertal skeletal morphology at the knee and ankle

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Abstract

We quantified Neandertal knee extensor and ankle plantarflexor moments to determine whether differences between Neandertal and recent human skeletal morphology represent important functional differences. Neandertal skeletal differences in the patella, tibial tuberosity, and calcaneus were used to modify a computer model of recent humans to calculate the moment arms and moments of Neandertal knee extensor and ankle plantarflexor muscles. We also conducted sensitivity studies on the effect of musculotendon parameters on the Neandertal moments. As expected, we found that Neandertal moment arms were greater than recent humans at the ankle (122–141%); however, the magnitude of the increase was not well-predicted from measurements of size differences between Neandertal and recent human skeletons. At the knee, Neandertal moment arms were greater than those of recent humans in the locomotor range (108%) but less so at more flexed knee angles (102%). Not all Neandertal skeletal adaptations at the knee contributed to increased moment arm. Knee extensor moments were enhanced in the Neandertal models in the locomotor range (111%), regardless of musculotendon parameters. At the ankle, however, Neandertal plantarflexor moment was greater than that of recent humans (149–200%) at all joint angles only if muscle fiber length increased proportionately with moment arm. Our results demonstrate that Neandertal skeletal morphology, compared to that of recent humans, generated greater moments at both the knee and ankle in the locomotor range but not at higher angles of knee flexion or ankle plantarflexion.

1. Introduction

Neandertal knee and ankle skeletal morphology is different from that of recent humans in several important respects. These differences include a thicker patella, a more prominent tibial tuberosity, and a longer calcaneus in Neandertals compared to recent humans. These differences in skeletal morphology have been explained as part of a Neandertal skeletal adaptation to sustained levels of locomotor activity over irregular terrain that increased the knee extensor and ankle plantarflexor moment-generating capacities in Neandertals (Trinkaus 1975, 1983, 1984, 1986).

These ideas about the functional consequences of Neandertal morphology are based on skeletal measurements obtained at single joint angles and may not adequately represent the actual joint biomechanics. Skeletal measurements that have been used to estimate the moment arms of muscles spanning a joint and, by inference, the moment-generating capacity of these muscles, are not necessarily constant over the whole range of motion at a joint, so conclusions drawn from a single joint angle may not accurately predict a functional difference (Delp et al., 1994; Grood et al., 1984). In addition, moment arm may not accurately predict musculotendon moment, especially for muscles with short fibers, long tendons and large moment arms like the triceps surae (Hoy et al., 1990). It is not known if these differences in

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skeletal morphology affect the functional interpretations of Neandertal morphology.

This study tested the hypothesis that skeletal differences between Neandertals and recent humans represent markedly different moment-angle relationships and therefore important functional differences. In particular, we tested whether the moment-generating capacity of musculotendon actuators at the knee and ankle was greater with Neandertal than with recent human skeletal morphology in the range of joint angles used during locomotion. Preliminary results have been reported elsewhere (Miller and Gross, 1995).

2. Methods

The skeletal differences between Neandertals and recent humans at the knee and ankle joints consist primarily of differences in size rather than shape, and include a thicker patella, a more prominent tibial tuberosity, and a longer calcaneus in Neandertals relative to recent humans (Trinkaus, 1975, 1983). Because the tibial length of Neandertals is short compared to recent humans (Trinkaus, 1983), skeletal differences are typically expressed as indices in which the patella, tibial tuberosity, and calcaneus dimensions are given relative to tibial length (Trinkaus, 1975, 1983). The three indices (Table 1) that are used to compare recent human and Neandertal samples are: (1) the tibial tuberosity projection index (length of tibial tuberosity relative to tibial length), (2) the patella thickness to tibial length index (maximum anterior–posterior patellar length relative to tibial length), and (3) the posterior tibio-pedal index (length of calcaneus from midtalar trochlea to the posterior margin of the calcaneal tuberosity relative to tibial length).

Recent human and Neandertal musculoskeletal models were constructed using Software for Interactive Modeling (SIMM) (MusculoGraphics, Inc). SIMM requires specification of bone surface topographies, muscle insertion sites relative to the bone surfaces, joint kinematics, and musculotendon parameters to compute the musculotendon moments (Delp, 1990; Delp et al., 1990). We used SIMM to compute the moment arms and moments for an adult male recent human model (Delp, 1990) and several Neandertal models. The Neandertal models were developed by modifying the muscle insertion sites in the recent human model without changing the bone surface topographies or the joint kinematics.

To represent the Neandertal knee morphology, three different models were constructed: (1) a “patella only” model, which accounted only for the patellar thickness to tibial length index, (2) a “tibial tuberosity only” model, which accounted only for the tibial tuberosity projection index, and (3) a “Neandertal” model, which accounted for both patellar thickness and tibial tuberosity indices. Moment arms were calculated separately for the four component muscles of the quadriceps femoris group and then were averaged to produce the knee extensor moment arm for each of the four models.

Neandertal ankle models were constructed that corresponded to the Neandertal skeletal indices that are 13% and 30% greater than recent human samples (Table 2). In these models (i.e., Neandertal (13%) and Neandertal (30%)), the combined tendon of the triceps surae was displaced posteriorly by either 13 or 30% to represent the longer calcaneus in Neandertals compared to recent humans. Moment arms calculated for the medial gastrocnemius, lateral gastrocnemius, and soleus were averaged at each joint angle to produce the ankle plantarflexor moment arm for the recent human and both Neandertal models.

The isometric moments of the knee extensors and ankle plantarflexors were calculated for the recent human and Neandertal models as the product of musculotendon force and moment arm. Musculotendon force was a function of the musculotendon parameters (i.e., muscle fiber length, muscle physiological cross-sectional area, pennation angle, and tendon slack length) which were specified for each musculotendon unit. Full activation of muscles was assumed. Moment arm was

<table>
<thead>
<tr>
<th>Sample</th>
<th>Tibial tuberosity projection index</th>
<th>Patella thickness to tibial length index</th>
<th>Posterior tibio-pedal index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neandertal</td>
<td>13.2*</td>
<td>6.60b</td>
<td>16.1*</td>
</tr>
<tr>
<td>Recent Human</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>European*</td>
<td>10.3</td>
<td>5.40</td>
<td></td>
</tr>
<tr>
<td>Amerindian*</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>North African*</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

*Sample includes: Shanidar 2 and 5, Tabun C1, La Chappelle-aux-Saints 1, La Ferrassie 2, Kiik-Koba 1 and Spy 2 (Trinkaus, 1983).
*Sample includes: Shanidar 1, 5, and 6, Tabun C1, La Chappelle-aux-Saints 1, La Ferrassie 2, Kiik-Koba 1 and Spy 2 (Trinkaus, 1983).
*Sample includes: Tabun C1, La Ferrassie 1 and 2 and Kiik-Koba 1 (Trinkaus, 1975).
*Trinkaus 1983.
*Trinkaus 1975.
calculated from the proportional relationship between change in musculotendon length and change in joint angle.

Since we cannot know the Neandertal musculotendon parameters, it was important to determine the sensitivity of the Neandertal moments to the musculotendon parameters. We calculated the Neandertal moments with two different sets of musculotendon parameters: (1) nominal and (2) scaled. The nominal set was the same set of parameters used in the recent human model. The scaled set was based on the assumption that muscle fiber length and tendon slack length scaled with moment arm so that the Neandertal muscles developed active force over the same range of joint angles, and that peak force occurred at the same joint angle, as in recent humans (Hoy et al., 1990; Delp et al., 1990). Muscle fiber lengths were increased for each muscle so that the muscle fiber length to moment arm ratio was the same as in recent humans; the average increase in muscle fiber lengths was 9% for the knee extensors and 22% and 41% for the ankle plantarflexors in the 13 and 30% Neandertal models, respectively. Tendon slack lengths were adjusted so that each muscle generated peak force at the same joint angle as recent humans.

3. Results

3.1. Knee joint

Neandertal moment arms were generally greater than recent human but the difference depended on knee angle. Neandertal moment arms were greater than recent human in the locomotor range (108%, shaded region), but were not much different at more flexed knee angles (102%) (Fig. 1). The Neandertal “tibial tuberosity only” model produced essentially the same moment arms as the recent human model. Thus, differences in patellar thickness accounted for virtually all of the differences between Neandertal and recent human moment arms.

Consistent with the increase in moment arm, the Neandertal knee extensor moments were much greater than recent human in the locomotor range (Fig. 2). The magnitude of the increase depended on the musculotendon parameters, however, so that the average increase in the locomotor range was 110.9% for the nominal Neandertal model and 111.4% for the scaled Neandertal model.

Fig. 1. Knee extensor moment arms for Neandertal and recent human models. Each curve is the average of rectus femoris, vastus medius, vastus intermedius and vastus lateralis moment arms. The shaded region indicates the range of joint motion used in locomotion. The recent human and tuberosity only models produced virtually the same moment arm curves indicating that Neandertal tibial tuberosity morphology did not affect knee extensor moment arm. Similarly, the Neandertal and patella only models produced virtually the same knee extensor moment arms, indicating that patellar morphology alone accounted for differences between recent human and Neandertal moment arms.

Table 2
Neandertal indices expressed as percent greater than recent human indices*  

<table>
<thead>
<tr>
<th>Sample</th>
<th>Tibial tuberosity projection index</th>
<th>Patella thickness to tibial length index</th>
<th>Posterior tibio-pedal index</th>
</tr>
</thead>
<tbody>
<tr>
<td>European</td>
<td>28% (0.98 cm)*</td>
<td>22% (0.57 cm)</td>
<td>30% (0.94 cm)</td>
</tr>
<tr>
<td>Amerindian</td>
<td></td>
<td></td>
<td>13% (1.87 cm)</td>
</tr>
<tr>
<td>North African</td>
<td></td>
<td></td>
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</tr>
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*[(Neandertal value-recent human value)/recent human value]*100.

Numbers in parentheses show the corresponding displacements of musculotendon attachments in the various Neandertal models.
3.2. Ankle joint

Both Neandertal (13%) and Neandertal (30%) models produced ankle plantarflexor moment arms that were greater than those of recent humans; the largest moment arms were associated with the Neandertal (30%) model (Fig. 3). The average increases in Neandertal moment arms compared to recent human moment arms in the locomotor range were 122% and 141% for the 13 and 30% Neandertal models, respectively; in the plantarflexion range the average increases were 121% and 139% for the 13 and 30% Neandertal models, respectively.

Although the Neandertal plantarflexor moment arms were larger than those of recent humans at all joint angles, the magnitude of the Neandertal moments compared to recent human moments depended on the musculotendon parameters. With the nominal parameters, the Neandertal plantarflexor moments were greater than those of recent humans in the locomotor range, but at more plantarflexed angles, the Neandertal moments were less than recent human moments because the muscle fibers were too short to generate force. The average increase in Neandertal plantarflexor moment in the locomotor range was 120% for the 13% model (Fig. 4, shaded region) and 137% for the 30% model (Fig. 5, shaded region); the average decrease in the plantarflexion range was 50% for the 13% model (Fig. 4) and 27% for the 30% model (Fig. 5). With the scaled parameters, however, the muscle fiber lengths were sufficient to maintain force in the plantarflexion region, and Neandertal plantarflexor moments were greater than those of recent humans over the entire range of ankle motion [149% for the 13% model (Fig. 4) and 200% for the 30% model (Fig. 5)].

4. Discussion

Previous studies have suggested that Neandertal skeletal modifications enhanced their ability to generate moment and enabled them to locomote more effectively over difficult terrain (Trinkhaus, 1983, 1984, 1986). An assumption of these studies, however, was that increased Neandertal skeletal dimensions corresponded to increased moment-generating capacity over the whole locomotor range of motion (Trinkhaus, 1983) although the
Fig. 4. Ankle plantarflexion moments for Neandertal (13%) and recent human models. Each curve is the sum of medial gastrocnemius, lateral gastrocnemius, and soleus plantarflexor moments. The shaded region indicates the range of joint motion used in locomotion. The solid line indicates the recent human model; the dashed line indicates the Neandertal (13%) model with nominal parameters; the dotted line indicates the Neandertal (13%) model with scaled parameters. The Neandertal moments were greater than recent human in the locomotor region. Scaled muscle fiber lengths were long enough to take advantage of the increased Neandertal moment arm to generate ankle moments greater than recent human.

actual increases in moment arm and moment associated with differences in skeletal morphology were not quantified. We calculated the effects of Neandertal skeletal modifications on the knee and ankle moments to determine whether these morphological differences represented functional differences between Neandertals and recent humans.

Our results showed that differences in skeletal size between Neandertals and recent humans did not accurately predict differences in moment arm. At the ankle, the index differences between Neandertal and recent humans underestimated the moment arm differences. The 13 and 30% posterior tibio-pedal indices for the Neandertals resulted in moment arm values that were 22% and 41% greater than those for recent humans, respectively. At the knee, the increase in Neandertal moment arm was not directly proportional to the increase in patellar thickness (22%), however, since the skeletal index overestimated the moment arm difference (8%). Further, the moment arm advantage was not constant over the whole range of knee motion, but decreased as knee flexion increased.

Fig. 5. Ankle plantarflexion moments for Neandertal (30%) and recent human models. Each curve is the sum of medial gastrocnemius, lateral gastrocnemius, and soleus plantarflexor moments. The shaded region indicates the range of joint motion used in locomotion. The solid line indicates the recent human model; the dashed line indicates the Neandertal (30%) model with nominal parameters; the dotted line indicates the Neandertal (30%) model with scaled parameters. The Neandertal moments were greater than recent human in the locomotor region. Scaled muscle fiber lengths were long enough to take advantage of the increased Neandertal moment arm to generate ankle moments greater than recent human.

The reason that patellar thickness enhanced moment arm over only part of the range of knee motion is explained by Yamaguchi and Zajac (1989). They established that the effective moment arm of the knee extensors was affected just as much by the levering action of the patella as by its function as a spacer. They found that the thickness of the patella influenced the effective moment arm of the knee extensors most at extended knee angles. However, the levering action of the patella due to patellar height and patellar ligament length was more important than the thickness of the patella in determining the effective moment arm of the knee extensors at knee flexion angles greater than 15°. Whether Neandertals took advantage of the levering action of the patella with a longer patellar ligament to generate a greater moment arm during knee flexion is not known. Thus, the Neandertal patella may have been thicker to accommodate increased cross-sectional area of the knee extensor muscles rather to increase moment arm alone.

Some Neandertal skeletal differences did not represent functional differences at all. Contrary to previous
interpretations (Trinkaus, 1983), the difference in tibial tuberosity projection between Neandertals and recent humans did not contribute to differences in knee extensor function. The greater prominence of the tuberosity can be explained more satisfactorily by the greater overall robustness of Neandertals.

Whether Neandertal knee extensor and ankle plantarflexor moments increased proportionately with moment arm depended on the musculotendon parameters. If muscle fiber length scaled with skeletal size so that the ratio of muscle fiber length to moment arm remained the same, then the shape of the moment-angle relationships were similar between Neandertals and recent humans (cf. recent human and Neandertal-scaled moments in Figs. 2–4). How the musculotendon parameters scale with body size is not known even among recent humans; it is not clear whether the same scaling assumptions can be applied to an earlier hominid population like Neandertals in which the functional requirements at the knee and ankle may have been different.

The sensitivity of the Neandertal moments to the musculotendon parameters was greater at the ankle than at the knee since the ankle plantarflexors have relatively short fibers and large moment arms (Hoy et al., 1990; Delp et al., 1990). At the knee, the moments were relatively insensitive to musculotendon parameters so that the increase in Neandertal moment arms produced greater extensor moments, regardless of musculotendon parameters. Neandertal plantarflexor moments, however, were very sensitive to the musculotendon parameters. Despite substantially greater moment arms, the Neandertal plantarflexor moments were not always greater than recent human but depended on how muscle fiber length changed with moment arm. If the same ratio of muscle fiber length to moment arm was maintained in Neandertals as in recent humans (scaled Neandertal models), the Neandertal moment arms resulted in greater moments at all joint angles. If the Neandertal moment arm increased relatively more than muscle fiber length (nominal Neandertal models), the plantarflexor moments would have been less than recent human at plantarflexed angles despite substantially larger Neandertal moment arms.

Although the physiological characteristics of Neandertal muscles are not known, it is likely that these people were at least as muscular as living humans and, based on their overall skeletal robustness, probably much stronger (Trinkaus, 1978, 1983, 1984; Wolpoff, 1996). If the muscle physiological cross-sectional areas were increased in the Neandertal models to reflect their greater robustness, the resulting muscle moments would be proportionately increased and the relative differences from recent human moments would be even larger. The shape of the moment curves, however, are not changed with muscle physiological cross-sectional area, so that our predictions about the differences between Neandertal and recent human moments would be quantitatively but not qualitatively altered.

We found that Neandertals did have a modest knee extensor and a large ankle plantarflexor moment arm advantage compared to recent humans, at least in the range of knee and ankle motions used in walking. Thus, our results are consistent with the reports of others regarding a functional advantage for Neandertals that arises from their skeletal morphology. An important difference, however, is that our results indicate that the Neandertal functional advantage did not depend on skeletal morphology alone but that morphological changes in muscles were necessary to accommodate the skeletal differences. Without an increase in plantarflexor muscle fiber length, for example, the Neandertal skeletal adaptations were potentially disadvantageous during motions that require extreme plantarflexion, such as climbing, lifting, or even walking over uneven terrain. Assuming that musculotendon parameters did change with the skeletal adaptations, however, Neandertals would have a distinct advantage compared to recent humans during demanding locomotor activities such as hiking.

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References


