The equine nuchal ligament 2: passive dynamic energy exchange in locomotion

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Summary
Head and neck movements in horses are characteristic of each gait, implying that the oscillation patterns are an intrinsic part of locomotion. In this study, we examined the head and neck movements of Standardbred horses exercising on a treadmill, and calculated the mechanical work performed by the head and neck segments at the walk, trot and canter. The position of the head and neck relative to the trunk was used to calculate the elastic strain energy stored in the nuchal ligament during the head movements of locomotion. These data allowed us to estimate the proportion of oscillatory work that is contributed by passive components of the equine neck. Elastic strain energy stored in the nuchal ligament contributes 55% of the work of moving the head and neck at the walk, and 33% and 31% respectively at the trot and canter. By substituting passive nuchal ligament work for active muscular work, the horse is able to reduce its metabolic cost of locomotion.

Keywords
Equine, Nuchal Ligament, Locomotion, Head and Neck, Biomechanics

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Introduction
A knowledgeable horse-person can tell whether a horse is moving at a walk, trot or canter by observing the head oscillations only. This changing pattern of head and neck movement suggests that head carriage is an intrinsic characteristic of the animal's fundamental gait mechanism. Indeed, it has been shown that the movement of the combined head and neck segment, relative to the trunk, is the most sensitive indicator of limb lameness (3, 12, 18), implying a profound integration of the body, the limbs and the head/neck complex.

The head and neck segments of the horse are cantilevered from the front of the body, and represent approximately 10% of the animal's total mass (4). The most appropriate simple mechanical model for the combined head and neck segments is that of a beam supported on one end, which can move independently of the body centre of mass (CM). However, this is an unusual beam in that it does not contain any large rigid elements, aside from the skull at the distal end. The cervical spine, while capable of acting as the beam's compression component, is flexible dorso-ventrally, laterally and rotationally. The passive tension element, the nuchal ligament (NL), is a support guy that is elastic and extensible, rather than rigid. Between these elements is a large muscular array, primarily oriented to span the distance between the trunk, the skull and the cervical vertebrae.

The nuchal ligament is primarily composed of elastin, a highly extensible biological polymer. The equine nuchal ligament is a compound structure with two anatomical elements (Fig. 1). The funicular, or cord-like section spans the top line of the horse from the withers (cranial thoracic spines) to the occiput, and the lamellar section is a series of broad bands between the funicular portion and the cervical spines. When the head is lowered, the nuchal ligament is stretched. When it is raised, the ligament returns to its previous length.

The nuchal ligament tends to be highly developed in ungulates. It has been suggested that it assists grazing animals in raising their heads after feeding (6, 8). Since elastic strain energy is stored in this structure whenever the head is lowered, it is also possible that the NL may contribute this elastic strain energy to the work of locomotion by reducing the muscular energy needed for the characteristic head oscillations of different gaits.

In this study, we examined the head and neck movements of Standardbred horses exercising on a high-speed treadmill, and calculated the mechanical work performed by the head and neck segments at the walk, trot and canter. The position of the head and neck, relative to the trunk, was then used to indirectly measure the elastic strain energy stored in the nuchal ligament, during the head movements of locomotion. Combining these data allows one to conservatively estimate the proportion of work contributed by passive components of the equine neck. Finally, we discuss the significance of head and neck movement to the mechanisms responsible for the three principle gaits used by horses.
Methods

Kinematics

Kinematic motions of six Standardbred horses, in racing condition, were measured in the course of their daily treadmill exercise at walk (1.8 m/s), trot (4 m/s), and canter (8 m/s). An automated kinematic analysis system was used, with four cameras, one viewing the treadmill from each corner. Video fields were recorded at 60 Hz. Spherical reflective markers were placed on the nose (8 cm. from the rostral edge of the nasal bone), the poll (the nuchal crest of the occiput), the highest point of the withers (spinoous processes of T4–T6), and the tuber sacrale. Markers were also placed on the cranio-lateral aspect of the front hooves to correlate head, neck and spine movement with foot placement. Each trial consisted of eight seconds, for a total of 480 fields. Video records were converted to 3-D orthogonal coordinates for each marker and exported as ASCII files to be analyzed via microcomputer in a spreadsheet and graphics programme.

Inverse Dynamics Analysis of the Head and Neck

The head and the neck were modeled as rigid bodies, rotating about the point where the neck joins the trunk of the horse, the junction of vertebral segments C7 and T1, hereafter called the “C-T hinge joint.” The positions of each segment’s CM, relative to the kinematic markers from the in vivo trials, were estimated by scaling segmental mass and inertia in Dutch Warmblood horses (3). The horses were videotaped with kinematic markers, plus markers indicating the terminal positions of the head and neck segments as defined by Buchner et al., and a marker for the position of the cervical thoracic junction. Images were captured and digitized from videotape, and a geometric relationship between the kinematic markers, the centres of mass and the C-T junction was determined. The mean values, as averaged over six subjects, were used to estimate the CM positions of the head and neck, and the position of the C-T hinge joint in the kinematic data sets. The mass of each segment was estimated from morphometric data (3) and adjusted proportionately to the individual mass of each subject used in the study.

The mechanical formulae used to derive the moments acting on the cervical-thoracic junction are presented in Appendix A. The calculated value is the moment acting on the hinge (C) about which the horse’s head and neck rotate. This moment is due to torque forces applied through the C-T hinge joint. These torques are generated by gravitational and inertial forces and are countered, primarily, by the nuchal ligament and the dorsal cervical musculature.

Moment due to Strain in the Nuchal Ligament

Since it would be extremely challenging technically to directly measure the moment due to NL strain in living animals without interfering with locomotion, it was estimated ex vivo using cadaver horses from a necropsy service (6). The strain in individual nuchal ligament segments (F1, F2, L4), at a range of neck angles, was characterized by regression equations, enabling nuchal ligament (true) strain to be estimated instantaneously for each kinematic data set. From in vitro testing of nuchal ligament material properties, the relationship of true strain to true stress, was determined. For each head position seen in vivo, the strain level...
associated with that position (as measured ex vivo) was plotted on the true stress/true strain curve. This process was repeated for each of the three nuchal ligament segments. The resulting stress was multiplied by the mean cross-sectional area of its respective segment, and then the three forces were summed to estimate total force. The moment (M) about the C-T hinge joint, due to nuchal ligament strain, was calculated as:

\[ M_{NL} = F_{NL} \times r_{CNL} \]  

(1)

where \( F_{NL} \) is the force generated by the nuchal ligament and \( r_{CNL} \) is the moment arm between the nuchal ligament and the C-T hinge joint (C).

**Power Calculations**

The power, used in oscillating the head and neck, was calculated as the moment times the angular velocity (\( \omega \)) of the combined head and neck segment about the C-T hinge joint.

\[ Power = M \times \omega \]  

(2)

The power was calculated for the total moment about the C-T hinge joint (due to gravitational and inertial forces as seen in Fig. 2), and the total moment minus the nuchal ligament moment. The moments about the C-T hinge are countered by moments generated by the nuchal ligament and the dorsal cervical muscles. After subtracting the NL contribution, the remaining moment is presumed to come from active contribution of the cervical muscles. The power curves were then plotted and integrated over three to four stride cycles for each animal at each gait. The integral (area under the power curve) represents the work done at the C-T hinge joint. For the purposes of this analysis, the absolute value of total work done at the hinge, whether positive or negative, was summed. The total work was compared to the work without the NL contribution, giving the percentage of nuchal ligament contribution to the total work:

\[ NL \text{ contribution} = \left[1-(W_{tot}-W_{NL})/W_{tot}\right] \times 100 \]  

(3)

**Statistical Analysis**

Head position and head angle were obtained by averaging over the portion of each kinematic data set used for the inverse dynamics analysis. Distribution of data points was normal (i.e. Gaussian). Tables 1, 2 and 3 show the means and standard deviations for each subject at all three gaits, and the mean of all subjects with standard error. A one-way analysis of variance was performed, comparing work at the C-T hinge joint among the three gaits. The significance was determined using Tukey's multiple comparison test (\( P \leq 0.05 \)).

**Table 1**  Walk – Results for individual animals (± S.D.) and overall mean (± S.E.)

<table>
<thead>
<tr>
<th>Subject</th>
<th>Poll Height (m)</th>
<th>Neck Angle (°)</th>
<th>Total Work (Joules/stride)</th>
<th>NL Work (Joules/stride)</th>
<th>Percent of Work done by NL (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.66 (0.04)</td>
<td>84.6 (3.6)</td>
<td>88</td>
<td>53</td>
<td>60</td>
</tr>
<tr>
<td>2</td>
<td>1.55 (0.04)</td>
<td>87.9 (3.7)</td>
<td>427</td>
<td>227</td>
<td>53</td>
</tr>
<tr>
<td>3</td>
<td>N.A.</td>
<td>N.A.</td>
<td>N.A.</td>
<td>N.A.</td>
<td>N.A.</td>
</tr>
<tr>
<td>4</td>
<td>1.55 (0.04)</td>
<td>91.3 (3.2)</td>
<td>464</td>
<td>246</td>
<td>53</td>
</tr>
<tr>
<td>5</td>
<td>1.66 (0.05)</td>
<td>79.9 (4.6)</td>
<td>264</td>
<td>137</td>
<td>52</td>
</tr>
<tr>
<td>Mean</td>
<td>1.61 (0.32)</td>
<td>85.9 (2.4)</td>
<td>311 (86)</td>
<td>166 (44)</td>
<td>55 (2)</td>
</tr>
</tbody>
</table>

**Table 2**  Trot – Results for individual animals (± S.D.) and overall mean (± S.E.)

<table>
<thead>
<tr>
<th>Subject</th>
<th>Poll Height (m)</th>
<th>Neck Angle (°)</th>
<th>Total Work (Joules/stride)</th>
<th>NL Work (Joules/stride)</th>
<th>Percent of Work done by NL (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.76 (0.03)</td>
<td>76.4 (2.2)</td>
<td>31</td>
<td>15</td>
<td>49</td>
</tr>
<tr>
<td>2</td>
<td>1.77 (0.03)</td>
<td>70.5 (2.3)</td>
<td>45</td>
<td>16</td>
<td>35</td>
</tr>
<tr>
<td>3</td>
<td>1.80 (0.03)</td>
<td>66.7 (2.5)</td>
<td>38</td>
<td>6</td>
<td>15</td>
</tr>
<tr>
<td>4</td>
<td>1.66 (0.02)</td>
<td>83.3 (1.2)</td>
<td>52</td>
<td>23</td>
<td>44</td>
</tr>
<tr>
<td>5</td>
<td>1.78 (0.05)</td>
<td>70.5 (3.8)</td>
<td>46</td>
<td>11</td>
<td>23</td>
</tr>
<tr>
<td>Mean</td>
<td>1.75 (0.02)</td>
<td>73.5 (2.9)</td>
<td>42 (4)</td>
<td>14 (3)</td>
<td>33 (6)</td>
</tr>
</tbody>
</table>
Table 3  Canter – Results for individual animals (± S.D.) and overall mean (± S.E.)

<table>
<thead>
<tr>
<th>Subject</th>
<th>Poll Height (m)</th>
<th>Neck Angle (°)</th>
<th>Total Work (Joules/stride)</th>
<th>NL Work (Joules/stride)</th>
<th>Percent of Work done by NL (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.70 (0.06)</td>
<td>78.1 (5.1)</td>
<td>160</td>
<td>56</td>
<td>35</td>
</tr>
<tr>
<td>2</td>
<td>1.71 (0.07)</td>
<td>74.8 (3.3)</td>
<td>66</td>
<td>16</td>
<td>25</td>
</tr>
<tr>
<td>3</td>
<td>1.71 (0.06)</td>
<td>73.7 (4.0)</td>
<td>112</td>
<td>33</td>
<td>29</td>
</tr>
<tr>
<td>4</td>
<td>1.68 (0.05)</td>
<td>81.5 (1.2)</td>
<td>35</td>
<td>14</td>
<td>42</td>
</tr>
<tr>
<td>5</td>
<td>1.75 (0.07)</td>
<td>72.9 (3.7)</td>
<td>93</td>
<td>22</td>
<td>24</td>
</tr>
<tr>
<td>Mean</td>
<td>1.71 (0.01)</td>
<td>76.2 (1.8)</td>
<td>93 (21)</td>
<td>28 (6)</td>
<td>31 (3)</td>
</tr>
</tbody>
</table>

Results

Examples of the data and derived calculations are presented in graphical form for a representative animal, in Figs. 3, 4 and 5. The results for the combined study group are presented in Tables 1, 2 and 3. At the walk (Fig. 3), the head and neck oscillate around an almost horizontal position, very close to the same height as the withers and tuber sacrale. At the trot, the head is routinely held 20 cm, or more, higher than at the walk. At the canter, the highest point of the head oscillations reaches trot height, and the lowest is close to walk height. In absolute terms, the largest head excursions are seen at the canter (mean 15 cm), followed by the walk (mean 10 cm) and the trot (mean 4 cm). However, when compared relative to the simultaneous oscillations of the whole body CM, the head excursions of the walk are the greatest (12-15 cm), with the canter second (9-11 cm) and the trot a modest (3-5 cm).

The maximum observed neck angle, with respect to a vertical projection at the withers, is greatest at the walk, and least at the trot (Fig. 4). The neck angle has important effects on the magnitude of strain energy of the nuchal ligament: the larger the neck angle, the lower the head, and the more the NL is stretched. The phase relationship of the head and back angle is also characteristic for each gait. At the walk, the head oscillates twice per stride, in rhythm with the placement of each forefoot. It rises in phase with the tuber sacrale, but out of phase with the withers, which accounts for the larger normalized head excursions (Fig. 3, shaded region). At the trot, the head, withers and tuber sacrale all move in phase, and bounce together with each diagonally paired step of the stride, giving two oscillations per stride. At the canter, the head and body oscillate only once per stride, and the peak vertical position of each anatomical marker, is slightly out of phase with one another (tuber sacrale leads, followed by the withers, then the head). Although the back angle changes very little when compared to the neck, the angles of the neck and back are almost one half cycle out of phase with each other, consistent with the visual impression of rolling undulation seen in the galloping gaits.

The difference between the total moment occurring at the C-T hinge and the moment contributed passively by the NL is the portion that must be provided by muscular activity (Fig. 5a). The nuchal ligament moment and the total moment at the C-T hinge are in phase with each other, confirming that the nuchal ligament is contributing to the total moment in a potentially useful way. The nuchal ligament moment is maximized when the head is low and the ligament is stretched.

Figure 5b shows the total power and power provided by the active structures at the C-T hinge joint. Both positive and negative work is performed during each gait cycle because the angular velocity is both positive and negative. In some analyses of power and work, negative work (work absorbed by the system) is counted as one fifth of the value of positive work (work done by the system) (14, 19). These analyses assume that positive work is generated solely by muscles, and so give a metabolic cost estimate. Since we have not measured any metabolic parameters in this study, only the mechanical work will be considered.

Figure 6 is a graphical representation of the sagittal rotation phases of the head/
The equine nuchal ligament

Discussion

The purpose of this study was to specify the contribution of the major passive anatomical components to the work of moving the head and neck during locomotion. While muscular work must also contribute to the observed motions, the animal may reduce its active muscular input between 31% and 55%, at the different gaits, by taking advantage of the nuchal ligament’s energy storage capabilities. Substituting passive work, for active muscular work, allows the animal to conserve its metabolic energy resources.
is "normal" for a biped at the walk, the gait is still functional when the arms are otherwise occupied. In contrast, it is difficult for a human to run effectively without swinging the arms.

Dynamic Effects

The results of the dynamic analysis are consistent with the kinematic observations. At the walk, the head is seen to have the largest excursions, and is carried lowest to the ground, maximally stretching the nuchal ligament. The work of moving the head and neck is largest at the walk, and the nuchal ligament contribution, as a percent of the total work, is the greatest. The percentage of nuchal ligament contribution at the trot and the canter is not statistically different, but the size of the head excursion is quite different between the two gaits (Fig. 3), and the amplitude of the power oscillations are much larger for the canter, when compared to the trot (Fig. 6b). It may be physiologically relevant to examine the trends of the means (Tables 2 and 3). The mean work per stride done by the nuchal ligament at the canter is twice that of the trot. Most locomotion data is presented using a stride, rather than a step, as a fundamental unit. In a stride cycle, each limb will step once, but for walk and trot, the head oscillates twice per stride. If one considers single head oscillations, rather than a full stride cycle, the mean work done by the NL for a single head bob in the cantering horse is four times that of the trotting animal. The mean nuchal ligament work of a single head oscillation at the walk is three times that of the canter and almost twelve times that of the trot.

Between subjects, the variability in calculated work performed at the C-T hinge joint is quite large. This reflects the system’s sensitivity to perturbations of acceleration, both linear and angular. Even though head oscillations are inevitable in locomotion, it is likely that a horse moving smoothly, without any rapid jerking of the head, is performing less mechanical work, and so using less metabolic energy. This concept may also be applied to limb movements. There is much interest, among equine and human gait researchers alike, in characterizing those qualities that separate average from gifted athletes. Perhaps, elite athletes have superior muscle control to manage more precisely their various segment accelerations, and so use their invested metabolic energy more effectively. This can also explain why even subtle, well-compensated, lameness can make an animal exercise intolerant.
Interactions with Fundamental Gait Mechanisms

Although the fluctuations of power in the head/neck segment are small, in comparison with those of the body centre of mass, they can be making a critical contribution to the dynamic energy balance of the horse. From this analysis, it is clear that the head/neck segment is used, very differently, in each of the three principal gaits. At the walk, head oscillations appear to be predominantly passive, following the pendular oscillations of the rest of the body (5). The nuchal ligament plays an important role in passively supporting the head/neck mass against gravity, and so reduces the muscular work that would otherwise be required to hold the head above the ground. It is likely that there are dynamic links between the pendular mechanisms of the limbs and that of the head/neck segment.

For the trot, a bounding gait, the animal must take advantage of strain energy stored in the distal tendons (7). Keeping the mass of the head and neck moving in synchrony with the remainder of the body mass will maximize distal tendon loading, and so return more energy for the next stride cycle. Therefore, oscillations of the head in response to the raising and lowering of the thoracic region are largely resisted by active muscular stabilization. Since the stabilizing muscles can act isometrically, there is little power requirement and the metabolic cost remains low. An alternative explanation might be that the bounce frequency of the trotting horse exceeds the intrinsic oscillation frequency of the head/neck system, so that it is more cost-effective for the animal to hold the head/neck relatively rigid than to actively respond to the trunk movement. The contribution of the nuchal ligament, at the trot, is probably too small to be an important factor in the gait energetics.

In contrast, the canter uses head and neck movement as an active element of the fundamental gait mechanism. It is an asymmetrical gait, with high impulse, single foot placements occurring twice during the stride cycle: trailing hind stance and leading fore stance. Mechanically, the distance between the body CM and the ground reaction force vector acts as a moment arm to rotate the trunk. This results in the characteristic body pitches seen at the canter. The body pitch is not seen at the trot because the front and hind limbs contact the ground simultaneously, and these moments balance during steady state locomotion (13). The sagittal pitching of the trunk and of the head/neck segment are out of phase with each other, which results in opposing motions during 50% of the total stride duration (Fig. 6b). The opposing head/neck pitches act during the single foot contacts of the canter stride (the trailing hind and the leading fore), countering the ground reaction force induced moments, and possibly helping return the trunk to the neutral horizontal position seen during the conjoined stance (leading hind and trailing fore) and flight phases of the stride. Since the oscillations of the head and neck are initiated in opposition to the pitching trends of the rest of the body, active muscular work must be added to reverse the direction of angular acceleration, and raise the head. Once the motion is reversed, the nuchal ligament can make a valuable contribution—nearly one third of the mechanical work of raising the head can be provided passively by the nuchal ligament alone.

It remains to be seen how much passive strain energy can be stored in the cervical musculature itself. The semispinalis muscle, which originates on the transverse processes of the cranial thoracic vertebrae and inserts on the articular processes of the cervical vertebrae and the occiput, is a large and complex muscle with many bands of connective tissue insertion and compartments containing up to 90% slow oxidative fibres (10). This muscle may have the capacity to generate force economically by using its slow oxidative fibres to contract isometrically against the gravity induced fall of the head, and so store strain energy in its aponeurotic bands. Using this strain energy to help raise the head would contribute even more energy savings to the system.

In these two studies, we have found that the head and neck movements of the horse are an intrinsic part of the whole animal's locomotory process and that the nuchal ligament has the capacity, through its structural and material properties, to contribute dynamically to locomotion through storage and release of elastic strain energy. Future experiments will need to quantitatively assess the active and passive muscular contributions to the internal work of the head...
and neck and compare the total energetic costs and gains of head motion.

Appendix A

The total moment at the C-T hinge joint (C) was determined using angular momentum balance at that point (Fig. 2, free body diagram).

\[ \sum M_{tc} = \dot{H}_{tc} \]

(1)

where \( M_{tc} \) is all moments about C, and \( H_{tc} \) is the rate of change of angular momentum about C. Gravitational forces act at each segment’s CM. A moment exists at the C-T hinge joint, which, together with the gravitational forces, opposes all of the dynamic influences of the body at the C-T hinge joint. Using unit vectors i, j and k, to express vector direction, for each segment, the angular momentum balance is:

\[ M_k + \left[ T_{G1C} \times mg(-j) \right] = i0k + \left[ T_{G1C} \times ma_{cm} \right] \]

(2)

where \( M \) is the total moment at the C-T hinge joint (C), \( T_{G1C} \) is the vector between the C-T hinge joint (C) and the segment centre of mass (G), \( m \) is the mass of the segment, \( g \) is the gravitational acceleration (9.81 m/s\(^2\)), \( I \) is the segment’s moment of inertia with respect to its CM, \( \dot{\theta} \) is the angular acceleration of the segment CM about C, and \( a \) is the linear acceleration of the segment CM. The head and the neck segments are treated separately, then summed. Resolving the cross products for each segment separately and dotting each side of the equation with \( k \), the total moment at the C-T hinge joint is found to be:

\[ M = I_k \dot{\theta}_k + d_m \dot{a}_m - e_m \dot{a}_m + \]

\[ I_e \dot{\theta}_e + d_m \dot{a}_m - e_m \dot{a}_m - \]

\[ (d_m \dot{g} + d_m g) \]

(3)

where \( d \) is the component of the vector \( r \) in the x direction (horizontal, in the direction of travel) and \( e \) is the component of the vector \( r \) in the z direction (vertical). Each of the terms is subscripted as per its reference segment.

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References


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