The role of motor and visual experience during development of bipedal locomotion in chicks

Gillian D. Muir*, K.S.V. Gowri
Biomedical Sciences, WCVM
University of Saskatchewan
Saskatoon, SK
Canada S7N 5B4

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*author to whom correspondence should be addressed:

Gillian D. Muir, D.V.M., Ph.D.
Biomedical Sciences, WCVM
University of Saskatchewan
52 Campus Drive
Saskatoon, SK
Canada S7N 5B4

phone 306 966 7353
fax 306 966 7376
gillian.muir@usask.ca

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The purpose of this research was to investigate the role of motor and visual experience during the development of locomotion in chicks. We have previously demonstrated that when locomotor activity is restricted immediately posthatching, chicks walk with shorter stride lengths and attenuated head bobbing movements. Head bobbing is an optokinetic response in birds, driven by the movement of the visual world across the retina (i.e., optic flow). During locomotion, optic flow is generated by forward translation, and we have shown that the magnitude of head bobbing movements and stride lengths are moderately correlated in walking chicks. In the present study, we investigated this relationship more closely by examining whether imposed changes in stride length could affect head excursions during head bobbing. We manipulated stride length by hobbling chicks immediately after hatching and subsequently quantified kinematic parameters, including step timing and head excursions, during walking. Imposition of shorter stride lengths induced chicks to take more frequent steps, spend less time in contact with the ground and shortened head excursions during head bobbing. Nevertheless, the developmental changes in head excursions were not fully accounted for by altered stride lengths, so in a separate experiment we investigated whether the development of head bobbing relies on the normal experience of optic flow. We raised chicks under stroboscopic illumination to eliminate chicks’ experience of optic flow, but found that this did not significantly alter head bobbing. These results are discussed along with related findings in other species, and the possible neural and biomechanical constraints underlying development of walking and head bobbing in birds.
INTRODUCTION

While there is much known about the experience-dependent development of sensory systems, less is known about the experience-dependent nature of motor system development. We are investigating how locomotor and visual experiences affect the development of bipedal locomotion in chicks. Very young chicks (i.e. 0 – 3 days old) naturally walk with shorter stride lengths, spend more time in contact with the ground and more time supported by two legs compared to older chicks (10 - 14 days old) (Muir et al. 1996). These same characteristics are seen during human locomotor development and may be related to constraints inherent to the development of bipedal locomotion (Forssberg 1985). We have previously demonstrated that manipulation of locomotor experience in chicks can alter their locomotor pattern (Muir and Chu 2002). When exercise restriction is imposed on chicks immediately after hatching for a minimum of 6 days, they move with shorter stride lengths and make smaller head excursions during head bobbing compared to control animals (Muir and Chu 2002). Head bobbing, which occurs during walking in birds, is an optokinetic response, driven by the movement of the visual world across the retina (i.e. optic flow) (Friedman 1975; Frost 1978; Troje and Frost 2000). During walking, the movement of the visual world is generated by forward translation and thus the relationships between locomotor parameters and the extent of head excursions could provide important insights into the control and development of head bobbing. For example, the shorter stride lengths which occurred in exercise-restricted animals might have accounted for the smaller head excursions seen in the same group of animals, since stride length determines the horizontal distance moved, and thus the amount of retinal slip occurring for each stride. Stride length and head excursions are, in fact, moderately correlated (Muir and Chu 2002). Nevertheless, other factors in addition to stride length must influence the extent of head excursions during posthatching development, because head excursions continued to increase for at least 10 days after hatching whereas stride length ceased to change after
4 days (Muir and Chu 2002). The current study aims to investigate the effect of stride length on head excursions more definitively by imposing shortened stride lengths on chicks and subsequently examining the effects on head bobbing excursions as well as on other stride parameters. Our previous results also demonstrated that maturation of the head bobbing response is sensitive to locomotor experience, suggesting a role for experience-dependent plasticity during early posthatching development. Experience-dependent changes have also been postulated to underlie the maturation of vestibulo-ocular and optokinetic responses in birds, because chicks have no visual experience prehatching, and thus their posthatching visual experience might be required for normal reflex maturation to take place (McKenna and Wallman 1985). Continued deprivation of visual stimuli, by dark-rearing for example, would be one method to examine the role of visual experience on optokinetic responses. Unfortunately, complete visual deprivation in chicks posthatching results in severe myopia (Wallman and Adams 1987; Wallman 1990; Stone et al. 1995). Nevertheless, because visual flow information requires continuous illumination, raising chicks in stroboscopic illumination will eliminate optic flow information without causing myopia (Wallman 1990). Cats reared in stroboscopic illumination display abnormalities in both optokinetic and vestibulo-ocular reflexes (Kennedy et al. 1982). In addition to investigating the contribution of stride length to head bobbing, the current study also investigated the extent to which early experience of optic flow plays a role in the maturation of head bobbing behaviour, by raising chicks under stroboscopic illumination and subsequently examining head bobbing behaviour and stride parameters during walking.

MATERIALS AND METHODS

Fertilized eggs were incubated at 37.5 C and rotated 4 times per day. Only animals which hatched between the hours of 8 am and 4 pm were used from each hatch to control for differences
in age between animals. The day of hatching was designated as posthatching day 0 (P0). All animals were cared for according to standards set by the Canadian Council on Animal Care. A total of 114 chicks were used for this study.

_Treatment groups – imposition of reduced stride length_

To impose a shorter stride length, all chicks were hobbled on P1 by placing loose plastic rings on each limb at the level of the distal metatarsal bones and tying the rings on right and left limbs together with a silk thread of pre-determined length. The length of the thread corresponded to 70% of the normal stride length for posthatching day 1 (P1) animals, obtained from earlier experiments (Muir and Chu 2002). The length of the hobble was adjusted every 2 days throughout the experiment to maintain the same proportion of stride length (ie. 70% of normal stride length) as the animals grew. For each hobbled animal, kinematic data was collected on P4, 8 and 12. To determine whether the length of time hobbled had an effect on locomotor development, a subset of randomly chosen animals were unhobbled on P2, 6 or 10. Data was collected from unhobbled animals 2 days after hobbled were removed, ie. P4, 8 and 12. Control animals were raised under the same conditions as hobbled animals, but were never hobbled.

_Treatment groups – elimination of optic flow_

To deprive animals of optic flow information, chicks were hatched and raised in a room lit only by a strobe light flashing at 2.0 Hz, consistent with frequencies used in related studies (Goode et al. 2001). Kinematic data was collected on P4, 8, 12 and 16. For each day of data collection, animals were randomly chosen and removed from the strobe lit environment. They were allowed to acclimatize to constant light conditions for 10 minutes prior to data collection. Preliminary experiments had determined that chicks would not walk down the runway for at least 10 minutes
upon being exposed to constant light conditions. Once animals were removed from strobe conditions for data collection, they were never returned to the strobe-lit environment. Thus, each chick was used for only one day of data collection.

Kinematic data collection and analysis

Data collection and analysis were performed as previously described (Muir and Chu 2002). Briefly, chicks were encouraged to walk and run unrestrained down a 50 cm long runway and were videotaped from the left side as they moved past a camera placed perpendicular to the runway. Two infra-red beams aligned across the runway provided a measure of the average velocity of each animal for each pass. Markers were placed over the greater trochanter of the hip and on the metatarsophalangeal joint.

Single frame analysis (60 frame/sec) was carried out on passes in which the chick maintained a constant velocity for 2 - 3 strides (Northern Eclipse, Empix Imaging Inc, Mississauga, Ontario). Gait parameters were collected from 1 complete stride for each pass and consisted of the duration of ground contact for each foot and stride length. Stride length was defined as the horizontal distance from foot position at onset of ground contact of one limb to the subsequent position of the same foot at onset of ground contact in the next stride. The horizontal distance between the hip and the eye was recorded for each frame throughout the stride by digitizing and recording the coordinate positions of the hip marker and the eye.

In order to compare chicks in different age groups, stride length, velocity and head excursions were normalized to body size. Stride length and velocity were normalized as previously described (Muir et al. 1998; Muir and Chu 2002) according to the method of Gatesy and Biewener (Gatesy and Biewener 1991). In brief, stride length was divided by hip height (h) and velocity was divided by gh^{0.5}, where g is the gravitational acceleration constant, 9.8 m/sec. Horizontal head movements were
normalized by dividing by neck length (obtained from age-matched cadaver specimens). References
to these variables in the remainder of this study refer to normalized values. Head excursions were
defined as the difference between the maximum and minimum horizontal distance between the hip
and the eye for each stride (see Figure 5, “Control P4” for an illustration of the head positions and
corresponding head-hip distance throughout the stride). For the remaining variables, stride duration
was defined the time between initial ground contact of one limb and the subsequent ground contact
of the same limb. Stance duration was the time between the initial ground contact of the limb and
the last ground contact of the same limb in the same stride. Double stance duration was the
proportion of the stride that the animal spent supported by both limbs.

Each variable (stride length, maximum head excursions, and durations of stride, stance and
double stance) was averaged for each animal when they were moving at walking speeds only
(normalized velocities of 0.2 to 0.4). Walking speeds were used because head bobbing only occurs
during walking (Muir and Chu 2002). Data from approximately 4 - 6 passes were used to obtain
averages for each individual. Averaged values from individuals were used to obtain group means for
each variable. Analysis of variance was used to determine statistical differences between groups
(SigmaStat, SSPS Inc). To compare head excursions throughout the stride, polynomial regression
was used to provide a representative curve for each age group (SigmaPlot, SPSS Inc.). A 6th order
polynomial produced the best fit in each case (Figure 5).

RESULTS

Imposition of reduced stride length

Hobbled chicks maintained stride lengths during walking which were 20% shorter than those of
age-matched control chicks throughout the experiment (Figure 1: F = 25.352, p<0.001). To
compensate for reduced stride lengths and maintain comparable walking speeds to age-matched
control animals, hobbled animals took more frequent steps, as indicated by reduced stride durations
(Figure 2: F=8.920, p<0.001). Stride timing measurements indicated that hobbled animals spent
much less time in stance and less time supported by two legs compared to age-matched control
animals (Figure 3A and B: for stance duration, F=13.567, p<0.001, for double support duration,
F=11.662, p<0.001).

Animals which had been previously hobbled (ie. unhobbled animals) walked with stride lengths
which were not different from control animals, indicating that early experience of shorter stride
lengths, even after being hobbled for 10 days, did not permanently shorten their stride. Unhobbled
animals tended to take more frequent steps compared to control animals, although this change was
only significant for those animals unhobbled on P6 and measured at 8 days post-hatching (Figure 2:
p<0.01). Similarly, unhobbled animals tended to move with reduced stance time and reduced time
supported by two legs, although these values were different from control values only on P8 (Figures
3A and B: p <0.001). Thus, there is some indication that gait modifications acquired during
imposition of shorter stride lengths for 6 days may be maintained for at least 2 days after stride
length is allowed to return to control values. Nevertheless, unhobbled animals which had been
hobbled for a shorter period (ie. 2 days) or a longer period (10 days) before unhobbling did not
move significantly differently from control animals.

As previously described, chicks normally undergo two cycles of neck extension and retraction
during each stride (Figures 4,5). This serves to hold the head stationary relative to the ground for
two separate periods of time during the stride cycle (Figure 4). The timing of these stationary phases
were similar between age-matched control and hobbled animals (Figure 4), but there were
differences between groups with respect to the distances moved by the head (Figure 5). Consistent
with our previous work, the maximum head excursions during head bobbing increased for up to 8 –
10 days after hatching (Muir and Chu 2002). This increase is evident in both control and hobbled
animals (Figure 5). Imposition of shorter stride lengths resulted in reduced head excursions during head bobbing (Figure 5, “Hobble”; Figure 6: F=28.622, p<0.001). This reduction is greatest at P4 but is still maintained up to 12 days posthatching (Figure 6). Head movements of P4 and P8 hobbled animals also occurred earlier in the stride cycle compared to control animals but returned to control values by P12 (Figure 5: maximum excursions occur at 0.15 and 0.75 proportion of stride cycle, compared to 0.2 and 0.8 for control animals). Unhobbled chicks showed reductions in head excursions, which were significantly different from controls up to and including 8 days posthatching (Figure 6: p<0.001).

Deprivation of optic flow

Animals raised under stroboscopic lighting conditions showed very few changes in their walking pattern compared to age-matched control animals. There was a small but significant reduction in stride length in animals raised for 16 days in a strobe environment (Figure 7A: F=5.248, p<0.001) and no differences in any other stride parameters compared to control animals (data not shown). Similarly, head bobbing excursions in animals raised in a strobe environment did not differ from those raised under normal lighting conditions, except for a small reduction in head excursions after 16 days in strobe lighting (Figure 7B: F=5.609, p<0.001). Thus, chicks deprived of optic flow information can walk and head bob in a manner similar to control animals.

DISCUSSION

The results presented here demonstrate that experimental reduction in stride length resulted in changes to the locomotor pattern in chicks, in that they moved with quicker steps and spent proportionately less time with their limbs in contact with the ground. Hobbled animals also walked with significantly smaller head excursions compared to control animals, consistent with previous
work which demonstrated that stride length and head excursions were correlated (Muir and Chu 2002). In both the previous and present studies, head excursions in all groups showed a developmental increase from hatching through to 12 days of age. Additionally, animals which had previously experienced hobble conditions, but which were no longer hobbled, moved with stride lengths similar to control animals, but changes in limb timing measurements and especially head bobbing excursions had a tendency to be more similar to those of hobbled animals. In contrast to the effect of hobbling, deprivation of optic flow information did not affect the manner in which chicks walked or head bobbed.

Hobbled chicks moved differently from very young (1-3 day old) chicks, which naturally move with disproportionately short stride lengths but spend more time with limbs in contact with the ground when compared with older animals (Muir et al. 1998). Instead, when shorter stride lengths are imposed on older animals, they actually spend less time in contact with the ground. Thus, hobbling does not delay development of walking in chicks. These animals simply adapted their stride timing to adjust for shorter stride lengths.

The imposition of shorter stride lengths affected head bobbing excursions in a different manner compared to stride parameters. Hobbled stride length was kept constant from 0 to 12 days posthatching (Figure 1, black bars), but unhobbled and control animals also maintained a constant stride length from P4 to P12. Concomitantly, stride frequency and limb support times (Figures 2 and 3) did not change from P4 to 12 days posthatching. In contrast, head bobbing excursions showed a dramatic increase with age in hobbled animals (Figure 6, black bars). This also occurred in control animals, although the increase was less dramatic. The differential increase in head excursions over time in hobbled vs control animals resulted in a stronger reduction in head excursions in hobbled animals at P4 (ie. 33% of control values) compared to p12 (80% of control values) (Figure 6). This
suggests that hobbling actually delayed the maturation of head bobbing behaviour, an effect which
was not seen for limb parameters.

The fact that head excursions in all groups of chicks continued to increase over time while stride
length remained constant suggests that there are factors in addition to stride length which affect
head bobbing behaviour in these animals. We investigated one possibility by examining the role that
visual experience of optic flow had on development of head bobbing. Although there was a slight
reduction in stride length and head bobbing excursions after 16 days of optic flow deprivation
(Figure 7), the evidence suggests that experience of optic flow is not necessary for the development
of head bobbing behaviour. This is in spite of the fact that optic flow, and specifically retinal slip,
has been shown to be the primary stimulus for this behaviour (Friedman 1975; Frost 1978; Troje
and Frost 2000). When birds are placed on a moving treadmill and do not begin stepping
immediately, head bobbing still occurs as the animals are moved backward by the treadmill relative
to the environment (unpublished observations). Frost has also described that very slow movement
of a treadmill belt will induce compensatory head movements (Frost 1978). Further experiments
have shown that retinal slip is particularly important during the phase of head bobbing in which the
head is held stationary relative to the environment (Troje and Frost 2000). The slight forward
translation of the head during this phase (ie. 3 mm s⁻¹) provides the necessary error signal for the
maintenance of head position (Troje and Frost 2000).

The apparent independence of head bobbing development, an optokinetic response, from the
experience of optic flow differs from the development of vestibulo-ocular reflexes in chickens.
Chicks raised for 8 weeks in a stroboscopic environment showed much smaller gains in vestibulo-
ocular responses (VOR) compared to birds reared in normal light (Goode et al. 2001). Although the
present study deprived chicks of optic flow for a much shorter period (up to 16 days compared to 8
weeks), Goode et al found reduced VOR gains after only two days in the strobe environment
(Goode et al. 2001). Importantly, VOR responses eventually recovered after several days in normal lighting. This, in turn, differs from the results of similar experiments in cats, in which both VOR and optokinetic responses do not recover under normal lighting in animals which were previously raised under stroboscopic lighting (Kennedy et al. 1982). Interestingly, vestibulocollic responses in chickens are not affected by stroboscopic illumination and it was suggested that additional information from neck proprioceptors provided sufficiently accurate information to maintain normal gains during head movements (Goode et al. 2001). It is possible that because head bobbing, like vestibulocollic responses, involves movements of the head, this behaviour may rely less on visual inputs for development than do other optokinetic and vestibulo-ocular responses.

If neither stride length reduction nor lack of exposure to optic flow can prevent the development of head bobbing, the question still remains as to what underlies this gradual increase in the magnitude of head excursions from hatching to 12 days of age. One possibility is that this change is not experience-driven, but instead relies on the maturation of underlying neural circuitry. Optokinetic responses in birds are thought to be controlled through the accessory optic system and the pretectum (Simpson 1984; Wallman and Velez 1985; McKenna and Wallman 1985; Simpson et al 1988). The major nucleus of the accessory optic system is the nucleus of the basal optic root (nBOR). This nucleus, and the major nucleus of the pretectum, the lentiform nucleus of the mesencephalon (LM) have been shown to be sensitive to the movement of optic flow fields at velocities which are consistent with the small head movements seen during the hold phase of head bobbing (Burns and Wallman, 1981; Morgan and Frost, 1981; Winterston and Brauth, 1985; Wylie and Crowder, 2000; Crowder et al 2003). Importantly, the responses of nBOR and LM undergo postnatal development in chickens (McKenna and Wallman 1985). These changes correspond to the increases in gain of optokinetic response which occur during the first weeks after hatching.
Thus, it is possible that the changes in head bobbing excursions over this time period correspond to maturation of responses in the nBOR and LM.

Another possibility is that factors other than optic flow are responsible for the changes in head excursions seen in chicks. There have been suggestions that biomechanical constraints also influence head bobbing behaviour. Work from our lab, including the present study, has demonstrated that stride length is correlated with, and can influence, head excursions (Muir and Chu 2002). It has also been observed that the peak speed of head movement during head bobbing occurs simultaneously with the peak speed of the body centre of mass in walking birds (Fujita 2003). The velocity of the body centre of mass may therefore indirectly affect head excursions during walking.

In conclusion, we have demonstrated that head bobbing behaviour can be influenced by biomechanical factors, such as the imposition of shorter stride lengths, but that visual factors such as the deprivation of optic flow did not appear to affect head bobbing behaviour. Further investigations into the neural and biomechanical constraints underlying walking and head bobbing in chicks will help to elucidate the experience-dependent nature of bipedal locomotor development.

**GRANTS**

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FIGURE LEGENDS

**Figure 1**
Stride length as a function of age for hobbled, unhobbled and control groups of animals. Stride length has been normalized to leg length to allow for comparisons between animals of different sizes. Stride length remained constant from 4 to 12 days of age within each group of animals. Hobbled animals walked with stride lengths that were approximately 20% shorter than those of age-matched control animals. The stride lengths of previously hobbled (ie. “unhobbled”) animals did not differ from those of age-matched control animals. Each bar represents the mean +/- S.E, hobbled n=22, unhobbled n=9, control n=9.

* significantly different from control values, p<0.001.

**Figure 2**
Stride duration as a function of age for hobbled, unhobbled and control groups of animals. Stride durations remained constant from 4 to 12 days of age within each group of animals. Hobbled animals walked with shorter stride durations (ie. higher stride frequencies) compared to those of age-matched control animals. The stride durations of unhobbled animals were shorter than those of age-matched control animals at P8. Each bar represents the mean +/- S.E, hobbled n=22, unhobbled n=9, control n=9.

* significantly different from control values, p<0.001 for hobbled, p<0.05 for unhobbed.
Figure 3

Stance duration (A) and double support duration (B) as a function of age for hobbled, unhobbled and control groups of animals. Both values are expressed as a proportion of stride duration. Within each group of animals, stance and double support durations do not change from 4 to 12 days of age. Hobbled animals walked with shorter stance durations and shorter periods of double support at all ages compared to age-matched control animals. Unhobbled animals walk with shorter stance and shorter double support durations at 8 and 12 days of age compared to age-matched control animals. Each bar represents the mean +/- S.E, hobbled n=22, unhobbled n=9, control n=9.

* significantly different from control values, p<0.001.

Figure 4

Head position relative to the ground during walking in P4, P8 and P12 chicks as a function of stride proportion. Each series of points on each graph represents the head positions of different individuals in each group. The data demonstrate that head bobbing is achieving a stable head position at two time periods within each stride (ie. from 0.20 – 0.50 and from 0.70 – 1.0 of the stride cycle) for ages P8 and P12, in both control and hobbled groups. Head position is less stable at P4, but this is similar between control and hobbled groups. The most notable differences between control and hobbled groups are the distances that the head moves from 0.0 – 0.20 of the stride cycle, further illustrated in Figures 5 and 6.
**Figure 5**

Horizontal distance between the head and the hip during walking in P4, P8 and P12 chicks as a function of stride proportion. Horizontal distances are normalized to neck length to control for size differences between chicks of different ages. Line drawings illustrate the corresponding head positions for the minimum and maximum head-to-hip distances produced twice during each stride. Horizontal distances increase in control animals up to P8. In hobbled animals, horizontal excursions are smaller than those produced by control animals at each age, but also undergo an increase from P4 through to P12. For each graph, thick lines represent 6th order regression through the data for all animals in each group, thin lines represent 95% confidence limits.

**Figure 6**

Maximum head excursions (= the difference between maximum and minimum head-to-hip distances in Figure 4) as a function of age for hobbled, unhobbled and control animals. Head excursions are normalized to neck length to allow for direct comparisons between chicks of different sizes. In all groups, head excursions increase with age up to P8 (control animals) and to P12 (hobbled animals). Hobbled animals produce smaller head excursions at all ages compared to age-matched controls. Unhobbled animals also produce smaller head excursions compared to controls at P4 and P8. Each bar represent the mean +/- S.E, hobbled n=22, unhobbled n=9, control n=9. * significantly different from control values, p<0.001.
Figure 7

Stride length (A) and head excursions (B) as a function of age for animals raised under stroboscopic illumination (strobe) and normal illumination (control). Stride length and head excursions have been normalized to leg length and neck length, respectively, to allow for comparisons between animals of different sizes. Both stride lengths and head excursions are smaller in strobe animals at P16 compared to P16 control animals. Each bar represents the mean +/- S.E., strobe n=12, control n=8. * significantly different from control values, p<0.01.
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Figure 1

Days posthatching

Stride length

Hobbled
Unhobbled
Control

*
Figure 2

The figure shows the stride duration of three groups of animals: Hobbled, Unhobbled, and Control, across three days posthatching: 4, 8, and 12.

- **Hobbled**: The stride duration for the hobbled group is represented by black bars.
- **Unhobbled**: The stride duration for the unhobbled group is represented by yellow bars.
- **Control**: The stride duration for the control group is represented by purple bars.

Significance is indicated by asterisks: * indicates a statistically significant difference. The bars for each day are labeled with their respective stride duration values.
Figure 3

A

Days posthatching

Stance Duration

B

Days posthatching

Double Support Duration

Hobbled
Unhobbled
Control

* * *

Hobbled
Unhobbled
Control

* * *

Hobbled
Unhobbled
Control

* * *
Figure 4

CONTROL

HOBBLE

P4

P4

P8

P8

P12

P12

head position (cm)

proportion of stride cycle

0.0 0.2 0.4 0.6 0.8 1.0 1.2

0.0 0.2 0.4 0.6 0.8 1.0 1.2

0.0 0.2 0.4 0.6 0.8 1.0 1.2

0.0 0.2 0.4 0.6 0.8 1.0 1.2
Figure 5

CONTROL

HOBBLE

Horizontal distance between head and hip

P4

P8

P12

proportion of stride cycle
Figure 6

![Bar chart showing head excursions over days posthatching.](chart.png)

- **X-axis**: Days posthatching (4, 8, 12)
- **Y-axis**: Head Excursions (0.0 to 0.5)

- **Legend**:
  - Hobbled
  - Unhobbled
  - Control

- **Significance**:
  - Asterisks indicate significant differences between conditions.

- **Note**: The chart illustrates the progression of head excursions with increasing days posthatching for hobbled, unhobbled, and control groups, highlighting changes over time.
Figure 7

A

Stride Length

Days Posthatching

B

Head Excursions

Days Posthatching