Posthatching Locomotor Experience Alters Locomotor Development in Chicks

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Muir, G. D. and T. K. Chu. Posthatching locomotor experience alters locomotor development in chicks. J Neurophysiol 88: 117–123, 2002; 10.1152/jn.00855.2001. We have previously demonstrated that, even though chicks are very precocial and can locomote within hours of hatching, they require a period of time to develop a mature stable walk. As an example, 1- to 2-day-old animals move with disproportionately small stride lengths compared with 10- to 14-day-old animals. The purpose of this study was to determine whether the maturation of walking, including the development of a mature stride length, depends on locomotor experience. We also investigated the development and experience-dependence nature of head bobbing, an optokinetic behavior that occurs during walking in birds. Chicks were randomly assigned to one of three groups receiving either increased locomotor experience (i.e., treadmill exercise), decreased locomotor experience (i.e., decreased housing space), or no alteration in locomotor experience. To assess the dependence of locomotor maturation on N-methyl-D-aspartate (NMDA)-type glutamate receptors, animals in each group were either given an NMDA antagonist (MK-801, 1 mg/kg intramuscularly daily) or saline control. Locomotor characteristics (stride length, leg support durations, horizontal head excursions) were quantified from videotaped recordings of chicks walking overground unrestrained on posthatching days 1, 2, 4, 6, 8, and 10. Animals subject to exercise restriction for at least 6 days moved with shortened stride lengths compared with age-matched treadmill-exercised or control animals, a change that was maintained for the duration of the study. NMDA antagonism also resulted in shortened stride lengths. Head bobbing behavior matured during the same posthatching time period. The rate of this maturation was also decreased by exercise restriction. Thus locomotor experience is required for normal development of locomotor behavior, even in very precocial animals. These results are discussed in terms of the possible neuroanatomical and neurophysiological mechanisms underlying experience- and activity-dependent changes during motor development.

INTRODUCTION

The purpose of this study was to determine whether experience-dependent processes are involved in the maturation of walking gait in the chick. We have previously shown that, although newly hatched chicks can walk and run within hours after hatching, they do not walk in the same manner as older birds (Muir et al. 1996). Evidence for this comes from both kinetic data (e.g., ground reaction forces) and kinematic data (e.g., stance and stride durations). In particular, the ground reaction forces produced by very young (1- to 2-day-old) chicks demonstrated that the normal vertical oscillations of the center of mass that occur during walking were smaller compared with those of older (10- to 14-day-old) birds, resulting in a less efficient gait. Young birds also walked with shorter stride lengths and spent disproportionately less time supported by a single leg during each walking stride when compared with older birds (Muir et al. 1996). This suggests that they are less stable than older animals and require time to develop a stable mature walking gait. Interestingly, although young birds have an immature walking gait, they appeared to run in the same manner as older birds. Many of these changes in limb timing and stride length are similar to those occurring during the development of walking in humans (Sutherland et al. 1988) and thus may be related to constraints inherent to bipedal locomotion.

We are currently investigating the extent to which development of this mature walking gait depends on experience, particularly locomotor experience. The role of experience during normal neural development has been studied in several neural systems, including sound localization and song-learning in birds, and the development of binocular vision in mammals. For example, it is well-established that visual experience is required for the development of ocular dominance columns in the visual cortex (Hubel and Wiesel 1970). Additionally, synaptic modifications underlying this development have been shown to be mediated by the N-methyl-D-aspartate (NMDA) subtype of the glutamate receptor (Kirkwood and Bear 1994).

Much less is known regarding the contribution of experience or activity-dependent reorganization to the development of locomotor systems (Muir 2000). Spinal motor circuitry, responsible for generating alternating limb activity, is established relatively early in development in many species (Bekoff 1976; Cazalets et al. 1995; O’Donovan 1999; O’Donovan and Landmesser 1987). Conversely, supraspinal locomotor pathways, necessary for the initiation and control of locomotion, project to the cord over a longer developmental time course, even postnatally in several mammals (Kudo et al. 1993; Okado and Oppenheim 1985; Schreyer and Jones 1982). Very little is known regarding the early synaptic reorganization of basic locomotor circuitry in any species, although it has been shown that NMDA-mediated synaptic modifications underlie the somatotopic organization of afferent projections in the chick.
spinal cord (Mendelson 1994). NMDA receptors may also be involved in the maturation of spinal locomotor networks in the postnatal rat (Maier et al. 1995). In chicks, it has been demonstrated that embryonic motility is altered by joint restraint in vivo, although the longer term effects of restraint have not yet been investigated (Bradley 2001; Bradley and Sebelski 2000). In rats, only temporary locomotor deficits occur when neonates have been prevented from using their hindlimbs for a period of time (Walton et al. 1992), and it is unclear whether these locomotor changes are due to effects on musculoskeletal physiology and/or from a change in locomotor circuitry. Thus the role of experience in the development of locomotor behavior is not well understood.

We addressed this question by manipulating the amount of locomotor experience that chicks receive early posthatching and subsequently quantifying the changes in their locomotor pattern using kinematic measures. We also examined the effect that NMDA receptor blockade had on locomotor development. Concurrently, we investigated the development of another locomotor-related behavior in birds: head bobbing. Chicks show characteristic repetitive horizontal head movements while walking, referred to as head bobbing or head nystagmus. Head bobbing is an optokinetic response involving structures of the accessory optic system (AOS) and functions to stabilize the visual world on the retina as the animal walks (Frost 1978; Wallman and Velez 1985). Importantly, this behavior only occurs during walking and not while running. We were therefore interested in whether the development of head bobbing is related to the development of a mature walk in this species.

METHODS

Fertilized eggs were incubated at 37.5°C and rotated 4 times per day. After hatching, chicks were moved to a brooder for 6 h before being randomly assigned to treatment groups as outlined below. Because the hatching for each batch of eggs usually occurred over a 12- to 24-h period, only animals that 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 considered to be day 0. All animals were cared for according to standards set by the Canadian Council on Animal Care. A total of 216 chicks was used for this study.

Treatment groups

Chicks were randomly assigned to one of three exercise groups (treadmill-exercised, restricted exercise, and control; n = 72 for each group). Animals in the treadmill-exercised group were housed in a standard chick brooder (67 × 100 cm, 670 cm²/bird) and additionally were given 2 × 30 min sessions of treadmill walking daily, at speeds ranging from 7 m/min for 1-day-old birds to 10 m/min for 10-day-old birds. Animals in the restricted exercise group were housed in 8 × 8 cm cages at a density of 20 cm²/bird. Animals in the control group were housed in a standard chick brooder at the same density as treadmill-exercised chicks (670 cm²/bird). In both the brooder and the restricted housing conditions, animals had sufficient room to walk around to obtain food and water, although restricted chicks had only to walk a few steps.

Chicks in each exercise group were also randomly assigned one of two drug treatment groups, MK-801 or vehicle control (n = 108 for each group). Chicks received a daily intramuscular injection of MK-801 (1 mg/kg) or an equivalent volume of saline beginning on posthatching day 1 (P1). Dosages were based on those used in previous studies (Kalb 1994; Mendelson 1994). Body weight and hip height were recorded daily from each chick.

Kinematic data collection and analysis

Chicks were encouraged to walk and run down a 50-cm-long runway with clear Plexiglas sides. Chicks were completely unrestrained as they moved spontaneously along the runway. They were videotaped from the left side as they moved past a camera placed perpendicular to the runway at a distance of 1.8 m. Two infrared beams were aligned across the runway and set 15 cm apart; when the chick broke the first beam, a light-emitting diode (LED) time clock in view of the camera was triggered. The clock stopped when the chick broke the second beam. In this way, the average velocity of each animal for each pass could be determined. To facilitate visualization of the position of the chick’s limb, the down over the left hip was plucked, and markers were placed over the greater trochanter of the hip and on the metatarsalphalangeal joint. Data were collected on P1, P2, P4, P6, P8, and P10 (n = 36 for each age). Each chick was used for only 1 day of data collection.

Single frame analysis was carried out on the videotaped data at a sampling rate of 60 frames per second. Video frames were digitized and stored on computer (Northern Eclipse, Empix Imaging, Mississauga, Ontario). Only passes during which the chick maintained a constant velocity for two to three strides were considered acceptable for analysis (approximately 1 of every 8 passes). Gait parameters, collected from one complete stride for each acceptable pass, consisted of the duration of ground contact for each foot, stride length, and horizontal head excursions. 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. Head excursions were defined as the horizontal distance between the eye and the hip throughout the stride.

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. 1996), according to the method of Gatesy and Biewener (1991). In brief, stride length was divided by hip height (h) and velocity was divided by gh₀.5, where g is the gravitational acceleration constant, 9.8 ms⁻². Horizontal head excursions were normalized by dividing by neck length (obtained from age-matched cadaver specimens). Maximum head excursions were obtained by determining the maximum horizontal distance between the hip and the eye within each stride. References to these variables in the remainder of this paper refer to normalized values.

For the remaining variables, stride duration was defined as the time between initial ground contact of one limb and the subsequent ground contact of the same limb. Duty factor, the proportion of the stride that each limb spends in contact with the ground, was calculated for each limb as the duration of ground contact for each limb divided by the stride duration. Single stance duration is the proportion of the stride that the animal spends supported by a single limb. It was calculated for each stride by summing the total time that one limb was in contact with the ground while the opposite limb was in the swing phase and dividing the sum by stride duration.

Each variable (stride length, duty factor, single stance duration, and maximum head excursions) were averaged for each animal at two different velocities: walking (normalized velocities of 0.2–0.4) and running (normalized velocities of 0.8–1.0). Data from approximately four to six passes were used to obtain averages for each individual. Averaged values from individuals were used to obtain group means for each variable at each of the two velocities. Three-way ANOVA showed no interaction between exercise level and the drug level, so two-way ANOVA (exercise level × age and drug level × age) was used to determine statistical differences between groups (SigmaStat, SSPS). To compare head excursions throughout the stride, polynomial regression was used to provide a representative curve for each age
group (SigmaPlot, SPSS). A sixth-order polynomial produced the best fit in each case.

RESULTS

There were no significant differences in body weight or hip height between any of the treatment groups used in this study. As a result, the hip heights for each age were averaged, and the averaged value was used in the normalization of stride length and velocity.

As previously documented (Muir et al. 1996), very young animals use significantly shorter stride lengths while walking compared with older animals (Fig. 1A, \( F = 30.957, P < 0.001 \)). There was also a small increase in running stride length as chicks matured (Fig. 1B, \( F = 4.86, P = 0.03 \)). Interestingly, chicks in the exercise-restricted group moved with significantly shorter stride lengths compared with the treadmill-exercised chicks at P6, and compared with both treadmill-exercised and control groups by P10 (Fig. 1, A and B). This effect was seen during walking (\( F = 3.107, P = 0.047 \)) and during running (\( F = 2.944, P = 0.050 \)). The drug MK-801 also had an effect on stride length, in that by P6, animals receiving MK-801 walked with significantly shorter stride lengths than did saline-treated controls (Fig. 2A, \( F = 4.080, P = 0.045 \)). No effect of MK-801 was seen during running gaits (Fig. 2B).

In contrast, neither exercise levels nor drug treatment had significant effects on the stride timing variables of single stance duration and duty factor during walking (data not shown). There was a significant effect of age on these variables as previously documented (Muir et al. 1996). \( P1 \) and \( P2 \) animals walked with smaller single leg support durations compared with older birds and with larger duty factors compared with older birds. No significant differences were found between these variables for MK-801 versus saline-treated controls. Similarly, no significant differences were found for these variables at running gaits for age, exercise group or drug treatment (data not shown).

Head bobbing movements normally underwent two cycles during each complete walking stride (e.g., Figs. 3 and 4). At the onset of stance for one leg (left leg in Fig. 3A; Fig. 4 at time 0.0), the head was maximally retracted, such that horizontal distance between the hip and the head was at a minimum.
During the first half of the stance phase, the head was extended forward relative to the body and reached its maximal extension at the midpoint of the stance phase of the limb, such that the horizontal distance between the head and the hip were normalized for neck length (Fig. 4, compare P1 through P10). The extent of head bobbing movements showed a gradual increase as the animal aged from P1 to P10.

To better illustrate the gradual change in the head bobbing movements over the first weeks posthatching, head excursions were compared at P2, P4, P6, P8, and P10 (Fig. 5). There was a significant effect of age on head excursions ($F = 19.859, P < 0.001$) in that P2 and P4 animals walked with significantly smaller head excursions than either P8 or P10 animals, and P2 animals also walked with significantly smaller excursions than P6 animals (Fig. 5A). Additionally, there was a significant effect of exercise level on the extent of head bobbing ($F = 3.326, P = 0.039$). By P8, animals that were exercise restricted walked with significantly smaller head excursions compared with treadmill-exercised or control animals (Fig. 5A). There was no effect of MK-801 treatment on the extent of head excursions at any age (Fig. 5B).

During the first half of the stance phase, the head was extended forward relative to the body and reached its maximal extension at the midpoint of the stance phase of the limb, such that the horizontal distance between the hip and the head was at a maximum (Fig. 3B; Fig. 4 at time 0.2). During the latter half of the stance, the head was retracted relative to the body, and the horizontal distance between the hip and the head was again at a minimum, which also coincided with the stance onset of the opposite limb (Fig. 3C; Fig. 4 at time 0.48). The cycle was repeated during the ground contact for the second limb (Fig. 3, D and E; Fig. 4, time 0.48–0.98), resulting in two complete head bobbing cycles per stride.

Head bobbing as described above occurred only at walking speeds, and not during running, for all ages of animals (Fig. 4, compare Walk and Run). Significantly, head bobbing movements of young chicks were much smaller compared with those of older birds, even after horizontal distance between the head and the hip were normalized for neck length (Fig. 4, compare P1 through P10). The extent of head bobbing movements showed a gradual increase as the animal aged from P1 to P10.
antagonism (Muir et al. 1996). Thus older (Fig. 1), whereas shortened stride length was only seen during walking in very young chicks (Muir et al. 1996). Thus older animals subject to exercise restriction moved differently than did young chicks.

There are several possible reasons for the change in stride length seen with exercise restriction. Shortened stride length could be due to a lack of muscle strength in exercise-restricted animals. This idea is supported by the fact that these animals had shorter stride lengths during both walking and running. During normal development of walking in chicks, muscular strength was not thought to be an important determinant of locomotor development, because young animals could run in a similar fashion to older animals, which requires larger muscle forces compared with walking (Muir et al. 1996). In exercise-restricted animals, lack of muscular strength could have contributed to shorter stride length seen during both running and walking, possibly by limiting the amount of muscle force that could be generated to propel the body forward during the stance phase. Nevertheless, it might be expected that if lack of muscular strength was the only underlying cause of the shortened stride length, then stride length would be much shorter during running in particular, when much larger muscular forces are required, an effect that did not occur in this study.

Shorter stride lengths in exercise-restricted animals could also result from a change in the neural regulation of the stride cycle (Hiebert et al. 1996; Whelan et al. 1995). If the onset of both the stance and the swing phase occurred sooner in the stride compared with nonrestricted animals, this would result in a shortened stride length without altering the proportion of stance to stride duration, consistent with the present results. Thus the inputs to the locomotor pattern generator and the circuitry of the pattern generator itself might be subject to experience- and/or activity-dependent plasticity after hatching.

In contrast to animals subject to exercise restriction, animals that were treadmill exercised did not show any alterations in stride length or stride timing variables during unrestrained overground locomotion compared with controls. It is possible that the amount of treadmill training provided was insufficient to result in changes to the pattern of overground locomotion. We judged, however, that the amount of training was near the maximum that very young chicks, at least, could accommodate without becoming fatigued. Additionally, animals receiving treadmill exercise might have walked less in the brooder compared with the brooder-housed controls, such that they actually did not receive as much extra locomotor experience as expected. It is also possible that increased locomotor experience of any amount would not affect locomotor patterns compared with controls, because control chicks obtained sufficient loco-

FIG. 5. Maximum head excursions as a function of age for treadmill-exercised, restricted exercise, and control groups of animals (A) and for MK-801–treated animals and saline-treated controls (B). Maximum head excursions are normalized to neck length to control for size differences between different ages of animals. Older animals undergo significantly larger head excursions compared with younger animals (A and B, P < 0.001). Asterisks indicate the ages at which animals in the restricted exercise group had significantly smaller head excursions compared with treadmill exercised or control animals (A, P < 0.05). Each bar represents mean ± SE, n = 12 (A), n = 18 (B).

**DISCUSSION**

The results presented here indicate that overground locomotion in the chick is affected by locomotor experience in the early posthatching period. In particular, animals subject to exercise restriction for at least 6 days posthatching moved with shortened stride length compared with control animals. Additionally, NMDA antagonism during the early posthatching period caused a reduction in stride length, suggesting that NMDA-dependent processes are involved in early locomotor development in the chick. Nevertheless, the changes in stride timing variables that occur normally during locomotor development were not affected by locomotor experience or NMDA antagonism (Muir et al. 1996). Thus older (P6–P10) animals subject to exercise restriction or NMDA antagonism since hatching moved with the shortened stride length of young chicks but without the increased ground contact time of young chicks. Importantly, this study has also demonstrated that head bobbing behavior, an optokinetic response, undergoes a distinct developmental change during the early posthatching period and is also sensitive to locomotor experience.

**Exercise restriction alters locomotion in posthatching chicks**

Exercise restriction, by producing a shortened stride length without causing changes in stride timing variables, altered locomotion in posthatching chicks differently than if it caused a delay in the normal sequence of locomotor development in chicks. During normal development, stride lengths are shorter, but duty factors are greater in young chicks compared with older animals (Muir et al. 1996). In the present study, the stride length reduction in exercise-restricted animals was not accompanied by an increase in duty factor, meaning that the proportion of time spent in stance compared with swing was unchanged by exercise restriction. In fact, duty factor was slightly, although not significantly, shorter in exercise-restricted animals. Additionally, stride length reduction in exercise-restricted animals occurred both running and walking (Fig. 1), whereas shortened stride length was only seen during walking in very young chicks (Muir et al. 1996). Thus older animals subject to exercise restriction moved differently than did young chicks.

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motor experience under the brooder conditions provided during the early posthatching period.

**NMBA antagonism alters stride length during walking in chicks**

Daily treatment with the NMDA-type glutamate receptor antagonist MK801 caused a reduction in stride length during walking in posthatching chicks, but caused no changes in stride timing nor did it alter stride length or stride timing during running (Fig. 2). Thus the normal sequence of posthatching locomotor development in chicks is not entirely dependent on NMDA receptors, but NMDA receptors may contribute to the maturation of stride length in the chick.

The mechanism by which NMDA antagonism resulted in shortened stride length is not known. One possibility is that antagonism of NMDA receptors is functioning at the spinal level. Antagonism of NMDA receptors in early development alters spinal afferent projections in chicks and spinal motoneuron morphology in rats (Kalb 1994; Mendelson 1994). NMDA-type glutamate receptors may also mediate the effect of normal weightbearing activity on spinal motoneuron morphology (Inglis et al. 2000; Walton 1998; Walton et al. 1992) and locomotor behavior in neonatal rats (Maier et al. 1995). The small effects of NMDA antagonism in the present study might be attributable to the precocial nature of the posthatching chick, such that earlier, e.g., in ovo, administration of NMDA antagonists would produce a greater effect on locomotor behavior after hatching than did posthatching administration.

**Head bobbing matures in the posthatching period and is sensitive to locomotor experience**

Head bobbing is a well-recognized behavior of birds that functions to stabilize the visual world on the retina as the bird walks overground (Frost 1978; Wallman et al. 1982). It is a response that is visually driven, i.e., by movement of the external world relative to the retina (retinal slip) and as such is thought to be primarily an optokinetic response (Frost 1978). Nevertheless, the low-frequency head movements characteristic of head bobbing necessarily result in vestibular stimulation, such that vestibuloocular and vestibulococil reflexes likely also play an important role in this behavior (Wallman et al. 1982).

In support of our present finding that head bobbing matures in the early posthatching period, there have been several studies that demonstrated developmental changes in both optokinetic and vestibuloocular reflexes in birds. These responses in young chicks were characterized, in part, by lower gain and differences in directional selectivity compared with older animals (Wallman and Velez 1985; Wallman et al. 1982). The anatomical structures thought to be involved in the vestibuloocular and optokinetic reflexes, e.g., vestibulocerebellum and parts of the accessory optic system, also show developmental changes posthatching (McKenna and Wallman 1985; Wallman et al. 1982). Thus there is anatomical, physiological, and now behavioral evidence for maturation of head bobbing in posthatching chicks.

Importantly, our results also demonstrate that maturation of the head bobbing response is sensitive to locomotor experience, suggesting a role for activity-dependent plasticity during early posthatching development. A similar mechanism has also been postulated for the maturation of vestibuloocular and optokinetic responses in these animals, in that newly hatched chicks have had no visual experience prehatching and thus this experience posthatching might be required for normal reflex maturation to take place (McKenna and Wallman 1985). Future studies in our laboratory will determine the extent to which early visual experience plays a role in the maturation of head bobbing behavior.

It is important that previous studies have invariably been performed using head restraint, so that only eye movements are recorded. Examination of actual head bobbing behavior during walking as in the present study allows us to investigate the combination of visual, vestibular, and locomotor influences. For example, the movement of the visual world during locomotion is self-generated, and thus the relationships between various locomotor parameters and the extent of head excursions could provide important insights into the control and development of head bobbing. In the present study, the shorter stride lengths that occur in exercise-restricted animals could account for a least part of 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 in each stride. Stride length and head excursions are, in fact, moderately correlated in P10 animals (r = 0.32, data not shown). Other factors therefore must influence the extent of head excursions, as evidenced by the differences in the pattern of head excursions at different ages compared with stride length; stride length normally matures within the first week after hatching, whereas head bobbing continues to mature past P10 (compare Fig. 1 and Fig. 5). Ongoing studies in our laboratory will determine the extent to which they contribute to development of locomotor behavior.

This is the first demonstration that locomotor experience is required for normal development of locomotor behavior, even in highly precocial animals such as the chick. This indicates that, even though the circuitry required for basic locomotor movements are established relatively early during embryonic development in many species, ongoing experience-dependent modifications may be required to produce mature locomotor behavior. The mechanisms by which experience affects this circuitry are as yet unknown, although evidence from the present study suggests that activity-dependent plasticity, mediated by the NMDA-type glutamate receptor, may be involved. Possible neuroanatomical sites for plasticity include spinal locomotor circuitry and structures of the accessory optic system. Further characterizations of these regions, through lesioning and electrophysiological studies, will help to determine the extent to which they contribute to development of locomotor behavior.

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