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Prematurely delivered rats show improved motor coordination during sensory-evoked motor responses compared to age-matched controls

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HIGHLIGHTS

- Rats were delivered prematurely into postnatal environment.
- Motor coordination was measured during species-typical behavior.
- Premature exposure to postnatal environment increased motor coordination.
- This suggests environmental factors influence development of motor coordination.

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ABSTRACT

The amount of postnatal experience for perinatal rats was manipulated by delivering pups one day early (post-conception day 21; PC21) by cesarean delivery and comparing their motor behavior to age-matched controls on PC22 (the typical day of birth). On PC22, pups were tested on multiple measures of motor coordination: leg extension response (LER), facial wiping, contact righting, and fore- and hindlimb stepping. The LER and facial wiping provided measures of synchronous hind- and forelimb coordination, respectively, and were sensory-evoked. Contact righting also was sensory-evoked and provided a measure of axial coordination. Stepping provided a measure of alternated forelimb and hindlimb coordination and was induced with the serotonin receptor agonist quipazine. Pups that were delivered prematurely and spent an additional day in the postnatal environment showed more bilateral limb coordination during expression of the LER and facial wiping, as well as a more mature righting strategy, compared to controls. These findings suggest that experience around the time of birth shapes motor coordination and the expression of species-typical behavior in the developing rat.

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1. Introduction

1.1. Experiential effects in sensory systems

Developmental and psychobiological research during the perinatal period has shown that manipulating sensory experiences, either by deprivation or enhancement, can profoundly affect developmental outcomes [1]. Classic studies on vision deprivation in kittens demonstrated cortical reorganization after sewing one or both eyes shut [2,3]. Congenitally deaf kittens fitted with cochlear implants showed increased auditory cortex activity compared to naïve deaf and hearing controls [4]. Deprivation studies of the whisker barrel cortex in developing rats also have shown cortical plasticity in the somatosensory system due to experience [5].

Other research has shown that premature enhancement of sensory input in a later developing modality can inhibit the development of other modalities [6–8]. For example, premature visual stimulation in young rats interferes with the normal development of olfaction [9] and facilitates exploratory and hindlimb rearing behaviors in young rats whose eyes were surgically opened one week early [10]. This shift in the timing of visual input had an effect on the development of other sensory and motor systems. A great deal of research is available on activity-dependent plasticity in sensory systems. However, less is known about the effects of experience on motor systems, particularly during early development.

1.2. Experiential effects in motor systems

Some evidence for the plasticity of motor systems during early development has been demonstrated in animal and human research. For example, changes in interlimb motor coordination in fetal rats have been shown to occur following interlimb yoke training [11]. Training consisted of yoking (physically linking) the fetus's hindlimbs together

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so that movement was constrained to in-phase, conjugate trajectories for a 30-minute training session. After training, the interlimb yoke was cut so that the hindlimbs could move independently. Overall hindlimb activity increased, as well as conjugate movements, both during yoking and afterward (as if the yoke were still constraining movement). Additional research with the yoke training paradigm has demonstrated modification of limb patterns between forelimbs, ipsilateral hind- and forelimbs, as well as hindlimbs [12]. Yoke training increased conjugate limb movement for trained limbs during the yoked and unyoked post-training periods. These results suggest that fetal rats can adapt their motor behavior in response to proprioceptive feedback to learn new motor patterns.

Viala et al. [13] determined that locomotor behavior in young spinalized rabbits is dependent on hindlimb experience. Infant rabbits were suspended in a sling with their hind paws secured to motor-driven pedals that moved in a synchronous pattern, an alternating pattern, or both. Animals trained on the synchronous or alternating pattern showed respective hopping or walking locomotor gaits exclusively, reflecting their training regimen. Animals trained on both patterns displayed both hopping and walking gaits. In addition, recent evidence from studies of human infants suggests that babies within the first year of life respond to sensory information, such as trip-inducing stimuli [14] and load [15], during brief stepping trials when tested on a treadmill.

Muir and Chu [16] showed that, even in precocial animals such as chicks, experience is necessary for the development of adult patterns of upright walking. Chicks trained on a treadmill showed more mature locomotor development than either the experience-restricted or the normal experience groups. Experience-restricted chicks showed shortened stride lengths and decreased horizontal head movements (characteristic of chick locomotion) compared to age-matched controls. Sindhurakar and Bradley [17] demonstrated that chick embryos exposed to increased amounts of light showed accelerated locomotor development due to early hatching, without impacting motor performance. However, extreme amounts of light exposure may have accelerated the development of neural circuitry used in locomotion. This suggests that motor systems utilize species-typical experiences in order to develop properly, just as sensory systems.

1.3. Purpose of current study

The studies described above provide examples of changes in motor behavior that result from providing immature animals with atypical experiences (e.g., yoke motor training and stepping on a treadmill). In contrast, the current study addresses the effects of typical kinds of experiences (e.g., labor, delivery, exposure to gravity, and maternal–infant interaction) on the development of species-typical action patterns. The current study examined the effect of an additional 24 h of postnatal experience on motor behavior in the in vivo perinatal rat, thus exposing rats prematurely to gravitation, variations in maternal care, skin-to-skin contact with siblings, and so on. Our hypothesis was that pups that had an extra day of postnatal experience would show more coordinated behavior during expression of species-typical action patterns, compared to age-matched pups with less postnatal experience. Motor coordination was examined in four different motor tasks/action patterns: the LER (a synchronous hindlimb task), facial wiping (a synchronous forelimb task), contact righting (axial coordination) and quipazine-induced stepping (an alternated forelimb and hindlimb task). Each of these action patterns has been shown to occur in the perinatal rat using the appropriate evoking stimulus (see Section 1.5 Action patterns).

1.4. Perinatal development in the rat

Although they are born furless, blind, and deaf, neonatal rats have some sensory capacities and behavioral abilities that are adaptive to and functional in the terrestrial environment. For instance, they have olfaction and are able to root for, attach to, and suckle at the dam's nipple. They also can emit ultrasonic vocalizations to solicit care from the dam. Rooting and suckling are good examples of coordinated behavior that involve coordinated movement of the head, mouth, and forelimbs. Such nascent behaviors start developing before birth and can be studied directly in the rat fetus. Over the past few decades, such research has demonstrated that the expression of coordinated behavior in the newborn emerges from initial spontaneous movements in the fetus [18].

1.5. Action patterns

In addition to expressing spontaneous motor activity, perinatal rats exhibit several action patterns, such as facial wiping, suckling, rooting, and forelimb treadling. Evidence for the development of these action patterns shows that the neural circuitry for these behaviors begins developing before birth. The action patterns of concern for this study are the leg extension response (LER), facial wiping, contact righting, and alternated fore- and hindlimb stepping.

1.5.1. The leg extension response

First described in newborn rats, the LER is expressed when the hind legs move from a resting posture to an immobile and stiffly extended posture with the hindquarters lifted [19]. Moore and Chadwick-Dias [19] demonstrated the LER occurs in rat pups in response to stimulation of the anogenital region and not in response to stimulation of other areas of the body, and continues into about the third postnatal week. This action pattern occurs in the neonate when the dam licks the pup's anogenital region to necessitate urination and defecation. In addition, the dam benefits by reclaiming fluids and nutrients lost through nursing [20,21]. The proximal function of the LER seems to be to provide better access to the pup's anogenital region in order to promote micturition and defecation. Rat fetuses tested two days before birth reliably show the LER when stimulated by a soft camelhair brush (mimicking stimulation by the dam), thus providing prenatal evidence of neural control of the response [22].

1.5.2. Facial wiping

Facial wiping is another action pattern expressed by the perinatal rat; it is the act of drawing one or both paws along the side of the face from the ears downward toward the nose. In adults, the action pattern is part of the stereotypical grooming repertoire and provides a good measure of interlimb coordination expressed by the forelimbs. Rat fetuses typically do not express the facial wiping response during spontaneous activity, although the response can be evoked in E20 (embryonic day 20; 2 days before birth) rats by infusing an aversive stimulus, such as lemon extract, into the mouth of the fetus through an intraoral cannula [23]. This same method has been used to evoke facial wiping in newborn rats [24].

1.5.3. Contact righting

Contact righting involves full body (axial) coordination and is used to test vestibular and tactile function [25]. Animals are typically tested by placing them onto a surface in a supine position, and observing the latency and motor strategy used to return to a prone posture. Pellis et al. [25] have shown that newborn rats are capable of righting, and that the righting strategy typically used changes during the early postnatal period. From the day of birth (postnatal day 0; P0) to P2, pups typically use the U-shaped posture to right themselves from supine to prone. When pups are held supine in contact with the ground, they raise the head and hindlimbs skyward, thus forming a “U” posture. This posture allows the pup to fall to one side and then rotate to a fully prone position. The corkscrew pattern develops subsequently and is used by rotating the head, neck, and shoulders in one direction while the pelvis rotates in the opposite direction. The percentage of pups using the corkscrew pattern increases from P0 to P2, as the U-shaped strategy decreases during the same period.