

Behavioral Complexity of Perinatally Underfed Lactating Rats: The Case of Swimming and Kyphotic Responses

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Abstract

In the rat, perinatal undernutrition associated with deficiencies in the mother-litter interactions, interferes with cortical subcortical networks underlying swimming and kyphotic responses of lactating dams. For swimming experiment, food restriction was achieved by separating pups from the mother (12 h daily) in an incubator from ages P4 - 13. Moreover, for kyphotic response, food intake was reduced from gestational day 6 (G6) with 50% (9.5 g) of the normal diet (Purina chow), from G13 to G19 with 70% (13.3 g), and with 100% (19 g) of the same diet until parturition. After birth, prenatally underfed pups were rotated between litter of two lactating dams, one with ligated nipples, for 12 h daily between ages of P2 - 25. We evaluated swimming maturation and the kyphotic posture of dams by exposing pups, correlated with their tentative cervical and lumbosacral spinal cord descending integrative mechanisms. Current findings suggest that the pattern of the spinal cord substrates in both behavioral responses affected by early undernutrition, changed according to the future complexity of the functional and incoming environmental sensory information.

Keywords

Early Undernutrition, Swimming and Kyphosis, Mother-Litter Bonds, Rats

1. Introduction

During the rat's nursing period, the mother promotes neuronal networks development in the young to integrate the increasing multimodal sensory activity propagated through ascending brain relays, which also maintain maternal care activity for pup survival and breeding. Thus, the lactating mother provides relevant olfac-

tory, tactile, thermal, and vestibular stimulation to the pups through body and anogenital licking, retrieval, whisking, and body manipulation [1]-[4]. Furthermore, maternal-like responses also activate ancient neuronal networks, concentrated in cortical and subcortical brain regions that we share with other species to elicit autonomic, motivational, and cognitive states [5]-[8].

In perinatally underfed rats, neuroanatomical and neurophysiological studies have shown deficiencies in sensory development and their interconnections with the neocortex, limbic structures, brainstem, and spinal motor neurons of lactating dams, interfering with pups' retrieval, nest building, kyphotic posture, motivation and emotional responses directed to the newborn [8]-[13]. Therefore, we hypothesize that the descending deficient sensory influences could be acting differently on the substrate of two behavioral responses, such as swimming and the kyphotic nursing response, by using different morphological and functional spinal cord mechanisms. Thus, nerve impulses for swimming follow a simple route of reduced superior corticospinal motoneurons generally underlying critical somatic movements, and the activation of a brainstem neuronal network for posture and body equilibrium [14]. Moreover, the nerve impulses for the maternal kyphotic response follow a more complex network including superior corticospinal motoneurons and subcortical neurons to modulate nursing posture, motivation, and emphatic emotional reactivity directed to the newborns [4] [8] [15]-[17]. The aim and relevance of the current study were to investigate whether the functional patterns of the spinal cord substrate in both behavioral responses of early underfed rats, are differentially reorganized according to the complexity of the incoming sensory information.

2. Undernutrition and Swimming Maturation

2.1. Animals and Experimental Design

Swimming ability was normally fed by infant rats from 4 - 30 days of age and in adulthood (120 days), and in rats that were chronically starved and tested for swimming in an aquarium. Chronic starvation was by maintaining the infant rats separated from the mother and littermates in an incubator at 29°C for a period of 12 hr. daily from 4 - 13 days of postnatal life (PD). Day 4 was the first day of the starvation period. The evaluation of swimming was according to the position of the nose and movements of front legs during 5 - 10 sec in an aquarium as previously described [18].

2.2. Results

The findings showed that before 4 days of age both experimental groups were unable to swim. They exhibited uncoordinated movements, floating motionlessly or entirely submerged under the water with hypertensive reflex activity. From days 4 - 12 both experimental groups swam in circles overlapping with floating activity. From 11 days of age onward, the rats gradually maintained their nose and a part of their head out of the water as adults. At this developmental age, rats started to

swim in a straight line, although overlapping with occasional rotating movements. After 12 days of age, the straight-line movements were consistent as in adult rats. In the early starved rats, maturation of swimming performance as measured by the nose and head position out of the water and the gradual decrease of front flexor-extensor foreleg activity were 2 - 3 days delayed as compared to controls. The high sensitivity of nervous tissue during critical periods of maturation and the relationship between undernutrition and the development of patterns of movement during swimming were directly associated with the sequence of brain development (Figure 1). During the first 7 PDs, there is a low or no response to hypothermia or brief periods of maternal separation as stressors [19]. Subsequently, the water of the aquarium was visually mixed with the fecal material of swimming rats, suggesting the activation of the neuronal substrate triggering the autonomic response to stress that gradually increased with age [17].

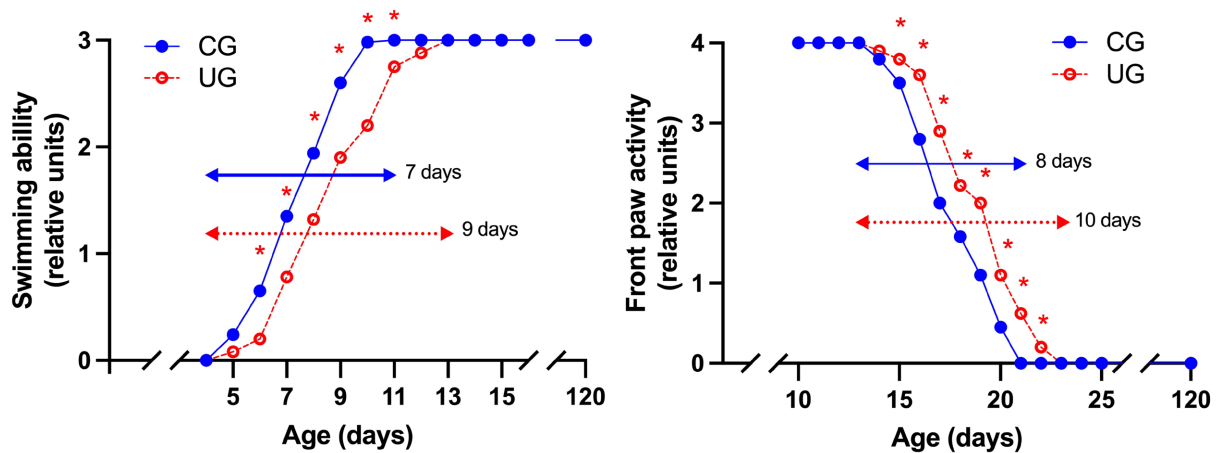


Figure 1. A. Nose position during swimming in normal and underfed rats at different ages. Each point in the graphs indicates the average of thirty-two values. B. Front paw activity changes during development of control and underfed rats. Horizontal lines in A and B show the stabilization days for swimming rats. *Points differing from controls at a level of significance of $p < 0.05$.

2.3. Discussion

The current findings provide evidence that chronic undernutrition affects the development of neuronal networks, underlying the complex neuromuscular adaptive mechanisms involved in swimming. In rats, swimming appears to be purely reflexive in lower mammals [15]. However, other studies have shown that swimming in rats is modulated by the wide interactions between the somatosensory cortex, labyrinthine, and cerebellum. Thus, the neuronal descending impulses from the motor cortex modulate space orientation, posture, voluntary movements and equilibrium. Furthermore, the vestibular nuclei have excitatory and inhibitory influences projecting to the cervical and lumbosacral motoneurons, underlying the space position of the head and limbs [16] [20] [21]. These functional deficiencies in swimming development associated with early undernutrition are supported by reduced corticospinal tract myelination, number of spines, basilar den-

dritic density, and dendritic thickness alterations in the pyramidal cells of layer V of the frontal cortex, Purkinje neuronal hypotrophy, and the altered electrical somatosensory responses elicited by the sciatic nerve electrical stimulation [22]-[24]. Thus, in the experimental model of swimming, early undernutrition interferes mainly with the direct descending cortical nerve impulses transmitted through one or two synaptic relays, to modulate spinal motoneurons and movements activity [17] [25] [26].

3. Kyphotic Response of Lactating Dams

3.1. Kyphotic Posture

During nursing behavior, the kyphotic posture shown by dams after birth is fundamental for the nutrition, development, and protection of pups in the nest, gradually declining before weaning [27]. Thus, ventral somatosensory stimulation provided by pup's activity elicits in the nursing dam quietness or immobility, bilateral symmetry, hyperextended limbs with the ventral part of the trunk over the pups, and a pronounced arching back mainly modulated by the midbrain caudal periaqueductal gray ventrolateral column (cPAGvl) projections [28]. Furthermore, in previous studies the role of perioral and ventral-trunk somatosensory stimulation of dams by pups was reduced by injections of lidocaine into the mystacial pads of pups or by the occlusion of the dam's ventrum with a full spandex jacket [29]. Compared with nursed inexperienced dams, early underfed pups showed longer latencies for suckling than controls that exhibited short latencies for nursing. Studies in neonatally undernourished dams with daily early separation for 12-h from half of the litter (placed in an incubator) along postnatal day 1 - 23, or with nipple ligation showed that underfed dams spent significantly reduced time crouching over the pups [30] [31]. However, these studies did not reflect neuronal evaluations on the types of nursing postures, and the modulatory mechanisms that affect the pup's development. Based on these antecedents, it may be helpful to use the immunocytochemical nuclear protein c-Fos elicited by immediate early gene c-Fos as a marker of cPAGvl neuronal activity for nursing following the exposure of pups to well-fed or early underfed mothers [32].

3.2. Methods

Perinatal undernutrition was achieved firstly in rats by reducing the percentage of food intake from gestational day 6 (G6) with 50% (9.5 g) of the normal diet (Purina chow), from G13 to G19 with 70% (13.3 g), and with 100% (19 g) of the same diet until parturition. This protocol was chosen because neurogenesis in the cortical and subcortical maternal circuit and afferent connectivity occurs mainly from day G21. At birth, prenatal underfed female young were fed by two gestationally underfed dams, in one of which the main galactophorous ducts had been tied subcutaneously. The two lactating dams were interchanging every 12 h between litters from PDs 1 to 24. Maternal tests were evaluated on PDs 4 and 12 when maternal activity was highly expressed [27].

3.3. Results

The ANOVA comparisons between controls (CG) and underfed (UG) groups showed that the duration of the high kyphotic posture (ventro-flexion) in UG dams decreased significantly, $F(1, 14) = 13.18$, $p < 0.002$; with no effects of age but with significant interaction between factors, $F(1, 14) = 11.96$, $p < 0.003$. Post hoc comparisons indicated that UG dams significantly reduced the duration of this behavioral component only on PD 12 of lactation. In the case of low kyphotic posture, the ANOVA comparisons did not indicate significant differences or a significant interaction between factors. The post hoc comparisons throughout the study did not indicate statistical differences between the experimental groups (Figure 2). The evaluation of the c-Fos protein, activated within the cPAGvl after suckling stimuli, indicates that the ANOVA comparisons between groups showed significantly reduced c-Fos immunolabeling in UG dams, $F(1, 32) = 476.52$, $p < 0.0001$, due to age, $F(1, 32) = 14.30$, $p < 0.0006$, suckling behavior, $F(1, 32) = 4514.43$, $p = 0.0001$ and interaction between factors, $F(1, 32) = 7.79$, $p < 0.008$. Post hoc comparisons showed that UG dams significantly reduced c-Fos immunolabeling after a suckling period on PDs 4 and 12 of lactation.

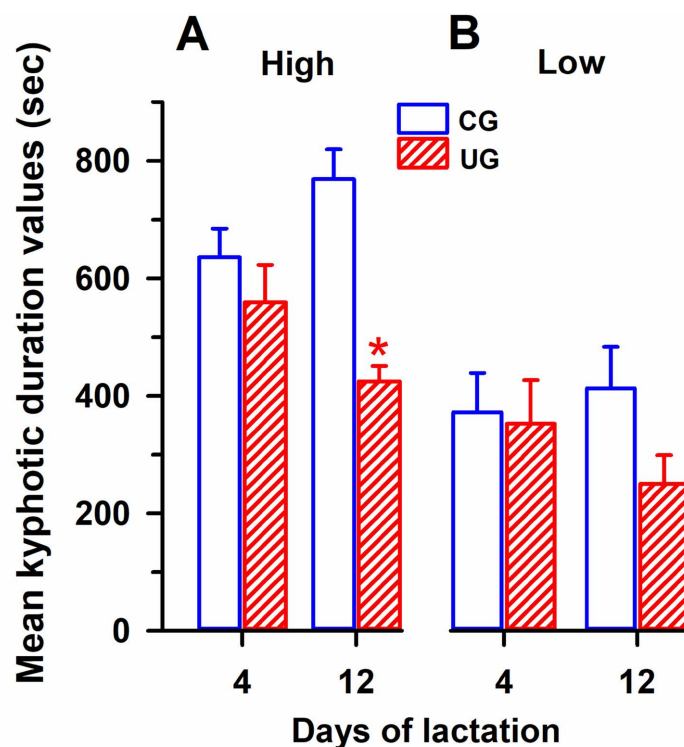


Figure 2. A. Mean (\pm SEM) of high kyphotic posture duration in CG and UG dams on PDs 4 and 12. B. Mean low kyphotic posture. Note that high kyphotic posture in UG mothers significantly reduced on PD12 vs. CG dams $*p < 0.001$. Low kyphotic posture was not significant during lactation. ($n = 8$ per condition).

3.4. Discussion

Present findings indicate that lactating dams with pre- and neonatal undernutri-

tion showed significant reductions in the kyphotic posture and nest rating scores durations after suckling, which reflect deficiencies in the social mother-litter bonds early in lactation. Furthermore, the dam's kyphotic alterations may result in significant decrements in the pups' activity, because of the reduction on weight gain, the delayed morpho-functional activity of muscle fibers in the newborn of UG dams, and/or the long-term alterations in the kyphotic mechanisms of the UG dams. The diminished outlet somatosensory stimulation provoked by the offspring of UG dams, may interfere with the expression of Fos IR at the brainstem cPAGvl, to influence spinal cord motoneurons activity [4].

4. Tentative Spinal Cord Mechanisms

4.1. Effects of Sensory Experience on Swimming Response

The anatomical and functional impairments on swimming development of early underfed rats are associated with delayed corticospinal tract myelination, reduced spines and basilar dendritic thickness of layer V pyramidal cells of the frontal cortex and Purkinje neuronal hypotrophy. Moreover, altered electrical somatosensory responses elicited by the sciatic nerve stimulation suggest reduced interactions and disorders in neuronal plasticity and experience. However, swimming performance deficiencies seem to be compensated from PD 25 onwards possibly by nutritional and neuronal rehabilitation. Taking together these findings, we suggest that the pattern of the reflex activity of the spinal cord substrate of underfed rats for swimming is reorganized according to the incoming environmental sensory information.

4.2. Effects Sensory Experience on the Kyphotic Response

Swimming and kyphotic activities have in common that their brain functional output occurs at the cervical and lumbosacral spinal cord motoneurons, before they impact the striatal musculature underlying adaptive environmental responses. In this regard, electrophysiological studies in cats have measured the reflex activity of the spinal stretch reflexes, by means of chronic long standing tenotomy or by spastic contralateral sensory-motor cortex injury. Thus, in adult animals, the electrical stimulation of afferent fibers to the L7 anterior root fibers of the lateral gastrocnemius is more efficient in evoking the monosynaptic reflex discharge. The temporal course of the excitability curve in the motor nucleus was measured by using the average magnitude of conditioned monosynaptic test reflexes at each interval, between conditioning and test stimulations. The variations of the excitability of intact animals showed a curve that describes the declining time course of direct facilitation as previously described [33]. The hyperactivity of the spinal reflexes following three-month spasticity showed a biphasic descending electrical potential with increased excitability, perhaps reflecting plastic neuronal sensory accumulated experience [34]. Similar experiments were performed to study the effects of reduction in stretch reflex activity, and experience following the gastrocnemius tenotomy. The results indicated that long-term tenotomy pro-

okes a declining excitability curve of neuronal facilitation. Moreover, in other experiments when a gastrocnemius tenotomy was introduced after fifteen days of previous spasticity, the effects of the conditioning afferent volleys provoked only a facilitatory declining curve. These last experimental findings suggest that the effects of the reduction in stretch reflex activity are independent of the degenerating pyramidal tract effects [34]. The study of the plastic changes occurring in a simple neuronal system associated with early undernutrition may be useful for a better understanding of the developmental mechanisms underlying the functional output of the integrated brain activity contributing to the maturation of kyphotic response in lactating dams.

4.3. Effects of Early Undernutrition and Stress on Swimming and Kyphotic Responses

Experimental studies in rats isolating pups from the mother in an incubator or by rotating between litters two lactating dams, one with ligated-nipples, for a 12 h daily between ages of P2 - 25, interfere with the programming of the hypothalamic-hypophysial-adrenal axis (HPA), which as a stressor restricts the neuroanatomy, neurochemistry, and behavioral adaptive responses [35]. Preliminary results on the effects of stressful conditions on swimming disorders indicate that during the first 7 PDs there is a low or no response to hypothermia or brief periods of maternal separation as stressors [19]. Subsequently, the water of the aquarium was visually mixed with the fecal material of swimming rats, suggesting the activation of the neuronal substrate triggering the autonomic response to stress gradually increased with age affecting the brain substrate underlying swimming motoric responses. Several studies on the impacts of early undernutrition upon the behavior of stressed lactating dams indicated consistently increased stressful self-grooming activity [30]. Current findings indicate that the kyphotic response was correlated with the derangement of a very complex neuronal network that severely interferes with the social mother-litter bonds, and their long-lasting effects disturbing movement activities, posture, affective, and autonomic responses in adulthood [4] [36] [37]. However, further studies using several models of food restriction, exposure to different stress manipulation, and evaluating the stressful impacts with neurochemicals approaches are necessary for a better understanding of the mechanisms underlying the adaptive behavioral responses.

5. Conclusion

In rats, perinatal undernutrition associated with deficient mother-young bonds interferes with cortical-subcortical networks underlying swimming and kyphotic responses. We compare the impacts of early food restriction on the limited morpho-functional organizations of swimming, with the complex cortical-subcortical descending pathways for social kyphotic response of lactating dams. Current findings suggest that the functional patterns of the spinal cord substrate in both behavioral responses of early underfed rats are reorganized according to the com-

plexity of the incoming sensory information. Moreover, early in life, exposure to stressful environmental factors increases the vulnerability to several brain disorders concerning adult brain functional plasticity.

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Conflicts of Interest

The authors declare no conflict of interest regarding this work.

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