Klotz communications: evolution of hormones during pregnancy

Neuroendocrine control of maternal behavior in non-human and human mammals

Le contrôle neuroendocrinien du comportement maternel chez les mammifères non-humains et humains

Frédéric Lévy

INRA, UMR85, CNRS, UMR7247, IFCE, physiologie de la reproduction et des comportements, université F.-Rabelais, 37380 Nouzilly, France

Abstract

Mammalian parental care is essentially provided by the mother and it occupies most of the reproductive period for female. The synchronization of maternal behavior with parturition and lactation ensures that the mother responds to the needs of the young at the appropriate time. This temporal synchrony is accomplished by hormonal changes that underly both the onset of maternal behavior and of parturition and lactation. The aim of this review is to describe and compare the hormonal mechanisms that regulate the onset of maternal behavior across a variety of mammals, including humans, that represent different behavioral strategies. Are involved the steroid hormones, estradiol and progesterone synthesized by the ovaries which primed the future mother to repond maternally. In response to these steroids, oxytocin release induced by vaginocervical stimulation and prolactin release affect the maternal brain. The medial preoptic area integrates the hormonal signals to regulate maternal behavior. The hormonal cocktail that stimulates maternal behavior varies across mammalian species. Because most of the studies in humans are correlative and because human environment is complex, direct causality between hormones and maternal behavior is unclear. However, one can reasonably think that hormones create a positive bias towards the baby increasing the occurrence of maternal behavior.

© 2016 Published by Elsevier Masson SAS.

Keywords: Maternal care; Steroids; Oxytocin; Prolactin; Hypothalamus

Résumé

Les soins parentaux chez les mammifères sont essentiellement prodigués par la mère et occupent la majeure partie de la période de reproduction chez la femelle. La synchronisation du comportement maternel avec la parturition et la lactation conduit à ce que la mère réponde aux besoins des jeunes au moment opportun. Cette synchronisation temporelle est réalisée grâce aux changements hormonaux qui sous-tendent l’apparition à la fois du comportement maternel et de la parturition. L’objectif de cette revue est de décrire et de comparer les mécanismes hormonaux impliqués chez de nombreuses espèces de mammifères, y compris notre espèce, qui représentent différentes stratégies de maternage. Sont impliqués les hormones stéroïdes, l’estradiol et de la progestérone qui sensibilisent la future mère à devenir maternelle. La stimulation vaginocervicale lors de l’expulsion du nouveau-né et la libération d’ocytocine concomitante sont des facteurs-clés chez de nombreuses espèces. L’augmentation de la libération de prolactine est primordiale uniquement chez les rongeurs. L’aire préoptique médiane est la structure cérébrale principale de l’action hormonale. Parce que la plupart des études chez l’homme sont corrélatives et étant donnée la complexité des interactions humaines, la causalité directe entre les hormones et le comportement maternel est incertaine. Cependant, on peut raisonnablement penser que les hormones créent une sensibilité spécifique vis-à-vis du bébé facilitant ainsi l’apparition des réponses maternelles.

© 2016 Publié par Elsevier Masson SAS.

Mots clés : Stéroïdes ; Oxytocine ; Prolactine ; Hypothalamus

E-mail address: levy@tours.inra.fr

http://dx.doi.org/10.1016/j.ando.2016.04.002
0003-4266/© 2016 Published by Elsevier Masson SAS.
1. Introduction

Survival of newborn young relies on the mother and her ability to provide food, warmth, shelter, and protection from predators and conspecifics. In placental mammals, the synchronization of maternal behavior with parturition and lactation ensures that the mother responds to the needs of the young at the appropriate time. This temporal synchrony is accomplished by finely-tuned physiological changes that underlie both the onset of maternal behavior and the preparation for and induction of parturition and lactation. The study of the biological mechanisms that influence and regulate pregnancy, parturition, and lactation is therefore important for a better understanding of maternal responsiveness.

Maternal behavior usually emerges at or close to parturition. Just after birth, the female shows a very rapid interest in the newborn. Cleaning of the neonate and the consumption of amniotic fluids and placenta are widespread behaviors among mammalian orders, except in fully aquatic mammals (Cetacea) or semi-aquatic mammals (Pinnipedia). Mothers of many mammals also emit characteristic vocalizations in response to their young and show retrieval, gathering, herding, or carrying behaviors that protect the young from predation and tend to keep the young in close proximity to the mother. As well, most new mothers protect their young from predators and conspecifics. However, the most important and common pattern of maternal behavior in mammals is nursing, which occurs shortly after the young are born.

In so-called “altricial” species (most rodents, canids, felids), the mother builds a nest in which she gives birth to a large litter of young that are not fully developed and have limited sensory and locomotor abilities. In rodents, once the mother has retrieved and gathered the pups together into the nest, she spends most of her time in a nursing posture [1–3] and she licks the young, a behavior that functions to promote urination and elimination by the offspring and to maintain the mother’s fluid balance [4]. In rabbits, a very different pattern is seen where the mother (doe) remains with and nurses her bunnies only once or twice a day for less than 10 minutes at a time [5]. In most altricial species, the young stay huddled together within the nest for the first 10 days and hence, there is little need for the mother to recognize individual members of her litter, as long as they remain in the nest. In the so-called “precocial” species (most ungulates), immediately after parturition, the mother licks her newborn until the young are cleaned of the amniotic fluid. She also emits maternal bleats and, as the lamb can stand, it searches for the udder; in turn, the mother responds by arching her body, thereby facilitating access to the udder. From these behavioral observations, licking behavior, emission of maternal bleats, udder acceptance and suckling are defined as “maternal acceptance” while aggressive behavior, emission of protest bleats and udder refusal are indicative of “rejection” of the lamb. These precocial species tend to have a small litter of fully developed young who are capable of following the mother shortly after birth. Mothers in these species develop discriminative maternal care favoring their own young, allowing them to suck while rejecting any alien young that may approach the udder. In this respect, the establishment of a selective bond within the first few hours after parturition represents one of the essential characteristics of maternal behavior in precocial species. Individual recognition of young has been demonstrated in sheep, goat, cattle, horse [6–10]. This characteristic is different from maternal responsiveness, which is a non-specific interest towards any newborn occurring immediately at birth in both altricial and precocial species.

A continuum of mothering styles can be found between the two extremes of altricial and precocial species. In some types of mammals, neonates have functional sensory systems but limited thermoregulation (e.g., pigs) or locomotion (e.g., primates). Sows build a nest and do not develop selectivity towards their piglets immediately after parturition, although they are able to recognize their young within 1 day of parturition [10]. Most primates do not build nests but instead, the mother carries the offspring on her body to which the infants attach, using their strong prehensile hands. In some primates, fathers, siblings and other group members participate in the carrying and caregiving [11]. Mothers act maternally only towards their own infants.

A cross-cultural survey of mothering practices in humans indicates that, although the biological mother is typically the primary caregiver, and in that role usually breastfeeds her infant [12], there is enormous variability in how mothers feel about, transport, and communicate with their infants and the extent of touching, vocalizing, and visual attention that is involved in those interactions [12–17]. As well, there are large variations in the extent to which siblings, fathers, and other relatives and friends participate in caregiving [17]. Despite this range of cultural variation in early maternal behavior and surrounding social systems, universal patterns and common functions of human maternal behavior are also suggested by a number of studies. For instance, particular maternal responses tend to follow particular infant behaviors: nurturant responses follow vocal distress, imitation follows nondistress vocalizations, and encouragement to the environment follows explorations [18]. Moreover, like other primates, humans are able to discriminate their own infants, and may show a preference for them, but, unlike the ungulates, they do not necessarily reject infants belonging to other mothers. Whatever the commonalities and variations in patterns of maternal behavior, adaptive mothering necessarily involves behaving so as to insure the infant’s survival and healthy development; thus, instrumental attitudes and behaviors (like nursing) that facilitate the infant’s growth, as well as emotional/nurturant attitudes and behaviors that promote the infant’s emotional development, comprise some of the more frequently used measures of maternal behavior in human beings.

The onset of maternal behavior depends first on the hormonal events occurring during pregnancy and parturition. This phase induces a maximal state of responsiveness to the sensory cues emanating from young which thereafter maintains maternal responsiveness [19,20]. The aim of this review is to describe the hormonal mechanisms that regulate the onset of maternal behavior across a variety of placental mammals including humans that represent different behavioral strategies.