Available online at www.sciencedirect.com
ScienceDirect
Hormones and Behavior 52 (2007) 92–98
Hormones and Behavior
www.elsevier.com/locate/yhbeh

Perinatal visceral events and brain mechanisms involved in the development of mother–young bonding in sheep

R. Nowak *, M. Keller, D. Val-Laillet, F. Lévy

《Equipe Comportement, Neurobiologie, Adaptation》, INRA UMR85 Physiologie de la Reproduction et des Comportements, CNRS UMR6175, Haras Nationaux, F-37380 Nouzilly, France
Université de Tours, F-37041 Tours, France

Received 27 March 2007; revised 27 March 2007; accepted 28 March 2007
Available online 1 April 2007

Abstract

In sheep the onset of maternal responsiveness and the development of the mutual mother–young bond are under the combined influence of hormonal and visceral somatosensory stimulations. These stimuli are provided in the mother by parturition (via steroids and vaginocervical stimulation) and in the neonate by the first suckling episodes (via cholecystokinin and oro-gastro-intestinal stimulation). In addition, each partner relies on specific chemosensory stimulation for reciprocal attraction: amniotic fluids for the mother, colostrum for the young. In the ewe parturition activates several brain structures to respond specifically to sensory cues emanating from the young. The main olfactory bulbs undergo profound neurophysiological changes when exposed to offspring odors at parturition. Additional activations in the hypothalamus – preoptic area – and the amygdala – medial and cortical nuclei – also contribute to maternal responsiveness and memorization of lamb odors. In the neonate, post-ingestive stimulations activate the brain stem via vagal afferents. Like in the ewe, several regions of the hypothalamus and the amygdala respond to colostrum ingestion suggesting common ground for the integrative neural processes involved in early learning and bonding. This leads to rapid visual and auditory recognition in both partners although olfaction remains important in the ewe to display selective nursing. It is concluded that the biological basis for the development of maternal and filial bonding in sheep presents striking similarities.

Keywords: Ewe; Lamb; Maternal behavior; Amniotic fluids; Vaginocervical stimulation; Suckling; Colostrum; Hypothalamus; Amygdala, Olfaction; Individual recognition; Bonding

Introduction

The pattern of the mother–young interactions in mammals is influenced by the combination of three factors: the developmental status of the neonate, the litter size, and gregariousness (Gubernick, 1981; Nowak et al., 2000). In the rat and the rabbit, the female seeks a sheltered area and builds a nest in which she gives birth to a large number of young that have limited sensory and locomotor abilities (altricial species). Early mother–young interactions occur within the nest and are not based on any preferential relationships. By contrast, sheep are characterized by a small litter of fully developed young that are capable of following the mother shortly after birth (precocial species). The rapid development of mutual bonding is a defining characteristic of maternal behavior in this mammal (Poindron et al., 1993). On the birth site, a close social bonding develops within hours after parturition. It is based on the maternal drive to care and nurse the young, and on mutual recognition between mother and offspring. It implies both a system of communication ensuring that contact is maintained at any time and highly efficient neurophysiological processes leading to the rapid learning of each other's individual cues. The aim of this review is to highlight similarities and differences between the ewe and the lamb in the physiological and neural mechanisms that are involved in both types of learning.

* Corresponding author. 《Equipe Comportement, Neurobiologie, Adaptation》, Unité de Physiologie de la Reproduction et des Comportements, UMR6175, INRA, F-37380 Nouzilly, France.
E-mail address: nowak@tours.inra.fr (R. Nowak).

0018-506X/$ - see front matter © 2007 Elsevier Inc. All rights reserved.
doi:10.1016/j.yhbeh.2007.03.021

Early mother–young interaction

Maternal behavior and recognition of the neonate

Ewes display maternal behavior immediately after expulsion of the fetus (Poindron and Le Neindre, 1980). They are initially attracted to any newborn lamb and the amniotic fluids (AF) that cover it are responsible for this attractiveness. These fluids are strongly repulsive throughout the estrous cycle and most of gestation. It is only around parturition that AF become highly attractive to the ewe triggering intense licking of the young (Lévy et al., 1983). This phenomenon of attraction–repulsion is mediated by olfaction and it is a necessary step for the development of maternal responsiveness. Removal of AF greatly disrupts the onset of maternal care (Lévy and Poindron, 1987). Conversely, wetting dry alien lambs with amniotic fluids facilitates their acceptance by parturient ewes even if fluids come from another female demonstrating that this attraction is not specifically oriented towards the mother's own fluids (Lévy and Poindron, 1984). While she is grooming, the dam emits frequent low-pitched bleats or rumbling noises with the mouth closed, and occasional high-pitched open-mouth bleats (Dwyer et al., 1998). Attraction to AF helps the ewes learn the individual characteristics of their offspring so that they develop rapidly a selective bond. This maternal bond is characterized by the acceptance of suckling attempts by the ewe's own lamb along with rejection of alien young. Many mothers show selectivity at nursing after only 30 min of contact with their young and after 2 h most ewes are selective (Keller et al., 2003). The primary developmental mechanism implicated in the establishment of the mother–young bond is the learning of the lamb's olfactory cues (Lévy et al., 2004). When ewes are made anosmic they subsequently nurse their own as well as alien young (Lévy et al., 1995). Sectioning the nerves of the accessory olfactory system is without effect indicating that the main olfactory bulb, in opposition to the vomeronasal organ, is the olfactory system mediating selectivity at suckling (Lévy et al., 1995). Maternal olfactory memory is rather labile if mothers do not remain in close proximity with their young. When lambs are temporarily removed 7 days after parturition mothers retain maternal selectivity over 36 h of separation but not after 3 days (Keller et al., 2005): most ewes lose their maternal drive thereafter.

Although ewes rely primarily on olfactory cues to recognize their lambs at nursing, they can also identify their neonate from a distance (>1 m) by using only auditory and visual cues (Ferreira et al., 2000; Keller et al., 2003). Non-olfactory recognition develops slightly later than olfactory recognition but it is fully effective by 6 h post-partum. The neural bases involved in either recognition process seem to be independent since anosmic ewes can discriminate between their own and an alien young from a distance even though they are willing to nurse any lamb (Ferreira et al., 2000). The respective roles of vision and hearing have not been clarified yet, although ewes do recognize the voice of their young (Searby and Jouventin, 2003; Shillito Walser et al., 1981).

Neonatal behavior and recognition of the mother

The behavior of the mother must be coordinated with the movements of the newborn lamb which has to be able to stand before it can orient and reach the mammary gland. Most lambs stand up within the first 30 min of delivery and begin to suckle 1–2 h later. They find the udder by exploring the underneath of the ewe's body from the chest to the udder. They are also guided by various cues emanating from the mother's body and many ewes will help the neonate by lowering their back and bending a hind leg to make access to the teat easier (Vince, 1993). The lambs learn the position and shape of the udder very quickly. This learning is sustained by the dynamic of mother–young interactions and the reinforcing properties of suckling. This tight relationship with the mother's udder, driven by the fact that lambs suckle at least on hourly intervals, bring the neonate in contact with maternal cues and behaviors required for the establishment of an individual recognition. Most lambs can display a clear preference for their dam by 12–24 h of age and their ability to discriminate their mother from an alien ewe improves markedly over the first few days of life (Nowak et al., 1989). While at 12–24 h identification of the mother is mostly based on cues that lambs can perceive at close quarters, lambs can clearly locate their mother from a distance of several meters when 3 days old. Olfactory cues are not necessary for newborn lambs to discriminate between two ewes at close quarters even though they do recognize maternal odors at birth (Vince, 1993). Instead, both auditory and visual cues are used (Nowak, 1991). Initial orientation towards the mother is based on rather general signals as 24-h-old lambs seem to choose a ewe on the basis of differences between acceptance behaviors (low-pitched bleats and suckling) and rejection behaviors (high-pitched bleats, aggression) (Terrazas et al., 2002). Step by step the lamb learns various individual features from its mother which results in an improved ability to recognize her from a distance (Nowak, 1991). The role of hearing seems to be important once lambs are several days old (Searby and Jouventin, 2003).

Peripheral changes associated with peripartum events

In the mother

Physiological control of attraction to a neonate

The onset of maternal behavior is brought about by a combination of hormonal factors, peripheral stimulation associated with parturition and cues from the lamb/amniotic fluids. Acceptance of a lamb occurs only when estrogen levels are high during estrus or at the very end of pregnancy (Poindron and Le Neindre, 1980). Evidence for an effect of estradiol on attraction to neonates has been reported on several occasions although results have not always been consistent. Steroid treatments using physiological doses led to the conclusion that steroids have priming effects permitting the action of other physiological factors. The synchrony between parturition and the occurrence of maternal responsiveness suggests that the actual process of expulsion of the fetus is of primary im-