

Neurobiology of Maternal Behavior in Nonhuman Mammals

Subjects: **Biology**

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Survival of the mammal offspring depends on the correct expression of maternal behaviors, particularly during the early postnatal period. Newborns must be a powerful source of incentive sensory stimulation to the dam, and in return, they must be capable of responding either actively or passively to such stimuli, expressing acceptance and motivation to invest energy and time and willingness to risk their physical safety. Hence, the capacity to express maternal behavior depends on the sensitivity to respond to the right stimuli under certain physiological, ontogenetic, or cognitive conditions. Accordingly, to understand the neurobiology of this behavior, it must be considered that neural systems are involved in acceptance, social recognition, motivation, and fear/rejection.

preoptic area

dopamine

recognition

brain

motivation

1. Active and Passive Maternal Behaviors

Maternal behavior involves the facilitation of acceptance, recognition, and motivation, along with the inhibition of rejection and fear toward offspring. Acceptance is inferred from behaviors that allow proximity to any newborn, whereas recognition involves selective acceptance of specific individuals. Thus, females may passively accept unfamiliar newborns (i.e., allowing nursing to any young) and recognize/accept only familiar ones. Similarly, rejection may involve active responses (i.e., aggression/infanticide) to discourage contact, whereas fear may be expressed via passive avoidance (i.e., not approaching them). Furthermore, care motivation involves active behaviors that indicate willingness to nurse and protect the young. So, although the expression of maternal behaviors varies considerably among species, the endpoints served are the same. For instance, some precocial species, such as sheep and horses, express very selective maternal behavior toward offspring they accept/recognize as theirs during the very first hours postpartum [1][2]. That kind of maternal selectivity requires strict mechanisms of acceptance/social recognition that occur via imprinting (i.e., associative learning) during a brief period following parturition. Disturbance of recognition between the dam and her offspring during the early imprinting period may result in rejection (perhaps fear), despite all the hormonal input or whelping experience. By contrast, altricial species with massive reproductive strategies, like rats, canids, or pigs, are considered less strict because they may accept alien offspring during extended periods [3][4][5]. In addition, some ungulates [6] and nonhuman primates [7][8] may display extensive maternal repertoires daily for weeks or months, whereas others, such as lagomorphs, will display only a few minutes of nursing once a day [9].

Some behaviors that start before parturition might be considered indirect maternal behaviors. For example, nest-building (e.g., digging, shredding paper, straw carrying, and hair pulling) and isolation from the pack or herd [10][11][12][13]. Other early behaviors, such as those observed in pregnant dogs, including restlessness, reduced appetite, lack of attention, drowsiness, aggression, anxiety, fickleness, capriciousness, irritation, and increase in attention request, may only reflect an imminent parturition [14][15]. Indeed, nest-building and isolation are associated with searching for and selecting the appropriate birthplace [16][17]. It is possible that nest-building is more likely observed in altricial species, whereas isolation from others may occur in precocial ones.

Direct maternal behaviors are observed after parturition, during the first contact with the newborns. Dogs will actively bite and tear the fetal membranes and cut the umbilical cord, which functions to prevent asphyxiation of the pups [18]. The dam actively licks the head and the mouth of the newborn to stimulate respiration and orient the pups toward the mammary gland [13][15]. They also lick the anogenital area to facilitate urination and excretion during the first 2 postnatal weeks [19]. Rats also express anogenital licking, especially toward males during the first 10 postnatal days [20]. Preference to lick males is evoked by attractive odors from preputial compounds, such as dodecyl propionate [21], which depend on the levels of systemic steroids. If female pups are treated with androgens (i.e., testosterone and dihydrotestosterone) on the day of birth, they receive an equivalent amount of active anogenital licking as males [22]. Enhanced anogenital stimulation appears to have positive long-term effects on male reproductive behavior [23]. Dams display other active responses as well, such as retrieving the pups, oral consumption of the placenta, and defense from predators and conspecifics, and passive behaviors such as huddling and crouching to regulate body temperature or allowing nursing. In the beginning, passive behaviors may depend on acceptance, whereas active behaviors may depend on enhanced motivation to care. Other species, such as cows, also express intense active licking for the first hour and will be very protective if someone approaches. Passive acceptance may occur within the first 30–120 min postpartum when the calf stands and searches for the udder [16].

The lack of maternal behaviors represents a serious problem that jeopardizes not only the survival of the offspring but also a very important mechanism of early socialization, cognitive development, and epigenetic changes associated with resilience to stress [24][25]. Good maternal behavior is associated with the so-called stress hyporesponsive period [24][26], which refers to a delay of the timing of glucocorticoid elevation in infants, associated with reduced stress response in adulthood [26]. Inappropriate maternal behaviors may occur in 50% of primiparous dogs, especially following cesarean section [27] or as a result of early separation during the postpartum period [28].

2. Natural Stimuli That Facilitate the Expression of Maternal Behavior

2.1. Hormones

Gregarious species have a natural predisposition to care for the young. However, the capacity to express appropriate levels of maternal behavior develops gradually with hormonal changes that occur throughout pregnancy. Then, drastic changes during parturition are needed to trigger the expression of behavior. In rats, for

example, concentrations of progesterone (P4) gradually start to increase from the very first day of pregnancy, reaching a peak at day 15, and are followed by a drastic reduction during the last 3 days before delivery. By contrast, the levels of estradiol (E2) and prolactin (PRL) stay relatively low at the beginning but increase dramatically during those last 3 days. The reduction of P4 and increase in hormones such as E2, PRL, oxytocin (OT), and corticosteroids, are the main hormonal drastic changes during parturition [29][30][31] and therefore are associated with sensitization of maternal behavior. For example, in the rabbit doe, digging is stimulated by changes in E2 and P4, while straw carrying and hair pulling are under the control of PRL. In the rat, the reduction in P4 and the increase in E2 and PRL levels facilitate active licking, retrieving, and gathering of pups. Pharmacological blockade of estrogen in the medial preoptic area (mPOA) and small interfering RNA silencing of estrogen receptors (ER α) disrupts maternal behavior in mice [32][33], whereas specific activation of ER α -positive mPOA neurons enhances pup retrieval [34][35]. Likewise, the blockade of PRL receptors within the mPOA in mice abolishes pup retrieval [36].

2.2. Vagino-Cervical Stimulation

In the ewe, licking, low-pitched bleats, and nursing are also evoked by changes in P4/E2 ratio and by the release of OT triggered by vagino-cervical (VCS) and nipple stimulation [37]. VCS caused by the passing of the young through the pelvic canal must be considered a powerful triggering stimulus to evoke maternal behavior after hormonal sensitization during pregnancy. For instance, artificial VCS (pressure on and stretching of the neck of the cervix provided by hand) in ewes can facilitate maternal acceptance toward an alien lamb up to 27.5 h postpartum [38][39]. This also occurs in other species, such as rats, in which normal expression of maternal behavior depends on the interaction between hormonal priming in the mPOA and VCS evoked by parturition. One study showed that, 24 h before parturition, only a few pregnant females exposed to pups (from a different female) expressed active pup retrieval, but 12 h before parturition, up to 80% of them retrieved pups. In addition, that study explored the maternal behavior of pregnant females implanted bilaterally in the mPOA with the antiestrogen 4-hydroxytamoxifen (OH-TAM). Accordingly, 12 h before parturition, none of the OH-TAM females expressed retrieving behavior, and in the absence of parturitional experience (delivery by cesarean section), maternal behavior was almost absent upon exposure to their own pups. By contrast, those OH-TAM females that were allowed to undergo normal parturition (with natural VCS) expressed normal retrieving behavior upon exposure to their pups [40]. Hence, hormones and VCS play a synergistic role in evoking the whole repertoire of maternal behaviors. Indeed, pseudopregnant female rats and mice that go through all the hormonal changes without parturition express only a few indirect maternal behaviors such as nest-building [41][42]. Similarly, pseudopregnant dogs (i.e., pseudocyesis) can also express some maternal behaviors (e.g., nesting, defense) toward pup-looking puppets [43]. In one case report, a sudden decrease in systemic P4 following ovariohysterectomy during the luteal phase of diestrus was reported as the triggering stimulus for maternal behavior, evoking a parturition-like drastic reduction of P4. Similarly, sudden maternal behavior has also been observed in pregnant rats following hysterectomy [44]. Males artificially exposed to E2 and P4 also expressed paternal behavior [45]. When those males received lesions in the mPOA, their behavior was significantly reduced, indicating the mPOA mediates parental behavior in both males and females.

Hormones and physical stimuli (VCS, nipple stimulation) that occur during parturition and lactation are the best natural stimuli that induce maternal behavior. Upon stimulation, magnocellular neurons in the supraoptic (SON) and paraventricular nuclei (PVN) fire high-frequency bursts of action potentials. Each burst generates a large pulse author's study shows, OT modulates acceptance, social recognition, learning, memory, emotions, reward, eating, drinking, sleep, wakefulness, nociception, analgesia, and sexual and maternal behaviors [47].

2.3. Exposure to Pups

Interestingly, exposure to pups can also result in sensitization of maternal behavior in male and nonpregnant female rats. One week of daily exposure to pups induces both active (e.g., nest-building, retrieving, licking) and passive behaviors (e.g., nursing posture) [48][49][50]. This indicates that gradual exposure sensitizes parental behavior without the need for any hormonal priming. This type of sensitization also occurs when juvenile rats are exposed to infant rats [51], and watching a conspecific perform maternal behavior (i.e., retrieval) activates OT neurons in the observer [52]. Accordingly, the putative neurocircuitry that mediates maternal behavior might be gradually activated and sensitized by daily exposure to pups, but hormones, parturition, and lactation function as triggering stimuli that accelerate its activation.

2.4. Mating

Similarly, copulation can also sensitize the neurocircuitry of parental behavior. In male rats [53] and mice [54], copulation blocks infanticide behavior (an expression of rejection) and facilitates active retrieving (an expression of care motivation) in future encounters with pups [55]. More than 90% of male mice will normally commit infanticide if exposed to pups between 1–4 days after mating with any female, indicating that during those immediate days males reject the pups. However, between 80–90% of those males will behave parentally and will not kill the pups if they are exposed to them 12–50 days after copulating to ejaculation. The actual mechanisms for sex-induced parental behavior in males are unknown but appear to require changes in the mPOA. This area is sensitive to mounts, intromissions, and ejaculations [56][57], such that consecutive copulatory series increase the number of firing neurons in the mPOA [58] and lesions impair consummatory sexual behavior [59]. Those changes may modify plasticity within the mPOA to facilitate parental behavior.

2.5. Maternal Experience

Former maternal experience also improves the expression of maternal responses. For example, multiparous dogs express more time of body contact with pups and constant maternal care during the 21-day postpartum period, whereas primiparous females show a gradual increase in licking, nursing, and contact with the puppies from day 1 to 21 [60]. Multiparous cows also express more maternal defense than primiparous [61] and isolate less from the herd [62], probably related to less intense fear, considering that multiparous female rats are less anxious in open field tests, compared to primiparous females [63]. In sheep, former maternal experience is associated with increased suckling, following, grooming, and low-pitched bleating and decreased aggressive behavior [64].

2.6. Environmental Enrichment

Environmental enrichment (EE) also improves maternal behavior. In one study with rats, EE condition consisted of housing seven females per cage; the EE cage (120 × 100 × 70 cm) was designed with four floors with lid ramps and contained plastic balls, tubes, and bedding material. The interactive objects and location of food were rearranged every three days to increase novelty and complexity, which resulted in a highly stimulating sensory and social environment with other females. Following parturition, EE females expressed less anxiety and displayed more licking, grooming, and crouching over pups during the first postpartum week as compared to females living in standard cages [65]. During that period, EE mothers also showed more aggressiveness to an intruder female. Associated with offspring-directed behaviors, EE females expressed more neural activity in the mPOA, PVN, and medial amygdala (MeA) but less activity in the basolateral amygdala (BLA) than standard-housed females [66]. As it is discussed, those brain areas are associated with maternal motivation and rejection, respectively. Taken together, the data indicate that the capacity to express maternal behavior develops as a consequence of hormonal priming but is triggered by stimuli such as parturition and lactation. In addition, cohabitation, copulation, former experience, and environmental enrichment facilitate its expression.

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