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Review article

Neural mechanisms of mother–infant bonding and pair bonding: Similarities, differences, and broader implications

Michael Numan [a,*], Larry J. Young [b]

[a] Rio Rancho, NM 87144, United States
[b] Center for Translational Social Neuroscience, Silvio O. Conte Center for Oxytocin and Social Cognition, Yerkes National Primate Research Center, Department of Psychiatry and Behavioral Sciences, Emory University, Atlanta, GA 30329, United States

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ABSTRACT

This article is part of a Special Issue "Parental Care".

Mother–infant bonding is a characteristic of virtually all mammals. The maternal neural system may have provided the scaffold upon which other types of social bonds in mammals have been built. For example, most mammals exhibit a polygamous mating system, but monogamy and pair bonding between mating partners occur in ~5% of mammalian species. In mammals, it is plausible that the neural mechanisms that promote mother–infant bonding have been modified by natural selection to establish the capacity to develop a selective bond with a mate during the evolution of monogamous mating strategies. Here we compare the details of the neural mechanisms that promote mother–infant bonding in rats and other mammals with those that underpin pair bond formation in the monogamous prairie vole. Although details remain to be resolved, remarkable similarities and a few differences between the mechanisms underlying these two types of bond formation are revealed. For example, amygdala and nucleus accumbens–ventral pallidum (NA–VP) circuits are involved in both types of bond formation, and dopamine and oxytocin actions within NA appear to promote the synaptic plasticity that allows either infant or mating partner stimuli to persistently activate NA–VP attraction circuits, leading to an enduring social attraction and bonding. Further, although the medial preoptic area is essential for maternal behavior, its role in pair bonding remains to be determined. Our review concludes by examining the broader implications of this comparative analysis, and evidence is provided that the maternal care system may have also provided the basic neural foundation for other types of strong social relationships, beyond pair bonding, in mammals, including humans.

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* Corresponding author at: 2409 Desert View Road, NE, Rio Rancho, NM 87144, United States.
E-mail address: numan@bc.edu (M. Numan).

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Introduction

The two most common prosocial behaviors in mammals are the sexual interactions that occur during mating and mother–infant interactions. In most mammals, sexual interactions are short lasting, while the mother–infant bond is long-term, persisting, at least, through weaning. The mother–infant bond, therefore, is the most common enduring social bond in mammals.

More specifically, about 95% of mammalian species exhibit a polygamous mating system (Kleiman, 1977), and although the two sexes are attracted to each other during mating, once mating is complete the two sexes leave each other. In these cases, the pregnant female gives birth and cares for her offspring by herself, giving rise to the typical mammalian maternal care system. In contrast, about 5% of mammalian species exhibit a monogamous mating system where one male engages in sexual activity preferentially with one female, and then the male–female pair remains together and both parents contribute to raising offspring (McGraw and Young, 2010; Young et al., 2011). Such a pair bond represents the formation of a selective and a long-term social attraction between two specific adults who recognize each other and remain together after sexual activity has terminated. Monogamy usually evolves under conditions where biparental care is necessary for infant survival (Brown, 1975).

Since the strong attraction between a mother and her infant(s) is common to all mammals, while the enduring pair bond in monogamy is rare in mammals, it can be suggested that the neural circuitry and mechanisms that underpin the long-term mother–infant attraction may have provided a primordial neural scaffold upon which other types of strong social bonds, such as pair bonds, have been built. Although many researchers have made this point (for a review, see Numan, 2015), the purpose of this paper is to compare the *details* of the neural circuitry and mechanisms that contribute to the formation of the mother–infant bond and the pair bond, where remarkable similarities (and some important differences) exist. In particular, in this review we will show that the amygdala and nucleus accumbens–ventral pallidum (NA–VP) circuits are involved in both types of bond formation, and that dopamine (DA) and oxytocin (OT) actions within NA appear to promote the synaptic plasticity that allows either infant or mating partner stimuli to persistently activate NA–VP attraction circuits, leading to an enduring social attraction and bonding. Further, we will present evidence that OT effects on the connections between the olfactory bulbs and the amygdala may play a role in the selective recognition processes that occur during maternal bonding in certain species and during pair bond formation. Such processes would allow for individual recognition of one's offspring or mating partner.

Most of the research we will review concerns maternal behavior in rats and sheep and pair bond formation in prairie voles. We will analyze the maternal bonding system first and then follow with the pair bond system because the former is proposed to be the primordial system. We will conclude with a comparative analysis of the two systems, along with broader implications.

Maternal behavior and mother–infant attachment

The development of a mother–infant bond consists of a two-step process: a recognition process and a persistent attraction process (Numan, 2015). The recognition process allows infant stimuli to gain access to those neural mechanisms that promote attraction and maternal care rather than rejection and avoidance of infant stimuli, while the persistent attraction process is the result of brain plasticity mechanisms that cause an enduring or long-lasting attraction to develop between a mother and her infant(s).

With respect to the recognition process, it can be either non-selective or selective. A non-selective recognition process typically occurs in mothers that give birth to altricial young, such as rats and many other rodents: maternal care is directed toward a generic infant stimulus rather than to particular infants, and mothers will care for any conspecific infant throughout the postpartum period. As a result, general infant stimuli are recognized as positive, rather than negative, social stimuli. In contrast, a selective recognition process operates in mothers that give birth to precocial young, such as sheep and other ungulates, or semi-mobile young, such as primates, where selective maternal care is ultimately directed toward the particular offspring that the mother gives birth to, while other (alien) young are rejected (Insel and Young, 2001; Nowak et al., 2011; Numan and Insel, 2003). *Experimental* manipulations show that postpartum rats will care for their own pups or pups from another mother, while sheep learn the olfactory characteristics of their lamb at the time of birth and will subsequently care for their own lamb while rejecting the advances of alien young. This difference in the selectivity of the recognition mechanism and the mother–infant bond is the result of evolutionary forces: selective recognition mechanisms are adaptive for sheep but have no adaptive significance for most rodents (Numan and Insel, 2003). However, the long-term attraction of a mother toward her infant(s) is an essential component of the mother–infant bond in all mammals.

It is worth pointing out that when one compares the mother–infant bond with the pair bond in monogamous species, the overall characteristics of the pair bond closely match the selective maternal bond that forms in such species as sheep. In both cases, a selective and long-term attraction is formed to a particular individual. However, please note that two processes are occurring during bond formation: one governing the nature of the stimuli that are relayed to an attraction mechanism (specific or generic stimuli), and one controlling the operation and modification of the attraction mechanism so that a persistent attraction develops to the relevant stimuli. Research on the maternal bond in species with precocial young, when compared with those with altricial young, will be shown to inform us about both processes. In particular, research on sheep has highlighted the mechanisms underlying the selective recognition process, while research on rats has provided significant insights into the mechanisms that underpin the development of an enduring attraction between a mother and her young. The research on pair bond formation in prairie voles, in the context of the maternal bonding data, provides hypotheses on how these two mechanisms are combined so that a selective and enduring attraction develops between mating partners.

In most mammals, the endocrine events associated with the end of pregnancy and parturition, in conjunction with OT release into the brain that results from the vaginocervical stimulation associated with the birth process, act on the brain to stimulate the immediate onset of maternal behavior at parturition, but after maternal behavior becomes established during the early postpartum hours, its maintenance until weaning becomes independent of hormonal control (Numan et al., 2006). Therefore, hormonal action on the brain, in conjunction with an initial maternal experience with infants, results in a long-lasting