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Review

New theoretical and experimental approaches on maternal motivation in mammals

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ABSTRACT

Maternal behavior is expressed in different modalities, physiological conditions, and contexts. It is the result of a highly motivated brain, that allows the female to flexibly adapt her caring activities to different situations and social demands. To understand how mothers coordinate maternal and other motivated behaviors we discuss the limitations of current theoretical approaches to study maternal motivation (e.g. distinction between appetitive and consummatory behaviors), and propose a different approach (i.e. motorically active vs. passive motivations) and a distinction between maternal motivated *state* and maternal motivated behaviors. We review the evidence supporting dopamine mediation of maternal motivation and describe how different phases of the dopaminergic response – basal, tonic, and phasic release in the nucleus accumbens – relate to increased salience, invigorating behavior, and behavioral switching. The existing and new experimental paradigms to investigate maternal motivation, and its coexpression and coordination with other social or non-social motivations are also analyzed. An example of how specificity of motivational systems (e.g. maternal and sexual behavior at postpartum estrus) could be processed at the neural level is also provided. This revision offers new theoretical and experimental approaches to address the fundamental question of how mothers flexibly adapt and coordinate the different components of maternal behavior with other motivated behaviors, also critical for the survival of the species.

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1. Introduction

Parental behavior is the result of complex internal processes and external factors that ensure that an individual takes care of the young, contributing to their survival by providing food, warmth, shelter, protection from predators and conspecifics, and appropriate stimulation. In mammals, lactating females are commonly responsible for providing all these benefits but, depending on the reproductive strategy of each species, males and other family members can also contribute to the care. In this context, mothers also interact socially with other members of their family or social group, besides their offspring. A flexible caregiving strategy by the mother requires a highly motivated and flexible brain to adapt to the different social contexts. These are the topics that brought the authors of this review together to participate in a Workshop that took place in Montevideo, Uruguay on September 3–5 of 2011. The workshop entitled *Neural basis of maternal motivation: relationship and coordination with other social motivational systems* was co-organized by Daniel Olazábal and Mariana Pereira. The aim of this workshop was to discuss how the brain adapts to and regulates maternal behavior in different species, and physiological and social conditions. The results of those discussions and of the academic exchanges that continued since then are presented in two separate reviews. The first review focuses on theoretical and experimental aspects of maternal motivation and the second review on the neural basis that supports the different forms and modalities of maternal behavior across mammals. Both of these reviews emphasize the mechanisms that provide flexibility and adaptation to the system. In the first two sections of the present review, we introduce the topics discussed at the Workshop and summarize the mechanisms of onset, maintenance and decline of maternal responsiveness in parturient and naive cycling animals and briefly describe the complex challenges of motherhood. In the third section we discuss the advantages and limitations of applying a number of concepts that are extensively used in the literature on behavioral motivation, to our studies on maternal motivation. In particular, we critique the distinction between appetitive and consummatory behaviors in the maternal behavior system, and propose new approaches and experimental models to study maternal motivation. We also put the existing evidence related to maternal motivation in the context of current theoretical interpretations of motivational processes (i.e. incentive salience, wanting vs. liking, etc.). In Section 4, we present a series of studies that investigates maternal motivation, either by manipulating or measuring the hormonal milieu or the dopaminerigc system, and integrate and discuss these findings with the new theoretical approaches proposed in Section 3. Section 5 describes some examples of the coexpression, coordination and switching between maternal and other motivations, and propose experimental approaches to understand its neural basis. Section 6 discusses the specificity of motivational neural systems underlying sexual and maternal motivation, in particular at the postpartum estrus. Finally, the last section brings the discussion full circle, where we summarize the main points that have come out of these discussions and raise some of the future challenges in the maternal behavior field.

2. Maternal behavior in parturient and naïve cycling animals

Parental behavior is essential for the survival of mammalian species, in which females are most commonly responsible for taking care of the offspring. The majority of lactating mammals share many behavioral features; they consume placenta, fetal membranes and amniotic fluids, clean off the neonates, exhibit a selective interest in the young and respond maternally to them, while at the same time defending the offspring from intruders or predators, for example when showing aggressive behavior (Numan et al., 2006).

The motivation to display parental behavior is very high at the time of parturition, when females (and in some cases males) show a very rapid interest in the newborn. In most rodents (e.g. rats, mice, hamsters) and primates, the mother builds a nest, transports or retrieves the newborn to the nest, cleans and licks them and adopts nursing postures (Numan and Insel, 2003).

However, in some species like the prairie voles, california mice, or marmosets, the father or other members of the family group assist the lactating female in the care of the young (Numan and Insel, 2003), indicating that maternal behavior can also emerge under different physiological and social contexts. For instance, virgin female rats eventually become maternal after several days of continuous exposure to foster newborn (Cosnier, 1963; Rosenblatt, 1967). This process (called pup-induction or sensitization of maternal behavior) leads to a pattern of behavior very similar to that of the lactating mother (Numan et al., 2006). During that continuous exposure to foster newborn, the animal often must overcome an initial aversion to pups before they approach, contact and start displaying all components of maternal behavior (Fleming et al., 1989). On the other hand, some non-lactating rodents (e.g. prairie voles) and primates (e.g. marmosets, humans) readily interact with newborns, displaying immediate maternal or paternal behavior without needing a prior period of sensitization (Kuroda et al., 2011; Lucas et al., 1998; Olazábal and Young, 2005).

2.1. Onset, maintenance, and offset of maternal behavior

Some of the behaviors typically displayed by mothers begin during pregnancy, like the construction of a maternal nest (González-Mariscal et al., 1994), and the preference for pup odors

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