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Review article

Dopamine dynamics underlying maternal motivation and reward

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ABSTRACT

Maternal behavior comprises a diverse set of caregiving actions essential for ensuring offspring survival and development. Shaped by evolutionary pressures, these behaviors range from goal-directed and coordinated overt motor actions such as nest building and pup retrieval to sustained akinetic states such as nursing and crouching. These can each be thought of as varying along two continua, one which captures the appetitive versus consummatory aspects of a given behavior, and the other describes the relative activity or passivity of the behavior. Since individual behaviors (1) vary substantially along these axes, and (2) evolve in time, we propose that motivated execution of them is likely accomplished through dynamic regulation by multiple circuits and neuromodulatory systems. One important regulator of maternal behaviors is dopamine (DA), a key neuromodulator that makes diverse contributions to behavior. Classically, dopamine is hypothesized to play a role in both the appetitive (e.g. pup retrieval) and consummatory (e.g. nursing, grooming) aspects of maternal behavior via distinct circuitry. Considering recent studies revealing the temporal dynamics of DA during maternal behavior, we examine the complexity of the concepts of appetitive and consummatory drive as maternal behavior unfolds in time. We propose that seemingly discrete behaviors, like pup retrieval, may be appreciated as evolving sequences of appetitive and consummatory components that reflect shifts in underlying neural dynamics at different timescales.

1. Introduction

In many species, attentive parental care is required for infant survival and overall species fitness. This is especially true of altricial offspring, such as humans and many other mammals, which are born in an underdeveloped state, entirely dependent on caregivers for warmth, nourishment, and protection. During infancy, the mother of the offspring devotes a significant amount of time and energy to infant care, making this period a crucial time for mother-infant social interactions. Beyond merely ensuring survival, the quality of mother-infant interactions is rewarding for both mother and infant, and provides social learning opportunities (Faust et al., 2020; Rincón-Cortés and Grace, 2020).

Rodents have been a leading laboratory animal model for parental care for nearly a century. Maternal behaviors typically seen in rodents include pup retrieval, nursing, licking/grooming, and pup defense. One key maternal behavior in rodents is pup retrieval, in which a mother detects the distress cries and location of scattered pups, picks them up, and transports them back to the nest (Ehret, 2005; Noirot, 1972; Sewell, 1970). This process involves multiple sequential steps that require sensory detection, motor coordination, and motivation of the animal. Following retrieval, the mother engages in close contact care, including nursing and licking/grooming. Licking/grooming serves multiple functions, including thermoregulation, bonding, and stimulation of pup physiology, such as elimination reflexes (Numan, 2020).

It is generally agreed that maternal behavior is governed by a broad network of interconnected brain regions, with the medial preoptic area (MPOA) serving as a key hub (Kohl et al., 2018; Numan et al., 2009; Numan and Stolzenberg, 2009). Prior studies of how sensory, motor, and reward-related processes are integrated to motivate maternal responses reveal the neurotransmitter dopamine (DA) as a key component of this regulation (Curry et al., 2013; Fang et al., 2018; Henschen et al., 2013; Numan, Numan, Pliakou, et al., 2005; Numan et al., 2009; Rincón-Cortés and Grace, 2020; Seip and Morrell, 2009; Stolzenberg et al., 2010). DA has widely acknowledged roles in movement initiation, motivation, and reward processing (Amo, 2024; Berke, 2018; Coddington et al., 2023; Hamid et al., 2016; Lerner et al., 2021). With regard to maternal behavior, there is considerable evidence implicating the mesolimbic dopamine system in the performance of certain maternal behaviors. The mesolimbic system includes a dopaminergic pathway from and the

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ventral tegmental area (VTA) to the nucleus accumbens (NAc) that is highly responsive to conventional rewards such as a sugar pellet or cocaine (Adinoff, 2004; Dunigan and Roseberry, 2022; Phillipson, 1979). As we discuss below, there is substantial behavioral evidence that access to pups is rewarding for dams. This is consistent with a model whereby DA signals for motivation and/or reward constitute a key mechanism by which caregiving behaviors are initiated and maintained.

The MPOA integrates hormonal, sensory, and environmental signals to coordinate maternal responses and projects to many other brain regions, including VTA and the periaqueductal gray (PAG). The MPOA-VTA network stimulates the release of DA into NAc and has been proposed as providing the drive for appetitive aspects of maternal behavior. The MPOA-PAG network, on the other hand, may serve to regulate consummatory aspects of maternal behavior (Numan, 2020). Here we discuss the historical use of "appetitive" and "consummatory" to classify behavior, including maternal behavior, and we evaluate their usefulness for characterizing the motivation for pup retrieval in light of several competing models.

Understanding the neurobiology of maternal care in species with altricial young has broad implications, from informing treatments for postpartum mood disorders to providing evolutionary insights into the origins of social bonding. In this review, we re-examine the use of the terms "appetitive" and "consummatory" to describe different aspects of maternal behavior, and review brain regions and circuits that are essential for these behaviors. We will address the following key questions while reviewing existing literature: How are different aspects of maternal behavior distributed across a network of regions and circuits? How does the reward system integrate into these maternal circuits?

2. Application of "Appetitive" and "Consummatory" to maternal behavior

Early ethologists identified action sequences that make up complex behaviors, such as maternal behaviors and reproductive behaviors, which are often essential to species survival. The concepts of "appetitive" and "consummatory" behaviors were first noted by Sherrington (1906) in his description of behavior as a sequence of reactions. He uses "precurrent" in his nomenclature to denote anticipatory behaviors that help the organism integrate sensory cues and motor movements to attain a goal stimulus He also hypothesizes that precurrent reactions are initiated by and dependent on "distance-receptors" that react to stimuli at a distance (e.g. olfactory receptors) originating from the cerebrum. One example of a precurrent reaction is a dog detecting prey via vision and turning its head to track the prey. Upon completion of the precurrent behavioral sequence, the organism will experience a consummatory reaction to the fulfillment of a biological need or purpose, such as ingesting food or mating. Craig (Craig, 1917, 1918) later substitutes the term "appetitive" for precurrent to describe a behavioral sequence serving the goal of attaining a stimulus for which the animal has an "appetite." Following the appetitive action(s), when the stimulus is acquired, the animal will perform an innate consummatory action (Craig, 1917, 1918), and if the goal stimulus is not satisfied, the animal will remain restless.

These terms were originally used only for description of behavior, not as a way to infer neural mechanisms (Ball and Balthazart, 2008). Nevertheless, Niko Tinbergen and Konrad Lorenz adopted the terminology to help organize physiological models of the neural control of behavior (Lorenz, 1935; Tinbergen, 1951). These models drew criticism (Beer, 1983; Hinde, 1953), leading some to argue that the terms appetitive and consummatory were not useful. Such conversations considering the use of appetitive and consummatory terminology are ongoing and include opinions that either endorse (Ball and Balthazart, 2008; Numan, 2020; Stolzenberg and Numan, 2011) or criticize (Hinde, 1953; Olazábal et al., 2013; Pfaus, 1996; Sachs, 2007) approaches that divide instinctual behaviors into two distinct categories.

With respect to maternal behavior specifically, Olazábal et al. (2013) argue that maternal behavior is highly adaptable and context-dependent, challenging the division between appetitive and consummatory phases. A more recent piece by Numan revisited these concepts (Numan, 2020), thoroughly reviewing evidence that is consistent with the appetitive vs consummatory dichotomy in terminology, circuits, and affiliated behavior. Numan also argued for maternal behavior to be produced by the "intersection between a specific appetitive motivational system and nonspecific mesolimbic DA system" (Numan, 2020). The appetitive behavior to satisfy the need of the stimulus could include pup retrieval (locating pup, picking it up, transporting it to the nest, and dropping it into the nest) and the innate consummatory behaviors could include crouching, nursing, grooming (Champagne et al., 2004; Numan and Insel, 2006; Numan and Woodside, 2010), however some have argued that components of retrieval could be consummatory (Van Hemel, 1973).

Van Hemel further explored Craig's hypothesis that appetitive behaviors toward a stimulus are reinforced by the satisfaction of consummatory behaviors using a lever pressing task (Van Hemel, 1973). She proposed that in this assay, operant actions would be reinforced by the ability to perform rewarding consummatory actions. Van Hemel trained virgin female mice to lever press for pups. This experiment allowed virgin female mice to choose to press a lever that gave access to pups that were either 1) behind a barrier and allowing limited interaction only, or 2) freely accessible, allowing the pups to be retrieved to a nest. Mice were given a choice between mere social interaction and the opportunity to retrieve pups to a nest. Van Hemel found that that virgin female mice could be trained to lever press for pups and consistently prefer the lever that granted access to retrievable pups. She concluded that in this paradigm, lever pressing was an appetitive behavior, and pup retrieval acted as the consummatory reward reinforcing that behavior.

In addition to disagreement over the terms appetitive and consummatory some groups have offered an alternative nomenclature of "active motivation" and "passive motivation" (Lonstein et al., 2015; Numan and Woodside, 2010; Olazábal et al., 2013; Terkel et al., 1979). This framework hypothesizes two distinct categories of maternal behavior: 1) active motivated behaviors, defined as nest building, grooming, search for pups, and retrieval, and 2) passive motivated behaviors including nursing and hovering over pups. Recently, another review described retrieval as "an appetitive or goal-directed" behavior and nursing as the "passive, consummatory component" (Rincón-Cortés, 2024).

Several behavioral variables that add complexity have not yet been considered in categorizing maternal behavior, including **temporal structure**, **repetition**, and **experience dependence**. Until recently, retrieval behavior has not been analyzed as a dynamic event that is subject to changing neural modulation within a trial. Observing ongoing neural activity during these events could reveal unexpected **temporal structure**. Next, many maternal tasks occur **repetitively**, for example, pup retrieval is often performed several times in a row to bring multiple scattered pups back to the nest. This behavior loop of multiple pup retrievals in quick succession could involve rapid shifts between appetitive and consummatory drives. Finally, maternal behaviors adapt with maternal **experience** and pup growth and development. As pups age, changes in their needs, capabilities, and size create shifting demands from birth to weaning, which are met in different ways depending on the dam's experience and ability to respond. Pup retrieval is often thought of as a single behavior; however, it can also be described as a series of events in which a dam 1) locates a pup, 2) approaches the pup 3) picks up the pup 4) carries the pup to the nest and 5) drops the pup into the nest. What happens after the pup is dropped in the nest depends on whether there are other scattered pups that need to be retrieved, or if pups in the nest are in need of other forms of maternal care. When considering pup retrieval as a behavioral sequence, it may be thought of as a hierarchically structured motivation, where the larger goal of moving all pups to the nest is satiated only after completing the smaller goal of moving one pup to the nest, repeatedly.

To better conceptualize the dynamic structure of maternal

motivation, we propose three hypotheses regarding the appetitive and consummatory components of pup retrieval (Fig. 1):

- **Classic appetitive/consummatory hypothesis**: The appetite is for getting the pup to the nest so it can be nursed and groomed, and it is satisfied by whichever action(s) bring about that result. In this case, the entire process of pup retrieval is appetitive, and subsequent actions of nursing or grooming is considered consummatory (Numan, 2020).
- **Rewarding pup hypothesis**: The appetite is for the rewarding stimulus, contact with the pup. In this case, any actions to search for and approach the pup are appetitive and subsequent picking up the pup, transporting it, and dropping it into the nest is consummatory (Van Hemel, 1973).

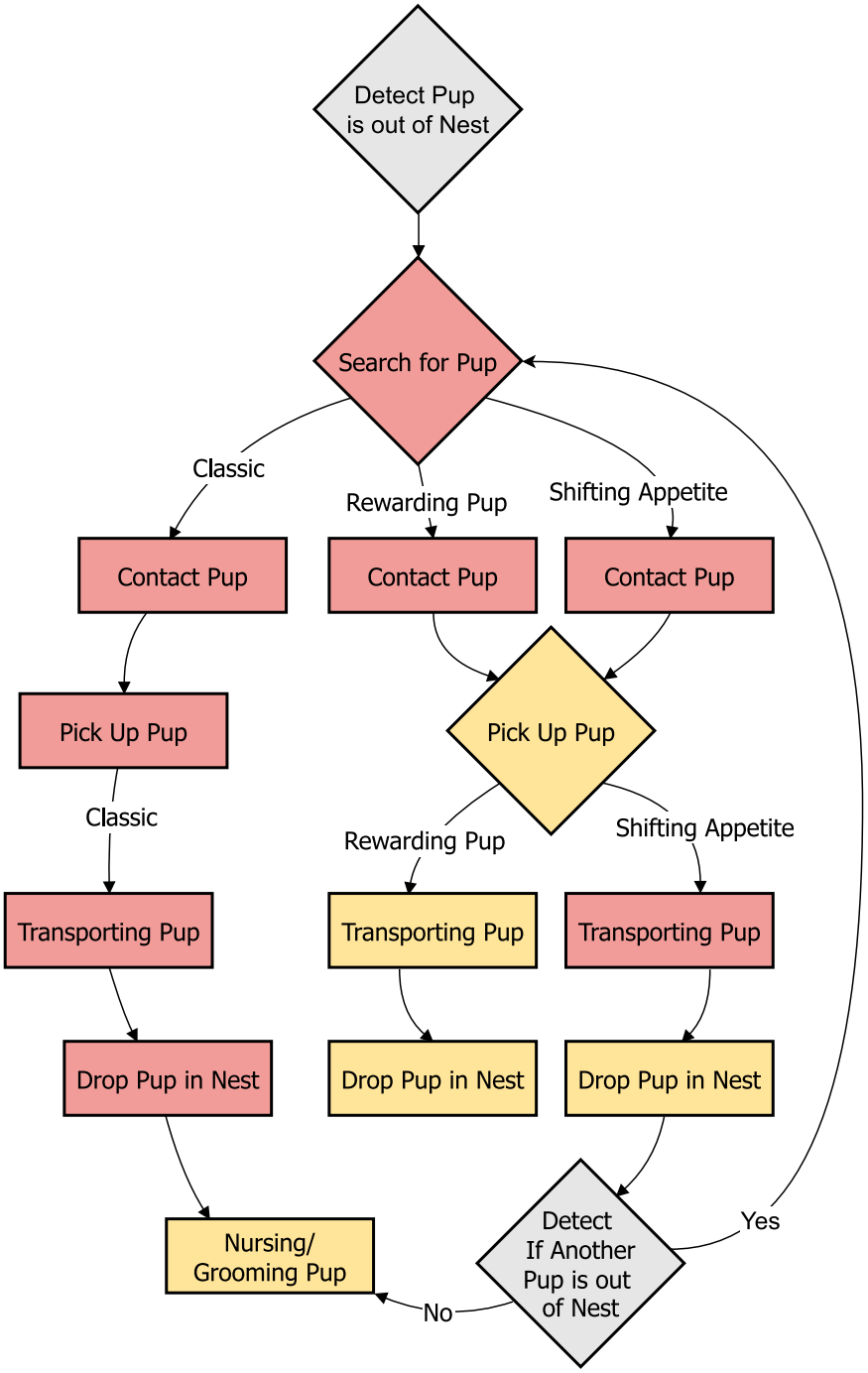

Fig. 1. Decision tree illustrating three hypothesized motivational structures underlying pup retrieval behavior. This schematic breaks down pup retrieval into discrete behavioral phases: search, contact, pick up, transport, and drop in nest. Each column represents one of three conceptual models for how motivational state transitions unfold during retrieval: Classic Hypothesis (left): Retrieval is driven by appetitive motivation (pink); consummatory motivation (yellow) initiates after the pup has been retrieved to the nest. Rewarding Pup Hypothesis (middle): The act of pup contact is itself rewarding, triggering a consummatory state in the subsequent steps of retrieval. Shifting Appetite Hypothesis (right): Motivational state evolves dynamically across the retrieval sequence, with behavior-dependent transitions from appetitive to consummatory phases. A loop at the end reflects re-initiation of the sequence for multiple scattered pups. Color coding denotes hypothesized motivational state: pink indicates appetitive behaviors, yellow indicates consummatory. Diamonds represent decision points; rectangles represent actions.

- **Shifting appetite hypothesis**: Initially, the appetite is for contact with the pup, and after the first appetite has been satisfied, the second appetite is for the nest. In this case, the appetitive behaviors would be searching for and approaching the pup, followed immediately by the consummatory action of picking up the pup. Next, the appetitive behavior would be for the dam to carry the pup to the nest, followed by the consummatory action of dropping the pup into the nest. In this case, picking up the pup, and dropping it into the nest are both considered the instinctual response of the dam, where the dam would remain restless until all pups are located and placed into the nest.

3. Networks & circuits of maternal behavior

A number of studies have shown that disruptions such as lesions, inactivation, or ablation to the MPOA result in immediate loss of maternal behaviors including retrieval, nestbuilding, and nursing behaviors in dams, as well as virgin rodents (Fleming et al., 1983; Franz et al., 1986; Gray and Brooks, 1984; Jacobson et al., 1980; Kohl et al., 2018; Lee et al., 2000; Numan, 1974; Numan et al., 1977, 1988, 1990; Numan and Callahan, 1980; Wu et al., 2014). While the MPOA is critical for several maternal behaviors, its projections to the VTA and PAG highlight the distinct yet interconnected neural networks that regulate different phases of caregiving (Fig. 2). Understanding these networks not only clarifies the neurobiological basis of maternal behavior but also provides insight into the evolutionary and adaptive significance of these behaviors. Based on these studies, projections to the VTA are hypothesized to regulate classical appetitive behavior and projections to the PAG to regulate classical consummatory behaviors.

MPOA neurons project to the VTA (Fang et al., 2018; Geisler and Zahm, 2005; Simerly and Swanson, 1988), making predominantly inhibitory contacts onto non-DA neurons, thereby indirectly activating

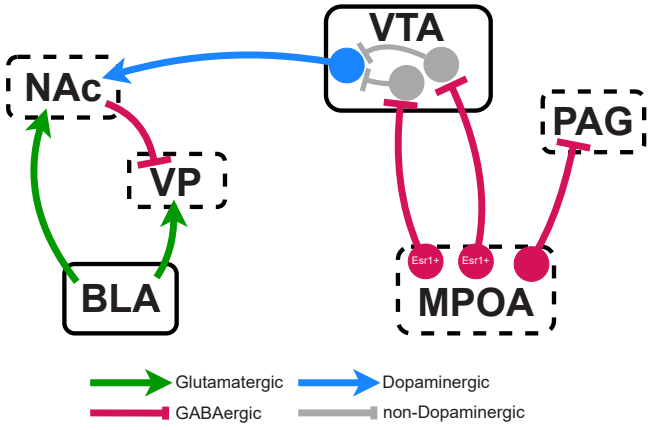

Fig. 2. Neural circuits underlying maternal motivation and caregiving behavior. This schematic illustrates key brain regions and neurotransmitter pathways involved in maternal behavior. The medial preoptic area (MPOA) projects to the ventral tegmental area (VTA) though $MPOA^{Esr1+}$ GABAergic (magenta) neurons that synapse on non-dopaminergic cells (gray), and potentially other yet to be determined mechanisms. The MPOA also projects to the periaqueductal gray (PAG) via GABAergic pathway. The VTA sends dopaminergic (blue) projections to the nucleus accumbens (NAc), which in turn sends GABAergic (magenta) projections to the ventral pallidum (VP). The basolateral amygdala (BLA) provides glutamatergic (green) input to both the NAc and VP. Gray arrows indicate projections that are less well-characterized or involve mixed neurotransmitter signaling. Outlines of brain regions indicate their place in classic appetitive vs consummatory networks, with consideration given to conflicting results. Solid outlines (VTA, BLA) are established as exclusively appetitive regions. Dashed outlines (MPOA, PAG, NAc, VP) indicate brain regions that may be involved in both appetitive and consummatory behaviors. In the classic appetitive vs consummatory brain networks the MPOA-VTA-NAc network in appetitive and MPOA-PAG is consummatory.

the mesolimbic dopamine system. VTA DA neurons project to NAc, releasing DA in the NAc (Dobi et al., 2010), and activating GABAergic medium spiny neurons that project to the ventral pallidum (VP) (Meredith, 1999; L. Zhou et al., 2003). Based on this circuit architecture and the effects of drug injections in various regions in the circuit, it has been hypothesized that the net effect of increased activity in the MPOA projections to VTA is to disinhibit VP, making it more sensitive to sensory pup cues (Numan, Numan, Pliakou, et al., 2005; Numan, Numan, Schwarz, et al., 2005; Numan and Woodside, 2010).The VTA has been considered an exclusively appetitive region, because chemical inactivation of VTA DA neurons (Numan et al., 2009), and lesions (Numan and Smith, 1984) disrupted pup retrieval but not nursing behaviors. Inactivation of VTA through optogenetic silencing of DA neurons disrupts pup retrieval, however that study did not investigate potential disruptions to nursing (Xie et al., 2023). Interestingly, when VTA is modified by other methods, such as oxytocin agonists (Pedersen et al., 1994), or GABA agonists (Numan et al., 2009), nursing patterns are disrupted, indicating that VTA DA neurons are essential in this circuit.

While past work highlights the projection from MPOA to VTA as an important part of the appetitive behavior network (Numan, 2020; Stolzenberg and Numan, 2011), it remains unclear that a single cell type or neurotransmitter is responsible for this connection. In the latter publication, the authors hypothesized that contributions could come from MPOA neurons releasing glutamate, GABAergic MPOA neurons releasing neurotensin, or a multisynaptic circuit where GABAergic MPOA neurons inhibit the non DA VTA cells that would normally provide GABAergic inhibition to DA VTA cells (Fang et al., 2018; Numan, 2020). The multisynaptic circuit was shown to arise from neurons in the MPOA that express the gene that codes for ER1α estrogen receptors (*Esr1*). Inactivation of the $MPOA^{Esr1}$ neural population revealed them to be essential for normal retrieval behavior (Fang et al., 2018).

Several pieces of evidence suggest that oxytocin may regulate involvement in the mesolimbic dopamine pathway during maternal behavior. First, oxytocin (OXT) promotes maternal behavior (retrieval and nursing) in the MPOA and VTA (Pedersen et al., 1994). Second, OXT producing neurons from the paraventricular nucleus of the hypothalamus (PVN) directly synapse onto VTA DA neurons, enhancing their activity and increasing prosocial behaviors (Beier et al., 2015; Hung et al., 2017; Xiao et al., 2017). Finally, oxytocin receptor (OXTR) expressing VTA DA neurons release DA into the NAc, which mediates maternal behaviors like licking and grooming pups (Melis et al., 2007; Peris et al., 2017; Shahrokh et al., 2010). While DA release in NAc alone is involved in the proposed appetitive behavior circuit, OXTR activation in NAc also increases social approach which interestingly is another appetitive behavior (Rincón-Cortés and Grace, 2020). Further research is needed to determine which neurotransmitters and cell types are responsible for different aspects of maternal behavior.

The VTA DA projection into NAc is a central to appetitive maternal behavior and reward processing, broadly. Prior studies that decreased or abolished DA activity in NAc with antagonists or chemical lesions disrupted maternal behavior. (Alsina-Llanes and Olazábal, 2024; Keer and Stern, 1999; Numan, Numan, Pliakou, et al., 2005; Silva et al., 2003). Yet, lesions to NAc itself have yielded conflicting results. Some studies show that electrolytic lesions (Lee et al., 1999), NDMA lesions (Alsina-Llanes and Olazábal, 2024), bilateral infusions of muscimol (Numan, Numan, Schwarz, et al., 2005) to NAc, or electrolytic lesions to the NAc core (Li and Fleming, 2003) have little no effect on pup retrieval or nursing behaviors. Electrolytic lesions to the NAc shell did, however, disrupt pup retrieval but not consummatory behaviors (nursing, grooming) (Li and Fleming, 2003). Other studies made electrolytic lesions in the dorsomedial NAc, resulting in impaired nursing and maternal behaviors (Smith and Holland, 1975), or bilateral electrolytic lesions reduced pup grooming and crouching (to nurse). Bilateral lesions of NAc did not alter the dam's ability to lever press for pups (Lee et al., 2000). Manipulations of DA in the dorsal striatum (DS) generally supports the hypothesis that this circuit exclusively drives appetitive

motivation; disrupting DA signaling the DS resulted in deficits for pup retrieval but not licking and grooming or nursing (Henschen et al., 2013).

One major output of the striatal medium spiny neurons of NAc is the VP of the basal ganglia, an important region for eliciting the motor response of appetitive behavior (Geisler and Zahm, 2005; Heidenreich et al., 1995; Meredith, 1999; Mogenson et al., 1993; L. Zhou et al., 2003). Interestingly, there is also evidence of opposing actions between GABAergic and glutamatergic VP neurons in influencing motivated behaviors. The GABAergic neurons are important for approach toward a reward, and the glutamatergic cells suppress movement in threatening situations (Ito and Hayen, 2011). In the VP, muscimol infusion interrupted pup retrieval and lowered nursing durations (as compared to muscimol infusion in NA), indicating changes to both appetitive and consummatory behaviors (Numan, Numan, Schwarz, et al., 2005).

The basolateral amygdala (BLA) is a more recently proposed addition to the appetitive brain circuit (Numan, 2020). Neurons in the BLA send glutamatergic projections to the NAc and VP independently from MPOA (Fuller et al., 1987). The ipsilateral BLA-NAc projections were identified as the source of D1-MSN activation in rewarding interactions that increase the likelihood of an appetitive response; this remains untested for pup retrieval or other maternal behaviors (Tian et al., 2024). Interestingly, different populations of neurons in the BLA were also recently reported to exhibit responses to pup odor and contact (Nowlan et al., 2024).

The consummatory network is proposed to centrally involve MPOA projections to PAG, however the evidence to support the PAGs role in nursing and licking and grooming behaviors this is less straightforward than the appetitive circuit studies (Stolzenberg and Numan, 2011). Notably, previous studies by Lonstein have shown that PAG is important for nursing (Lonstein et al., 1998; Lonstein and Stern, 1997a, 1997b, 1998). In these experiments, lesions to cPAG, but not the rPAG were responsible for disruption of arch back (kyphosis) and increase of supine nursing (Lonstein and Stern, 1998). Lonstein reported that the nursing deficits induced by prepartum lesions to cPAG resulted in lower litter weights, and increased maternal aggression (Lonstein et al., 1998). These same studies also observed that when the rPAG was lesioned, it disrupted retrieval, and dams had difficulty dropping the pups from their mouth at the end of a retrieval event, indicating that the PAG may have overlap with appetitive behaviors as well (Lonstein and Stern, 1998). These findings emphasizes the PAG's role in integrating both consummatory *and* appetitive aspects of maternal behavior, further blurring the lines between these categories using the classic definitions (Lonstein et al., 2015). A different study focused on the effects of MPOA lesions on PAG cFos activity where maternal behavior was associated with an increase in cFos in the cPAG, but lesions to MPOA/vBST, which putatively disables the MPOA-PAG consummatory circuit, also resulted in increased cFos expression in the cPAG. Moreover, maternal behavior resulted in indistinguishable cFos staining in animals with NDMA-induced lesions and controls (Stack et al., 2002). It is possible that the MPOA projections to PAG in maternal behavior are GABAergic (Láng et al., 2024); prior studies show that GABAergic MPOA-PAG circuit promotes maternal grooming (Dimén et al., 2021) and inhibiting the glutamatergic MPOA-PAG circuit promotes pup retrieval (Zhang et al., 2021). While further studies are warranted to better understand which neurotransmitters and cell types are involved in this circuit, these discrepancies suggest that the relationship between the MPOA and PAG in regulating maternal behavior is multifaceted and may involve yet unidentified neural mechanisms.

4. Dopamine dynamics of maternal behavior

Although anatomical studies have mapped essential circuits for maternal behaviors, less is known about how these circuits are modulated during the unfolding of caregiving sequences. Given that maternal behaviors may involve shifting appetitive and consummatory drives, it is essential to explore how dopamine dynamics contribute to transitions between motivational states during caregiving.

Maternal behavior is not only essential for offspring survival but also intrinsically rewarding for the mother (Rincón-Cortés and Grace, 2020). The mesolimbic DA system, a key mediator of reward and reinforcement learning, plays a central role in maternal motivation. While DA's role in reward processing and reward prediction error (RPE) has been extensively studied in other contexts such as learning, addiction, and disease (Chang et al., 2017; Deng et al., 2023; DiCarlo et al., 2019; Schultz, 2016; Schultz et al., 1997; Springer and Nawrot, 2021; Steinberg et al., 2013; Watabe-Uchida et al., 2017), the precise mechanisms by which it shapes maternal behavior remain an area of active investigation. Below we discuss DA's involvement in maternal reward processing, highlighting how rewarding interactions with offspring and RPE signals reinforce caregiving behaviors.

In vivo studies including fiber photometry, voltammetry, and microdialysis have shown that DA activity is involved in multiple steps of maternal behavior including pup retrieval, grooming and nursing (Afonso et al., 2008, 2009; Borland et al., 2019; Champagne et al., 2004; Hansen et al., 1993; Shnitko et al., 2017; Song et al., 2016; Xie et al., 2023). Pups themselves are highly rewarding stimuli (Fleming et al., 1994; Hauser and Gandelman, 1985; Swart et al., 2023; Wilsoncroft, 1968), to such a degree that dams prefer interacting with pups over cocaine at postpartum day 8 (Mattson et al., 2001). Notably, this preference strengthens with increasing maternal experience, suggesting a learning-dependent process (Afonso et al., 2008; Shnitko et al., 2017).

The mesolimbic dopamine system, which includes projections from the VTA to the NAc, plays a central role in reward processing. Rapid fluctuations in DA release from the VTA are observed in in various learning contexts, including social and maternal behaviors (Cai et al., 2020; Deperrois et al., 2019; Heymann et al., 2020; Robinson et al., 2003). One leading framework for the interpretation of dopaminergic activity in the VTA is the concept of RPE. RPE is defined as the expected reward minus the reward received, and this computed value is an important component of most reinforcement learning algorithms (Schultz et al., 1997; Watabe-Uchida et al., 2017). Putative VTA DA neurons have been shown repeatedly to signal this quantity in many circumstances and behavioral paradigms (Mininni et al., 2018). An alternative framework, **F**lexibly **L**earned **E**rrors in **E**xpected Reward (FLEX), proposes that DA signals emerge through plastic, experience-dependent representations of time. Unlike fixed-time assumptions in classic RPE models, FLEX accounts for gradual and cue-specific development of dopaminergic responses (Cone et al., 2024). This model may better explain dopamine dynamics in contexts like maternal behavior, where cue-reward timing is learned, however there have not yet been any experiments to test this theory.

Several recent studies investigated whether a similar prediction error could be found for social reward. The first study found that DA signals were evoked by social contact, and that showed using a social instrumental task that responses were negative to omission of an expected social encounter, thus conforming to RPE (Solié et al., 2022). Xie et al. (2023) examined the dynamics of VTA DA neuronal responses to pup retrieval and concluded that phasic bursts of VTA DA neurons during pup retrieval also reflected social RPE, reinforcing retrieval with the reward of encountering a pup (Xie et al., 2023). One key question was whether DA was involved in the entire series of actions required for pup retrieval, or primarily one step, and Xie et al. observed that optogenetic silencing of the VTA DA neurons at pup contact disrupted future retrieval attempts. The VTA is also sensitive to social and hormonal cues that modulate maternal motivation. For instance, OXT release from the PVN enhances VTA DA neuron activity, promoting social reward and maternal care (Borland et al., 2019; Song et al., 2016). Conversely, social isolation during the postpartum period leads to hyperexcitability of VTA DA neurons projecting to the prefrontal cortex (PFC), which may disrupt maternal behavior (Musardo et al., 2022). These findings highlight the importance of the VTA-NAc pathway in integrating social and

hormonal signals to regulate maternal motivation.

DA release in the NAc has been extensively studied in maternal behavior, corroborating the intrinsically rewarding quality of pups established behaviorally (Afonso et al., 2008, 2009; Dai et al., 2022; Shnitko et al., 2017; K. Zhou et al., 2022). Interestingly, the NAc core (NAcC) and shell (NAcSh) appear to serve complementary functions. While the NAcSh requires DA for motivated behaviors like pup approach and retrieval (Dai et al., 2022; Keer and Stern, 1999), the core seems to encode RPE (Saddoris et al., 2015), suggesting that the NAc integrates both learning and motivational signals. DA offers an interesting connection between appetitive and consummatory behaviors, where it is believed to help transition from appetitive to consummatory via the mesolimbic pathway (Numan, 2020). Interestingly, there is evidence that NAc is implicated in both appetitive and consummatory behaviors. DA antagonists impair pup retrieval and licking and grooming, while enhancing nursing behavior of lactating rats (Keer and Stern, 1999), raising additional questions. Does increased nursing result from a decreased drive to perform appetitive behaviors like retrieval, due to reduced DA-mediated motivation? Or is DA acting more directly within the NAc to suppress nursing circuits, such that its loss disinhibits consummatory behavior? These questions highlight the complexity of DA's role in maternal behavior and suggest that the NAc may serve as a critical node for integrating both appetitive and consummatory processes, and for dynamically balancing these behaviors based on motivational state and circuit-level modulation.

Despite these advances, several questions remain. What are the precise circuit mechanisms that shape maternal motivation over time, and how do individual differences in DA signaling contribute to variations in maternal behavior? Additionally, how do disruptions in these circuits contribute to postpartum mood disorders, where maternal motivation is often impaired? Future research using advanced techniques, such as cell-type-specific recordings and perturbations of multi-region circuit manipulations will be critical for addressing these questions and elucidating the neural mechanisms underlying maternal reward processing.

5. Downstream consequences of DA

Rodent models provide valuable insights into the neural mechanisms of maternal behavior, but species differences must be considered. The majority of the studies discussed in this paper include rats, and there are many investigating mice. It should be noted that rats require several days of pup exposure or hormonal intervention for maternal behaviors to emerge (Cohen and Bridges, 1981; Wiesner and Sheard, 1933), whereas virgin mice can exhibit pup retrieval without such interventions. While lactating dams outperform virgin female mice in pup retrieval tasks, including t-tests and straight alley retrievals (Gandelman et al., 1970), the social transmission of maternal behavior has been observed in virgin mice through visual and observational learning from experienced dams, with PVN OXT neuron activation playing a key role (Carcea et al., 2021). Hormonal state is well known to influence maternal motivation in mice, but maternal behavior persists even in the absence of circulating ovarian hormones. Studies show that ovariectomized (OVX) mice continue to find pups rewarding and engage in pup retrieval (Hauser and Gandelman, 1985). OVX virgin mice, as well as OVX aromatase knockout virgins with prior pup experience, continue pup retrieval (Stolzenberg and Rissman, 2011). This suggests that maternal motivation is not exclusively hormonally driven and may involve experience-dependent mechanisms in mice.

Receptor interactions play an essential role in maternal behavior. Heterocomplex formation between dopamine and oxytocin receptors has been observed in key maternal brain regions and could play a role in behavior. Evidence suggests facilitatory interactions between dopamine D2 and oxytocin receptors in the amygdala (de la Mora et al., 2016; Hernández-Mondragón et al., 2023), potentially contributing to anxiolytic effects relevant to maternal behavior. OXTR-D1 interactions can also be considered, especially in NAc, as OXTR signaling in NAcSh is necessary for the onset of maternal behavior (Witchey et al., 2024). Interestingly, the co-release of DA and OXT in the NAc has been demonstrated in prairie voles, further supporting a role for these heterocomplexes in social bonding (Romero-Fernandez et al., 2013).

Finally, DA plays a role in additional processes beyond reward and maternal care that must be considered when interpreting results and designing future experiments. DA is also involved in motor control and invigoration (Barter et al., 2015; Bova et al., 2020; da Silva et al., 2018; Hughes et al., 2020; Panigrahi et al., 2015), most well-known for its role in Parkinson's disease (Z. D. Zhou et al., 2023).

6. Future approaches

While significant progress has been made in understanding the neural mechanisms underlying maternal behavior, several critical questions remain. Future efforts should aim to refine our conceptualization of maternal behaviors, expand methodological approaches, and explore the branches of the proposed maternal behavior network that are still uncertain.

6.1. Reevaluating pup retrieval language

The "classic" designation of pup retrieval as an appetitive behavior may warrant reconsideration. Craig's definition of consummatory action emphasizes that these behaviors fulfill an emotional need and result in satisfaction. This framework lays foundation for further investigation of the reward value and dopamine dynamics associated with maternal behavior. Pup retrieval is particularly interesting because it could be viewed as a sequence of events or a single event. Although many studies treat pup retrieval as a single appetitive event, we propose considering this behavior as a series of discrete actions, pup search, pup approach, pup contact, lifting the pup, carrying the pup, dropping the pup, and deciding whether to retrieve another pup, or care for the last retrieved pup. Each of these steps may involve appetitive processes, but some stages may be more consummatory, a distinction that needs further exploration. It is also critical to consider species-specific factors when working with rodents, who typically birth litters of pups, requiring them to care for multiple pups at once, balancing the needs of the entire litter.

Van Hemel's (1973) work strongly suggests that pup retrieval is rewarding, and as a satisfying reward it should be considered consummatory. Van Hemel's findings use the multi-step paradigm to deconstruct the series of events leading up to pup retrieval and show that pup retrieval is more rewarding than pups alone. Xie et al.'s (2023) study indicates that DA activity in the VTA peaks when the mouse contacts and lifts the pup during retrieval, suggesting that this phase of the behavior may be inherently rewarding. Importantly, Xie also used an assay to isolate individual steps of pup retrieval, where pup approach is disrupted by a physical barrier (door) to separate specific steps in a cued retrieval task. This cued retrieval task provided evidence that VTA DA reflects RPE, and how disrupting the temporal flow of pup retrieval affects motivational and reward signaling.

Together, these studies emphasize the critical role of timing and sequencing in pup retrieval, using physical barriers to break the behavior into distinct phases. Further investigation is needed to determine whether pup retrieval should be considered 1) a consummatory action, 2) a multi-step sequence with shifting appetitive and consummatory components, or if 3) its rewarding properties are distinct from its motivational processes. Future studies should employ optogenetic manipulations to selectively inhibit different phases of pup retrieval and use barriers (such as timed doors, levers, or obstacles) to interrupt the canonical steps of pup retrieval (locating, approaching, lifting, carrying, or dropping the pup into the nest).

6.2. Tools for monitoring dopamine activity

To address questions about the temporal dynamics and rewarding properties of pup retrieval, increasingly sophisticated tools are needed to monitor dopamine activity with high spatial and temporal precision. Recent advances in neurotechnology have enabled real-time measurement of dopamine fluctuations during distinct phases of maternal behavior. Genetically encoded dopamine sensors such as dLight (Patriarchi et al., 2018) and $GRAB_{DA}$ (Sun et al., 2020), paired with fiber photometry or microendoscope imaging, allow the ability to capture dopamine dynamics across different stages of maternal care, from initiation to maintenance. Future experiments should leverage these tools to dissect dopamine activity at specific steps of pup retrieval, asking whether dopamine release shifts dynamically within a single retrieval sequence, across successive retrievals of multiple pups, or with increasing maternal experience over days. Key questions for future studies include: Does dopamine release shift dynamically across successive retrievals within a single session? Does DA release differ between the first and last pup retrieved from a scattered litter? Which steps of pup retrieval (or other maternal behaviors) trigger DA activity in different brain regions? Answering these questions may help refine our understanding of how maternal motivation and learning interact at the neural level.

6.3. Circuit-level mechanisms of maternal motivation

While the MPOA-VTA-NAc circuit is well established as a key regulator of maternal motivation, several aspects remain unresolved. The specific cell types and neurotransmitters mediating MPOA-VTA communication are still under debate, with hypotheses ranging from glutamatergic, GABAergic, neurotensinergic, to oxytocinergic pathways (Numan, 2020). Future studies should consider cell-type-specific manipulations to dissect the precise contributions of these neurotransmitter systems to maternal motivation.

Many other branches of the maternal behavior network also warrant deeper investigation. The BLA-NAc, MPOA-NAc-VP, and MPOA-PAG circuits have all been implicated in maternal behavior, however additional research is needed to better understand how the circuits function, which cell types or neurotransmitters are involved, and the role they may play in how maternal behaviors are reinforced and maintained over time. Exploring how these circuits interact with other networks, such as the mesolimbic dopamine reward system, may reveal how maternal motivation is shaped not only by biological factors but also by a broader neural network that underpins motivation and decision-making. Future research should also investigate whether similar circuits are involved in caregiving behaviors across species, and how the number of offspring (singleton vs litter) influences activation of these circuits, potentially altering maternal motivation across different species and contexts.

Within circuit-level analyses, the molecular dynamics of receptor interactions also warrant closer examination. Heterocomplexes between dopamine and oxytocin receptors have been implicated in social bonding and maternal behaviors, but their precise function remains poorly understood, making them a promising subject of future studies. In the amygdala, D2-OXTR receptor complexes have been shown to modulate anxiety-related behaviors (de la Mora et al., 2016; Hernández-Mondragón et al., 2023), which may have implications for maternal motivation and stress responses. Additionally, OXTR signaling in the NAcSh is necessary for the onset of maternal behavior (Witchey et al., 2024), suggesting that DA-OXT interactions may directly influence maternal reward processing. Future studies using fluorescence or bioluminescence resonance energy transfer (FRET or BRET) based receptor interaction assays, proximity ligation assays (PLA),or cryo-EM could help elucidate how these receptor complexes function at a molecular level. Understanding these mechanisms is particularly important given that disruptions in in DA-OXT signaling have been implicated in postpartum mood disorders like dysphoric milk ejection reflex (D-MER)), where abrupt decreases in dopamine during nursing trigger emotions of dysphoria in mothers (Deif et al., 2021). This research may have important translational implications for developing targeted treatments for maternal mental health conditions that are often underdiagnosed or misattributed, such as D-MER and postpartum depression (PPD).

6.4. Translational implications: from rodent models to human maternal behavior

Given the emerging evidence linking DA-OXT signaling disruptions to maternal mood disorders like D-MER, it is critical to consider how these mechanistic insights from rodent models may translate to human maternal behavior and mental health. While rodent models have provided crucial insights into maternal motivation, species specific differences must be carefully considered when translating findings to humans. Unlike rats, which require days of pup exposure or hormonal priming to exhibit maternal behaviors (Cohen and Bridges, 1981; Wiesner and Sheard, 1933), virgin mice and humans often display caregiving behaviors without hormonal intervention. Additionally, social transmission of maternal behavior has been observed in mice, with PVN oxytocin neurons playing a key role in the observational learning of pup retrieval (Carcea et al., 2021). Further research should explore how these findings translate to humans, particularly in the context of PPD and D-MER. The VTA-NAc mesolimbic DA system is well known for its role in motivation and reward in both rodents and humans, as well as major depressive disorders, making this circuit a promising target for future PPD studies (Admon and Pizzagalli, 2015; Post and Leuner, 2019). Moreover, longitudinal studies in humans using fMRI and PET imaging could assess how changes in reward-related brain activity correlate with shifts in maternal behavior over time. Are differences in striatal dopamine release associated with variations in maternal sensitivity or bonding? Do species with litters versus single offspring engage in reward circuits differently during caregiving? Can we recapitulate these depressive states in mice to better understand the brain regions and neurotransmitters involved in, so we can develop better treatments? Addressing these questions could have significant clinical and societal implications.

7. Conclusion

Maternal behavior is a dynamic process shaped by experience, external cues, neural circuits, and motivational states. Although major progress has identified key brain regions such as the MPOA, VTA, NAc, PV, PAG, and BLA, critical questions remain. Integrating refined behavioral classifications, temporally sensitive recording techniques, and cell-type specific circuit manipulations will deepen our understanding of maternal behavior across multiple levels of analysis.

Reframing maternal motivation as a dynamic, evolving sequence, rather than a static state, opens new directions for both basic science and clinical research. Future studies should integrate real-time measurements of neuromodulatory activity with high-resolution behavioral analysis to capture how motivation shifts within and across caregiving episodes. This framework may reveal general principles of motivated behavior, better inform the biological basis of caregiving across species and guide more effective strategies to support maternal mental health.

Ultimately, advancing a dynamic view of maternal caregiving is not only critical for neuroscience, but also essential for shaping public health policies that protect maternal care, support women's health research, and recognize caregiving as foundational to societal well-being.

Author contributions

Conceptualization, K.R.D.; writing – original draft, K.R.D.; writing – review and editing, all authors; supervision and funding acquisition, S.

D.S.

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