



Research report

Parents induced- conditioned place preference and the neuronal expression of oxytocin and tyrosine hydroxylase in preweaning female pups



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HIGHLIGHTS

- ICR mice pups established CPP when conditioned with their mother or father alone.
- ICR mice pups failed to show any preference in mother versus father conditioning.
- The pups showed more TH-IR neurons in the VTA when conditioned with their mother or father alone.
- The pups showed more OT-IR neurons in the SON when conditioned with their mother rather than father.
- The pups showed higher levels of OT and TH in mother versus father conditioning.

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ABSTRACT

Parents-offspring bonding is critical for development of offspring in mammals. While it is known that pups stimuli provide rewarding effects on their parents, few studies have assessed whether parental stimuli serve as a reinforcing agent to their pups, and what the neural mechanisms underlying this reward process may be. In addition to maternal care, male ICR mice display pairmate-dependent parental behavior. Using the conditioned place preference (CPP) paradigm, we examined the effects of maternal and paternal conditioning on the postnatal day 17–21 female ICR mice pups, and compared the expression of oxytocin (OT)- and tyrosine hydroxylase (TH)- immunoreactive (IR) neurons. We found that the pups established dam- or sire- induced CPP when using mother conditioning (MC) or father conditioning (FC) alone. However, the pups failed to show any preference when using mother versus father conditioning (MFC). Compared to the control group, the MC and MFC groups displayed more OT-IR neurons in the supraoptic nucleus and more TH-IR neurons in the ventral tegmental area (VTA). The FC group showed more TH-IR neurons in the VTA compared to the control group, but there were no significant differences in OT-IR neurons. These findings indicate that female ICR mice pups may establish mother- or father- induced CPP. The underpinnings of preference for parents are associated with the activity of VTA dopaminergic neurons, and the preference of pups for mother in particular appears to be associated with OT levels.

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1. Introduction

Parental care in mammals includes providing food, warmth, shelter and protection to the offspring, and is a crucial component

Abbreviations: CPP, conditioned place preference; DA, dopamine; FC, father conditioning; ICR, Institute of Cancer Research; MC, mother conditioning; MFC, mother versus father conditioning; MPOA, medial preoptic area; OT, oxytocin; PVN, paraventricular nucleus; SN, substantia nigra pars compacta; SON, supraoptic nucleus; TH, tyrosine hydroxylase; VMH, ventromedial nucleus of hypothalamic; ZI, zona incerta.

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of mammalian fitness [1]. In addition, parents are a rich source of sensory and emotional stimulation that plays an important role in the neurobiological and behavioral development of the offspring [2–6]. The mother and the pup maintain close physical proximity throughout the preweaning period [7], where pups provide natural rewards that have some intrinsic value to the mother. The pup-exposure, regardless of length, is sufficient to support strong maternal motivation [8]. In rats, the rewarding value of pup stimuli is dependent upon full interaction between the mother and her pups [9,10], and pups can become reinforcing to a mother throughout the entire postpartum period [10,11]. In the monogamous mandarin vole (*Microtus mandarinus*), tighter father-pup attachment is established where pups become a reinforcer to fathers [12].

The CPP paradigm is widely used to explore the reinforcing effects of natural and pharmacological stimuli [13]. Bolanos et al. posited that reward processes are functionally mature in preweanling rats (at least by 10 days of age) [14]. For example, cocaine or morphine can induce conditioned place preference (CPP) in preweanling mice or rats [15,16]. Although there is strong evidence to support that pups provide a significant reinforcing effect on their parents, fewer studies have addressed whether the rewarding effects of father or mother are also available in preweanling pups. This parallel investigation about the parents' rewarding effects on the offspring would provide insights into parents–offspring bonding.

The oxytocin (OT) is a well-known neuropeptide that is produced by the hypothalamic paraventricular nucleus (PVN) and supraoptic nucleus (SON), and is implicated in parental behavior [17–19]. OT co-activates the dopaminergic circuits that are involved in motivation and reward, and can facilitate close social attachment and enhance the reward value of social interactions, leading to the formation of social-bonds between individuals [20–22]. The mesolimbic dopamine (DA) system is crucial for creating the motivation to seek rewards [23], and is also implicated in the expression of parental behavior [19,24,25]. Some studies indicate that different “prosocial” behaviors have similar neuroanatomical and neurochemical organization [26,27], pointing to the possibility of a common brain circuit underlying behaviors as diverse as infant and mother affiliation, juvenile play, sexual, and parental behaviors [27]. Thus, OT and DA could also play a role in mediating pup preferences for parents.

Male ICR (Institute of Cancer Research) mice display mate-dependent parental retrieval behavior only for their own biological pups [28,29]. This unique ability of the ICR sires contributes to the increased survival rate after reproduction and to the high level of social attachment and interaction [29]. Pup retrieval as a parental behavior is rare among laboratory mice that are not genetically monogamous [30,31]. This behavior is strain-specific to ICR mice, and is not observed in other mice strains such as C57BL/6 and BALB/c [29], making ICR mice a model for studying the reinforcing property of parents. Female ICR mice show superior learning and memory abilities than males [32]. Therefore, we used female ICR pups for our experiments. Our first objective was to determine whether parents have reinforcing effects on preweanling pups using the CPP paradigm. Next, we measured neuronal expression levels of OT and the tyrosine hydroxylase (TH), which is a rate-limiting enzyme for DA synthesis and an indicator of DA production, in pups that experienced mother or father conditioning.

2. Methods

2.1. Subjects

ICR mice were purchased from Ningxia Medical University Laboratory Animal Center (Yinchuan, China). The animals were housed in groups of four in polycarbonate cages (32 × 21.5 × 17 cm, length × width × height) and had ad libitum access to food and water. The colony room operated on a 12-h light/dark schedule (lights on at 0800 h) and was maintained at an ambient temperature of 23 ± 2 °C. Virgin females and males were paired, and females were checked daily for signs of labor 20 days after pairing. The day pups were born was denoted as postnatal day (PND) zero (day of birth = day 0). ICR mice were weaned at approximately 22–23 days. PND 17–21 female pups were used for present study. All animals were treated humanely according to guidelines approved by the Animal Care and Use Committee of Beifang University of Nationalities.

2.2. CPP test

The place preference apparatus consisted of two large compartments (34 cm × 25 cm × 32 cm, length × width × height) with different visual cues (gray walls or white-black striped walls) separated by a small middle compartment (11 cm × 25 cm × 32 cm, length × width × height). The middle compartment served as the acclimation compartment, with a door (7 cm × 9 cm, height × width) in the center of the base.

2.2.1. Pre-test

On the day prior to conditioning, PND 17 pups from different litters (n = 12) were tested to determine whether they had any innate individual preferences to either of the two lateral compartments. A pup was given free access to each decorated compartment, and the time spent in two lateral compartments was recorded for 15 min by a camera (Sony, HDR-XR260E) mounted 70 cm above the arena. Additionally, motor activity was simultaneously obtained by measuring the total frequencies of pups crossing the doors of the chambers. After each trial, the compartment was wiped cleaned using 70% ethanol. Pups showed no inherent preference for either compartment.

2.2.2. Conditioning with mother (MC)

Pups were conditioned in an alternate half-day design. In the morning, a pup (n = 14, each from different litters) cohoused with her mother for 1 h in one of the outer compartments; in the afternoon, the pup was placed alone in the opposite chamber. We followed this counter balanced sequence for 4 days. The pup therefore underwent four consecutive days of conditioning, where it was alternately reinforced with the mother or empty chamber for 1 h in the morning or afternoon. On the fifth day, the pup was given a 15 min test (post-test) without the presence of the mother.

2.2.3. Conditioning with father (FC)

A different subset of pups (n = 14, each from different litters) were alternately reinforced with their father or empty chamber. Conditioning sessions and post-test procedure were the same as the mother conditioning described above.

2.2.4. Conditioning with mother versus father (MFC)

To test for whether there is a difference in the rewarding strength of mother versus father cues, we compared the two reinforcing stimuli using another subset of pups (n = 16). Pups underwent four consecutive days of conditioning where they were alternately reinforced with dams or sires for 1 h in the morning or afternoon. On the fifth day, pups were given a 15 min post-test without the presence of dams and sires.

2.3. Tissue collection and immunochemistry

We used a different subset of conditioned pups for OT- and TH-immunoreactive (IR) neurons test. Pups were assigned to one of the four treatment groups: MC group (n = 6), FC group (n = 6), MFC group (n = 6), and the control (CK) group (n = 6), which received no dam or sire conditioning, where animals were exposed to each cue-decorated compartment for 1 h in an alternating sequence, matching the parameters for the treatment of the experimental group.

After post-test, animals were deeply anesthetized and perfused with 0.1 M phosphate buffer solution (PBS, pH 7.4) and 4% paraformaldehyde in 0.1 M PBS. The brain was removed, and placed in 4% paraformaldehyde overnight. Brains were immersed in 30% sucrose until saturated prior to dissection. Coronal sections (40 μm) were cut on a cryostat, and consecutive sections were collected in two vials containing 0.01 M PBS for immunostaining.

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