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The effects of fathering experience on paternal behaviors and levels of central expression of oxytocin and dopamine-2 type receptors in mandarin voles

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ABSTRACT

Mothers' brains change dramatically in response to the release of hormones related to pregnancy and labor; however, fathers' brains are also sensitive to the experience of paternal care. Thus, fathers with differing fathering experience may exhibit different behavioral responses towards pups. Using socially monogamous mandarin voles (*Microtus mandarinus*), effects of fathering experience on levels of paternal behavior as well as oxytocin (OT) and dopamine-2 type (D2) receptors in the nucleus accumbens (NaCC) and medial nucleus of the amygdala (MeA) were investigated. The obtained results showed that experienced fathers displayed more active paternal behaviors such as licking, retrieval, and nest building than new fathers; however, new fathers spent more time in inactive huddling than experienced fathers. Western blot analysis showed that new fathers had significantly higher levels of OTR, but lower levels of D2R compared to experienced fathers in the NaCC. Levels of OTR and D2R in the NaCC and MeA of new and experienced fathers changed with the age of pups. OTR levels in the NaCC of both new and experienced fathers significantly decreased in response to increasing age of pups. Levels of D2R in the NaCC of new fathers on postnatal day 7 (PND 7) were significantly higher than on PND1 and PND14, and levels of D2R in the NaCC of experienced fathers increased with the age of pups. OTR levels in the MeA of new fathers decreased with the age of pups. In contrast, OTR levels of experienced fathers significantly increased with the age of pups. The D2R level in the MeA of new fathers did not change significantly, while the D2R levels of experienced fathers increased with the age of pups. These data illustrate that fathering experience could increase the active components of parental care and alter the expression levels of OTR and D2R in a region- and time-dependent way.

1. Introduction

Previous studies reported the biological effects of prior reproductive experiences on maternal behaviors, including biochemical [1], epidemiologic [2,3], hormonal [3–5], and behavioral changes in female mammals [5–7]. For example, mothers' brains change considerably in response to the release of hormones related to pregnancy and labor [8]. Although males cannot experience pregnancy or lactation, paternal behavior can be facilitated via stimulation by the female during mating, via cohabitation with a pregnant mate, and in particular, via stimuli from pups. Such external stimuli may also activate neuroendocrine changes underlying paternal behavior [9]. Furthermore, fathers' brains are sensitive to and can be changed by the paternal care experience [10]. Thus, fathers with differing fathering experience may exhibit different behavioral responses towards pups.

Most of the previously reported behavioral studies focused on effects of mothering experience on maternal behavior. Previous studies found that mothering experience affected subsequent maternal behavior and offspring development via a process that could either involve learning or hormonal priming. For example, multiparous mothers have been reported to exhibit increased maternal responsiveness to young. This behavior is relatively stable across pre-weaning stages in comparison to that seen in primiparous mothers [11–13]. In addition, multiparous mothers retrieve their young more rapidly and successfully than primiparous mothers [14].

There is less known about the relationship between paternal parity and paternal care behaviors. Some lines of evidence suggest a species-specific effect of fathering experience on paternal care. For example, Hartung and Dewsbury reported significant effects of fathering experiences in Deer mice (*Peromyscus maniculatus*) in which second time

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fathers spent less time licking their pups than both the new paired males and first time fathers; however, no effects of fathering on parental behavior were found in white-footed mice (*P. leucopus*) [15]. In addition, Wang and Novak reported that the parental experience caused no significant effects on fathers in prairie voles [16]. Thus, effects of fathering experiences on paternal care may be species-specific. Therefore, an investigation is required in other species on whether paternal behavior is affected by fathering experience. Whether fathering experience affects paternal care differently across lactation periods also remains unclear.

Reproductive experience may affect brain activities and subsequently result in different parental behavior. The hormone oxytocin (OT) plays a central role during the process of parent-infant bonding via early parental care across a range of mammalian species, including rats, prairie voles (*Mirotus ochrogaster*), sheep, and rhesus macaques (*Macaca mulatta*) [17–20]. Level of central OT is positively correlated with levels of paternal care in mandarin voles (*Microtus mandarinus*) [21]. Pharmacological study also revealed an important role of dopamine in mediating paternal behavior [22]. The medial nucleus of the amygdala (MeA) and nucleus accumbens (NaCC) has been reported to be involved in the control of paternal behavior [23]. New fathers showed higher levels of dopamine-1 type receptors (D1R) and dopamine-2 type receptors (D2R) mRNA expression in the NaCC and higher oxytocin receptor (OTR) mRNA expression in the NaCC and MeA; D1R and D2R mRNA expression was reduced in the MeA compared to new paired males [24]. The change in mRNA expression levels in fathers either with or without fathering experience is only one mechanism that generates diversity in paternal behaviors at the transcript level. Changes in mRNA expression levels of a relevant gene and levels of protein transcribed and translated from the same gene were not always consistent in many previous studies [25]. Ultimately, only proteins translated from the mRNA originating from relevant genes can regulate paternal behaviors. Therefore, OTR and DR expression need to be explored at protein levels to further elucidate effects of reproductive experiences on functional OTR and dopamine receptor (DR) expression. Here, we hypothesize that the fathering experience itself could affect levels of paternal behavior possibly via alterations of OTR and DR levels in both the NaCC and MeA.

Variation in DR density in the NaCC has also been found to be associated with occurring variations in maternal care of rats [26]. Reproductive experience has been reported to reduce the activity of the hypothalamic dopaminergic system in female rats [27]. A considerable amount of work emphasized the role of two types of DA receptors for the expression of maternal behavior [28–31]. In addition, previous studies suggested D1R function to be more important for the immediate expression of maternal behavior and indicated that it does not substantially affect the formation of the memories of the maternal experience [28]. A previous study reported that the selective D1R antagonist SCH23390 only significantly decreased licking in postpartum dams [32]. Since pup retrieval and nest-building were not greatly disrupted [32] by this treatment, the effects of dopamine on other components of the maternal behavior are more likely mediated by D2R [28]. Thus, we predict that the fathering experience may affect paternal behaviors via changes in level of D2R in the NaCC and MeA.

The mandarin vole (*Microtus mandarinus*) is a monogamous rodent and fathers exhibit a high level of paternal care [33]. Therefore, the mandarin vole is an ideal animal model to investigate the impact of the fathering experience on paternal behavior and changes in the brains of fathers throughout the reproductive cycle. The goals of the current study were to answer: (1) whether the fathering experience affects the paternal behavior during postnatal periods in mandarin voles, and (2) whether the hormone OT and/or DR receptor binding densities in the NaCC and MeA differ between males that had different fathering experiences during different postnatal days (PNDs).

2. Materials and methods

2.1. Subjects

Male mandarin voles of the F2 generation with ancestors that originated from a wild population in Henan, China, were used as experimental animals. All subject animals were assigned to one of two age-matched groups at an age of 70 days: new fathers (NF) who were first-time fathers and experienced fathers (EF) who were fathers for the second time. Animals were maintained on a 14:10 light:dark cycle (light on at 2000 h) and were allowed free access to food (carrots and rabbit chow) and water. Animals were housed in polycarbonate cages (44 cm × 22 cm × 16 cm) containing cotton as nesting material. All procedures were in accordance with the guide for the care and use of laboratory animals of China and were reviewed by the institutional animal care and use committee at Shaanxi Normal University.

Males that were eventually assigned to the EF group were mated on or around day 70. Upon delivery (~day 95, depending on time of mating), litters were culled to two to three pups, thus providing equivalent postnatal stimulation to the fathers, and all pups were weaned on postnatal day 21. Ten to 14 days after the first litter was weaned, mates of the EF were confirmed to be pregnant again. Males were left undistributed until the second parturition of their mates, at ~160 days. At this time, litters were culled to two to three pups again and weaned on postnatal day 21 (at day 181).

Males from the NF group were housed together with a male sibling until they were paired with females and their first mating occurred around day 135. They were allowed to go through pregnancy undisturbed and had their litters culled to two to three pups at day 160. Consequently, paternal behaviors of EF and NF groups were scored at approximately 160 days of age to avoid age-related effects [16].

2.2. Experiment I: effects of fathering experience on paternal behavior

2.2.1. Subjects

The physical properties of pups as stimulus varied across postnatal periods [34]. The day of birth was considered the postnatal day zero (day of birth = day 0). After pup stimuli became available for the males, levels of paternal behaviors and OT/D2R receptors of fathers were measured at three different stages of pup development: On PND1 when the stomachs of pups were full of milk [35]; On PND 7, a visible pelage appeared in pups; On PND 14, pups had opened their eyes, were more self-sufficient, and began to walk stably [36]. Twenty adult males with different levels of fathering experiences (first-time fathers and second-time fathers) were used (n = 10 at different PNDs in per group).

2.2.2. Paternal behavior test

Paternal behavior was observed in the breeding cages and in the breeding room. Pups were raised entirely undisturbed, i.e. both parents lived together with their pups throughout the entire observation period except the conditions of the animals were checked every two days through removing some nest material on the top of the nest. The paternal behavior was videotaped at PND 1, PND7, and PND14 for a cumulative time of 30 min per day, consisting of three 10-min samples obtained daily during the following time blocks: 0600–0800 h, 1300–1500 h, and 2100–2300 h. The observation cage was equipped with a video camera on the roof before one hour of recording. To improve observation, before the behavioral recording, some nesting material was removed from the top of the nest, leading to a bowl-like nest, thus exposing parents and litter to the camera. We usually checked the condition of the animals in this way, so the animals were likely habituated to this type of interruption. Every effort was made to reduce the interruption of parents and litter. After the recording, the nest material was restored.

During each observation session, we recorded the time the male voles spent huddling with pups, retrieving pups, licking pups, and

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