

Effects of paternal deprivation in social rodents

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ABSTRACT. The article concerns the effects of paternal deprivation in social rodents (California mice, Mongolian gerbils, mandarin and prairie voles and degus) whose social organizations are characterized by a family-group lifestyle and biparental care. Paternal deprivation was found to have a dramatic effect on pup survival (e.g. in California mice), as well as negatively affect pair bonding and adult parental behavior in other social rodents. Paternal deprivation resulted in reduction of central expression of some steroid and neuropeptide receptors in offspring. Besides, paternal deprivation was found to alter the regional density as well as the homeostatic balance of distinct interneuron populations in an age- and brain region-specific manner; it also affects maturation of excitatory spine synapses in prefrontal cortical and limbic regions. The father-deprived individuals showed the behavioral differences resulted from altered brain circuits. As a result, cognitive and emotional competence might be essentially changed in father-deprived animals. These findings indicate the importance of paternal care and paternal bonding as a unique source of sensory and socio-emotional stimuli, which may protect the offspring from developing an increased vulnerability towards stress-related life events.

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Влияние отсутствия самца на его потомство у социальных видов грызунов

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РЕЗЮМЕ. В статье рассматривается влияние депривации, связанной с удалением самца перед рождением детенышей, на потомство у социальных видов грызунов, для которых типичны устойчивые парные связи и совместная забота о детенышах: калифорнийский хомячок, монгольская песчанка, китайская и прерийная полевки, а также дегу. Установлено, что отсутствие самца-родителя может быть критическим для выживания потомства (как, например, у калифорнийских хомячков) и негативно влиять на формирование парных связей и родительского поведения взрослых особей. В результате депривации в головном мозге детенышей снижалась экспрессия рецепторов некоторых половых стероидов и нейропептидов, а также изменялась локальная плотность различных популяций нейронов (в зависимости от конкретных мозговых центров и возраста особей) и нарушался их гомеостатический баланс. Помимо этого, депривация влияла на созревание возбуждающих синапсов нейронов в префронтальной коре и структурах лимбической системы. В итоге, у детенышей, воспитанных самками в отсутствие самца-родителя, обнаруживались отклонения в поведении, обусловленные изменениями функциональных связей в головном мозге. Это негативно отражалось как на когнитивных способностях, так и на эмоциональной устойчивости потомства. Результаты проведенных экспериментов указывают на важность отцовской заботы как уникального источника сенсорных и социально-эмоциональных стимулов, которые защищают потомство от повышенной уязвимости в стрессовых ситуациях.

КЛЮЧЕВЫЕ СЛОВА: грызуны, совместная забота о потомстве, влияние отсутствия самца.

Introduction

Numerous studies on rodent parental behavior have primarily focused on maternal behavior, with little research directed at observing paternal behavior. Paternal care, though rare among mammals, is routinely displayed by not numerous social or biparental rodent species, i.e. species with long-lasting pair bonds and a family-group lifestyle (Eisenberg, 1966; Dudley, 1974a; Hartung & Dewsbury, 1979; McGuire & Novak, 1984; Gromov, 2011a, 2013, 2020). In family-groups, both mothers and fathers engage in direct care of offspring; moreover, paternal care plays a role as important as maternal care in the development of offspring providing warmth, tactile stimulation and protection (Dewsbury, 1985; Kentner *et al.*, 2010; Gromov, 2011b, 2013, 2020), and having caring father around may increase chances of survival for offspring (Gubernick *et al.*, 1993; Gubernick & Teferi, 2000).

Depending on the species, different components of male experience as well as different exogenous cues are involved in the organization and activation of paternal behavior. Specifically, the early social environment in terms of the presence or absence of the father in the natal nest plays a critical role in leading to divergent developmental pathways due to its influence on the adult brain and behavior. The influence of the early social environment on behavioral development is found to be a long-term, continuous, and complex process. In other words, father-offspring interaction during the neonatal period is essential to establishment of future behavioral patterns, and this effect is both constant and intense during the entire developmental period of the offspring (Cushing & Kramer, 2005). In particular, the results of artificial rearing and cross-fostering of infants in prairie voles (McGuire, 1988; Roberts *et al.*, 1998; Gonzalez *et al.*, 2001), as well as the experiments with Mongolian gerbils (Gromov, 2009) showed that participation of males in rearing their offspring is the important factor of subsequent development in individuals of the same sex of the 'careful father' behavioral stereotype that is so typical of many rodent species with a family-group lifestyle. Moreover, additional tactile stimulation of infants due to pup-directed licking and grooming promotes reinforcement of social bonds and peaceful relationships in family groups (Gromov, 2013, 2020).

Parental care is shown to be an extremely important early environmental factor that influences both behavioral and neuroendocrine development of offspring (Ahern & Young, 2009; De Jong *et al.*, 2009; Ahern *et al.*, 2011; Bales & Saltzman, 2016; Feldman *et al.*, 2019; Gromov, 2020). Several hormones, including steroids (testosterone, estradiol, progesterone) and neuropeptides (prolactin, vasopressin, oxytocin), are involved in the onset, the maintenance, or both the onset and the maintenance of parental behavior, and paternal care as well. Neuropeptides, especially oxytocin, are also involved in the establishment and maintenance of pair bonds, which are typical of socially monogamous species (Insel & Young, 2001). Steroid hormones and neuropeptides primarily affect specific brain structures,

especially of the limbic system, including the anterior and ventromedial hypothalamus, the bed nucleus of the stria terminalis, lateral septum, the medial preoptic area of the hypothalamus, the amygdala, and some other ones where there are many receptors of steroid hormones as well as oxytocin and vasopressin receptors (Numan & Insel, 2003; Shepard *et al.*, 2009). The limbic system is known to be implicated in a variety of socially relevant functions including sexual and affiliative behavior, social memory, parental care and attachment (Kling & Brothers, 1992; Kirkpatrick *et al.*, 1994; O'Connell & Hofmann, 2011). Therefore, paternal deprivation (i.e., a situation when father is removed from neonatal pups and mother alone raised the offspring) could be critical for many aspects of the offspring development. One can expect that removal of the father in social species may have long-lasting effects on behavior, as well as on the neuroendocrine systems, in offspring.

The present review concerns the effects of paternal deprivation in several social rodent species, i.e. species with persistent pair bonds and biparental care. The main purpose of this review is to determine the long-term effects of paternal deprivation on the development of parental behavior in offspring, pair bonding, social behavior, social recognition, and cognitive development in the species under consideration.

The effects of paternal deprivation in different rodent species

The California mouse, *Peromyscus californicus* (Gambel, 1848)

California mice are reported to be socially monogamous in the wild, show mating exclusivity and have persistent pair bonding and biparental care (Dudley, 1974a; Ribble & Salvioni, 1990). DNA-fingerprinting and paternity exclusion analyses indicated that only the paired male sired his mate's offspring. No cases of multiple paternity were revealed (Ribble, 1991, 1992). Family groups in California mice usually consist of a breeding pair and their male and female offspring (usually up to four young individuals). However, litters of four pups are seldom observed in the wild because resources are not sufficient to support litters this large (Cantoni & Brown, 1997). Males exhibit extensive care of the young both in the laboratory (Gubernick & Alberts, 1987) and in the field (Gubernick & Teferi, 2000). Males display all the components of parental behavior shown by mothers (nest attendance, retrieving, huddling over and grooming pups) and to the same extent, except lactation (Dudley, 1974a; Gubernick & Alberts, 1987; Ribble & Salvioni, 1990). In the laboratory, and in the absence of any maternal care, direct male care of young, in the form of huddling over pups and keeping them warm, was found to enhance offspring survival (Dudley 1974b). When California mice were housed under cold ambient temperature or had to forage for food by running in a wheel, more pups survived when the father was present

than when the female alone reared the pups (Gubernick *et al.*, 1993). Thus, presence of the male appears to be beneficial for the offspring survival in the California mouse.

Cantoni & Brown (1997) examined the effects of the male's presence on the reproductive success of *P. californicus* pairs in a semi-natural environment in which the mice had to run in a wheel to obtain their food. As measures of reproductive success, pup survival and body mass at weaning were examined in litters reared in the presence or absence of the male. The results of the study showed that the effect of removing the male on litter survival depends on litter size. Few litters of one pup survived, whether reared by the female alone or by both parents. One reason for this result could be that the cost of rearing one pup is too high, and females alone or in pairs let a single pup die to prepare for a larger litter. When the litter size was large (four pups), removal of the male had a dramatic effect on pup survival, because no females alone who had to work for food were able to rear their pups to weaning. When the male was present, however, both parents were able to rear four pups to weaning. Thus, the presence of the male is essential for the survival of a large litter when the parents have to forage for food as they do in the field. When males were removed in the field, a small portion (about ¼) of the young survived to weaning (Gubernick & Teferi, 2000).

Bearing in mind that paternal behavior is adaptive if it leads to increased pup survival and/or growth, Wright & Brown (2002) have conducted an experimental study to determine if the parental behavior provided by male *P. californicus* would increase pup survival and pup growth under different 'foraging' requirements. In this study, mice were placed in three housing conditions that differed in the amount of wheel running required for obtaining food: mice either (1) had a wheel present and had to run for food (wheel contingent, WC), (2) had a wheel present but were fed *ad lib* (wheel non-contingent, WN) or (3) had no wheel present and were fed *ad lib* (no wheel, NW). In each housing condition, males either remained with females and their pups to weaning (male present, MP) or males were removed before the birth of their pups (male absent, MA). The results of the study showed that females in the MP and MA groups spent about the same amount of time engaged in parental behavior. There was also no difference in the amount of time spent engaged in parental behavior by females in the three housing conditions. The amount of parental behavior the male engaged in was not influenced by housing, but males spent more time in parental behavior, as pups aged. A comparison of males and females in the MP groups indicated that females spent significantly more time in parental behavior than males. Besides, pups reared with both parents received almost twice as much parental grooming as pups reared with the mother alone. Moreover, significantly more pups were found to survive in the MP group (77.5%) than in the MA group (61.2%). Also, more pups survived in the NW condition (78.8%) than in the WC condition (61.7%). In the WC condition significantly more pups survived in the MP group than in the MA group. There were no significant differences

in pup survival between the MA and MP groups in the NW and WN conditions. In the MP group, 27 of 36 litters (75.0%) survived while 21 of 37 litters (56.8%) survived in the MA group. Although more litters survived in the MP group, this difference was not significant. At 24 days of age, pups weighed significantly more in the NW condition than in the other two housing conditions.

In general, paternal deprivation resulted in decreased pup survival when mice were required to forage for food, but not when food was available *ad lib*. This finding is consistent with the data of other studies suggesting that effect of paternal deprivation on the survival of offspring is most evident in poor quality environments. Specifically, the absence of the male led to a decrease in pup survival in California mice in cold environmental temperatures, but not in warm temperatures (Gubernick *et al.*, 1993).

The effects of male removal on offspring survival and growth were examined in *P. californicus* under three laboratory conditions: (1) warm ambient temperatures with food and water provision *ad lib*, (2) warm ambient temperatures when parents were required to forage for food (i.e., wheel running) and (3) cold ambient temperatures with food and water provision *ad lib* (Gubernick *et al.*, 1993). The results of this experimental study have shown that there was no effect of the male removal on offspring survival in warm ambient temperatures. However, substantially less pups survived in father-absent families than in father-present families in cold ambient temperatures (55 vs 90%) and when parents had to forage for food (45 vs 83%). Nevertheless, infants that survived, with or without their father, were similar in body mass from birth to weaning. This finding indicates that under conditions of adequate food, water and warm ambient temperatures, the presence of the father is not important for survival of young in *P. californicus*. However, the father's presence appears to enhance offspring survival when parents are challenged by cold temperatures or by foraging demands.

The effects of paternal deprivation in California mice in the wild were studied by Gubernick & Teferi (2000). The authors manipulated male presence and compared offspring survival in father-present and father-absent family groups using a capture-recapture technique. Males were removed within three days following the birth of their first litter, and the reproductive success of females without partners was compared with that of females with partners. Reproductive success was defined as the number of young that emerged from the nest burrow. The study has shown that there was no difference in the number of young born to father-present (in average 1.9 ± 0.2 , $n = 14$) and father-absent (in average 2.1 ± 0.2 , $n = 11$) family groups. To the contrary, significantly more young emerged from father-present (1.5 ± 0.1) than from father-absent (0.6 ± 0.2) family groups. Thus, significantly fewer young emerged than were born in father-absent family groups. Almost 81% of young born into father-present family groups emerged, whereas only 26% of young born into father-absent family groups survived to emergence. Every female with a partner

(14 out of 14) raised young, whereas only three out of 11 (27.3%) females without partners weaned any offspring. Gubernick & Teferi (2000) suggested that the female's inability to raise young was the result of male absence. The results of their study indicate that male care seems to be crucial for offspring survival. Some females were able to raise young without male assistance, but male investment in young significantly enhanced offspring survival compared with 'non-investing, absent' males.

In the laboratory, experiments with California mice have revealed that family structure impacts the development of at least two learning and memory tasks, with more slowly learning in animals reared by single mothers (Bredy *et al.*, 2004). This study was designed to examine the interactions between neonatal handling and biparental behavior during the early postnatal period, and their effects on cognitive function in adult *P. californicus*. Besides, the parental behavior of handled and non-handled biparental (male present, MP) and uniparental (male absent, MA) family units over days 3–15 of life was characterized. The handling procedure was conducted daily from day 1–21 post-parturition. The authors expected that (1) neonatal handling would increase parental grooming toward the young from birth to weaning, and (2) pups reared without their father would be groomed less often in infancy and exhibit poorer learning and memory in adulthood. The results of the study have shown that pups in the MP family units were groomed more than those in the MA family units. Overall, there was a significant main effect of handling on the average percentage of observation periods with grooming of pups, as handled pups were groomed more than non-handled pups. There was also a significant interaction between handling and paternal presence on the average percentage of observation periods with grooming of pups: handled, MP pups received the most grooming, while non-handled, MA pups received the least grooming. It was also found that neonatal handling enhanced spatial learning in adulthood by reducing the latency, and number of errors made, in finding the escape hole in the Barnes maze. However, contrary to the authors' predictions, increased grooming provided by the male in the non-handled, MP family units did not enhance spatial learning. These results suggest that under standard laboratory conditions, the presence of the father may not enhance offspring cognitive development. Bredy *et al.* (2004) concluded, however, that changes in parental care could contribute to offspring cognitive performance in *P. californicus*, and the importance of paternal investment might only become clear when environmental demands are such that maternal care is compromised, i.e., when the mother may neglect pups.

The Mongolian gerbil, *Meriones unguiculatus* (Milne-Edwards, 1867)

Mongolian gerbils live in extended family groups and have persistent pair bonding and biparental care. Family groups usually include one adult male, one or two, less frequently three adult females, and their offspring. The

total number of members in a large family group can amount to 28 individuals (Leont'ev, 1954, 1962; Gromov, 1981, 2000, 2011a; Ågren *et al.*, 1989).

Mongolian gerbils are a cooperative breeding species. Cooperation in breeding is related, first of all, to biparental care of young: the adult male engages in all care-giving activities observed in the female, except for nursing (Elwood, 1975, 1979; Clark *et al.*, 1997; Gromov, 2009, 2011b, 2014). The male and female gerbils form an integrated parental unit when rearing their offspring (Elwood & Broom, 1978). Both adults were reported to cooperate also via their synchronised presence with the young (temporal coordination or time sharing in the nest) (Weinandy & Gatterman, 1999). Besides, young gerbils that remain in the natal area become non-breeding helpers within family groups assisting in the rearing of the infants (Ostermeyer & Elwood, 1984; French, 1994). Specifically, young gerbils interact extensively with their younger siblings from the next litter, exhibiting care-giving activities such as nest attendance, retrieving, huddling over and grooming pups. The presence of the male and helpers is thought to be beneficial to physical and behavioural development of young gerbils, and their major contribution appears to be warmth and additional tactile stimulation of the pups (Elwood, 1975; Gromov, 2009, 2011b, 2013).

Elwood & Broom (1978) conducted a study to examine whether the presence of the male influences the development of the young and, if there is an influence, is it beneficial to the offspring or not? In their study, shortly after birth, litters were reduced to three pups (without regard to their sex) and then assigned to one of three experimental groups. In the first group, litters were left with the mother and father (male present: MP). The second group of litters had the male removed on the day of birth (male absent day 0: MA0). The third group of litters had the male removed on day 2 after the female's postpartum estrus (male absent day 2: MA2). The study showed that there was no essential difference in the mean body mass of the pups at 25 days of age in the MP, MA0 and MA2 groups. However, the mean age at which 50% of the eyes were open for the MP, MA0 and MA2 groups was 17.9, 19.3 and 19.1 days, respectively. Thus, those pups reared with their fathers were advanced in their eye-opening in comparison with pups of other two groups. Besides, pups reared without the male spent more time not with adult than did those reared with the male. This situation results in that pups without the male lose more body-heat. The data obtained suggest that pups reared by a single female are less advanced in their behavior and eye-opening than those reared by both parents.

When a male is present, he interacts with the pups to a large extent (Elwood, 1975; Gromov, 2009, 2011b, 2013). He licks them, walks and huddle over them, and thus provides a large amount of tactile stimulation. Such neonatal stimulation is an important factor in the development of young in biparental rodents (Russel, 1971; Gromov, 2013). The increased tactile stimulation provided by the male may accelerate behavioral and physical development of the young; alternatively, a

lack of additional stimulation provided by the male may have a negative effect that was found in the experiments with removal of adult males from the family groups of Mongolian gerbils (Gromov, 2009).

In this experimental study, the pair-bonding and parental behaviors of the animals reared in biparental (BP) and single-mother (SM) family units were compared. During the observations, total time spent in the nest (in minutes per 1 h of observations) and total duration of the mate grooming and grooming pups (in seconds per 1 h of observations) were calculated. All interactions between the parents were also recorded. For a comparative analysis, the entire observation period (24 days) was divided into four six-day periods: 1–6, 7–12, 13–18, and 19–24 days after the birth of pups. In BP-reared animals, grooming of females by males was found to be considerably more prolonged (in average 34.6 ± 5.8 s) than grooming of males by females (in average 6.0 ± 1.4 s). In SM-reared animals, the duration of grooming initiated by females (in average 5.4 ± 1.8 s) was not considerably changed compared to BP-reared females, while in SM-reared males it was found to decrease almost threefold (in average 11.2 ± 8.4 s). No other obvious differences in the social interactions of adult individuals reared in BP and SM family units were found. Among BP-reared animals, there was no significant sex difference in total time spent in the nest: this parameter averaged 45.1 ± 2.9 min in females and 47.7 ± 2.4 min in males, and almost was not changed throughout the entire observation period. In females, the duration of pup-directed grooming was found to be increased during the 1st and 3rd six-day periods and then decreased by the end of observations. In males, this parameter remained almost invariable during the entire observation period. SM-reared females spent essentially less time in the nest with pups compared to BP-reared females. As for SM-reared males, they spent a considerable part of time outside the nest during the first week after the birth of the pups compared to BP-reared males. As a result, females in SM family units remained in the nest for a considerably longer time without the partner compared to BP family units. As for the duration of pup-directed grooming, no significant difference in this parameter was found between BP- and SM-reared females. On the contrary, SM-reared males were significantly less active in pup grooming than BP-reared males, especially during 2nd six-day period. The behavior of SM-reared males with respect to pups was normalized only by the end of observation period. Thus, paternal deprivation was found to affect negatively both pair bonding and parental behaviors of the offspring in adulthood, and the most remarkable effect was revealed in SM-reared males. The latter exhibited less affection towards their mates (this was expressed particularly in terms of essential decrease in nest attendance and duration of the mate grooming) and lower rate of caregiving activities, especially during the first two weeks after the birth of pups. In SM-reared males and females, a complete recovery of the rate of parental care to normal values occurred only by the end of observations. Any

way, pups reared by parents with lower levels of direct paternal care obviously experienced a deficiency of both warmth and tactile stimulation, and this deficiency might result in essential behavioral deviations in adulthood (Gromov, 2009, 2011b, 2013, 2020).

The prairie vole, *Microtus ochrogaster* (Wagner, 1842)

Prairie voles are a socially monogamous and biparental species that lives in family groups and maintain varied and often complex social structures (Gruder-Adams & Getz, 1985; Getz & Hofmann, 1986; Carter & Getz, 1993; Getz & Carter, 1996). For most of the year, approximately one-third of family units are single mothers, one-third are male/female breeding pairs, and one-third are extended family groups (often called communal) consisting of a breeding pair and several reproductively inactive alloparents, usually elder offspring (Getz & Carter, 1996). Partner preference behavior is well characteristic of prairie voles, but pair bonding is not the only type of family-relevant behavior displayed by these rodents. Nest sharing, mate guarding, paternal and biparental care, spontaneous alloparenting, and communal nesting are also exhibited (Getz et al., 1981, 1993; Getz & Carter, 1996; Roberts *et al.*, 1998; Lonstein & De Vries, 1999). As for alloparental care, juveniles spend a significant amount of time in the natal nest, so that the litter is seldom left alone. Juveniles also show active forms of parental behavior such as retrieving, huddling over and grooming younger pups. Besides, juveniles contribute to nest and run way construction (Thomas & Birney, 1979; Gruder-Adams & Getz, 1985; Getz *et al.*, 1987; Solomon, 1991).

Wang and Novak (1994) performed a study (1) to characterize and quantify the alloparental behavior of juvenile prairie voles when housed with one or both parents and their younger siblings throughout lactation and (2) to assess the effects of fathers on juvenile behavior by comparing the alloparental behavior of juveniles when housed with their mother and younger siblings or with their mother, father and younger siblings. The results of this study showed that the presence of father had an impact on the spatial location and behavior of juveniles. The latter spent more time in the natal nest when housed with both parents (BP) than when housed with mothers only (SM, single-mother family units). BP-reared juveniles also spent less time in passive-alone behavior (resting outside of the nest away from other animals) than SM-reared juveniles, and made a greater mean number of direct body contacts with their younger siblings than did SM-reared juveniles. Besides, alloparental behavior changed differentially across pup development. When both parents were present, juveniles showed a gradual decrease in the time spent huddling-over and grooming pups, whereas contacting pups increased over days. No such developmental changes were detected when fathers were absent. Generally, this study indicates that alloparental care by juvenile prairie voles is affected by the presence of fathers. Juveniles spent less time

alone, more time in the natal nest, and had more body contact with their younger siblings when fathers were present than when fathers were absent. Besides, male juveniles spent more time in the natal nest and less time in passive-alone behavior in the father-present than in the father-absent condition. This pattern, however, was not characteristic of female juveniles. Therefore, prairie vole juvenile males may be more sensitive than juvenile females to the stimulation associated with the presence of their male parents. It is suggested that male could serve as a passive social or olfactory stimulus, and thus elicit increased contact by juveniles, and/or they might actually serve as a model for the acquisition of parental skills (Mugford & Nowell, 1972). Thus, the absence of father negatively affects the alloparental behavior of juvenile prairie voles, especially of juvenile males who in turn may become less responsive to their own offspring in terms of parental care.

Ahern & Young (2009) exploited some of the natural variations in prairie vole family structure to examine the influence of early life social experience on later-life social behavior. Specifically, these authors examined the developmental trajectories and adult social behavior of prairie voles raised in single-mother (SM) or biparental (BP) rearing conditions. They also explored the neurobiological correlates of this behavioral variation and suggested that early life rearing conditions can profoundly affect adult prosocial behavior, and that these effects may be mediated by alterations in neuropeptide systems. The study has shown that SM-reared offspring experienced a greater frequency of time alone in the nest during postnatal days 2–10 than BP-reared pups. Besides, during postnatal days 2–10, SM-reared offspring experienced a significantly lower frequency of licking and grooming than BP-reared counterparts. There was a significant effect of rearing condition on pup body mass as well: SM-reared animals weighed less at weaning than BP-reared animals, regardless of sex. By adulthood (postnatal day 60), however, SM-reared animals from both sexes had achieved body mass statistically indistinguishable from BP-reared animals. SM-reared females were found to exhibit significantly less licking and grooming and less time immobile (huddling) over pups. Males, however, showed equal amounts of both licking and grooming and huddling over pups across rearing conditions. SM-reared females spent more time away from the stimulus pups than BP-reared females; males showed no group difference.

Quantification of *in situ* hybridization of oxytocin (OT) mRNA silver grains in the paraventricular nucleus (PVN) of the hypothalamus revealed that SM-reared females had significantly greater numbers of OT mRNA clusters in the PVN than BP-reared females, whereas males showed no statistical difference. An analysis of oxytocin receptor (OTR) binding density in the bed nucleus of the stria terminalis (BNST), lateral septum (LS), medial preoptic area (MPOA) of the hypothalamus, central amygdala (CA) and basolateral amygdala revealed no group effect for any of the brain regions. Lastly, an analysis of vasopressin 1a receptor

(V1aR) binding density in LS, BNST, CA, mediodorsal thalamus and posterior cingulate revealed no effects of group for any of the brain regions as well. These findings demonstrate that SM- and BP-reared animals experienced different levels of care during the neonatal period and that these differences significantly affected parental and bonding social behaviors in adulthood. Ahern & Young (2009) hypothesized that removing the male would have significant consequences on the quantity and quality of care received by offspring. Comparisons of SM and BP family units revealed that SM-reared pups experienced significantly less care, including greater exposure and less licking and grooming in comparison to BP-reared counterparts. Group differences in the level of licking and grooming arose as a function of the father's absence in the SM group. Compared to BP-reared animals, SM-reared adult females exhibited remarkably low spontaneous parental behavior, and both males and females exhibited a delayed onset of partner-preference formation.

Unexpectedly, the neurophysiological investigations provided little insight based on *a priori* predictions of Ahern & Young (2009). These authors hypothesized that variation in ventral forebrain OTR and V1aR densities would track behavioral performance differences, and that this relationship would be a function of parental care. Contrary to these predictions, no group differences were found in the density of OTR and V1aR in key ventral forebrain regions. However, the OT system in other brain areas was revealed to be sensitive to natural variations in early care. Compared to BP-reared animals, SM-reared adults had increased OT mRNA clusters in the PVN, and a modestly higher density of OTR in the lateral BNST. Overall, this study demonstrates that early social experience plays an important role, and a lower level of spontaneous parental behavior and a delayed onset of partner-preference formation may result in part from differences in oxytocin gene expression. Given the greater foraging demands in natural environments, SM-reared adults in the wild are likely to spend even less time with their pups. Thus, the decrease in adult social contact may have important consequences for adult social behavior of the offspring. Manipulations of family structure in one generation may indirectly affect parental care in the next generation by directly altering tactile stimulation (via licking and grooming) and subsequently OTR circuits.

Ahern *et al.* (2011) continued the investigations and performed a study to test the hypothesis that manipulations of family structure in one generation can affect primiparous family behavior in the next. In particular, the authors compared parental behavior of prairie voles reared in biparental (BP) and single-mother (SM) family units and expected SM-reared animals to exhibit significantly lower levels of nest attendance as well as pup-directed licking and grooming. In Experiment 1, the authors established that BP- and SM-reared offspring experienced significant differences in their early social environment: as predicted, BP-reared females showed a significant group partner preference, whereas SM-reared females did not; besides, BP-reared females and males

exhibited a higher frequency of pup-directed licking and grooming than SM-reared parents. Therefore, BP- and SM-reared pups experienced significant differences in the rates of tactile stimulation, including total huddle time and licking and grooming received, because of the father in the BP condition. In Experiment 2, the authors examined whether differences in early family structure would alter parenting of the next generation (in SM/SM- and BP/BP-reared animals). The results of Experiment 2 showed that SM/SM- and BP/BP-reared animals again showed differences in partner preference formation, with BP/BP-reared females seeming to form stable partner preferences more quickly than SM/SM-reared females. Both sexes in the SM/SM group showed decreased pup-directed licking and grooming in comparison to BP/BP counterparts. The authors noted that the cause of this intergenerational effect on pup-directed licking and grooming is currently unclear, but it may depend on early life tactile stimulation (via licking and grooming) and oxytocin receptor (OTR) densities in the BNST, like, for example, in female rats (Francis *et al.*, 2000, 2002). In prairie voles, SM-reared pups received less licking and grooming than BP-reared animals; they also had lower densities of OTR in the BNST (Ahern & Young, 2009). Therefore, manipulations of family structure in one generation may indirectly affect parental care in the next generation by directly altering tactile stimulation and subsequently OTR circuits.

The mandarin vole, *Lasiopodomys mandarinus* (Milne-Edwards, 1871)

Mandarin voles are a socially monogamous species inhabiting steppe regions of southern Siberia (Russia) and China (Smorkatcheva, 1999; Tai *et al.*, 2001; Tai & Wang, 2001). Reproduction within mandarin vole family groups is commonly restricted to one female and one male, with family group founders exhibiting persistent pair bonds. Males engage in all care-giving activities observed in the female, except for nursing. Alloparental care, when juveniles assist the breeders in rearing younger siblings, is also typical of mandarin voles (Smorkatcheva, 2003; Jia *et al.*, 2009; Song *et al.*, 2010). This species is an interesting model to study developmental influences of early neuroendocrine environment, paternal and early deprivation on adult social behaviors (Jia *et al.*, 2008a, b). The previous work indicated that paternal deprivation significantly increases anxiety and reduces sociability of adult offspring (Jia *et al.*, 2009).

Neurobiological studies have shown that, along with other steroid hormones, estradiol is also involved in the initiation and maintenance of paternal care (Brown & Moger, 1983; Rosenblatt & Ceus, 1998; Trainor & Marler, 2002). The actions of estradiol in males involve the medial preoptic area of the hypothalamus (MPOA), which expresses aromatase enzyme (for the conversion of peripheral testosterone to estradiol) as well as estrogen receptor alpha, ER α (Rosenblatt & Ceus, 1998; Trainor *et al.*, 2003; Cushing & Wynne-Edwards, 2006). ER α expression in the MPOA was found to increase in females

exhibiting high level of parental care (Champagne *et al.*, 2003). The same effect is expected in males (Martínez *et al.*, 2019).

Jia *et al.* (2011) hypothesized that estrogen binding to estrogen receptors might play a very important role in mediating paternal behavior and have performed a study to test the hypothesis that early deprivation (including paternal deprivation) has long-term effects on the development of parental behavior in offspring, and that this effect may be associated with central ER α expression. To test this hypothesis, male and female of F1 generation mandarin voles were paired and then divided into three experimental groups: the biparental care (BP) group, the neonatal paternal deprivation (PD) group, where the father was removed immediately after offspring were born while the mother took care of the offspring on her own, and the early deprivation (ED) group, where offspring were removed from their natal cages for 3 h every day and placed inside an incubator from postnatal day 0 to postnatal day 13. Parental behaviors of F2 generation mothers and fathers with different neonatal treatment (BP, PD, ED) were examined.

The results of this study have shown that levels of maternal behavior and sociability were significantly reduced by both paternal deprivation and early deprivation. Females that experienced neonatal early deprivation (ED group) and neonatal paternal deprivation (PD group) showed significantly less huddling than those with early biparental care (BP group). Females from the BP group spent more time licking and grooming their own offspring than females from the PD and ED groups. Females from the PD and ED groups exhibited significant increase in non-kyphotic behavior (sitting flat on pup or next to it, while touching, but without an arched back) than those from the BP group. Levels of paternal behaviors were also suppressed due to neonatal paternal deprivation and early deprivation. Males from the PD and ED groups huddled with their own pups for significantly less time and less frequently than those from the BP group. Males from the ED group spent less time in pup-directed licking and grooming than those from the BP group. Males from the PD and ED groups showed more non-kyphotic behavior than did the males from the BP group. It was also found that there were significantly more ER α -IR neurons in the BNST, MPOA and ventromedial hypothalamic nucleus (VMH) of BP females than in those of PD and ED females. In addition, PD females had significantly more ER α -IR neurons in the BNST than ED females, and BP females displayed more ER α -IR neurons in the arcuate hypothalamic nucleus (Arc) than did PD females. The number of ER α -IR neurons in the BNST, MPOA, VMH and Arc of BP males were significantly more than those of PD and ED males. Additionally, PD males had significantly more ER α -IR neurons in the BNST and MPOA than ED males. Within only the BP group did females display significantly more ER α -IR neurons in the BNST, MPOA and VMH than males, while the number of ER α -IR neurons in the Arc of females was significantly less than in males. In the ED

group, a similar difference between the sexes was also found in the BNST and MPOA. Thus, this study showed that both paternal and early deprivation suppressed the parental behavior of adult offspring, suggesting that male presence and social contact play an important role in the development of parental behavior. Drastic changes in central ER α expression were also induced by paternal deprivation and early deprivation. These findings prove the hypothesis that paternal deprivation and early deprivation have long-term effects on the development of parental behavior that may be associated with central ER α expression. Offspring that experience paternal deprivation or early deprivation can in turn significantly reduce their own level of parental behavior (Jia *et al.*, 2011).

All social relationships are known to be based on the ability to recognize and remember conspecifics. Experimental studies have shown that maternal care influences many aspects of the cognitive ability of offspring in adulthood, and maternal separation impairs social recognition performance (Lukas *et al.*, 2011) and exacerbates age-related learning impairments in adult rats (Meaney *et al.*, 1988, 1991; Oitzl *et al.*, 2000; Tang, 2001). Cao *et al.* (2014) performed a study to examine whether paternal deprivation would have the same effect in mandarin voles. The authors hypothesized that paternal deprivation possibly alters oxytocin receptor (OTR) and estrogen receptor alpha (ER α) mRNA expression in the medial amygdala (MeA) and nucleus accumbens (NAcc) which are known to be associated with social recognition performance (Young *et al.*, 1998; Hammock & Young, 2002; Kang *et al.*, 2009), and subsequently affects social recognition. In this study, breeding pairs of mandarin voles were randomly assigned to two groups: biparental care (BP) and paternal deprivation (PD). In the BP group, all family members were housed together in their home cage and left undisturbed until pups were weaned. For the PD treatment, the male parent was removed during the first 24 h following birth of the pups, and only the mother reared the offspring. Using the habituation/dishabituation test paradigm, the authors of the study found that social investigatory behavior in BP-reared offspring followed normal social recognition patterns in which the duration of olfactory investigation declined across four exposures to the same individual, and increased when presented with a novel one. In contrast, animals of the PD-treatment group failed to show any habituation and dishabituation behaviors, spending similar amounts of time investigating the stimulus animal in all five trials, indicating impaired social recognition. Impairments in social recognition in PD animals could be a result of the reduction of tactile stimulation such as licking and grooming from parents, because such stimulation appears to be a critical factor for hippocampal development which plays an important role in recognition (Bredy *et al.*, 2004). It was also found that the PD treatment significantly reduced the expression of OTR mRNA in the NAcc of both sexes and in the MeA of the males as well as ER α mRNA expression in the MeA in the females. Thus, paternal deprivation may subsequently

down-regulate OTR and ER α . Additionally, BP-reared females had significantly greater serum OT levels than PD-reared females, but no difference was found for males. Difference in the effect of paternal deprivation on oxytocin levels between males and females may be due to the different roles played by this neuropeptide between the sexes. It is suggested that impaired social recognition induced by paternal deprivation may be associated with a reduction in serum OT levels in females. Similarly, OTR mRNA expression in the MeA suppressed by paternal deprivation may also contribute to impairment in social recognition. There is strong evidence that estrogen and oxytocin systems regulate each other (Young *et al.*, 1998; Mitra *et al.*, 2003). Thus, interaction between reduced OTR and ER α in the MeA and NAcc, and reduced serum OT caused by paternal deprivation may contribute to the impairment of social recognition in mandarin voles (Cao *et al.*, 2014).

Postpartum paternal care has been hypothesized to be an important facilitator for the subsequent formation of pair bonds in socially monogamous rodent species. This hypothesis is supported by empirical evidence using early social manipulation (Gromov, 2009). Bearing in mind such evidence, Yu *et al.* (2012) predicted that paternal care might affect social behavior during male–female interaction as well as selective aggressive behaviors that are important for pair bonding. It is known that several brain regions including the NAcc, MPOA, MeA, ventral pallidum (VP) and supraoptic nucleus (SON) of the hypothalamus are involved in pair bonding (Bales *et al.*, 2007). In addition to the important roles played by the central oxytocin and vasopressin systems in the formation and maintenance of pair bonds (Bamshad *et al.*, 1993; Insel & Shapiro, 1992; Insel *et al.*, 1994), dopamine receptor types 1 (D1R) and 2 (D2R) in the NAcc have been also shown to play different roles in pair bonding. D2R facilitates the formation of the pair bond, whereas D1R prevents pair-bond formation with another subject during the maintenance period (Aragona *et al.*, 2006; Gingrich *et al.*, 2000). Glucocorticoids have been shown to be involved in regulating the mesencephalic dopaminergic system as well (Koob, 1992; Deroche *et al.*, 1995; Willner, 1995).

Yu *et al.* (2012) conducted an experimental study to determine the long-lasting effects of paternal deprivation on pair bonding and social behavior in mandarin voles and assess whether the central D1R and D2R expression in NAcc and serum corticosterone (CORT) are involved in these effects. Animals in this study were a laboratory-reared generation derived from a wild population of mandarin voles from China. Breeding pairs of the voles were randomly assigned to two groups: biparental care (BP) and paternal deprivation (PD). In the BP group, all family members were housed together in their home cage and left undisturbed until pups were weaned. For the PD treatment, the male parent was removed during the first 24 h after the birth of the pups, and only the mother reared the pups. The results of the study showed that paternal deprivation inhibited the formation of a preference for the male partner in females: adult female offspring from the

BP family groups spent significantly more time with the partner than with the stranger, whereas female offspring from the PD family groups did not show a preference for either the partner or the stranger. Female offspring from the BP family groups showed more body contact with the partner and less body contact with the stranger than did females from the PD family groups. Besides, PD-reared females increased aggression toward both the partner and the stranger, whereas BP-reared females never directed any attack behavior toward the partner. As for males, the PD treatment did not affect the direction of the preference for partners over strangers in adult male offspring, but increased the level of aggression to the strangers.

It was revealed that the PD treatment affected dopamine receptor mRNA expression in the NAcc differently for the females and the males. In adult female offspring, neonatal PD treatment significantly reduced the expression of both D1R mRNA and D2R mRNA before pairing and after 3 days of cohabitation with a male partner. In contrast, D1R mRNA expression and D2R mRNA expression both increased significantly after cohabitation in PD-reared females. BP-reared males exhibited decreased expression of D1R mRNA, whereas PD-reared males exhibited decreased expression of both D1R mRNA and D2R mRNA after three days of cohabitation with a female. Only the expression of D2R mRNA in BP-reared males showed an increasing trend after cohabitation. In addition, PD-reared males enhanced the expression of both D1R mRNA and D2R mRNA prior to cohabitation, but reduced D2R mRNA expression after cohabitation. Besides, 3 days of cohabitation reduced the serum CORT levels in BP-reared females, but increased serum CORT levels in both BP- and PD-reared males.

Thus, the effects of paternal deprivation on pair bonding and social behavior in mandarin voles were found to be sexually dimorphic (Yu *et al.*, 2012): paternal deprivation inhibited the formation of partner preferences and selective aggression in females, but not in males. In both female and male offspring, however, paternal deprivation reduced social contact with the partner and increased aggression towards the partner and the stranger. The effects of paternal deprivation on dopamine receptor mRNA expression and serum corticosterone levels were also sex-specific: the PD conditions essentially reduced the expression of D1R mRNA and D2R mRNA in the NAcc in females, but had the opposite effect in males; similarly, the PD treatment reduced the CORT levels in the females, but increased male CORT levels. Cohabitation for 3 days essentially reduced serum CORT concentrations in BP-reared females, but increased concentrations in BP- and PD-reared males. CORT has been found to have sex-specific effects on pair bonding: decreased CORT facilitates partner preference formation in females, but increased CORT promotes pair bonding in males (De Vries *et al.*, 1995, 1996; 2002). Therefore, the decreased serum CORT levels observed in BP-reared females and the increased serum CORT levels seen in BP- and PD-reared males after 3 days of cohabitation

likely facilitated partner preference formation, and this finding is consistent with predictions of Yu *et al.* (2012). The results of this study provide substantial evidence that paternal deprivation inhibits the formation of the pair bond in mandarin voles, especially in females. The inhibition of the pair-bond formation is possibly associated with sex-specific alterations in the expression of two types of dopamine receptors in NAcc, and serum corticosterone levels induced by paternal deprivation.

Yu *et al.* (2015) continued the investigations and performed a study to examine the effects of early biparental separation (BS) and neonatal paternal deprivation (PD) on paternal behavior in the adult offspring of mandarin voles and assess whether serum levels of CORT, mRNA expression of dopamine receptors (DR) and oxytocin receptors (OTR) in the NAcc, and mRNA expression of OTR and ER α in the MPOA are associated with paternal care. The authors hypothesized specifically that early biparental separation and neonatal paternal deprivation may affect OTR and ER α levels in the MPOA, OTR and DR levels in the NAcc, and impact the mediation on offspring paternal behavior. In this study, breeding pairs of mandarin voles were randomly assigned to three experimental groups: biparental care (BP), PD and BS. In the BP group, all family members were housed together in their home cage and left undisturbed until pups were weaned. For the PD treatment, male parents were removed during the first 24 h after birth of the pups, and only the mother reared the offspring. For the BS treatment, all pups were separated from their parents 3 h per day from postnatal days 1 to 13. All pups were weaned at 23 days of age, and a same-sex sibling pair from each litter was housed in one cage. Female and male offspring from each of the three groups were paired as adults at about 100 days of age. It was revealed that compared to the BP group, the BS treatment reduced crouching behavior of males, whereas the PD treatment reduced retrieval behavior of males. Besides, compared to the BP group, BS-treated males had higher serum CORT concentrations in adulthood when their own pups were at postnatal days 5–7. Increased serum CORT concentration was found to be associated with reduced paternal crouching behavior. Compared to the BP group, PD treatment had no effect on CORT. Further, compared to the BP group, BS-treated males displayed higher levels of D1R mRNA expression in the NAcc, but lower levels of OTR and ER α mRNA expression in the MPOA. Reduced expression of OTR was associated with altered crouching behavior and increased expression of D1R. However, compared to the BP group, PD-treated males only exhibited less ER α mRNA expression in the MPOA. These findings indicate that both early biparental separation and neonatal paternal deprivation negatively affect some paternal care-giving activities at adulthood. Besides, both the BS and PD treatments reduced ER α mRNA expression in the MPOA, but only the BS treatment suppressed OTR mRNA expression in this brain region. It is remarkable that reduced expression of OTR was closely associated with alteration of paternal crouching behavior and increased expression of D1R.

The results of the study also suggest that the OT system in the MPOA might interact with the NAcc dopamine system to regulate paternal behavior, and that the BS treatment may affect interactions between the MPOA and NAcc (Yu *et al.*, 2015).

As it is mentioned above, oxytocin (OT) is one of the most important neurotransmitters that regulate social behavior including parental responsiveness. However, many of the effects of the OT system, especially those associated with social behavior, are estrogen-dependent, i.e. require ER α . Feng *et al.* (2019) conducted an experimental study to investigate the effects and mechanisms of paternal deprivation on parental behavior of mandarin voles. Considering the role of the early social environment on parental behavior and the long-term effects of both OT and ER α on social behavior, the authors hypothesized that both early social deprivation and paternal deprivation could decrease OT expression in pups. This, in turn, could affect the parental behavior via alterations of ER α levels in specific brain regions at the adult stage. In Experiment 1, breeding pairs were randomly assigned to three experimental groups: the biparental care (BP) group, the paternal deprivation (PD) group, where the father was removed immediately after the offspring were born, and the early social deprivation (ESD) group, where the offspring were removed from their natal cages for 3 h every day from postnatal day 0 to postnatal day 13 and placed inside an incubator. At postnatal day 21, brains of all pups were collected for OT immunohistochemistry. In Experiment 2, breeding pairs were randomly assigned to one of the following groups, according to whether they received a single subcutaneous injection of: isotonic saline (SAL), oxytocin (OT), or oxytocin antagonist (OTA). At postnatal day 75, the animal were paired with unfamiliar, untreated, and sexually naïve voles of similar age and opposite sex. Parental responsiveness of the animals to their offspring was assessed at postnatal days 0, 13 and 21. In Experiment 3, animal treatment was the same as in Experiment 2. At postnatal day 75, brains of the animals were collected for ER α immunohistochemistry.

The results of Experiment 1 have shown that both the BP-reared females and males displayed significantly more OT-IR neurons in the paraventricular hypothalamic nucleus and the supraoptic nucleus than did voles of the PD and ESD groups, while there were no significant difference between the PD and ESD groups. The results of Experiment 2 have shown that females from OT-treated group had significantly more maternal behavior than did females from SAL-treated group. Neither single neonatal injections of OT nor OTA affected paternal behavior. Besides, males from OTA-treated group spent more time nesting than males from SAL-treated group. The results of Experiment 3 have shown that there were significantly more ER α -IR neurons in the MPOA and the ventromedial hypothalamic nucleus (VMH) of OT-treated females than in those of SAL-treated group. OT-treated females also displayed significantly more ER α -IR neurons in the BNST, MPOA, VMH and the arcuate hypothalamic nucleus (Arc) than did OTA-treated

females. Besides, OTA-treated females had significantly fewer ER α -IR neurons in the BNST, VMH and Arc than did SAL-treated females. The numbers of ER α -IR neurons in the BNST, MPOA, VMH and Arc of OTA-treated males were found to be significantly fewer than those of SAL- and OT-treated males. Overall, this study demonstrated that paternal deprivation as well as early social deprivation resulted in reduced OT expression in both the paraventricular hypothalamic nucleus and the supraoptic nucleus that in turn might negatively affect parental responsiveness. Neonatal exogenous OT promoted maternal but not paternal behavior. Changes in the OT system also had long-term effects on ER α expression in mandarin voles that also might lead to significant deviations in parental responsiveness of the species.

The degu, *Octodon degus* (Molina, 1782)

Degus are caviomorph social rodents inhabiting rocky biotops in Chilean savanna and living in extended family groups consisting of 1–2 adult males, 2–5 adult females and their offspring (Fulk, 1976; Meserve *et al.*, 1983; Lacey & Ebensperger, 2007). Groupmates of both sexes share the same burrow system, including a communal nest site (Ebensperger & Bozinovic, 2000; Ebensperger *et al.*, 2004). It has been shown that male degus invest enormous efforts in rearing their offspring, and while the mother–pup contacts gradually decrease within the first postnatal weeks, the father–pup contacts increase with the offspring’s age (Wilson, 1982). Thus, to a similar degree as the mother, the father is a source of a variety of sensory as well as emotional stimulation for his offspring and provides an “enriched environment” to stimulate and optimize brain development (Fuster, 2002).

Helmeke *et al.* (2009) carried out a study to assess the effect of paternal deprivation on neuronal and synaptic development in the orbitofrontal cortex, a prefrontal brain region which is essential for emotional and cognitive function. In this study, biparental family groups were compared with single-mother (father-deprived) family groups (pups were raised without father, who was removed from the home cage 1 day after the birth of his offspring). Dendritic length and the density of dendritic spines were compared between biparentally raised (BP) and father-deprived (PD) animals in the orbitofrontal cortex (OFC), which has been shown to play an essential role in social behaviors (Kolb *et al.*, 2004; Rolls, 2004). This study has shown that in biparental family groups the fathers engaged significantly less frequently in pup-directed licking and grooming compared to the mothers. However, degu fathers showed similar activity for huddling with pups as the mothers. Single mothers displayed the same frequency of huddling, licking, grooming and nursing as mothers in biparental family groups. Due to the activity of the father in BP family groups, the total amount of huddling with parents was 2.7-times higher than in PD family groups. Besides, in BP family groups pup-initiated parent allogrooming was doubled compared to PD family groups. Morphological analysis has shown

that at the age of 3 weeks the father-deprived animals displayed significantly lower densities of dendritic spines on the apical and basal dendrites compared to animals raised by both parents. In adulthood, the father-deprived animals displayed significantly shorter apical dendrites. Thus, the lack of paternal care significantly interferes with dendritic and synaptic maturation and refinement in the OFC. As the OFC is activated by touch, taste, smell, visual stimuli, somatosensory and emotional input (Rolls, 2004), paternal care stimulates the establishment of neuronal and synaptic networks of cortical and limbic regions in the brain of the offspring during early infancy. Therefore, the observed synaptic and dendritic changes in the fatherless animals may be the result of reduced huddling activity in fatherless family groups (Helmeke *et al.*, 2009). It is suggested that the reduced spine numbers and densities in the OFC of father-deprived animals might be indicative of an OFC hypofunctionality and dysfunction of OFC connectivity, including OFC–amygdala circuits (Pitkänen, 2000).

Another similar study has been conducted by Pinkernelle *et al.* (2009) who aimed to test the impact of paternal deprivation on dendritic and synaptic development of pyramidal neurons in the somatosensory cortex (SSC). This study has shown that paternal deprivation resulted in significantly altered somatosensory circuits and induced hemispheric asymmetry of pyramidal neurons in the SSC. Specifically, it was found that somatosensory pyramidal neurons in layer II/III in the SSC of left hemisphere of father-deprived degus displayed significantly shorter and less complex basal dendrites, as well as decreased numbers of presumably excitatory spine synapses on their basal dendrites. Therefore, one can conclude that environmental factors contribute to the development of hemispheric asymmetry. Hemispheric lateralization appears to be characteristic of the adequate function of sensory cortices, and also for prefrontal and limbic regions (Sullivan *et al.*, 2009). With respect to the SSC, evidence for hemispheric asymmetry as well as its functional interpretation is still controversial. However, the results of the study indicate that the two hemispheres may be differentially affected by paternal deprivation, and the observed deprivation-induced asymmetry in the SSC dendritic network may affect the behavioral outcome as well (Pinkernelle *et al.*, 2009).

Braun *et al.* (2010) continued investigations and performed a study to test the hypothesis whether paternal care also affects the development of inhibitory circuits to maintain a 'homeostatic' balance between excitation and inhibition within prefrontal and limbic pathways. This study focused on the expression of Ca-binding proteins Parvalbumin (PARV) and Calbindin-D28k (CaBP-D28k) in two GABAergic interneuron subpopulations, which predominantly innervate and inhibit the dendrites (CaBP-D28k-expressing neurons) or somata (PARV-expressing neurons) of pyramidal neurons, where a reduction of excitatory spine synapses has been found in father-deprived degus (Helmeke *et al.*, 2009). Like in other similar research, biparentally-raised animals

were compared with father-deprived animals. The study revealed region-specific deprivation-induced changes in the density of PARV- and CaBP-D28k-expressing cells. Some deprivation-induced changes were only seen at postnatal day 21: elevated CaBP-D28k-positive neurons in the orbitofrontal cortex, hippocampal CA1 and CA3 sub-regions, as well as dentate gyrus, and elevated PARV-positive neurons in the lateral orbitofrontal, prelimbic/infralimbic, dentate gyrus, and hippocampal CA1 regions, nucleus accumbens, and amygdala. Some deprivation-induced changes were only seen in adulthood: increased CaBP-D28k-positive neurons in the amygdala and decreased PARV-positive neurons in the prelimbic/infralimbic and hippocampal CA3 sub-regions. In hippocampal CA1 sub-region, PARV-positive neurons were increased at postnatal day 21 and decreased in adulthood. The developmental decrease in PARV-positive neurons deserves special attention, because these cells have been identified as the key player for critical period plasticity in the visual cortex (Hensch, 2005). Thus, the effects of paternal deprivation allow one to suggest that paternal care essentially affects the development of inhibitory neurons in specific brain regions. It is important to note that even small and transient readjustments within inhibitory circuits during specific developmental time windows can affect long-term development of the same or other afferent/efferent brain regions. The establishment of balanced excitation and inhibition is critical during cortical development as well as for adult cortical function, and altered activity levels of specific inhibitory interneuron subpopulations in specific prefrontal and limbic brain areas may result in altered cognitive and emotional competence. In particular, altered density of PARV- and CaBP-D28k-expressing neurons in the amygdala, hippocampus, nucleus accumbens and medial and orbitofrontal prefrontal cortex of father-deprived animals may affect learning and memory formation as well as emotionality (Braun *et al.*, 2010).

In the study of Seidel *et al.* (2011), effects of paternal deprivation on the development of neurons in prefrontal-limbic brain regions, which express corticotropin-releasing factor (CRF), were analyzed. CRF is a polypeptide hormone, which is expressed and released by a neuronal subpopulation in the brain. CRF is known to be essential not only for regulating stress and emotionality, but also involved in cognitive functions. As in previous studies (Helmeke *et al.*, 2009; Pinkernelle *et al.*, 2009; Braun *et al.*, 2010), biparentally-raised degus were compared with father-deprived animals. Seidel *et al.* (2011) have shown that at weaning age (postnatal day 21) paternal deprivation resulted in an elevated density of CRF-containing neurons in the orbitofrontal cortex and the basolateral amygdala of male degus, whereas a reduced density of CRF-expressing neurons was revealed in the dentate gyrus and stratum pyramidale of the hippocampal CA1 sub-region at this age. With the exception of the hippocampal CA1 sub-region, the deprivation-induced changes were no longer evident in adulthood, which suggests a transient change, which in

later life might be normalized by other socio-emotional experience. It is known however that in addition to its direct functional effect on neuronal circuits, CRF is also critically involved in neuronal dendritic and synaptic development, and alteration in density of CRF-containing neurons even during a short-time ontogenetic window may affect dendritic and synaptic development of pyramidal and/or inhibitory neurons, and thereby can induce structural changes, which are still maintained even after normalization of CRF regulation. Thus, the results of the study of Seidel *et al.* (2011) demonstrated a critical role of paternal care in the maturation of central CRF circuits in specific brain regions, which are essential for emotional and cognitive functions.

General discussion

Experimental studies in social rodents have shown that paternal deprivation does delay the development of offspring, increases levels of anxiety, reduces sociability, negatively affects parental and alloparental behaviors, and inhibits the formation of pair bonds. Specifically, paternal deprivation is shown to result in decreased pup survival in California mice, when parents were challenged by cold temperatures or by foraging demands. In Mongolian gerbils, pups reared by a single female are less advanced in their behavior and eye-opening than are those reared by both parents. Paternal deprivation was found to negatively affect both pair bonding and parental behaviors of the offspring in adulthood. The absence of father negatively affects the alloparental behavior of juveniles in the prairie vole, especially of juvenile males who in turn may become less responsive to their own offspring in terms of parental care. Paternal deprivation significantly affects parental and bonding social behaviors in adulthood: adult females exhibited remarkably low spontaneous parental behavior, and both males and females exhibited a delayed onset of partner-preference formation; the decrease in adult social contact may have negative consequences for adult social behavior of the offspring.

Experiments with mandarin voles have shown that paternal deprivation resulted not only in a decrease of levels of parental care and sociability in males and females in adulthood, but in a significant reduction of ER α -IR neurons in the bed nucleus of the stria terminalis, the medial preoptic area and the ventromedial hypothalamic nucleus both in males and females. As a result, the parental behavior, associated with central ER α expression, was significantly suppressed in adult offspring of both sexes. In other words, offspring that experience paternal deprivation can significantly reduce their own parental behavior in adulthood. Besides, paternal deprivation significantly reduced the expression of OTR mRNA in the nucleus accumbens of both sexes and in the medial amygdala of males as well as ER α mRNA expression in the medial amygdala in females (these brain regions are known to be associated with social recognition performance and involved in pair bonding). Therefore, paternal deprivation may

negatively affect social behavior of offspring related to pair bonding. The inhibition of pair-bond formation is possibly associated with sex-specific alterations in the expression of two types of dopamine receptors in the nucleus accumbens, as well as of serum corticosterone levels induced by paternal deprivation. Effects of paternal deprivation were also associated with that male mandarin voles exhibited (1) less ER α mRNA expression in the medial preoptic area and, as a consequence, reduced retrieval behavior; (2) reduced OT expression in some brain regions involved in regulating parental behavior that in turn might negatively affect parental responsiveness. Thus, paternal deprivation negatively affects some paternal care-giving activities in adulthood.

In degus, paternal deprivation was shown to negatively affect the establishment of neuronal and synaptic networks of cortical and limbic regions in the brain of the offspring as a result of reduced huddling activity in fatherless family groups. Besides, paternal deprivation induced asymmetry in the dendritic network of the somatosensory cortex that might affect the behavioral outcome as well. Additionally, paternal deprivation was found to essentially affect the development of inhibitory neurons in specific brain regions that could lead to significant behavioral deviations, because even small and transient readjustments within inhibitory circuits during specific developmental time windows could affect long-term development of the same or other afferent/efferent brain regions. As a result, cognitive and emotional competence might be essentially altered in father-deprived animals.

Thus, experimental studies show that various types of disturbances within early life may essentially affect the development of the brain and consequently social behavior in biparental rodent species. During this process, related brain regions and nuclei, neurotransmitters, and their corresponding receptors integrate abundant and complex information from the environment and then regulate various types of social behavior. Specifically, interruption or lack of father-offspring interaction resulted from paternal deprivation may be associated with inhibited parental behavior in adulthood, mediated particularly via changes in central oxytocin system which subsequently alters the estrogen-dependent binding of ER α (Feng *et al.*, 2019). Therefore, social interactions are a most important factor in the early social environment that affects the development of the oxytocin system as well as adult social behavior including parental care.

It appears likely that the behavioral differences of father-deprived individuals result from altered brain circuits, which have been formed under conditions of paternal deprivation. This view is supported by findings in the biparental rodents, which revealed that paternal care significantly affects maturation of excitatory spine synapses in prefrontal cortical and limbic regions (Bredy *et al.* 2004; Helmeke *et al.* 2009; Pinkernelle *et al.* 2009; Braun *et al.*, 2010). Paternal deprivation alters the regional density as well as the homeostatic balance of distinct interneuron populations in an age- and region-specific manner (Braun *et al.*, 2010).

All these findings, in addition to that mentioned above, indicate the importance of paternal care and paternal bonding as a unique source of sensory and socio-emotional stimuli, which may protect the offspring from developing an increased vulnerability towards stress-related life events.

Summarizing this review, it needs to note that experimental studies on social rodents may be relevant in understanding of neurobiological mechanisms related to adult pair-bond stability, maternal and paternal investment, and long-term behavioral and mental health outcomes, including cognitive performance, emotional regulation, behavioral control, and sociality in many mammalian species as well as in humans.

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