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Sex differences in the parental behavior of rodents

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Abstract

The reproductive strategy of many mammalian species that give birth to altricial young involves intense and prolonged care of their offspring. In most cases, the mother provides all nurturance, but in some cases fathers, older siblings, or unrelated conspecifics participate in parental care. The display of these behaviors by animals other than mothers is affected by numerous factors, including their sex. We herein review the literature on similarities and/or differences between male and female laboratory rodents (rats, mice, voles, gerbils, and hamsters) in their parental responsiveness and discuss how the parental behavior of males and females is influenced by hormones, developmental processes, and prior social experiences. Understanding the mechanisms that generate sex differences in the parental responsiveness of rodents may indicate how similar sex differences in parental care are generated in other mammals. © 2000 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The behavior of male and female animals differs in numerous ways, often most strikingly for behaviors associated with reproduction [108,181]. Parental behavior, which is arguably one of the most complex and intriguing behaviors displayed, is no exception and virtually all animal species ranging from insects [53,229] to primates [253] exhibit sex differences in their behavior towards offspring. In many mammalian species, the young are relatively altricial at birth, requiring intense and prolonged nurturance and protection to insure their growth and survival until reproductive age. In most cases these parental behaviors are predominantly shown by lactating females who undergo pregnancy and parturition. However, in very rare exceptions such as canids [133] or some monogamous primates [149,237], fathers provide almost exclusive care of the offspring with the exception of nursing. Yet in other species, both parents contribute to the rearing of their young. Neonates may also receive parental care from conspecifics other than their biological parents [208]. Unfortunately for the neonates, older conspecifics can display a wide range of responses towards them and nurturance is often tempered by indifference, avoidance, or even infanticide.

Whereas several excellent reviews have focused on

the physiological basis of postpartum maternal behavior in rats [13,58,161,213], the goal of the present review is to describe sex differences, or lack thereof, in the parental responsiveness of some widely studied laboratory rodents. This review will not focus on specific care-giving activities, such as retrieval, licking of the young, or nest building. A comprehensive cross-species comparison of such behaviors would be particularly difficult for numerous reasons. For example, different laboratories often do not evaluate parental behaviors in the same manner and there may also be species differences in whether particular behaviors are even displayed at all (e.g. parental rats readily retrieve pups whereas parental prairie voles do not [123,148,163,206]). We will instead primarily review sex differences in three general responses towards pups: nurturance, indifference/avoidance, and infanticide. The term *parental responsiveness* is used hereafter to indicate the general propensity of an animal to act parentally towards young. The term *parental behavior* will be used in a few cases to indicate specific nurturant behaviors, which may include nest construction, retrieval or licking of pups, as well as huddling or nursing behaviors. We will further examine the hormonal and non-hormonal factors during development and in adulthood that contribute to sex differences in these behaviors. Lastly, we will examine the ethological significance of sex differences in parental behavior and discuss how they may be relevant for offspring development in mammals.

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2. Laboratory rats

2.1. Sex differences in the parental responsiveness of subadult rats

As is true for most other behaviors, laboratory-bred Norway rats (*Rattus norvegicus*) have been the most extensively studied species with regards to sex differences in parental responsiveness. Rats are naturally non-gregarious and uniparental animals with the lactating dam normally providing sole care of the offspring [29]. Unlike most sexually and parentally naive adult rats, which avoid physical contact with pups when they are first introduced to them [227], subadult rats (prepubertal or pubertal, ~18–42 days old) readily approach pups and make physical contact with them. Contact is often followed by carrying, licking, and huddling over the pups, and the behavior of subadults resembles that of lactating dams. Careful observation, however, reveals numerous differences between subadult and adult behavior. In particular, the reliability of the display of parental behavior across testing and the patterning of the individual behaviors differs between subadult and adult rats [24,80,138,139,152]. Sex differences in parental responsiveness appear very early in development, and contrary to what may be expected, subadult male rats are more parentally responsive than subadult females. More males are spontaneously parental towards pups than females, and males that are not immediately parental eventually become parentally responsive after continuous exposure to pups [sensitization; 192] faster than females. Males also initiate contact with pups faster, retrieve them more readily, spend more time with them, and generally display parental behaviors more consistently than females [15,25,80,110,111,138,214,245,255]. Although some of these behaviors have not always been found to differ between males and females [24–26,138,139,141,170,210,255], there are no reports of a sex difference in the opposite direction (i.e. subadult females acting more parentally than males).

The sex difference in parental responsiveness changes as the laboratory rat ages. The high parental responsiveness displayed by young rats declines soon after weaning [141] and changes even more dramatically around puberty (~30 days old). Studies that reported sex differences either in the percentage of prepubertal subjects becoming parentally sensitized or in the number of days of pup exposure necessary for sensitization (sensitization latency) also reported an increase in sensitization latency around the time of puberty for both sexes [15,210,214]. This increase was particularly large in males, to the point where their latencies became similar to that of females [210,214]. Conversely, in studies where no sex differences were found prior to puberty, sensitization latencies increased for pubertal males and decreased for females to a point where a sex difference existed, with females being more parentally responsive than males [139,141].

2.2. Sex differences in the parental responsiveness of adult rats

Regardless of the ambiguity regarding how sex differences in parental responsiveness change during puberty in young laboratory rats, distinct and well-defined sex differences are consistently found by the time they are adults (>45 days old). Among groups of gonadally intact virgin animals, females are less likely to be infanticidal [20,104,105,150], and are either more spontaneously responsive to pups or more likely to become parentally sensitized than are males [54,127,139,147,174,176,192,197]. Females also display particular parental behaviors more consistently [80,141,192] and require lower doses of exogenous hormones to stimulate a rapid-onset of parental responsiveness [131] than do males. Two studies that reported no significant sex differences in the percentage of subjects becoming parentally sensitized are exceptions [14,177]. Although most studies have not found a sex difference in the sensitization latency of virgin adult rats that eventually showed parental behavior, a few have reported shorter latencies for responding females than for responding males [54,110,139,141,174,197].

2.3. Hormonal influences on sex differences in parental responsiveness in rats

The change from indifference to pups to high parental responsiveness in female rats that undergo the fluctuations in ovarian and pituitary hormones associated with pregnancy, parturition, and lactation [13,161,211] strongly suggest that hormones influence the propensity to act parentally. In fact, treating virgin female rats with a hormonal regimen that imitates these hormonal fluctuations dramatically reduces their latency to become parentally sensitized [13]. Furthermore, fluctuations or sex differences in circulating levels of gonadal hormone at any age can potentially contribute to sex differences in responses towards pups. The rat testes are steroidogenic both prenatally and postnatally, whereas the developing ovary may be relatively quiescent [204]. Only males, therefore, are exposed to significant levels of gonadal hormones during perinatal life and this early hormone exposure can have dramatic effects on behavioral development [252]. Although the role of perinatal gonadal hormones in the generation of sex differences in the parental behavior of subadult rats has not been studied, perinatal hormone levels may influence sex differences in parental responsiveness just as they influence sex differences in other reproductive behaviors. Infusions of blood plasma from parturient females facilitates parental responsiveness more in juvenile females than in juvenile males [25]. This suggests that sex differences in the ability to respond to gonadal hormones and other blood-borne factors for the display of parental behavior already exist before puberty, possibly because the behavioral response to exogenous hormones in males is already masculinized by

this time. It is surprising that unmanipulated juvenile males are more parentally responsive than females, because endogenous or exogenous testosterone does not facilitate parental responding in adult males [20]. It may be that neural systems that inhibit parental responsiveness or facilitate infanticide in adult males are not fully developed prior to puberty. Other blood-borne factors that may affect parental responding in juveniles may include prolactin, which stimulates parental responsiveness in adult rats [13], and is greater in juvenile males than in juvenile females [109].

As with prepubertal sex differences in parental responsiveness, few studies have examined the influence of prenatal gonadal hormones in generating sex differences in the parental responsiveness of adult rats. This influence may be inferred, however, from the increase in parental responding in male offspring of dams subjected to stress during pregnancy [110], a procedure that sometimes curtails other indexes of masculinization as well [31,240]. Numerous studies have examined the influence of postnatal gonadal hormones on paternal responsiveness in adult males. The most common finding is that gonadectomy before puberty decreases infanticide and increases parental responsiveness, with castration soon after birth being the most effective [20,127,147,174,190–192]. The one study reporting that castration as late as 60 days after birth still decreased infanticide is the exception [187], although this finding is consistent with the stimulation of infanticide by exogenous testosterone in males that are castrated as adults [20]. In addition to their own testicular secretions, males are also exposed to gonadal hormones from their mother. For example, they are exposed to progesterone and glucocorticoids of maternal origin prenatally via the placenta and postnatally via her milk [159,178]. Neonatal administration of the progesterone and glucocorticoid receptor blocker, RU 486, however, does not significantly change the percentage of males that become parentally sensitized as adults [127].

The influence of prenatal hormones on the development of maternal responsiveness in adult female rats is equivocal, with prenatal exposure to testosterone either masculinizing, (i.e. reducing) [100,107] or having no effect on their parental responsiveness as adults [175]. Although neonatal castration decreases infanticide and facilitates parental responsiveness in male rats, a single administration of testosterone to neonatal females does not masculinize their adult behavior towards pups [14,100,118,176,177,190]. In one case, however, neonatal treatment with testosterone did reduce females' parental responsiveness in adulthood [174] and relatively prolonged testosterone treatment neonatally followed by additional testosterone treatment during adulthood increased their infanticide [188,189]. Similar to males, neonatal exposure to progesterone or glucocorticoids does not appear to play a role in the development of parental responses in females since administration of RU 486 after birth has no significant effect on their sensitized or postpartum maternal behavior [127].

The role of endogenous ovarian hormones in the parental

responsiveness of virgin female rats is ambiguous because ovariectomy before puberty has been observed to either reduce [139,176], or have no effect on [210], their behavior during adulthood. However, ovariectomy during puberty decreases later maternal responsiveness [139] whereas ovariectomy after puberty has no effect on sensitization in subjects that are tested soon after surgery [78,127,192]. A decrease in parental responsiveness can be found in females that are tested many months after postpubertal gonadectomy, though [139].

In addition to gonadal hormones, sexual experience can also change the propensity of adult rats of both sexes to display parental or infanticidal behavior. In male Long-Evans rats, infanticide is inhibited after copulation and cohabitation with a female [20], which may prevent males from killing their own offspring. The mechanisms controlling this inhibition are unknown but may be similar to the reduction in male infanticide following continued exposure to pups, which is associated with reduced circulating prolactin [21]. In female rats, some aspects of maternal behavior appear even before parturition [140], indicating that ovarian secretions during gestation facilitate the onset of maternal behavior. In some strains of rats (Long-Evans) in which virgin or gestating females are highly infanticidal [168], pup killing is suppressed during the first two weeks of lactation but resumes again after weaning of the litter [169]. In females from other strains of rats, maternal responsiveness can be retained for much longer after exposure to gestational hormones and postpartum experience with pups [58]. Whether or not the effects of social experiences on parental responsiveness can be explained by changes in hormone levels, sex differences in social experience may also contribute to sex differences in parental behavior.

3. Mice

Mice (*Mus musculus*) are also highly popular rodents used in the study of parental responsiveness, and given the rapidly increasing use of mice as models of genetic influences on behavior, may one day surpass rats as the model of choice to study the physiological basis of parenting. Several studies have already examined the effects of highly specific genetic mutations (i.e. gene deletions) on parental behavior [19,121,162]. However, this topic is beyond the scope of our review and we will consider only the genetic influences resulting from selective breeding rather than from molecular engineering.

Unlike rats, mice can show great variability in their parental responsiveness across different studies, which is the result of numerous factors. One such factor is that the various strains of laboratory mice can dramatically differ in their responses to neonates, suggesting genetic influences on their parental responsiveness. Furthermore, domestication influences their parental responsiveness and we will discuss sex differences in the parental responses of laboratory strains of mice separately from those of wild house mice.

3.1. Sex differences in the parental responsiveness of subadult laboratory mice

Given the variability of parental behavior across different strains of mice, we will include their genetic background, if possible. Within some laboratory environments, mice of the Rockland-Swiss (R-S) and CFLP strains are biparental and males share in the caring for offspring [7,172]. In other cases, Rockland-Swiss and C57BL/10Gin males may share a nest with the lactating female but are not necessarily parental [70]. Unlike rats, sex differences in the parental responses of R-S laboratory mice are not evident early in life and most prepubertal mice of both sexes ignore pups. After they are approximately 32 days old, however, juvenile R-S male mice are likely to kill them [63]. Maternal responses in subadult R-S females are also low and while prepubertal females ignore pups, pubertal females tend to kill them [64].

3.2. Sex differences in the parental responsiveness of adult laboratory mice

By adulthood, virgin laboratory mice display a pronounced sex difference in their responses towards pups such that most adult virgin females are spontaneously maternal [R-S, Swiss-Webster, C57BL: 39,62,69,70,155–159¹,193,219] whereas many males (30–80%) are infanticidal [R-S, Swiss-Webster, CF-1, C57BL/6JxBALB/cCF strains: 6,62,63,132,165,193,220,221,232]. One study that did not demonstrate this sex difference is the exception [C57BL: 103]. The magnitude of the sex differences in parental responsiveness, particularly regarding the propensity of adult male laboratory mice to act parentally, varies in these studies. This variability may, in part, be explained by differences in the ages at which subjects are tested because young adult males are less likely to kill pups than older males [144,220]. Genetic differences between the various strains of laboratory mice are also likely responsible for differences between studies. In a direct comparison between adult C57BL/6J and DBA/2J mice, fewer DBA/2J males were infanticidal and more were parental compared to C57BL/6J males, whereas females from both strains were similarly maternal [220,223]. However, when young (<45 days old) females were compared, more DBA/2J than C57BL/6J females were parental [134]. Different strains of lactating female mice also show differences in their parental behaviors [16,22,119,241], indicating that genetics not only influence sex differences in the parental responsiveness of virgin mice but also these behaviors in lactating females.

3.3. Hormonal influences on sex differences in parental responsiveness in laboratory mice

Similar to rats, little is known of the mechanisms that

generate prepubertal sex differences in the parental responsiveness of laboratory mice. The increase in infanticide observed in 32-day-old male mice does not appear to be due to sudden increases in circulating testosterone that may accompany puberty because exogenous testosterone propionate administered to 22-day-old R-S mice does not elicit pup killing [63] and circulating androgen levels do not rise precipitously in peripubertal male R-S mice before they are 32 days old [222]. The change in parental responsiveness that occurs as females age is also not governed by gonadal activity because ovariectomy just before weaning has no effect on parental responsiveness at most ages, although early ovariectomy decreases maternal responsiveness in older R-S females [64].

Much is known about the role of gonadal hormones in the development and maintenance of sex differences in adult mice. Exposure to gonadal hormones during the perinatal period has an unusual influence on the later responses of virgin adult mice towards pups. Female R-S mice that have been exposed to testosterone neonatally and then again during adulthood are often infanticidal [62]. Neonatal testosterone treatment alone does not produce this effect and adult testosterone administration alone produces only a small increase in infanticide [62]. A similarly modest increase in infanticide [39,62,67] can also be elicited in adult R-S females by administration of the testosterone metabolites estrogen and dihydrotestosterone [219]. This increase in infanticide is reversed after hormonal treatment is terminated [39]. In contrast, other studies have found that R-S females that were exposed neonatally to exogenous androgens or estrogens are less likely to kill pups in response to adult treatment with testosterone propionate [68,198]. Similarly in males, neonatally castrated R-S subjects are more likely to kill pups in response to adult testosterone treatment than males castrated during adulthood [67,68]. These data generally suggest that neonatal exposure to androgens primes the mouse brain to be less responsive to the infanticide-inducing effects of later androgens. In support, the highly infanticidal C57BL/6J male mouse has much lower testosterone levels throughout their lifetime than do males from other strains [220,223]. Furthermore, the intrauterine position of male fetuses influences later parental responsiveness. In polytocous (litter-bearing) species such as laboratory rodents, male CF-1 fetuses flanked by two male fetuses (2M males) in utero are exposed to greater levels of androgens than males flanked by two females (0M males) [233,234] and are less likely to commit infanticide than 0M males [165]. Intrauterine position has no effect on the behavior of virgin female R-S mice [112]. It is possible that pre- and neo-natal exposure to androgens affects parental responsiveness of males and females differently under normal conditions or when they are administered exogenous testosterone during adulthood.

Similar to rats [131], the physiological substrates for parental behaviors are sexually differentiated and adult female CFW mice are more responsive than males to

¹ Noirot [155–160] describes her mice only as “from an outbred strain”.

exogenous hormones for the stimulation of some maternal behaviors such as nest building [122]. In adult virgin female R-S and other² strains of inbred mice, circulating pituitary and gonadal hormones are not necessary for their high levels of maternal responsiveness because neither hypophysectomy nor ovariectomy affects their behavior [39,64,117], although one study of NMRI females found a decrease in maternal responsiveness after adult ovariectomy [114]. On the other hand, infanticide in R-S males is greatly influenced by circulating gonadal hormones. Although their responses to pups do not correlate well with levels of circulating androgens [221], males that are castrated during adulthood show lower levels of infanticide than intact males, but only if they do not have prior killing experience [67].

Differences in parental responsiveness between mouse strains may be partly due to genetic differences in responsiveness to hormones, as well as to differences that are independent of hormones. Even after neonatal ovariectomy followed by identical hormone treatments during adulthood, C57BL/6J and DBA/2J female mice still differ in their propensity to kill pups [134]. No differences between strains are found, however, if females are ovariectomized during adulthood and then receive exogenous testosterone [220]. In contrast, castrated adult DBA/2J males are more infanticidal than castrated C57BL/6J males either with or without daily injections of testosterone and regardless of the time of castration [220,223]. Furthermore, perinatal treatment of C57BL/6J males with TP cannot increase infanticide to the levels displayed by DBA/2J males in adulthood [223].

Mating dramatically changes parental responsiveness in laboratory mice. Mated female mice show an abrupt decrease in parental responsiveness within a day after insemination followed by a gradual increase until the normally high levels of responsiveness return within one week of parturition [159]. Perhaps not surprisingly, lactating R-S females are also highly maternal towards pups from other dams, and cannot be provoked to kill pups even if administered testosterone [66]. Once the pups are weaned, however, some primiparous females will commit infanticide [66]. Mated R-S, CFLP, and C57BL/10G males cohabitating with their mates are also highly parental [7,172], or at least not infanticidal [70]. The full inhibition of infanticide in mated CF-1 male mice is first observed around the time when their mates are due to give birth and the stimuli associated with copulation, particularly that of ejaculation, are necessary for this inhibition [165,231,232].

3.4. Sex differences in the parental responsiveness of wild house mice

In natural or semi-natural environments, wild house mice live in extended familial groups consisting of a dominant male, several breeding females and their pups, and several subordinate males [17,180]. We are not aware of any scien-

tific reports on the parental behavior of wild house mice within their natural environment, but biparental behavior is likely in animals living under these communal conditions. In contrast to laboratory strains of adult mice, which display a sex difference in parental responsiveness prior to mating, virtually all virgin wild adult house mice of both sexes are infanticidal when tested in the laboratory [103,142–145,166,207]. There are also no sex differences in the parental responsiveness of juvenile wild house mice (<40 days old), but juveniles of both sexes are generally less likely to kill pups than adults [143,144].

3.5. Influences on parental responsiveness in wild house mice

Adrenal or ovarian hormones are not responsible for the high frequency of infanticide in adult virgin female wild house mice; adrenalectomy alone or in conjunction with ovariectomy either before or after puberty does not prevent later pup killing [146]. Unlike rats, ovarian hormone fluctuations during pregnancy do not inhibit infanticide in female mice, at least not rapidly, because they are infanticidal throughout pregnancy [143,207]. Only after parturition do most dams refrain from killing pups [143,207], though some are still infanticidal [143]. There is apparently no lasting effects of maternal experience in wild female house mice because wild female mice quickly resume their infanticidal behavior after weaning or removal of their young [143,207].

Although there appears to be no sex differences in parental responsiveness in unmanipulated wild house mice, they show sex differences in the effects of exposure to pups during development on parental responsiveness in adulthood. Whereas prepubertal experience with pups significantly facilitates parental responsiveness in adult virgin males, similar early experience has no permanent effect on the behavior of females [103,142]. Furthermore, whereas repeated exposure to pups during adulthood eventually renders males more parental, it does not in females [207].

Male wild house mice are much more flexible in their parental responsiveness than females. Not only do they more readily show sensitization after repeated pup exposure as weanlings or adults, but they stop killing pups during their mate's pregnancy more rapidly than their mates [145,207]. The precise time at which mated males begin displaying parental behavior is unclear since it has been demonstrated to begin both early [207] and late [145] in their mate's pregnancy. Unlike their mates, males show a lasting effect of mating and interaction with pups on their parental responsiveness and only half of the males resume killing pups after removal of their own young [207]. The stimuli critical for the inhibition of infanticide in mated wild male house mice is also not clear. Although one report demonstrates the need for copulation [145], another report shows that cohabitation with a pregnant female alone inhibits infanticide in virgin males [115,207] as well as in

² Strain of mice used by Le Blond and Nelson described as "inbred".

sexually experienced males [115]. This inhibition of infanticide after mating is context-specific and is not observed if males are returned to their own home cage in the absence of their mates [144,145].

As could be suspected, genetic influences also largely underlie differences in parental responsiveness between wild house mice and laboratory mice. Furthermore, these genetic influences are sex-specific. In hybrids obtained from mating laboratory and wild mice, the behavior of males virtually always reflects the maternal phenotype. If the mother was wild, most males are infanticidal. Conversely, if the mother was of a laboratory strain, fewer males kill pups and more are parental. The behavior of female hybrids, however, is always similar to that of the laboratory strain [166].

3.6. California mice

Male and female California mice (*Peromyscus californicus*), which belong to a different genus of the murid family than laboratory and wild house mice, form long-term, monogamous pairbonds after copulation [42] and display biparental behavior after the birth of pups [83]. Unlike young rats, relatively few juvenile and young virgin adult California mice of either sex are spontaneously parental [86], and even fewer older virgin mice are parentally responsive. Exposure to younger siblings only temporarily facilitates parental responsiveness in juvenile California mice, but this effect is completely lost by adulthood [86]. Whereas most adult virgin males are non-parental [87,88], parental responsiveness increases in many male California mice soon after copulation and cohabitation with their pregnant mate [85,88]. Most males, however, remain infanticidal until the birth of the pups [88], after which they are highly parental. Exposure to pups is not necessary to maintain parental responsiveness in males for the first three days after birth [87], but if both dam and pups are removed after parturition, fewer males act parentally and those that displayed a propensity for infanticide prior to the birth of the pups will commit infanticide when re-exposed to them [87,88]. These changes in parental responsiveness indicate that sensory cues from the lactating dam maintain parental responsiveness in males. Direct tactile cues from the dam are not a critical factor because sires remain paternal even if they are separated from their mate by a wire barrier. Instead, males may require exposure to their mate's excretions for the maintenance of their paternal behavior, suggesting that olfactory cues are necessary [85].

California mice are also an interesting example of how sex differences in specific physiological needs contribute to sex differences in particular parental behaviors. In the first two weeks after birth, females display more anogenital licking of pups, and accordingly, ingest more pup urine than males. The sex difference in anogenital licking disappears three weeks after birth of pups, when the osmolarity of the urine is reduced [83,84]. Because ingesting urine partly

offsets the loss of water and electrolytes that occurs during lactation, females would presumably benefit more from anogenital licking than males. It is not known whether other biparental species show similar sex differences in anogenital licking.

The hormonal basis of parental behavior in male California mice is unknown, but plasma prolactin levels are higher in fathers than in other males [87] and increases in circulating oxytocin levels after copulation and during their mate's pregnancy have also been suggested to play a role [91]. Little is known about the regulation of maternal behavior in female California mice, but stimulation from pups after parturition is necessary to maintain their maternal behavior whereas the continued presence of the sire is not [88].

4. Voles

4.1. Meadow voles

Members of the genus *Microtus*, which also belong to the murid family, provide a unique model in which to examine closely related species that differ considerably in their social organization and reproductive strategies, including the display of parental behavior. In polygamous and seasonally breeding meadow voles (*M. pennsylvanicus*) trapped in the northeastern United States, only lactating dams care for the young [148,163] and sexually experienced males do not readily display parental behavior [4,163,238,246]. However, the degree of parental responsiveness displayed by adult male meadow voles depends on numerous factors including their geographic origin, photoperiod, ambient temperature, testing conditions, as well as reproductive history [216,217,243,244]. In meadow voles trapped in high latitudes of North America, virgin males are highly infanticidal [216,217,244]. However, if they are housed under long daylight conditions that simulate their natural breeding season, they are more likely to be parental than males housed under short daylight conditions [164]. Even during short daylight conditions, however, males may nest with their mate and offspring during extremely cold temperatures [243]. Males with recent sexual experience also not only resist killing their mate's pups but act paternally towards them [216,218,244], although they may still kill the offspring of unfamiliar females [244]. In mated male meadow voles, it is not clear which stimuli inhibit infanticide after sexual experience. Copulation itself does not enhance paternal responsiveness and males are parental only relatively late in their mate's gestation [215], and the importance of copulation may be influenced by photoperiod [164]. Furthermore, continuous cohabitation with the pregnant female is also unnecessary for the sire's inhibition of infanticide towards his own pups [244], but chemosensory and tactile cues from the dam and pups inhibit his killing of unrelated pups [217]. Apparently, nothing is known about

possible differences in the parental responsiveness of virgin, pregnant, and lactating female meadow voles.

4.2. *Prairie voles*

4.2.1. *Parental responsiveness in pairbonded prairie voles*

In contrast to meadow voles, prairie voles (*M. ochrogaster*) are a socially monogamous species in which members form stable pairbonds after copulation and show biparental behavior under natural and laboratory conditions [30]. The repertoire of parental behaviors displayed by pairbonded male and female prairie vole parents is identical [123,206]. In fact, both males and females display kyphosis (upright crouched nursing/huddling posture), even though male prairie vole do not lactate or have nipples upon which the pups can suckle [123]. This is surprising considering the importance of suckling for the display of kyphosis in lactating rats [213]. Although the repertoires of parental behaviors are identical in male and female prairie voles, the patterning of these behaviors during interactions with pups differ between the sexes [123], likely reflecting the different somatosensory inputs that male and female parents receive from their offspring (e.g. suckling).

Sexually experienced female prairie voles are infanticidal in the early stages of pregnancy [230], and similar to rats, the hormonal fluctuations during late gestation and parturition are probably responsible for the onset of maternal behavior around the time of parturition. Of course, pairbonded males do not undergo the changes in gonadal hormones experienced by their pregnant mates so other, yet unknown, mechanisms must be responsible for their high parental responsiveness [124].

4.2.2. *Parental behavior in virgin prairie voles*

In contrast to the similarities between the parental behaviors of pairbonded and parentally experienced male and female prairie voles, there are striking sex differences in the parental responsiveness of virgin prairie voles. Upon their very first exposure to pups, most adult virgin males are highly parental whereas most virgin females are infanticidal [4,5,124,125,185,239]. Virgin female prairie voles show an age-related decline in their maternal responsiveness such that the nurturant responses towards pups observed in juvenile females gradually declines by three months of age, after which most are infanticidal [126]. Neither ovariectomy at weaning nor altering the sex ratio of littermates in the postweaning environment prevents this decline in females' maternal responding [126]. Similar to rats [214], extensive or relatively short interactions with pups beginning immediately after weaning does, however, permanently render virgin females more parentally responsive [126,185]. Furthermore, adult virgin females that continue to interact with their dam and sire after weaning are also highly parental, to the point where the percentage of parental females is similar to that of adult virgin males [123]. This is true even if the dam and sire do not have

any other litters of pups, and it is possible that an olfactory cue emanating from one or both of the parents maintains a juvenile-like level of parental responsiveness in their adult virgin daughters.

4.2.3. *Hormonal influences on parental behavior in prairie voles*

The hormonal basis for the similarities between male and female prairie voles in their parental responsiveness after pairbonding, or the differences between the sexes prior to copulation, is unknown. In virgin animals, sex differences are not due to circulating gonadal hormones after the perinatal period because gonadectomy at weaning or during adulthood has no effect on the later behavior of either sex towards pups [124,126, Lonstein, unpublished data]. Circulating prolactin also does not appear to mediate this sex difference because inhibition of prolactin release from the pituitary gland with the dopamine agonist bromocriptine (0.4 mg/day, intraperitoneal injection for 10 days) [8], also does not affect the behavior of either sex [Lonstein, unpublished data]. Similarly, the paternal behavior of adult virgin males is apparently not influenced by glucocorticoid or progesterone receptor activity because antagonism of these receptors with RU 486 (1 mg/day subcutaneously for four days) does not reduce paternal behavior [Lonstein, unpublished data].

As detailed above for laboratory rats and mice, differential exposure to gonadal hormones during the perinatal period can be important for the generation of sex differences in parental responsiveness. In virgin prairie voles, however, gonadal hormones during the prenatal or early postnatal period seem to have only a small role in the development of parental or infanticidal responses. Neither prenatal nor postnatal exposure to testosterone, nor their combination, masculinizes the behavior of females (i.e. inhibits infanticide or promotes maternal behavior). If anything, prenatal testosterone tends to increase females' infanticide [125]. In males, inhibition of androgenic or estrogenic activity via the anti-androgen flutamide or the aromatase inhibitor ATD, respectively, during either the prenatal or postnatal period does not feminize their paternal responsiveness (i.e. promote infanticide or inhibit paternal behavior) [125]. Eliminating the influence of gonadal hormones throughout most of their life by prenatal inhibition of steroid hormone activity in conjunction with neonatal castration also does not have much effect on the behavior of males [128]. Hormones from other sources, such as glucocorticoids from the adrenal glands, may act perinatally to influence the development of parental behavior of adult virgin prairie voles. Neonatal administration of corticosterone reduces later parental responding in juvenile and young adult female prairie voles [186], but it is unknown whether it has any effect on the already very low maternal responsiveness of older virgin females.

5. Hamsters

5.1. Golden hamsters

Sex differences in the parental responsiveness of hamsters have not been extensively investigated and depend on the species observed. Golden hamsters (*Mesocricetus auratus*) are solitary animals and mothers presumably provide exclusive care of the offspring [195]. Pregnant and lactating females are extremely aggressive towards males, thereby preventing their mates from approaching the pups [247]. However, males may sometimes be accepted into the natal nest by their mates and allowed to contact the young [137].

In juvenile golden hamsters, both sexes are highly parental and infanticide is first observed when subjects are approximately 37 days old. Interestingly, this increase in infanticidal tendencies happens only in hamsters living in the natal nest with their dams. Young adults that are weaned from the natal nest are highly parental [196], suggesting that sensory cues from the dam actually promote infanticide in her offspring. Since female hamsters do not have a postpartum estrus [82], maternal encouragement of infanticide in her weanlings could be beneficial from an evolutionary perspective because young pups that are present in the natal nest during the first litter's weaning period could not possibly be the offspring of the dam and must be unrelated.

Sex differences in parental responsiveness become pronounced once virgin golden hamsters reach adulthood. Unlike rats, in which virgin females are more responsive to pups than virgin males, virgin female golden hamsters are much less parentally responsive than virgin males. Whereas the majority of adult virgin males are spontaneously parental, most virgin females are infanticidal [136,151,182,183,196,225,247]. Furthermore, the neural substrates responsive to hormones for some components of parental behavior in hamsters may be sexually dimorphic as well because a regimen of exogenous hormones that stimulates parenting in virgin females does not change parental responsiveness in males [184]. These sex differences may partly depend on the conditions under which parental behavior is tested because one study that tested subjects in their home cage instead of in an unfamiliar testing chamber found that both sexes displayed relatively low levels of spontaneous parental behavior and that virgin females were more responsive than virgin males [225].

5.2. Hormonal and experiential influences on parental responsiveness in golden hamsters

Similar to other rodents, sex differences in the parental responsiveness of adult golden hamsters do not depend on circulating gonadal hormones and gonadectomy during adulthood does not affect the behavior of either sex towards pups [136]. Parental responsiveness of virgin females is probably influenced by multiple factors, including the age

of the stimulus pups [183], but it is not clear whether experience with pups influences their behavior as it does in other rodents because repeated exposure to the same-aged pups does not reduce females' likelihood to be infanticidal [135,160]. In other cases, however, virgin females may become maternally sensitized very rapidly (within 24 h), though the sensitization experience is not permanently retained [225].

The onset of maternal behavior in pregnant golden hamsters is relatively sudden compared with the more gradual increase in responsiveness sometimes observed in pregnant rats; only within hours before parturition do most female hamsters desist from killing pups [28,38,202]. Even postpartum female golden hamsters are infanticidal, often cannibalizing a portion of their litters within 72 h after parturition or killing unfamiliar pups that are introduced into her cage [40,182,194]. This postpartum infanticide appears to be the rule rather than the exception but can be influenced by many factors including litter size [40], food accessibility [116,199], the possibility of food hoarding [151], and population density [76,77].

5.3. Siberian hamsters

Like golden hamster pups, Siberian hamster pups (*Phodopus sungorus*) are reared solely by their dams [250]. Similar to rats and mice, juvenile Siberian hamsters are less likely to attack pups than adults, but there is no significant sex difference in their behavior at this age [74]. In contrast to golden hamsters, virgin adult male Siberian hamsters are less parental than females and often attack pups [73,74]. Remarkably, this sex difference reverses after sexual and parental experience. A small number of male Siberian hamsters do provide minimal parental assistance starting as early as the dam's parturition [106] and males that have cohabitated with their mates until weaning of their offspring are invariably parental towards test pups [74]. Conversely, a small percentage of their mates are still infanticidal [74].

5.4. Djungarian hamsters

The Djungarian hamster (*Phodopus campbelli*) has a different reproductive strategy than its close relative, the Siberian hamster, and is biparental both in laboratory and natural environments [106,249–251]. Nothing is known about sex differences or similarities in the behavior of virgin or sexually experienced Djungarian hamsters. Virgin adult females may not be infanticidal because lactating dams living with a virgin female sibling can successfully rear a litter to weaning [249,250], though this may be due more to the dam's protection of her litter rather than the behavior of the Djungarian hamster "aunt". The hormonal basis for the biparental behavior of Djungarian hamsters is also unknown but an increase in circulating testosterone after mating and its precipitous reduction after the birth of pups concomitant with an increase in prolactin has been suggested to be important

Table 1

Sex differences in the parental behavior of laboratory rodents (U = uniparental lactating female provides almost exclusive care of young. B = biparental both lactating female and mate provide care)

Species	Biological parents	Virgin animals		
	Parental strategy	♀ high/♂ low	♀ low/♂ high	♀ = ♂
<i>Rattus norvegicus</i>	U [29]			
Juveniles		–	[15,25,80,110,11,138,214,245,255] ^a	[24–26,138,139,141,170,210,255] ^a
Adults		[20,54,104,110,127,139,141,147,150,174,176,192,197]	–	[14,177] ^b
<i>Mus musculus</i>	B [7,172,115,145]			
Laboratory juveniles		–	–	[63,64] ^c
Laboratory adults		[6,39,62,63,69,70,132,155–159,165,193,219,220,221,232]	–	–
Wild juveniles		–	–	[133,134] ^c
Wild adults		–	–	[103,142–5,166,207] ^c
<i>Peromyscus californicus</i>	B [83]			
Juveniles		–	–	[86] ^c
Adults		? ^d	?	?
<i>Microtus pennsylvanicus</i>	U [148,163]			
Juveniles		?	?	?
Adults		? ^d	?	?
<i>Microtus ochrogaster</i>	B [30,123,206]			
Juveniles		? ^e	?	?
Adults		–	[4,5,123–126,185,239]	–
<i>Mesocricetus auratus</i>	U [195]			
Juveniles		–	–	[196] ^b
Adults		[225]	[136,151,182,183,196,247]	–
<i>Phodopus sungorus</i>	U [250]			
Juveniles		–	–	[74] ^b
Adults		?	?	?
<i>Phodopus campbelli</i>	B [106,249–251]			
Juveniles		?	?	?
Adults		?	?	?
<i>Meriones unguiculatus</i>	B [1,45,49,242]			
Juveniles		–	–	[47] ^c
Adults		–	[47]	–

^a Only true for some measures.

^b Both sexes moderately or highly parental.

^c Neither sex highly parental, most either ignoring or killing pups.

^d Males not parental, females unknown.

^e Females parental, males unknown.

for their parenting [179]. As with voles, the close relationship between Siberian and Djungarian hamsters makes these animals a useful model for studying which factors contribute to species differences in parental behavior.

6. Gerbils

Mongolian gerbils (*Meriones unguiculatus*) are biparen-

tal [1,45,49,242]. Juvenile gerbils of both sexes are unlikely to cannibalize pups, but are apparently not parental either, and become more infanticidal as they age [47]. This is particularly true for females, which as adults are much more likely to kill pups than males [47]. The nature of the social environment prior to weaning seems to have little effect on the behavior of virgin males. Males reared with their dam alone, both parents, or both parents and the parent's subsequent litters show similar frequencies of

infanticide [47]. After mating, female and male gerbils display different types of changes in parental responsiveness. Most pregnant females remain infanticidal until approximately one week before parturition, when nest construction increases [235] and infanticide decreases—but does not disappear [48]. Infanticide is virtually absent after parturition [34,48] and the presence of the litter is critical for the dam's inhibition of infanticide. If females are permitted to remain with their litters, infanticide of pups other than their own is suppressed during the first two weeks postpartum but resumes thereafter. Sensory cues emanating from younger pups are particularly effective in inhibiting infanticide in lactating dams because this inhibition can be prolonged if older litters are replaced with younger ones [48]. Unlike rats [12,209], gerbils show no long-term effects of parturition or brief contact with pups on parental responsiveness because if the pups are permanently removed soon after birth, dams become infanticidal within a few days [48]. Moreover, prior maternal experience also does not facilitate parental responding to pups or to auditory cues from pups when females are pregnant with a second litter or are no longer breeding [46,113]. Although there are no data on the role of gonadal hormones on the development of parental responsiveness in female gerbils, it varies according to the rate that they reached sexual maturity [35], suggesting that hormones facilitate their parental behavior.

Like virgin male gerbils, sexually experienced male gerbils are less infanticidal than their female counterparts and show an even further decline in infanticide within two weeks prior to their mate's parturition [46,47,51]. Sensory cues from the pregnant female gerbil mediate this decline because males resume pup killing within three days after being removed from their mates [40]. Direct physical contact with the lactating dam [50] rather than pheromonal cues and other olfactory stimuli emanating from her [71,235] are responsible for this inhibition of infanticide. Unlike parentally experienced females, once males obtain parental experience, they are never again infanticidal [46,50].

There is only indirect evidence suggesting that gonadal hormones influence parental responsiveness in male gerbils. Males that were gestated between two other male fetuses have higher levels of circulating testosterone as adults and are less parental towards their own offspring than males gestated between two females [34,36]. Although these lower levels of parental responsiveness suggest that higher levels of testosterone inhibit paternal responsiveness, it is unclear when testosterone generates this effect. If testosterone acts primarily in adulthood to alter parental responsiveness, the slow rise in circulating androgens after mating followed by the sharp decline after the birth of pups may inhibit infanticide and increase paternal responsiveness [23].

7. Proximate mechanisms underlying sex differences in parental responsiveness

It is clear that sex differences in behavioral responses towards pups are common in many species of laboratory rodents (Table 1). One question that arises regarding the proximate mechanisms underlying these sex differences is exactly how hormones act to produce these differences. One obvious answer is via their actions on the central nervous system. Unfortunately, very little is known about the neural regulation of parental behaviors in any rodent species other than rats and we believe that it is rather unlikely that this information wholly extends to the control of parental behaviors in all other rodents. However, at least one neural site that is responsive to hormones for the onset of some parental behaviors in rats, the medial preoptic area (mPOA) [161], contains a sexually dimorphic subnucleus (the sexually dimorphic nucleus, SDN) that is several times larger in males than in females [79]. Sex differences in this structure may be related to the sex differences in parental behavior in virgin rats, and possibly other species. For example, the sex difference in SDN-POA volume of voles is much smaller in the monogamous and biparental prairie vole than in the polygamous and uniparental montane vole (*Microtus montanus*) [201]. Numerous examples, however, fatally undermine an argument that sex differences in mPOA morphology alone can explain sex differences in the parental responsiveness of all rodent species. First, the sexual dimorphism in the mPOA of rats also exists before puberty [102], when sex differences in their parental responsiveness are reversed (i.e. males are more responsive than females). Second, adult virgin laboratory mice also show sex difference in their responses to pups similar to that of adult virgin rats, even though mice of most strains have no SDN at all [18,254]. Third, the mPOA of virgin gerbils shows one of the most extremely sexually dimorphic structures found in the mammalian brain, such that males have a structure (sexually dimorphic area, pars compacta; SDAPc) that is not even identifiable in females [37]. Although the direction of the sex difference in gerbil SDAPc is similar to that of the rat SDN, the sex difference in the parental behavior of virgin gerbils is the opposite of that found in rats (i.e. females are less parentally responsive than males). Furthermore, the magnitude of the sex difference in the size of the mPOA is larger in adult virgin California mice compared with sexually experienced counterparts [89]. In this case, however, there are no sex differences in their behavior but only differences according to reproductive state; virgin adult California mice of both sexes are not parental whereas sexually experienced males and females are.

Other sexual dimorphisms in the rodent brain have also been suggested to be important for sex differences in parental behavior, but are as unlikely as sex differences in the structure of the mPOA to be singularly important for sex differences in parental responsiveness. Central projections of the neuropeptide arginine-vasopressin (AVP) that arise in

the medial amygdala (mAMY) and bed nucleus of the stria terminalis (BNST) terminate in the lateral septum and lateral habenula and are highly sexually dimorphic in many animals, including all rodent species investigated, such that males express much more AVP than females [41]. Although changes in septal AVP after mating and birth of pups have been suggested to be related to high levels of parental behavior in male prairie voles [4,5], and septal injection of an AVP antagonist may decrease paternal behavior in virgin male prairie voles [27,239], it is not essential for male nurturant behavior because castrated males with virtually no AVP in their septum are highly parental [124]. Similarly, virgin male golden hamsters are parental even though they do not express AVP in their septum at all [52]. Any relationship between septal AVP and parental behavior in rodents cannot be simply correlational because the direction of the sex difference in central AVP expression is similar in prairie voles, rats, and mice — three species that show very different patterns of parental responsiveness between males and females.

Sex differences also exist in central opioid peptides, which inhibit maternal behavior in postpartum rats when applied to the mPOA [13]. This system also cannot explain sex differences in parental responsiveness in virgin rats because even though females have fewer β -endorphin immunoreactive fibers in the mPOA than males [203], they may be more sensitive to central opioid peptides because they have more μ receptor binding sites [92].

Although singular sex differences in these higher neural structures are unlikely to explain how sex differences in parental behavior are generated, prenatal and postnatal exposure to gonadal hormones must somehow influence the development and/or sexual differentiation of central and peripheral nervous system structures that are ultimately necessary for parental responding. It is unlikely that this sexual differentiation affects the systems involved in the motor control of parental behavior given that there are no obvious sex differences in the mechanics of specific parental behaviors, merely in the likelihood that such behaviors are displayed. Rather, it is more likely that sex differences in the perception and processing of sensory cues from pups are responsible for sex differences in parental responsiveness [200]. Indeed, there are sex differences in the function of numerous sensory systems and gonadal hormones have profound effects on sensory perception and discrimination [65]. For example, gonadal hormones can affect somatosensory processing, which is critical for parental responding in female rats [213]. Estrogen can enhance somatosensation in the perioral region in rats [9], which is necessary for oral components of parental behavior such as retrieval [213]. Sex differences can also be found in the sensitivity of the ventral trunk of rats, such that virgin females are more likely than males to show the kyphotic nursing/huddling posture in response to non-suckling stimulation from pups [212]. Interestingly, male prairie voles are almost as likely to show kyphosis in response to non-suckling ventral stimulation as their mates are to suckling stimulation [123]. Sex differ-

ences in other sensory systems such as the olfactory system [200], which may be involved in discriminating pups from other conspecifics, can be readily related to sex differences in parental or infanticidal behaviors. Olfactory cues from pups stimulate multiple neural sites within the main and accessory olfactory systems that are inhibitory to parental responsiveness in virgin rats [56,57,59,150,200]. One olfactory site — the medial amygdala — is larger in male rats than female rats [97]. The larger size in males seems to be correlated with their greater reluctance to act parentally. Sexually dimorphic characteristics in the olfactory pathways of other rodents [101,224] may also contribute to sex differences in their propensity to be parental. However, a comparison of this sex difference across species and ages may reveal similar inconsistencies as those indicated above for the other sexually dimorphic systems that have been related to parental behavior. Rather than correlating sex differences in neural structure with sex difference in function, studies that focus on sex differences in neural activation to specific sensory stimuli and sex differences in parental responsiveness may give a better understanding of the neural mechanisms that contribute to these sex differences in behavior.

It is also likely that sex differences in behaviors that at first may seem completely unrelated to parental behavior contribute to sex differences in nurturance. One example is the vulnerability to fear- or anxiety-provoking stimuli. Virgin rats [127], mice [3], meadow voles [167], and Mongolian gerbils [33] show sex differences in the levels of fearfulness, and the sex that is less fearful may also be less susceptible to novelty-induced anxiety generated by pups. Since a reduction of fear could be necessary for parental responses in some rodents [55,94,129], sex differences in basal levels of fear may translate to sex differences in parental responding. This hypothesis could be tested by administering anxiolytics, which may eliminate sex differences in parental responsiveness [93], provided that there are no sex differences in sensitivity to the anxiolytics themselves.

8. Ultimate mechanisms underlying sex differences in parental behavior

A second question that arises regarding sex differences in parental or infanticidal behaviors of rodents involves the ultimate mechanisms driving these sex differences. That is, why are these sex differences selected for, and how do they affect individual survival, population dynamics, and propagation of genes to the next generation within the natural environment? Large sex differences in nurturant behavior of biological parents may simply be due to sex differences in reproductive costs that promote high maternal and low paternal care [228]. In cases where parents show no sex differences, such as biparental species that are socially

monogamous, and where the certainty of paternity is high (e.g. mice, prairie voles, Djungarian hamsters, and Mongolian gerbils), it may be obvious that the parental contributions of both the dam and sire would be advantageous for survival and development of the offspring [49,90,238,251]. Even within these species, however, the sire's presence has sometimes been shown to have either no effect, or even detrimental effects, on pup survival within laboratory environments [2,72,172]. This may, in part, be due to the relatively benign conditions within the laboratory; the sire's presence may be more advantageous under the relatively harsh conditions of a natural environment [205,236].

The ethological significance of sex differences, or lack of them, in the parental behavior of sexually inexperienced laboratory rodents is completely unknown. Infanticide under certain conditions may be important for reproductive fitness of the killer, perhaps by reducing competition for resources or terminating suckling-induced anovulation in lactating females, which could hasten a male's opportunity to mate [95,98]. In most cases, however, the relevance of infanticide is not obvious. Similarly, the nature of sex differences and the mechanisms underlying them cannot easily be related to the social organization and reproductive strategy of each species, as patterns of parental behavior differ even between species with very similar social structures. For example, species with communal social organizations such as prairie voles and mice do not show similar sex differences in parental responsiveness, nor do non-gregarious species such as rats and golden hamsters. Although these inconsistencies may be due to peculiarities specific to the environmental demands of each species, one has to consider that similarities or differences in parental responsiveness of males and females may sometimes be an artifact of the laboratory setting. In most rodent species, parturient dams undergo a postpartum estrus [75] and would, in nature, probably be inseminated soon after parturition and give birth to a second litter of pups three to four weeks after birth of the first litter. Since most three- to four-week-old juvenile rodents have probably not yet dispersed from the natal nest [32,226], their first experience with newborn pups would likely be with their younger siblings. Although dams may discourage continued suckling by the older litter, the weanlings continue to spend a great deal of time in the natal nest and have extensive physical interactions with the neonates [29,153,214]. In these cases, it would be beneficial for the dam and her younger pups if the weanlings displayed low levels of infanticidal behavior and provided parental assistance. As noted above, juveniles of many rodent species such as rats, mice, and prairie voles are highly parental and their presence in the natal nest can contribute to, or at least have no significantly negative consequence on, the development of the neonates [205,248]. Since prepubertal interactions with pups renders virgin rats, mice, and prairie voles more parental when re-exposed to pups as adults, the parental behavior of adult virgin animals in natural environments must differ from that observed within

the laboratory, where juveniles are typically removed from the natal nest and housed with same-sex littermates at weaning.

9. Implications of sex differences in rodent parental behavior

It is clear that more research is required to understand how and when gonadal and other hormones influence the development of parental behaviors in male and female rodents. Even in rats and mice, which have been the most extensively examined species, experiments manipulating perinatal (particularly prenatal) androgen or estrogen activity with receptor antagonists or aromatase inhibitors are necessary to define the "critical periods" during which gonadal hormones influence the development of sex differences in parental responsiveness. Cross-species comparisons would be particularly useful for understanding these mechanisms, because they reveal the range of possibilities by which these behaviors can be influenced during development. As indicated above, another avenue of investigation that is sorely lacking is determining how sex differences in parental care influence offspring development in semi-natural or natural environments. Investigation of these sex differences within a laboratory environment can be exploited to unravel the pathways possibly involved in parental behavior, but since the sex differences may only be an artifact of the laboratory condition, there are limits on the amount of information that this experimental path can provide. In some cases, the relevance of sex differences in parental responsiveness may be demonstrated only under natural circumstances.

Examining the mechanisms underlying sex differences or similarities in parental responsiveness of rodents may provide insight into the mechanisms underlying parental behavior in other species, including non-human and human primates. In some non-human primates such as rhesus macaques [130] as well as humans [11], sex differences in parental responsiveness present themselves very early in life. These sex differences may result from early sex differences in exposure to gonadal hormones. Sex differences in non-human and human behavior towards neonates or time spent conducting caregiving activities can also extend into adulthood [60,61,171]. A possible example of hormonal influences on parental responsiveness in humans may be found in females with congenital adrenal hyperplasia (CAH), a condition caused by a deficiency in the enzymes necessary for steroidogenesis within the adrenal glands, ultimately resulting in a hypersecretion of adrenal androgens [154]. In addition to physical masculinization, females with CAH are less interested in infants [43,120], score lower on measures of parental or nurturant tendencies [96], and show less parenting "rehearsal" behaviors such as doll play or infant care [44] compared with unaffected females. These differences in females with CAH may be particularly due to their greater exposure to androgens

during prenatal, rather than early neonatal, life [10]. Although hormones may play a role in generating sex differences in human caregiving behaviors, social, cultural, and economic factors are often viewed as equally or more important influences [99] and human parents can display very similar attitudes and behavioral responses towards their newborn offspring [81,171,253]. Although we believe that there are risks involved in considering sex differences in the darker side of human responses to infants, such as neglect or abuse, from a purely biological perspective, not considering such factors may be equally irresponsible by impeding the prevention or treatment of such behaviors.

10. Summary and conclusions

In most mammalian species, males and females respond differently to neonates. In rodents, numerous factors influence the motivation to act parentally [173], and many of these factors contribute to sex differences in parental responsiveness. Sex differences or similarities in the parental responsiveness of laboratory rodents cannot be easily predicted by the social organization of a species, and a myriad of influences on parental behavior (e.g. hormonal, sensory, experiential, social, motivational, genetic, environmental) interact to produce specific patterns of parental care. While decades of research have provided answers as to how some of these factors influence parental behavior, many questions remain. At the level of the nervous system, sex differences in parenting are likely to be regulated at numerous levels, from peripheral sensory afferents up to higher integrative centers. The high variability in the patterns of sex differences across species suggests that it is not likely that a single neural basis for sex differences in parental responsiveness is conserved across species. An experimental approach that considers both differences between species in the factors influencing parental responsiveness, as well as how parental care is displayed within their natural environments, will prove to be the most productive in unraveling the complexities of mammalian parental behavior.

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