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Parenting in Animals

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Abstract

The study of parenting in animals has allowed us to come to a better understanding of the neural and physiological mechanisms that underlie mammalian parental behavior. The long-term effects of parenting (and parental abuse or neglect) on offspring, and the neurobiological changes that underlie those changes, have also been best studied in animal models. Our greater experimental control and ability to directly manipulate neural and hormonal systems, as well as the environment of the subjects, will ensure that animal models remain important in the study of parenting; while in the future, the great variety of parental caregiving systems displayed by animals should be more thoroughly explored. Most importantly, cross-talk between animal and human subjects research should be promoted.

The study of parenting in animals is fascinating both in its variety and as a reflection of ourselves and our experiences. We ask ourselves, what makes a good parent? Is it hormones, experience, or both? What effects does parenting have on the offspring, and what are the mechanisms for those effects? Animal models for these processes are crucial for many reasons, including our ability to experimentally control the experiences of the parents and offspring, to manipulate hormonal, environmental, and neural processes, and sometimes to look into the brain itself.

The great variety of parenting behavior in animals in nature; and the subset of these systems in the laboratory

Animals display many different forms of parenting behavior, based on their socioecology, the energetic constraints of their reproduction (ex. litter size), and their mode of delivering nutrients to the offspring [1]. In mammals, due to the necessity of infant nutrition by lactation, uniparental female care is the norm and the ancestral state. However, many species display shared care (“alloparenting” or “cooperative breeding”) in which relatives or group-mates help to care for offspring [2]. In socially monogamous mammals, which are a minority estimated at 3–5% of species [3], adult males also often care for offspring [4].

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Biparental care is hypothesized to co-evolve with monogamy (as either a precursor or a consequence): for instance, to increase survival of the offspring, to gain further mating opportunities with the pair mate, or as an indirect consequence of exposure to young. Modeling suggests that relative mortality rates of males and females may contribute to biparental care [5].

However, the most extreme forms of parenting exist outside of mammals; for instance, with many amphibians and reptiles not providing care at all [6], and more than 80% of birds providing biparental care [7]. In birds, this phenomenon is generally attributed to the ability of male birds to engage in all parental behaviors except for egg-laying, and thus to present the opportunity both for more plastic systems and for inter-sexual conflict (ex. the possibility of female desertion) [7]. Consideration of the selection pressures for each different group of bird species, and the evolutionary transitions between types of parenting, suggests that parental care patterns are determined by the costs and benefits of desertion for each sex, as well as the benefits of additional care for the offspring, all of which may be affected by environmental variables [8]. Another particularly fascinating group is the poison dart frogs, various species of which display uniparental male care, uniparental female care, and biparental care [1,9]. While uniparental male care is ancestral in this group, careful consideration of phylogeny and ecology has shown that in at least one species, the need to breed in smaller pools drove the development of costly parenting strategies (feeding unfertilized eggs to the tadpoles), which then drove the evolution of biparental care in that species, *Ranitomeya imitator* [10]. These non-mammalian groups represent some of the most interesting opportunities to study the selection pressures that result in different types of parenting.

While there is great variety in parenting behavior in nature, the parental systems used for laboratory research have been far more restricted. In mammals, the most commonly studied species are most likely rats, mice, and rhesus monkeys, all of which have uniparental female care. In PubMed, a search on “maternal” and “rat” returns 20,536 citations; “maternal” and “mouse” 15,809 citations, and “maternal” and “rhesus”, 1703 citations (search performed on 11/6/2016). Some strains of these species, such as house mice, actually display alloparenting in the wild [11], but are often housed in such a way that they cannot display these behaviors in the laboratory. Laboratory species that display less common forms of care include biparental species such as California mice (*Peromyscus californicus*), Octodon degus (*Octodon degus*), and titi monkeys (*Callicebus cupreus*; Figure 1); as well as cooperative breeders such as prairie voles (*Microtus ochrogaster*), mandarin voles (*Microtus mandarinus*), and marmosets and tamarins (family Callitrichidae).

Neurobiology of mothering

The neurobiology of mothering has been well studied for decades [12]. In short, the hormones associated with late pregnancy and birth (falling progesterone, rising estrogen, prolactin, and oxytocin) act in the medial preoptic area (MPOA) to make pup stimuli salient to the new mother (also see [13], this issue). This results in release of dopamine and involvement of the mesolimbocortical, “motivation” system [12]. These processes allow for the motivation to interact with the pups; the long-term persistence of maternal behavior, also

known as “maternal memory”, is also maintained by oxytocin and dopamine action in the nucleus accumbens shell [14]. Recent work has detailed the ways in which epigenetic pathways, including histone acetylation/deacetylation and gene methylation, contribute to the display of mothering behavior [15].

In turn, mothering changes the female [16]. Among the best studied of these changes are in cognition, spatial memory and hippocampal plasticity [17]. Rodent mothers display long-lasting improvements in spatial memory associated with reproductive experience; however, human mothers do not show the same phenomenon [17]. Due to this difference, rodents may not be the best model for changes associated with human mothering. A study in owl monkeys (*Aotus spp.*) demonstrated a longer duration of time interacting with high quality foraging sites in reproductively experienced animals, of the same age as the reproductively inexperienced animals [18]. One interpretation is that reproductively experienced animals had a slight (gone by the second trial) learning advantage; an alternative might be that reproductively experienced animals perseverated longer than inexperienced ones. Further experiments in non-human primates are needed to determine if they more closely resemble rodents or humans in the effects of parenting, or of maternal hormones, on cognition.

Mothering can also change emotional regulation in females [19]. A reduction in anxiety-like behavior is associated with pup care in female rats [20], a phenomenon which is associated with pup stimuli [19]. Study of this change and its associated mechanisms is important for many reasons, including the occurrence and potential severity of postpartum depression in human mothers [21].

Finally, in animals as in humans, sometimes parents display poor caregiving [22]. Experimental manipulations that induce disordered caregiving or maternal neglect in rodents, such as maternal separation, have been utilized for decades and are still major tools in our investigations of effects on offspring (see below, also [23], this issue) [24]. However, these experimental manipulations do not shed light on naturally occurring neglect or abuse. One of the few animal models for naturally occurring abuse is found in rhesus monkey (*Macaca mulatta*) mothers, some of which drag, throw or sit on their infants [25]. Abuse and neglect has also been demonstrated in other Old World monkeys such as sooty mangabeys (*Cercocebus atys*) [26] and pigtail macaques (*Macaca nemestrina*) [27]. Research has associated abusive behavior in rhesus monkeys with altered serotonin function, and higher levels of corticotropin-releasing hormone [28,29]. However, the neurobiology of abusive or neglectful parents in animal models remains an important area for further exploration.

Neurobiology of fathering

The neurobiology of fathering is far less studied than the neurobiology of mothering, partially because of its relative rarity in mammals and especially its absence in common laboratory models such as rats and rhesus monkeys [30,31]; but see [32], this issue. Experiments in male mammals examining hormones in relation to fathering behavior have often been inconclusive and inconsistent across species. It is unclear if these are species differences or if there are more important neurobiological or hormonal factors that have yet to be examined [30]. For example, the most consistent finding from the animal literature is

that testosterone is usually antithetical to male parenting [31]; however, in California mice it is actually necessary [33]. Other hormones that have been implicated in male care include oxytocin, vasopressin, and prolactin, although a recent review concluded that prolactin is unlikely to be a major hormone promoting male care in mammals, as it seems to be in birds [7,30].

These studies have been done in a number of the biparental and cooperatively breeding species noted above; however, they are often divorced from actual fathering and examined in virgin males (alloparents). Therefore, the amount of information on actual fathers is even smaller than it appears in Table 1. In addition, a lot of work has been carried out in species that do not normally show male parenting in nature, but can be induced to do so in the laboratory (Table 1).

In the past few years there has also been an emerging focus on the switch from infanticide to fathering behavior in laboratory mice [1,34]; Table 1. It has been known for a long time that some rodents that do not display male parenting in nature may do so in the laboratory [35], either as the result of extended exposure to young or as the result of becoming a father. These males are usually infanticidal until their parenting behavior is “turned on”. One laboratory has focused on the neuroanatomy of this switch, implicating neurons in the rhomboid nucleus of the bed nucleus of the stria terminalis (rhBNST) in infanticidal behavior in male mice, and neurons in the central medial preoptic area (cMPOA) as involved in fathering [34]. This study, however, did not focus on the neurochemical identity of the cells. Another study [36] showed that activation of galanin neurons in the mPOA suppressed infanticide and induced male parenting in mice.

Effects of parenting on offspring in animal models

There are clear and pervasive effects of parenting on many characteristics of offspring in animal models. This has been best studied in rats, where the effects of maternal licking (also known as licking/grooming, or arched-backed nursing/licking/grooming), have been linked to changes in the offsprings’ behavior including maternal behavior and anxiety-like behavior [37]. In addition, maternal licking alters offspring glucocorticoid receptors [38], oxytocin and vasopressin receptors [39], estrogen receptors [40], etc. Epigenetic changes associated with behavioral and neurobiological changes in the offspring have been identified [41–43].

More recently, the effects of parenting have also been studied in a socially monogamous, biparental species, the prairie vole (*Microtus ochrogaster*) [44]. Vole parents were classified into high, medium, and low contact pairs [45]. These classifications were stable across litters, and were associated with behavior in the juvenile offspring; low-contact offspring were less social and displayed more anxiety-like behaviors [45]. As adults, stress reactivity differed between high- and low-contact offspring, with high-contact offspring especially vulnerable to social stressors [46]. In a cross-fostering study, social behavior followed the foster parent, while some aspects of oxytocin and vasopressin receptor binding were correlated with that of the biological parents [47]. Finally, parental contact was associated with patterns of cortical connectivity; high-contact offspring having more intrinsic

connectivity within somatosensory cortex, and low-contact offspring having more dispersed connectivity between somatosensory cortex and other areas [48].

Effects of paternal care specifically on offspring are much less defined, and have primarily been studied by removing the father from biparental species [31], which can have numerous and lifelong effects. Number and identity of caregivers are therefore confounded in most studies, which makes it difficult to isolate effects due to paternal behavior. Changes caused by differential paternal care are presumably subserved by epigenetic changes, which are also mostly still undefined. Studies of genomic imprinting [49] and other modes of inheritance [50] have found evidence for paternal effects unrelated to behavior in both primates [51] and rodents [52]. However, changes in methylation or histone acetylation subsequent to paternal behavior have not yet been studied.

Finally, many experimental manipulations exist in order to up- or down-regulate parenting behavior, including maternal separation as mentioned above; “handling”, or short separations, which can lead to increased parenting behavior [53] and potentially resistance to stress [54]; and other manipulations that disorganize parenting [55], including models of limited bedding that mimic poverty-related stress in humans; and models of prenatal stress [56]. While these have been used primarily in females, a few have also been used in males. Early “no handling” manipulations drastically reduce alloparental behavior in male voles [57], although these males as fathers actually retrieve their own pups more [58]. Post-natal chronic variable stress led to small reductions in paternal care in California mice [59], while acute treatment with corticosterone did not [60].

Frontiers in animal studies of parenting

What are the important new frontiers in the study of parenting in animals? They will need to include both depth and breadth; depth in our understanding of mechanism, and breadth in our incorporation of new information on non-traditional species and on non-maternal caregivers. Major contributions to this field may be made by additional, detailed field studies of parental behavior in both mammalian and, perhaps even more importantly, non-mammalian systems that display types of caregiving not seen, or not often seen, in mammals.

As discussed above, we also critically need new information on the neurobiology of male parenting; the neurobiology of abuse and neglect; and the effects of parenting (both female and male) on other aspects of cognition, behavior and emotion regulation in animal models. We need to apply cutting-edge technology to our studies of parenting behavior; for instance, see recent neurobiological [61] and genetic [62] applications to parenting (also see [63], this issue). Most importantly, we need to advance cross-talk and collaboration between animal and human work, creating animal models to test theoretical models of parenting and parental effects on offspring first developed in humans.

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Highlights

- Animals display a wide variety of parenting systems
- Laboratory models allow for experimental control and manipulation of parenting
- Parenting causes numerous neurobiological and behavioral changes in offspring



Figure 1. Titi monkey father carrying infant at the California National Primate Research Center. Photo by: Kathy West Studios ©2016



Figure 2.
Prairie vole family. Photo by: Karen L. Bales

Table 1
Rodent species used in the study of male parenting

PubMed searches were performed on Latin species names with the words “father”, “paternal”, and “alloparental”, with numbers of studies listed here (search performed on 11/6/2016). This table includes all database hits, both empirical studies and reviews.

Species name	Care System	“father”	“paternal”	“alloparental”
Prairie vole (<i>Microtus ochrogaster</i>)	Obligate male care in wild	8	39	19
California mouse (<i>Peromyscus californicus</i>)	Obligate male care in wild	34	54	0
Djungarian hamster (<i>Phodopus campbelli</i>)	Obligate male care in wild	8	24	1
Mongolian gerbil (<i>Meriones unguiculatus</i>)	Obligate male care in wild	2	8	1
Degus (<i>Octodon degus</i>)	Obligate male care in wild	9	14	0
Mandarin voles (<i>Microtus mandarinus</i>)	Obligate male care in wild	7	15	1
Laboratory rat (<i>Rattus rattus</i>)	Induced male care in lab	188	426	8
Norway rat (<i>Rattus norvegicus</i>)	Induced male care in lab	187	426	8
C57BL/6J mouse (<i>Mus musculus</i>)	Induced male care in lab	527	2205	12