Paternal Behavior and Offspring Aggression

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ABSTRACT—*Aggression can have a critical impact on the functioning of societies. Some aspects of aggression have received considerable attention, such as links between parenting behavior and offspring aggression in humans. Although acknowledged as being important to the understanding of human aggression, animal aggression has been relatively unstudied. Recent mammalian animal research is emerging that addresses issues relevant to the study of parenting and aggression. This has been accomplished primarily by focusing on nontraditional mammalian model systems. We integrate human and nonhuman animal studies to (a) further elucidate the potential impact that the behaviors of fathers have on offspring aggression, (b) study the influence of paternal behavior on the behavior of offspring and transfer of aggression across generations, and (c) explore neural and physiological underpinnings for variation in paternal behavior and aggression.*

KEYWORDS—*aggression; paternal behavior; arginine vasopressin; testosterone; progesterone*

The developmental origins of aggression have long been a subject of discussion in psychology. There is a widespread belief that the behavior of parents has potent effects on aggression in their offspring, but the vehicle for these effects is usually unclear. An important research priority is to identify the biological mechanisms that underlie and help guide changes in both aggression and parental behavior, particularly in response to social conditions. We have identified particular aspects of parental behavior that have a strong long-term influence on the aggressive behavior of their offspring and have identified the mechanisms through which this influence occurs in an animal species.

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AGGRESSION AND PARENTING IN HUMANS

The most extensive research on associations between parental and offspring behavior has focused on human maternal behavior. Child abuse and neglect by mothers have both been associated with higher levels of offspring aggression (Serbin & Karp, 2004). Furthermore, a positive association has frequently been found between offspring aggression and such parental behaviors as restrictive discipline. In comparison, a more responsive or warm style of mothering has been associated with lower levels of aggression. Paternal behavior also has emerged as a strong predictor of offspring aggression. For example, harsh parenting has been found to have a stronger effect on children's aggression when it originates from the father than when it originates from the mother (e.g., Chang, Schwart, Dodge, & McBride-Chang, 2003). Overall, offspring aggression has been found to be negatively associated with warmer parenting styles and positively associated with harsh or restrictive discipline. Recently, researchers have begun investigating whether parental behaviors and aggression can be transmitted behaviorally across multiple generations. For example, harsh and punitive parenting has been found to transfer across generations, possibly through learning, and has been associated with high aggression levels in subsequent generations (Serbin & Karp, 2004). This far-reaching impact of parenting behavior on subsequent generations can potentially influence the functioning of societies.

A NEED FOR CAUSAL ANIMAL-MODEL SYSTEMS

Animal studies are important for establishing the behavioral, physiological, and neurological mechanisms underlying variation in paternal and aggressive behaviors, largely because of the difficulties in experimentally altering those mechanisms over a long period of time in humans (Serbin & Karp, 2004). Because paternal involvement in raising offspring is rare among mammals, the impact of the father's behavior on paternal and aggressive behavior of offspring has been understudied. However, rodent species in which both parents care for offspring, such as the prairie vole (*Microtus ochrogaster*) and the California mouse

(*Peromyscus californicus*), are emerging as valuable model systems, particularly for studying the physiological and neurological bases of paternal behavior. Studies of these animals complement those that have investigated the role and biological underpinnings of maternal behavior.

BEHAVIORAL MECHANISMS UNDERLYING CHANGES IN PATERNAL OR AGGRESSIVE BEHAVIORS

The most extensive studies of how parental behavior affects offspring behavior have examined, at a physiological and neural level, the influence of maternal licking and grooming on stress reactivity in rat pups (Meaney, 2001). Interestingly, these maternal behaviors are transferred nongenetically across generations; rats raised by mothers that expressed less maternal care showed less maternal care as adults even when the mothers were not directly related to them genetically. However, animal studies have neglected to examine changes in offspring aggressiveness in response to such maternal behaviors as licking and grooming. One recent correlational study suggested that maternal huddling with pups and grooming of pups may decrease aggression of adult male offspring when individuals encounter other males in neutral or unfamiliar territory, but does not decrease aggression in resident males when they encounter an intruder in their home cage or territory (Bester-Meredith & Marler, 2003). Neutral-arena aggression tests may be more stressful for the animal in question than resident–intruder tests are for residents, and therefore changes in maternal huddling and grooming may influence neutral-arena aggression. This will be an interesting target for further research.

Only recently have animal models focused on how paternal behavior influences offspring aggression and whether resident–intruder aggression can be transferred across generations nongenetically via paternal behavior, particularly pup retrievals. Retrievals back to a nest or away from danger may be a protective style of parenting analogous to protective behaviors found in primates (Fairbanks, 1996). Alternatively, they may be a rougher style of parental behavior, as pups are grasped just behind the forelegs and lifted off of the ground and can be brought back to the nest or to some other location. Studies have revealed that male California mice raised by the less paternal and less aggressive white-footed mouse display less aggression and fewer pup retrievals as adults than those raised by their own species, without a difference in paternal huddling or grooming behavior towards pups. In California mice, there is a positive association between adult-offspring resident–intruder aggression and paternal retrievals but not other paternal behaviors (Bester-Meredith & Marler, 2003). Furthermore, artificially increasing paternal pup-retrieval behavior (by placing pups outside of the nest) without causing a change in paternal huddling/grooming behavior increases resident–intruder aggression of both male and female pups (Frazier, Cravens, Trainor, & Marler, 2005). Thus we have identified how a specific paternal behavior can influence offspring aggression in California mice.

The data suggest a difference between paternal behaviors such as pup retrievals and other paternal behaviors such as huddling and grooming in their effects on offspring behavior. In the retrieval manipulation study discussed above, we also decreased paternal huddling and grooming in a subset of animals by castrating the males (Marler, Bester-Meredith, & Trainor, 2003; Frazier, Cravens, Trainor, & Marler, 2005). This manipulation of the fathers caused an increase in corticosterone (a stress hormone) in the adult male offspring (Frazier, Cravens, Trainor, & Marler, 2005). Such a result would be predicted in light of studies by Meaney and colleagues demonstrating that a decrease in maternal huddling and grooming can affect the stress responsiveness of offspring (Meaney 2001). Castrating the fathers did not alter resident–intruder aggression of the offspring. In contrast, while the retrieval manipulation altered resident–intruder aggression, it did not alter corticosterone levels of offspring. The independence of these paternal behaviors in their effects on offspring is further supported by the finding that the frequency of pup retrievals is statistically independent of the frequency of other parental care behaviors such as huddling and grooming (Marler et al., 2003). These data suggest that paternal retrievals may influence offspring resident–intruder aggression independently of huddling and grooming. As mentioned earlier, however, changes in paternal huddling and grooming may influence aggressive responses to stress in adult offspring.

The effect of retrievals on aggression may go beyond a single generation. Male California mice that were raised by white-footed mice and were therefore exposed to fewer paternal retrievals during development also retrieved their own pups less (reviewed by Marler et al., 2003). Some paternal and aggressive behaviors are positively correlated in males (Marler et al., 2003). Based on these studies, we predict that future generations exposed to fewer paternal retrievals will also be less aggressive. We hypothesize that certain parental and aggressive behaviors are positively associated and are perpetuated from generation to generation. Future studies investigating physiological or neurological mechanisms mediating this effect in California mice may prove valuable as an animal model for understanding the underlying mechanisms for the intergenerational transmission of aggression in humans.

NEURAL AND PHYSIOLOGICAL MECHANISMS UNDERLYING CHANGES IN PATERNAL AND AGGRESSIVE BEHAVIORS

To understand human parenting and aggression, it will be of the utmost importance to integrate animal behavioral studies with studies of the biological mechanisms underlying changes in paternal and aggressive behaviors. The simplest set of mechanisms for shaping aggression and paternal behavior within the same sex and species would be hormones or neurochemicals that influence both behaviors. The first steps are being made toward understanding this integration of biological mechanisms and behavior, and here we briefly review a set of neuroendocrine compounds, including arginine vasopressin, testosterone, and progesterone, that influence both paternal behavior and aggression. Moreover, and perhaps more importantly, neuroendocrine levels can change in response to social conditions.

Vasopressin can influence a number of social behaviors, including aggression, paternal behavior, and pair bonding, depending on social conditions that raise or lower levels of this neurochemical (reviewed by Marler et al., 2003). Raising or lowering vasopressin experimentally can change dominance status or alter aggression toward an intruding male in golden hamsters, as well as modulate paternal behavior in voles; it can even induce paternal behavior in the meadow vole (a species in which paternal behavior is expressed only under some conditions; reviewed by Marler et al., 2003). Vasopressin levels can also be altered in response to social conditions. When male California mice are raised by the less-aggressive, less-paternal white-footed mouse, they express not only lower levels of aggression and paternal behavior but also less vasopressin in a brain area associated with aggression (reviewed by Marler et al., 2003). Furthermore, vasopressin and aggression are decreased in male golden hamsters that are threatened and attacked by members of their own species during puberty (Delville, Melloni, & Ferris, 1998).

These animal studies have stimulated researchers to investigate the aggression-related functions of vasopressin in humans, although, as yet, little attention has been paid to paternal behavior. Cerebrospinal vasopressin has been positively correlated with aggressive life histories in humans (reviewed by Thompson, Gupta, Miller, Mills, and Orr, 2004). Furthermore, vasopressin may cause human males to respond more aggressively (via changes in facial muscle activity) towards emotionally ambiguous facial expressions (Thompson et al., 2004).

Testosterone also influences both aggression and paternal behavior in animals and humans. For example, testosterone increases temporarily in California mice after they win an aggressive encounter, and this temporary increase influences future aggression and ability to win subsequent encounters (Oyegbile & Marler, unpublished data; Trainor, Bird, & Marler, 2004). Winning without a change in testosterone (i.e., when males have been castrated and given testosterone implants to mimic stable baseline levels) causes no such increase in future aggression (Trainor et al. 2004). These studies involving testosterone manipulations in California mice are important because they identify a function for the temporary increases in testosterone found in a variety of human studies. Numerous human studies demonstrate a significant, albeit weak, positive correlation between testosterone and aggression (reviewed by Book, Starzyk, & Quinsey, 2002), and a number of studies have demonstrated temporary testosterone increases in response to competitive interactions among males (reviewed in Trainor et al., 2004).

Testosterone is also positively associated with paternal huddling and grooming in California mouse pups (Marler et al., 2003). In some species, however, testosterone is negatively associated with these paternal behaviors; testosterone's effects on paternal behavior are thus likely to depend on a species' behavioral traits and ecology (Marler et al., 2003). Hormonal correlates of human paternal behavior have only recently been measured. Testosterone levels tend to be lower in more responsive fathers, but testosterone increases in fathers upon hearing cries from unrelated infants (Fleming, Corter, Stallings, & Steiner, 2002). Testosterone also decreases when male California mice become fathers, but testosterone is nevertheless positively linked with paternal behavior. The enzyme aromatase (which converts testosterone to estrogen) is increased in the medial preoptic area (a brain area that modulates parental behavior) of California mouse fathers. This increase allows for an increase in the effect of testosterone on paternal behavior that is at least partially independent of testosterone levels in the blood, since aromatase primarily modifies testosterone levels in very localized brain regions (Trainor et al., 2003). The relationship between testosterone and paternal behavior in humans remains uncertain and may be difficult to unravel without the necessary testosterone manipulations described above that can be performed more readily on animals.

Progesterone, which is negatively associated with aggression, is the final candidate for influencing both aggression and paternal behavior. Progesterone can inhibit aggression and decreases temporarily in female California mice after an aggressive encounter with another female of the same species (Davis & Marler, 2003). Furthermore, intruding male California mice experiencing losing encounters have increased progesterone levels (Trainor et al., 2004). These studies demonstrate progesterone's responsiveness to social conditions and its potential role in aggressive interactions. Evidence for inhibitory effects of progesterone on paternal behavior is also emerging. Increased paternal behavior occurs in male house mice treated with chemicals that block the reception of progestin (a steroid hormone with progesterone-like effects) and in mice with deactivated progestin-receptor genes (Schneider et al., 2003). Also, progesterone levels are lower in California mouse fathers compared to sexually inexperienced males (Trainor, Bird, Alday, Schlinger, & Marler, 2003). Furthermore, progesterone is negatively correlated with aromatase activity in the medial preoptic area; thus, lower progesterone levels and higher aromatase levels in the medial preoptic area are associated with higher levels of paternal behavior (Trainor et al., 2003).

CONCLUSION

Comparisons between human and animal studies demonstrate that the developmental environment provided by the father is likely to have critical and long-lasting effects on behavior and its biological underpinnings. There is evidence that variation in parenting behavior can alter aggression and parental behavior in offspring. Moreover, there are hints that, in humans and animals, paternal and aggressive behaviors are transmitted behaviorally across generations. Finally, studies investigating the biological mechanisms influencing both aggressive and parental behaviors have identified hormones and neurochemicals that may modify interactions between fathers and offspring and potentially influence paternal and aggressive behavior of future generations. Which of these hormones and neurochemicals play such a role needs to be confirmed, and how much they change in response to altered social conditions needs to be determined. Many other unanswered questions remain. How reversible are these changes? What suites of behaviors are influenced by each mechanism? If one behavior or neurochemical is altered, how does this influence other behaviors and neurochemicals? How does altering the behavior of one parent affect the parenting behavior of the other parent? Through what sensory mechanisms (e.g., visual, tactile) do fathers influence the behavior of their offspring? Does a given parenting behavior in mothers and fathers influence offspring in the same way and is the effect similar for sons and daughters? Insight into these interactions between behavior and physiological and neural mechanisms in animals will help in the interpretation of complex interactions among humans and add to our understanding of the social pathologies that exist in human societies.

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