Kim Wallen

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Abstract

Kim Wallen is an American behavioral neuroendocrinologist known for his studies on sex differences in behavior in rhesus macaques. His work has emphasized the importance of studying animals in naturalistic contexts to understand organizational and activational effects of hormones. Kim Wallen investigated the Organizational Hypothesis in a large study in which animals received flutamide or physiologically relevant doses of testosterone prenatally. He studied the effects of these hormonal manipulations on a wide variety of complex social behaviors. Wallen's work has provided important information about the timing and sensitivity of social behaviors, hormones, the nervous system, and developmental milestones to prenatal androgens. His work in adult monkeys has challenged the notion that female monkeys are passive during sexual encounters, that females are always motivated to mate, and that androgens regulate female sexual desire. Kim Wallen's findings have elucidated the importance of social factors and context in studying hormone-behavior relationships.

Keywords

Organizational Hypothesis · Sex difference · Social context · Testosterone · Flutamide · Estrus · Puberty · Vocalization · Rough play · Mating

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Kim Wallen was born 3 September 1947 in Asheville, NC. His father was a social psychologist at Black Mountain College. At a young age, his father moved the family out to Estacada, Oregon, to start a communal farm. Wallen lived there until he was 8 years old. Farm life shaped his interest in animal behavior and biology. One of his earliest recollections was at 5 years of age when his dad decided to become a goat herder. Wallen observed newly acquired female goats finding their place in the hierarchy and the fierce aggression that bucks display during rut. He also processed the goats with his father, which allowed him to observe their internal physiology.

As a child, Wallen was a self-proclaimed behaviorist. Inspired by Skinner, whom his dad had known at Harvard, Wallen created his own Skinner box and trained a rat. Unfortunately, the rat eventually escaped and was killed by the family dog. Later, when Wallen went out to Antioch College for his undergraduate studies, he avoided the Psychology department because it was largely focused on behaviorism at the time. However, Antioch College afforded Wallen the opportunity to explore various career options, including photography. The college had a co-op program in which students attended classes for 6 months and worked for 6 months. Elliot Valenstein, who was at Antioch at the time, encouraged Wallen to reach out to Robert Goy at the Oregon Primate Center for his first co-op experience. After hesitating a bit, Wallen contacted Goy and spent the next 6 months conducting research. As we will see, this relationship was enduring and had a major impact on Wallen's career.

Most scientists start by publishing in small journals, but Wallen's first publication was in *Science*. Wallen had a work opportunity at the UCLA Neuroscience Institute with Lyn Clemens and Roger Gorski. They found that, after applying potassium chloride (KCl) to the cortex of ovariectomized female rats treated with estradiol, they immediately went into heat, seemingly proving that progesterone was unnecessary to induce estrus (Clemens et al., 1967). Their conclusions were later disproved (the KCl treatment actually induced adrenal activity and resulted in high progesterone levels), but Wallen learned an early lesson that one can never think of every possible alternative explanation.

Wallen earned a B.A. in Biology from Antioch College in 1970. Once he graduated, he was faced with the prospect of being drafted into the Vietnam War – his lottery number was 5. He therefore applied for alternative service. His first application was to work in photography, but it was determined the service project was likely to further his career (he had taken a photography class during college). Strangely enough, they instead agreed to alternative service in the lab of Bob Goy.

Wallen's older brother, Kurt, was also working with Bob Goy at the time. Kim Wallen did 3 years of research with Goy, following Goy from Oregon to the Wisconsin Regional Primate Center. Wallen was not sure that he wanted to do a PhD, but realized it was necessary after talking with a former director of the primate center at Cayo Santiago. Wallen was admitted to the Neuroscience program in 1973 when it was in its infancy (the program was only in its second year). Wallen earned his PhD from the University of Wisconsin-Madison in 1978.

After completing a year as a postdoctoral fellow at the Wisconsin Regional Primate Research Center, Wallen joined the Psychology department at Emory College (now Emory University) in 1979. David Edwards, a professor at Emory,

had encouraged him (via David Goldfoot) to apply. Wallen was ultimately Emory's second choice, but the other candidate (Chris Coe) turned them down to do a post-doc elsewhere. Wallen has been at Emory University ever since. He is presently Samuel Candler Dobbs Professor of Psychology and Behavioral Neuroendocrinology at Emory University. Wallen has been a huge contributor to the field of behavioral neuroendocrinology. He has over 135 publications and has graduated 16 PhDs, all of them women. He has served as President of the Society for Behavioral Neuroendocrinology (1999–2001) and was Editor-in-Chief of Hormones and Behavior from 2012 to 2019.

Effects of Social/Environmental Context on Adult Female Sexual Behavior: Activational Effects on Estrogens

When Wallen arrived at Emory, there was little funding for research (he was given a mere $600 to purchase a modem to dial into the college server). One thing he did have, however, was access to the Yerkes Regional Primate Research Center Field Station, which allows monkeys to live outdoors in socially complex groups of approximately 100 individuals. Wallen's first project was to investigate the effects of space on mating throughout the cycle. At the time that Wallen initiated this research, the prevailing belief was that male rhesus monkeys initiated most sexual encounters and that, because they were able to, females mated continuously throughout the estrous cycle. Thus, sexual behavior in female monkeys was deemed to be uncoupled from hormonal influences. The conceptualization of the passive female was largely born out of Harlow's work on socially isolated monkeys (reviewed in Wallen (1996)). Wallen's first project published at Emory demonstrated that the size of the enclosure affects how much animals mate throughout the cycle, mating more frequently in the luteal phase when they were housed in a small cage than when they were housed in a larger enclosure (Wallen, 1982). Next, Wallen et al. (1984) investigated sexual behavior in monkeys housed under the semi-naturalistic conditions of the Yerkes Field Station and determined that over 90% of sexual encounters were initiated by female monkeys. Furthermore, in these complex social groups, mating was tightly coupled with the estrous cycle (Wallen et al., 1984). One important social factor determining when mating occurs is female-female competition. In lower-ranking females, mating was more tightly linked to the estrous cycle than in higher-ranking females (Wallen, 1990). Thus, Wallen's studies of sexual behavior in adult female rhesus monkeys highlighted the female's role in determining when mating occurs and emphasized the need to consider the social and environmental context of the testing environment.

In complex social groups, mating occurs during female estrus, suggesting that ovarian hormones play a role in female sexual motivation. Historically, however, researchers had assumed that androgens, not estrogens, regulate sexual behavior in females, particularly women (reviewed in Cappelletti and Wallen (2016)). When Wallen ovariectomized females and gave them estrogens or aromatizable androgens, female proceptive behaviors increased, indicating that estrogens are effective

in increasing female sexual behavior (Wallen & Goy, 1977). Mating by females treated with a GnRH agonist decreased sharply, but was restored when ovarian function was restored, further suggesting that ovarian hormones are key in regulating sexual behavior (Wallen et al., 1986). However, in these studies, male behavior was a potential confound. To eliminate this confound, Wallen and colleagues (Zehr et al., 1998) tested ovariectomized females during the nonbreeding season. Estradiol-treated ovariectomized females initiated sex more frequently than ovariectomized females who did not receive estradiol or nonpregnant controls (Zehr et al., 1998). Thus, research by Wallen and his colleagues conclusively demonstrated that it is estrogens and not androgens that regulate female rhesus monkey sexual behavior.

Effects of Social Context on Sex Differences in Behavior: Organizational Effects of Androgens

Another important contribution to the field of behavioral neuroendocrinology is Wallen's work on the organizational effects of hormones on social behavior. As stated above, Kim trained with Robert Goy during his undergraduate career, as a postbaccalaureate, as a PhD student, and as a postdoctoral fellow. Goy had been a co-author on the well-known 1959 article that set forth the Organizational Hypothesis, that hormones, through their actions early in development, cause sex differences in behavior (Phoenix et al., 1959). This famous study used female guinea pigs as a model, but Goy applied the Organizational Hypothesis to the study of rhesus monkeys. Goy was perfectly situated to do this, as he had learned about rhesus monkey behaviors while visiting Harry Harlow's lab, and had succeeded Harlow as the director of the Wisconsin Regional Primate Center in 1971.

Wallen first studied the effects of social context on the development of male rhesus monkey behavior. Most experimental approaches to studying behavior controlled and restricted the social environment to eliminate potential confounds. Thus, most of the early work in rhesus monkeys used subjects that had been taken from their mothers at an early age and raised with only minimal access to peers. This contrasts markedly with how free-ranging rhesus monkeys live. Rhesus monkeys live in large social groups, where matrilineally related females have tight social relationships and matrilines are ranked in a strict hierarchy. Each group contains only a couple of adult males and males migrate out of their natal group at sexual maturity.

Wallen sought to examine which social experiences during development are necessary for normal adult male mating behavior. Wallen found that male monkeys who had greater exposure to mothers and peers had the highest rates of mounting behavior and were the most successful at engaging in sexual behavior in adulthood (Goy & Wallen, 1979). Juvenile male rhesus monkeys who had only 30 min per day of access to peers were less likely to exhibit foot-clasp mounting (the posture that allows intromission during mating) than were males who had continuous access to peers (Wallen et al., 1981). Wallen and colleagues concluded that "under (our) circumstances, only alterations in the more intimate and cooperative aspects of social

behavior are evident, rather than pronounced deficiencies in all aspects of social interaction" (Wallen et al., 1981, p. 308). Thus, rearing by the mother is an important component of behavioral development, as is exposure to same-aged peers, with animals faring better if they had continuous exposure to both. By controlling the rearing environment, therefore, previous researchers were creating behavioral results that had little connection to normal rhesus monkey behavior.

Wallen's early research demonstrated that social context matters for males, but what about females? At a time when most researchers in scientific fields studied only males (a trend that persists to some extent today), Wallen's contribution to studying both sexes cannot be underestimated. Wallen, at the Yerkes Regional Primate Center Field Station, was in a prime position to study the Organizational Hypothesis in socially living monkeys of both sexes.

Although previous researchers had examined the Organizational Hypothesis in developing female rhesus monkeys (Wallen's was the fourth such study), his studies differed from previous ones in four important ways. First, previous studies had studied these effects in females that were raised with varying degrees of social isolation. In contrast, Wallen studied socially reared monkeys living in stable groups in outdoor enclosures of 75–125 individuals from established matrilines. This allowed Wallen to study organizational effects of hormones in animals that could freely socially interact with mothers, peers, siblings, and related adult females, along with exposure to adult males and unrelated adult females (Wallen, 2005). Such social complexity allowed Wallen and his lab to study social behaviors, like interest in infants and vocalizations, that were not possible in simpler social contexts. Second, Wallen used a lower dose of testosterone, which allowed him to explore the sensitivity of various behaviors to testosterone (Wallen, 2005). Although the dose used in his studies was somewhat of an accident, the dose was one that would be more likely to occur naturally. In contrast, previous studies had used supernormal doses of testosterone, essentially blasting the system with hormones. Third, Wallen was the first to study demasculinization in males by exposing them to flutamide, an androgen receptor antagonist. All in all, Wallen's study had ten different treatment groups: control females, control males, androgen-treated females, flutamide-treated males, as well as flutamide treatments in females and androgen treatments in males (it was difficult to determine sex in utero). Within each treatment group, animals were exposed to one of two 30–35-day treatments, one during the second trimester (considered the "early" treatment) and one during the third trimester (considered the "late" treatment). This huge undertaking allowed Wallen and his colleagues to simultaneously study effects of hormonal manipulations in both sexes during two different sensitive periods of prenatal development. Finally, most studies of development had looked solely at sexual behaviors. Although rough play was included in most studies of primate behavior, it was included mostly because it was thought to be preparation for adult sexual behavior (reviewed in Goy and Wallen (1979)). Wallen expanded our understanding of the organizational effect of hormones by studying a variety of nonsexual behaviors, many of which were not possible to study in impoverished rearing conditions.

The lower dose of testosterone resulted in 83% lower testosterone concentrations in mothers compared to previous studies and resulted in no significant effects on female genital morphology (Herman et al., 2000). Early (second trimester) flutamide treatments in males resulted in incomplete masculinization; some early flutamide males had penises posterior to their scrotum (Herman et al., 2000). Late (third trimester) flutamide males developed a smaller penis in comparison to control males (Herman et al., 2000). Through this study, Wallen and colleagues were able to determine that the threshold of androgen sensitivity was higher than the dose provided and that flutamide had the capacity to demasculinize male genital morphology.

One might expect that these minor effects on genital morphology would translate to no effects on behavior. However, Goy and colleagues had already determined that the effects of hormones on behavioral sex differentiation could be independent of the effects on genital sex differentiation (Goy et al., 1988). While genital differentiation primarily occurs during the second trimester, behavioral differentiation can also be impacted by exogenous androgens administered during the third trimester (Goy et al., 1988). The use of a lower dose of testosterone in Wallen's studies allowed him and his research team the ability not only to test the extent to which effects on behavior are separable from the effects on genital morphology but also to determine whether behavior (central effect) is more sensitive to hormones than genital morphology (peripheral effect).

Classically, studies of the effects of prenatal androgens on behavior have focused on foot-clasp mounting and rough play. This is because rough play is one of the largest sex differences in infant and juvenile monkeys, with males engaging in more rough play than females (Wallen, 1996). Foot-clasp mounting is also more common in developing males than in females, as it prepares males to successfully mate later in life (Goy & Wallen, 1979). Previous studies had found that testosterone administered late in gestation resulted in higher rates of rough play in females and that treatments both early and late in gestation increased mounting (Goy et al., 1988). In Wallen's study, the lower dose of testosterone had no statistically significant effects on rough play or mounting in females (Wallen, 2005). In males, flutamide treatments late in gestation paradoxically increased mounting behavior relative to control males (Wallen, 2005). Thus, Wallen and colleagues demonstrated that lower doses of testosterone were insufficient to significantly increase female rough play and mounting and challenged the assumption that flutamide acts centrally to potently block androgen receptors.

In addition to studying classic behaviors such as rough play and mounting, Wallen's use of monkeys living in complex social groups enabled him and his colleagues to study the organizational effects of hormones on behaviors that had not been previously studied. One such category of behavior is interest in infants. In contrast to play and mounting, juvenile females are more likely to engage with infants than are males: they often touch them, play with them, carry them around, and even "kidnap" them (Herman et al., 2003). This sort of behavior can only be studied in large social groups, in which offspring of multiple ages can interact. However, the only prenatal treatment that altered interest in infants was flutamide

administered late in gestation to females, in which interest in infants was decreased, a paradoxical result (Herman et al., 2003).

Vocal behavior is another social behavior that had not yet been studied in the context of prenatal androgens. Rhesus monkeys use many vocalizations to communicate with each other and, in adulthood, females use recruitment screams to solicit help from matrilineal relatives during agonistic encounters, whereas males are unlikely to use these vocalizations. These screams convey information about the severity of aggression and the relative rank of the opponent (Gouzoules et al., 1984). I met with Harold Gouzoules (also at Emory) when I was applying to graduate school, because I was interested in studying sex differences in vocal development. While there, I met Wallen, and we discussed the possibility that the sex differences observed in rhesus monkeys (namely, that females are more vocally voluble than males) might be due to prenatal androgens. Wallen readily agreed to be a co-advisor and invited me to join his study. This demonstrates Wallen's commitment to understanding sex differences broadly defined and also demonstrates his openness to exploring new avenues of research. I had no prior experience in the field of behavioral neuroendocrinology, so he was also really taking a chance on me.

We began by studying sex differences in infant vocalizations. One of the primary contexts in which infants vocalize is when they are separated from, or rejected by, the mother. The fact that the monkeys were housed in large outdoor enclosures made this possible. Females and males both vocalized a lot during maternal separation but used different calls. Females used the harmonically rich "coo," which sounds exactly like "oo" (Tomaszycki et al., 2001). Males, in contrast, used geckers, which are short, broadband (i.e., noisy) calls given in rapid succession, typically accompanied by convulsive jerking of the body (envision a child throwing a tantrum in a store) (Tomaszycki et al., 2001). As one might expect based on the types of calls employed by each sex, mothers responded more to calls by males than by females (Tomaszycki et al., 2001).

Prenatal hormones affected these sex differences. Early androgen treatments completely masculinized female calling behavior, and late androgen females were somewhat masculinized (half of the call features were male-typical) (Tomaszycki et al., 2001). Contrary to expected, early flutamide treatments in females also masculinized vocalizations (Tomaszycki et al., 2001). Also surprising was that masculinization of calling behavior did not affect maternal responsiveness to females (Tomaszycki et al., 2001). Flutamide treatments in males (both early and late) demasculinized vocal behavior to some extent, and, in contrast to findings in females, maternal responsiveness to these individuals was decreased (Tomaszycki et al., 2001).

As monkeys reach 1 year of age, they become more independent from their mother. This makes them vulnerable to aggression. Rhesus monkeys are a highly aggressive species, and therefore referential agonistic screams become important, with adult females using these screams more than adult males. A young monkey must learn not only to produce an acoustically correct version of the scream but also to produce it in the appropriate context. We found no sex differences in proper contextual usage of screams but found that juvenile females produced more adultlike

screams than did juvenile males (Tomaszycki et al., 2005). Androgen and flutamide treatments administered to females late in gestation resulted in screams that were less adultlike, but no treatment in males resulted in more adultlike screams (Tomaszycki et al., 2005).

Taken together, we demonstrated that prenatal androgens have organizing effects on rhesus monkey vocal behavior. Furthermore, vocal behavior may have a lower threshold of sensitivity than other behaviors, such as mounting and rough play. Finally, mothers may not be paying attention to the calls themselves, but instead to the genital morphology of the infant, as maternal responsiveness was only altered in the treatment groups that had altered genital morphology (early and late flutamide males).

Wallen and his team continued to study the effects of prenatal androgens in adulthood. During early puberty (3.5 years of age), early flutamide males had increased testosterone and luteinizing hormone compared to control males, and both early and late flutamide treatments resulted in increased testes volume (Herman et al., 2006). Thus, Wallen and colleagues concluded that flutamide likely decreases negative feedback on luteinizing hormone and that flutamide treatments cannot compensate for this effect. These findings suggest that hormonal systems are resilient. These effects on hormone levels in males were no longer apparent a year later. There were also no effects of prenatal hormones on timing of puberty or first ovulation in females (Zehr et al., 2005). Treatments also did not eliminate mating behavior. All males engaged in sexual behavior with few differences according to treatment (Herman et al., 2006), and all females conceived at least once during their first three breeding seasons (Wallen, 2005). However, Wallen determined that social rank impacted the timing of puberty in both sexes, such that higher-ranking animals went through puberty earlier than lower-ranking animals (reviewed in Stephens and Wallen (2013)).

Wallen was also the first to consider sex differences in cognition in rhesus monkeys and the first to test them in outdoor enclosures. Herman and Wallen (2007) conducted tests of spatial navigation using spatial cues and local markers; they found that females outperformed males when relying solely on either one of these cues. Flutamide treatments in both sexes resulted in poor performance, such that more flutamide-treated animals were removed from the study due to this compared to any other group (Herman & Wallen, 2007). There were no effects of androgen treatments (Herman & Wallen, 2007).

Although much of Wallen's research interests were based on social behavior, he also collaborated with researchers at other institutions to understand as much as possible about the effects of prenatal androgens on developing monkeys. With Dennis McFadden, Wallen explored the effects of prenatal hormones on click-evoked otoacoustic emissions in adult male and female rhesus monkeys. They were the first to determine that female rhesus monkeys had stronger click-evoked otoacoustic emissions than did males (McFadden et al., 2006). Flutamide treatments in males, regardless of timing, resulted in more female-like otoacoustic emissions, and androgen treatments in females administered late in gestation resulted in more male-like otoacoustic emissions (McFadden et al., 2006). Late androgen-treated

males were hyper-masculinized (McFadden et al., 2006). It is interesting that the two sets of studies focused on vocal/auditory work (this study and the studies on infant/juvenile vocalizations) both showed effects of prenatal androgens in the predicted direction. Taken together, Wallen's findings suggest that vocal and auditory processes, an important component of communication in rhesus monkeys, are more sensitive to the effects of prenatal androgens than are other social behaviors.

Wallen also collaborated with Nancy Forger to understand how these treatments affect underlying circuitry. They focused on Onuf's nucleus, a motoneuron region that innervates the muscles involved in erectile function and ejaculation (Forger et al., 2018). Males had more motoneurons in this region and larger soma sizes in comparison to females (Forger et al., 2018). Males treated early in gestation with flutamide had slightly fewer motoneurons in Onuf's nucleus, and androgen treatments in males had no effects (Forger et al., 2018). This study established a sex difference in Onuf's nucleus and suggests that prenatal androgens play some role in the emergence of this effect.

In sum, Kim Wallen's contributions to our understanding of the Organizational Hypothesis are extensive. His research has provided important information about the relative contributions of prenatal androgens and complex social rearing environment to sex differences in behavior. Wallen considered many types of social behaviors, going beyond many studies that only focus on male-biased and sexual behavior, and including studies that considered the timing of developmental milestones (such as puberty). He explored behaviors not studied before in rhesus monkeys, like spatial navigation and otoacoustic emissions, and effects on underlying circuitry. Wallen also further established that different behaviors have different timing and sensitivities to prenatal androgens. Some behaviors, like rough play and mounting, seem to be less sensitive, whereas vocal behavior and otoacoustic emissions seem to be more sensitive. Finally, through using lower doses of testosterone that had few effects on genital morphology, Wallen was able to further establish that the effects of prenatal androgens on behavior are independent of their effects on genital morphology (Fig. 37.1).

This tremendous project was not without its problems. This work required a large crew of individuals to administer injections 7 days per week, morning (7 am) and afternoon (4 pm), even through the holidays. To administer injections, we had to walk into the large outdoor enclosures with 100 monkeys, identify individual females, and get them to run into the indoor enclosure to receive their injection. Once inside, the females were trained to transfer into a box, and then into a cage, where they would present their leg for the injection. Minutes later, they were returned to the outdoor enclosure. We had the females trained very well, but we also had new adult males from Cayo Santiago. During a training session in 1996, one of the adult males jumped on my back, leaving a large gouge. Rhesus monkeys transmit Herpes B. To monkeys, it is much like Herpes A in humans. When it is transmitted to humans, it is almost always fatal. I was lucky – the monkey who attacked me was not shedding the virus at the time and I did not get sick. To this day, I have a scar. I was a bit scared to go back into the enclosures, but Wallen counseled me to go back in as soon as possible. It was good advice, as I got over my fear rather

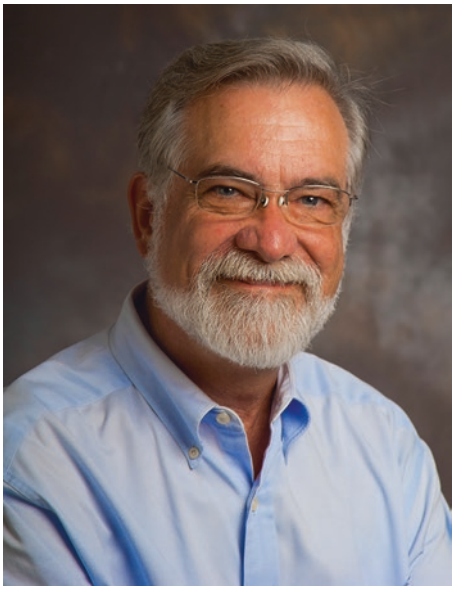

Fig. 37.1 Kim Wallen

quickly (and the monkey who attacked me had been removed from the enclosure). However, another member of our lab was not so lucky. Elizabeth (Beth) Griffin began her work as a volunteer undergraduate assistant working with me, but eventually transitioned to a paid position as a technician in Wallen's lab. Annually, we assisted the veterinarians in bringing all animals in our study into the indoor enclosure. Once inside we anesthetized them and checked their health. During one such health check at the end of October 1997, Griffin got something from a monkey (urine or feces) in her eye. Within 2 weeks, she was hospitalized. She died on 10 December 1997. The impact on all of us in the Wallen lab cannot be described. Wallen considered leaving academia and we all reconsidered studying monkeys. But we all came together for mutual support and somehow managed to continue.

Recent Research Contributions to Behavioral Neuroendocrinology

Luckily for the field, Wallen chose to remain in academia and continue research. Griffin's death occurred when the animals were between 1 and 2 years of age. Wallen continued studying these animals into puberty and beyond. More recently, he has focused on two different avenues of research that are especially noteworthy in terms of their contributions to behavioral neuroendocrinology. First, in collaboration with Mar Sanchez and Jocelyne Bachevalier, among others, he embarked on another enormous project to study the effects of neonatal amygdala lesions on behavioral development in rhesus monkeys. They found few behavioral effects, although these lesions reduced time females spent with the mother in infancy

compared to control females (Raper et al., 2014) and advanced puberty in females (Stephens et al., 2015). The few effects of amygdala lesions challenge our current thinking about the role of the amygdala in social behavior. Second, Wallen has translated his findings in monkeys to humans by studying hormone-behavior relationships, mainly in relation to visual sexual stimuli. Wallen and his colleagues again focused on the amygdala and determined that males have greater activation of this region in response to viewing sexual stimuli than do females (Hamman et al., 2004). Furthermore, 46, XY women with complete androgen insensitivity syndrome are female-typical in response to visual sexual stimuli, with less activation of the amygdala compared to males (Hamann et al., 2014). Thus, Wallen extended his research program to consider central effects and to consider how his research in monkeys translates to humans.

Conclusion

The focus of this chapter has been on Wallen's research on the effects of social context on hormones and behavior. His studies have shaped how we design experiments in the field of behavioral neuroendocrinology. Wallen has emphasized the need to consider social and contextual factors when studying hormone-behavior relationships. Wallen has contributed to our understanding of both organizational and activational effects of hormones on social behavior, through studies that mimic naturalistic conditions by focusing on rhesus monkeys living in complex social groups in outdoor enclosures. Wallen has also examined central effects on behavior, examining the role of the amygdala on social behavior in rhesus monkeys living in semi-naturalistic conditions. He has then translated those findings to the human condition. Wallen has instructed us that hormone-behavior relationships cannot be separated from the social and environmental contexts in which they occur.

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