Biology of Aggression

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Modern discussions on the roots of violence in human society have tended to focus increasingly on the internal determinants of aggression.[1] The general impression derived from this emphasis is that the pervasiveness of violence and war in human history stems in large measure from biological bases: a legacy of our animal ancestry facilitated by endocrinological and neurogenic processes. It is important to reiterate that many of the evolutionary and physiological tenets of this view still need to be clarified, and that other research has continued to demonstrate the important role of environmental factors.[2-4] We hope to provide here an overview of new findings in animal research as an aid to forensic psychiatrists concerned with the biological basis of aggression. While it is not possible to fully resolve the nature/nurture aspects of aggressive behavior — in part because the dichotomy between nature and nurture is a false one — we can provide an up-to-date summary of pertinent factors that affect the manifestation of aggression in animals. A series of studies our laboratory has conducted on nonhuman primates will be used to illustrate the ways hormones influence the manifestation of aggression and to show how changes in social relationships can, in turn, influence the individual's endocrine system.

Definitional Problems

One difficult problem, even in studies on animals, has been how to develop a comprehensive, yet operational, definition of aggression. Contrary to the thoughts of some theorists,[5-6] most modern biologists have shifted from viewing aggression as a primary motivational drive. More typically, the complexity of aggressive behavior is emphasized by separately defining its causes, functions, and motoric elements.[7] Attempts to classify aggressive acts have focused on their consequences (for example, injurious harm to others, attainment of social dominance) or on the stimuli that elicit aggression. Thus, Moyer[8] has described seven categories of aggression in animals: predatory, inter-male, fear-induced, irritable, territorial, defense, and instrumental.

We make a primary distinction between aggression that occurs within the context of establishing and maintaining social relationships and aggression that is elicited as a response to frustrating situations. As investigators of aggression in humans have found,[3] frustration and aversive stimulation can potentiate aggressive behavior in animals. Electric shock, for example, will

induce fighting behavior between two previously non-hostile rats.[9] The emphasis herein on the social aspects of aggression reflects our belief that a division should be made between aggression involved in the attainment of specific biological ends and aggression induced by irritating stimuli that raise an individual's aggressive propensity beyond the normal level. Indeed, under natural conditions injurious aggression is a rather infrequent event, and aggressive intent is usually conveyed by ritualized behavior, such as displays and threat gestures.

Outright aggression occurs primarily when two unfamiliar animals first meet or when there is irreconcilable conflict over commonly desired goals. Typical examples of situations resulting in aggression include competition over limited food and spatial resources or conflict over priority of access to desired sexual partners. In these contexts aggression may be more appropriately described as a mode of interacting directed toward achieving a specific goal rather than as a primary motivational drive. One goal or function of this kind of aggression in animals is the attainment of a certain dominance with respect to other conspecifics of the same sex. In species that have a solitary life style, dominance is manifest in the maintenance of a territory; in gregarious species, it is evident in attainment of a position in the social group's dominance hierarchy. One aim of the endocrine studies we will describe later was to evaluate the hormonal consequences of establishing and maintaining a certain rank within the social hierarchy.

Organizational and Activational Role of Hormones

Although bouts of aggression are relatively infrequent in natural animal populations and aggression is typically expressed in a noninjurious form, this does not lessen the importance of the underlying physiological processes. For example, studies on animals have demonstrated clearly the role of prenatal exposure to testosterone in establishing sex differences in the propensity for aggression. This so-called organizational effect of testosterone during differentiation has been shown to affect the precursor of aggression in young monkeys, the occurrence of "rough and tumble" play,[10,11] as well as the disposition for fighting in adult rodents.[9,12] Similarly, studies on children who were exposed to exogenous steroids *in utero* have indicated that the predilection for certain play patterns and personality traits can be influenced by hormones in humans.[13]

As puberty approaches, a second stage of hormonal influence emerges, when rising titers of gonadal hormones exert an activational influence on behavior. At this time, gonadal hormones stimulate the emergence of species-typical forms of adult social and sexual behavior. In addition to heightened aggressivity between peers, the level of aggression shown by males typically rises after puberty in many primate species because now they are forced to compete with adult males — either expelled from the social group or compelled to enter the adult dominance hierarchy.[14] Coinciding with the behavioral changes, hormones initiate the maturation of

secondary sexual characteristics in males, including enlarged stature, canine development, and adult coloration. Although it is not as easy to generalize about the effect of pubertal hormone increases in females, it should be mentioned that aggressive behavior may increase after menarche due to more frequent dominance interactions with adult females, especially in monogamous species.[15] More typically, however, the level of aggression among females continues to remain lower than among males, and the primary behavioral changes associated with menarche are related to initiation of the adult maternal phase.

We recently obtained an excellent example of the activational effect of hormones on male aggression in a study we conducted on the development of display behavior in our closest evolutionary relative, the chimpanzee. In adulthood male chimpanzees use dramatic, charging displays to convey aggressive intent, and we were interested in assessing the maturational features of this behavior pattern. Thus, the frequency of display behavior by developing male chimpanzees was systematically recorded while they lived under semi-free-ranging conditions in 1.5 acre enclosures.* As can be seen in Figure 1, there was a marked increase in all aspects of the display behavior, beginning with the rudimentary motoric elements, at six years of age when testosterone titers first begin to rise. The occurrence of displays continued to increase through the pubertal period, which occurs at approximately nine to ten years of age in captive chimpanzees. Maturation of display behavior by this age is essential since males begin using the charging display to establish a position in the adult social hierarchy.[16]
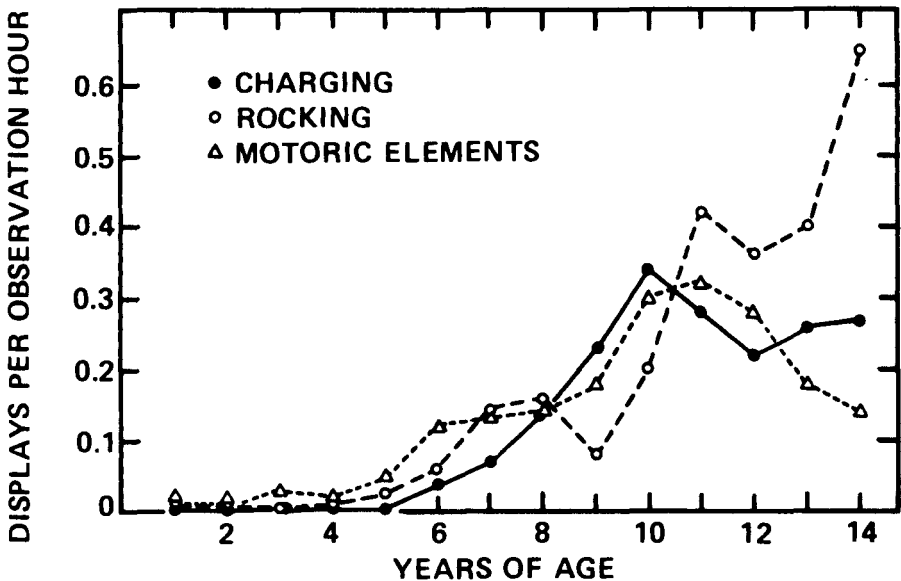

Figure 1. Maturation of charging display behavior in male chimpanzees. Note initiation of displays coincides with the onset of initial rises in testosterone levels prior to puberty.

* The reader is referred to Kraemer *et al.*[67] for details on the recording procedure and to Coe and Levin[16] for information on the facilities and subjects.

Notwithstanding the evidence of a strong influence of hormones on the development of aggressive behavior, studies on castration have yielded much more equivocal data in primates than in other species. For centuries it has been known that castration produced docility in farm animals. Similarly, laboratory experiments on reptiles, birds, and rodents have shown that gonadectomy causes a marked diminution of fighting behavior, which can be reinstated by hormone administration.[17] Yet, in primates the effect of castration appears to be considerably less pronounced once adult behavior has been established. Castration of the dominant male in groups of squirrel monkeys, for example, did not lead to a fall in rank;[18] nor did the natural occurrence of an agonadal condition in the dominant male of a rhesus monkey group.[19] Not only do previously established interaction patterns have a prevailing influence in primates, but castration post-pubertally does not appear to lower aggressiveness toward strangers. Epple[20] reports that castrated marmosets were just as likely as intact animals to attack unfamiliar subjects presented to them.

This generalization about that relatively minimal effect of castration on aggression in adult primates must be given one important qualification, however. In most studies there are usually some subjects in which castration does produce a dramatic change in behavior. An example of the variable influence of castration on dominance and aggression is portrayed in

DOMINANCE HIERARCHIES

RECIPIENT

INITIATOR		I₁	C₁	C₂	I₂	I₃	
	I₁	■	3	1	39	32	75
	C₁		■	15	3	3	21
	C₂		1	■	3	12	16
	I₂	1		2	■	15	18
	I₃	2	1	4	1	■	8

RECIPIENT

	I₁	I₂	C₁	I₃	C₂	
I₁	■	23	21	18	12	74
I₂		■	16	15	7	38
C₁		4	■	15	16	35
I₃	1	11	1	■	5	18
C₂	2	2	1		■	5

I = INTACT

C = CASTRATED

Figure 2. Male dominance hierarchies in two groups of squirrel monkeys. Castrated males exhibit normal levels of display behavior, although they tend not to be in the top-ranking positions and some show a tendency to be of low social rank.

Figure 2 from a study on squirrel monkeys.[21] Observations were conducted on two heterosexual groups, each consisting of three intact and two castrated males plus ten females. The display behavior of the males during the first four months following group formation revealed that, while gonadectomized males can exhibit normal levels of dominance-related behavior, castrates were not in the top-ranking positions in either group, and two were of low social rank in one of the groups. Studies on rhesus monkeys also have indicated marked individual differences in the effects of castration.[22] Why some subjects in each species are more susceptible to influence remains to be determined, but it is noteworthy that similar idiosyncratic effects have been reported in studies on sex behavior after castration. In a number of species, not all males show the typical decline in copulations following castration,[23,24] and in humans the variable effect of castration has been especially evident in studies of castrated sex offenders.[25]

Attempts to alter aggressivity by raising testosterone levels in males have also tended to indicate that hormone secretion does not directly cause aggression in male primates.[26,27] For example, aggression between male chimpanzees was not affected by the administration of LH-RH even though plasma levels of both luteinizing-hormone and testosterone were raised.[28] One notable exception occurred in a study on castrated talapoin monkeys.[14] Testosterone implants increased aggression directed toward subordinate animals. However, varying hormone level did not have a differential effect, and aggression was not increased toward males of higher dominance rank.

Hormone Medication of Sex-Related Aggression

Although testosterone does not appear to directly cause aggression in male primates once adult behavior has been established, there is considerable evidence that hormone facilitation of sex behavior can indirectly increase the manifestation of aggression. In many animals that breed seasonally there is a marked rise in aggression coinciding with the onset of the mating period. Common examples of this type of aggression, which is related to the process of mate selection, include the rookery behavior of seals and the rutting of deer and elk. Similarly, aggression is usually much higher during the months of mating in those primate species that show an annual reproductive cycle.[29,30] Examination of the females' reproductive status in these primates indicates that the rise in aggression is often induced by the presence of receptive females, although in some species there appears to be an endogenous annual cycle of aggression that is independent of female stimuli.[31]

One of the most potent experimental manipulations for eliciting aggression between male animals, in fact, is the introduction of receptive females. For example, prior exposure of male rodents to females will significantly increase fighting when the males are subsequently paired with another male.[32] Another example of this potentiation of male aggression was obtained in a recent study on factors influencing dominance-related behavior in male bonnet macaques.[33] In one phase of the study, the social relations of

five pairs of males were assessed while they lived alone and also while in the presence of estrogen-treated females. Observation of the males' interactions indicated they engaged in high levels of affiliative behavior, such as grooming and huddling, in the absence of females (Figure 3). However, when a receptive female was added to each male pair, the positive nature of the males' social relations was dramatically altered. Affiliative behavior between the males virtually disappeared, and marked increases in dominance-related behavior and aggression occurred. Moreover, in another phase of this study it was shown that visual presentation of a female behind Plexiglas was sufficient to induce these behavioral changes in the males.
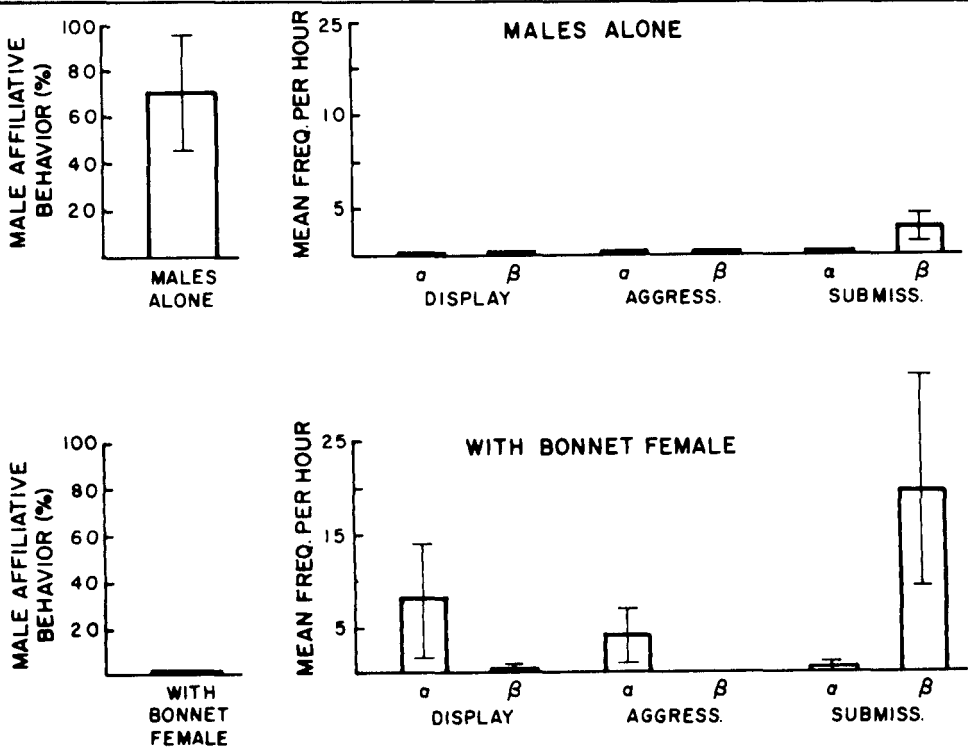

Figure 3. Mean levels of affiliative and dominance-related behavior between male bonnet macaques while alone and after the introduction of an estrogen-treated female.
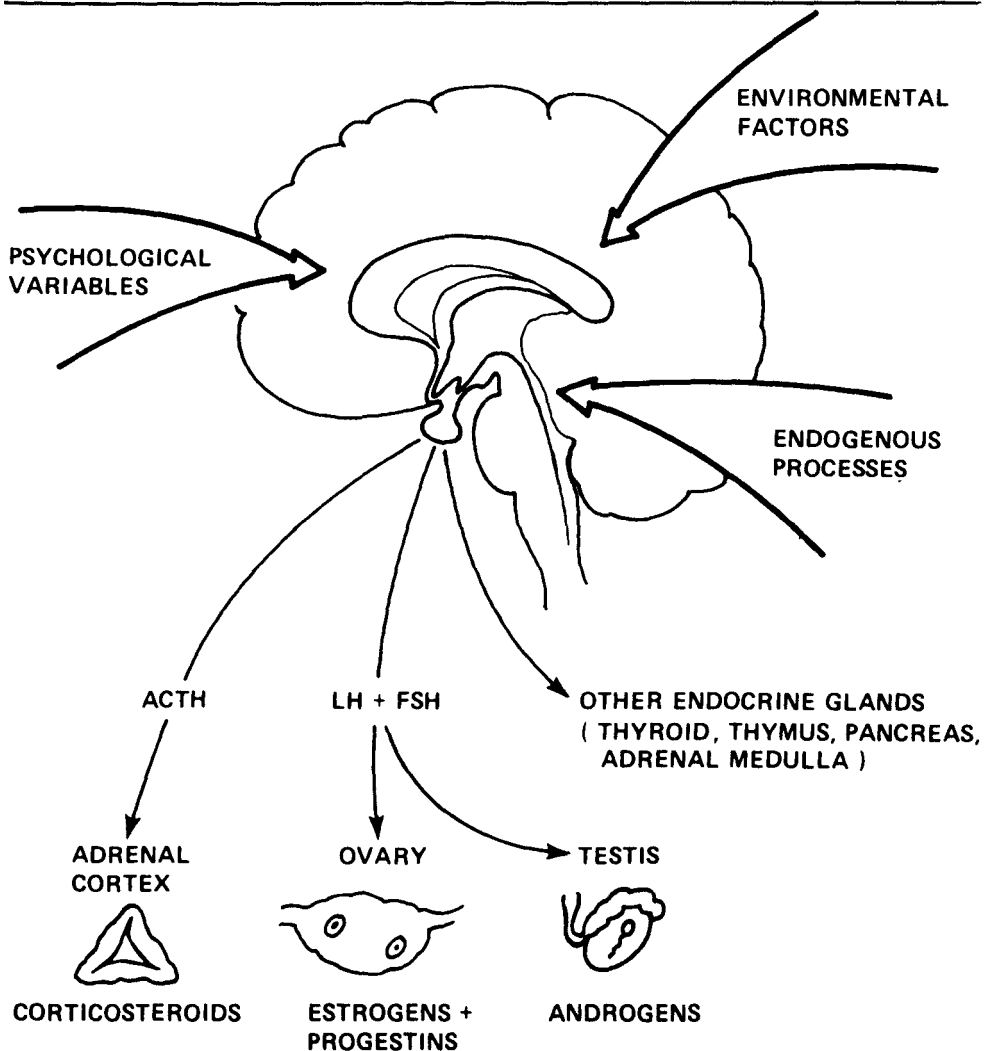
Effect of Dominance and Aggression on Endocrine System

One of the most significant realizations concerning the relationship between physiology and aggression has been that the manifestation of aggressive behavior itself can have a profound influence on the endocrine system. In our studies on the hormonal correlates of social behavior in the squirrel monkey, we found that aggression and dominance can exert protracted effects on the secretion patterns of both adrenal and gonadal hormones. These findings have far-reaching implications because the hormonal

changes can subsequently affect reproductive physiology and behavior as well as the individual's responsiveness to stress.

The sensitivity of the endocrine system to a variety of environmental and psychological stimuli has become increasingly evident over the last several decades. The importance of environmental stimuli first emerged in investigations of biorhythms when it became apparent that factors such as light, temperature, and humidity were critical for synchronizing reproductive cycles. As an outgrowth of the extensive research on stress and psychosomatic illness, however, we now know that many other aspects of the internal milieu are greatly influenced by events occurring in the outside world.[34,35] As illustrated in Figure 4, it is primarily through the hypothalamic regulation of the endocrine system that environmental factors and

ENVIRONMENTAL
FACTORS

PSYCHOLOGICAL
VARIABLES

ENDOGENOUS
PROCESSES

ACTH　　　LH + FSH　　　OTHER ENDOCRINE GLANDS
(THYROID, THYMUS, PANCREAS,
ADRENAL MEDULLA)

ADRENAL　　　OVARY　　　TESTIS
CORTEX

CORTICOSTEROIDS　　　ESTROGENS +　　　ANDROGENS
PROGESTINS

Figure 4. Schematic diagram of the diverse inputs influencing the endocrine system via the central nervous system.

psychological variables exert an effect on the timing and pattern of hormone release. A multitude of neural pathways converge on the basal hypothalamus, influencing the secretory pattern of releasing factors and, in turn, the output of the pituitary and various target glands. The pituitary-adrenal system, in particular, appears to be extremely responsive to psychological stimuli;[36] although it is now apparent that the hormone secretion from most glands, including the gonads, is not as invariant as once believed.[37]

With these findings in mind, we began to examine the influence of dominance and aggression on the adrenal and gonadal systems of the squirrel monkey. The hormone levels shown by the squirrel monkey are extremely conducive to this kind of evaluation because plasma levels of both adrenal corticosteroids and testicular androgens are unusually high even under normal conditions.[38–40] Figure 5 portrays the adrenal and gonadal responses of male squirrel monkeys to being confronted with another male.
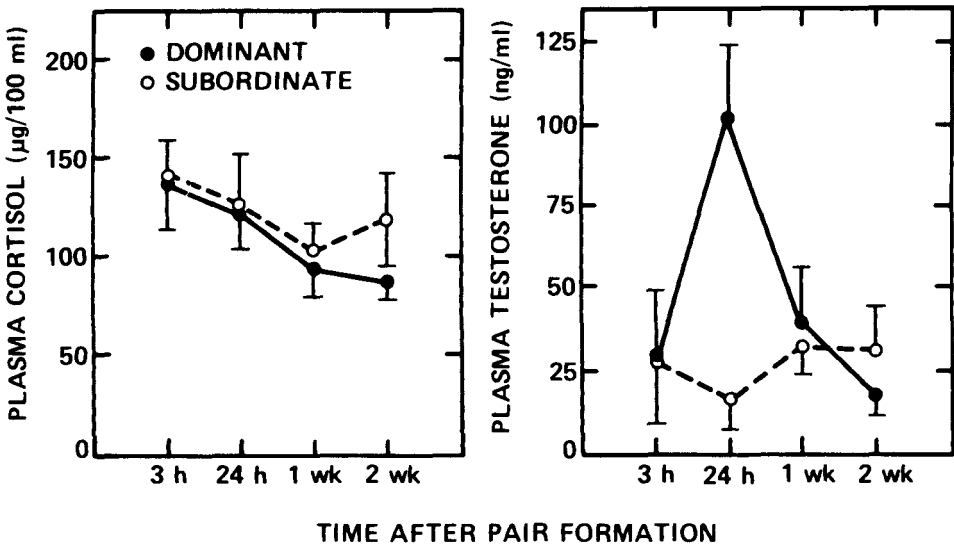

Figure 5. Adrenal and gonadal responses of male squirrel monkeys following the establishment of dominance relations.

Fourteen males were established as seven pairs, and plasma levels of cortisol and testosterone were determined at 3 hours, 24 hours, 1 week, and 2 weeks after pair formation. Examination of the males' social relations via food and water competition tests indicated that a dominant and subordinate monkey rapidly emerged in each pair, and these relationships remained consistent across the study. Dominant males showed striking elevations in testosterone output at 24 hours after the pairs were formed; whereas testosterone levels in subordinates either remained the same or tended to decline. In contrast to the selective response of the gonads, both dominant and subordinate males underwent significant elevations in plasma cortisol levels

during the first day.

These findings on the endocrine responses accompanying dominance contention in the squirrel monkey concurred with previous research on other species. As observed in fighting studies in rodents, both winners and losers showed adrenal activation due to the general arousal induced by dominance interactions. In the current study, the dominance relationships were quickly resolved, but if the fighting continues, such as under conditions of overcrowding, high adrenal activity may persist in the subordinates and eventually result in adrenal hypertrophy.[41] The selective gonadal response was also in keeping with previous research on rhesus monkeys that demonstrated that attainment of high rank in newly formed groups caused an increase in testosterone, while defeat or a fall in rank resulted in a lowering of gonadal output.[42] Even in humans, this type of endocrine response can be observed, since mock combat or competitive tennis matches have been reported to cause similar alterations in testosterone levels.[35,43]

In other studies on the squirrel monkey, we have demonstrated that dominance relationships also can have more protracted effects on the endocrine system. The previous experiment had been conducted during the nonmating season when overall hormone levels tend to be relatively low. In the next study, we compared the effects of dominance during both the mating and nonmating seasons. Males were paired with previously unfamiliar partners and allowed to acclimate to the new housing conditions for three weeks. Thereafter, repeated blood samples were obtained at weekly intervals for six to eight weeks. As expected, both cortisol and testosterone levels were elevated during the mating season, and dominant males showed significantly higher output than subordinates at this time (Figure 6). During the nonmating season, when hormone levels were generally lower, the protracted effect of dominance was no longer apparent. Thus, when dominance rank can potentially exert its greatest influence on reproductive behavior, we find that it has a sustained effect on the endocrine system. Moreover, in further assessments of these subjects, we have determined that the changes in basal levels caused by dominance rank also altered the hormonal response to stress. Examination of the acute response to either stress revealed that relatively high or low basal levels differentially affected the magnitude and temporal parameters of the stress increment.[44] At present, it is not possible to put a value judgment on the type of stress response observed, since the functional significance is still unclear, but it is noteworthy that the increments tended to be smaller in dominant animals.

Perhaps of greater importance, is the potential effect of dominance on reproductive physiology. In other longitudinal studies we have found that dominance rank in stable social groups can influence the onset and magnitude of seasonal hormone surges. At the start of the mating season, the dominant males in each social group typically show the initial testosterone rises before subordinate males, and they also tend to show higher pulsatile surges during the period of high hormone output.[45] This effect of dominance
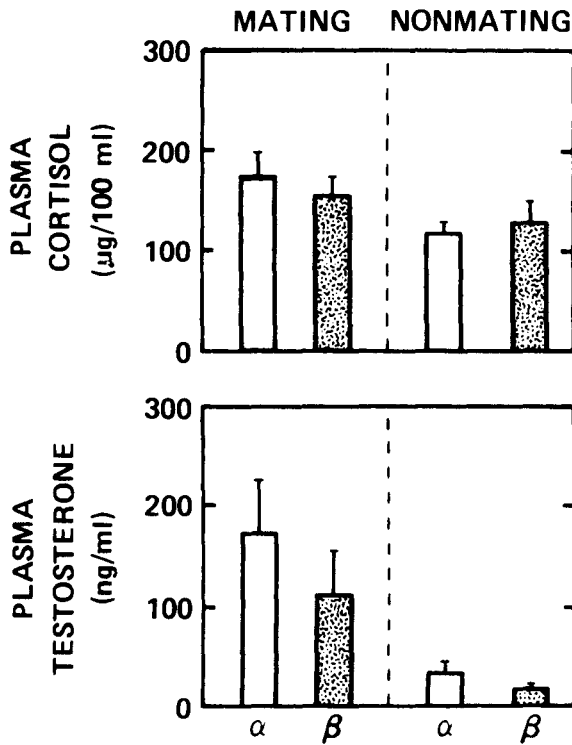
Figure 6. Hormone levels of dominant and subordinate squirrel monkeys during the mating and nonmating seasons.

on reproductive physiology is best illustrated by a study we conducted on the psychoendocrine responses of males to the introduction of females. Although the squirrel monkey is a seasonal breeder, it is possible to induce fertile mating simply by forming new social groups even when the monkeys are in a period of reproductive quiescence. In the next two experiments, we attempted to decipher the hormonal changes accounting for this intriguing phenomenon of induced breeding, as well as to ascertain the possible effect of dominance interactions.

The first experiment assessed changes in the secretion of adrenal and gonadal hormones during three social manipulations.[46] In June, after the normal mating season in our laboratory had ended, nine males were initially housed alone to determine basal levels of cortisol and testosterone. The males were then housed together in three social groups, each consisting of three males, and across the next month four blood samples were collected from every subject at weekly intervals. During the second month after group formation, five females were added to each all-male group, and four more blood samples were collected from the male subjects at weekly intervals (Figure 7).

Behavioral observations of the three social groups indicated that linear dominance hierarchies emerged soon after group formation, and male

dominance relations had a pervasive effect on subsequent interactions and hormone changes. Analysis of the hormonal data revealed that attainment of high social rank was accompanied by a sustained elevation of plasma testosterone levels, whereas subordinate males underwent progressive decreases in testosterone output (Figure 7). The significant changes in circulating testosterone titers that began during the all-male phase became even more striking during the male-female phase. By 24 hours after the introduction of females, mean testosterone levels in dominant males had risen to mating season values, while testosterone secretion in β and γ males either declined or did not respond to the female stimuli. The pattern of change in plasma cortisol levels also revealed strong adrenocortical response to the three social conditions. Plasma cortisol levels increased in all males following group formations, but dominant males again showed the highest hormone levels, especially after the introduction of females.

The particularly strong effect of social rank on hormone levels during the male-female phase seemed to be related to the induction of mating activity, which began soon after the females were added. At least one female in each group became pregnant and the first births occurred 5.5 months later, indicating that some conceptions happened almost immediately. Thus, as previous reports had suggested, the formation of new social groups did indeed induce fertile mating even in the nonmating season. Moreover, this
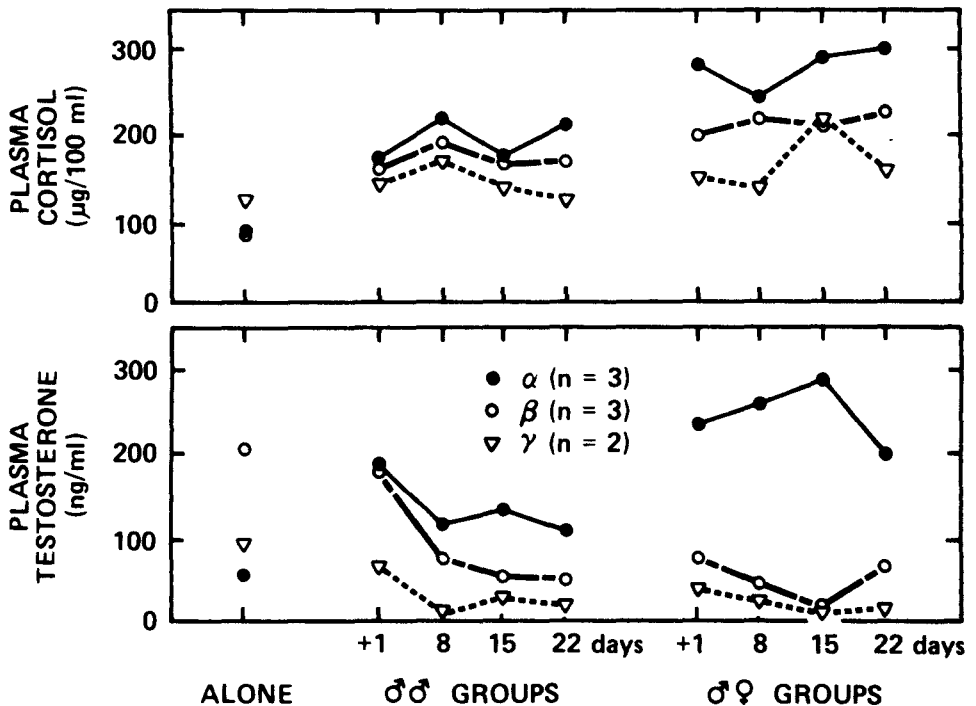

Figure 7. Hormonal responses of male squirrel monkeys to the formation of all-male and male-female groups.

induced mating was accompanied by rather dramatic hormonal changes in the males that reflected a strong influence of behavior on endocrine physiology. Some of the endocrine changes were nonspecific, in that the overall increase in cortisol seemed to reflect a generalized sensitivity to the heightened behavioral agitation that occurs in new social groups. However, the stratification of hormone levels by social rank indicated that specific psychoendocrine relationships are also established that, in turn, can determine subsequent responses to new stimuli. Prior to group formation, neither cortisol nor testosterone levels were predictive of the ranks obtained, but once the hierarchical relationships had developed, they influenced subsequent psychoendocrine responses such that only dominant males showed testosterone elevations to the presence of females. Since dominance was expressed primarily in ritualized displays and spatial displacement, this effect of social rank was not due to injurious aggression, a variable previously shown to affect hormone levels,[35] although periodic dominance contention in one group was serious enough to result in the wounding and forced removal of the most subordinate male.

It was not possible to ascertain the functional significance of the altered hormone levels in this experiment, so a follow-up study was designed to examine whether specific benefits are accrued by increasing testosterone secretion. To see if reproductive ability was actually enhanced, the ejaculatory responses of males were evaluated before and after group formation in the nonmating season.† Partial results of this more elaborate study are presented in Figure 8. As previous research on electro-ejaculation in male squirrel monkeys had demonstrated,[47] the volume of ejaculatory fluid had decreased, and the latency to ejaculate had become prolonged during the nonmating season. However, within 24 hours after the formation of either all-male or male-female groups, the males' ejaculatory responses were suddenly transformed in the direction of mating season levels. These data thus proved that the psychoendocrine changes induced by group formation could cause males to shift rapidly from a state of relative testicular inactivity to one of fertile reproductive potential. It should be noted that the facilitation of ejaculation change occurred in both unisexual and heterosexual groups. Therefore, the enhancement of ejaculation may reflect a synergistic influence of several hormonal or neural mechanisms related to general arousal, especially since the change persisted whether the initial testosterone rises were transitory or sustained during the weeks after group formation.

To date, we do not have equivalent information on ovarian responses to group formation in females, although the occurrence of fertile mating is certainly indicative of a similar activation of reproductive hormone secretion. Given the evidence that females are typically acyclic during the nonmating season, the rapid occurrence of conceptions following group formations suggests that ovulatory cycles can be quickly initiated via social facilitation. This effect of male-female interactions is not the first demonstration of a social influence on female reproductive physiology, since it
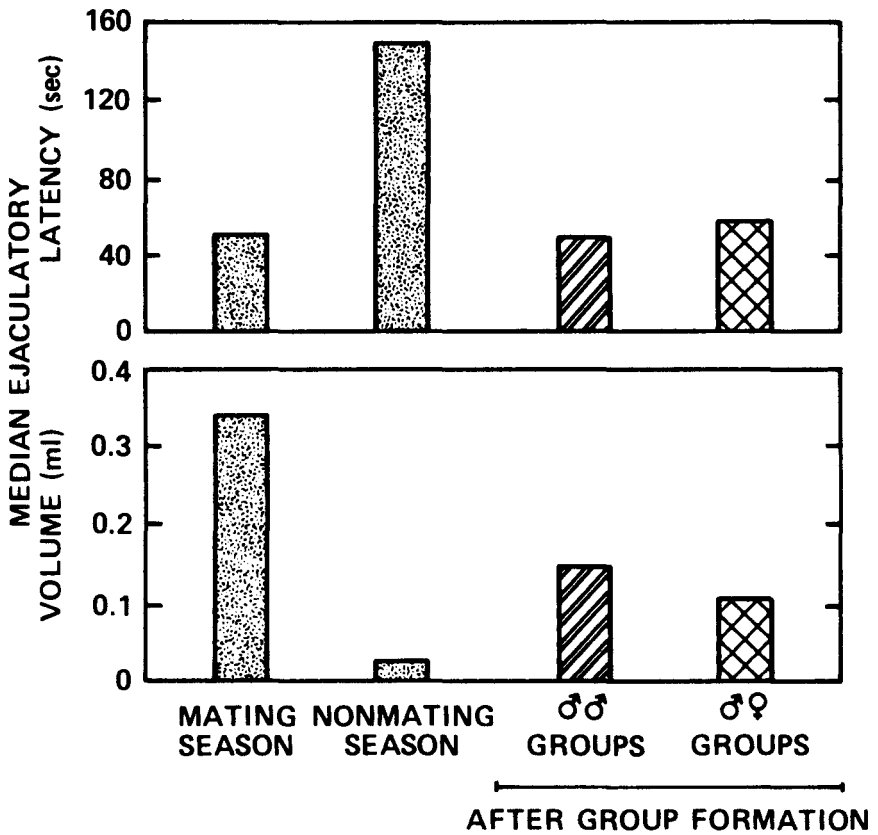
Figure 8. Ejaculatory responses of male squirrel monkeys during the mating and nonmating seasons as well as after the formation of social groups.

concurs with the finding that the onset and termination of cycling is highly synchronized between females during the normal mating season.[21,48,49] In addition, as with males, the occurrence of aggressive and sexual behavior by females appears to be related to increased adrenocortical output. Evaluations of plasma cortisol levels in females have shown that they undergo marked increases in adrenocortical secretion following group formations, and the hormone levels attained reflect the degree of social agitation within the social group.[50]

General Discussion

Viewing our studies within the context of other recent research on aggression in animals, we can draw a number of important conclusions about the biological basis of aggression. First, it must be emphasized that aggression is typically expressed in a non-injurious form, and in most species, there are ritualized behaviors, such as displays or threat postures,

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† In addition to S. Levine, this study was conducted by C. Gonzalez, E. Smith, J. Chen, and G. Gray.

which convey aggressive intent without the need to resort to outright fighting. As a consequence it is usually only under conditions of privation or overcrowding that one finds aggression manifested to the point of severe wounding and death. Recent reports by Goodall[51] of lethal fights in chimpanzees, for example, do not reflect our ''killer'' ancestry as much as they reveal how easily pathological levels of aggression can be induced when normal spatial relations are disturbed; in this case, by extensive food provisioning and habitat destruction in surrounding areas.[52] As Kummer[53] has aptly stated, under natural conditions, ''spacing behavior remains the ultimate refuge when social relationships become unmanageable.''

One exception to the generally noninjurious nature of aggression in animals occurs when two unfamiliar individuals first meet. As Schjelderup-Ebbe[54] described in his classic studies on 'pecking orders' in birds, aggression of this type serves to establish a dominance-subordinance relationship. The establishment and maintenance of dominance relationships is perhaps the most common source of aggression in animals, especially in territorial species and in those animals that aggregate annually for mating purposes. Nevertheless, it is important to bear in mind that the ultimate aim of the aggressive behavior is not to inflict injuries and that fighting usually subsides as soon as the subordinate animal indicates ''no contest'' by withdrawal or submissive gestures.[55] In fact, the hierarchical nature of the social relations may actually serve to reduce subsequent aggression in the future: if food resources or mates become limited, subordinates will acquiesce to more dominant individuals, granting priority of access without the need of further fighting.[56]

As reviewed here, an understanding of the association between aggression and social dominance as well as between aggression and sexual behavior is particularly important for evaluating the physiological factors underlying aggression. Given the significance of inter-male competition in the reproductive strategies of most species, it should not be surprising that the male sex hormone, testosterone, also has a predominant influence in aggressive behavior. Thus, prenatal exposure to testosterone exerts a masculinizing influence on aggressive propensities, and pubertal increases in testosterone serve to activate adult forms of both aggressive and sexual behavior. In many animals, testosterone continues to facilitate the manifestation of aggression in adulthood, but in primate species there has been a radical departure from this reliance on the hormone facilitation of aggression. Presumably due in part to the greater role of learning and socialization in primates, castration does not cause a dramatic lessening of aggressive behavior in adult primates.

There appears to be little evidence from primate studies, therefore, to support the view that altered endocrine physiology can account for the violent dispositions or deviant sex behavior of some members of our own species. Indeed, most studies on testosterone levels in violent criminals and sex offenders have not revealed marked differences from hormone titers in normal men,[57,58] and the few reports of positive correlations may have been

due to the effect of aggressive behavior on hormone output.[59,60] Similarly, the diminished effect of castration in nonhuman primates raises serious questions about its use as a means of reducing violence in humans. Aside from the important ethical issues (do we believe in *jus talionis* only for sex offenders?), castration will probably not reduce overall hostility, and in an appreciable number of cases, the men will even be spared the decline in sex drive.[61] The primary reports of success with hormone manipulation in humans have come from lowering libidinal urges with estrogens or anti-androgens and, thereby, sex-related violence in sex offenders.[62] However, even these treatments have been of mixed success becuase of the marked individual variation in the physiological and psychological responses to the medication, and some physicians have felt the need to include phenothiazines in the treatment.[63]

Since aggression in adult primates does not appear to be caused directly by hormones, it may come as some surprise that the endocrine system is so responsive to the manifestation of aggression. Our laboratory, as well as others,[14,35] has repeatedly found a strong influence of aggression on both adrenal and gonadal physiology. With regard to the gonadal system, the data are relatively straightforward. Fighting or attainment of high rank causes heightened testicular output, whereas wounding or defeat results in lower circulating levels of testosterone. The effect is usually transient although, as our studies demonstrate, during the mating period the influence of dominance on testosterone levels may be extended for many weeks. These data thus suggest that fighting may have an imporant role in establishing the physiological basis for mating in animals in addition to serving in the process of mate selection. Some legacy of this animal heritage can still be observed in humans, since mock combat and competitive tennis matches can cause similar testosterone changes in men.[35,43] It remains to be determined whether the activating effect of aggression on the pituitary-gonadal system is in any way involved in the reinforcing aspects of violent behavior for the sexual gratification of certain sex offenders.

It should be emphasized that some of the behavioral effects resulting from psychoendocrine relationships may be mediated nonspecifically by alterations in the general level of behavioral and physiological arousal. As exemplified by the now classic study of Barfield and Sachs,[64] increases in arousal caused by painful stimulation prior to or concurrent with testing can facilitate the sexual performance of male rats. Similarly, in our studies the increased agitation accompanying the formation of new social groups altered hormone levels and facilitated ejaculatory responses even in the absence of females. These transformations may be partially mediated by changes in adrenocortical output that can cause beneficial or deleterious effects depending on the degree of activation. Under conditions of moderate arousal, for example, the assertion of dominance results in the greater output of corticoids in high-ranking male monkeys, whereas following sustained social harassment in conditions of overcrowding, adrenal hyper-

trophy and accompanying pathologies are typically observed in subordinates.[41,65]

These examples of the complex influence of environmental and psychological factors on adrenal and gonadal physiology have led us to question the view that aggressive propensities emerge simply from neurological or endocrinological events. The strong influence of aggression and dominance behavior on endocrine physiology indicate that it is essential to describe the association between the internal milieu and the external environment in a holistic manner. Some theorists have stated that it is not important to determine "whether aggression is primary or secondary, endogenous or reactive, but . . .to correctly gauge the importance of aggressive forces in personality structure."[66] Our studies on the physiological consequences of aggression and dominance behavior are more cautionary because of the profound influence of psychological processes on internal functions. Since these psychological processes are directly affected by learning and environmental events that evoke frustration, our studies provide added weight in favor of the argument for a primary facilitation of aggression by environmental and situational factors. Clearly, there is a reciprocal relationship between aggression and physiology, but whether aggression is expressed or not depends to a large degree on needs and goals engendered by factors external to the individual.

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