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The Emotions: Focus on Inter-Male
Aggression and Dominance Systems
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DOMINANCE

by

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INTRODUCTION

Studies on dominance abound and cover a range of species from the Stellar Jay to the White rhinoceros. Unfortunately, there is relatively little research on humans. Because of the plethora of studies, it is clearly not possible to cover all of them. Thus, one must be highly selective. The emphasis in this paper will be on human and non-human primates. Because of a variety of problems encountered in experimental design and because of financial considerations, the amount of research in the higher mammals, particularly in the physiological manipulations, is limited. It is therefore necessary, in some cases, to turn to the work on other mammals. Rats and mice, of course, are not people and the results obtained through the study of those subjects may not have any relationship to similar phenomena in humans. Certainly one cannot transfer findings on animals, and particularly lower animals, to humans. However, these studies can provide us with hypotheses that can be tested on humans.

There are situations in which females form dominance hierarchies and engage in threat and fighting behavior if their status is threatened. However, the dominance hierarchy is primarily the province of the male in most species. The antagonists are other males of the same species. Contests between males reflect a dominance interaction whether it involves a fight associated with a particular position in a hierarchy or simply a fight that involves the dominance of one animal over another. The later type of fighting is frequently called intermale aggression.

There are many different forms of social organization in the various animal species. Professor Itani has provided us with an excellent introduction to the many social organizations in primates. It will therefore not be necessary to include that material in this report.

DEFINITIONS

An individual may be said to be dominant if it has a high probability of winning hostile encounters. A win occurs when one subject leaves the field of altercation, or makes "submissive gestures". Submissive gestures are species-specific responses that operationally decrease the probability of attack by a dominant foe. In the case of humans, the range of submissive responses is very broad and are frequently verbal, such as "I am sorry."

CHARACTERISTICS OF FIGHTING IN DOMINANCE DETERMINING SITUATIONS

From mouse to man, with few exceptions, the male of the species is more aggressive than the female[1] and the most frequent target of that hostility is a male conspecific. Intermale aggression is unique and can be differentiated from other types of hostile behavior on the basis of the kinds of stimuli that elicit it, the stimuli that inhibit it, the species-specific topography, and its particular physiological basis.

Although there are particular situations in which the female can display intense and effective aggression (in the defense of the young, for example), in most day-to-day encounters among animals it is the male that shows the highest and most consistent level of spontaneous aggression.

Among non-human primates, most of the aggressive behavior that does occur is manifest by males. For example, Thompson (1967), who studied fascicularis macaques and observed dyadic encounters within and between sexes in a laboratory situation, reports that the principal interactions between pairs of males consisted of biting or rough handling of one male by the other. Pairs of females manifested

almost no aggressive behavior, but spent their time in grooming and inspecting one another. In male-female pairs, the males initiated most of the social interactions, which involved mounting, grooming, and anogenital inspection with relatively little hostile behavior.

Although there are some species differences, the naturalistic observations of a variety of non-human primates tends to support the laboratory findings that indicate that intraspecific aggression is displayed more by the males than by the females (Kummer, 1968; Chance & Jolly, 1970; Carpenter, 1964). A number of additional studies are cited in Gray (1971).

Humans are no exception to this general zoological principle. Although hostile behavior is by no means the exclusive province of the male, he is the primary perpetrator of violent crimes. One of the major findings of the National Commission on the Causes and Prevention of Violence (1969) is stated in unequivocal terms, "Violent crime in the city is overwhelmingly committed by males." In 1968, for example, the homicide rate in the United States was five times higher for males than it was for females, and the rate for robbery was 20 times higher.

It has been suggested that the trait that has the greatest statistical significance in differentiating criminals from noncriminals is that of sex status (Cressey, 1961). Broom and Selznick (1957, p. 639) summarize the particular propensity of the male for all types of criminal behavior as follows: "Compared with females, males have a great excess of crimes in all nations, all communities within nations, all age groups, all periods of history for which we have statistics and all types of crime except those related to the female sex, such as abortion."[2]

Although actual fighting does not generally occur until endocrine maturation takes place, the males in some species seem to have an early predisposition to rough-and-tumble play that simulates adult aggressive behavior.

Among chimpanzees and baboons, males spend considerably more time engaging in aggressive play than do females (Hamburg, 1971a). Infant male rhesus monkeys wrestle and roll and engage in sham biting significantly more than do females, and from 2 1/2 months of age, males show more threat responses than do females. These results were obtained during the study of infant monkeys raised with inanimate surrogate mothers who could hardly transmit cultural differences to the young (Harlow, 1965). Sexual dimorphism in regard to frequency of threat, rough-and-tumble play, and chasing play in the infant rhesus has also been confirmed by Goy (1968); it seems unlikely that this difference between the sexes is due to blood levels of testosterone since that hormone is undetectable in the blood at that age (Resko, 1967). Furthermore, these sex differences are maintained even though the males are castrated at 3 to 4 months of age (Goy, 1966). Field studies have also confirmed the tendency for the young male monkey (old world) to engage in the rough-and-tumble play (DeVore, 1965).

Human children also show sex differences in aggressive tendencies at a very early age. Large amounts of data have been collected in various parts of the United States on the amount and kinds of aggression displayed in relatively standardized doll play situations and there is a clear distinction between the sexes on these variables as early as the age of 3. Boys spend more time in aggressive play than do girls and the type of aggression shown by boys tends to be more vigorous, destructive, and hurtful than that shown by the girls (Sears, 1965). Careful observation of nursery school children reveals that boys more frequently engage in mock hostile play than do girls. This activity involves rough contact with considerable running, chasing, jumping up and down, and laughing (Blurton, 1969). Preschool boys manifest more physical aggression than do girls (McIntyre, 1972). It has also been reported that boys up to the age of 6 or 7 in a Melanesian society show much more rough-and-tumble play than do girls (Davenport,

RESPONSE TOPOGRAPHY IN INTERMALE AGGRESSION

A number of authors have emphasized the stereotyped ritualized nature of fights between male conspecifics (Lorenz, 1964; Eibl-Eibesfeldt, 1967, 1970; Fox, 1969b; Ardrey, 1966). The behaviors displayed by fighting males are characteristic of the species and differ considerably from aggressive behavior involved in the capture of prey or defense against predators.

The response sequences characteristic of intermale aggression have been referred to as fixed action patterns, and although there is some increase in the precision of the movements and an increase in coordination with practice, there is little evidence that these response sequences are learned.

The ritualistic aspect of intermale aggression can also be readily seen in higher animals. An excellent description of the fighting topography in the baboon is given by Kummer (1968):

> Fighting technique consists of each opponent aiming bites at the shoulder or neck of the other. Among hundreds of such scenes we have only seen a male actually take hold of another's coat on two occasions. The analysis of films shows that the animals fence rapidly with open jaws without really touching each other and that the heads are often held back. During a fight each opponent also hits out at the face of the other with his hand, usually missing here as well. The biting and hitting ritual goes on with tremendous speed for a few seconds, silently, the opponents facing each other. Then, one of them turns to flee. At this moment the other often snaps out at him, producing an occasional scratch on the anal region. The vigorous chasing, interrupted by some more fencing, usually lasts no longer than 10 seconds. Most fights come to an end when one opponent flees.

The threat response is also a portion of the topography of intermale aggression. Unless an opponent responds to threat with a submissive posture, a fight is likely to ensue. The threat of the squirrel monkey is particularly easy to

observe and consists of a genital display in which one monkey approaches another and bends over it, making penile thrusts toward the second animal (Candland et al., 1970; Ploog, 1967).

THREAT RESPONSES IN THE CHIMPANZEE

Once a dominance hierarchy is established, the amount of actual fighting is reduced and the submissive animals respond with the responses of submission. The threat responses in the lower mammals may be relatively simple. In the chimpanzee, the threat responses are quite complex and may be considered ritualistic. This does not mean that they are rigid. In fact, they are remarkably flexible and a full-blown threat response may combine any of the following:

1. Staring directly at another animal and making eye contact.

2. The subject may raise one arm above the head, and/or hunch the shoulders.
3. The dominant animal may show foot stamping.
4. It may show hooting, hair erection, and head tipping or jerking.

5. More directly hostile, the dominant member may throw rocks at the animal that is lower in the hierarchy.
6. Finally, it may grab a bush or small tree, shake it vigorously, and even uproot it.

If the opponent does not flee, a full-scale fight may occur (Van Lawick-Goodall, 1968).

THE SUBMISSIVE RESPONSE

Fighting for dominance among males is unique in that it can be blocked or inhibited by specific, generally species-specific stimulus input.

The defeated animal successfully avoids serious injury by engaging in particular ritualized behaviours that function to prevent further attack by the superior contestant. These behaviors have been referred to as submissive

(Matthews, 1964) or appeasement (Lorenz, 1966) responses. Schenkel (1967) has characterized "active submission" in the wolf and dog as "impulses and effort of the inferior toward the friendly harmonic social integration," or as a request for "love" from the superior animal. It is important to recognize that one need not project such complex cognitive-affective mental states onto animals in order to recognize that a particular behavior in one animal has a high probability of eliciting a particular behavior on the part of a responding animal. The terms submission, appeasement, love, and so on, are descriptive of mental states recognizable by humans. They may, of course, have nothing at all to do with the mental states (if any) that occur in animals behaving in the manner described as submissive appeasing, and so on.

Although the intent and the derivation of these ritualized aggression-inhibiting responses have been variously interpreted, there can be little doubt that active, ongoing intermale aggression can be immediately blocked by the assumption of a particular stance or posture by the defeated animal. The ethological literature is replete with examples (Darwin, 1896; Eibl-Eibesfeldt, 1961, 1970; Cloudsley-Thompson, 1965; Lorenz, 1966). Lorenz (1966) devotes an entire chapter in his On Aggression ("Behavioral Analogies to Morality") to descriptions of various aggression-inhibiting signals. The wolf, it is said, turns its head away from its opponent and offers the jugular vein, which immediately inhibits further aggression from its rival. Or when the fight is clearly lost, the weaker wolf throws itself on its back, exposing all the vulnerable parts of the body to the victor, who "cannot" then follow up his advantage (Matthews, 1964).

Detailed observations on the mouse indicate that the defeated animal "sits on its rump and rears without displaying the aggressive face." The posture is accompanied by vocalization. The submissive animal does not attempt to bite the attacker, but may push it away with the front feet. This posture reduces the

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aggressiveness of the attacker. If the defeated mouse attempts to flee, the victor follows for some distance in hot pursuit, with the result that the fleeing mouse is frequently bitten on the rump (Brain & Nowell, 1970). Brain and Nowell also indicate that the inhibition of aggression by posturing is found only in intermale aggression. The submissive posture in several laboratory animals is described by Grant and Mackintosh (1963). Grant (1963) constructed ethograms of the social behavior of the rat and showed that the submissive posture occurs as a response much more frequently than it is responded to. The opposing animal most frequently reacts to submission by refraining from further social behavior and by moving away from the social interaction. Aggression-inhibiting postures have also been described in detail by Barnett (1963) and Seward (1945).

As one might suspect, the submissive behaviors in the chimpanzee are quite complex. The defeated animal may raise its rump toward the opponent in a sexual presentation or it may reach out to be touched. The submissive chimp may bow or crouch or bob. A common gesture is to retract the lips, exposing the teeth and gums (Van Lawick-Goodall, 1968).

The submissive postures, in general, tend to be quite different from those displayed during threat or actual fighting, and it may be that there are few components in the submissive posture that elicit aggression. Darwin (1896), in developing his principle of antithesis in emotional expression, emphasized that gestures of greeting and gestures of affection present a stimulus pattern that is quite the opposite of the pattern presented during threat. In the anecdotal methods of the times, he presents some rather convincing examples. "When a dog approaches a strange dog or man in a savage or hostile frame of mind, he walks upright and very stiffly; his head is slightly raised, or not much lowered; the tail is held erect and quite rigid; the hairs bristle, especially along the neck and back; the pricked ears are directed forwards and the eyes have a fixed stare."

Darwin suggests that the demeanor of the friendly greeting dog is just the reverse of threat. Instead of walking upright, the body sinks downward or even crouches, and is thrown into flexous movements; his tail, instead of being held stiff and upright, is lowered and wagged from side to side; his hair instantly becomes smooth; his ears are depressed and drawn backwards, but not closely to the head; and his lips hang loosely. From the drawing back of the ears, the eyelids become elongated, and the eyes no longer appear round and staring.

An analysis of many of the submissive postures manifest by mammals seems to indicate that, at least in a general way, Darwin's principle of antithesis appears to hold (Eisenberg, 1963). The animal that appears large in threat appears small in submission. The erect stance of threat is replaced by the supine posture of submission. The canines, which in many species are prominently displayed during threat, are hidden, covered, or turned away during gestures of appeasement.

SUBMISSIVE BEHAVIOR AS A REMOTIVATING DISPLAY

However, it seems likely that more is involved in the act of submission than merely the absence of aggression-eliciting stimuli. Lorenz (1966) makes the salient point that in the aroused and "angry" animal there is considerable emotional momentum and that the shift from one motivational state to another tends to be gradual rather than abrupt. Thus it seems that the appeasement postures provoke direct response inhibition on the part of the attacking animal.

Nothing is known as yet about the neurological mechanisms underlying the aggression-inhibiting capacity of submissive postures. However, the descriptive literature available suggests the possibility that elements of the submissive pose function to activate neural systems that are incompatible with the neural system for

intermale aggression. Morris (1964) has referred to the submissive gestures as "remotivating displays"; that is, the submissive posture elicits from the attacking animal a response that is incompatible with further attack behavior. He suggests that an important component in the display in many species is pseudoinfantile and pseudosexual behavior. The behavior of the submissive wolf is frequently identical to the food begging of a puppy. Or, as indicated previously, the wolf may roll on its back and remain still. Such behavior does expose the vulnerable belly, but perhaps more important, it constitutes a "ritualized presentation for cleaning of the anal region," as is common in puppies (Fox, 1969). The submissive wolf may urinate, which elicits an actual cleaning response on the part of the dominating victorious animal (Eibl-Eibesfeldt, 1970).

A frequent component of submissive behavior in a number of subhuman primates involves sexual presentation. That is, the submissive animal turns and presents the hindquarters to the dominant animal (Kreveld, 1970; Chance & Jolly, 1970; Altman, 1962; Hall & DeVore, 1965). The presentation posture results in the elicitation of a perfunctory mounting response, which is incompatible with continued attack.

Aggression-inhibiting postures have not evolved in all species of animals. Neither the cotton rat (Bunnell & Smith, 1966) nor the dove (Lorenz, 1966), for example, seem to have developed such mechanisms; consequently, when escape is not possible, aggression may lead to the death of one of the animals. In general, however, in species in which efficient weapons of defense or of predation have evolved, there has been a parallel development of aggression-inhibiting mechanisms. The resultant value to the species is obvious in that intraspecific confrontations do not generally have serious or lethal consequences.

LIMITED WOUNDING FROM INTERMALE ENCOUNTERS

One of the most remarkable characteristics of intermale aggression is the relatively small amount of injury that occurs during fighting. In other kinds of aggression, the animal uses its available weapons as effectively as possible to dispatch the antagonist. The terminal behavior in the predatory aggression sequence is the killing of the prey. Most typically, there is a bite directed at the cervical spine, which is both efficient and lethal. In contests between males, however, the fighting behaviors have evolved in such a way that the encounters result in a demonstrable superiority of one animal over the other with little physical damage. At a given stage in the conflict one of the animals may flee and his opponent is unlikely to pursue for any distance, or the defeated animal may assume a posture that results in the inhibition of aggression on the part of the victor. In other instances, the attack is aimed at portions of the opponent's anatomy that have evolved in such a way as to minimize injury.

Fighting among male elephant seals, for example, is vigorous and intense. It is conducted with the large upper canine teeth, which have considerable potential for damage. The bulls are frequently wounded and the older, more dominant veterans of many encounters display a large number of wrinkled scars in the neck region, where the attacks are directed. However, the elephant seal is well equipped by tough skin and fat pads to take a great deal of punishment in that part of the body (Matthews, 1964).

The agonistic behavior between males of the same species is highly ritualized and stereotyped. Again the nature of the response is such that the possibility of serious wounding is minimized. Among fallow deer (Dama dama), rival stags engage in vigorous fighting. Their encounters consist of headlong charges against one another. However, they charge only when facing, with the result that

the contact is antler to antler. An attack is never directed against the more vulnerable parts of the body. Fighting among male giraffes is common. They engage in neck-to-neck pushing matches or they swing their heads against the opponent's body or legs. They do not, however, attack with their sharp and dangerous hooves, which are reserved for defense against predators. The oryx and other antelopes may have extremely sharp horns for use in interspecific defense. In intraspecific interactions they are used only to lock the heads of the animals together during intermale pushing contests (Cloudsley-Thompson, 1965).

Another aspect of the hostile interactions among male conspecifics that tends to minimize serious injury is the role of learning. As indicated above, after a limited number of agonistic contacts between a given pair of animals, a dominance-submission relationship is set up between them. When this is accomplished, the probability of actual fighting is diminished because the more submissive animal has learned to respond to anticipatory aggressive responses (threat behavior) with submission or escape, which terminates the encounter. Thus the threat gestures functionally replace actual fighting.

In spite of several safeguards that have evolved to minimize serious consequences from intraspecific conflict, "fractricidal accidents" do occasionally occur and some animals are badly wounded. Pedersen (1962, quoted in Matthews, 1964) reports that a bull musk-ox is sometimes killed as a result of fractures in the frontal part of the skull received during an intermale head-butting match. Bull elephants have been killed as a result of a tusk stab by a rival. Defeated hippos have died from heart penetration by the tooth of another male (Cloudsley-Thompson, 1965). In the fights between seals, an eye may be burst or knocked out, and rarely an animal is killed (Bartholomew, 1967). Fights between male gibbons sometimes result in serious wounds, including broken bones (Carpenter, 1940). All these examples, however, are the exception rather than the rule.

As with most behaviours, the two major factors influencing dominance include environmental inputs and physiological processes. Other things being equal, any factor that increases the probability of other types of aggression occurring will also have a probability of increasing a given subject's rank in a dominance hierarchy, or of increasing the likelihood that it will defeat any given individual.

ENVIRONMENTAL VARIABLES

There are a multitude of environmental inputs, from a drunken father to the observation of the "A TEAM" on television that may have an influence on dominance. Learning in the broadest sense is important. The functions of reward and punishment are obvious, as are the influences of various types of modeling. Conditioning in some circumstances may also influece the status of a given individual in a dominance submission relationship. Miller et al. (1955) have clearly shown that it is possible to manipulate social hierarchies in monkeys by punishing a dominant animal in the presence of a subordinate.

There are a variety of environmental inputs consisting of sign stimuli that may alter dominance relationships. Humans, of course, use many signs. Some are verbal and quite straight forward, such as "Now I shall have to kill you." Meltzoff (1983) in the paper Lethal Dance describes a variety of signs used to express dominance and designed to intimidate others as practiced by New Guinea tribesmen.

Southwick (1969) has shown that the physical and the social environments are of the utmost importance in the aggressive behavior of the Rhesus monkey. Animals in forest habitats are less aggressive than are those living in rural villages and temple areas. A captive group showed the greatest number of aggressive interactions. The social climate had a more profound effect on aggression than did

the physical environment. When strangers were introduced to the group, agonistic behaviors increased as much as tenfold, presumably in an attempt to reorganize the social order. Also see Teas et al. (1982) in this regard.

An important environmental variable that has an influence on dominance relationships is territoriality. It is generally agreed that aggressive encounters that occur within the territory (or central home range) of an animal will usually be won by the resident. The win occurs even though the resident, in other situations, may be subordinate. Although the relationship between dominance and territoriality is an interesting one, there are a number of problems with the concept of territoriality. One of the earliest definitions suggested that "territory is any defended area" (Noble, 1939). Many authors have adopted this definition (Ruffer, 1968; Jewell, 1966; Brown, 1966, and many others). For an historical account of this concept, see Carpenter's excellent review (Carpenter, 1958).

It has been repeatedly pointed out that home ranges may overlap, but territories generally do not because the various animals under study "defend" their territories and "protect" them from encroachment by conspecifics, or by male conspecifics, or by any intruder. How intensive a "defense" the animal puts up depends on the species under consideration and on how broad the experimenter wishes to make the definition.

Motivational states are not only attributed to the territory holder but are also not uncommonly attributed to the intruder. For example, Hamilton (1947, quoted in Wynne-Edwards, 1962, p. 187) suggests that the blue wildebeest (Gorgon taurinus) "strongly resents" encroachment on its grazing land. He also describes an instance in which intruders are chased by a territory-holding bull and then says, "Not the least remarkable phase of the incident was the sense of wrong-doing exhibited by the trespassers, which displayed not the smallest tendency to offer any resistance." (Emphasis added.)

Defend, protect, and resent are all terms that are descriptive of human motivational states. When these terms are applied to animals they are inferred from the behavior, and there can be no assurance that the animal has any mental process even remotely similar to those implied by such words. Observation indicates only that many kinds of animals live within certain restricted areas and that some of them engage in fighting behavior. It can also be said that, in general, the closer they are to the center of their territory, the more intense will be threatening gestures and fighting responses. It is really no more reasonable to suggest that the animal is "defending" his territory than it is to believe that the intruder is defending his God-given right to territorial expansion. Crook (1968) makes the important point that, "In animal societies, individuals do not fight because they have territories, they have territories because, among other things, they fight."

It contributes very little to our understanding of the phenomenon to suggest that certain animals have an innate tendency for territorial defense. Understanding comes only when we can specify the variables of which this behavior is a function. We need to spell out specifically the stimulus characteristics that elicit this kind of behavior in a given animal. Further, since many animals engage in aggression within the home range only at particular times in the seasonal or life cycle, it is necessary to specify the physiological state of the animal during that aggressive period.

One need not impute unobservable need states, or motivations in order to understand the phenomenon of territoriality. There are alternative explanations.

There is evidence, of course, that animals do confine their activities to particular geographical location, and within a given location... many animals spend a greater amount of time in so-called core areas. There is also abundant evidence that many animals engage in intraspecific fighting within home ranges and that

many species tend to win encounters that are fought close to their core areas; that is, the animals on unfamiliar ground are chased away, infrequently injured, and on very rare occasions killed.

It is of little explanatory value to suggest that the large variety of factors contributing to fighting within an animal's home range are related to an innate tendency or need to defend a territory. The fact that the animal closest to the center of its home range is more likely to be successful in an encounter with an intruder is certainly not evidence that territorial defense is involved. Barnett (1969), for example, has suggested that aggressive behavior in the rat is territorial because the animal must be on familiar ground before it will attack a conspecific. By the same reasoning, one should refer to territorial sexual behavior and territorial eating behavior.

Animals are more "successful" in all their behaviors when they are on familiar ground. If one wishes to study sexual behavior, predation, or simply eating and drinking, it is essential that the animal be adapted to the environment. In a strange area, the predominant behavior of most animals is cautious investigation, which is incompatible with aggressive, sexual, or consummatory behavior. Exploratory behavior overrides eating or drinking even under conditions of extreme deprivation. It has been repeatedly reported that a mouse in its home cage is more likely to initiate and to win a fight against an introduced intruder. However, Urich observed in 1938 that the stranger spends most of its time investigating the unfamiliar cage whereas the home cage mouse concentrates on fighting.

There are a variety of stimulus conditions that facilitate the tendency for one male to attack another. There is also a tendency on the part of most animals to investigate and/or escape from unfamiliar situations. There are a variety of ways in which motivational states can be mutually inhibitory. Thus if an animal is on unfamiliar ground, it has investigatory and escape tendencies that are

incompatible with a full-blown aggressive response of whatever kind. If, under the pressure of attack, the animal flees to the familiar stimuli of its own core area, the factors producing escape and investigation tendencies are eliminated and the stimulus of its attacker elicits full and uninhibited aggressive proclivities. It is now likely to win an encounter with the aggressor, who is now itself on unfamiliar ground and has escape and investigation tendencies to compete with its hostile behaviors. In a series of chases and counterchases, it would be expected that the animals might end up at the borders of their home ranges manifesting a combination of escape and aggressive behaviors that are frequently components of the threat response.

Since, as Carpenter (1958) suggests, the so-called territorial behavior is a higher-order construct that results from the action of a variety of sub-systems. It is not possible to attribute this behavior to particular physiological mechanisms. In different seasons and in different species, fighting in relation to a geographical location may be primarily between males, as in the Uganda kob (intermale aggression); restricted to a nest area and confined to lactating females, as in certain female mice (maternal aggression); or related to the herding of a harem, as in the Pinnipedia (sex-related aggression). The amount and intensity of fighting must also undoubtedly be a function of the success or failure of these various aggressive interactions and is therefore partly instrumental aggression.

PHYSIOLOGICAL FACTORS INCLUDE NEURAL AND HORMONAL MECHANISMS.

The two basic physiological methods used for the neurological study of dominance and related problems have been brain stimulation and brain lesions. It has been shown repeatedly that brain lesions may reduce a subject's status in the

hierarchy. The areas lesioned have included the amygdala, the orbital frontal area, as well as the prefrontal and temporal lobes. It is important to note that the situation in which the animals are tested is critical to the outcome. Amygdalectomized animals tested in the laboratory manifest no aggressive tendencies toward humans. However, if the amygdalectomized animals are released among normal animals in a natural setting, or in a natural group in a large cage, the subjects generally show a lack of fear or escape responses in relation to humans. At the same time, they tend to avoid social interactions with other animals and become social isolates. The dominance rank of the operated animals is reduced and they manifest inappropriate social behaviors which elicit aggression from the normal animals (Kling & Cornell, 1971; Kling et al., 1968). In a completely natural setting, operated animals released into their own group withdrew from all attempts by their peers to interact with them. The operates appeared fearful and eventually left the group (Kling et. al., 1970). Briefly, the amygdalectomized animals in a fairly normal social setting appear to show an increase in fear in all social interactions.

In an attempt to resolve the discrepancy between the apparent loss of fear of man and the increase in fear of normal social interactions with other monkeys, Kling (1972) suggests the interesting hypothesis that the removal of the amygdala results in an inability to comprehend complex visual input. The inability to sort out visual communications may result in a state of "depersonalization" such as had been reported in some human patients after amygdalotomy.

The studies on the orbital frontal area (Snyder, 1946), the prefrontal area (Brody & Rosvold, 1952), and portions of the temporal lobe (Plotnik et al., 1968), have all been done using non-human primates and they all find that the lesions interfere with social adjustment and cause the social status of the individual to drop.

One cannot assume, however, that because dominance is affected by a given brain lesion, that the damaged area is responsible for dominance behavior. The relationship may be a circuitous one indeed. In addition to the suggestions of Kling, the actual effect may be due to neurological systems removed from the lesion. Some other deficiency, partial facial paralysis for example, may prevent the monkey from giving adequate social signals. Or, some other unmeasured variable may be critical to the finding, such as a reduction of spontaneous activity. The effect may also be due to the dependent variable used. Dominance relationships may very well lack stability if a single measure is used to represent the complex interactions between two or more animals. One can only begin to understand the subtle relationships if the detains of behavioral mechanisms are observed. Benton (1982) puts it well when he says,

> The problem remains that those who have used competitive measures of dominance often did so because they were unable to observe overt fighting. One answer may be to take more detailed ethological descriptions of social interactions.

> Benton (1981) noted that too frequently, the complex dynamic interaction between animals is reported as one measure. An additional benefit from a more ehtological analysis of behavior is that drugs and hormones do not influence all behavioral postures usually described as characteristically dominant or subordinate in the same way. It seems likely that the ethological approach will demonstrate that subcategories of dominant behavior have different biological bases. Alternatively if subcategories of behavior are influenced in a similar way by particular drugs or hormones, then we may feel safer in using a range of behavior in composite scores.

STIMULATION STUDIES

Stimulation studies are also difficult to interpret. Frank Ervin (Ervin et al., 1969, pp. 54-55) has indicated many of these interpretation problems:

> 1. A synchronous electrical discharge is quite different from the exquisitely patterned afferent volley of physiologic signals.

> 2. In a complex neural aggregate, the electrical input may activate excitatory and inhibitory, afferent, efferent, and integrative, or cholinergic

and adrenergic systems indiscriminately.

3. The instantaneous state of cerebral organization--i.e., all the other influences acting on the object structure at the time of stimulation--is unknown.

4. At best, the site stimulated is part of an integrated system, so that the stimulus is like a rock thrown in a pond--perhaps influencing by waves a distant lily pad. The stimulation of a structure says what it can do under certain circumstances, not what it does do normally.

5. It should be further emphasized that ablation is not the reciprocal of stimulation in other than very simple input and output systems.

It might best be said that both stimulation and ablation experiments should be described with the emphasis on how the organism functions in the new state of cerebral organization necessitated by the experimental intervention.

In spite of the above cautions, stimulation studies do provide us with some insights into the neurological mechanisms involved.

Robinson, et al. (1969) have produced what seems to be clearly an example of intermale aggression in the primate M. mulatta. An electrode was implanted in the anterior area of hypothalamus. It was bolted to the animal's skull and connected to a radio receiver that the subject wore on its head. When the stimulated animal was confined to a primate chair, it made no attempt to attack the experimenter, nor did it manifest a random type of aggression against inanimate objects. When in a colony situation, however, the brain stimulation resulted in an attack on another male that was dominant to the experimental monkey. Other investigators have found that it is difficult to change a dominance hierarchy by brain stimulation (Delgado, 1965). In this case, however, the attacks by the experimental animal were so intense that the formerly dominant subject became submissive.

This appears to be a rather clear cut case of an intermale activity that resulted in dominance change. The experimental animal showed no tendency to attack. Although it is complex and, without doubt, interacts with other

neurological mechanisms, there appears to be an identifiable neurological system associated with intermale aggression, and thus with the systems relating to dominance. It is characteristic of the nervous system that active neural systems have associated with them inhibitors which tend to block the active system when the inhibitors are active. A series of studies by Delgado (1963, 1965) indicate that inhibitory systems also exist for the intermale aggression mechanisms. Delgado also used a telestimulation device so that the animal could be stimulated by remote control.

In a classic experiment, it was shown that remote stimulation of the caudate nucleus of the boss monkey in a colony blocked his spontaneous aggressive tendencies. His territoriality diminished and the other monkeys in the colony reacted to him differently. They made fewer submissive gestures and showed less fear. When the caudate was being stimulated it was possible for the experimenter to enter the cage and catch the monkey with bare hands. During one phase of the experiment, the button for the transmitter was placed inside the cage near the feeding tray and thus made available to all the monkeys in the colony. One of the submissive animals learned to press the button during periods when the boss monkey showed aggressive tendencies. When the boss made threatening gestures, the smaller monkey would frequently look him straight in the eye and press the button, thus directly calming him down and reducing his hostile tendencies (Delgado, 1963, 1965).

Winning an encounter may be its own reward regardless of other rewards, such as availability of sex or food. That is to say, the win may produce positive affect in and of itself. Since animals do not respond well to questioning, it is difficult to get good data. However, at least one study has shown that monkeys will press a bar in order to receive stimulation that produced intermale aggression (Robinson et al., 1969). One might infer from this that the activation of the

intermale system produced positive affect because the animal would work to turn it on. However, there are other interpretations possible. The current may activate more than one neural system at the same time. These systems may be functionally discrete even though they are anotomically proximal. Thus the affective state generated by the stimulation may be irrelevant to the manifest behavior. More definitive information on the problem must come from work with humans who can provide verbal reports on the affective states that accompany dominance oriented responses. There are other animal experiments, however, that do give some insight into the problem of the reward value of intermale aggression.

There are several lines of evidence to indicate that the opportunity to engage in intermale aggression may be positively reinforcing to the participants. The opportunity for one male to attack another will suffice to support the learning of new response patterns. Male mice trained as fighters using the "dangling" procedure of Scott (1958) learned a positive response in a T-maze when the only reinforcer used was the opportunity to attach a "victim" mouse. When the reinforcer was withdrawn, the response extinguished and the position response was reversed when the victim mouse was moved to the oppisite side of the T (Tellegren et al., 1969).

It has also been shown that trained fighters run faster in a runway if the running behavior results in a 5-second opportunity to attack a victim mouse. The starting latency for these animals is shorter than that of controls; they acquire the running response in fewer days and take longer to extinguish than do control subjects (Legrand, 1970). Further, Fredericson (1949, 1951) showed many years ago that the latency for "spontaneous" fighting between male mice decreased over days when they were permitted to fight once a day. If a fight between mice is interrupted, the victorious mouse will push open a door and run from one compartment to another to get at its opponent, as will one of a pair of evenly

matched mice. The only reward for this behavior is a opportunity to continue the fight. The latency of this response is significantly shorter than that of either defeated mice or mice not involved in an aggressive incident (Lagerspetz, 1964). If a fight immediately precedes a trial, aggressive mice will also cross an electrified grid to get at a defeated opponent. Again there is no reward available except the opportunity to fight (Laperspetz, 1964).

ENDOCRINE MECHANISMS

One must also be cautious in the interpretation of the many studies which demonstrate that social hierarchies are influenced by various endocrine mechanisms. A given preparation may serve as a precursor to the actual active hormone, and it may influence more than one endocrine system. For example, one of the corticosteroids (hormones from the adrenal cortex) may reduce the amount of ACTH put out by the pituitary.

It is only recently that adequate measures of androgens and other hormones in the blood stream have become available. The behavioral effects of hormones must operate through their effects on the brain. These brain hormone interactions are, of course, incredibly complex. Additionally, experiments and clinical observations on humans frequently present problems in interpretation. Because experiments frequently lack some desirable controls, it is difficult to determine the role of variables not specifically considered in a particular study. Manipulations of blood chemistry, either experimental or natural, do not occur in a vacuum. A large number of factors are, of course, constantly interacting to affect the changes in aggression potential that result from blood changes. There are wide individual differences in susceptibility to various hormones.

Changes in hormone levels cause changes in subjective experience that may be interpreted differently by different individuals because of their prior learning. The individual's expectations may strongly influence his behavior, and the experience he has after a given manipulation will be influenced by his interpretations of the expectations of others about how he should be affected.

In spite of all the difficulties, however, it is possible to draw some tentative conclusions about the role of blood chemistry changes and aggressive behavior in humans. Much of the evidence in this section is clinical and some of the studies have a small number of subjects and fewer controls than one would find with comparable animal experiments. These findings must be interpreted with considerable caution. However, the result are frequently suggestive of hypotheses that should be followed up and tested more carefully in the future.

At the lowest level of complexity, endocrine studies are relatively easy to do, which may account for the large number of such studies in the literature. It is simplicity itself to do the operation of castration, and it requires relatively little sophistication to give an injection, as any ten year old diabetic knows. It also takes very little more skill to implant pellets of testosterone under the skin.

Interpretation is always a problem. Whereas it is generally the case that changes in hormonal balance which increase intermale aggression also show a measurable increase in social dominance, it is not necessarily so. The treated subject may be a violent isolate that will win a one to one encounter but removes itself from social interactions, thus having no position on the dominance scale.

ANDROGEN LEVELS AND DOMINANCE

Indirect evidence of the relationship between levels of androgens and

aggressive behavior can be derived from studies of the seasonal fluctuations of this type of behavior in primates. Wilson and Boelkins (1970), in a study of the colony of rhesus monkeys on Cayo Santiago Island, have shown that high levels of aggression (as measured by amount of wounding and deaths) occur most frequently in males during the mating season and in females during the birth season. These authors cite evidence to show that the testes are larger during the breeding season (Sade, 1964) and that the relative spermatogenesis occurs during the spring birth season and maximum spermatogenesis during the mating season (Conaway & Sade, 1965). They conclude from these data that the most plausible interpretation of the elevated frequencies of aggression during the mating season is indirectly due to the hormonal changes at that time in the mature males. Alexander (1970) also reports seasonal changes in the behavior of adult male Japanese monkeys, indicating that increases in affiliative behavior result from the seasonal withdrawal of androgens.

The plasma testosterone levels of male rhesus monkeys have been shown to correlate with a number of agonistic behaviors. Threatening and chasing behavior and being submitted to by another member of the colony all correlate significantly with testosterone plasma levels. Submissive behavior is negatively correlated with testosterone level, but not significantly so. This is interpreted as indicating that an animal with a high frequency of aggressive contacts with its subordinates will generally show a higher testosterone level, regardless of how frequently he responds submissively to those above him in the dominance hierarchy. (See Table 1.) Dominance rank within the colony is also correlated with plasma testosterone concentration. The animals in the higher quartile had significantly higher testosterone levels than those animals lower in hierarchy (Rose et al., 1971).

Table 1

Testosterone and Behavior

A. Testosterone and behavioral correlations

Total aggression	0.469
Non contact agression	0.515
Receives submission	0.516
Tension	0.534
Dominance rank	0.350 (rho)
Submission	-0.320 NS

B. Behavioral intercorrelations

Agression and receives submission	0.543
Agression and dominance rank	0.710 (rho)
Submission and dominance rank	-0.650
Agression and tension	0.344 NS
Tension and dominance rank	0.490 (rho)

All correlations listed are Pearson's r except those shown as p, which are Spearman's rank-order correlations. All are significant to at least p⊥0.05, except those followed by NS. For all correlations, n = 34.

From R.M. Rose et al., Plasma testosterone, dominance rank and aggressive behavior in male rhesus monkeys, Nature, 1971, 231, 367.

There are numerous studies that show an increase in intermale aggression scores when the subject is treated with one of the androgens, while, conversely, gonadectomy results in a reduction of such scores. Much of this information has been collected on rodents and it must be recognized that the same findings do not necessarily apply to primates. See Dixson (1980) for an excellent and detailed review. Recent evidence also indicates that endogenous levels of androgens are influenced by the subject's fighting behavior. In general, winning an aggressive encounter results in increasing circulating levels of testosterone and other steroids. This has been shown in mice (McKinney & Dejardins, 1973). Animals defeated in a fight have lower levels of circulating plasma testosterone (Bronson & Dejardins, 1971). This general finding has been substantiated in the male rhesus monkey. Defeat in dominance encounters causes a significant decrease in testosterone levels. Rose et al. (1971, 1972) indicate that dominant males show relatively high circulating levels of testosterone. Although there are wide individual differences, there appear to be dramatic increases in testosterone and androstenedione (a biologically active form of testosterone) levels in adolsecent human males. There are differences between the sexes prior to puberty, but after the age of 9, boys show a gradual increase in testosterone levels. At ages 10 to 15, the increase is on the order of tenfold. Adolescent boys do, of course, show an increase in aggressive behavior, but the increases in testosterone levels have not yet been related to any measures of aggression in adolescents (Hamburg, 1971b).

Until recently, essentially no information has been available relating the endocrine function and affective response tendencies in man. However, with improvement in assay techniques (see Hamburg & Lunde, 1966), such studies are beginning to appear. A suggestive relationship was found between the activity of the pituitary (luteinizing hormone) testicular axis and feelings of hostility, anger, and aggression (Persky et al., 1968). A further study was undertaken on the basis

of those findings using more refined techniques involving the measurement of plasma testosterone level and testosterone production rate (Persky et al., 1971). Two groups of men were studied. The 18 individuals in the younger group ranged from 17 to 28 years of age, and the 15 older men were between the ages of 30 and 66 years. The average testosterone production rate of the older men was about half that of the younger men and when all the subjects were considered as a group, a significant negative correlation (r = -.062) was shown between age and testosterone production rate. This is an interesting finding in itself, inasmuch as it has been shown that violent crime in the United States is most prevalent among males between the ages of 15 and 24.

This study also showed that in the younger men the production rate of testosterone was highly correlated with a measure of aggression derived from the Buss-Durkee Hostility Inventory,[3] and a multivariate regression equation was obtained between the testosterone production rate and four different measures of aggression and hostility. This equation accounted for 82 percent of the variance in the production rate of testosterone for the younger men. In the older age group, the only variable that correlated highly with testosterone production was age, and the regression equation that was highly predictive for the young men was not valid for the older age group.

In another study, aggressive behavior and plasma testosterone were assessed in a young criminal population (Kruez & Rose, 1972). The subjects were selected to provide a high-aggression and a low-aggression group using the number of times that an individual had been placed in solitary confinement as the index for assignment to the two groups. That index was associated with fighting behavior and results in highly differentiated groups. Fighters were defined as those individuals who had been in more than one fight during their imprisonment. Plasma testosterone was measured in six plasma samples taken within one hour of

awakening. Although there was a significant difference between the two groups in terms of actual fighting behavior and verbal aggression, the differences on plasma testosterone were not significant. Paper and pencil tests were also given to the subjects. Hostility was measured by the Buss-Durkee Hostility Inventory but no significant correlation was found between the hostility test scores and fighting in prison, and the hostility scores did not correlate with plasma testosterone. However, an investigation of the type of crime for which the subjects were incarcerated revealed that those individuals who had committed violent and aggressive offenses during adolescence had a significantly higher testosterone level than men who had not committed that type of offense. There was also a significant correlation between the age of the first conviction for a violent crime and the plasma testosterone level. However, the past history of assaultive behavior was not correlated with either fighting in prison or hostility as measured by the paper and pencil test.

The results of the Kreuz and Rose (1972) study are somewhat surprising in light of the Persky et al. (1971) study, which used the same hostility inventory. It may well be that a variety of potent pressures in the prison setting influence the instrumental aggression of the subjects. Reinforcement in the prison tends to be swift and severe and may be a more important determinant of actual behavior than whatever internal tendencies to hostility are set up by the testosterone level. The behavior that did correlate with plasma testosterone took place outside the prison. The reason for the lack of relationship between the scores on the Buss-Durkee inventory and testosterone level are not clear at the moment.

The preceding studies on blood levels of testosterone and aggressive tendencies use males as subjects, but it is not possible from the data to determine whether the hostility measured is a form of intermale or irritable aggression, or some combination of both.

Although uncontrolled clinical studies must be interpreted with caution, several reports on humans offer support for the idea that exogenous androgens enhance aggressive tendencies. One series of schizophrenic patients showed a decrease in fearfulness and apprehension and increased self-confidence when treated with Diandrone (dehydroisoandosterone) (Strauss, et al., 1952). A decrease in feelings of inferiority, timidity, and apathy with an increase in self-confidence occurred in young males with "inadequate personality" after four days to four weeks of therapy with the same preparation (Sands & Chamberlain, 1952). Diandrone is also reported to exert an androgenic effect in the social and psychological rather than in the physical or sexual field. Masculine activity, aggression, and self-confidence are enhanced. The timid "shrinking violet" becomes more adequate, and aggressive tendencies in individuals with manifest hostility are made flagrantly worse (Sands, 1954).

Although the evidence is far from conclusive, it certainly suggests a relationship between testosterone level in the male and some indications of aggressive behavior. This is what one might expect from the numerous studies on animals. One could also expect the relationship to be less powerful because learning is such a potent factor in aggressive behavior in humans. Learned inhibitions can, of course, prevent an individual from acting on relatively strong aggressive feelings that might occur because of the sensitivity produced in the neural systems for aggression by a relatively high androgen level.

A more recent study (Elias, 1981) investigated the levels of testosterone and cortisol (a steroid from the adrenal cortex) in male wrestlers after either a win or a loss. Winners of competetive matches showed greater increases in both cortisol and testosterone than losers. The author concludes, "These findings indicate that humans, like other social mammals may undergo specific endocrine changes in response to victory or defeat."

CAN DOMINANCE BE INHERITED?

The answer to that specific question must be "no." However, the concept must not be discarded too easily. One cannot inherit behaviors or behavioral tendencies. One inherits only structures. However, if, as clearly indicated above, there are a variety of physiological mechanisms, both neural and endocronological, on which dominance aggression is based, it can be seen that the inheritance of particular structures or patterns of structures will, of course, predispose the individual to the expression of dominance. If that is true, it should be possible to breed dominant types of subjects and non dominant subjects.

There can be no doubt that animals can be bred specifically for particular kinds of aggression; for example, fighting cocks, fighting bulls, and pit dogs have been selectively bred for fighting behavior. There are clear-cut strain-differences in the probability of predatory attack. Seventy percent of Norway rats kill mice, whereas only 12 percent of the domesticated Norways do (Karli, 1956). A significantly higher percentage of Long-Evans hooded rats kill chickens than do Sprague-Dawley albinos (Bandler & Moyer, 1970).

There are also strain differences in intermale fighting (Scott, 1942; Southwick & Clark, 1968). A number of experimenters have shown that it is possible, through selective breeding, to develop aggressive and non-aggressive strains of animals. In these cases, the behavior studied was also intermale aggression (Hall & Klein, 1942; Lagerspetz, 1964; Stone, 1932, Yerkes, 1913). The most extensive study of the genetics of aggression has been done on mice selectively bred for high and low aggressiveness according to a seven-point scale of behavior during a period in which formerly isolated mice were paired. It is interesting to note that the

selection process was carried out only on males, since the females did not show enough aggression to score. Table 2 shows the mean aggression score for each successive generation. As McLearn (1969) points out, "In combination with the differences among inbred strains in aggressiveness, this success in selective breeding for aggressive behavior constitutes unassailable evidence of the importance of hereditary factors in determining individual differences in mouse aggressiveness."

Table 2

The Selective Breeding Experiments

Generation	Number of selected males		Age at selection (months)	Range of test scores of selected animals		Number of successful matings			Number of offspring		
	A	N		A	N	A	N		A	N	
P	3	3	3-6	5.3-7.0	1.8-2.1	4	3	10	8	12	8
S$_1$	4	4	4.5	4.1-5.9	1.5-1.9	5	4	25	8	7	10
S$_2$	6	4	4.5	4.1-6.6	1.3-2.4	7	7	29	22	22	19
S$_3$	6	6	4.5	5.0-6.2	1.1-1.9	7	7	20	15	22	14
S$_4$	7	7	4.5	6.1-7.0	1.0-1.7	6	6	30	24	27	23
S$_5$	7	8	4.5	5.9-6.9	1.4-1.7	9	9	31	37	26	31
S$_6$	9	9	4.5	6.4-6.9	1.0-1.6	10	13	34	30	28	34

There are, of course, no comparable data on humans. However, there must be hereditary factors contributing to the determination of individual differences of some kinds of aggression in humans. Certainly there are vast inherited differences in the human nervous and endocrine systems. If, in fact, there are specific neural systems which are responsible for particular types of aggression, one would expect genetic variability in the sensitivity of those structures. If, as appears to be the case, the sensitivity of these systems varies as a function of the level of certain circulating hormones, one would also expect genetic variability in the factors that contribute to the determination of the hormone levels in the blood stream.

A consideration of the concept that there is the possibility of innate mechanisms that may increase the probability of aggressiveness in humans frequently leads to conclusions about the inevitability of war. And, the concept that the mafia and the beast of Buchenwald must, then, forever be with us is concluded. Philsophical questions are raised: Are humans innately evil, and are the discussants at scientific meetings born with the hostility they so frequently display? The answers to those kinds on questions are well beyond the scope of this paper. However, some points must be made. Human aggression of any kind is not inevitable. There are no behaviors based on physiological mechanisms (as all behaviors must be) that cannot be modified through a multiplicity of environmental inputs. These include all kinds of learning. It can be convincingly shown that aggressive responses can be learned. The inhibition of aggression can also be learned, as it has been by hundreds of millions of people around the world. The probability of innate mechanisms for aggression is food for thought, but not despair.

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FOOTNOTES

1. Exceptions to this general rule include hamsters and gibbons. When hamsters are tested in pairs in a neutral area, considerable agonistic behavior occurs with overt fighting in about half the cases. However, no sex differences are discernible (Payne & Swanson, 1970). After extensive field observations, Carpenter (1940) has concluded that male and female gibbons are generally equally dominant and aggressive.

2. In humans, of course, there are potent social and environmental influences on the aggressive behavior displayed by the males, but the sex differences are clear.

3. The Buss-Durkee inventory provides a measure of aggression and hostility. It was developed through the use of standard test contruction techniques. It was subjected to an item analysis and factor analysis and a collection of norms are available. Responses to the items on the inventory seem to be relatively free from the influence of the social desirability variable. (See Buss, 1961.)