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AGGRESSIVE INTERACTIONS IN NON-HUMAN PRIMATES: SOME GENETICAL AND ENVIRONMENTAL FACTORS

A Discussion Paper

Ъу

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SOME ASPECTS OF AGGRESSION AND REASSURANCE IN MACQUES

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During the 1980 biannual meeting of the International Society for Research on Aggression, at Groningen, we watched the Dutch film "Bij de beesten af," made by BERT HAASTRA, one of the best documentary cineasts in the world. This film, nominated for an Oscar, illustrated shots taken in the wild and in laboratory showing how important ethological studies in animals are for the understanding of the mechanisms underlying human behavior. In fact, instead of the inadequacy of standardized tools for the evaluation of aggressiveness reporting only on a few measures or behavioral categories, as too frequently happens, especially in biological studies, an ethological approach can give a better understanding of complex behaviors as the aggressive interactions in primates. As BENTON (1981) pointed out, ethology has the advantage of describing the variety of behavioral elements shown simultaneously in any complex social interaction and their variable sequence, timing and orientation. And that is why our psychobiological research dealing with human and animal aggressiveness has a bioethological approach. Being necessary to work with lower animals, because of financial considerations, we have constructed ethograms of agonistic patterns and submissive postures showed by pigeons, rats, squirrels and monkeys (MARTIN RAMIREZ, DELIUS 1979, MARTIN RAMIREZ 1980, MENDOZA, submitted).

As students of animal behavior, we have been chosen to make some comments on aggressive interactions, with special emphasis to non-human primates.

Aggressive behavior, although rooted in genetic determinants — as every behavior, it is a biologically-based behavior — , is developed and modified through interactions with other life forms and with physical environment, i.e., through a variety of sociological and ecological imputs. (On the utmost importance for behavior of genetics and learning see details in MARTIN RAMIREZ 1978.)

Here we will attempt to examine some biological and environmental variables modifying animal aggression. Before we proceed to our comments on a number ofpotential influences involved in aggressive interactions, let us make one point of a general introductory nature on the concept of aggression.

NATURE OF AGGRESSION

Although people generally seem to be in agreement about what the word "aggression" stands for, research workers show much disagreement about its meanings, ranging from an overt response that delivers noxious stimuli to another organism to an internal state such as a personality trait (HINDE, 1974). This term is used so broadly that it becomes virtually impossible to formulate a single and comprehensive definition (MARTIN RAMIREZ 1981).

In order to better understand this complex phenomenon, it would be more convenient to consider each dimension or strategy in its conceptualization in terms of its functional value suggested (for instance BANDURA 1974, NAGEL, KUMMER 1974) or in terms of how it is expressed (STOKES, COX 1970 considers it as a group of behaviors that lead to attack more than to retreat) or even in terms of the performers' intention (MOYER 1976: an action carried out with the intent to harm another individual or object).

In the real world, aggressiveness is articulated by a number of different types of behavior, subsumed under the general rubric of "aggression". Among the several tentative classifications focused on dichotomies (for instance VALZELLI 1981 distinguished spontaneous from induced aggression), or on the situations which trigger an aggressive response (for instance the classical MOYER's division in eight classes (1968)), we propose, following McGUINNESS's (1981) suggestion, three types: interspecific, intraspecific and reactive aggression, which would be an indiscriminate response to frustration or threats from any source. More details have been discussed elsewhere (MARTIN RAMIREZ 1981). The major emphasis here shall be on intraspecific aggression, especially in primate males.

GENETIC FACTORS OF AGGRESSION

Agressive interactions are affected by genetic factors. Since one of us has recently written on the physiological factors (MARTIN RAMIREZ, NAKAYA, HABU 1980), let us add here just two remarks: there are species-specific differences and sexual ones, related to aggression.

1) Species-specific differences

MOYER (in this ICUS) has reviewed the more characteristic agonistic patterns of several primate species: baboons, squirrel monkeys, chimpanzees..., showing how fighting topography, threat patterns and dominance systems are species-specific. ITANI (in this ICUS) has shown how sociality and aggression vary among species and provide us with a very interesting taxonomy of the many forms of social organization in primates: a) "elemental" or "asocial" societies, consisting only of solitaries with few social interactions (ex., nocturnal prosimians and orangutan), and b) "stable family groups", with a basic social unit a bisexual unit which allows inflow and outflow of certain individuals. ITANI distinguishes two kinds of primate societies as well: one based on the inequality principle, having a very clear linear dominance system (ex., Japanese monkeys), and the other based on the equality principle, sharing a sense of social identity, as SCHELLENBERG points out (ex., apes). The prevalence of either principle would depend on situational structure and on phylogeny. If we accept this point of view, and it is very attractive indeed, it would be not more valid than the old dominance concept, initially used as a social behavior, according to which all groups were thought to be organized in a linear hierarchy. For a more detailed comment on dominance see the recent reviews by SNOWDON, 1983, and MOYER, (in this ICUS).

Although differences in aggression among different species are obvious, there are few studies where aggression has been compared for several species sharing the same habitat. HAKK, 1965, and JOLLY, 1972 observed that in free living conditions macaques and baboons were in general more aggressive than other Old World monkeys such as patas monkeys or guenons. However, baboons seem to adjust better to captivity: killings are less frequent in them than in guenons (ROWELL 1971); probably this is related to the frequent appeasement and conciliation behaviors (lip smacking and presenting) shown by baboons, but not by guenons (NAGEL, KUMMER 1974). The cercopithecoids are probably the most aggressive among the primates.

Nevertheless there are also conspicuous differences in regard to aggression and sociality among closely related species, as BERTRAND (1969) found comparing stumptails and liontails living in the same captive conditions and with equal group composition, and SORENSEN (1974) studying several tree

shrew species living in semi-captive conditions.

2. Sex differences

Naturalistic observations support laboratory findings that in most primate species, including humans, males are generally far more aggressive and more frequent target of hostility than females. There are, however, exceptions, such as gibbons, where males and females are equally dominant and aggressive (CARPENTER 1940).

This prominency of male aggressiveness has been already documented at a very early age of life. Two month old male Rhesus displayed more threat responses than females of the same age (HARLOW 1965, GOY 1966). Field studies (DEVORE 1965) have also confirmed the tendency for the young male monkeys to engage in the rough—and—tumble play. Infant male chimpanzees and baboons spend considerably more time than females engaging in aggressive play (HAMBURG 1967). In humans, boys spend also more time in aggressive play and have a more physical, vigorous, destructive and hurting type of aggression, as SEARS (1965) observed in 3 year—old children and we confirmed in 7 year—old ones (MENDOZA, MARTIN RAMIREZ, in press).

The quality of the aggression shows also sexual dimorphism in primates. In tree shrews, males chase and bite more often than females do and, in turn, the latter ones display more lunges, slaps, threat calls and postures (SORENSON 1974). In Rhesus monkeys, females show milder forms of agonistic behavior, such as threatening gestures (MALLOW 1981) and more instigation than males (TEAS, FELDMAN, RICHIE, TAYLOR, SOUTHWICK 1982). In general, then, males seem to compensate for their strength and danger by giving ample warning before they attack (NAGEL, KUMMER 1974), and their confrontations are quick, clean and one by one (ERWIN personal communication, August 1982), whereas female aggressiveness is sometimes less predictable and, in this sense, more dangerous. Somebody talking about another primate species – the human one – said: "Woman does not fight fairly because she does not know how to be a gentleman."

Finally, there is an additional credence to the possibility that males inhibit aggression among females: in the direct presence of males, there is seldom any reciprocal fighting by females, and their eventual aggressive encounters usually consist of a single act such as a grab or bite (ERWIN 1979).

ENVIRONMENTAL FACTORS

A number of potential social and ecological variables of utmost importance on aggressive behavior of primates have been suggested (for instance SOUTHWICK 1969, NAGEL, KUMMER 1974, ERWIN 1979). Let us comment on a few of them.

1) Social factors

1.1. Social bonds

Although there are so-called asocial species, such as the prosimians, already mentioned, whose level of social interaction is very low, one of the general characteristics of most monkeys is their social nature, which allows a relatively stable social organization, which varies little from one group to another. For many primate species, the maintenance of group integrity and cohesion appear to be based in part on specific long-term emotional bonds between individuals within groups (ERWIN 1979). Those social bonds may develop at any age or sex: the earliest bond is established between the infant and its mother, and later by increasing the interaction with peers. These peerrelationships are typically closest among individuals of the same gender.

Studies in captive macaques have found that the familiarity - unfamiliarity dimension influences the aggressiveness: animals who know each other form coalitions against unfamiliar intruders, who are attacked and repelled with the exception of their infants, which were accepted, even adopted: BERNSTEIN 1964, SOUTHWICK 1967, ERWIN, FLETT 1974, ERWIN, MITCHELL 1975). Familiarity, therefore, endures as a deterrent to violence and unfamiliarity contributes to the risk of violence.

Fieldwork (BERNSTEIN 1967, RICHARD 1970) has showed that in free ranging primates overt interactions between different species are minimal and physical contact is particularly rare: there is a social organization only within groups of cospecifics. WILLIAM's studies (1983) have showed that wild hybrid macaques were socially integrated in their respective troups. They formed an integrated social unit similar to that of a non-hybrid macaque group although with less proximity and contact and without the female social nucleus.

In sum, familiarity between animals creates social bonds which in turn permit a stable organization of social relationship between individuals of the same species.

1.2. Social Deprivation

Rearing conditions have a big influence in the socialization of primates. These early influences are not only maternal, but also paternal: males play an important role in socialization. Parental behavior may be described as varying along two scales: one from overprotective and possessive mothering ot brutal responses to the infant's demands (see details in ARLING HARLOW 1966, MITCHELL 1968). An incompetent parental behavior would result in neglect and abuse of offspring (SUOMI 1978), aggression to the offspring to promote their independence (NEGAYAMA 1981) and, what is even worse, infanticide (HRDY 1979).

A well known case of maternal deprivation is the classical research done by the HARLOW and HARLOW (1969) on the behavioral effects of social isolation of the infant Rhesus monkeys from their mathers in the early stages of development. Animals deprived of social experiences (especially tactile) at an early stage of life become fearfull and disturbed and less socially active, tend to less social exploration and play, and display increased, intensity of aggressiveness. On the contrary, an assessment of the effects of short-term maternal deprivation (12 weeks) in Papio monkeys followed by peer group rearing showed that the nursery-reared infants were less aggressive and dominant than those reared by the mother and in contact with other infants (COELHO, BRAMBLETT 1981).

One of us has had the occasion to observe a case of orphanhood in a two-week-old squirrel monkey, which we will consider in some detail. This monkey lost his mother when he was two week old and was hand-reared up to the age of two weeks, when it was reincorporated to his former colony. At the beginning of this stage he was extremely fearful and threated any individual who walked near him. Later, at the age of three months he seemed to readjust and showed less threats than before. After being back in the colony his social interaction was almost null, except when any other monkey approached him. In these instances he threated and screamed at it. At this stage abnormal behaviors were also observed such as thomb (or any other digit) sucking as well as penus sucking. After a month of being reincorporated into the colony, most of these behaviors ceased and he seemed to behave almost like any other of his peers. The data obtained up to the age of six months indicates that he remained more threatful than any other member of the colony. He was characterized by a low rate of activity, while the normal reared infants of the group were the most active of the colony. Returning back to the main point we were discussing the low level of social activity showed by the orphan monkey. It is consistent with the results obtained by Fairbanks (1974), who indicates that the normal-reared juvenile and infant males of her study were involved in 83% of the 401 recorded behavioral interactions.

Most infanticide cases (HRDY, 1979) reported for many primate species (SUGIYAMA (1965) in langurs, FOSSEY (1979) in gorillas, and SING PIRTA, SING (1981) in Rhesus monkeys occured during inter-groups episodes. In these situations more male infants were killed by conspecifics than females, especially when the captors of the infants were males (KAWANAKA 1981). According to SACKETT (1981), fetal gender appears to influence the aggression received by pregnant pigtail monkeys. Female-pregnant mothers receive more bites than male-pregnant mothers. The explanation given is that something in their appearance or physiology is linked to the sex of the fetus and in some way is detectable by other monkeys.

2) Physical factors

Although social factors usually outweigh the physical ones, some ecological variables have been reported to have profound effects on aggressive behavior in primates. Let us comment how aggressiveness varies according to season and space.

2.1. Season

Males are more aggressive during the mating season, and females during birthseason (EATON, MODAHL, JOHNSON, 1981, TEAS, FELDMAN, RICHIE, TAYLOR, SOUTHWICK, 1982). During the mating season, males usually fight for estrous females, although even within the same species great variations can be observed which seemingly are a function of social traditions (NAGEL, KUMMER 1974). Free-ranging squirrel monkeys, as well as captive ones, display a low level of aggression outside the mating season; on the contrary, during this season, their fights increase, especially those of a ritual nature, where behavioral patterns characteristics of the species can be readily observed: genital display (MENDOZA, submitted).

2.2 Space

Although the supposition that crowding produces an increase in aggressiveness in many species is well accepted (summarized by ARCHER 1970), results are ambiguous at the present time; for instance, experimental studies on crowding effects of non-human primate aggression (BERNSTEIN, GORDON 1974) have failed to produce more than temporary increases in intragroup aggression. This may be partly due to an unclear formulation of problems related to crowding. There should be differentiations between spatial density (by changing the available space while the number of individuals is not changed) and social density (by changing the group size while the available space remains unchanged).

In macaques: a) a higher spatial density resulted in an increase of dyadic male aggressive interactions and in a decrease of the female ones.

ALEXANDER and ROTH (1971) suggest that the more crowded conditions lowered the risk of trauma due to contact aggression, and b) the social density has not yet been experimentally investigated, but field observations on growing populations

suggested that the tension resulted from its increase was normally resolved by group fusion (FURUYA 1969, NAGEL, KUMMER 1974). In humans, McGREW (1971) has compared both kinds of density changes in preschool children, finding that:

a) at higher spatial density, proximity and peers contacts increased proportionally, whereas b) at higher social density, the children tended to avoid each other. For a more detailed summary of non-human studies on density effects on stress, see ELTON (1979).

2.3. Captivity

Although fighting is a fairly common occurrence even in a natural wild setting, captivity intensifies the destructive violence of primates. For instance, hamandryas baboons in the Zurich Zoo and savanna baboons in the Vincennes Zoo were nine to fifteen times and three to ten times, respectively, more aggressive than the wild population of the same species (KUMMER, KURT 1965, MASURE, BOURLIERE 1971). The greatest aggressive interaction in captive groups may be caused, among other possible factors, by: a) spatial limitations and excessive social density (it is very important to keep it in mind for an adequate maintainance of captive primates), with their subsequent restriction of movements; and b) "artificial" composition of groups, forcing a familiarity between individuals previously alien or even incompatible, which is uncommon to feral populations, that can solve such incompatibilities by emigration. These distortions of social rules imposed by captivity may result in the probably most devastating problem encountered in captive primates: their social disruption.

FINAL REMARKS

We are conscious of the high risk of a premature assessment, before doing a careful research based both on biological findings and on social and physical environments, operating within the still poorly understood agonistic interactions and other social processes. Let us conclude, however, saying that aggressiveness cannot be assessed as a merely negative drive to be avoided. On the contrary, it seems to be an essential element in the organization of a

social group. Interacting with other forces, such as social attraction, escape, submission, rearing conditions, space availability, and the familiarity to a place, the aggressive behavior plays an important role as an organizing factor, which serves to establish and maintain the social structure (NAGEL, KUMMER 1974, ERWIN 1979). The cercopithecoids are a good example for this assertion: they are probably the most aggressive, as already mentioned, and they have the most clearly organized societies among non-human primates.

Rather than a way of destruction, the biological aim of aggressiveness, therefore, is a way of competition for vital ressources (food, territory, partners...). The aggressive intraspecific episodia in non-human primates tends to end up with just the submission of the looser and rarely causes severe damage or death. But this strategy is effective only at distances short enough to perceive appeasing signals and submissive gestures. That is why in fighting at too long distances, as in human wars, where weapons are used (lances, arrows, bombs, rockets...), aggression becomes impersonal. "Bastarding" its real positive function produces those terrible massacres that destroy mankind.

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