

Agonistic Rank, Aggression, Social Context, and Testosterone in Male Pigtail Monkeys

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Two groups of pigtail monkeys were merged, a third was formed, and individual males were introduced into a group in a series of experiments examining the effects of social context upon agonistic rank, aggressive expression, and testosterone levels. In the first experiment, two heterosexual groups, containing adult males unfamiliar to the other group, were merged. The two groups fought, and the smaller group was defeated. The alpha and beta males of the defeated group were singled out for repeated attack and both showed significant drops in circulating levels of testosterone. Both males were removed from the group during the first day, but testosterone levels did not recover to baseline levels for several days. The alpha male of the victorious group, on the other hand, showed a significant rise in testosterone, which was apparent only on the day following the merger.

In order to study the influence of previous social familiarity on male reception into a group, another group was formed by removing males from the victorious group and placing them in a separate enclosure. The males in the new group established a dominance hierarchy unrelated to their previous social ranks with one another. Three months later, each of the six adult males remaining in the parent group was individually introduced into the new group for one day or less.

Each of the males introduced into the new group accepted a social position at the lower end of the dominance hierarchy without regard to his previous rank relationships with the host males when they were all in the parent group.

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Even the alpha and beta males of the parent group were relegated to low rank positions in the new group, despite having ranked over each of the host males since birth.

In contrast to the aggression directed at the unfamiliar males in the first experiment, a minimum of aggression was directed to the familiar males introduced into the new group in the second experiment. Although the males introduced accepted low social ranks, it appeared that each was readily integrated into the group with a minimum of aggressive interaction during the time he was scheduled to remain in the group. There were no significant changes in circulating levels of testosterone in any of the males during the introductions of familiar males to one another.

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 Key words: dominance determinants, group formation, testosterone, pigtail monkeys, familiarity and aggression

INTRODUCTION

In studies of individual introductions of rhesus monkeys (*Macaca mulatta*) to established groups we have reported consistent defeat of the newly introduced animal, often accompanied by a depression of circulating levels of testosterone in male subjects [Bernstein et al, 1974; Rose et al, 1972]. Similarly, the merger of rhesus monkey groups has resulted in the defeat of one group by the other with high-ranking males in the defeated group showing plasma testosterone depressions, whereas the victorious alpha male showed a brief but dramatic rise in hormonal level [Bernstein et al, 1974; Rose et al, 1975]. In a few rare cases when introduced individuals were not defeated by the host group, successful defendants showed hormonal rises [Bernstein et al, 1974], whereas mere membership in the victorious group did not produce hormonal rises in resident males not participating in vigorous successful attacks against intruders.

The present study was designed both to test for the generality of these findings to a second macaque (*Macaca nemestrina*) and to determine what influence previous social familiarity has upon the reception of an intruder into a group. If, in fact, dominance was an individual attribute expressed in social relationships, then a knowledge of relative ranks in a previously long-established social relationship should allow for prediction of ranks after the introduction of animals into a new social setting. If, on the other hand, rank positions were a reflection of the current established social order, then past histories of rank relationships would not influence the new rank order established in a new social situation. If individual familiarity due to past association had no influence on the reception of a newcomer, then both social and hormonal responses to introductions should be the same for intruders regardless of past associations with animals in the host group. If, on the other hand, such associations did influence the receptions received, there should be perceptible differences in receptions between familiar and unfamiliar animals introduced into a new social group.

METHOD

Unfamiliar Male Introduction

Two groups of pigtail monkeys were used in the first experiment. The first consisted of four adult males (Ob, Z, Ya, C), four females, and an infant, whereas the second contained approximately 50 animals of all ages and both sexes, including six adult male subjects (Z, Kb, Hb, Lb, Ec, Tb). Both groups had been maintained undisturbed for at least six months prior to the period of study in outdoor compounds with access to indoor quarters.

The groups were merged by releasing the smaller group (group I) into the 30 m square compound containing the larger group (group IIa). The behavior of the ten males was observed and systematically scored using a standard vocabulary during the merger and for several hours thereafter. Additional observations were made during the following days.

Blood samples were drawn from each of the ten males six and four days prior to the merger, and on the morning of the merger, and on the first, third, and ninth days after the merger at approximately 1,000 hours in each instance. The collection of blood samples and the analysis of testosterone by radioimmunoassay were conducted using procedures that have been previously described [Gordon et al, 1976]. All assays were run in duplicate, and the coefficient of variation of duplications was reported as 2.18%, with sensitivity at 5 pg and blank values not significantly different from zero.

Familiar Male Introduction

The second experiment was conducted ten months after the first. Five adult males from group IIa (Hb, Rb, Ec, Lb, and Tb), two males from group I (Z and C), and several females were placed in another 15 m square compound to form a new group, group III. These animals formed a new dominance hierarchy with Hb as alpha. Male Z failed to be integrated into the group and was removed. Dominance ranks were determined using the method of dyadic analysis of the directionality of agonistic encounters.

Three months after group formation the females were removed, and six other males from group IIb (Kb, Q, Lc, Yb, Ya, Zb) were removed one at a time, placed in an individual cage for one week, introduced to group III for one hour, returned to their individual cage for another week, and then returned to group IIb. (Group IIb was the remainder of group IIa after III was formed.) Removals from IIb were done at two-week intervals so that only one animal was out of the group at any time. The order of introduction was not related to the rank of the animals, which had changed since the removal of the animals to form group III so that Q, who had been the alpha male of the group, was now second to Kb.

The experiment was thus divided into four conditions with three blood samples drawn in each condition. Baseline draws in the group took place minus 6 and minus 4 days and at the time of removal. During the week in the individual cage prior to introduction, in the week following introduction, and in the week after return to the group, blood samples were obtained at +24 hrs, +72 hrs, and 1 week. Behavior was scored during the first hour of introductions and summarized into 20-minute blocks. Data collection in this case used the introduced animal as focal subject.

A summary of male subjects used in each of the two experiments and the manipulation procedure appears in Table I.

RESULTS

Introduction of Unfamiliar Males

Shortly after the animals in group I were released into the compound that housed group IIa, fighting broke out between the dominant males of the two groups. Q, the alpha male of the larger group, led his group and vigorously attacked Ob and Z, the alpha and beta males of the smaller group. Both Ob and Z received high levels of noncontact and contact aggression, and displayed redirected aggression to the subordinate males of their own group. The attacks on Ob and Z were persistent and severe, and both animals received multiple wounds and had to be removed from the compound within two hours after being introduced.

The other two introduced males, Ya and C, received comparatively less noncontact aggression and very little contact aggression and engaged in nonagonistic social interactions with members of group IIa. In fact, within a few hours after the introduction, Ya repeatedly mounted a female and was no longer involved in agonistic episodes. C was the only introduced male to exhibit more noncontact aggression than he received, and this was directed primarily toward three group IIa males (Kb the beta male of group IIa), Hb, and Rb. Although C generally avoided group IIa members he would threaten any animal approaching the corner in which he spent most of the time. C was removed during the night for protection and on return to the group fought briefly with Q. He was removed again during the second night and was attacked by Kb on return, defeated, and removed to avoid further injury. Ya was the only male to remain with group IIa and, of the four males from group I, Ya was the only one who had lived in group IIa within the last five years.

The two males who were clearly defeated by the larger group, Ob and Z, each showed a dramatic fall in testosterone level. The mean measures and the three follow-up measures are shown in Table I. A z score was calculated for all follow-up measures to test for significance. Figures 1 and 2 express testosterone concentrations as the percent of the mean value for the period of the study, and

TABLE I. Adult Male Subjects in Each of the Study Groups

Unfamiliar Male Experiment		
Subjects		Procedure
Group I	Group IIa	Groups I and IIa merged
Ob	Q	
Z	Kb	
Ya	Lc	
C*	Rb*	
	Lb*	
	Yb	
	Hb*	
	Zb	
	Ec*	
	Tb*	

At conclusion, males were drawn from group I and group IIa to establish group III. Asterisks designate males forming group III. Males Ob and Z of group I were not used in the second experiment.

Familiar Male Experiment		
Subjects		Procedure
Group IIb	Group III	
Kb	Hb	Each group IIb male was individually introduced to group III for 24 hours or less.
Q	Lb	
Lc	Rb	
Ya	Tb	
Yb	Ec	
Zb	C (removed during first trial)	

both Ob and Z show falls to less than 20% of mean values following introduction (z scores of 5.9 and 2.8 are significant $P < 0.001$ and $P < 0.01$, respectively.) The hormonal levels of the two undefeated males, C and Ya, fluctuated during the period of the study, but all of their measures following introduction were within one standard deviation of their mean baseline values. (Defeat was defined as having occurred when the subject crouched, emitted submissive signals, and no longer responded with aggression to aggressive signals or attack or took any active steps to fend off attack.)

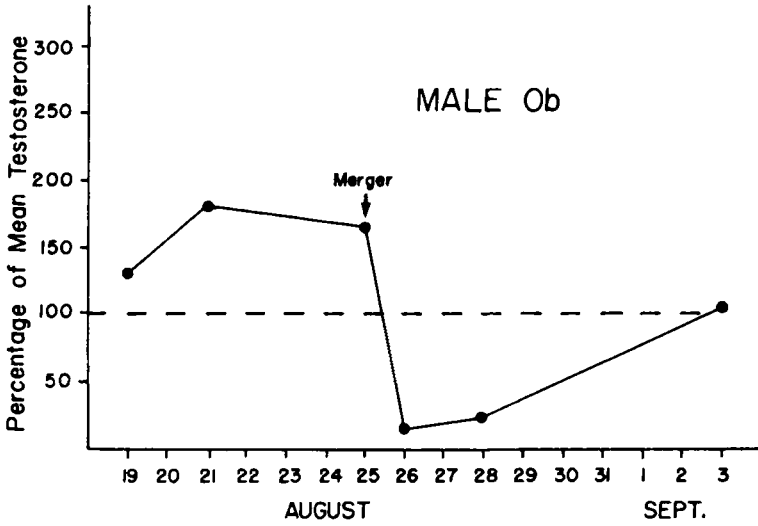


Fig. 1. Testosterone levels of alpha male of the defeated group when two groups were merged. All points are expressed in terms of the percent deviation from the grand mean. Group merger occurred on 25 August immediately following the last baseline measure.



Fig. 2. Testosterone levels of the beta male of the defeated group when two groups were merged. See caption, Figure 1.

The alpha male of group IIa, Q, who led the attack on the group I males, showed a brief rise in testosterone (see Table II and Fig.3) to a value almost two and one half times greater than his mean value for the period of the study. (z score of 9.0 significant $P < 0.001$.) Neither the beta male, Kb, nor any subject male in group IIa, with the exception of Ec, showed a significant hormonal rise on the day following the introduction. Male Ec did show a significant 300% rise in testosterone, although he was only observed to participate in a few agonistic episodes. (z score 83.2 significant $P < 0.001$.) Significant drops in Hb's levels and the rise in Kb's levels did not seem to relate to the group merger, but rather to events within group IIa itself.

Introductions of Familiar Males

In the second experiment, the social order of group III was maintained during each of the introductions of group IIb animals. Despite the fact that both Q and Kb had been dominant over all of the group III males since their births and up until the time they were removed from group IIb, all of the group IIb males yielded immediately to Hb as the alpha male in group III. There were no massed attacks against any of the six familiar intruders, although signs of tension [see Maxim, 1978a, b] such as yawning and puckering [Bernstein, 1970; elsewhere described as LEN, Kaufmann and Rosenblum, 1966; or jaw thrust, Bobbit and Jensen, 1964] were observed throughout the first hour. Virtually no aggression was observed during the introduction of Lc who (as also with Ya and Zb) was quietly accepted

Table II. Testosterone Values (ng/ml) of Males Prior to Group Merger and Changes

Subject	Mean baseline	+24 hours	+72 hours	+1 week
Group IIa				
Q	4.36	14.20*	6.89*	3.35
Kb	17.17	16.34	24.99	32.00*
Hb	17.99	10.12	17.95	12.12*
Lb	24.34	34.14	23.03	23.93
Tb	2.98	1.43	2.96	1.46
Ec	3.69	23.23*	3.83	5.67*
Group I				
Ob	26.08	2.58*	4.18*	18.19*
Z	19.25	1.23*	1.24*	1.37*
C	16.08	26.92	13.16	19.78
Ya	8.62	3.27	3.02	6.47

*Significant z scores at $P < 0.005$.

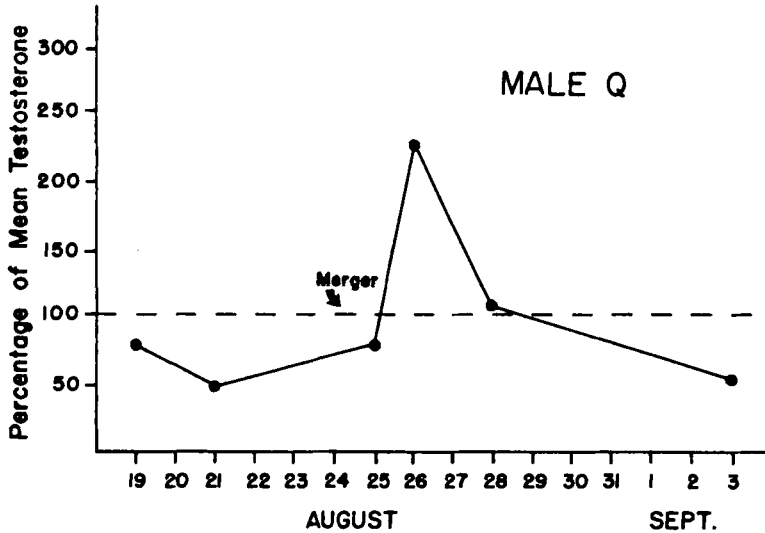


Fig. 3. Testosterone levels of the alpha male of the victorious group when two groups were merged. See caption, Figure 1.

as lowest ranking group member. Males Yb and Kb received similar amounts of aggression and submitted appropriately, but male Q promptly attacked C upon entry into group III. C had to be removed from the group as a consequence, and Q proceeded to direct aggression to the lower ranking members of group III while submitting only to the higher ranking group II members, who attacked him and established their positions over him in the first 20 minutes. Although all introductions had been scheduled for one hour, Lc, Ya, and Zb were allowed to remain overnight to see if any of them would eventually be attacked. They were not.

Table III summarizes the agonistic and other social response frequencies of each of the males upon introduction to the group. The high frequency of aggression expressed by Q reflects his attacks against C, the only group III member not familiar to Q. Despite these attacks against C, Q, as all the other introduced males, accepted low rank in the group.

The returns of Yb, Lc, and Ya to group IIb were also uneventful, consisting mainly of group inspection of the returnee with no agonistic episodes. When Q was returned he showed submission to Kb and redirected aggression to Ya. During Kb's absence from group IIb, Q resumed the alpha position, so that when Kb returned to the group, the two fought briefly. Kb defeated Q, who redirected aggression to Ya and Lc. When Zb returned he was chased by Q, and then redirected aggression toward the younger males of the group.

TABLE III. Frequency of Three Categories of Behavior (hourly rate) Scored During the Introduction of Each Group II Male to Group III (familiar males)

	Aggressive		Submissive		Social	
	Does	Receives	Does	Receives	Does	Receives
Q	130.2	21.0	31.2	142.2	27.0	24.0
Yb	9.0	51.0	163.2	0.0	37.2	48.0
Lc	0.0	3.0	1.8	0.0	15.0	1.8
Ya	7.8	15.0	37.8	0.0	7.2	34.8
Kb	7.8	33.0	97.2	0.0	15.0	43.2
Zb	1.8	21.0	48.0	0.0	7.2	10.2

The testosterone levels of the introduced males showed no systematic hormonal response to any of the changes of social environment apparent in the group as a whole. When examined individually the animals showed considerable variability in testosterone level, but there were no changes that could be attributed to the manipulations of the study.

DISCUSSION

The suppression of testosterone in the male members of a group defeated by another group in a group merger experiment was previously reported for rhesus monkeys [Rose et al, 1975] and was replicated in this study using two pigtail monkey groups. In the present study, the alpha and beta males of the defeated group were singled out for attack by the other group and showed hormonal depressions, whereas the other two males in their group avoided the initial confrontation, did not suffer group attack, and did not show significant changes in their levels of circulating testosterone. Although the differential wounding received cannot be discounted as related to differential hormonal responses it has been suggested that social defeat, not wounding, was the major cause of hormonal depression in rhesus males [Rose et al, 1975].

An increase in testosterone in the alpha male of the victorious group had likewise been reported in the previous rhesus monkey study and was confirmed in the present study as well. Resident males in the victorious group do not all experience this transient elevation in circulating level of testosterone, although one group member, who participated to only a limited extent in the defeat of the other group males, also showed the same hormonal elevation.

The factor of removal of the defeated males from the group can be discounted as causal for hormonal depression inasmuch as in the second experiment none of

the males removed from his original group and placed in a small cage, or removed from the host group and placed in a small cage, showed any sign of hormonal depressions.

Experiment two demonstrated that social familiarity greatly influences the outcome of initial encounters by lessening, and sometimes eliminating, the amount of aggression received from the hosts upon introduction. None of the familiar males introduced into group III were attacked by the group nor did any of them experience hormonal depressions. The one subject (Q) who did show aggression during his introduction to group III directed his responses to the only member of group III who was not socially familiar to him. After the removal of this male, Q did direct aggression to some low-ranking males of the host group while submitting to the high ranking members. His response was appropriate to the ranks of the host animals in their present group and unrelated to their ranks relative to him or to each other in the previous group in which they had all lived.

In the study in which socially familiar group IIb males were subjects, they showed a great deal of variability in hormonal levels throughout the study with some changes during baseline and follow-up periods of magnitudes comparable to that seen in other manipulation studies. It is not clear why these males showed so much hormonal variability in this experiment despite relatively stable levels in the first experiment, but it is possible that the spontaneous reorganization of the dominance hierarchy, which had occurred in the interim, resulted in a period of instability in the group which was reflected in the variable testosterone levels. In spite of the variability, it is clear that no single hormonal response was characteristic of removal from the home group, introduction to the new group of familiar males, or return to the home group. Although these manipulations include a variety of changes that have the potential to influence gonadal hormones, perhaps most important is that each subject male yielded to the social organization of the host group and none suffered mass attack such as unfamiliar male intruders face on introduction [Bernstein, 1969].

Thus, only the introduction of unfamiliar males in the first experiment produced conflicts leading to social victory or social defeat, and when such victory or defeat was recorded we saw significant changes in circulating levels of testosterone. When male subjects with a past social history with host group members were introduced, we saw little aggression and recorded neither social defeats nor victories. None of these males, hosts or subjects, showed significant changes in circulating levels of testosterone. All testosterone levels were, of course, measured at the same time of day, and the influence of these manipulations on the diurnal curve at other points is unknown.

On the other hand, the past social relationships of subject and host males did not determine rank relationships following the experimental introductions. All subject males accepted the alpha male of the host group as dominant. Further, a period of time as a low ranking male in the host troop did not influence the resumption of previous rank positions upon return to their home group. It is true that the beta male in the subject group had asserted himself as number one

during the time that the alpha was out of the group, but the alpha promptly re-asserted himself upon return despite having recently accepted subordinate rank in the host group. Thus, in agreement with Wade [1977, 1978], we would conclude that rank is not an attribute of the individual, nor a reflection of dyadic relationship, but rather an outcome of group dynamics within a particular social organization.

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