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Effects of *d*-Amphetamine on Grooming and Proximity in Stumptail Macaques: Differential Effects on Social Bonds

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PEFFER, P. G., L. D. BYRD AND E. O. SMITH. *Effects of* d-*amphetamine on grooming and proximity in stumptail macaques: Differential effects on social bonds*. PHARMACOL BIOCHEM BEHAV **24**(4) 1025–1030, 1986.—An experiment was conducted to determine the effects of *d*-amphetamine on the expression of certain social behaviors, i.e., grooming and proximity, initiated by adult male stumptail macaques living in a large group comprised of both sexes and all ages. Traditionally, grooming behavior and proximity behavior have been considered indicators of social affinity. Under the non-drug conditions of the present study, the two types of behaviors were initiated in greatly different proportions toward individual members of the group. The acute administration of *d*-amphetamine (0.01–0.3 mg/kg IM) resulted in marked increases in the rate of self-grooming, i.e., the number of self-grooming bouts initiated per hour, for all subjects and in decreases in the rate at which subjects groomed other monkeys, but the drug appeared to have no effect on the rate at which a subject positioned itself near another monkey (proximity). Consequently, the drug had different effects on the two relationships represented by grooming behavior and proximity behavior. Drug administration also produced changes in the distribution of grooming and proximity initiated by the subjects toward various classes of interactants in the group. Furthermore, the changes were not of the same magnitude for the two behaviors. These data provide additional evidence that different group members receive differential behavioral interactions from drugged subjects.

d-Amphetamine Social behavior Grooming Proximity Stumptail macaques

d-AMPHETAMINE is a sympathomimetic drug that readily penetrates the blood-brain barrier and enters the central nervous system, facilitating the release of brain catecholamines. It is also a psychotomimetic agent that can affect mood and psychomotor behavior in humans [17,44]. Therefore, the drug has been of interest to behavioral scientists, and its effects on various behaviors have been studied in a number of contexts. The effects of *d*-amphetamine on behavior maintained under various schedules of reinforcement have been well documented [12,19]. Recently, knowledge of *d*-amphetamine's effects has been expanded by studies involving social behaviors in group-housed nonhuman primates [39]. The studies showed that amphetamine can have distinct, non-global effects on different types of social behaviors. For example, the drug increased the rate of aggression and decreased the rate of affiliative behavior in drug-treated subjects in a group [16, 22, 40, 45].

These results and others dealing more specifically with neurotransmitter activity [28, 31, 32, 33, 34, 36] indicate a possible role of neurotransmitter systems, especially dopamine, in the mediation of some nonhuman primate behavior. Furthermore, the involvement of dopamine systems in psychosis has been suggested by studies relating the chronic administration of amphetamine and other dopamine agonist drugs to the production of a condition closely resembling paranoid schizophrenia [3, 11, 31, 42]. These studies reveal the usefulness of amphetamine research and indicate the need to determine whether the drug may have other behavior-specific effects.

Although behavioral research with amphetamine has focused on aggression and perseverative behavior, the effect on affiliative responses and isolation is also of significance. In order to characterize further the effect of amphetamine on the latter types of behavior, two social measures, grooming and proximity, were studied. Grooming occurs in most nonhuman primate species and, based on its prevalence [18], appears to be a major component of affiliation. Consequently, many hypotheses have been advanced regarding the function of grooming behavior. The two most prominant hypotheses state that (1) grooming is an indication of a network of social attachments and is involved in establishing and maintaining group cohesion (cf. [9, 21, 25, 26, 27]), and (2) grooming is a mechanism for appeasement and for reduction of tension (cf. [25, 26, 43]). Neither of these hypotheses provides an explanation for self-grooming, i.e., grooming behavior directed toward self, yet there is a high incidence of self-grooming in social groups of nonhuman primates.

Goosen [14] has provided evidence that a relationship

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exists between grooming and proximity, another behavior which is purported to indicate affiliation and social stability [10,15]. However, Ehardt-Seward and Bramblett [13] caution that the assessment of social attachment by a single measure creates an oversimplified concept which masks the existence of different types of positive relationships. In the present study, partners in both grooming and proximity were determined, and the effect of *d*-amphetamine on these relationships was investigated. The examination of singular behaviors that relate to group organization and cohesion can increase our understanding of the effects of *d*-amphetamine in a social setting.

METHOD

Subjects

Adult male stumptail macaques *(Macaca arctoides),* maintained in a heterogeneous social group of 37 animals, served as subjects. Group members ranged in age from newborn to old adult (over 20 years). The five male subjects ranged in age from 5 to 11.5 years and occupied various positions in the group's dominance hierarchy. Two of the male subjects (M-18 and M-24) were known to be related matrilineally to certain other members of the group; monkey M-18 was related to five individuals, and monkey M-24 was related to nine others.

The group was housed in a 28.4×32.7 m outdoor enclosure with environmentally-controlled indoor quarters that were accessible via two metal tunnels during non-testing periods (see Smith and Byrd [39] for a detailed description and diagrams of the housing conditions).

Procedure

Group members were restricted to the outdoor enclosure on a prescribed daily schedule, weather permitting. Observations of the subjects and acquisition of the data were accomplished from a tower located along one side of the enclosure, 4.3 m above the floor. Data were collected during 15-minute observation periods at preselected, post-injection times using the focal-animal technique described by Altmann [1]. This technique involved 15 minutes of continuous observation of the experimental subject and recording all instances of grooming behavior and proximity behavior initiated by the subject toward other monkeys. Hourly rates of behaviors initiated by the subject were then derived. Data were collected and stored in a digital format using a microprocessor-based data collection device, the Datamyte 900 [38], and then processed, analyzed and stored on-site in a Digital Equipment Corporation PDP 11/23 microcomputer.

Grooming behavior was scored whenever a subject spread and inspected body hair, picked out particles by mouth or from hand to mouth, or licked the body surface continuously. Self-grooming and grooming another animal were scored separately. Therefore, the term "groom" will be used to refer only to grooming others and "self-groom" will describe a subject grooming itself. Grooming bouts were analyzed both by the number of times a subject initiated them per hour and by their duration. Grooming was rescored after a pause in the behavior of at least two seconds. Proximity behavior was scored whenever a subject was within arm's reach of another animal following a non-aggressive approach. A subject could initiate proximity to more than one animal at a time by moving itself close to other monkeys in a group. If both proximity and grooming were already ongoing when an observation period began, only grooming was scored.

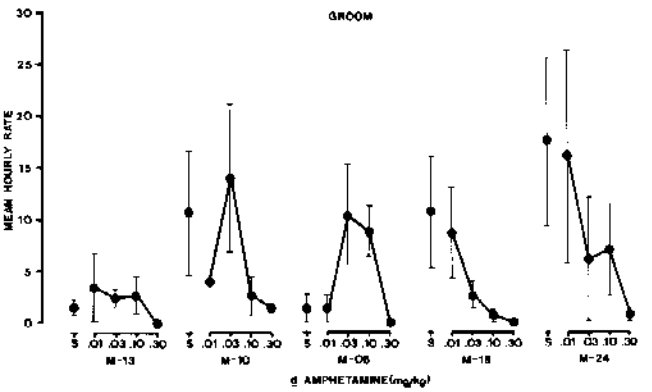

FIG. 1. Effect of *d*-amphetamine on the rate of initiation of grooming behavior by each of five adult male stumptail macaques. Each data point is the mean (+SEM) rate during the period 90–180 minutes post-injection based on three administrations. Data points to the left of the dose-effect curves were obtained when saline (S) was administered as a control.

In order to examine the involvement of other monkeys as different interactants in grooming and proximity behaviors, individual monkeys were identified by age/gender, dominance rank and genetic relatedness. The age/gender classification included adult males (5 years of age or older with full dentition and fully developed temporal musculature), adult females (4 years of age or older and exhibiting ovarian cycling), subadults (4–5 years of age for males and 3–4 years of age for females), juveniles (2–4 years of age for males and 2–3 years of age for females), and immatures (birth to 2 years of age). Identification of high- and low-ranking animals, excluding immature monkeys, involved daily, random distribution of fruit into the compound and observing and scoring priority of access to the fruit among the animals. A computer-based ranking program linearly ordered the animals into a matrix according to the number of wins of each animal over others in the group. This was then divided into high and low rank. Identification of kin and non-kin animals was based on known matrilineal relationships.

d-Amphetamine was dissolved in sterile normal saline (0.9%), and the resulting solution was injected intramuscularly in a volume of less than 1.0 ml. Sodium chloride solution (0.9%) served as a control (placebo) injection. Each subject received, in an unsystematic order, three administrations of 0.01, 0.03, 0.1 and 0.3 mg/kg *d*-amphetamine. On a given experimental day, the drug was administered to only one adult male, and data characterizing the behavior of the drugged subject were collected during the day. At least two days separated successive experimental days, and any one subject received a drug injection no more than once per week.

In order to administer injections without alarming or exciting the animals with physical restraint, each subject was trained to enter a small cage [37] connected to one side of the enclosure, and to extend an arm through a circular opening in the cage according to procedures described previously [7,8]. On a given day, each of the five male subjects received either a drug injection, saline (placebo) injection, or no in-

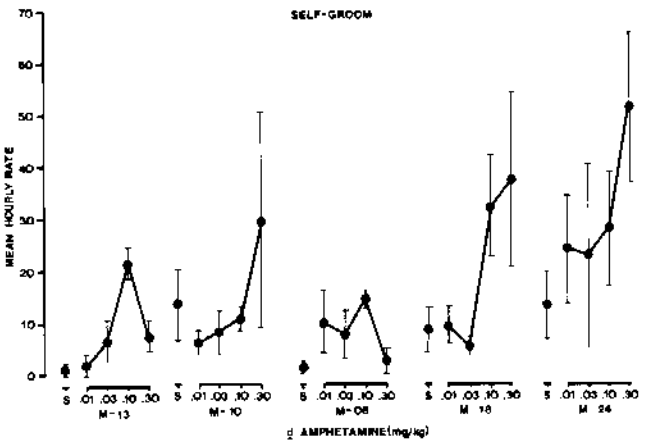

FIG. 2. Effect of *d*-amphetamine on the rate of initiation of self-grooming behavior by each of five adult male stumptail macaques. Each data point is the mean (±SEM) rate during the period 90–180 minutes post-injection based on three administrations. Data points to the left of the dose-effect curves were obtained when saline (S) was administered as a control.

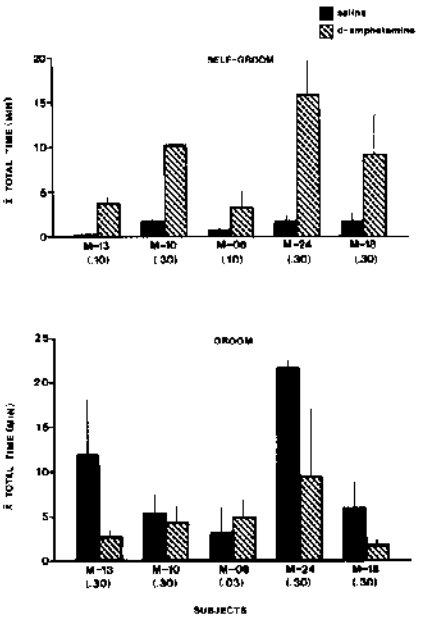

FIG. 3. Effect of *d*-amphetamine on duration of self-grooming (top) and grooming of others (bottom) behavior. Data obtained with the dose of *d*-amphetamine (striped bars) that produced the maximum effect are shown with saline's effect (solid bars) for each of five adult male macaques. The data were derived from the period 90-180 minutes post-injection and were averaged over three administrations.

jection; however, only the experimental animal for that day received the drug. The persons responsible for data collection did not know whether saline or a drug dose had been administered to a given animal.

RESULTS

Mean hourly rates of initiation of grooming behavior, self-grooming behavior and proximity behavior were determined for each subject based on four 15-minute observation sessions during the period 90–180 minutes following drug or saline administration. Following saline administration, the rate of initiation of grooming for the five subjects ranged between 1 and 18 occurrences per hour, the rate of initiation of self-grooming ranged between 1 and 13 occurrences per hour, and the initiation of proximity ranged from 25 to 47 occurrences per hour.

The four doses of *d*-amphetamine had contrasting effects on the rates of grooming, self-grooming and proximity. With the exception of monkey M-06, all subjects exhibited a monotonic decrease in the rate of grooming other monkeys over the range of doses studied (Fig. 1). Rates were lowest after a dose of 0.3 mg/kg, and lower doses had either no effect or less of a decreasing effect. The dose-effect curve for monkey M-06 was of an inverted U-shape indicating no effect after the lowest dose, increased grooming after the two intermediate doses, and decreased grooming after the highest dose (Fig. 1). A Student's paired *t*-test comparing level of grooming after the drug dose (0.3 mg/kg) producing the greatest decrease with level of grooming after saline was significant ($t=3.08$, $p<0.05$).

In contrast to the effect on grooming others, *d*-amphetamine resulted in marked increases in the occurrence of self-grooming for all subjects (Fig. 2). The results of a Student's paired *t*-test comparing saline levels to the dose producing the greatest increase indicated that the effect was significant ($t=-3.66$, $p<0.05$). For two subjects, M-13 and M-06, the dose-effect curves described an inverted U-shape, with the largest increases after a dose of 0.1 mg/kg. For the other subjects, the dose-effect curves were monotonic, and maximum increases were observed after the highest dose studied (0.3 mg/kg). The greatest increases in self-grooming were observed in monkey M-24, where an increase to 383 percent of control value was obtained after 0.3 mg/kg.

In addition to the effect on rate of occurrence, *d*-amphetamine had an effect on the duration of grooming and self-grooming behaviors. The total time each subject was involved in grooming or self-grooming after *d*-amphetamine was compared to the time involved in either behavior after saline administration. For purposes of comparison, the dose of *d*-amphetamine that produced the greatest change from saline, as described above and in Figs. 1 and 2, was chosen for each subject and used in the analysis. When the data for all five males were analyzed using a Student's *t*-test, the results indicated that *d*-amphetamine increased significantly the total amount of time devoted to self-grooming behavior ($t=-4.55$, $p<0.05$) (Fig. 3, top). The increase was greater for some subjects (e.g., M-24 and M-10) than for others, but all increased the time engaged in self-grooming. In contrast, there was a general decrease in grooming others after the administration of *d*-amphetamine (Fig. 3, bottom). With the exception of M-06, all monkeys showed a decrease in duration of grooming others. Moreover, the decrease in total time devoted to grooming others when the focal-animal subject was drugged was significant ($t=2.71$, $p<0.05$). In spite of these effects, the mean duration of each grooming or self-grooming bout did not change.

In contrast to the effect of *d*-amphetamine on grooming and self-grooming behaviors, the drug had little effect on the initiation of proximity behavior in the same subjects. Overall, there was little change from saline values in the occurrence of proximity behavior following *d*-amphetamine administration (Fig. 4). For one subject (M-18), there was no

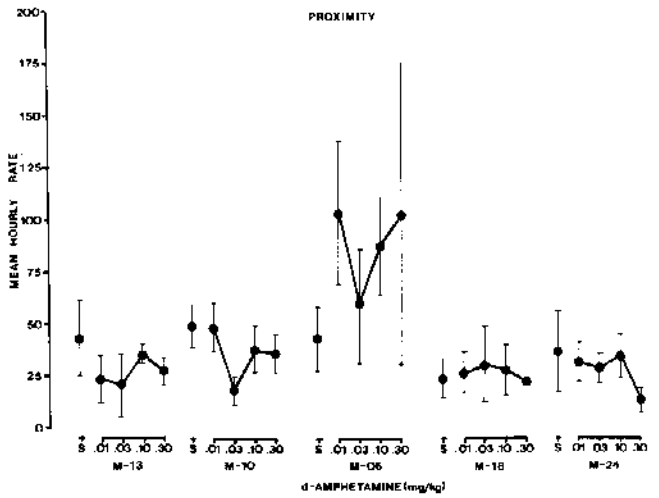

FIG. 4. Effect of *d*-amphetamine on the rate of initiation of proximity behavior by each of five adult male stumptail macaques. Each data point is the mean (±SEM) rate during the period 90–180 minutes post-injection based on three administrations. Data points to the left of the dose-effect curves were obtained when saline (S) was administered as a control.

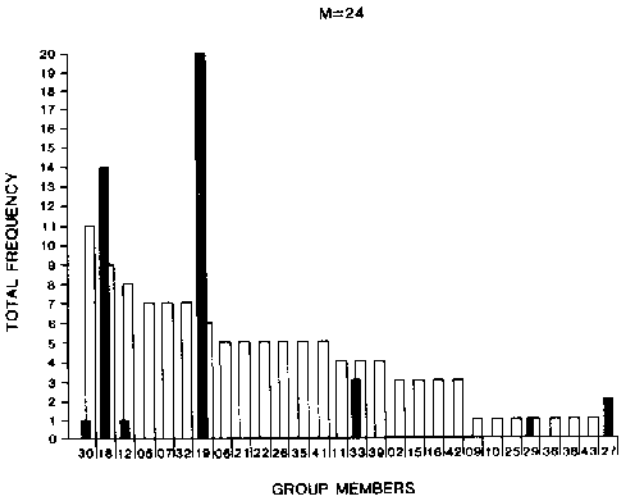

FIG. 5. Frequency of proximity (light) and grooming (dark) behavior initiated by monkey M-24 toward other group members during three administrations of saline. Group members not shown did not receive grooming or proximity behavior from the subject during this time.

effect over a range of four doses, and for three of the subjects (M-13, M-10 and M-24), there were only slight decreases in proximity after any dose (Fig. 4). Data for monkey M-06 reflected an increase in proximity after two doses of *d*-amphetamine, but there was little indication of a relation between dose and effect. Results of the Student's *t*-test indicated no significant difference between saline and the dose producing the greatest change ($p<0.05$).

To assess the independence and separateness of grooming behavior and proximity behavior, the initiation of these behaviors by one representative subject (M-24) toward other individuals in the group under non-drug conditions was determined and plotted (Fig. 5). Even though monkey M-24 engaged in both types of behavior with certain members of the group, grooming and proximity were not initiated by M-24 toward an individual partner in the same proportions. This type of pattern was also characteristic of the other male subjects, and it suggested that two different types of affiliative relationships were ongoing. Additionally, when individual subjects were classified by dominance rank, kin versus non-kin, and age and gender, Chi-square goodness-of-fit tests revealed that the initiation of grooming toward others was not consistent with expectation based on the initiation of proximity. For the kin versus non-kin analysis, data were analyzed for the only two subjects with known genealogy; for all other analyses, however, data for all five subjects were included. Significant differences in distribution were obtained for age/gender ($\chi^2=27.73$, $p<0.05$) and for kin versus non-kin ($\chi^2=64.88$, $p<0.05$). In order to evaluate each age/gender class separately, cells in the Chi-square table were examined for significant departures between standardized cell residuals and the appropriate Chi-square distribution following a procedure outlined by Bishop *et al.* ([5], pp. 136–137). This separate-cell analysis revealed that the male subjects initiated grooming toward subadult and immature group members less frequently than would be expected from the proximity data. Furthermore, significantly more grooming occurred with kin compared to non-kin than would be expected based on the proximity scores. Analysis by high versus low dominance rank revealed no discernible distinction between grooming and proximity partners.

Chi-square goodness-of-fit tests were used also to assess drug-induced departures from saline patterns of interaction and to determine whether *d*-amphetamine produced changes in which animals the drugged subject chose as recipients of grooming and proximity behavior. Because the mean hourly rate of grooming following administration of 0.3 mg/kg *d*-amphetamine was either zero or near-zero for all subjects, it was necessary to use a dose that produced a less dramatic effect. Therefore, a dose of 0.1 mg/kg was chosen to examine changes in the distribution of interactions by the subject with other individuals in the group.

When group members were classified by age and gender (adult males, adult females, subadults and juveniles), *d*-amphetamine was found to alter the distribution of grooming initiated by the focal animals toward members of these classes ($\chi^2=12.33$, $p<0.05$). Immature animals were not included in this analysis because physical access by adult male subjects to immature animals was typically limited, and because the rate at which male subjects groomed immatures under saline conditions was zero. A separate-cell analysis, following Bishop *et al.* [5], revealed an increase in the initiation of grooming by the drugged subjects toward other adult males and an increase toward high-ranking group members compared to the saline condition ($\chi^2=8.77$, $p<0.05$). Moreover, grooming was initiated more frequently toward group members that were not related matrilineally to the drugged subjects (M-24 and M-18) based on interactions with kin and non-kin under saline conditions ($\chi^2=12.94$, $p<0.05$).

Interactants were also grouped by age/gender, high and low dominance rank, and kin versus non-kin in order to analyze changes in the occurrence of proximity behavior. There was a significant change from saline rates in the distribution of proximity initiated by the male subjects toward the various age/gender classes ($\chi^2=13.76$, $p<0.05$). However, a separate-cell analysis did not identify any single class of in-

teractants that received proximity at a rate that deviated significantly from saline conditions. Drugged subjects initiated proximity behavior toward high-ranking animals more frequently than would be expected based on the distribution of interactions following saline administration ($\chi^2=5.83$, $p<0.05$). However, there was no change from saline conditions in the initiation of proximity toward kin versus non-kin.

DISCUSSION

Results of the present study support previous findings of a reduction in the rate of initiation of grooming behavior following the acute administration of *d*-amphetamine [20, 23, 24, 29, 30, 35, 46]. In contrast, self-grooming behavior increased. This difference in effect suggests that there may be different functions for grooming and self-grooming. The rate of self-grooming behavior was also enhanced by acute doses of *d*-amphetamine in previous studies [4, 23, 29, 45]. Poignant and Avril [24] found, however, that self-grooming decreased at doses higher than those used in the present study.

Different experimental conditions (e.g., group size, chronic vs. acute drug administration, individual vs. concurrent dosing) have yielded a variety of results concerning the effect of *d*-amphetamine on proximity behavior. In a study of dyadic interactions between mother and infant vervet monkeys, Schiørring and Hecht [29] found a reduction in the rate of initiation of proximity behavior by the drugged animal. Similar results have been reported for studies involving the chronic administration of *d*-amphetamine [31,45]. Some investigators have reported an increase in proximity behavior, however [2,6]. Haber [16] did not find an increase in the average distance between the drug-treated animal and others, but did report that each drug-treated animal maintained closer contact to the individual with which it affiliated most under saline conditions and had less contact with others.

That *d*-amphetamine affects the rates of certain behaviors selectively and non-uniformly is interesting. Moreover, examination of group members involved in these behaviors with the drugged subjects contributes to a better understanding of the effects of *d*-amphetamine on behavior in a social setting [41]. This type of analysis also emphasizes the value of a large, heterogeneous group of nonhuman primates in revealing drug effects which might not be readily apparent in smaller groups and, yet, which may be relevant to human society. In the present study, rate of initiation of grooming by the subjects decreased and proximity behavior appeared to remain unchanged. Therefore, reduction in the initiation of grooming behavior was not dependent upon a decrease in the initiation of proximity and, thus, to less opportunity for grooming. Closer examination of the individuals involved, however, showed that for both behaviors, changes occurred in the distribution of acts initiated by the subjects toward various members of the group.

As with the effect on rate of initiation of grooming and proximity behavior, changes in the distribution of interactions toward other group members also were not uniform with respect to these behaviors. High-ranking individuals received increased grooming and increased proximity from the experimental animals after drug administration; however, more grooming was initiated toward non-kin animals by the drugged subject in contrast to little change in the initiation of proximity toward related and non-related animals. Although there were changes in the distribution of grooming and proximity when interactants were analyzed by age and gender, grooming was initiated more frequently toward other adult males, and proximity did not deviate from saline rates for any single class of individuals. Under non-drugged conditions, grooming and proximity, behaviors proposed previously as indicators of bonds or affiliations among animals, were initiated predominantly to two different sets of group members. The disparate effect of *d*-amphetamine on these two behaviors suggests that the drug may affect ongoing relationships differentially. In that case, the drug would serve as a useful tool for differentiating among various behaviors.

In humans, *d*-amphetamine can produce irritability and paranoid behavior which can be described as schizophreniform [3, 11, 42]. The nonhuman primate literature is consistent in reporting increased aggression and decreased affiliation associated with this drug [39]. Ehardt-Seward and Bramblett [13] provide evidence that grooming can serve as appeasement and as a mechanism for the reduction of tension in adult male vervet monkeys. In the present study, significantly more high-ranking animals received grooming from the drugged subjects than occurred under saline conditions, a finding that would support the appeasement theory. However, this does not rule out the existence of grooming relations which are more indicative of social attachment.

In conclusion, *d*-amphetamine was found to affect grooming, self-grooming and proximity behaviors dissimilarly. Previously, grooming and proximity behaviors have been used as measures of social affinity, but in the present study, they appear to reflect two different types of bonds. *d*-Amphetamine did not appear to affect these relationships similarly, and the effect did not depend on the baseline rate of occurrence of the behaviors. These findings require greater recognition of the role of the specific behavior and of the social variables controlling the behavior in determining the behavioral effects of drugs. The results also emphasize the important role drugs can play in understanding the complex variables controlling behavior in a group.

ACKNOWLEDGEMENTS

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