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A New Context for the Social Amygdala

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An abstract of

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Abstract

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By Daniela M. Sánchez

Among primates, male emigration presents sex-specific social challenges. Male rhesus macaques (*Macaca mulatta*) emigrate from their natal groups and must successfully integrate into new social groups in order to ensure their survival and reproductive success. Thus, juvenile male rhesus monkeys are a unique model in which to study the neural mechanisms of social behavior. The amygdala has long been implicated in various aspects of social behavior, and lesions of the amygdala have been shown to produce deficits in producing appropriate social responses. In the present study, I have examined social behavior following neonatal amygdalectomy in juvenile male rhesus monkeys (n = 18) reared in semi-natural social groups to determine the extent to which social rearing environment attenuates the behavioral effects of neonatal amygdala lesions. MRI-guided, ibotenic acid-induced lesions of the amygdala (n = 9) or sham procedures (n = 9) were performed at 4 weeks of age. Males then spent the next two years of life in large, mixed-sex, multifamily groups. At 2-2.5 years of age, subjects were removed from their natal groups and all-male groups of age-matched animals were formed in order to present males with an ecologically relevant social challenge. Results indicate that operated males are less likely to initiate social interaction during acute social challenges, but are not impaired in their ability to produce and respond to contextually appropriate social signals. However, this effect is attenuated by social context; observations conducted over a period of months in stable social groups reveal no significant differences between operated and control males and also provide evidence that operated males do not characteristically assume low social rank, as has been previously suggested. These results suggest that a complex social rearing environment compensates for early loss of the amygdala and underscore an important difference in behavioral outcomes as a result of the testing environment. Thus, a relevant social context is crucial to facilitating a deeper understanding of the neural mechanisms of social behavior.

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I. INTRODUCTION

Male rhesus monkeys face unique social challenges. They are born into a female-centric hierarchical social structure, in which the maintenance of dominance relationships depends upon an array of subtle affiliative and agonistic interactions, which young males must learn to recognize and to which they must respond appropriately. Secondly, unlike females, males leave their natal group and enter one or more unfamiliar groups in their lifetime. Their integration into new social groups, and hence their long-term survival and reproductive success, hinges upon their ability to correctly interpret and generate appropriate social behavior. Specific neural systems involved in social cognition may modulate social behavior by altering the perception of signals from others and influencing the production of appropriate responses. The amygdala has long been implicated in several aspects of social cognition. In humans, the amygdala is involved in the recognition of emotions and facial expressions (see Adolphs, 2006 for a review). In rhesus monkeys, removal of the amygdala has been shown to affect aggressive, affiliative, and fearful behaviors (Bauman et al., 2004b; Emery et al., 2001). Numerous studies have addressed the effects of loss of the amygdala on adult rhesus monkey social behavior, and more recently, studies of amygdalectomy early in development have been conducted to determine the amygdala's role in the development of social behavior. However, these studies have employed a variety of surgical techniques, some more precise than others (see Meunier et al., 1999), and have studied behavior in generally restrictive social settings, thus providing little definitive evidence of the social behavioral effects of amygdalectomy in social groups of rhesus monkeys. This small part of the limbic system might be particularly important for rhesus males because of the sex-specific social challenges they face.

Rhesus monkeys naturally live in highly structured, hierarchical social groups (Southwick et al., 1965). Hierarchies are linear, and relationships are maintained through subtle interactions involving agonistic and affiliative behaviors (Altmann, 1962; Sade, 1967). These hierarchies contribute to group stability and serve to reduce aggressive interactions between group members (Vessey, 1984). Rhesus monkey groups are matrilineal; females are philopatric and inherit ranks just below their mothers. Female ranks are generally stable and maintained by support from their mother and other female family members (Sade, 1972; Vessey, 1984). While adolescent males also inherit rank from their mothers, they typically undergo a change in rank around the onset of puberty when they disperse from their natal groups (Boelkins & Wilson, 1972; Drickamer & Vessey, 1973). Adult males in a group also exhibit a linear hierarchy, separate from that of the females (Southwick et al, 1965; Kaufmann, 1967), perhaps because their group membership is transient. Since most adult males in a group are immigrants, they lack the kin-based support system that females use to maintain their rank, and hence have less stable ranks in a group (Bernstein et al., 1974). This pattern of group-changing by males produces social challenges that are sex-specific, and the strategies males use to face these challenges are still unclear.

Natal male emigration

The dispersal or emigration of males from their natal groups is a common occurrence among mammals (Greenwood, 1980) and occurs in nearly all species of Old World monkeys (Pusey & Packer, 1987). Among free-ranging rhesus monkeys, dispersal occurs in early adolescence, around the age of puberty (Boelkins & Wilson, 1972; Carpenter, 1942; Drickamer & Vessey, 1973; Koford, 1963). Evidence suggests that which sex emigrates depends on the species-typical reproductive strategy (e.g., whether males provide parental care) and ecological factors, such as whether food resources are clumped/defensible or distributed (see Pusey & Packer, 1987). Dispersal itself likely prevents inbreeding (Melnick et al., 1984), though evidence on this point is inconclusive. That male emigration is reproductively motivated is supported by observations that dispersal typically occurs during mating season (Boelkins & Wilson, 1972; Drickamer & Vessey, 1973; Lindburg, 1969; Vandenbergh, 1967), and that males successfully mate with females in the new group they join (Berard, 1999; Lindburg, 1969). Thus, dispersal of natal males likely serves important reproductive functions.

Evidence suggests that natal male dispersal likely serves important social functions as well. Males from high-ranking mothers have occasionally been observed to remain in their natal groups and integrate into the existing male hierarchy through both kin (Koford, 1963; Tilford, 1982) and nonkin alliances with peers (Tilford, 1982), thereby avoiding the social difficulties of changing groups. However, the presence of natal males may compromise group stability. In a free-ranging population at La Parguera (a transplanted and provisioned population along the southern coast of Puerto Rico), Tilford (1982) found that subadult natal males from high-ranking matrilines used male alliances to attain a high rank among the adult nonnatal males, but were likely to fall in rank with the onset of the mating season, perhaps due to a loss of support as their male supporters sought access to females. During the postmating season, these natal males rose in rank again, resulting in rank instability over time. Beisner, et al. (2010) contend that in captive populations, juvenile natal males with more frequent kin alliances are more likely to use intense aggression, and that groups with higher proportions of high-ranking juvenile males experience higher rates of wounding, perhaps contributing to group instability. In contrast, the presence of unrelated adult males seems to increase group cohesion and reduce wounding, thereby promoting group stability.

Though males from high-ranking mothers may attain a high rank in their natal groups, remaining in the natal group is an exception to the norm; males will typically emigrate, and they will assume low rank when joining a new group in both free-ranging populations and captive groups (Bernstein et al., 1974; Carpenter, 1942; Drickamer & Vessey, 1973; Koford, 1963). Natal dispersal typically occurs during adolescence, around the age of puberty, with the vast majority of males leaving their natal groups during their third or fourth years (Boelkins & Wilson, 1972; Carpenter, 1942; Colvin, 1986) and having changed groups at least once by six years of age (Drickamer & Vessey, 1973). In new groups, rank is typically determined by an interaction of age (reflected by size) and seniority (i.e., length of time in the group; Berard, 1999; Bernstein et al., 1974; Drickamer & Vessey, 1973). Among males that change groups together, maternal rank seems to exert an effect through the first year of membership in the new group (Drickamer & Vessey, 1973). Interestingly, this maintenance of maternal rank has also been seen for a period of at least one year in an experimentally formed group of all-juvenile animals taken from a free-ranging, mixed-sex group (Loy & Loy, 1974) and in a captive group at the Yerkes National Primate Center Field Research Station (Wallen, unpublished observations).

When leaving their natal group males may either join an existing mixed-sex group, an all-male peripheral group, or become semi-solitary. Males that become semi-solitary tend to do so at a later age (5-6 years) and these changes do not correspond with the mating season (Boelkins & Wilson, 1972; Drickamer & Vessey, 1973). However, these males may join mixed-sex groups briefly during mating season, in particular by interacting with females on the periphery of larger groups. Though males may temporarily leave their group and become solitary for several days at a time (Southwick et al., 1965) this is less common than changing groups, particularly for immature males, who may be at a higher risk of predation (Pusey & Packer, 1987) or lack sufficient experience to live alone (Drickamer & Vessey, 1973). Thus, leaving a group to become semi-solitary may be considered to operate via a different mechanism or serve a different purpose than moving from one group to another.

Group changes occur almost exclusively during the breeding season (Boelkins & Wilson, 1972; Drickamer & Vessey, 1973, Lindburg, 1969), and female sexual interest in unfamiliar males during the breeding season is critical to male integration into a new social group (Tannenbaum, 1997; Wallen & Tannenbaum, 1999). Hence, for young males that have not yet reached sexual maturity, all-male groups may be more accepting than are mixed-sex groups. To emigrating males, the attractiveness of all-male groups may be attributed to any number of factors: their fluctuating and flexible composition, tolerance of extra-group males, and their existence on the periphery of larger, mixed-sex groups, providing the possibility of mating opportunities within the larger group (Boelkins & Wilson, 1972; Drickamer & Vessey, 1973; Vandenbergh, 1967). Among free-ranging rhesus monkeys on Cayo Santiago (a transplanted, provisioned island population off the coast of Puerto Rico), young emigrating males have not been observed to join mixed-sex groups, instead associating in all-male groups until early adulthood (Carpenter, 1942).

Juvenile males are more likely to emigrate with peers than are older males, particularly in seasonally breeding species, perhaps because multiple males enter puberty at around the same time (Pusey & Packer, 1987). Among free-ranging macaques on La Cueva and La Parguera in Puerto Rico, males tended to change groups with peers and/or brothers of similar age, and were more likely to join groups that contained an older brother (Drickamer & Vessey, 1973; Meikle & Vessey, 1981). Colvin (1983) found no evidence of males emigrating with brothers among rhesus on Cayo Santiago, but did not comment on males emigrating to groups already containing brothers. Meikle et al. (1984) reported that wild rhesus in Nepal dispersed randomly with regard to adjacent social groups, but provided no data regarding the previous natal relationships and affiliations among the animals entering into the same new group. Three of five adjacent groups received more than one male immigrant from the central group, indicating the possibility that the group was chosen preferentially due to the presence of brothers or prior affiliates. Meikle & Vessey (1981) found that younger brothers tended to join an older brother's group, but found no evidence for unrelated males from the same natal group being clustered in nonnatal groups as brothers were. Differences among studies may result from different observational techniques, as males from the same natal group may preferentially migrate with affiliates but not necessarily with any male from the natal group. Social histories of the animals prior to emigration would be necessary to more fully understand the inconsistencies among studies in this aspect of male emigration.

Though the evidence for males changing groups together is mixed, Meikle & Vessey (1981) provided evidence that joining a group containing a brother can have reproductive benefits. Males in groups with brothers spent more time in those groups (thus acquiring seniority) than did males in groups without brothers, a factor which was not explained by effects of maternal rank or age, and which the authors posit could increase reproductive success (Meikle & Vessey, 1981). Berard (1999) found inconsistent evidence for increasing reproductive success among immigrant males after reaching a point of long-term residency in the group, but Meikle & Vessey (1981) only observed animals over a period of one year, during which time Berard’s (1999) results support increased reproductive success for these newly emigrated males. This evidence suggests that while it is unclear whether long-term reproductive success in a group is affected by the presence of brothers, short-term success may be increased. Addressing another possible mechanism of increased reproductive success among brothers, Meikle & Vessey (1981) found that the disruption of male-female mating consortships by competing males was less than expected by chance between brothers, though it is not clear whether this effect was mediated by the rank of the animals and the authors do not address whether brothers in a group are more likely to attain high rank than males in a group without a brother. Thus, it is unclear whether the benefits of emigrating with brothers are strictly reproductive, or perhaps derived elsewhere. Of males who participated in agonistic coalitions (providing support or aid to an animal engaged in an agonistic encounter with another animal), aid was more likely to be given to a brother than to an unrelated male (Meikle & Vessey, 1981), which could have important effects on rank in a new group. Thus, emigrating with brothers may have important social benefits. It is not clear whether these benefits also apply to unrelated males who change groups together, as the evidence for unrelated males changing groups together remains inconclusive.

Affiliations between unrelated males are important for social integration. Boelkins & Wilson (1972) reported affiliative relationships between emigrating males and males already members of all-male groups. These relationships were characterized by mutual grooming and support from the group-member male, facilitating the entry of the new male into the group. While the specifics of all-male group formation remain unclear, the formation of affiliative relationships appears very important to group stability, cohesion and integration of new members.

The matrilineal social structure of rhesus monkey groups is based almost entirely on affiliations between female group members. However, the importance of affiliations among males in maintaining group structure and stability is poorly understood. First, the transient nature of male membership in groups may impede the formation of long-lasting affiliations characteristic of female family members, as males must join new groups where they lack kin-based support (Bernstein et al., 1974; Drickamer & Vessey, 1973; Koford, 1963; Southwick et al; 1965). Secondly, males must compete in order to reproduce, and this sexual competition has been thought to preclude the formation of cooperative affiliations among unrelated males in mixed-sex groups. Since fertilizations cannot be shared, cooperation may not provide direct benefits to reproductive success. Males often attempt to disrupt the mating opportunities of other males in order to maximize their own reproductive success (Van Hooff & Van Schaik, 1994; except among brothers, Meikle & Vessey, 1981). That competition for females prevents the formation of cooperative bonds is supported by observations that all-male groups are characterized by peaceful, affiliative interactions between members, in contrast to the agonistic interactions between these immigrant males and resident males in mixed-sex groups

(Pusey & Packer, 1987). Clearly, males are capable of forming affiliative bonds with other males, but perhaps belonging to a mixed-sex group, and the associated sexual competition, limits the formation of such relationships. However, affiliative relationships among males in mixed-sex groups can and do occur (Southwick et al., 1965), though the factors which contribute to these affiliative relationships remain poorly understood as they are typically not driven by kinship ties.

Although some information on the social factors affecting emigration and subsequent social integration exists, little is known about specific neural mechanisms that might facilitate this process. The neural systems underlying social memory and judgment must play a role in social integration, but the specific neural networks or nuclei involved have not been clearly elucidated. One area of the limbic system, the amygdala, has been implicated in processing facial expressions of emotion and the recognition of social signals (see Adolphs, 2006) and thus is an excellent candidate for investigating the role of neural function in male social integration.

The amygdala and social behavior

Successful navigation of complex social situations is dependent on the ability to interpret and appropriately react to social signals. Much of this ability can be attributed to making accurate judgments about others and social context. The amygdala has been implicated in the modulation of social behavior in humans and nonhuman primates via its importance for making accurate social judgments. This modulation may occur at the level of perception, attention, and/or memory of social stimuli. In humans, the amygdala is important for recognizing emotions from facial expressions, gaze-following, and assessing the motivational states of others, as well as understanding others' intentions and social relationships (Adolphs, 2006). All of these processes contribute to making social judgments and attributing mental and/or emotional states to others (see Adolphs, 2006 and Phelps, 2006 for reviews). Studies in humans with amygdala damage have focused on these individual attributes, as well as on the impairment of fear conditioning and processing of fear-inducing stimuli, but have not directly addressed how amygdala damage affects the nature of social interactions in such individuals.

Functional imaging studies have confirmed the activation of the amygdala in normal individuals when viewing untrustworthy faces, indicating its importance in making appropriate social judgments (Winston et al., 2002). Thus, it is surprising that social interactions following amygdala damage have not been extensively studied in humans, and this may be a reflection of our reliance upon spoken language. Adolphs (2006) suggests that social impairment in individuals with amygdala damage may be attenuated by social cues available from language. In this view, individuals with amygdala damage may glean declarative social information through language rather than implicit understanding; for example, a patient may appropriately describe fearful behaviors, even though she is unable to recognize a fearful facial expression (Adolphs, 2006). This suggestion is supported by evidence that individuals with amygdala damage are impaired when asked to judge unfamiliar faces as trustworthy/approachable and tend to rate untrustworthy faces as trustworthy, compared to controls. However, they show no impairment of social judgment if given verbal biographies or specific adjectives describing trustworthy or untrustworthy individuals (Adolphs et al., 1998).

Obviously, the extent of experimental manipulation in human studies is limited. Nonhuman primate studies have provided opportunities for greater manipulation of social contexts as well as direct control over the extent of brain damage in subjects. These studies have been conducted across a broad range of circumstances, and consequently have produced varying but nonetheless measurable effects on behavior, which may, at least in part, reflect changes similar to those seen in humans. Different lesion techniques provide varying degrees of control over the precision and specificity with which structures are damaged, whether surrounding tissue is preserved, and whether fibers of passage are damaged. Aspiration lesions physically remove brain tissue, affecting tissues surrounding the area of interest and damaging fibers of passage. The extent of tissue removal may vary widely across animals. Hence, effects produced by aspiration lesions cannot be easily attributed to removal of the area of interest, in this case the amygdala, when portions of the amygdala may be spared while neighboring areas of the brain are damaged. Neurotoxic lesions (also referred to as excitotoxic lesions) allow more precise targeting of tissue damage. Such lesions are performed by injecting a neurotoxin, such as ibotenic acid, into selected brain areas. Ibotenic acid binds to NMDA receptors, causing calcium channels to open and exciting the neurons to fire excessively, eventually killing the cells in the target area, while sparing fibers of passage.

Thus, interpretation of the nonhuman primate literature on the effects of amygdalectomy is affected by the specific type of lesion technique employed (see Meunier et al., 1999 for a comparison of amygdalectomy via aspiration versus neurotoxic lesions in rhesus monkeys). Early studies used aspiration lesions, often large and imprecisely targeted, while more recent studies use ibotenic-acid induced lesions under MRI guidance and with post-lesion MRI verification of lesion extent while the animal is still alive. Therefore, the wide variety of behavioral consequences of amygdalectomy on social behavior, in part, reflects the markedly different techniques employed to produce brain damage.

Early reports by Klüver and Bucy (1939) suggested that temporal lobe lesions markedly affect behavior. However, these very large lesions involved removal of the entire temporal lobe, including the amygdala. Resulting changes in behavior included an increased tendency to indiscriminately explore objects by mouth (hyperorality), a decreased fear of objects, a decreased fear of other animals (including humans) and a tendency to compulsively react or attend to any stimulus (hypermetamorphosis; Klüver & Bucy, 1939). The authors suggested that the changes in behavior were so profound as to seriously impair normal social functioning: "the outstanding characteristic of the behavioral changes…[is] that they affect the relation between animal and environment so deeply" (Klüver & Bucy, 1939).

In order to more precisely investigate the effects of damage localized to the amygdala, Rosvold et al. (1954) investigated the effects of aspiration amygdalectomy on social rank in rhesus monkeys. Using an 8-member all-male social group, aspiration amygdalectomies were performed sequentially on the three highest-ranking, young male rhesus monkeys. Ages of the animals are not given, but based on weights that were provided (2.90-3.85 kg), they can be assumed to be 1.5-2.5 years old and prepubertal. Subjects were observed for a total of 36 weeks (12 weeks preoperatively), during which they spent alternating two-week periods in either individual or group housing. It is unclear whether they were familiar with each other prior to the beginning of the study, or whether they could view each other when housed individually. Several manipulations were performed by the experimenters in order to increase levels of social interaction, as well as to clarify aspects of the hierarchy that were not well-understood (Rosvold et al., 1954). These included splitting the group into two smaller groups, with one containing the four top-ranking animals and the other the four lowest-ranking animals, reducing the cage space by half, and removing the lowest-ranking animal. These methodological choices make the interpretation of these data particularly challenging as social interactions in a group of potentially unfamiliar animals in a continual state of separation and reintroduction are unlikely to reflect social processes occurring in species-typical rhesus monkey groups. In free-ranging rhesus monkey groups, temporary removal of males often results in changes in rank upon their reintroduction (Vessey, 1971). It has also been suggested that in captive populations, repeated separation and reformation of groups impedes the process of social integration (Bernstein et al., 1974). Thus, the exact relevance of this study to typical social processes remains obscure.

Experimental surgeries were performed sequentially, starting with the highest ranking male and proceeding down the hierarchy, at two-month intervals. Time in the group was thus confounded with timing of surgery, with later-operated males having less time to reintegrate than earlier-lesioned males. Histological examination, while indicating inconsistency of lesion placement, did not allow determination of which areas were removed in common across all three animals, so we cannot be confident in attributing any of the results of this study specifically to amygdala damage. When individually housed, all three lesioned animals appeared to behave more aggressively towards the observer. However, the nature of the ethogram used to collect the data make interpretation of the results nearly impossible, as behaviors like remaining in the front of the cage (while the experimenter provided food) were classified as indicating aggression.

Analysis of the components of the ethogram indicates that rather than measuring aggression, the experimenters were measuring some combination of aggression, disinhibition, reduced fear responses, or some combination thereof. Upon return to the group two weeks post-recovery, the former alpha and beta males exhibited decreased aggression and fell in the dominance hierarchy. The last lesioned male, who had taken over the alpha position with the fall of the two other lesioned males, remained in the alpha position for the last four weeks of the study. The authors interpret this difference in behavior post-surgery as reflecting the social environment facing the animal upon its post-surgery return. The retention of dominance by the third-operated animal may have reflected his being faced with seven relatively submissive animals upon his return to the group (Rosvold et al., 1954). The sequential nature of the surgeries affected not only the length of time each animal spent in the group postoperatively, but necessarily meant that by the time of surgery, the third-operated animal had elicited submissive responses from other animals for 16 weeks, as opposed to the 6 weeks that the original alpha had been dominant (Rosvold et al., 1954). Furthermore, the animal that had been fourth-ranked at the outset of the study was originally described as “placid [and] unaggressive”, and thus by the time of the third and final surgery, this animal (now second-ranked) likely made no attempt to achieve or maintain the position of alpha male. Thus, the social environment facing the third-operated male upon his return was quite different than previously, when each of the first two males were faced with relatively active and aggressive animals in the top ranks upon their return to the group. Finally, the means by which the social hierarchy was determined are not stated, thus discussing the social structure with any certainty is difficult. Although numerous uncontrolled variables make these results nearly impossible to interpret, it is often cited as evidence of decreased social rank following amygdalectomy (e.g. Amaral et al., 2003 and Emery et al., 2001).

In order to assess the effect of amygdalectomy in a more natural setting, Dicks et al. (1969) conducted a behavioral study on four males from a free-ranging rhesus group on Cayo Santiago. The subjects, between 2 and 9 years old and of intermediate dominance rank, were removed from their social group and underwent complete, bilateral amygdalectomies. Two other subjects received more extensive bilateral lesions of that included the uncinate cortex, but both were unsuccessful in rejoining social groups and died (perhaps lending credence to the assertion put forth by Klüver & Bucy in 1939). Animals were allowed 9-12 days of recovery time before being taken back to their home group and released. All four amygdalectomized animals demonstrated a period of social isolation after release, but of particular interest is that the two youngest animals (2 and 3 years old) were able to rejoin and associate normally with their groups after a short period (6 days) of social isolation, indicating that perhaps early insult to the amygdala is overcome more easily than in adulthood. The two oldest subjects (4 and 9 years old) never rejoined their groups, and were found dead one and three weeks, respectively, after release. Their deaths were attributed to starvation or infection, as neither was reported to show signs of severe wounding. Unfortunately, very little quantitative data were provided, with only a few anecdotal observations regarding specific encounters. The authors concluded that amygdalectomy produces “social indifference”, in that the animals were able to interact socially, but demonstrated no interest in initiating interactions or reestablishing group membership. It is also suggested that they were “banished” from their social groups, presumably for displaying inappropriate social behavior, and when left in isolation demonstrated a reduced ability to compete for food (Dicks et al., 1969). In striking contrast to these conclusions, however, the two youngest animals apparently reintegrated into their social groups, at least for the remaining 22 days of the study. Furthermore, the timing of and lack of information regarding the deaths of the two older animals raises the speculation that they may have died from physical complications of recovery from the surgery instead of from a failure to socially reintegrate. As in the case with Rosvold, et al. (1954) this study has fatal challenges to interpretation, yet it is often cited as evidence that amygdalectomy produces severe social deficits (e.g., Amaral, 2002; Amaral et al., 2003).

Providing further evidence of the submissiveness seen by Rosvold et al. (1954), a study of 15 individually-housed adult males by Meunier et al. (1999) found that ibotenic acid-induced neurotoxic lesions of the amygdala produced animals that displayed low levels of aggression and high levels of submission compared to controls in reaction to several nonsocial stimuli. Furthermore, this study compared the effects of aspiration versus neurotoxic lesions and found that monkeys with aspiration lesions were significantly more submissive than those with neurotoxic lesions in trials involving an unfamiliar human face. In addition, both groups of amygdalectomized subjects were significantly more likely to investigate a toy snake, a stimulus that reliably elicits fear in normal rhesus monkeys. The differences between these results and those of previous studies may, in large part, have had to do with the greater degree of specificity and precision with which neurotoxic lesions can be performed, hence limiting damage of surrounding brain areas and thus reducing associated symptomatology. These animals were also tested 7 months after surgery, providing ample time for recovery, an important consideration ignored in earlier studies. The authors conclude that as opposed to the social indifference proposed by Dicks et al. (1969), amygdala-lesioned animals produce indiscriminate and inappropriate emotional responses to external stimuli, thereby likely negatively impacting social relationships, though these subjects were never tested in social situations with conspecifics (Meunier et al., 1999). Though social behavior was not directly studied, these results nevertheless provide strong evidence for differences in behavioral effects of aspiration versus neurotoxic amygdala lesions.

Testing with conspecifics has produced mixed results. Emery et al. (2001) performed ibotenic acid-induced amygdala lesions in 12 adult male rhesus monkeys (mean age 5-6 years) from mixed-sex group housing enclosures in which they had been born and raised. Subjects were individually-housed during the study, and tested in dyads, 3 months post-surgery, with unfamiliar conspecifics as stimulus animals in a novel testing room. Bilaterally lesioned subjects appeared less socially inhibited than controls. In dyadic interactions, amygdalectomized males initiated more positive social behaviors than did controls, including: approaching, contacting, soliciting grooming from and mounting unfamiliar conspecifics. However, they also displayed more fear grimacing and less aggression than did controls. The stimulus animals reciprocated many of the positive social behaviors, more frequently spending time in proximity with, grooming, and presenting to amygdala-lesioned animals than to controls, though whether this was a response to the behavior of the amygdalectomized subjects or a judgment made by the conspecifics about the social style of the subjects was unclear. Results similar to the dyadic encounters were obtained when tested in a “round robin” format, with each subject experiencing a 20-minute dyadic interaction with every other subject.

Amygdalectomized subjects both initiated and received more positive social behaviors than did controls, regardless of whether they were paired with controls or other amygdalectomized subjects. The apparent disinhibition of these subjects would seem to indicate decreased fear of social interaction, however this is in contrast to their increased production of fearful signals, such as grimaces, and may actually provide evidence of an indiscriminate behavioral profile as suggested by Meunier et al. (1999). Four months later, the same 12 monkeys, now 7-10 years old, were combined in tetrads composed of two lesions and two control animals, for 2-hour sessions over a period of 32 days during which 10 minutes of focal observations were performed on each animal (Machado et al., 2008). Amygdalectomized animals still initiated more affiliative behaviors, but also directed these behaviors towards control animals more often than towards other amygdalectomized subjects. In return, amygdalectomized animals received more affiliative behaviors from control animals than did other control animals. However, lesioned animals also initiated and received more aggression from other lesioned animals than did controls. The animals' housing conditions during the 4 months between studies are not clearly described, so it is impossible to conclude whether the changes in behavior are attributable to a return to group living or a the condition of larger testing groups (tetrads vs. dyads) allowing for more varied social interaction. The results suggest that amygdala-lesioned animals came to engage in aggressive behaviors, and to direct affiliative behaviors preferentially towards control animals, neither of which was seen in the original dyadic interactions. Whether this shift in directing positive behaviors towards controls came as a result of receiving more aggression from other lesioned animals, or whether the increased aggression received from other lesioned animals was an effect of reduced positive social interactions is unclear. These results, while partially consistent with those from the 2001 study (Emery et al.), are difficult to interpret given the brief periods of behavioral observation for each animal, but seem to suggest that a change occurred over time, with lesioned subjects eventually engaging in more positive social behaviors with control animals and more agonistic behaviors with other lesioned animals.

Machado & Bachevalier (2006) utilized a repeated measures design in order to address individual personality differences among subjects by studying the behavior and social dominance of a group of juvenile (2-3 year old) males pre- and post-surgery. Subjects were given one hour of group interaction (in tetrads) per day, for 15 days, one month prior to surgery. Six months after neurotoxic lesions of the amygdala, animals were allowed to interact in the same groupings and 10-minute focal samples of behavior were taken to observe changes in behavior and dominance rank. Unlike the results presented by Rosvold, et al. (1954), dominance ranks were unchanged by amygdalectomy, however amygdalectomized animals were more aggressive, avoidant, anxious, excitable, and less affiliative. The authors suggest that the lack of changes in rank may have reflected the less socially-challenging environment of tetrads as opposed to monkeys who were placed into a larger social group, or an effect of familiarity, whereby previously established dominance rankings remained unchallenged. This argument is somewhat inconsistent with the results reported by the Rosvold et al. (1954) study, in which animals had an established hierarchy before and after surgeries, and in which the experimenters split the 8-animal group into two 4-animal groups at several points during the study. However, it is possible that these differences can be attributed to the more frequent disruptions of social structure in the Rosvold et al. (1954) study, and thus perhaps the changes in rank can be attributed to methodological factors as opposed to loss of the amygdala.

These studies indicate that distinct behavioral effects result from removal of the amygdala, however specific effects are difficult to deduce because of wide methodological variation. It is clear that the amygdala is involved in the modulation of affiliative behavior, fear, and aggression, but the mechanism by which these behaviors are specifically affected (e.g., through perception of others' behavior, inappropriate production of behaviors, or dysregulation of emotional responses) and the result of these changes on social interactions within a naturalistic group setting cannot be deduced at present. The age at which surgery is performed appears to be important, but direct comparison is difficult across different housing, rearing, and social contexts. The results from Dicks et al. (1969) illustrate that perhaps early insult to the amygdala is overcome more easily than is insult in adulthood, and in fact, it was suggested by Kling & Green as early as 1967 that age mediates the effects of amygdalectomy. Investigators have since begun to study the effects of neonatal lesions of the amygdala on the development of social behavior in rhesus monkeys. Whether or not these animals develop a species-typical repertoire of behavior and use it appropriately in social interactions will perhaps be indicative of not only the importance of the amygdala in a social context, but also the extent to which other brain regions may be capable of compensating for its loss, perhaps helping to elucidate the mechanism by which the amygdala influences social behavior.

Thus far, studies of neonatally amygdalectomized animals are limited, and have produced mixed results. In 1969, Thompson et al. studied the behavioral effects of amygdala lesions on 6 female, infant rhesus monkeys. Unilateral aspiration lesions were performed at 1.8 months of age, and the contralateral lesions were performed at 2.5 months. Beginning at 2.9 months, animals were tested daily in pairs (lesioned and control), for 20-minute sessions, over a period of 10 days. Two more 10-day period of testing occurred at 4.8 (lesioned with lesioned) and 8.3 months (lesioned with control). At 13 months, the animals were placed in group housing with one or two other animals for 18 days. The authors found no change in behavior when animals were observed alone in their cages. When tested socially, lesioned females demonstrated more fear responses, which notably increased from the 2.9- to 8.3-month testing sessions and remained high during the 13-month observations. Both lesioned and control animals more frequently directed positive social behaviors towards lesioned animals, and lesioned animals tended to demonstrate fewer fear responses when paired with other lesioned animals than with controls. The authors suggest that this may have been in response to the behavior of the control animals, which tended to be more active as time in the testing situation went on, as they became more accustomed to the novel environment (Thompson et al., 1969). It was concluded that lesioned animals demonstrated more social fear, but less nonsocial fear (e.g. of a new environment), and that this difference was made apparent as time in the testing situation progressed, at least partly due to the changing behavior and responses of the control animals.

Similarly, Prather et al. (2001) found that three subjects (two males, one female) with ibotenic acid lesions of the amygdala at 2 weeks of age exhibited greater fear responses during dyadic social interactions with other infants, but displayed greater exploration of novel objects. These infants were housed with their mothers until 5.5

months of age, when they were weaned and housed individually, and given daily access to one peer for three hours per day. The dyads always consisted of one lesioned and one control animal. A more extensive study was performed by the same group, with five female and three male lesioned subjects in similar housing and weaning conditions, with the exception that subjects were provided access to "socialization cohorts" for three hours per day instead of social interaction restricted to dyads (Bauman et al., 2004b). Subjects were observed in home cages and in socialization groups of varying size (4-12 animals, including other mother-infant pairs prior to weaning) from 6 to 12 months of age. Lesioned subjects exhibited more fearful behaviors in social situations, displaced fewer animals, more frequently solicited grooming from other animals (particularly from other lesioned subjects), groomed others less frequently, spent more time in proximity with other lesioned animals, and spent more time in contact with their mothers when in socialization groups, compared to controls (when tested in a mother-preference task on the day after weaning, however, lesioned animals did not demonstrate a preference for their mother over a stimulus adult female, Bauman et al., 2004a). Control animals spent more time in proximity with other controls. The authors conclude that amygdala-lesioned animals were able to develop a species-typical repertoire of social behaviors, and that rather than impairment of social cognition, removal of the amygdala prevents accurate assessment of potential threats. Hence, these animals are unable to determine if a situation (e.g. separation from the mother in a novel environment) is dangerous, and do not respond as though they are in danger (Bauman et al., 2004a). Similarly, their heightened fear responses in novel social situations may reflect an overestimation of the threat posed by other animals. However, it is not clear why these animals might overestimate danger in one social context while underestimating it in another. Possibly, this difference reflects a disconnect between context and emotion such that amygdalectomized monkeys have difficulty exhibiting contextually appropriate emotions, and display the indiscriminate behavioral profile suggested by Meunier et al. (1999). Another study with the same subjects evaluated dominance among ranks at 1.5 years old by assessing latency to gain access to a preferred food in a group setting (Bauman et al., 2006). Lesioned animals took longer to access the food, displayed less aggression and produced more fear behaviors than controls, leading the authors to conclude that they ranked below all other subjects. Specific hierarchical data are not provided, but the mean rank of amygdala-lesioned animals was significantly lower than that of control animals. The usefulness of reporting mean rank is unclear, as it does not provide any information about the distribution of amygdala-lesioned animals within the hierarchy. It is not clearly specified how a linear hierarchy was determined by the authors, but it is suggested that lesioned animals take longer to access the preferred food because of their low social rank, and that their lack of aggression and heightened fear is responsible for their low social rank. However, this argument is confounded in a number of ways. Aggression and dominance rank have been shown to be positively correlated in rhesus males (Rose et al., 1971), though it is not necessarily the case that aggression precedes dominance. Low-ranking animals must produce more submissive behaviors than high-ranking animals by definition (this is typically how dominance hierarchies are determined by observers). Thus it is not clear whether lesioned animals demonstrated less aggression and more fear because they were low-ranking, or whether they were low-ranking because they displayed less aggression and more fear. Analysis of the behaviors within rank categories (e.g., whether low-ranking lesioned animals are less aggressive than low-ranking control animals) might help to elucidate the nature of this relationship. As the animals were still very young at the time of testing, it is not unlikely that the social structure could change over time, particularly as these animals were permanently separated from their mothers at 6 months of age and approximately one year had passed by the time dominance testing began. It is not known what type of social hierarchy might have been present among the mothers of these subjects during the daily socialization time provided, though the authors suggest that the influence of maternal rank was absent as a result of separating the animals from their mothers (Bauman et al., 2006). As mentioned above, maternal rank is known to affect dominance rank in familiar juvenile animals through the first year of membership in a new group (Drickamer & Vessey, 1973, Loy & Loy, 1974). Thus it is difficult to interpret whether these results are indicative of low social rank among lesioned animals, or perhaps reflect previously existing relationships that were established during the first 6 months of life, when individual traits would have been less important than maternal dominance status.

Until recently, no studies have thoroughly examined the social behavior of amygdalectomized animals in species-typical social groups. A pilot study of four males (two neonatally lesioned, two control) reared by their mothers and housed in semi-natural social groups consisting of both kin and nonkin found that amygdalectomized males exhibited early independence from their mothers, and surpassed controls in age-appropriate increases in social play, dominance displays and mounting, and both initiated and received more aggression than controls as they aged (Raper, 2009). Few differences were seen in fear and anxiety-related behaviors, with lesioned animals showing a slight decrease in fear as they aged, and with both groups showing increased anxiety over time. These findings are in partial agreement with those of previous studies that reported increases in aggression and affiliative behaviors, though not both (Emery et al., 2001; Machado & Bachevalier, 2006). Interestingly, Machado et al. (2008) reported both increases in affiliative behavior and increases in aggression when animals were observed in larger social groups, even when previous dyadic pairings of the same animals produced different results, indicating the importance of social context in eliciting behavioral responses.

The existing body of literature currently points to a role for the amygdala in the judgment of social stimuli and regulation of appropriate behavioral expression. Marked differences exist not only in lesion techniques, but also in recovery time prior to behavioral assessment, between earlier and more recent studies. It is also apparent that lesions of the amygdala performed in adulthood produce different effects than when performed immediately after birth, indicating that the plasticity of other brain regions may compensate for loss of the amygdala, which may mediate some behavioral effects. In summary, lesions of the adult amygdala have been found to both increase or decrease aggression (Emery et al., 2001; Machado & Bachevalier, 2006; Meunier et al., 1999; Rosvold et al., 1954), affiliative behaviors (Emery et al., 2001; Machado & Bachevalier, 2006; Machado et al., 2008), and fear responses (Emery et al., 2001; Machado & Bachvalier, 2006; Meunier et al., 1999). Amygdalectomy in adults also possibly contributes to lower rank and a higher frequency of submissive behaviors, however these results come from two studies each using markedly different lesion techniques (neurotoxic lesions – Meunier et al., 1999; aspiration lesions – Rosvold et al., 1954).

Neonatal amygdala lesions have produced increased fear responses (Bauman et al., 2004; Prather et al., 2004), increased affiliative behaviors (Bauman et al., 2004; Raper, 2009), decreased or increased aggression (Bauman et al., 2006; Raper, 2009), and lower rank (Bauman et al., 2006). Both adult and neonatally lesioned animals demonstrate decreased fear of normally fear-inducing objects, such as rubber snakes (Meunier et al., 1999; Prather et al., 2001). Clearly, more study is needed to elucidate the effects of amygdalectomy on social behavior in this species, particularly under species-typical social conditions.

Current research

Previous research implicates the amygdala in the appropriate regulation of social signals, and hence successful social integration, though the mechanism of this regulation (e.g., perception, response, production) remains unclear. As male rhesus monkeys are faced with the challenge of changing social groups throughout life, they are under unique pressure to repeatedly and successfully navigate new social situations. In the present study, we examined the formation of three all-male groups of juvenile males comprised of neonatally amygdalectomized and control animals, in order to determine the role of the amygdala in social integration during male group formation. As natal emigrant males are often not sexually mature, they would likely not be accepted into a mixed-sex group and hence, all-male "bachelor" groups were formed in order to emulate the species-typical experience of emigration (Carpenter, 1942).

The current study is unique in a number of ways. Few data exist on the behavior of neonatally amygdalectomized animals reared in large, mixed-sex, multi-family social groups. These are even fewer with regard to observation of animals in semi-natural social groups, as opposed to acute, short-term group formations that are typically impermanent and thus data are collected in short bursts as animals are given limited access for social interaction. In the current study, animals have been reared in semi-natural social groups, and observed in groups which are permanent and remain relatively stable over time, allowing for long-term data collection on the behavior of these animals in a stable social context, as opposed to one of either frequent upheaval or constant manipulation. Thus, general predictions were made, but the circumstances under which the present study was conducted made directional predictions based on an already tenuous interpretation of the literature speculative at best.

Several aspects of behavior were of interest at the outset of this study. In particular, I sought to determine whether the absence of the amygdala would impair the ability of these males to face an ecologically relevant social challenge integrate into an all-male group. Furthermore, I hoped to determine whether loss of the amygdala affected the ability of these males to exert and interpret the appropriate displays of affiliation, dominance, submission, and aggression that would be necessary for the formation of a social hierarchy. I expected that maternal rank might predict rank in the bachelor group (Boelkins & Wilson, 1972; Drickamer & Vessey, 1973; Loy & Loy, 1974), however as males joining new groups typically assume low ranks (Drickamer & Vessey, 1973; Koford, 1963) it was also possible that an entirely new hierarchy would be formed, or that the effect of maternal rank would wane over time as males became responsible for maintaining rank through their own abilities. Lastly, this design provided an opportunity to explicitly observe the relationships between and within controls and lesioned animals, and to further clarify whether differences exist in how these animals react to social signals given or received in complex social environment.

II. METHODS

Subjects

Male rhesus macaques living in large, mixed-sex groups at the Yerkes National Primate Center Field Research Station were randomly assigned to one of three conditions: complete, bilateral lesions of the amygdala (AMY, *n* = 9), sham surgical procedures (S-SHAM, *n* = 5) or behavioral sham procedures (B-SHAM, *n* = 4). At four weeks of age, subjects and their mothers were removed from their social groups so that procedures could be performed. AMY subjects underwent complete, bilateral amygdalectomies using MRI-guided placement of ibotenic acid injections (*n* = 9). S-SHAM subjects underwent the same preparation procedures as AMY animals as well sham surgical procedures. B-SHAM subjects underwent the same treatment as S-SHAM subjects (separation from mother, anesthetization), but were not subjected to sham surgical procedures. The extent and location of lesions were verified by MRI one week later. Infants were returned to their mothers within 24 hours post-surgery, for increasing periods of time daily, until they began nursing. Once nursing, each animal was housed with his mother and spent a minimum of two weeks in recovery (recovery was as needed, and typically ranged from 2-4 weeks) before the mother-infant pair was returned to their social group. Subjects were since raised in semi-natural, mixed-sex social groups housed in large, outdoor compounds at the Yerkes Field Station. Subjects were drawn from one of two separate natal groups; hence, animals from different groups were completely unfamiliar to each other (see Table 1).

Surgical procedures

Subjects and their mothers were removed from their social group and pair-housed prior to surgery. AMY subjects were separated from mothers, anesthetized (Ketamine hydrochloride, 100mg/ml) and given isoflurane. A stereotaxic apparatus was used to secure the animal's head so that the MRI-coordinates for acid injection could be determined. The scalp and dura were cut to expose the brain, and bilateral injections (0.6-0.8 μl) of ibotenic acid (PH 7.8-7.9, 10 mg/ml concentration) were given bilaterally and simultaneously at each of four injection sites. The incisions were sutured and subjects were allowed to recover from anesthesia.

Subjects were returned to their mothers and observed for signs of normal nursing. If nursing did not occur, the infant was removed and cared for overnight. These reintroductions continued until the infant was nursing normally. MRI scans were performed one week post-surgery to determine the extent and location of the lesions.

S-SHAM animals underwent the same procedures with the exception that a needle was not lowered into the brain, and an MRI was not performed one week post-surgery. These animals were separated from their mothers for the same period of time as the AMY animals who underwent the MRI scans.

B-SHAM animals experienced several exceptions to the procedures performed on S-SHAM animals. These subjects did not have any surgical procedures or MRI scans performed, but the separation from the social group and from the mother, and the preparation procedures (anesthetization, shaving the head) were the same as in the AMY and S-SHAM animals. These animals were separated from their mothers for the same period of time as the AMY animals who underwent the MRI scans.

Pair introductions

At approximately 2.5 years of age, six males from the first cohort were removed from their natal groups, in order to mimic natal emigration. Males were initially individually housed. Over approximately two months, unfamiliar pairs of males were introduced to each other to form a total of three pairs (see Table 1). A total of 12 males from the second cohort were removed from their natal groups (six at a time), at approximately 2 years of age. Pair introductions were performed in order to ease the stress of the group introduction and to provide an opportunity for the formation of affiliative relationships. As free-ranging macaques have been observed to change groups with peers (Drickamer & Vessey, 1973), it was hoped that these relationships would facilitate the transition to a new group.

All caged introductions took place under video observation. Pairs were housed in adjacent cages with a solid, opaque barrier between them and given time to acclimate to new housing conditions. The time spent in individual housing varied between subjects, as the conditions under which males were removed from their natal groups could not be controlled (for colony management reasons), and varied from 1 week to 4 months. The first stage of introduction involved replacing the opaque barrier between the cages with a solid, clear barrier. After an acclimation period (see below), this was replaced with a clear barrier with three rows of 1-inch holes, through which animals could smell and touch each other. Finally, this barrier was removed and the pairs shared the adjacent cages with no barrier until the group formation. The acclimation period at each stage of the caged introductions varied between cohort 1 and 2. Cohort 1 animals spent 2 weeks at each stage (in order to ensure the safety of the animals). When these introductions went smoothly, the acclimation period was shortened to facilitate more rapid introductions. Thus, cohort 2 pairs spent 3 days with a clear panel and 5 days with holed panels prior to removal of the barrier. All pairs spent a minimum of 12 days in paired housing before the group formation.

Group introductions

To form each group, all six males were released into an enclosed, outdoor 4.9x4.9x2.4m observation area enclosed by a chain-link fence. Males were released sequentially, as pairs, in as simultaneous a manner as possible (housing constraints made precisely simultaneous release impossible). The observation area provided several perches and ample space in which the animals could be apart from one another, while also allowing for both live data collection and video-recording of the group formation. Males were dorsally marked with unique dye marks for individual identification. Subjects were allowed to interact freely while three trained observers (one designated to record observations) observed all occurrences of specific agonistic and affiliative behaviors (see Table 2). For all three groups, conditions appeared stable at the day's end, and subjects were moved as a group to a permanent, indoor housing enclosure where they remain under regular observation.

Behavioral observations

Thirty minute focal-animal observations took place between the hours of 0700 and 1700, once per week for 16 weeks. Focal observations include all behaviors performed by the focal animal, or directed toward the focal animal by other animals (Altmann, 1974; see Table 2). Order of observations was randomized within each bachelor group. After 16 weeks, observations were reduced to thirty minutes every other week. All but three of the focal-animal observations were performed by the same observer. The ethogram was updated throughout the course of observation to more accurately capture the frequency of common behaviors. Thus, several categories were expanded as needed.

Data analysis

All frequency behaviors were analyzed and reported as frequency per hour (see Tables 3 and 5). All duration behaviors were analyzed and reported as minutes per hour (see Tables 4 and 6). All behaviors were analyzed individually, but if no significant differences were found they were reported categorically (e.g. aggressive behaviors). Two-tailed independent *t*-tests were performed to assess differences in frequency or duration of behavior between AMY and sham-operated animals, using Levene's test for equality of variances. If the results of Levene's test indicated that variances were significantly different, corrected degrees of freedom and *p*-values are reported. For the purposes of this analysis, S-SHAM and B-SHAM males were considered as part of the same control group (SHAM). Because each bachelor group contained different numbers of AMY and SHAM animals, chi-squared goodness-of-fit tests were performed to compare recipient effects to expected values based on chance. Thus, for a SHAM male in group 1, the probability of initiating proximity to another SHAM male would be 0.2. Probabilities were calculated for all subjects in all groups, and used to calculate expected values based on behavior totals. For behaviors which might be affected by rank, two-way analysis of variance (ANOVA) was used to examine differences among high- and low-ranking AMY and SHAM animals. For these analyses, social dominance rank was specified as either high (rank 1-3) or low (rank 4-6). Analyses involving social dominance rank were performed using current rank, which represents rank at the time of this writing. Use of this measure allows for combined analysis of the data across all three groups. At the time of this writing, group 1 is 13 months post-introduction, group 2a is 7 months post-introduction, and group 2b is 5 months post-introduction.

III. RESULTS

Group introductions

Data from the three bachelor group introductions were combined for analysis.

Affiliative behaviors

SHAM animals tended to be in proximity more frequently with one or more other animals than were AMY animal, though this difference was not statistically significant ($t(16) = -2.07$, $p = .056$, Figure 1). Further analysis revealed that SHAM animals initiated proximity to other animals more frequently than did AMY animals ($t(16) = -2.13$, $p = .049$), but were not recipients of proximity more often ($t(16) = -0.81$, $p = .431$). Duration of proximity did not differ between treatment groups ($t(16) = -0.57$, $p = .578$).

SHAM males more frequently initiated proximity with other SHAM animals ($\chi^2 = 8.17$, $p = .004$) and spent more time in proximity with other SHAM animals ($\chi^2 = 12.32$, $p < .001$) than would be expected by chance (Figures 2 and 3). SHAM animals initiated proximity with AMY animals at a rate that did not differ from chance ($\chi^2 = 2.30$, $p = .129$). AMY animals initiated proximity with other AMY animals less frequently ($\chi^2 = 6.91$, $p = .009$) but did not spend less time in proximity with other AMY animals ($\chi^2 = 1.08$, $p = .298$) than would be expected by chance. AMY animals initiated proximity with SHAM animals at a rate that did not differ from chance ($\chi^2 = 2.35$, $p = .125$). AMY and SHAM males spent less time in proximity to one another than would be expected by chance. ($\chi^2 = 4.93$, $p = .026$).

The results of Levene's test for homogeneity of variances was significant for the frequency of grooming interactions ($p = .005$), initiating grooming ($p = .002$) receiving grooming ($p = .015$), and duration of grooming ($p = .003$), so corrected values for the test statistic (t), degrees of freedom, and p are reported. SHAM animals demonstrated significantly higher rates of grooming than did AMY animals (*t*(9.219) = -2.29, *p* = .047), but neither rates of initiating grooming (*t*(8) = -1.46, *p* = .183) or receiving grooming (*t*(10.783) = -1.28, *p* = .227) differed between AMY and SHAM males (Figure 4). Analysis by social group revealed that SHAM animals demonstrated higher rates of grooming only in group 1 (*t*(4) = -36.18, *p* < .001; but see discussion). AMY and SHAM males did not differ in the duration of grooming interactions (*t*(8.079) = -1.93, *p* = .089). Chi-squared analysis of grooming behavior for actor/recipient effects was not performed for these data because so few grooming interactions occurred during the introductions.

Aggressive behaviors

Overall rates of aggressive behaviors performed (*t*(16) = -0.17, *p* = .867) or received (*t*(16) = 1.07, *p* = .299) did not differ significantly among AMY and SHAM males (Figure 5). No significant differences emerged when analyses were performed for individual aggressive behaviors (attack, hit, bite, grab, threat, chase), performed or received (see Table 3).

Dominance-related behaviors

AMY and SHAM males did not differ in the rates of withdraw (*t*(16) = 1.02, *p* = .324) or receiving withdraw (*t*(16) = -0.19, *p* = .855, Figure 8). The results of Levene's test for homogeneity of variances was significant for the frequency of grimace (*p* = .041), so corrected values for the test statistic (*t*), degrees of freedom, and *p* are reported. AMY and SHAM males did not differ in the rate of grimace (*t*(8.009) = 1.06, *p* = .319, Figure 9).

Play behaviors

SHAM males engaged in higher rates of social play (Figure 10) than did AMY animals ($t(16) = -2.98$, $p = .009$). SHAM animals also more frequently initiated social play ($t(16) = -2.65$, $p = .017$) and received initiation of social play from others ($t(16) = -2.21$, $p = .042$). The duration of social play did not differ between treatment groups ($t(16) = -1.79$, $p = .092$).

AMY animals initiated play less frequently with other AMY animals than would be expected by chance ($\chi^2 = 8.18$, $p = .004$, Figure 11), though the duration of play was not different ($\chi^2 = 1.10$, $p = .294$, Figure 12). AMY animals also initiated play more frequently with SHAM animals than would be expected by chance ($\chi^2 = 4.92$, $p = .027$), but again the duration of play did not differ ($\chi^2 = 0.95$, $p = .331$). SHAM animals initiated play with other SHAM males at a rate that did not differ from chance ($\chi^2 = 0.82$, $p = .366$), and initiated play with AMY males at chance rate ($\chi^2 = 0.67$, $p = .412$).

Very little solitary play (including eat-object play) occurred during the group introductions, and there were no significant differences in either the frequency ($t(16) = 0.17$, $p = .868$) or duration ($t(16) = -0.47$, $p = .647$) of solitary play. Eat-object play, which involves mouthing, chewing or licking non-food objects, was also rarely observed during the group introductions. When eat-object play was analyzed alone, Levene's test for homogeneity of variance was significant for the duration of eat-object play ($p = .005$), so corrected values of the test statistic (t), degrees of freedom, and p are reported. AMY and SHAM animals did not differ in the frequency ($t(16) = -0.88$, $p = .391$) or duration ($t(8.134) = -1.33$, $p = .221$) of eat-object play.

Sexual and other behaviors

During the group introductions, males that established themselves as high- or low-ranking animals did not differ in the frequency of initiating (*t*(16) = 0.98, *p* = .343) or receiving (*t*(16) = 1.03, *p* = .318) mounts. SHAM animals tended to initiate mounts as compared to AMY animals, though this difference was not statistically significant (*t*(16) = -2.09, *p* = .053). There were no differences between treatment groups in the frequency of receiving a mount (*t*(16) = -1.50, *p* = .153, Figure 13).

Rates of scratch (*t*(16) = -0.82, *p* = .424) and yawn (*t*(16) = -0.03, *p* = .978, Figure 14) did not differ between AMY and SHAM males, suggesting that the two groups did not differ in levels of anxiety.

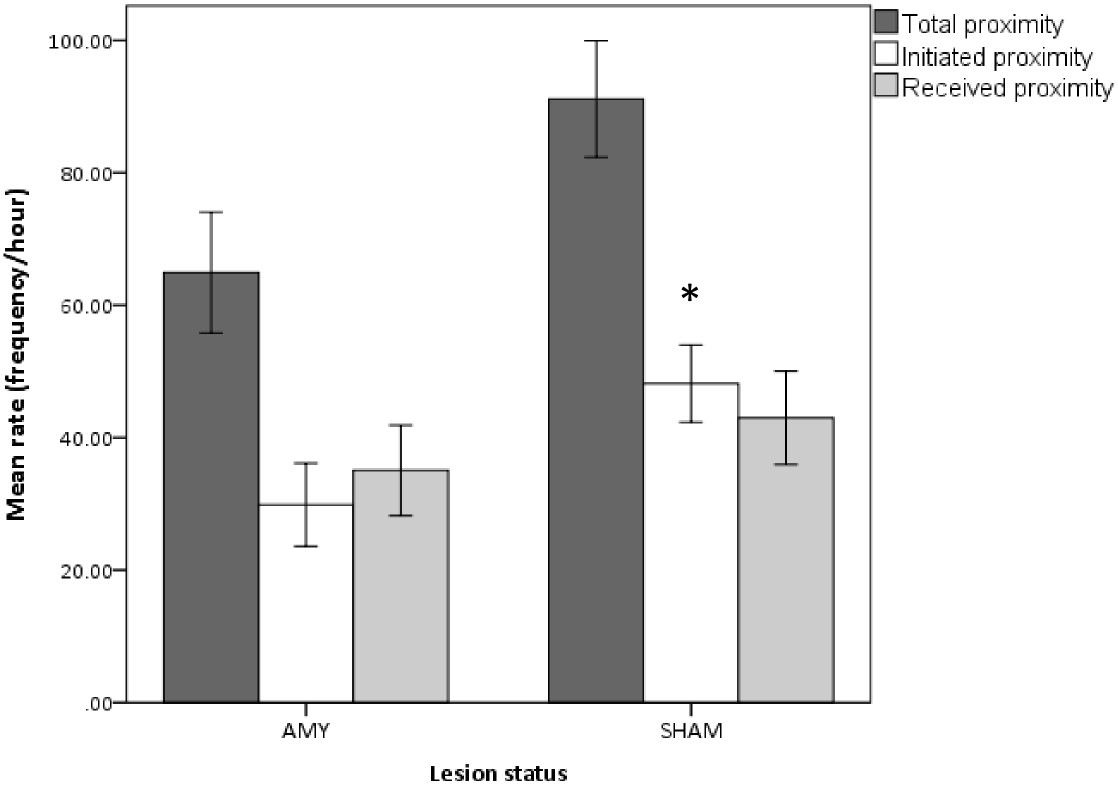

Figure 1. Mean rate (frequency/hour) of proximity with one or more animals during group introductions. Error bars represent ±SEM. * indicates significance at *p* < .05 between AMY and SHAM.

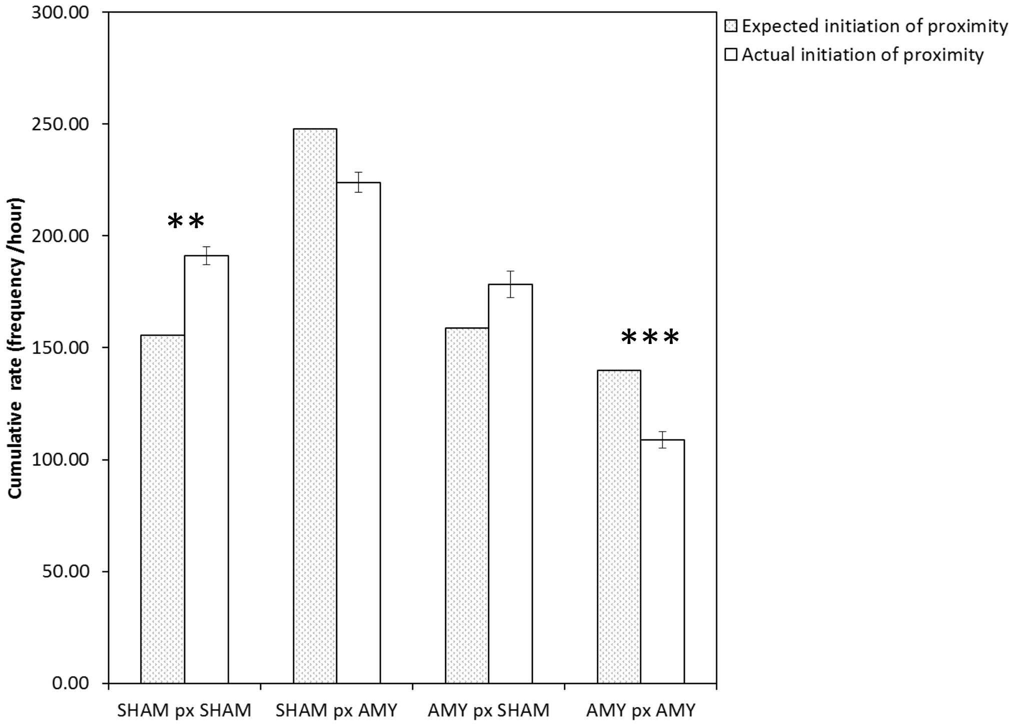

Figure 2. Cumulative rate (frequency/hour) of initiating proximity (px) to either SHAM or AMY animals during group introductions. Error bars represent +SEM. ** indicates significance at *p* < .01 between actual and expected values, *** indicates significance at *p* < .001 between actual and expected values.

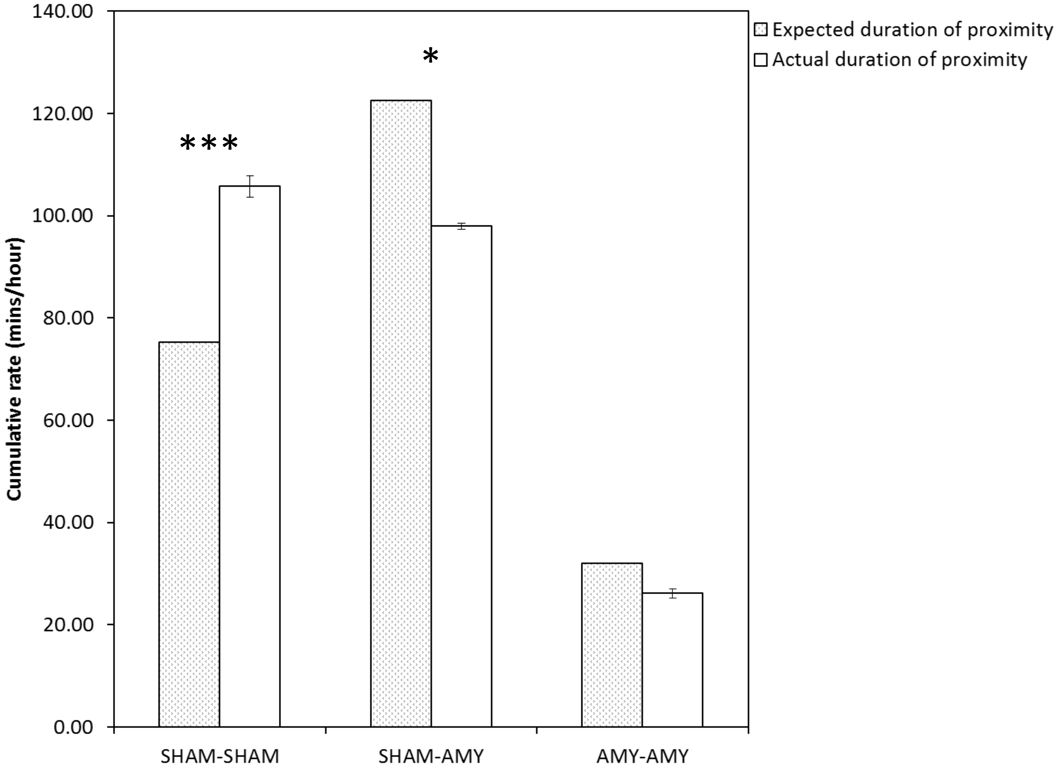

Figure 3. Cumulative rate (mins/hour) of time spent in proximity to either SHAM or AMY animals during group introductions. Error bars represent +SEM. * indicates significance at *p* < .05 between actual and expected values, *** indicates significance at *p* < .001 between actual and expected values.

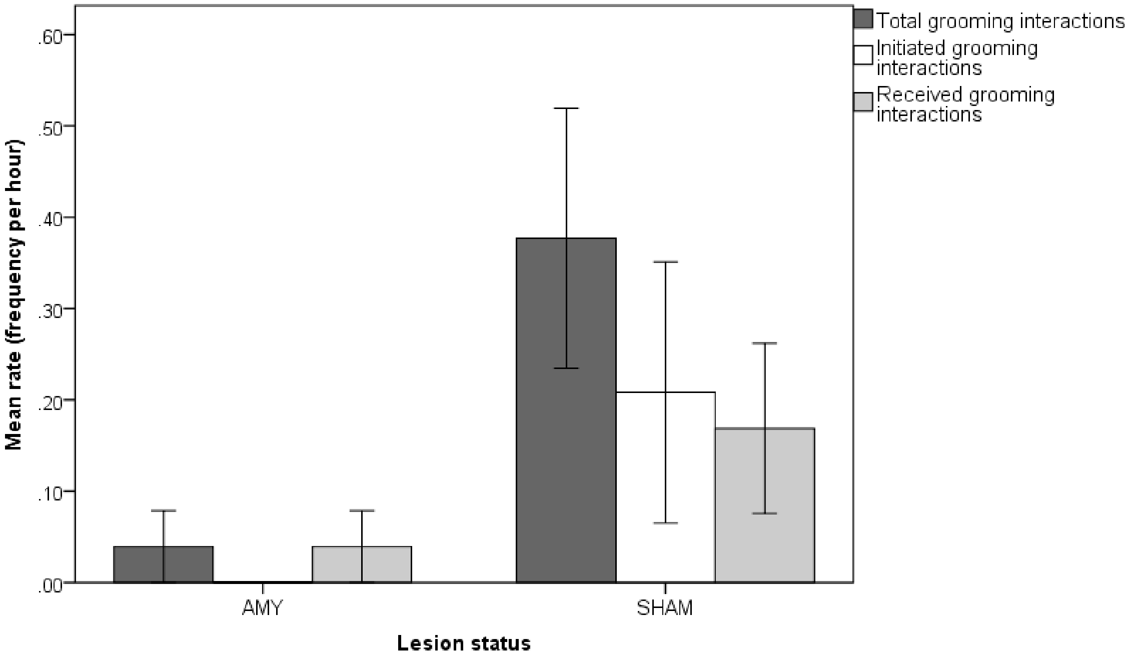

Figure 4. Mean rate (frequency/hour) of grooming interactions during group introductions. Error bars represent ±SEM. * indicates significance at $p < .05$ between AMY and SHAM.

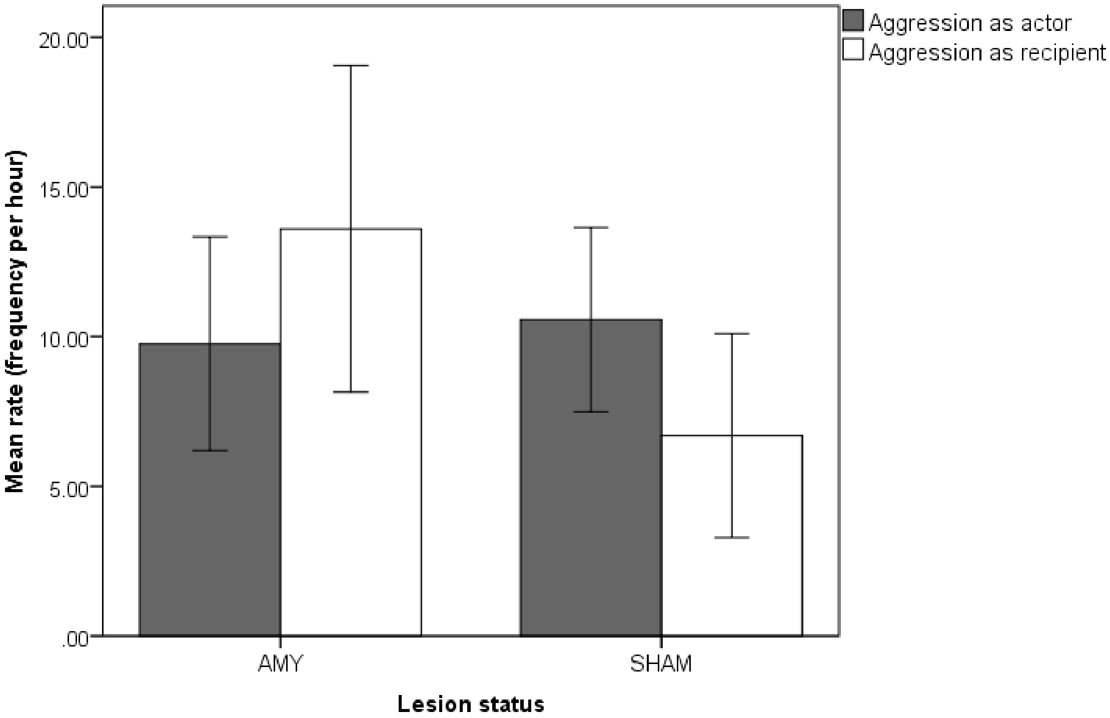

Figure 5. Mean rate (frequency/hour) of aggressive behaviors during group introductions. Error bars represent ±SEM.

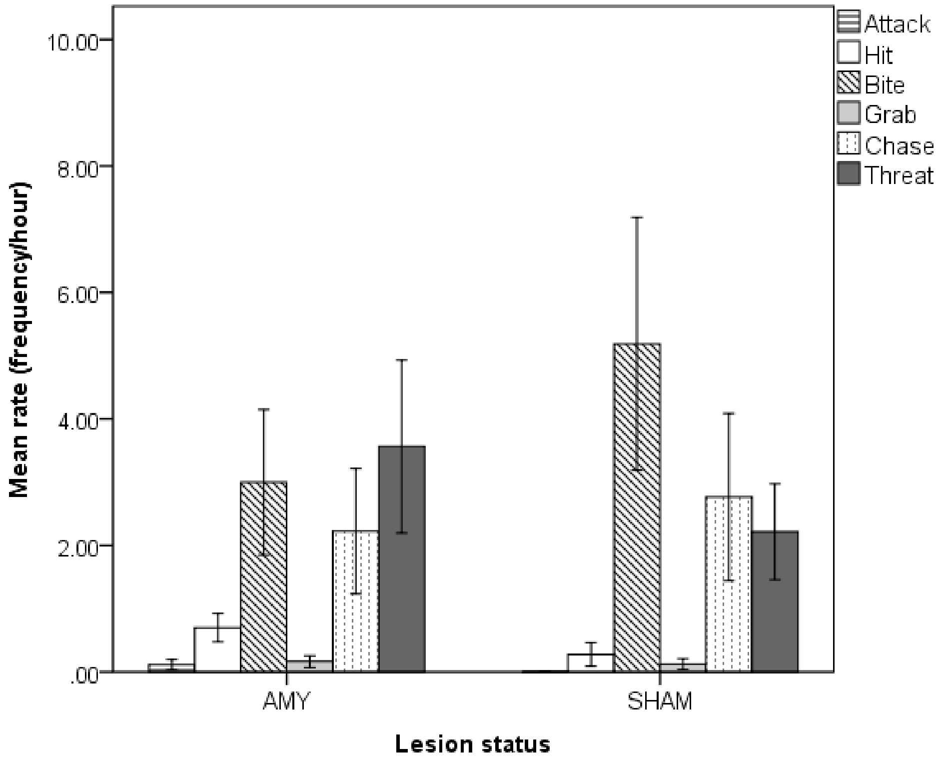

Figure 6. Mean rate (frequency/hour) of individual aggressive behaviors performed during group introductions. Error bars represent +SEM.

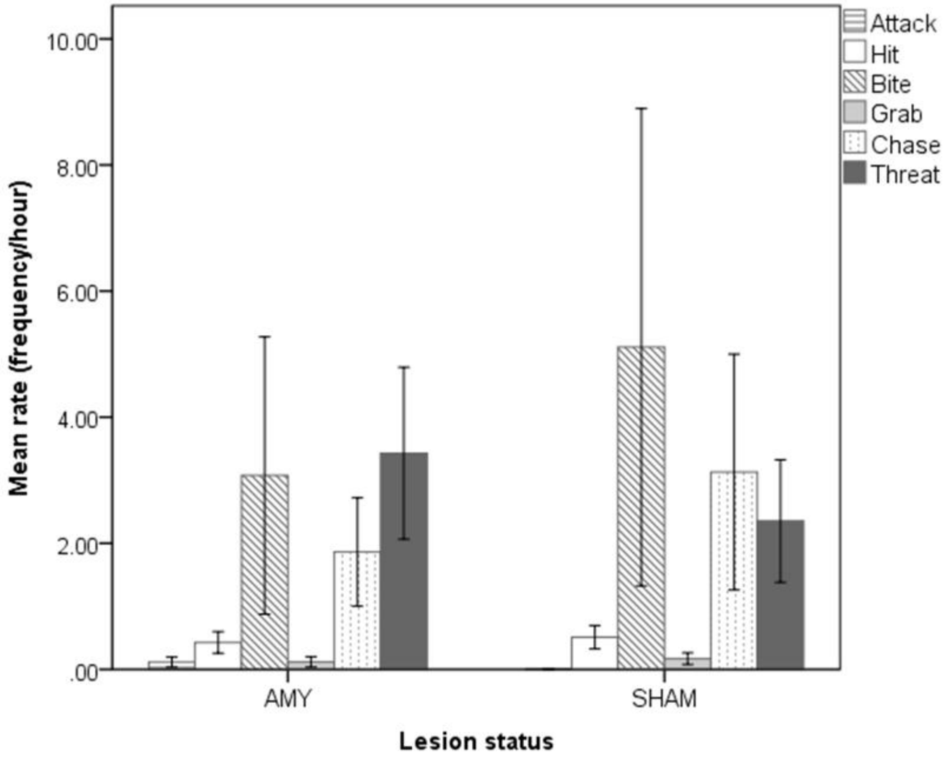

Figure 7. Mean rate (frequency/hour) of individual aggressive behaviors received during group introductions. Error bars represent +SEM.

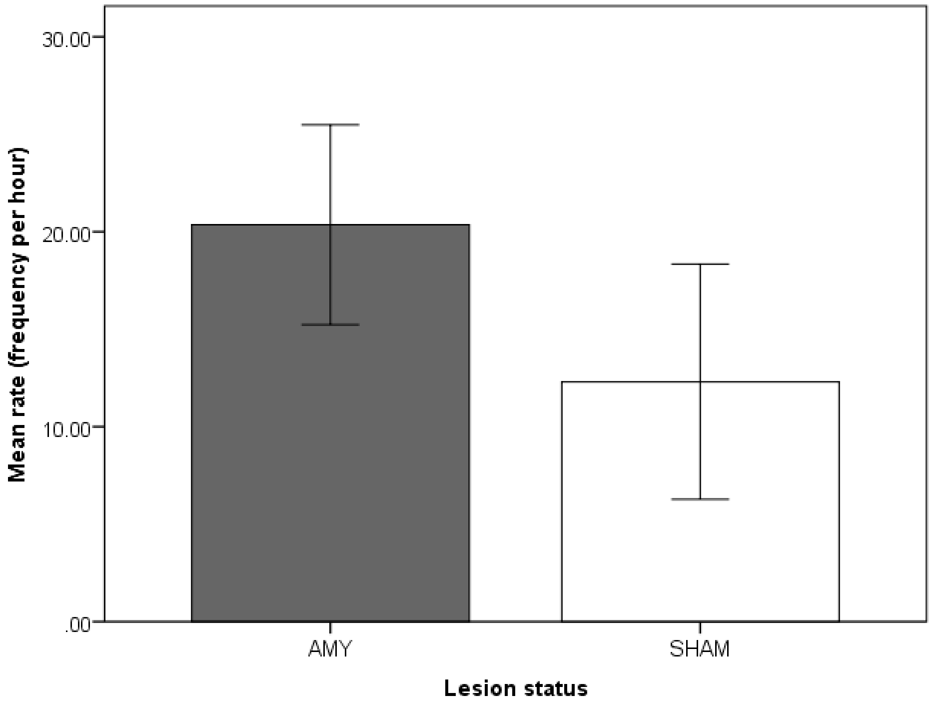

Figure 8. Mean rate (frequency/hour) of withdraw (as actor) during group introductions. Error bars represent +SEM.

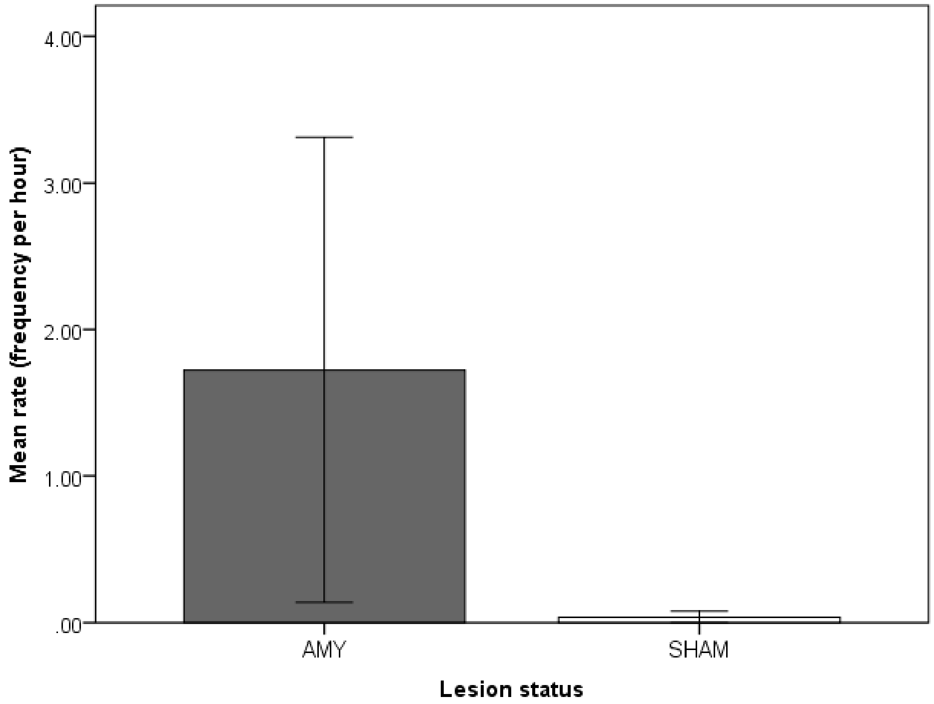

Figure 9. Mean rate (frequency/hour) of grimace (as actor) during group introductions. Error bars represent +SEM.

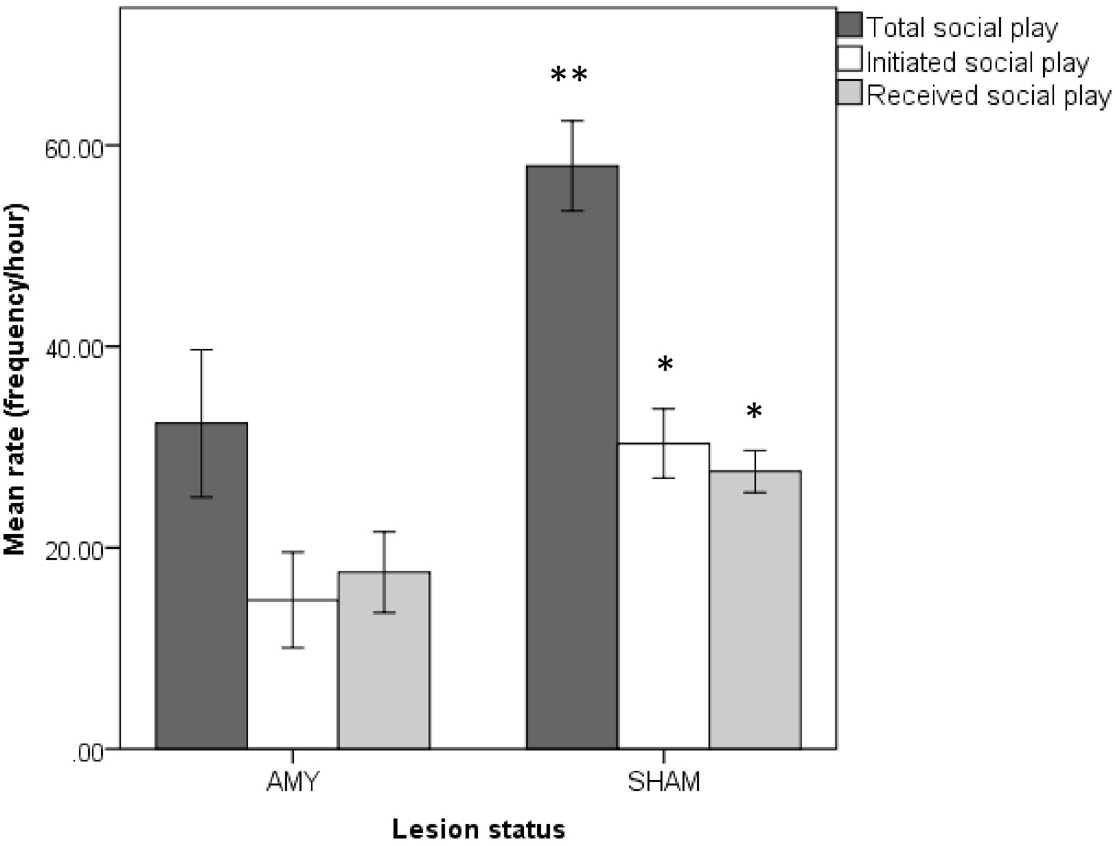

Figure 10. Mean rate (frequency/hour) of social play during group introductions. Errors bars represent ±SEM. * indicates significance at $p < .05$ between AMY and SHAM, ** indicates significance at $p < .01$ between AMY and SHAM.

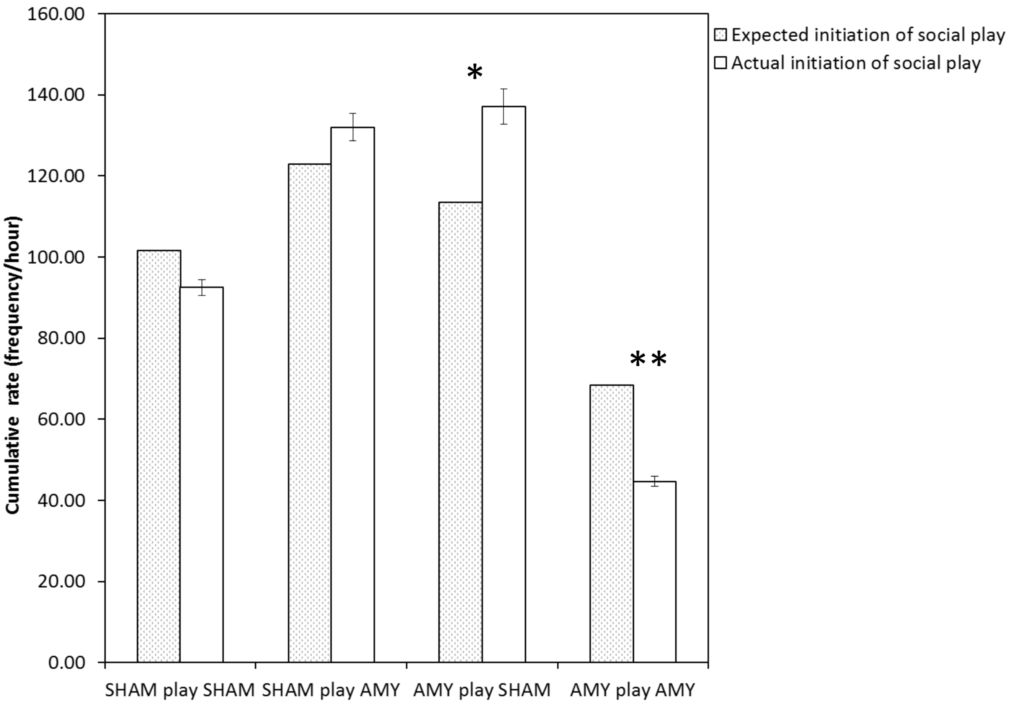

Figure 11. Cumulative rate (frequency/hour) of initiation of social play by partner during group introductions. Error bars represent ±SEM. * indicates significance at *p* < .05 between actual and expected values, ** indicates significance at *p* < .01 between actual and expected values.

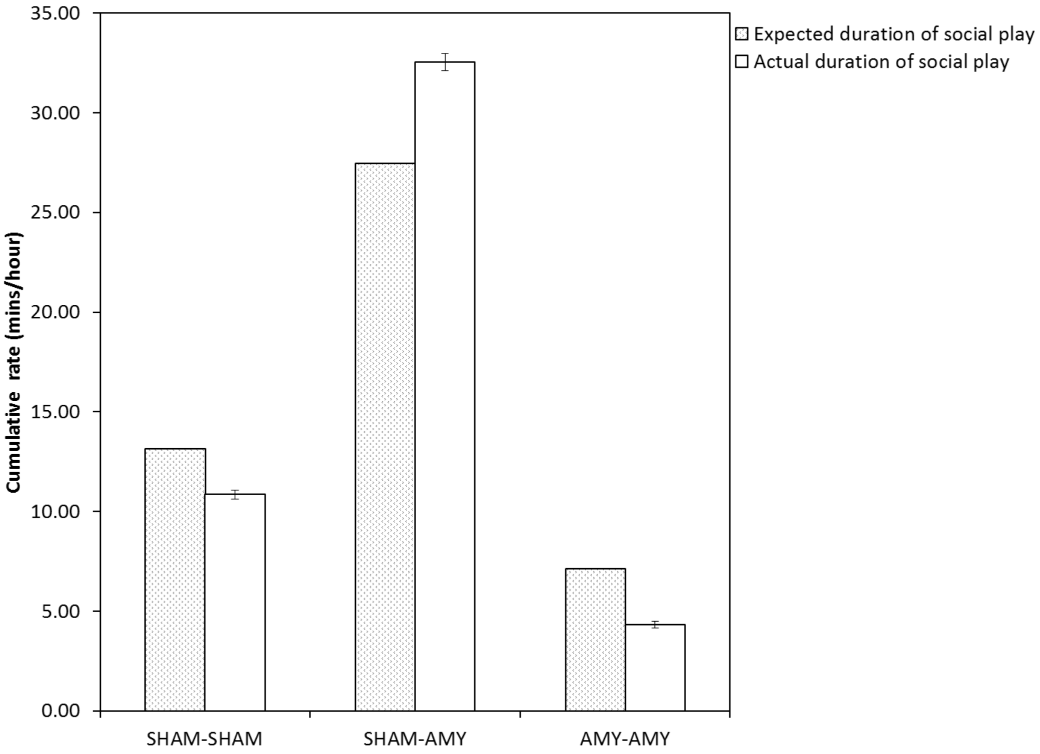

Figure 12. Cumulative duration (mins/hour) of social play duration by partner during group introductions. Error bars represent ±SEM.

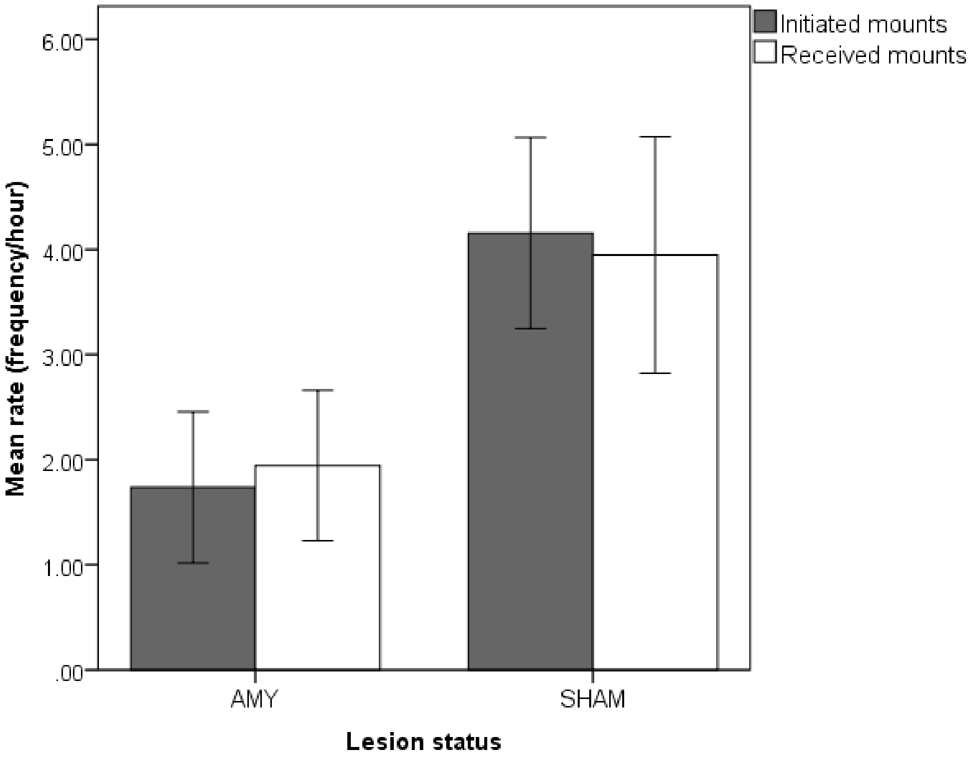

Figure 13. Mean rate (frequency/hour) of initiating and receiving mounts during group introductions. Error bars represent +SEM.

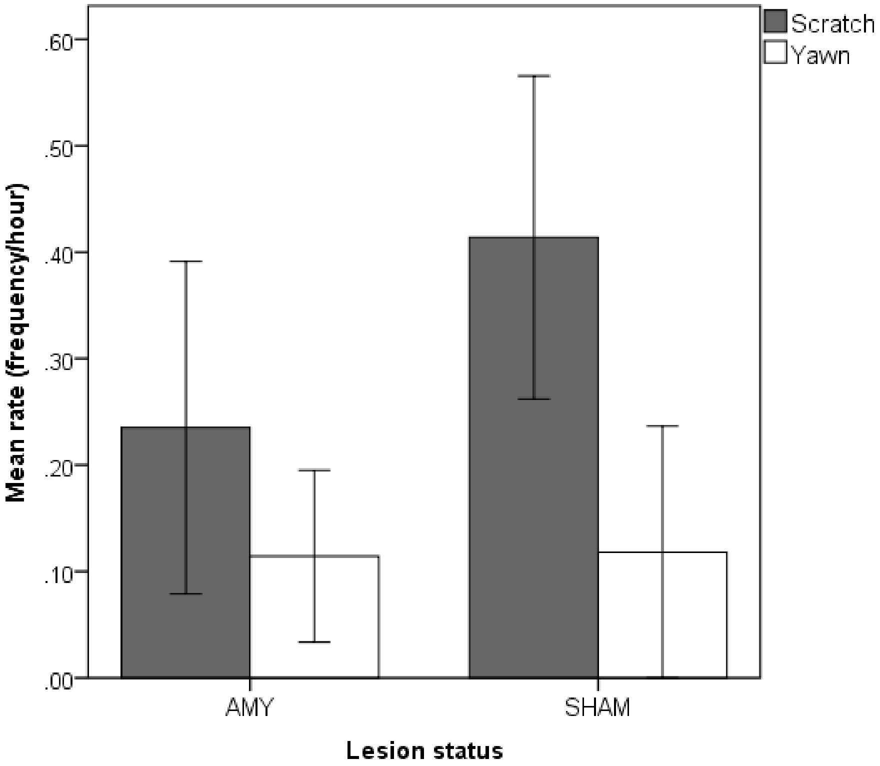

Figure 14. Mean rate (frequency/hour) of scratch and yawn during group introductions. Error bars represent +SEM.

Focal observations

Focal observation analyses include data collected up to and including January 2012, except for rank data, which are current at the time of this writing. Behaviors not analyzed from the group introductions due to their relative infrequency were analyzed in the focal observation data.

Affiliative behaviors

There were no significant differences among AMY and SHAM animals in the frequency ($t(16) = -1.77$, $p = .096$) or duration ($t(16) = -1.27$, $p = .223$) of proximity to other animals (Figure 16). Contrary to what was found in the group introductions, SHAM animals did not initiate proximity more frequently than did AMY animals ($t(16) = -1.95$, $p = .069$). Further analysis revealed that AMY animals initiated proximity with other AMY animals more often than would be expected by chance ($\chi^2 = 5.25$, $p = .022$, Figure 16), but did not spend more time in proximity with other AMY animals ($\chi^2 = 3.03$, $p = .082$, Figure 17). This is the opposite of what was seen in the group introductions, when AMY animals less frequently initiated proximity with other AMY animals. AMY animals initiated proximity with SHAM animals at a rate that did not differ from chance ($\chi^2 = 3.14$, $p = .076$), as was seen in the group introductions. Contrary to what was found in the group introductions, SHAM animals did not differ from chance probabilities in the frequency of initiating proximity to other SHAM animals ($\chi^2 = 0.54$, $p = .461$) nor in the duration of time spent in proximity with other SHAM animals ($\chi2 = 2.45$, $p = .118$). SHAM animals did not differ from chance probabilities in the frequency of initiating proximity to AMY animals ($\chi^2 = 0.473$, $p = .493$). As was found in the group introductions, AMY and SHAM animals spent less time in proximity to one another than would be expected by chance (χ^2 = 4.16, *p* = .041).

AMY and SHAM males did not differ significantly in the frequency of grooming interactions (*t*(16) = -0.80, *p* = .435), nor in the frequency of initiating (*t*(16) = -1.32, *p* = .204) or receiving (*t*(16) = -0.19, *p* = .848) grooming (Figure 18), contrary to the higher rates of grooming seen among SHAM animals during the group introductions. SHAM animals did not differ significantly from chance probabilities in the frequency of initiating grooming of other SHAM animals (χ^2 = 0.07, *p* = .798) or AMY animals (χ^2 = 0.05, *p* = .821), nor in the duration of grooming SHAMs (χ^2 = 0.55, *p* = .460). AMY animals also did not initiate grooming at a rate different from chance with either SHAMs (χ^2 = 0.38, *p* = .534) or other AMY animals (χ^2 = 0.62, *p* = .432). The time that AMY and SHAM animals spent in grooming interactions with one another did not differ from chance (χ^2 = 0.43, *p* = .515).

Aggressive behaviors

Aggressive behaviors were analyzed using a two-way ANOVA between high- and low-ranking AMY and SHAM animals. The main effect of lesion status was not significant for initiating aggression (*F*(1,14) = 0.002, *p* = .962), indicating that AMY animals did not perform aggressive behaviors more frequently than did SHAM animals. This is concurrent with results from the group introductions. The main effect of rank was significant, with low-ranking animals performing aggressive behaviors less frequently than high-ranking animals (*F*(1,14) = 6.25, *p* = .025). There was no significant interaction effect (*F*(1,14) = 0.57, *p* = .461). The main effect of lesion status was not significant for receiving aggression (*F*(1,14) = 0.64, *p* = .438), indicating that AMY animals did not receive aggression more frequently than SHAM animals. The main effect of rank was significant, with low-ranking animals receiving aggression more frequently than high-ranking animals (*F*(1,14) = 11.70, *p* = .004). There was a significant interaction effect (*F*(1,14) = 5.35, *p* = .036), indicating that the effect of rank was greater among SHAM animals.

Among individual aggressive behaviors, main effects of rank were found for bite and threat, and an interaction effect was found for receiving grab. No other individual analyses were statistically significant (see Table 4). There was a significant main effect of rank for the frequency of bite (*F*(1,14) = 5.31, *p* = .037) and of receiving bite (*F*(1,14) = 9.34, *p* = .009). A significant interaction effect was found for receiving grab (*F*(1,14) = 8.74, *p* = .010), indicating that that the effect of rank was greater among SHAM animals. A significant main effect of rank was found for receiving threat (*F*(1,14) = 5.84, *p* = .030), with low-ranking animals receiving more threats than high-ranking animals.

Dominance-related behaviors

Dominance-related behaviors were analyzed using a two-way ANOVA between high- and low-ranking AMY and SHAM animals. A significant main effect of rank was found for withdraw (*F*(1,14) = 6.88, *p* = .020), with low-ranking animals performing withdraw more often than high-ranking animals. As was found during the group introductions, the main effect of lesion status was not significant (*F*(1,14) = 1.54, *p* = .235, Figure 22). Nor was there a significant interaction effect (*F*(1,14) = 0.60, *p* = .452). The main effect of rank for receiving withdraw was not significant (*F*(1,14) = 0.08, *p* = .788), nor was the main effect of lesion status (*F*(1,14) = 4.18, *p* = .060) or interaction effect (*F*(1,14) = 0.39, *p* = .544). A significant main effect of rank was found for grimace (*F*(1,14) = 5.66, *p* = .032), with low-ranking animals producing more fear grimaces than high-ranking animals. The main effect of lesion status was not significant (*F*(1,14) = 0.03, *p* = .866, Figure 23), nor was the interaction effect (*F*(1,14) = 0.12, *p* = .733).

Play behaviors

During the group introductions, SHAM males engaged in higher rates of social play overall, and both initiated and received initiation of social play more often than AMY males. In contrast, there were no significant differences between AMY and SHAM animals in frequency of social play (*t*(16) = -0.50, *p* = .624, Figure 24) during focal observations. AMY and SHAM males did not differ in frequency of initiation of social play (*t*(16) = -0.90, *p* = .384) nor in receiving social play from others (*t*(16) = -0.07, *p* = .944). Duration of social play did not differ between treatment groups (*t*(16) = -0.32, *p* = .756). Also in contrast to the group introductions, no significant recipient effect was found for initiation or duration of social play (Figures 25 and 26). No significant difference was found in the frequency (*t*(16) = 0.95, *p* = .358) or duration (*t*(16) = 0.55, *p* = .590) of solitary play. AMY and SHAM males did not differ in frequency (*t*(16) = -0.41, *p* = .691) or duration of eat-object play (*t*(16) = -0.58, *p* = .571).

Sexual and other behaviors

Levene’s test for homogeneity of variances was significant for frequency of initiating mount (*p* = .026) and receiving mount (*p* = .031) among high- and low-ranking animals, so corrected values for the test statistic (*t*), degrees of freedom, and *p* are reported. As was seen during the group introductions, there were no significant differences between high- and low-ranking animals in the frequency of initiating (*t*(8.464) = 1.69, *p* = .127) or receiving (*t*(10.549) = -1.02, *p* = .323) mounts.

AMY and SHAM animals did not differ in the frequency of initiating (*t*(16) = -0.72, *p* = .483) or receiving mounts (*t*(16) = -0.26, *p* = .795, Figure 27), as was seen in the group introductions. There were no significant differences in frequency (*t*(16) = 0.55, *p* = .588) or duration (*t*(16) = 0.29, *p* = .774) of masturbation. Nor were there significant differences in the frequency (*t*(16) = 0.82, *p* = .426) or duration (*t*(16) = -0.67, *p* = .513) of oral-genital contact.

Levene's test for homogeneity of variances was significant for the frequency of masturbation (*p* = .006), so corrected values for the test statistic (*t*), degrees of freedom, and *p* are reported. The frequency of masturbation was slightly higher in cohort 1 males than in cohort 2 males, though this difference was not statistically significant (*t*(5.397) = 2.13, *p* = .082). However, the duration of masturbation was significantly higher in cohort 1 males (*t*(16) = 3.17, *p* = .006). This difference in behavior is likely because of the one-year age difference between the two cohorts, with the older males demonstrating more sexual behavior. Thus, further analysis was performed comparing masturbation behavior between AMY and SHAM animals within group 1 only. No significant differences were found in either frequency (*t*(4) = 0.29, *p* = .790) or duration (*t*(16) = -0.11, *p* = .922) of masturbation between AMY and SHAM animals.

As in the group introductions, there were no significant differences in the frequency of scratch (*t*(16) = 0.123, *p* = .90) or yawn (*t*(16) = -0.50, *p* = .626, Figure 28). Two-way ANOVA between high- and low-ranking AMY and SHAM animals did not reveal any significant main effect of rank or significant interaction effects for any of these behaviors (Table 4).

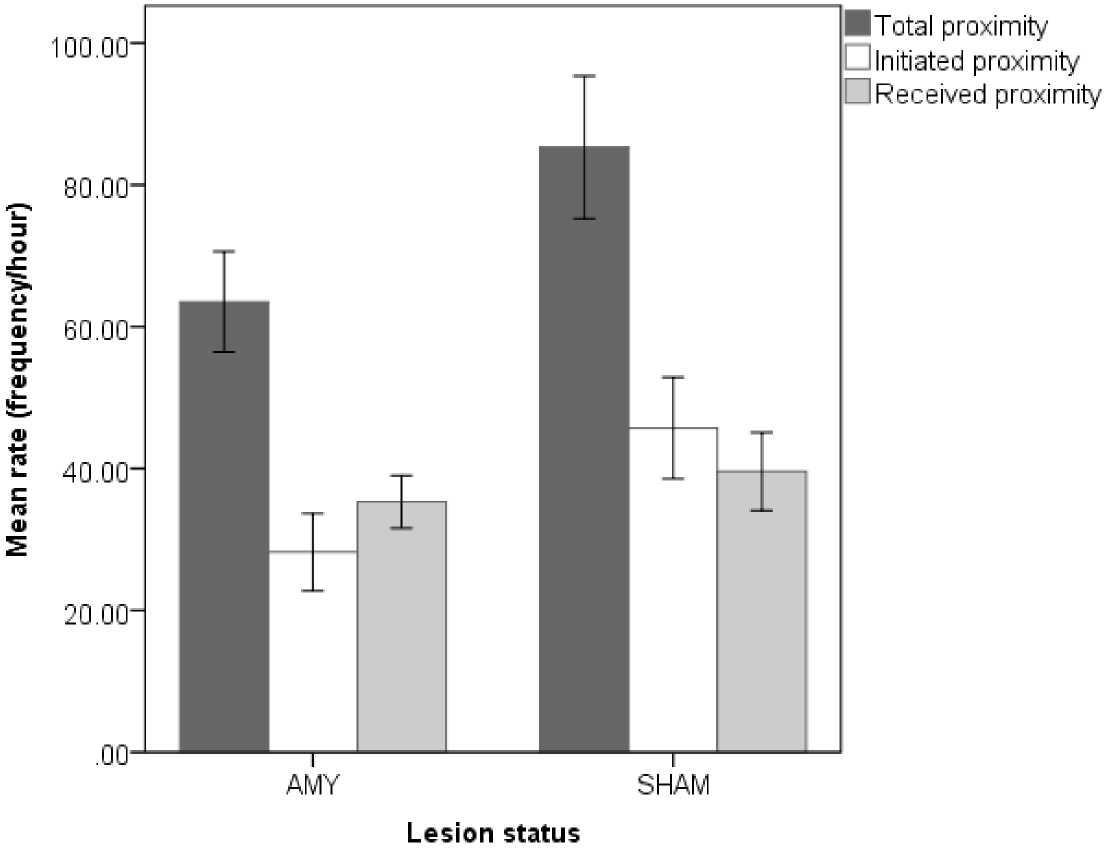

Figure 15. Mean rate (frequency/hour) of proximity with one or more animals during focal observations. Error bars represent ±SEM.

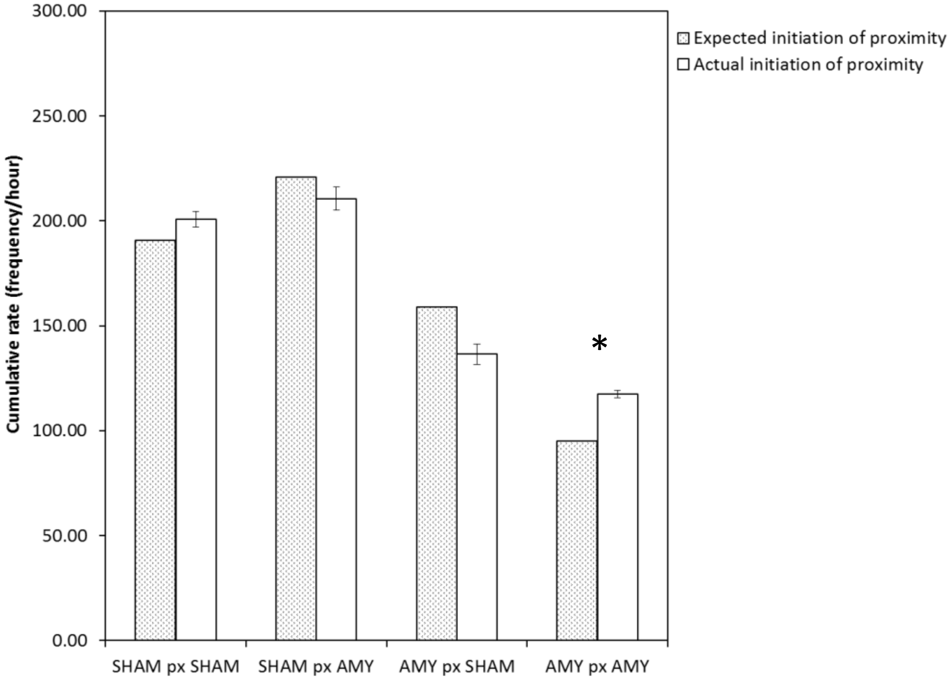

Figure 16. Cumulative rate (frequency/hour) of initiating proximity (px) to either SHAM or AMY animals during focal observations. Error bars represent ±SEM. * indicates significance at $p < .05$ between actual and expected values.

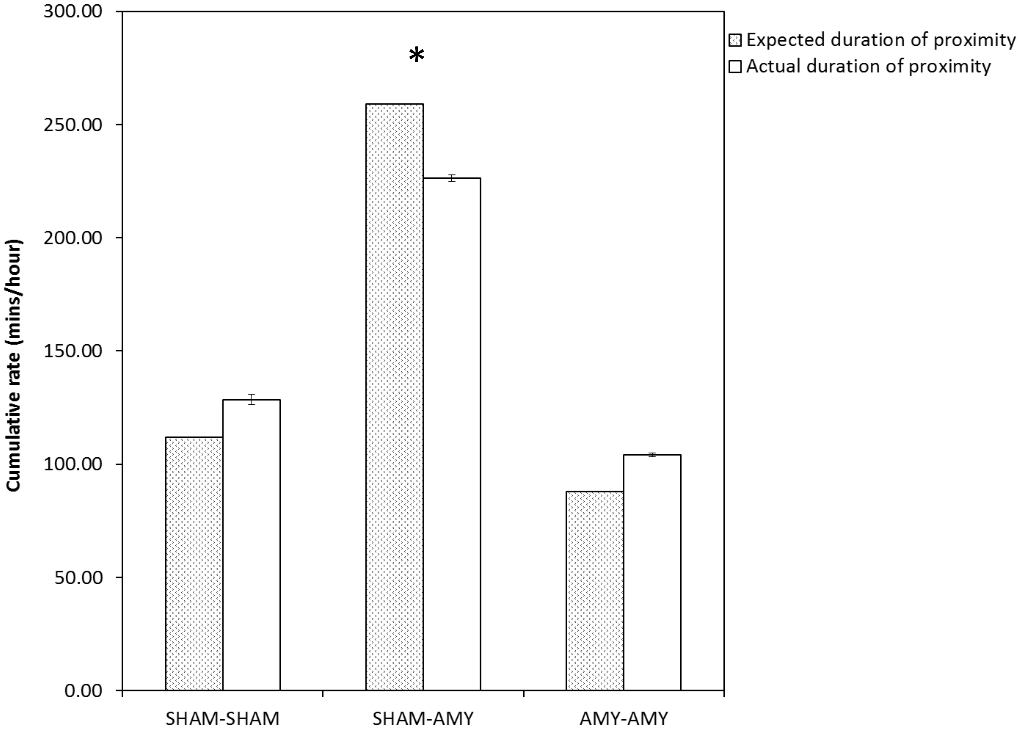

Figure 17. Cumulative rate (mins/hour) of time spent in proximity to either SHAM or AMY animals during focal observations. Error bars represent ±SEM. * indicates significance at $p < .05$ between actual and expected values.

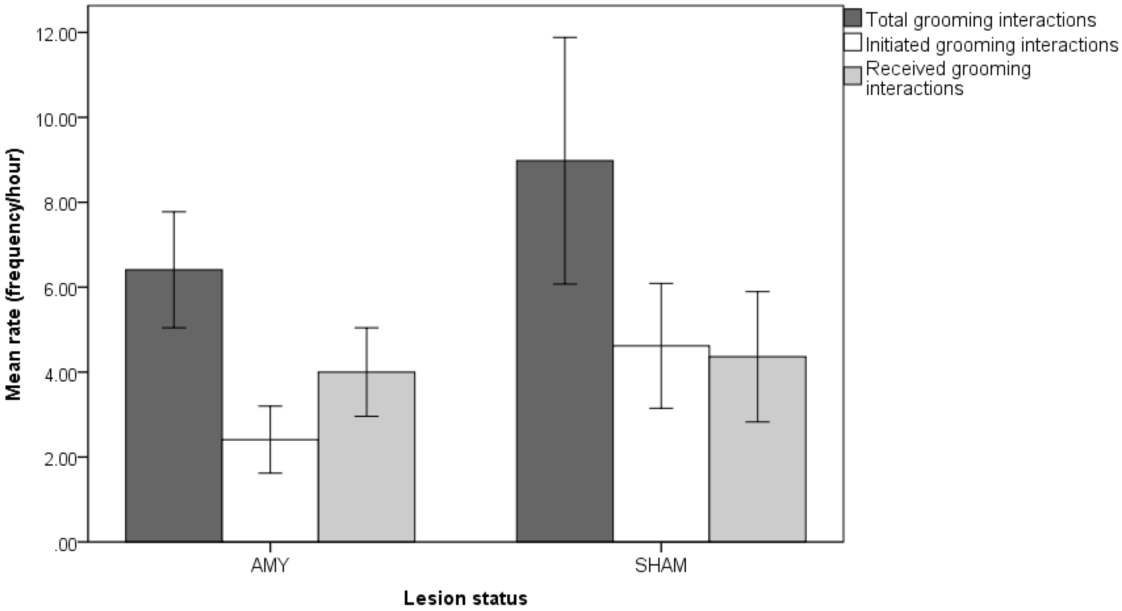

Figure 18. Mean rate (frequency/hour) of grooming interactions during focal observations. Error bars represent ±SEM.

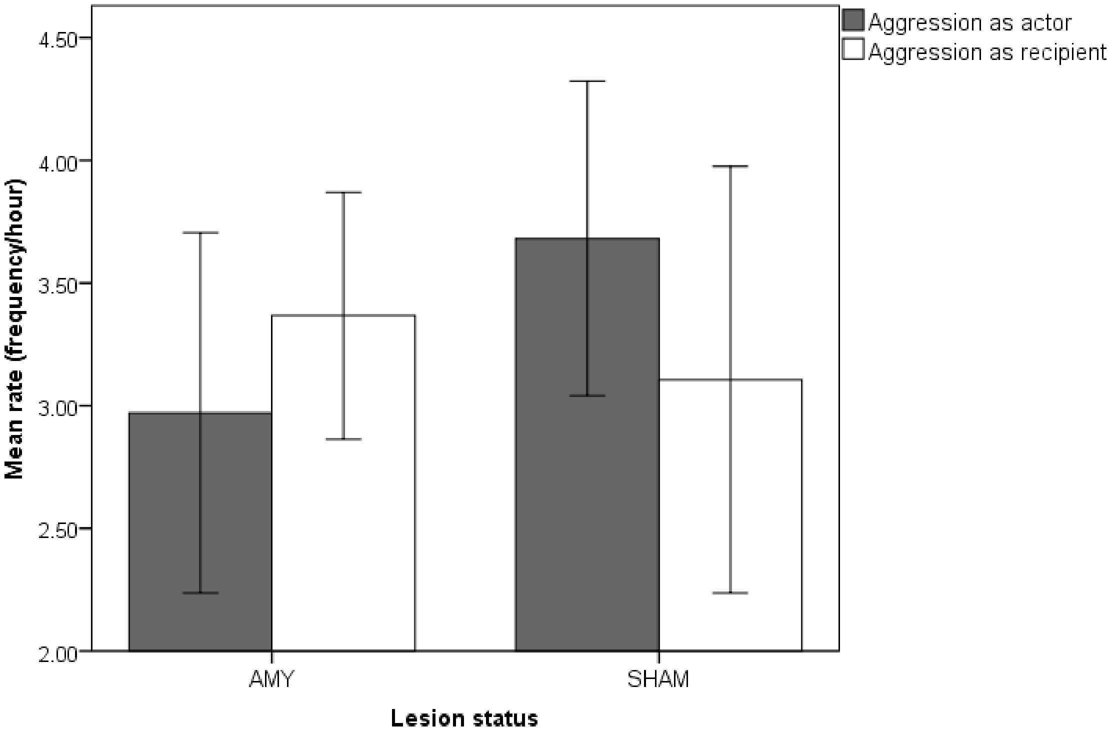

Figure 19. Mean rate (frequency/hour) of aggressive behaviors during focal observations. Error bars represent ±SEM.

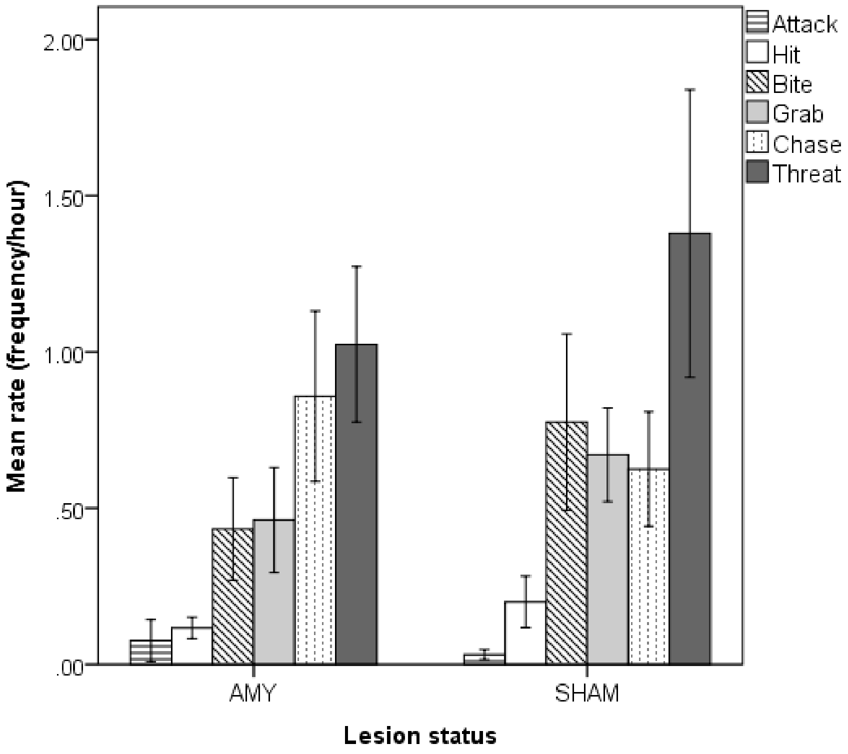

Figure 20. Mean rate (frequency/hour) of individual aggressive behaviors performed during focal observations. Error bars represent +SEM.

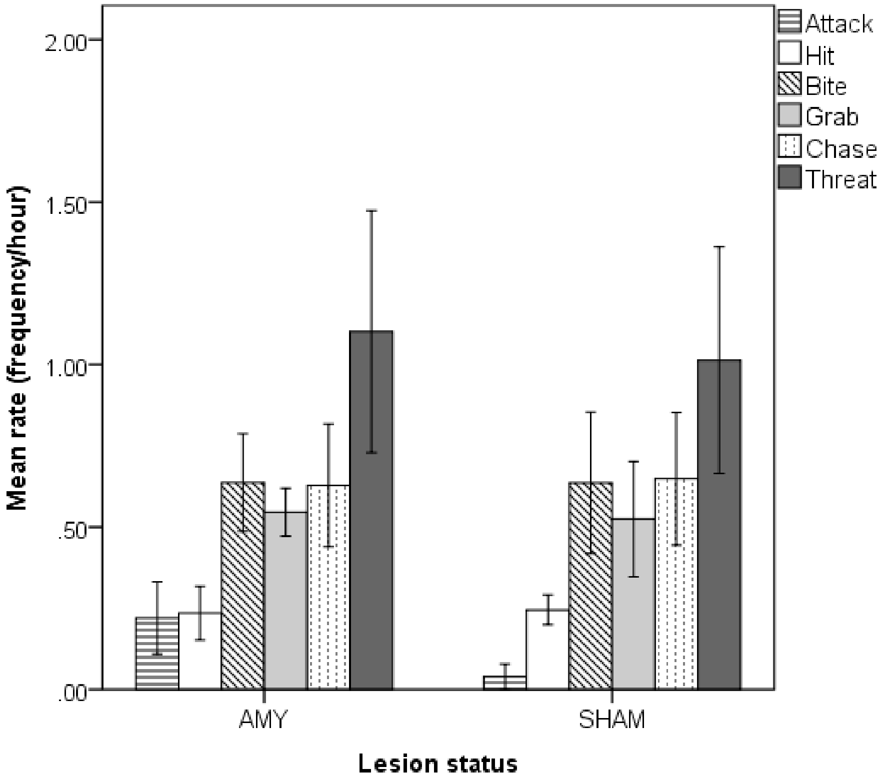

Figure 21. Mean rate (frequency/hour) of individual aggressive behaviors received during focal observations. Error bars represent +SEM.

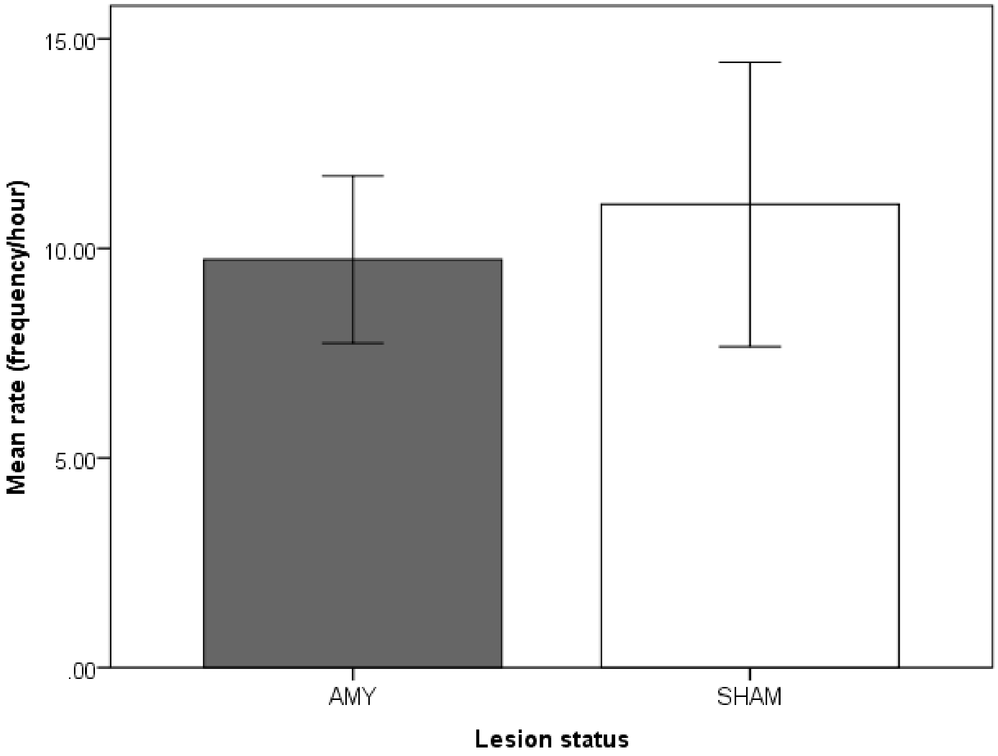

Figure 22. Mean rate (frequency/hour) of withdraw (as actor) during focal observations. Error bars represent ±SEM.

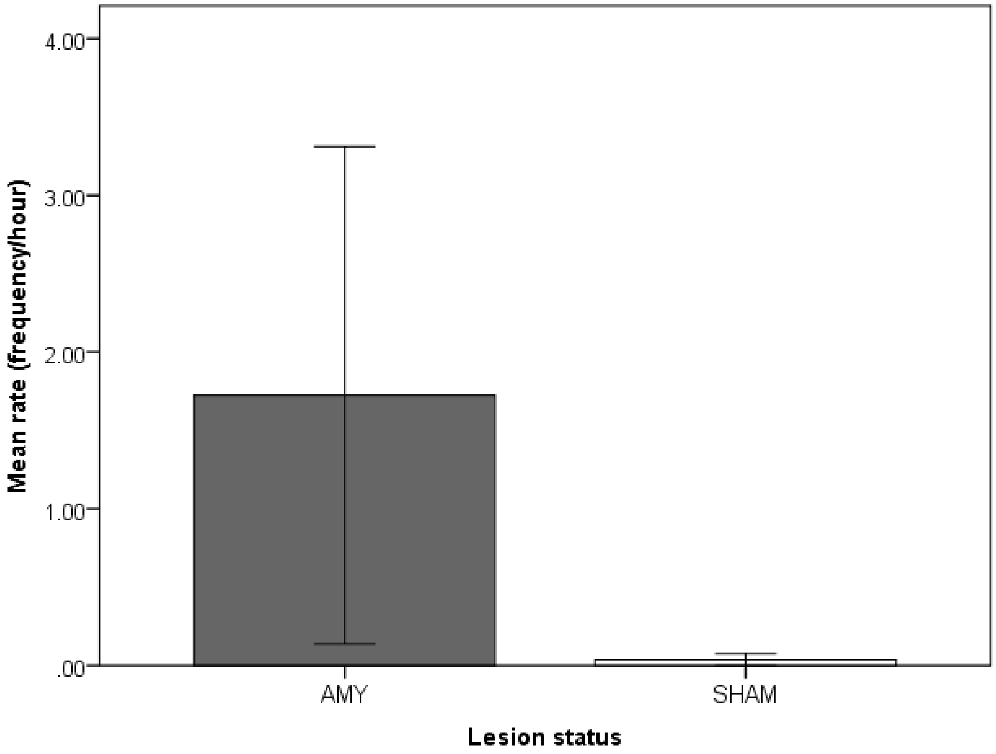

Figure 23. Mean rate (frequency/hour) of grimace during focal observations. Error bars represent ±SEM.

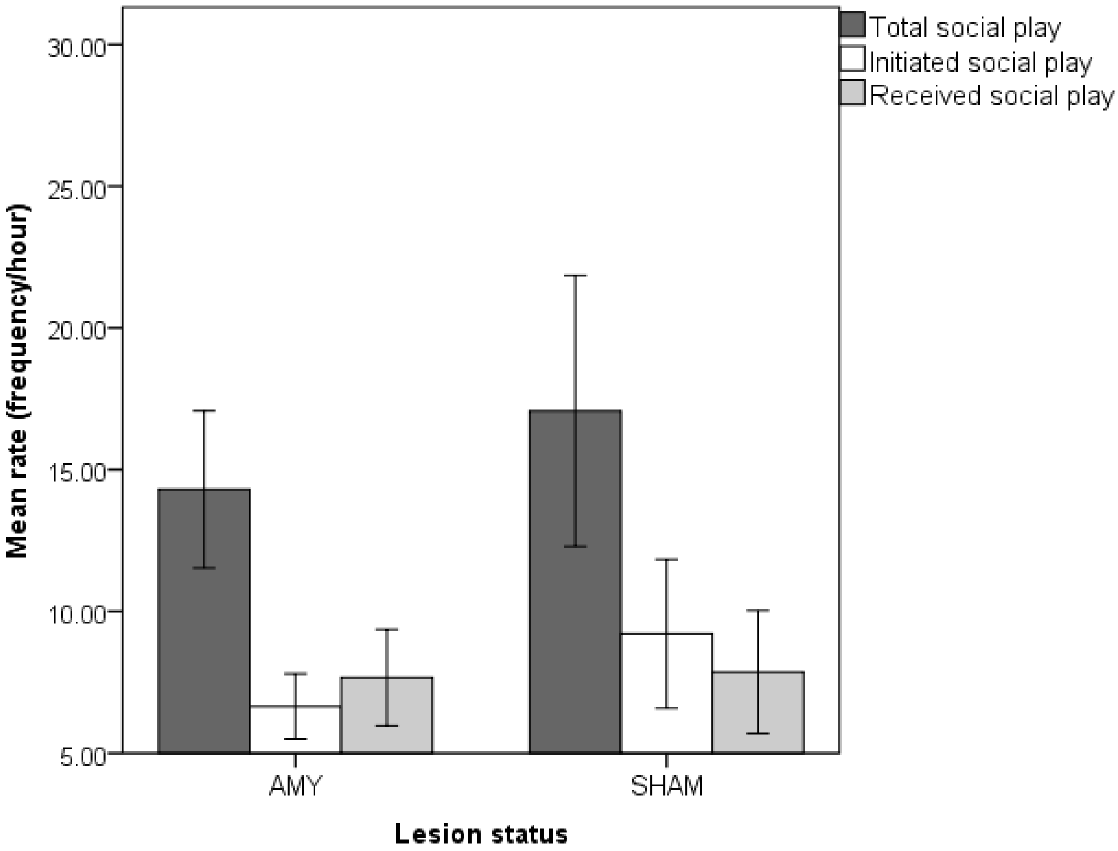

Figure 24. Mean rate (frequency/hour) of social play during focal observations. Error bars represent +SEM.

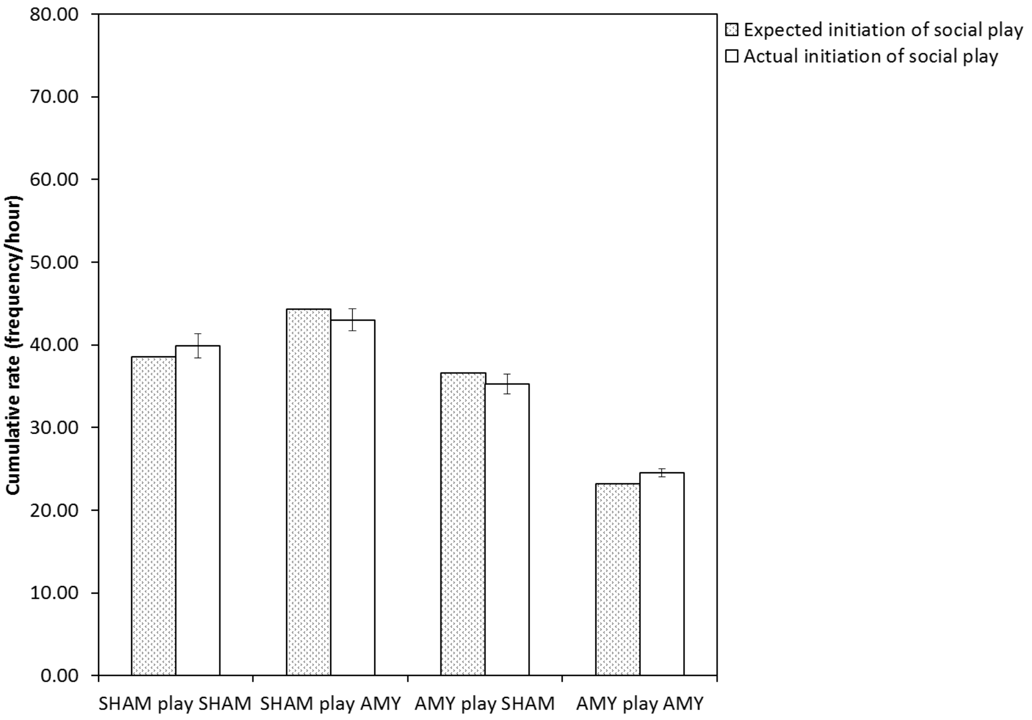

Figure 25. Cumulative rate (frequency/hour) of initiation of social play by partner during focal observations. Error bars represent ±SEM.

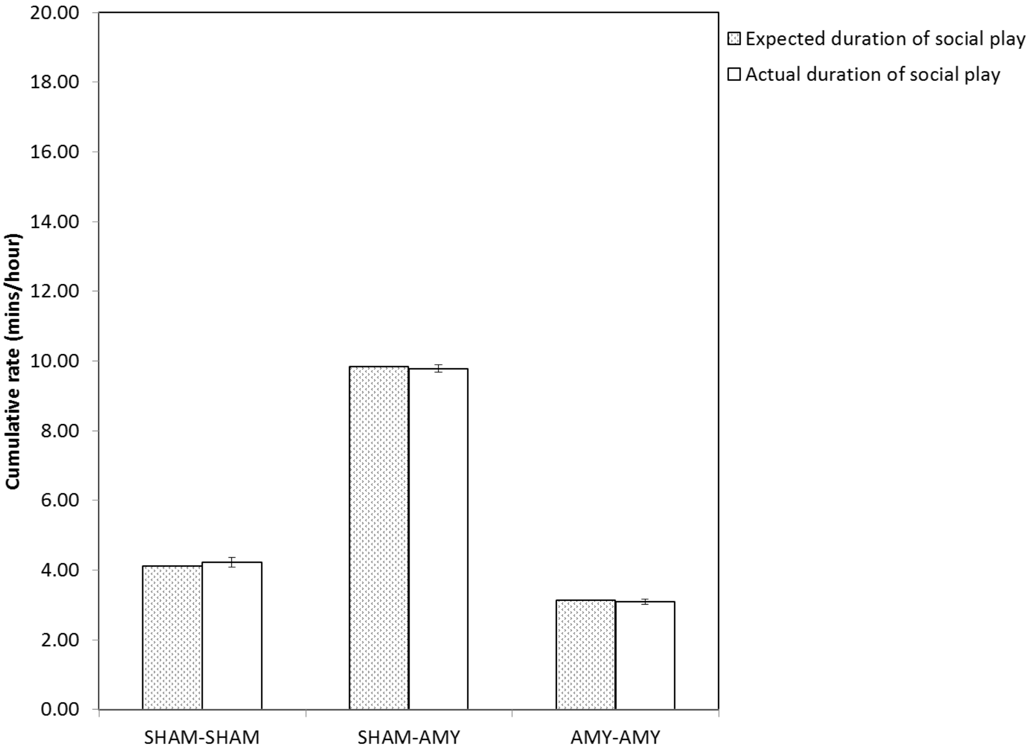

Figure 26. Cumulative rate (mins/hour) of social play duration by partner during focal observations. Error bars represent ±SEM.

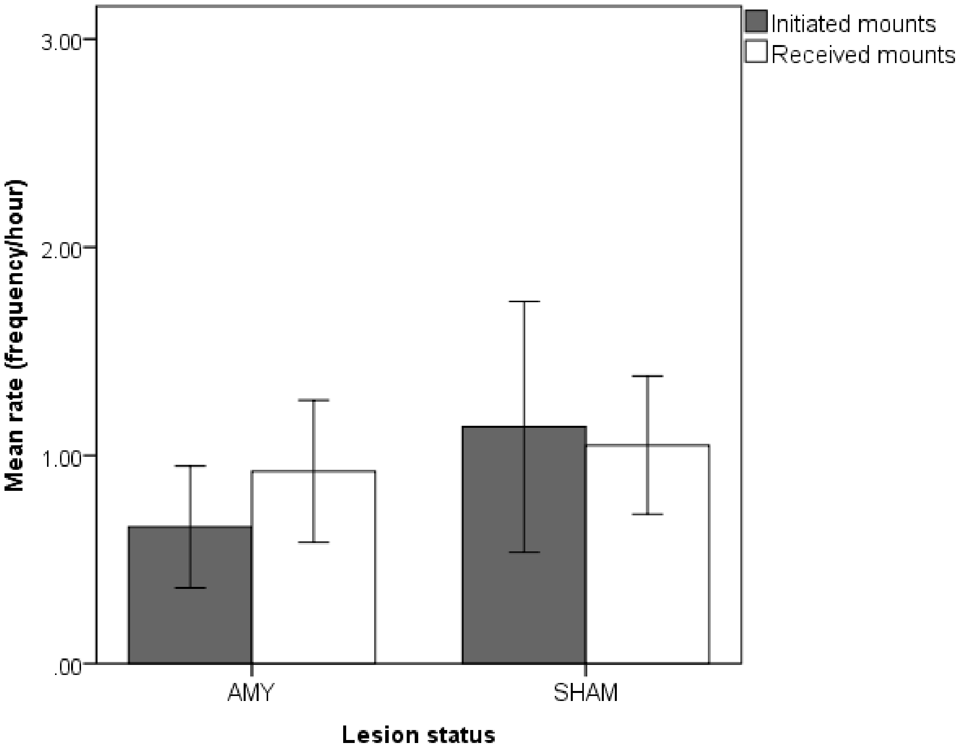

Figure 27. Mean rate (frequency/hour) of initiating and receiving mounts during focal observations. Error bars represent ±SEM.

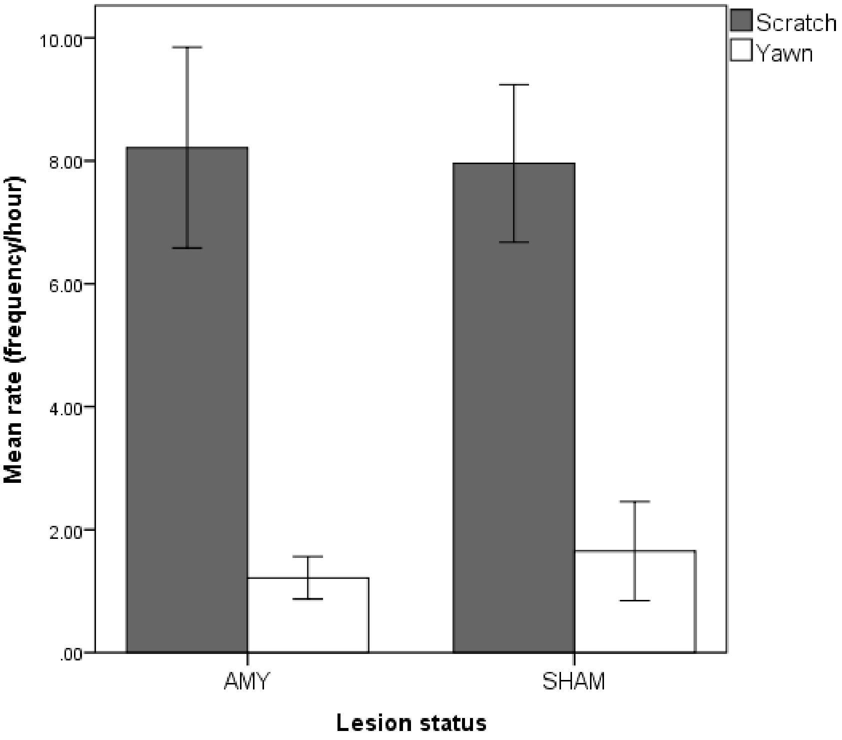

Figure 28. Mean rate (frequency/hour) of scratch and yawn during focal observations. Error bars represent ±SEM.

Social dominance rank

For all three groups, dominance hierarchies were constructed based on the occurrence of several dominance-related behaviors, including withdraw, grimace and aggressive behaviors. Rank in the natal group was calculated as a composite rank score based on matrilineal rank as a proportion of all possible matrilineal ranks. Thus, if an animal was in the alpha family in a group comprised of ten families, the animal would be assigned a score of 1/10, or 0.10. Each animal was assigned a score within their natal group. The six males for each bachelor group were then ordered in terms of matrilineal rank in relation to one another, and each was assigned a unique rank from 1 to 6. In instances when animals were from the same matriline, maternal rank within the matriline was used to determine relative rank among those animals. In this manner, a measure of natal rank was calculated for all males in two ways: rank at the time of removal from the natal group (natal rank), and rank at the time of birth (birth rank).

As it has been suggested that rank in the natal group influences rank in a new group, particular among males from the same natal group, Spearman correlation coefficient tests were performed to determine if a positive relationship existed between either measure of natal rank and rank in the bachelor group (Table 5). There was no significant relationship between natal rank and rank at the time of group formation ($r_s(7) = -.18$, $p = .237$), or between birth rank and rank at the time of group formation ($r_s(7) = .08$, $p = .382$). There were also no significant correlations between either measure of natal rank and rank at any point in the bachelor group ($p > .10$).

Among males who came from the same natal group, a relative natal rank from 1 to 3 was calculated for each subgroup of males. Thus, the natal rank of three males from natal group D1 were transformed to a rank from 1 to 3, only in relationship to one another. The same was done for birth rank, rank at the time of group formation, and current rank, again ranking males from the same natal group only in relationship to one another. In this manner, relative ranks were assigned to all three males from natal group D1 in bachelor group 1, all three males from natal group D2 in bachelor group 1, and so on for all three bachelor groups.

Spearman correlation coefficient tests were used to analyze the extent to which relative rank in the natal group was related to relative rank in the bachelor group. There was no significant correlation between relative natal rank or relative birth rank and relative rank in the new group, indicating that rank relationships among males in this study were not significantly influenced by rank in the natal group (Table 6).

A representation of the social hierarchy in each group over the span of the study is presented in Figure 29. Analysis of the change in rank that occurred at the time of group formation (as compared to natal rank) was performed using Wilcoxon's signed rank test to compare the magnitude and direction of rank changes (subjects with no change in rank were excluded). This analysis revealed that changes in rank were not significantly different from the expected median of zero within either AMY ($W(8) = 18$, $p = .574$) or SHAM animals ($W(7) = 7$, $p = .173$). A second comparison, of natal rank with current rank, was not statistically significant for AMY ($W(9) = 16$, $p = .405$) or SHAM animals ($W(7) = 7$, $p = .173$).

Approximately 4 months after the group introduction, the lowest-ranking male in group 1 (Lo12) moved to the fourth-ranked position with support from the second- and third-ranked males (Um12, Ro12). Approximately 1 month later, the group experienced a social overthrow in which these three males formed a coalition and successfully defeated the alpha male. These three males maintained their relative rank to one another, but all moved up one position in the social hierarchy. Since that time (5 months post-introduction), the hierarchy has remained stable.

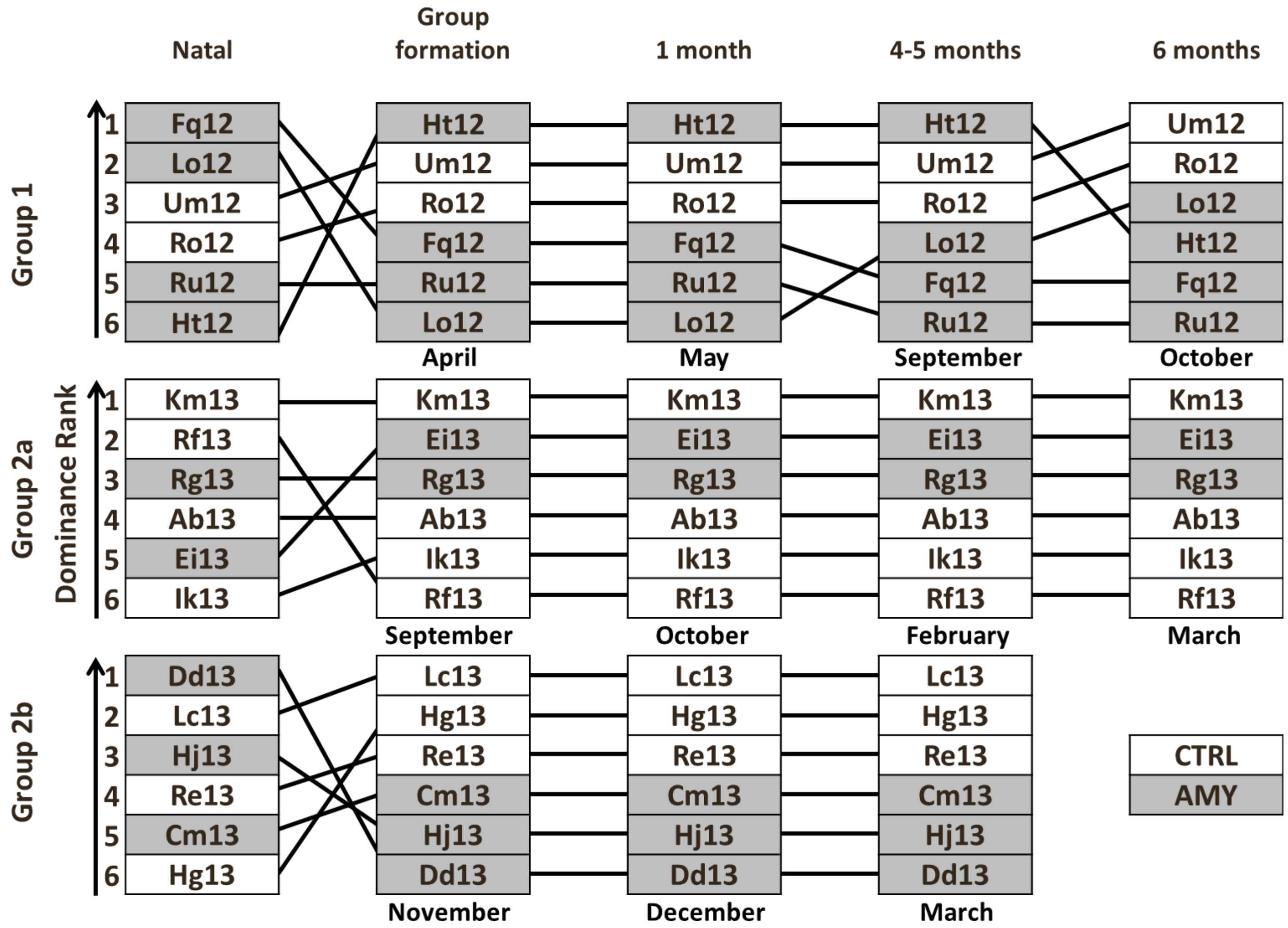

Figure 29. Representation of the social hierarchy in each group over time (1 = highest rank, 6 = lowest rank). Natal rank refers to maternal rank at the time of removal from the natal group. Changes in rank from natal to group formation did not significantly differ from the expected median of zero for either AMY ($W(8) = 18$, $p = .574$) or SHAM animals ($W(7) = 7$, $p = .173$); nor were changes in rank from natal to current significant for AMY ($W(9) = 16$, $p = .405$) or SHAM animals ($W(7) = 7$, $p = .173$). Current ranks in each group are the same as in last listed month.

IV. DISCUSSION

Group introductions

In each of the three groups, the introductions occurred with little aggression. There was no evidence to suggest that amygdalectomized males have difficulty socially integrating or are socially isolated, as proposed by Dicks, et al. (1969). Social interactions were typical of those seen among brain-intact males and a hierarchical structure emerged rapidly in each group. There was little indication during the initial group formations that amygdalectomized males do not recognize social status signals. There was also little evidence to suggest that amygdalectomized males cannot occupy or maintain high social status, as some have suggested based on the study by Rosvold et al. (1954).

Overall there were few behavioral differences between AMY and SHAM subjects during the introduction phase of this study. SHAM animals did more frequently initiate proximity to other animals than did AMY animals, preferentially directed this initiation towards other SHAM animals, and spent more time in proximity to other SHAM animals than to AMY animals. Bauman et al. (2004b) reported control subjects spending more time with other controls when subjects were observed from 6-12 months of age in socialization groups. However, the authors also found that lesioned animals spent more time in proximity with other lesioned animals. In the present study, AMY animals initiated proximity with other AMY animals less than would be expected by chance, though they did not spend significantly less time in proximity with other AMY animals. The frequency and duration of grooming interactions were generally low during the group introductions, which is likely attributable to the fact that animals were in an unfamiliar physical and social environment, and thus time for extended grooming interactions was limited. However, SHAM males engaged in higher rates of grooming than did AMY males, though it should be noted that there number of grooming interactions overall were limited. When the data were analyzed within each group , the two SHAM animals in group 1 spent significantly more time grooming each other than did AMY animals, which spent no time grooming at all. This difference was not found in group 2a or 2b. This may be explained by social history of the two group 1 SHAM animals. Subjects Ro12 and Um12 were co-reared by the same female in their natal group, and thus likely share a stronger affiliative relationship than would animals raised by different females within the same natal group. Colvin & Tissier (1985) found that among male siblings, time spent in proximity was characterized by significantly more grooming and resting together than in other affiliative peer relationships. Among males in the same nonnatal group, more time is spent in proximity with a brother than with any unrelated males (Meikle & Vessey, 1981). Thus, it is not unlikely that these males behave as siblings and as a result, spend more time together than would be expected by chance.

Social play is common among juvenile primates and at an early age, play becomes sexually-differentiated, with males more commonly engaging in rough-and-tumble play interactions (Poirier & Smith, 1974). Play interactions may serve important functions in social development, integration and perhaps even establishing dominance relationships among juveniles, though the incidence of play decreases with age. In the present study, SHAM animals initiated and received social play interactions at higher rates than did the AMY subjects. This pattern was apparent across all three group introductions, and does not appear to be explained by the specific social histories of group members. Taken together with the differences in other affiliative behaviors (proximity, grooming), these results do not support the notion that AMY animals are more social or more affiliative than control animals (nor do they direct their affiliative behavior preferentially towards control animals) as in some studies (Emery et al., 2001; Machado et al., 2008); instead, AMY males appear to show less frequent positive social behaviors during these initial group interactions, as has also been previously observed (Machado & Bachevalier, 2006; Prather et al., 2001). Because social dominance rank was being established throughout the course of the group introduction, it is unlikely that is effect can be completely explained by effects of dominance rank, and thus it may represent a subtle difference in the social "style" of AMY animals that hinders their initial interactions with others, in particular, with other AMY males. Contrary to the present results, Thompson et al. (1969) observed that neonatally amygdalectomized animals engaged in more social play and produced fewer fear responses when paired with another lesioned animal than with a control, though these data were collected under conditions of acute, dyadic testing, in contrast to the social group setting of the present study. These authors suggest that lesioned animals were less fearful of nonsocial stimuli (e.g novel testing environment) than controls, but were more fearful in response to the behavior of control animals. It may be that under the conditions of the group introduction, AMY males are more socially unsure, perhaps providing further evidence for a profile of increased social fear. This is supported by the current findings that SHAM males initiated proximity with other animals more frequently, indicating less social fear or a more outgoing social style. AMY males initiated proximity and played less frequently, and also directed these behaviors less frequently towards other AMY males. However, AMY males did not demonstrate typical fearful or anxiety-related behaviors, and thus rather than fearful, their behavior could be described as cautious or reserved. This may indicate that the outgoing nature of the SHAM males encouraged reciprocation of positive social behaviors from all other animals, both AMY and SHAM. Thompson et al. (1969) observed changes in behavior as time in the testing situation progressed. When paired with a control animal in a novel environment, lesioned animals initially showed less fear than the controls in response to the testing situation, but as the control animals became less fearful, the lesioned animals became more withdrawn. It is possible that AMY and SHAM animals in the present study spent less time together for this reason, in that the AMY animals were reacting to the behavior of SHAMS in a way that suggests social uncertainty, but not necessarily generalized fear, as AMY males did not display higher levels of fear- or anxiety-related behaviors. Thus, the present data do not provide evidence for the "social disinhibition" seen after lesions of the amygdala in adult animals (Emery et al., 2001), nor for the "social indifference" suggested by Dicks et al., (1969), but rather for a more subtle difference in approach to social interaction that is likely moderated by the social style of one's partner.

Klüver and Bucy (1939) observed that temporal lobe lesions produced hyperorality in animals. Similarly, Emery et al. (2001) found that adult males with amygdala lesions more frequently engaged in oral exploration of the environment in dyadic testing situations than did control animals. Results in studies of neonatally lesioned animals are inconsistent. Bauman et al. (2004b) found that lesioned animals engaged in less frequent oral exploration both during social and nonsocial observation. Prather et al. (2001) also found less oral exploration under social conditions, but found more frequent oral exploration during nonsocial conditions. The present study found no significant differences among AMY and SHAM males in the frequency or duration of oral exploration (eat-object play). Eat-object play is also considered as a component of solitary play. In general, solitary play behaviors were fairly infrequent during the group introductions, which is not surprising given the novelty of the social environment.

Aggressive interactions between unfamiliar rhesus males establish dominance relationships. As these males were juvenile at the time of the group introductions, no severe aggression was anticipated. Though aggressive interactions occurred, there was no apparent wounding and overall, the interactions were of low intensity. There were no significant differences between AMY and SHAM males in aggressive behaviors, neither when analyzed by individual behavior nor as a composite variable. Nor were there differences in the likelihood of performing an aggressive act as compared to receiving aggression from others, indicating that AMY animals were neither less aggressive, nor were they the recipients of aggression more often, as seen in previous studies (Bauman et al., 2004b; Emery et al., 2001), which may be attributable to the rearing history of the animals in the present study. The current results support the notion that while AMY animals may use a different social strategy to integrate with unfamiliar animals, their apparent social strategy is not outside the range of species-typical social behavior, as they are not being targeted by their intact peers. It is important to note that the subjects in the present study were reared in large, mixed-sex groups, providing a social environment in which there were a multitude of opportunities for observing social interactions among other animals, as well as participating in social interactions with animals of different sex, age and social rank. Thus, it is likely that our animals gained significant social knowledge under these circumstances that were unavailable to animals weaned from their mothers and placed in small “socialization cohorts” for 3 hours per day (as in Bauman et al., 2004b). Our subjects’ prior social experience might have prepared them for the challenge of social integration with unfamiliar peers, and it is possible that this compensated for the behavioral effects of amygdala lesion during an acute social challenge.

Focal observations

Focal observations were performed over a period of months after the acute group formation phase and thus provide more detailed information about the degree to which AMY males have become socially integrated, formed social bonds, and established and maintained social rank in an environment that does not provide the same degree of social support as did their natal groups.

Some of the behavioral differences seen during the group introductions were not significantly different during the post-introduction period, while others appeared. SHAM animals no longer initiated proximity with other SHAM animals more frequently. AMY animals, however, were more frequently in proximity to other AMY animals than would be expected by chance, the opposite of what was seen in the group introductions. This may indicate that over time and with increasing social experience with group mates, AMY animals overcame any initial uncertainty about the novel social situation, but may have developed stronger affiliations with other AMY animals because of their similar social styles. In contrast, in a more limited social context, Machado et al. (2008) observed that adult-lesioned animals tested in a second round of behavioral observations directed more positive behaviors towards control males and engaged in more agonistic behavior with other lesioned males. Thus, under the conditions of the Machado et al. (2008) study, lesioned animals were observed to exhibit a shift towards exhibiting more positive social behavior over time, perhaps as a result of being tested with animals that were not completely unfamiliar. It is possible that the increased agonistic encounters among the lesioned males were a result of the increased social uncertainty associated with the testing condition, as suggested above. This uncertainty may have been exacerbated by the daily separation and reintroduction of the tetrads used in the study design requiring the animals to repeatedly renegotiate their social status. I found no increase in agonistic interactions among AMY males, perhaps because the stable social environment provided social continuity which allowed AMY males to exhibit more positive social behaviors and have less need for agonistic behavior. The acute stress of the group introductions may have amplified specific behavioral differences which resulted in SHAM males engaging more often with other SHAM males, but once this acute stressor passed, the effect was no longer apparent. However, SHAM and AMY males spent less time together overall, though the reasons for this are not immediately clear. This may be a secondary effect of social rank.

Examination of the social hierarchy reveals that AMY and SHAM males are frequently divided between the high-low rank division (between ranks 3 and 4). Animals tend to associate more frequently with others of a similar social rank, and thus it may be that the distribution of males along this social division contributed to decreasing the amount of time that AMY and SHAM males spent in proximity to one another. Thus the change in social behavior may be an artifact of the social hierarchy and not reflect a direct effect of specific behavioral differences.

There were no significant differences in behaviors signifying social dominance or social fear, except as would expected based on social rank, indicating that AMY animals recognized hierarchical relationships and understood social signals. Taken together with the finding that AMY animals did not initiate or receive more aggressive behaviors than did SHAM animals, this indicates that AMY animals were not behaving in a manner inappropriate to the social context. They produced appropriate social signals, and did not exhibit heightened fear, submissiveness, or aggression, as reported in previous studies (Bauman et al., 2004b; Bauman et al., 2006; Prather et al., 2001; Rosvold et al., 1954; Thompson et al., 1969). In terms of social rank, these animals were able to successfully assess the social environment and interpret interactions with peers, and all three groups quickly formed a clear linear hierarchy.

Analysis of the rank changes that occurred among both AMY and SHAM animals revealed that the median changes in rank did not differ from zero in either AMY or SHAM animals, indicating that AMY animals were no more likely to experience a decrease in rank (from maternal rank in the natal group) at the time of group formation than were SHAM animals. It has been suggested that AMY animals tend to exhibit lower social rank in a group environment (Bauman et al., 2006; Rosvold et al., 1954). The current data do not support this finding. Further analysis of factors that might predict rank in a new group (e.g., hormone levels, body weight) will help to shed light on whether AMY males are attaining social status via the same mechanisms as are SHAM males.

It has been suggested that maternal rank in the natal group determines initial rank in a new group of juvenile males who emigrate together (Drickamer & Vessey, 1973).

The present study found that this was not the case across all of our males, but there was a large amount of variability. Within certain triads, males maintained relative rank relationships, but this pattern was not consistent across all males, again reflecting the need for further analysis of the factors contributing to rank in an all-male group.

After the acute group formation phase there were no significant differences in the frequency or duration of grooming or social play interactions, nor did these differ when analyzed by partner. I found no evidence of hyperorality or hypersexuality (Klüver & Bucy, 1939), though the latter has not been reported for animals with neonatal lesions of the amygdala. In the present study, no differences were found in the frequency or duration of any sexual behaviors as a function of lesion status, though older animals engaged in more masturbation than did younger animals. This difference may be accounted for by the relatively young age of males in the study, and further observation as these animals become pubertal and adult will help to clarify whether the lack of a difference found in the present study is consistent over time.

Overall, these results indicate that AMY animals were neither social outcasts nor ignored by SHAM animals, nor did they appear to be "more attractive" as has been previously suggested (Emery et al., 2001). Our data do not support characterizing AMY animals as being either highly affiliative or highly avoidant, but rather seem to suggest a different style of social interaction that may enable stronger affiliations to form between AMY males, though perhaps requiring extended time.

General discussion

The results presented here represent a unique perspective on the question of how lesions of the amygdala affect social behavior in rhesus monkeys. Differences between the group introduction and focal observations likely represent subtle differences in the way that AMY animals face acute social challenges. Previous research has focused almost exclusively on acute social interaction, thus finding that many of these differences disappear when animals are observed under more stable circumstances is important. Future research in this area might be improved by considering at the outset whether the goal is to observe an animal's response to an acute social challenge, or to observe an animal's ability to function in an ecologically relevant social environment. The present study addressed aspects of both of these questions, and the present data support the finding that neonatally amygdalectomized male rhesus monkeys display a full repertoire of species-typical behaviors that are not used indiscriminately, but rather are generated appropriately in response to the social context and behavior of others.

Comparison of the data from the group introductions and the focal observations seems to indicate a behavioral profile for AMY animals that can be described as more socially reserved, as compared to SHAM animals. However, this does not impede the formation of social relationships, nor does it appear to persist over time as animals have more experience with the social environment. Thus it may be that loss of the amygdala produces deficits in dealing with acute stressors and that these deficits are overcome when placed in a consistent social context. This is not surprising as the literature on damage to the amygdala in humans confirms their ability to function socially. It has been suggested that human patients with damage to the amygdala are able to overcome deficits in recognition of facial expressions through the use of spoken language or other contextual cues (Adolphs, 2006), and it is possible that mechanisms for compensation exist in other species as well, particularly in those adapted for life in complex environments.

The social overthrow that occurred in group 1 approximately five months after the group formation is an excellent example of the ability of these males to navigate the challenges associated with group-living. For some males, this is through the formation and exploitation of beneficial social bonds. Approximately four months after group formation, the lowest-ranking male (Lo12, AMY) moved to the fourth-ranked position with the support of the second and third-ranking males (Ro12, Um12, both SHAM). As suggested by Meikle & Vessey (1981), emigrating with a brother can have important social benefits, and the social history of these two males supports this notion. This type of “bridging” coalition, in which higher-ranking animals support a lower-ranking animal’s rise to a rank just below theirs, has been suggested to be maximally beneficial when the lower-ranking individual is related to the higher-ranking individual (van Schaik, 2004). However, it is possible that the benefit of “helping” an individual achieve higher rank may come in the form of a new coalition member. In this case, once Lo12 had achieved fourth rank, he joined with Ro12 and Um12 to form an “all-up rank-changing” coalition (van Schaik, 2004), in which all three males received the benefit of moving up in the dominance hierarchy by successfully defeating the alpha male. Revolutionary coalitions among free-ranging rhesus males are more likely to be formed between brothers (Meikle & Vessey, 1981) and to occur during the mating season (Higham & Mastripieri, 2010). The mating season at the Yerkes Field Station typically lasts from August through March, and thus the social overthrow occurred just at the beginning of the mating season. The ranks of the males involved are typical of those involved in revolutionary coalitions (mid-high ranking, Higham & Mastripieri, 2010) and it is of particular interest that these males were likely just entering puberty. Analysis of hormone levels surrounding this period of social instability will help to further elucidate factors which may have influenced what occurred; the important point at present being that an AMY male was able to form sufficient social bonds with two SHAM animals as to improve his own social rank, which he has maintained since the social overthrow occurred.

These results clearly demonstrate the importance of context in studies of social behavior. Males with neonatal lesions of the amygdala demonstrated behavior consistent with increased social fear during an acute social challenge, but were nonetheless able to produce, interpret, and reciprocate appropriate social signals with both lesioned and brain-intact conspecifics. Observations that took place in the months after the acute challenge confirmed that lesions of the amygdala did not impair the ability to socially integrate, establish and maintain rank, and function within a stable hierarchical structure. Thus, the effect of neonatal amygdala lesion was mediated by both the social context in which observations took place as well as the social environment in which these males were reared. This has important implications for future research, such that in order to gain a fuller understanding of the neural mechanisms of social behavior social behavior cannot be completely divorced from a relevant social context.

V. APPENDIX

Table 1. 18 male subjects, their treatment condition (A = bilateral amygdala lesion, S = SHAM surgical procedure), natal groups, and pair-introduction partners.

	Subject (treatment) Natal group D1	*paired with*	**Subject (treatment) Natal group D2**	**Group formed**
Group 1	Ro12 (S)	--	Lo12 (A)	April 2011
	Ru12 (S)	--	Fq12 (A)	
	Um12 (S)	--	Ht12 (A)	
Group 2a	Ei13 (A)	--	Rg13 (A)	September 2011
	Km13 (S)	--	Ab13 (S)	
	Rf13 (S)	--	Ik13 (S)	
Group 2b	Dd13 (A)	--	Re13 (S)	November 2011
	Hj13 (A)	--	Cm13 (A)	
	Lc13 (S)	--	Hg13 (S)	

Table 2. Abridged ethogram for behavioral observations. Frequency behaviors are scored each time the behavior occurs. Duration behaviors are scored with a beginning and end.

Affiliative *(duration behaviors)*	
Proximity	Animal is within arm's reach of another animal.
Groom	One animal combing through the hair of another.
Agonistic *(frequency behaviors)*	
Attack	High-level aggressive contact between any two animals.
Hit	
Bite	
Grab	
Chase	Both animals are running, not in the context of play.
Threat	Non-contact aggression; lunge, open-mouth woofing, or slap without contact.
Grimace	Animal pulls back lips to reveal teeth with a closed jaw.
Withdraw	Clearly avoiding another animal; does not imply any distance.
Play *(duration behaviors)*	
Social play	Any play between two animals, not agonistic. Includes brief contact play, rough and tumble play, and chase play.
Solitary play	Play by oneself; includes vigorous play and quiet play.
Eat-object play	Animal is mouthing or licking non-food objects.
Sexual	
Mount *(frequency behavior)*	Animal's pelvis is oriented towards the hindquarters of the recipient. Feet may or may not be clasped on recipient's ankles. Typically, the animal grabs the recipient's waist.
Oral-genital contact/grooming *(duration behavior)*	May be solitary or partnered.
Masturbation *(duration behavior)*	Manual manipulation of the genitals that is rhythmic and repetitious.
Other	
Scratch *(frequency behavior)*	A self-directed behavior. Scored for each bout of scratching or each body part scratched.
Yawn *(frequency behavior)*	Wide-mouthed yawn.
Self-groom *(duration behavior)*	Animal combing through own hair.
Genital groom *(duration behavior)*	Animal grooming his own or another's genitals, is not rhythmic.

Table 3. Frequency behaviors in group introductions. Rates (frequency/hour) are reported with focal animal as actor, except when otherwise noted. Total rate = rate as actor + as recipient. For χ^2 comparisons, +/- indicates initiation of behavior is greater/less between SHAM (SS), AMY (AA), SHAM and AMY (SHAM initiates with AMY, SA) or AMY and SHAM (AMY initiates with SHAM, AS) than expected by chance. When Levene's test for homogeneity of variance was significant, corrected values for the test statistic (t), degrees of freedom, and p are reported.

Behavior	**Lesion Mean (SD)**	**Sham Mean (SD)**	**Test statistic (two-tailed p)**	**Significant χ^2 comparisons of recipient effect (p)**
Affiliative				
Proximity	29.88 (18.84)	48.15 (17.47)	t(16) = -2.13 (.049)	AA-; χ^2 = 6.91 (0.009); SS+; χ^2 = 8.17 (0.004)
Groom	0.04 (0.19)	0.38 (0.43)	t(9.219) =-2.29 (.047)	
Aggressive				
Attack	0.11 (0.24)	0.00	t(8) = 1.41 (.195)	
Attack (recipient)	0.11 (0.24)	0.00	t(8) = 1.41 (.195)	
Hit	0.70 (0.67)	0.28 (0.55)	t(16) = 1.46 (.165)	
Hit (recipient)	0.62 (0.51)	0.31 (0.51)	t(16) = 1.29 (.216)	
Bite	3.00 (3.44)	5.18 (6.00)	t(16) = -0.95 (.356)	
Bite (recipient)	6.86 (12.44)	1.33 (1.71)	t(8.302) = 1.32 (.222)	
Grab	0.16 (0.28)	0.12 (0.26)	t(16) = 0.34 (.742)	
Grab (recipient)	0.08 (0.16)	0.20 (0.33)	t(11.687) = -1.01 (.331)	
Chase	2.22 (2.97)	2.77 (3.97)	t(16) = -0.33 (.747)	
Chase (recipient)	2.45 (2.62)	2.54 (5.67)	t(16) = -0.05 (.964)	
Threat	3.56 (4.11)	2.22 (2.28)	t(16) = 0.86 (.403)	
Threat (recipient)	3.48 (4.01)	2.30 (3.01)	t(16) = 0.70 (.493)	
Dominance-related				
Grimace	1.72 (4.76)	0.04 (0.11)	t(16) = 1.06 (.319)	
Withdraw	20.36 (15.39)	12.31 (18.10)	t(16) = 1.02 (.324)	
Play				
Social play	14.79 (14.27)	30.36 (10.30)	t(16) = -2.65 (.017)	AA-; χ^2 = 8.18, (0.004); AS+; χ^2 = 4.92, p = 0.03
Social play (recipient)	17.56 (12.06)	27.59 (6.25)	t(16) = -2.21 (.042)	
Sexual				
Mount	1.74 (2.15)	6.69 (10.22)	t(16) = -2.09 (.053)	
Mount (recipient)	19.44 (2.15)	3.95 (3.38)	t(16) = -1.50 (.153)	
Other				
Scratch	0.24 (0.47)	0.41 (0.46)	t(16) = -0.82 (.424)	
Yawn	0.11 (0.24)	0.12 (0.35)	t(16) = -0.28 (.978)	

Table 4. Frequency behaviors in focal observations analyzed using two-way ANOVA between high/low ranking AMY/SHAM animals. Rates (frequency/hour) are reported with focal animal as actor, except when otherwise noted.

Behavior	**Lesion Mean (SD)**	**Sham Mean (SD)**	**Test statistic (*p* value)**
Aggressive			
Attack	0.08 (0.20)	0.03 (0.05)	F_{rank} = 0.69 (0.420); F_{lesion} = 0.10 (0.759); $F_{\text{rank x lesion}}$ = 0.46 (0.507)
Attack (recipient)	0.22 (0.33)	0.04 (0.12)	F_{rank} = 0.43 (0.524); F_{lesion} = 1.35 (0.265); $F_{\text{rank x lesion}}$ = 0.06 (0.817)
Hit	0.12 (0.10)	0.20 (0.25)	F_{rank} = 2.41 (0.143); F_{lesion} = 0.15 (0.708); $F_{\text{rank x lesion}}$ = 0.17 (0.685)
Hit (recipient)	0.23 (0.25)	0.24 (0.14)	F_{rank} = 0.29 (0.599); F_{lesion} = 0.08 (0.787); $F_{\text{rank x lesion}}$ = 0.04 (0.845)
Bite	0.43 (0.49)	0.78 (0.85)	F_{rank} = 5.31 (0.037); F_{lesion} = 0.10 (0.753); $F_{\text{rank x lesion}}$ = 0.16 (0.697)
Bite (recipient)	0.64 (0.45)	0.64 (0.65)	F_{rank} = 9.34 (0.009); F_{lesion} = 1.03 (0.327); $F_{\text{rank x lesion}}$ = 3.58 (0.079)
Grab	0.46 (0.50)	0.67 (0.45)	F_{rank} = 3.61 (0.078); F_{lesion} = 0.09 (0.765); $F_{\text{rank x lesion}}$ = 0.82 (0.381)
Grab (recipient)	0.55 (0.22)	0.52 (0.53)	F_{rank} = 2.21 (0.160); F_{lesion} = 0.13 (0.720); $F_{\text{rank x lesion}}$ = 8.74 (0.010)
Chase	0.86 (0.82)	0.63 (0.55)	F_{rank} = 0.45 (0.514); F_{lesion} = 0.77 (0.394); $F_{\text{rank x lesion}}$ = 1.01 (0.332)
Chase (recipient)	0.63 (0.57)	0.65 (0.61)	F_{rank} = 2.46 (0.140); F_{lesion} = 0.36 (0.561); $F_{\text{rank x lesion}}$ = 2.95 (0.108)
Threat	1.02 (0.76)	1.38 (1.38)	F_{rank} = 2.09 (0.170); F_{lesion} = 0.03 (0.876); $F_{\text{rank x lesion}}$ = 0.03 (0.868)
Threat (recipient)	1.10 (1.12)	1.01 (1.05)	F_{rank} = 5.84 (0.030); F_{lesion} = 0.38 (0.545); $F_{\text{rank x lesion}}$ = 0.74 (0.405)
Other			
Scratch	8.21 (4.89)	7.96 (3.84)	F_{rank} = 3.02 (0.104); F_{lesion} =0.49 (0.496); $F_{\text{rank x lesion}}$ = 0.18 (0.674)
Yawn	1.22 (1.04)	1.65 (2.41)	F_{rank} =3.66 (0.076); F_{lesion} =0.02 (0.890); $F_{\text{rank x lesion}}$ = 0.28 (0.608)

Table 5. Correlation matrix of social dominance rank over time. Natal = rank at time when removed from natal group, Born = rank when born, Formation = rank at time of bachelor male group formation, Months = number of months after group formation. Each cell contains Spearman correlation coefficient r_s, *p*, and *n*. ** indicates significance at $p < .01$, *** indicates significance at $p < .001$.

	A.	**B.**	**C.**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
A. Natal	1.00 . *18*	-.30 .118 *18*	-.18 .237 *18*	-.18 .237 *18*	-.18 .237 *18*	-.18 .237 *18*	-.18 .237 *18*	-.03 .465 *12*	.24 .231 *12*	.12 .413 *6*	.12 .413 *6*	.12 .413 *6*	.12 .413 *6*	.12 .413 *6*	.12 .413 *6*
B. Born	-.30 .118 *18*	1.00 . *18*	.08 .382 *18*	.08 .382 *18*	.08 .382 *18*	.08 .382 *18*	.08 .382 *18*	-.04 .456 *12*	.08 .404 *12*	.58 .114 *6*	.58 .114 *6*	.58 .114 *6*	.58 .114 *6*	.58 .114 *6*	.58 .114 *6*
C. Formation	-.18 .237 *18*	.08 .382 *18*	1.00 . *18*	1.000^{***} . *18*	1.000^{***} . *18*	1.000^{***} . *18*	1.000^{***} . *18*	$.91^{***}$ .000 *12*	$.686^{**}$ .007 *12*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*
1 month	-.18 .237 *18*	.08 .382 *18*	1.00^{***} . *18*	1.00 . *18*	1.000^{***} . *18*	1.000^{***} . *18*	1.000^{***} . *18*	$.91^{***}$ .000 *12*	$.686^{**}$ .007 *12*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*
2 months	-.18 .237 *18*	.08 .382 *18*	1.00^{***} . *18*	1.000^{***} . *18*	1.00 . *18*	1.000^{***} . *18*	1.000^{***} . *18*	$.91^{***}$ .000 *12*	$.686^{**}$ .007 *12*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*
3 months	-.18 .237 *18*	.08 .382 *18*	1.00^{***} . *18*	1.000^{***} . *18*	1.000^{***} . *18*	1.00 . *18*	1.000^{***} . *18*	$.91^{***}$ .000 *12*	$.686^{**}$ .007 *12*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*
4 months	-.18 .237 *18*	.08 .382 *18*	1.00^{***} . *18*	1.000^{***} . *18*	1.000^{***} . *18*	1.000^{***} . *18*	1.00 . *18*	$.91^{***}$ .000 *12*	$.686^{**}$ .007 *12*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*
5 months	-.03 .465 *12*	-.04 .456 *12*	$.91^{***}$ .000 *12*	$.91^{***}$ .000 *12*	$.91^{***}$ .000 *12*	$.91^{***}$ .000 *12*	$.91^{***}$ .000 *12*	1.00 . *12*	$.829^{***}$ .000 *12*	.66 .08 *6*	.66 .08 *6*	.66 .08 *6*	.66 .08 *6*	.66 .08 *6*	.66 .08 *6*

Table 5, continued. Correlation matrix of social dominance rank over time. Natal = rank at time when removed from natal group, Born = rank when born, Formation = rank at time of bachelor male group formation, Months = number of months after group formation. Each cell contains Spearman correlation coefficient r_s, p, and n. ** indicates significance at $p < .01$, *** indicates significance at $p < .001$.

	A.	**B.**	**C.**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
6 months	.24 .231 *12*	.08 .404 *12*	.686** .007 *12*	.686** .007 *12*	.686** .007 *12*	.686** .007 *12*	.686** .007 *12*	.829*** .000 *12*	1.00 . *12*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*
7 months	.12 .413 *6*	.58 .114 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.66 .078 *6*	1.00*** . *6*	1.00 . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*
8 months	.12 .413 *6*	.58 .114 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.66 .078 *6*	1.00*** . *6*	1.00*** . *6*	1.00 . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*
9 months	.12 .413 *6*	.58 .114 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.66 .078 *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00 . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*
10 months	.12 .413 *6*	.58 .114 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.66 .078 *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*
11 months	.12 .413 *6*	.58 .114 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.66 .078 *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00 . *6*	1.00*** . *6*
12 months	.12 .413 *6*	.58 .114 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.37 .234 *6*	.66 .078 *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00*** . *6*	1.00 . *6*

Table 6. Correlation matrix of social dominance rank relative to natal group members. Relative birth rank = relative rank when born, Relative natal rank = relative rank at time when removed from natal group. Each cell contains Spearman correlation coefficient r_s, p, and n. *** indicates significance at $p < .001$.

	Relative birth rank	**Relative natal rank**	**Relative rank at group formation**	**Relative current rank**
Relative birth rank	1.00	.25	.17	-.08
	.	.159	.254	.371
	18	*18*	*18*	*18*
Relative natal rank	.25	1.00	.17	.17
	.159	.	.254	.254
	18	*18*	*18*	*18*
Relative rank at group formation	.17	.17	1.00	$.75^{***}$
	.254	.254	.	.000
	18	*18*	*18*	*18*
Relative current rank	-.08	.17	$.75^{***}$	1.00
	.371	.254	.000	.
	18	*18*	*18*	*18*

VI. REFERENCES

Adolphs, R., Tranel, D. & Damasio, A.R. (1998). The human amygdala in social judgement. *Nature*, 393:470-473.

Adolphs, R. (2001). The neurobiology of social cognition. *Current opinion in neurobiology*, 11:231-239.

Adolphs, R. (2006). Is the human amygdala specialized for processing social information? *Annals of the New York Academy of Sciences*, 985:326-340.

Amaral, D.G. (2002). The primate amygdala and the neurobiology of social behavior: Implications for understanding social anxiety. *Biological Psychiatry*, 51(1):11-17.

Amaral, D.G., Capitanio, J.P., Jourdain, M., Mason, W.A., Mendoza, S.P. & Prather, M. (2003). The amygdala: is it an essential component of the neural network for social cognition? *Neuropsychologia*, 41:235-240.

Bauman, M.D., Lavenex, P., Mason, W.A., Capitiano, J.P., & Amaral, D.G. (2004a). The development of mother-infant interactions after neonatal amygdala lesions in rhesus monkeys. *The Journal of Neuroscience*, 24(3):711-721.

Bauman, M.D., Lavenex, P., Mason, W.A., Capitiano, J.P., & Amaral, D.G. (2004b). The development of social behavior following neonatal amygdala lesions in rhesus monkeys. *Journal of Cognitive Neuroscience*, 16(8):1388-1411.

Beisner, B.A., Jackson, M.E., Cameron, A. & McCowan, B. (2010). Effects of natal male alliances on aggression and power dynamics in rhesus macaques. *American Journal of Primatology*, 71:1-12.

Berard, J. (1999). A four-year study of the association between male dominance rank, residency status, and reproductive activity in rhesus macaques (*Macaca mulatta*). *Primates*, 40(1):159-175.

Bernstein, I.S., Gordon, T.P. & Rose, R.M. (1974). Aggression and social controls in rhesus monkey (*Macaca mulatta*) groups revealed in group formation studies. *Folia primatologica*, 21:81-107.

Boelkins, R.C. & Wilson, A.P. (1972). Intergroup social dynamics of the Cayo Santiago rhesus (*Macaca mulatta*) with special references to changes in group membership by males. *Primates,* 13(2):125-140.

Carpenter, C.R. (1942). Sexual behavior of free ranging rhesus monkeys (*Macaca mulatta*). II. Periodicity of estrus, homosexual, autoerotic and non-conformist behavior. *Journal of Comparative Psychology*, 33(1):143-162.

Colvin, J. (1983). Influences of social situation on male emigration. In Hinde, R.A. (Ed.), *Primate social relationships*, (p. 160-171). Sunderland: Sinauer Associates Inc.

Colvin, J. (1986). Proximate causes of male emigration at puberty in rhesus monkeys. In Rawlins, R.G. & Kessler, M.J. (Eds.), *The Cayo Santiago macaques: History, behavior & biology*, (p.131-158). Albany: State University of New York Press.

Colvin, J. & Tissier, G. (1985). Affiliation and reciprocity in sibling and peer relationships among free-ranging immature male rhesus monkeys. *Animal Behavior*, 33:959-977.

Dicks, D., Myers, R.E., Kling, A. (1969). Uncus and amygdala lesions: Effects on social behavior in the free-ranging rhesus monkey. *Science*, 165:69-71.

Drickamer, L.C. & Vessey, S. H. (1973). Group changing in free-ranging male rhesus monkeys. *Primates,* 14(4):359-368.

Emery, N.J., Capitanio, J.P., Mason, W.A., Machado, C.J., Mendoza, S.P. and Amaral, D.G. (2001). The effects of bilateral lesions of the amygdala on dyadic social interactions in rhesus monkeys (*Macaca mulatta*). *Behavioral Neuroscience,* 115(3):515-544.

Greenwood, P.J. (1980). Mating systems, philopatry, and dispersal in birds and mammals. *Animal Behaviour*, 28:1140-1162.

Higham, J.P. & Mastripieri, D. (2010). Revolutionary coalitions in male rhesus macaques. *Behaviour*, 147:1889-1908.

Kaufmann, J. (1967). Social relations of adult males in a free-ranging band of rhesus monkeys. In S. Altmann (Ed.), *Social communication among primates*, (p. 793-98). Chicago: University of Chicago Press.

Klüver, H. & Bucy, P.C. (1939). Preliminary analysis of functions of the temporal lobes in monkeys. *Archives of Neurology and Psychology*, 42(6):979-1000.

Koford, C. B. (1963). Ranks of mothers and sons in bands of rhesus monkeys. *Science*, 141:356-357.

Lindburg, D.G. (1969). Rhesus monkeys: Mating season mobility of adult males. *Science*, 166(3909):1176-1178.

Machado, C.J. & Bachevalier, J. (2006). The impact of selective amygdala, orbital frontal cortex, or hippocampal formation lesions on established social relationships in rhesus monkeys (*Macaca mulatta*). *Behavioral Neuroscience*, 120(4):761-786.

Machado, C.J., Emery, N.J., Capitanio, J.P., Mason, W.A., Mendoza, S.P. & Amaral, D.G. (2008). Bilateral neurotoxic amygdala lesions in rhesus monkeys (*Macaca mulatta*): Consistent pattern of behavior across different social contexts. *Behavioral Neuroscience*, 122(2):251-266.

Meikle, D.B., & Vessey, S.H. (1981). Nepotism among rhesus monkey brothers. *Nature*, 294:160-161.

Melnick, D.J., Pearl, M.C. & Richard, A.F. (1984). Male migration and inbreeding avoidance in wild rhesus monkeys. *American Journal of Primatology*, 7:229-243.

Meunier, M. Bachevalier, J., Murray, E.A., Málková, L. & Mishkin, M. (1999). Effects of aspiration versus neurotoxic lesions of the amygdala on emotional responses in monkeys. *European Journal of Neuroscience*, 11:4403-4418.

Meunier, M. & Bachevalier, J. (2002). Comparison of emotional responses in monkeys with rhinal cortex or amygdala lesions. *Emotion*, 2:147-161.

Phelps, E.A. (2006). Emotion and cognition: Insights from studies of the human amygdala. *Annual Reviews in Psychology*, 57:27-53.

Prather, M.D., Lavenex, P., Mauldin-Jourdain, M.L., Mason, W.A., Capitiano, J.P., Mendoza, S.P., & Amaral, D.G. (2001). Increased social fear and decreased fear of objects in monkeys with neonatal amygdala lesions. *Neuroscience*, 106(4):653-658.

Pusey, A.E. & Packer, C. (1987). Dispersal and philopatry. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, T. Struhsaker & R.W. Wrangham (Eds.), *Primate societies*, (p. 250-266). Chicago: University of Chicago Press.

Raper, J. R. (2009). *Behavioral and neuroendocrine effects of neonatal amygdala lesion on rhesus monkeys living in a semi-naturalistic environment* . Unpublished master's thesis. Emory University, Atlanta, GA.

Rosvold, H.E., Allan, F.M. & Pribham, K.H. (1954). Influence of amygdalectomy on social behavior in monkeys. *Journal of Comparative and Physiological Psychology*, 47, 173-178.

Sade, D.S. (1967). Determinants of dominance in a group of free-ranging rhesus monkeys. In S. Altmann (Ed.), *Social communication among primates*, (p. 99-113). Chicago: University of Chicago Press.

Southwick, C.H., Beg, M.A. & Siddiqi, M.R. (1965). Rhesus monkeys in North India. In I. DeVore (Ed.), *Primate behavior: Field studies of monkeys and apes*, (p.111-159). New York: Holt, Rinehart and Winston, Inc.

Tannenbaum, P. (1997). Biobehavioral mechanisms of male rhesus monkey social integration. Unpublished doctoral dissertation, Emory University.

Tilford, B.L. (1982). Seasonal rank changes for adolescent and subadult natal males in a free-ranging group of rhesus monkeys. *International Journal of Primatology*, 3(4):483-490.

Wallen, K. & Tannenbaum, P. (1993). Hormonal modulation of sexual behaviore and affiliation in rhesus monkeys. In Carter, C.S., Lederhendler, I.I., Kirkpatrick, B. (Eds.), *The integrative neurobiology of affiliation*, (p. 101-118). Cambridge: The MIT Press.

Winston, J.S., Strange, B.A., O'Doherty, J. & Dolan, R.J. (2002). Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nature Neuroscience*, 5(3):277-283.

Van Hooff, J.A.R.A.M. & Van Schaik, C.P. (1994). Male bonds: Affiliative relationships among nonhuman primate males. *Behaviour*, 130(3/4):309-337.

Vessey, S.H. (1971). Free-ranging rhesus monkeys: Behavioural effects of removal, separation and reintroduction of group members. *Behaviour*, 40(3/4):216-227.

Vessey, S.H. (1984). Dominance among rhesus monkeys. *Political Psychology*, 5(4):623-628.