Bilateral Neurotoxic Amygdala Lesions in Rhesus Monkeys (*Macaca mulatta*): Consistent Pattern of Behavior Across Different Social Contexts

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Although the amygdala has been repeatedly implicated in normal primate social behavior, great variability exists in the specific social and nonsocial behavioral changes observed in nonhuman primates with bilateral amygdala lesions. One plausible explanation pertains to differences in social context. This study measured the social behavior of amygdala-lesioned and unoperated rhesus monkeys (*Macaca mulatta*) in 2 contexts. Monkeys interacted in 4-member social groups over 32 test days. They were previously assessed in pairs (N. J. Emery et al., 2001) and were therefore familiar with each other at the beginning of this study. Across the 2 contexts, amygdala lesions produced a highly consistent pattern of social behavior. Operated monkeys engaged in more affiliative social interactions with control partners than did controls. In the course of their interactions, amygdala-lesioned monkeys also displayed an earlier decrease in nervous and fearful personality qualities than did controls. The increased exploration and sexual behavior recorded for amygdala-lesioned monkeys in pairs was not found in the 4-member groups. The authors concluded that the amygdala contributes to social inhibition and that this function transcends various social contexts.

Keywords: amygdala, social behavior, nonhuman primate, affiliation, personality

Deficits in social behavior are prominent symptoms of many human psychiatric disorders (see the *Diagnostic and Statistical Manual of Mental Disorders,* 4th ed., text revision; American Psychiatric Association, 2000), but the neural substrates of such deficits remain largely unknown. Research with both human and nonhuman primates has demonstrated that the neural network responsible for normal social behavior, although still largely unidentified, is likely to be complex and widely distributed (Adolphs, 2001; Bachevalier & Meunier, 2005). One brain structure that has drawn particular interest is the amygdala, a collection of 13 sub-

nuclei buried deep within the temporal lobes. Neuroanatomical evidence indicates that the amygdala receives sensory information from all modalities and is heavily interconnected with other brain regions thought to participate in memory, emotional expression, and reward assessment (Amaral, Price, Pitkänen, Carmichael, & Aggleton, 1992; Barbas, 1995; Cavada, Company, Tejedor, Cruz-Rizzolo, & Reinoso-Suarez, 2000; Ghashghaei, Hilgetag, & Barbas, 2007; Suzuki, 1996; Suzuki & Amaral, 1994; Witter & Amaral, 1991).

Early studies of nonhuman primates with large lesions that included the amygdala demonstrated profound changes in behavior. In a laboratory setting, operated monkeys displayed hyperexploration, hypersexuality, and hypoemotionality; a spectrum dubbed the Klüver–Bucy Syndrome (Brown & Schäfer, 1888; Klüver & Bucy, 1939). Social interactions within pairs, in small groups, or in the wild were also profoundly disturbed. The most common alterations included decreased dominance, decreased initiation of affiliative interactions, and increased aggression from others, with the operated monkeys sometimes being ostracized from their social group (Dicks, Myers, & Kling, 1968; Kling, 1968; Kling & Cornell, 1971; Kling, Lancaster, & Benitone, 1970; Rosvold, Mirsky, & Pribram, 1954). It is interesting that observations in social environments typically did not detect the profound Klüver–Bucy characteristics (Kling, 1972; Kling & Brothers, 1992; Kling & Steklis, 1976).

These early studies provided an important framework for the design and interpretation of social behavior studies. First, behavioral impairments appear to be highly dependent upon species, gender, age at time of lesion, previous experience with social

partners, and especially the complexity of the social environment. Second, lesion specificity is important in concluding how individual neural regions contribute to social behavior. Third, the lack of precisely defined and quantifiable behavioral categories complicates the comparison of deficits across studies.

Recent advancements in selective lesioning procedures, as well as techniques to reliably classify and record nonhuman primate behavior, have rekindled interest in studying the neural network underlying nonhuman primate social behavior. Emery and colleagues (2001) studied the social behavior of adult male rhesus macaques (*Macaca mulatta*) with bilateral neurotoxic amygdala lesions. Social behavior was assessed while monkeys interacted in pairs. In two experiments, unoperated control and amygdala-lesioned monkeys interacted with a common group of age-matched male or female monkeys. In another context, each control or amygdala-lesioned monkey received one 20-min paired interaction with each of the other 11 experimental monkeys. A common theme developed from these three experiments. Relative to controls, and contrary to expectations, amygdala-lesioned monkeys initiated and received more positive or affiliative social behaviors (grooming, physical contact, sexual behavior, etc.), engaged in less aggression (contact aggression, chasing, etc.), and displayed fewer tension-related behaviors (tooth grinding, dominance displays, yawning, etc.). These differences were most prominent during the earliest encounters with unfamiliar partners. This was especially surprising because normal adult male rhesus monkeys typically fight or temporarily refrain from interacting with unfamiliar partners, presumably to ascertain each other's abilities, intentions, and threat level (Mendoza, 1993). In terms of nonsocial behavioral abnormalities, amygdala-lesioned monkeys also consistently displayed increases in locomotion, autoerotic behavior, and oral and tactile cage exploration.

Complementary findings have been provided by Málková and colleagues (2003), who studied social interactions between pairs of pigtail macaques (*Macaca nemestrina*) that received unilateral infusions of the GABA$_A$ antagonist, bicuculine methiodide. By blocking the inhibitory influence of GABA, this drug effectively disinhibits or hyperactivates the amygdala. Relative to untreated controls, monkeys who received the drug displayed less physical contact with social partners, a complete loss of play, and increased incidence of active avoidance by partners. Infused monkeys also received more aggression from untreated partners. Thus, the reports by both Emery et al. (2001) and Málková, Barrow, Lower, and Gale (2003) support the view that an active amygdala inhibits social interaction in rhesus monkeys.

An example of how social context may alter behavioral outcomes was reported by Machado and Bachevalier (2006). Rhesus macaques with bilateral neurotoxic amygdala lesions were evaluated in four-member social groups both pre- and postsurgery. The four-member groups consisted of a sham-operated rhesus macaque, a rhesus macaque with an amygdala lesion, one with a hippocampal lesion, and one with an orbital frontal cortex lesion. In this case, amygdala-lesioned macaques did not show the social disinhibition, hypersexuality, or environmental exploration demonstrated by Emery and colleagues (2001). In the present study, we sought to address the issue of how social context might modify the social behavior of monkeys with amygdala lesions. Observations reported here for four-member groups were made on the same monkeys that Emery et al. (2001) studied in two-member groups.

On the basis of that study, we predicted that amygdala-lesioned monkeys would continue to produce greater frequencies and durations of affiliative social behaviors; therefore, they would potentially be preferred as social partners.

Method

Materials

All experimental procedures were carried out in accordance with the National Institute of Health Guide for the Care and Use of Laboratory Animals and developed through consultation with the veterinary staff at the California National Primate Research Center (CNPRC). All protocols were also approved by the University of California, Davis, Institutional Animal Care and Use Committee.

Subjects and Housing

Twelve adult male rhesus monkeys (*Macaca mulatta*) were randomly assigned either to receive bilateral ibotenic acid lesions of the amygdala (A-IBO; $n = 6$) or to act as unoperated controls (CON; $n = 6$). Each was born and raised at the CNPRC in one of 12 half-acre enclosures containing approximately 70 monkeys each. The monkeys were chosen after trained behavioral observers watched each monkey for two 30-min sessions over a 2-week period. The observers ascertained that all monkeys displayed a moderate level of social behavior, and no monkeys displayed unusual or inappropriate aggressive behavior or motor stereotypies. All selected monkeys were of mid-dominance rank. Each monkey was raised in a different corral from all other monkeys but had previously encountered the other experimental monkeys during one 20-min interaction in a round-robin dyad study (Emery et al., 2001). Before the present experiment, these monkeys also participated in studies of emotional reactivity to potentially dangerous objects (Mason, Capitanio, Machado, Mendoza, & Amaral, 2006), social behavior in three paired settings (Emery et al., 2001), resting hormonal stress response (Emery et al., 1998), as well as emotional reactivity to video presentations of social stimuli. Approximately 4 months intervened between the end of the paired social behavior experiments (Emery et al., 2001) and the beginning of the present experiment, during which no other behavioral testing took place.

Rhesus monkeys were relocated to indoor housing at the CNPRC when they were between 5 and 8 years old. The present study did not begin until the monkeys ranged in age from 7 to 10 years and weighed 10–15 kg. For complete housing details, refer to Emery et al. (2001). Briefly stated, monkeys were housed in individual cages (66 cm width × 61 cm length × 81 cm height) and allowed visual access to other male macaques participating in a separate study. The housing room was maintained on a 12-hr light/dark cycle. All monkeys were maintained on a diet of fresh fruit, vegetables, and monkey chow (Lab Diet 5047, PMI Nutrition International Inc., Brentwood, MO), with water available ad libitum.

Neuroimaging, Surgeries, and Histological Lesion Assessment

Neuroimaging, surgical, and histological lesion assessment procedures have been reported in detail previously (Emery et al.,

2001). Briefly, each rhesus monkey assigned to the A-IBO group underwent an initial aseptic surgical procedure. Monkeys were initially sedated with ketamine hydrochloride (8 mg/kg), had their heads shaved, were intubated with an endotracheal cannula, and brought to a surgical level of anesthesia using isoflurane (1–2%). The monkey's vital signs were monitored by CNPRC veterinarians throughout the procedure. After a midline scalp incision and reflection of the underlying fascia, two small glass beads filled with copper sulfate were cemented to the skull at known stereotaxic coordinates. These beads were visible on magnetic resonance images (MRIs) and were used as landmarks to create individualized stereotaxic coordinates for ibotenic acid injections into the amygdala (Saunders, Aigner, & Frank, 1990).

For the MRI scans, A-IBO monkeys were anesthetized with Telazol (10 mg/kg) and placed in an MRI-compatible stereotaxic apparatus (Crist Instruments Co., Inc., Damascus, MD). A Phillips 1.5T Gyroscan magnet was used for imaging, with 3.0-mm coronal and 3.0-mm sagittal sections taken with a T1-weighted Inversion Recovery pulse sequence; repetition time (TR) = 2084, inversion time (TI) = 708, echo time (TE) = 20, number of excitations (NEX) = 2, field of view (FOV) = 18 cm, matrix size = 154 × 256. Once acquired, these images were overlaid with a 1 mm × 1 mm square matrix, and the stereotaxic locations of intended ibotenic acid injections throughout the amygdala were determined.

For the neurotoxic lesion surgeries, A-IBO monkeys were anesthetized and monitored by CNPRC veterinarians as described earlier for the bead implantation surgeries. Five A-IBO monkeys underwent a two-stage lesion of the amygdala, with each stage separated by 1 week. One monkey (Case no. 26085) underwent a single-stage bilateral lesion surgery, and all monkeys recovered similarly. A midline incision was made, followed by reflection of the periosteum and temporalis muscles. Craniotomies were made over the amygdala. The dorsoventral location of the amygdala was verified electrophysiologically. Once the dorsal and ventral borders of the amygdala were verified, the electrode was withdrawn and a 10-μl Hamilton syringe (26-gauge beveled needle) was lowered to the appropriate coordinates. At each injection site (20–24 per hemisphere), 0.5–1.5 μl ibotenic acid (Biosearch Technologies Inc., 10 mg/ml in 0.1 M phosphate-buffered saline) was injected at a rate of 0.2 μl/min. The single-stage bilateral lesion was carried out with two identical Hamilton syringes to simultaneously inject ibotenic acid into each amygdala. After all injections were completed, the dura was closed, the craniotomy was filled with Gelfoam (Pharmacia & Upjohn, Peapack, NJ), and the temporalis muscles were replaced and sutured. The wound was then closed in layers. The monkey was removed from anesthesia and monitored continuously for 24 hr by veterinary staff. All A-IBO monkeys received prophylactic doses of the antibiotics Cefazolan (20 mg/kg tid) and Baytril (BVP; 5 mg/kg sid) and the analgesic Oxymorphone (0.15 mg/kg tid) as needed and were allowed to recover for 4 weeks before any behavioral testing commenced.

Monkeys assigned to the CON group did not receive any invasive surgical procedures (bead implantation or neurotoxin injections), nor did they receive MRI scans. However, these monkeys were sedated as described earlier for the bead implantation surgeries, were brought to the surgical suite, had their heads shaved, were intubated, and were brought to a surgical level of anesthesia with isoflurane gas. These monkeys remained sedated for the average length of the neurotoxic lesion surgeries experienced by the A-IBO monkeys. After recovery, the CON monkeys were returned to their home cages.

At the completion of all behavioral testing, the A-IBO monkeys were immobilized with ketamine hydrochloride (8 mg/kg), deeply anesthetized with Nembutal (50–100 mg/kg iv) and perfused intracardially. Perfusates were 4% paraformaldehyde in 0.1 M sodium phosphate buffer (pH 7.2 at 40°C), 250 ml/min for 10 min and 100 ml/min for 50 min. The brain was then blocked stereotaxically, removed from the skull, and postfixed in the same 4% paraformaldehyde solution for 6 hr. The brain was then cryoprotected in a solution containing 10% glycerol and 2% dimethylsulfoxide (DMSO) overnight, followed by submersion in a solution containing 20% glycerol and 2% DMSO for 3 days. Brains were frozen through an isopentane method (Rosene, Roy, & Davis, 1986) and stored at −70°C until sectioned. Frozen sections were cut on a sliding microtome in the coronal plane at a thickness of 30 μm. The sections were then placed in a cryoprotectant tissue-collecting solution (30% ethylene glycol, 25% glycerin in 0.005 M sodium phosphate buffer). The sections were stored at −20°C until every eighth section was mounted onto glass slides. These sections were subsequently stained for Nissl with 0.25% thionin solution.

The volumes of the entire amygdala, as well as the lateral, basal, accessory basal, and central nuclei were measured in the left hemisphere of 5 normal-age and weight-matched rhesus monkeys (kindly provided by Peter Rapp, Mount Sinai School of Medicine, NY). For each of these control cases and the 6 A-IBO monkeys, the amygdala and the four amygdaloid nuclei noted earlier were drawn on a template rhesus monkey atlas using a Leica stereomicroscope and camera lucida (Wetzlar, Germany). Drawings were digitized with a Summasketch II digitizing tablet connected to a PC running Sigma Scan software. We computed the volume of the remaining amygdaloid tissue for each case by multiplying surface area by the distance between each coronal section (240 μm for the A-IBO monkeys and 400 μm for the controls). The volume of remaining amygdala and the four subnuclei were then compared with the normal volume of the amygdala and these subnuclei to calculate the percentage of the total volume damaged in the left and right hemispheres, as well as the arithmetic mean across hemispheres. Similar percent unintended damage measurements were made for the subjacent entorhinal cortex.

Apparatus

Behavioral measures were collected while monkeys interacted in a large indoor enclosure (3.05 m × 2.13 m × 1.83 m; Figure 1), constructed from galvanized steel pipe and chain link fencing. The floor was constructed from heavy-gauge (2.5 cm × 2.5 cm) galvanized steel mesh, which was suspended 15 cm above the concrete laboratory floor. A chain link door (0.81 m × 1.89 m) was located at the front of the cage, 0.81 m from the right side. The monkeys entered the enclosure through a rectangular chute (1.2 m × 0.45 m × 0.39 m) attached to the front of the cage. This chute was constructed from steel mesh (2.5 cm × 2.5 cm), and the bottom was 54 cm above the floor of the enclosure. Monkeys entered the main enclosure through a door (30 cm × 45 cm) at the far left end of the chute, which the experimenter could raise and lower using a pulley system. Three perches were located inside the enclosure, each constructed from PVC-coated galvanized steel
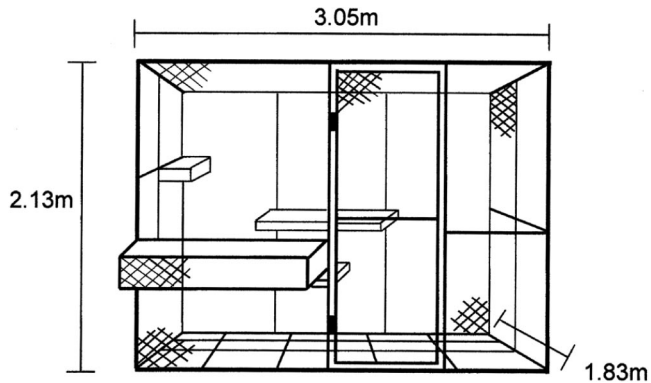
Figure 1. Diagram with dimensions of the testing enclosure where all social interactions took place. The cage was located indoors and raised 15 cm from the concrete floor. A 3 × 5 square matrix was painted on the floor for the collection of inter-animal distance data.

pipes (2.5-cm diameter). The perches were 0.9 m, 1.5 m, and 1.29 m in length and were positioned 0.425 m, 0.8 m, and 1.08 m respectively above the mesh floor, as shown in Figure 1. Before the present experiment began, all monkeys were trained to enter and exit the chute and main enclosure to reduce the intersession interval and minimize stress for each monkey that could result from handling procedures.

Experimental Design

The 12 rhesus monkeys were randomly divided into three, four-member social groups, with the only constraint being that each group consisted of two A-IBO and two CON monkeys. Each group was allowed to freely interact in the testing enclosure for 2 hr on 32 test days (4 days/week: Tuesday–Friday). To control for circadian effects on social behavior, we conducted observations during three sessions throughout the day (0805–1010, 1045–1250, and 1315–1520) and testing time was balanced for all groups.

At the beginning of each interaction session, the experimenter released the four members of a group into the testing enclosure in reverse dominance order (lowest ranked monkey entered first) on the basis of the experimenter's experience with the monkeys. The experimenter remained in the room during the entire interaction session and sat behind a rolling computer cart approximately 2 m from the front left corner of the interaction cage. The experimenter conducted behavioral assessments during the 2-hr interaction session (see Figure 2).

Social and Nonsocial Behavioral Assessments

With The Observer software package (Noldus, Trienes, Hendriksen, Jansen, & Jansen, 2000) and a desktop PC, the experimenter used ad lib and focal sampling techniques (Altmann, 1974) to record social and nonsocial behaviors during eight 10-min collection periods. The software also allowed the experimenter to record the specific rhesus monkey that initiated or received a social behavior, as well as specify the identity of its social partner. Table 1 describes all behaviors that the experimenter could record during these eight collection periods. As shown in Figure 2, the data collection began with two ad lib samplings, a technique that is

particularly useful for collecting behavioral data during periods of extremely high or low activity (i.e., the beginning and ending of an interaction session). With this technique, the observer continuously scans the enclosure in a clockwise motion and records behaviors produced by all subjects as soon as they are seen. After the two ad lib samplings, four focal samples were collected. This technique requires the observer to record the behavior of one "focal" subject per collection period, along with the identity of all interaction partners. Only behaviors that the focal subject produces or receives are recorded. The focal sampling technique is ideal for recording behavior in social groups once activity levels have stabilized. Each member of the group served as the focal subject once during these four collection periods, and the temporal sequence of focal observations across monkeys was balanced by Latin square. After the four focal samplings, two additional ad lib samplings were conducted as described earlier.

Inter-Animal Distance

As shown in Figure 2, after each ad lib or focal behavior collection period, the experimenter recorded the spatial location of all monkeys in the group on paper forms. Fifteen squares were painted on the cage floor in a 3 × 5 matrix (see Figure 1) to allow for quick and reliable spatial localization in the horizontal plane. The three rows were designated as A, B, and C (back to front, respectively), and the five columns were designated as 1–5 (left to right, respectively). Location of all group members was noted four times during each 1-min sampling interval, with notation based on the specific square where a monkey's head was located. The letter and number designation of the square (e.g., A3) was recorded, and the monkey's position in the vertical plane was noted as floor, perch, wall, or ceiling. These spatial coordinates were then transformed into linear distances (in meters) between individuals with in-house software programmed in Q-Basic to serve as an indirect measure of sociability.

Attitude Ratings

At the end of every 2-hr social interaction session (see Figure 2), the experimenter subjectively rated each individual monkey on seven adjectives describing various aspects of macaque social and nonsocial personality or attitude, using a 5-point Likert-type scale (Capitanio, 1999; Stevenson-Hinde & Zunz, 1980). Table 2 describes each of these attitude assessment categories. Definitions for the rating points are as follows: 1 = *definition not at all descriptive*, 2 = *definition slightly descriptive*, 3 = *definition moderately descriptive*, 4 = *definition mostly descriptive*, and 5 = *definition completely descriptive*. All ratings were made solely on the basis of the interactions observed on a given day. Observers were explicitly instructed not to use previous knowledge about the monkeys to influence how each session was scored.

Data Analysis

Data from the three measures above were divided into four 8-test-day blocks to capture changes in the groups' behavior over time. The frequency and duration of discrete social and nonsocial behaviors collected during ad lib and focal samplings were summed within each block, whereas the inter-animal
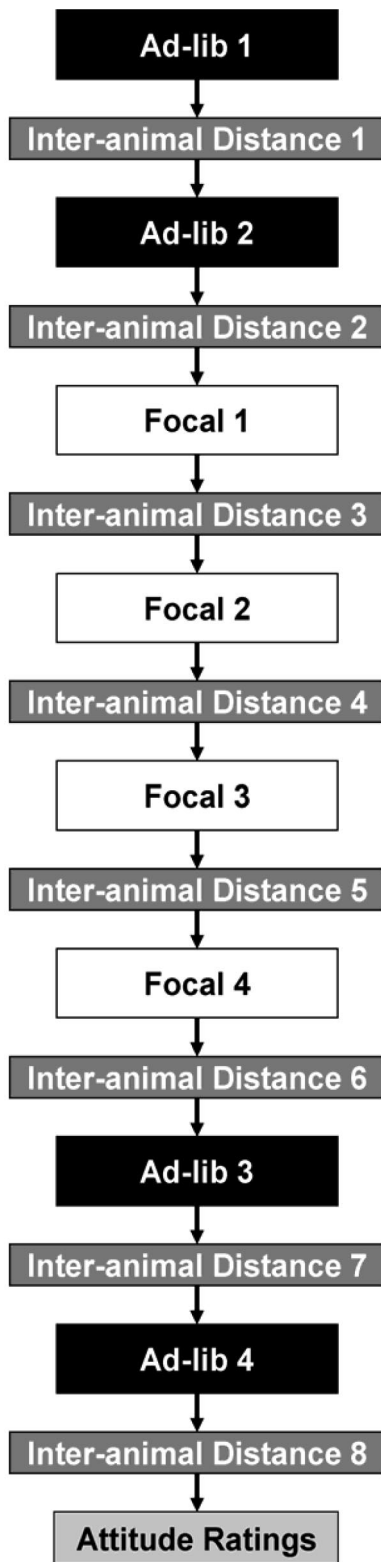
Figure 2. Schematic representation of the structure of each testing session. A total of four ad lib and four focal sampling sessions were used to capture social and nonsocial behaviors. Eight sampling sessions were made to measure mean inter-animal distance. The final measurement each day captured aspects of each monkey's attitude or personality.

distance and attitude assessment data were averaged within each block. Attitude rating data were normally distributed for both groups, as determined with the Shapiro–Wilk test and by inspecting the skewness and kurtosis ratios. However, these normality assessments indicated that the inter-animal distance data set and a majority of behavioral frequency and duration measures were not normally distributed. These data were therefore $\log_{10}(x + 1)$ transformed before statistical analyses were conducted (Sokal & Rohlf, 1995), but nontransformed values were used for illustration purposes. We analyzed all data using general linear model analyses of variance (ANOVAs), with group (2) as a between-subjects factor and block (4) as a within-subjects factor with repeated measures using the SPSS 12.0 statistical analyses package. For analysis of inter-animal distances and behavioral frequencies and durations, we also included partner (2) as a second within-subjects factor to differentiate between interactions with lesioned or control monkeys. A Huynh–Feldt correction was used to adjust the degrees of freedom if group variances did not remain equal across the four testing blocks. Alpha was set at $p < .05$. However, given the low number of monkeys in each experimental group and the variation of lesion extent in Group A-IBO, we occasionally report results for which p values fall above this threshold. Results are identified as marginally significant if their p value is greater than .05 but less than .08.

Because main effects of block do not provide any specific information regarding amygdala function, these effects were omitted from the Results section. Post hoc examinations of Group × Block interactions or Group × Partner interactions were accomplished with separate independent-samples t tests for each block or partner, respectively. Partner × Block interactions and changes in behavior between blocks were examined using paired-sample t tests. If any variable under post hoc evaluation had a group mean equal to zero, nonparametric versions of the preceding tests (such as the Wilcoxon signed-ranks test and Mann–Whitney U test) were used.

Finally, for A-IBO monkeys, Pearson product–moment correlation matrices were generated to determine whether the extent of intended damage to the amygdala (as a whole or as separate subnuclei) or unintended damage to the entorhinal cortex significantly influenced any behavioral parameters measured.

Interobserver Reliability Assessments

The two behavioral observers (Christopher J. Machado & Nathan J. Emery) for this study had extensive previous experience observing adult male and female rhesus macaques, collecting inter-animal distance data, and rating attitude or personality qualities. These observers were aware of the lesion status of the macaques in the present study and had observed them previously as they interacted in pairs (Emery et al., 2001) but never in four-member groups. Therefore, before the present study began, the two observers were tested for interobserver reliability on all behavioral measures described earlier using nonexperimental adult male rhesus monkeys. The observers simultaneously recorded the behavior of these monkeys using the ad lib sampling technique (33 trials total), and the mean percent agreement across these trials was $89.5 \pm 1\%$ (range = 74.2–100%). The observers also simultaneously recorded the

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Table 1
Social and Nonsocial Behavior Ethogram

Behavior category and specific behavior	Brief definition
Affiliative social behaviors	
Approach[b]	Movement to within arm's reach of partner for more than 3 s
Proximity[a,b]	Remaining within arm's reach for more than 3 s
Contact[a,b]	Direct physical contact with partner for more than 3 s
Groom[a,b]	Picking through or licking partner's fur for more than 3 s
Play[b]	Rough-and-tumble play or grappling, with play face
Mount[b]	Hands on partner's hips, double foot clasp and thrusting
Incomplete mount[b]	Missing hands on partner's hip, double foot clasp or thrusting
Anogenital explore[b]	Sniffing, touching, or licking anogenital area of partner
Grunt vocalization	Soft, bubbly, guttural sound, made in affiliative situations
Affiliative social signals	
Lipsmack[b]	Rhythmic lip movements, often with pursed lips
Groom solicitation[b]	Rigid posture with presentation of body part for grooming
Mount solicitation[b]	Stiff four-point stance, rump oriented toward partner with tail up
Dominance-related behaviors	
Cage aggression	Rapid shaking of enclosure walls or perch, body slams against walls
Crooktail	Animal struts with tail held up in a "?" shape
Aggressive behaviors	
Chase[b]	Hostile, rapid movement after another animal
Aggression[b]	Physical contact with intent to harm: grabbing, hitting, biting or slapping
Threat[b]	Two or more of open-mouthed stare, head bobbing, ear flaps, and lunges
Displace[b]	Take over another animal's position in the enclosure for more than 3 s
Bark vocalization	High-intensity, low-pitch, guttural bark vocalization
Self-directed behaviors	
Self-bite	
Self-clasp	
Self-groom	
Self-sex	
Urine drinking	
Anxious behaviors	
Tooth grinding	Audible rubbing of lower premolars on upper canines
Scratch	Crude, rapid, hand movements, using fingers to scratch
Fear grimace[b]	Large grin, exposing teeth
Yawn	Fully open mouth, with lips fully retracted and teeth showing
Motor stereotypy	Abnormal and repetitive motor behaviors: bucking, bouncing, circling, etc.
Scream vocalization	High-pitched, high-intensity vocalization or alarm call
Exploratory behaviors	
Tactile exploration	Use of hands to explore the physical environment
Oral exploration	Use of the mouth to explore the physical environment
Avoidant/solitary behaviors	
Withdraw[b]	Animal moves out of arm's reach of another animal for more than 3 s
Nonsocial[a,b]	Animal remains out of arm's reach for more than 3 s
Other behaviors	
Extended social[a,b]	Describes a mount, chase, aggressive episode or play bout lasting more than 3 s
Coo vocalization	High-pitched, soft "oooo" vocalization
Walk by[b]	Movement into and out of proximity in less than 3 s

Note. List of all social and nonsocial behaviors recorded during live behavioral observations. All behaviors were analyzed for frequency (total number of occurrences). Self-bite = hair-plucking, self-biting, or other self-mutilation; self-clasp = abnormal grasping of the torso; self-groom = picking or licking at one's own fur or nonfur body part; self-sex = manual or oral manipulation of one's own genitals; urine drinking = drinking of one's own urine from penis; hand, or ground.
[a] Behavior for which total duration was also measured during focal observations. [b] Behavior for which a specific partner was recorded.

behavior of these macaques using the focal sampling technique (9 trials total), and the mean percent agreement was 94.8 ± 1.6% (range = 83.1–100%). The two observers were also tested until their interobserver reliability for collecting inter-animal distance data was greater than 90% agreement and until their interobserver reliability for making attitude assessment ratings was greater than 85% agreement for all adjectives. To further counteract any biases, the observers were pseudorandomly as-

Table 2
Attitude Assessment Ethogram

Category and adjective	Brief definition
Sociable	
Confident	Monkey freely moves within the cage. Movements are fluid, not furtive, and the monkey may strut with a crooktail posture.
Affiliative	Monkey actively seeks to be near and/or in friendly contact with another monkey or facilitates contact by the other monkey.
Interaction inhibiting	
Avoidant	Monkey actively refrains from engaging in positive or negative social interactions.
Aggressive	Monkey attempts to, or actually causes, physical harm to several other group members.
Nervous	Monkey's behavior is characterized by fidgeting, picking at the cage or perches, motor stereotypies, fear grimacing, yawing, or furtive movements.
Fearful	Monkey is anxious in the presence of others, readily fear grimaces, and appears overly vigilant to the movements of others.
Other	
Active	Monkey moves around the enclosure excessively and remains stationary only for short periods of time.

signed to observe different social groups on different days, and the total number of observations per group for the two observers was counterbalanced.

Results

Lesion Extents

A detailed description of each A-IBO monkey's lesion has been provided by Emery et al. (2001). However, a brief description of this group as a whole is given here and a summary of the histological lesion assessment for each monkey is provided in Table 3. Ibotenic acid injections were intended to damage the entire amygdaloid complex but primarily targeted the lateral, basal, and accessory basal nuclei, as these nuclei have the most substantial direct connections with the neocortex. For the most part, the lesions across the A-IBO group were quite successful in achieving their goal, with average bilateral damage to the amygdala as a whole ranging from 66.5% to 84.0%. Damage to the lateral and basal nuclei was even more complete, ranging from 84.2% to 99.3% in the lateral nucleus bilaterally and from 82.2% to 98.3% in the basal nucleus bilaterally. Average bilateral damage was slightly less in the accessory basal nucleus, ranging from 55.7% to 93.8%. The central nucleus was damaged extensively but less than the deep nuclei (range = 55.8%–83.4%). The more superficial

areas of the amygdala, such as the medial nucleus and the peri-amygdaloid cortex, were typically spared. Nevertheless, it is likely that these superficial nuclei were heavily denervated, as a majority of their input arises from the lateral, basal, and accessory basal nuclei (Pitkänen & Amaral, 1998).

Unintended damage to adjacent areas was mild in most cases. Five of six cases showed minor cell loss in the rostral hippocampus, but more caudal portions of this structure were completely undamaged. All monkeys received minor to extensive cell loss in the piriform cortex and ventral claustrum, and all cases received extensive damage to the rostral field of the entorhinal cortex that is located ventral to the amygdala.

Inter-Animal Distance

Inter-animal distances within each social group were averaged into four consecutive 8-day blocks to investigate changes over time depending on lesion condition. Between-groups comparisons were made with partner (amygdala-lesioned or control) and block as within-subjects factors. Only the Group × Partner interaction attained significance, $F(1, 10) = 9.015$; $p = .013$. Post hoc examination revealed that mean distance between CON and A-IBO monkeys was significantly lower than the distance between two CON monkeys, $t = 2.20$, $p = .05$ (see Figure 3). Distance

Table 3
Lesion Extents for Monkeys With Bilateral Ibotenic Acid Amygdala Lesions

Case	Amygdala			Lateral nucleus			Basal nucleus			Accessory basal nucleus			Central nucleus			Entorhinal cortex		
	L	R	Avg	L	R	Avg	L	R	Avg	L	R	Avg	L	R	Avg	L	R	Avg
24349	61.2	89.7	75.4	79.1	100.0	89.5	77.9	100.0	88.9	49.6	100.0	74.8	46.1	68.0	57.1	49.3	40.7	45.0
25468	75.6	87.7	81.7	93.2	99.5	96.3	95.2	100.0	97.6	81.0	99.6	90.3	59.5	84.4	72.0	83.6	83.5	83.6
25571	95.5	70.4	82.9	100.0	89.2	94.6	100.0	90.3	95.2	100.0	70.2	85.1	90.9	75.9	83.4	49.9	78.0	64.0
25627	71.9	80.3	76.1	98.5	92.5	95.5	97.2	96.8	97.0	58.3	89.1	73.7	47.9	63.7	55.8	57.3	66.6	62.0
25942	73.6	59.3	66.5	94.5	73.9	84.2	94.4	70.0	82.2	66.0	45.5	55.7	60.2	61.3	60.8	60.2	77.9	69.1
26085	83.3	84.7	84.0	98.5	100.0	99.3	97.2	99.4	98.3	93.0	94.6	93.8	59.6	65.4	62.5	33.1	57.7	45.4
Mean	76.8	78.7	77.8	94.0	92.5	93.2	93.6	92.7	93.2	74.6	83.2	78.9	60.7	69.8	65.2	55.6	67.4	61.5

Note. Data are the percentage of normal volume damaged within the amygdala as a whole, the lateral, basal, accessory basal, and central nuclei, and the entorhinal cortex. L = percentage of damage to the left hemisphere; R = percentage of damage to the right hemisphere; Avg = average of L and R.
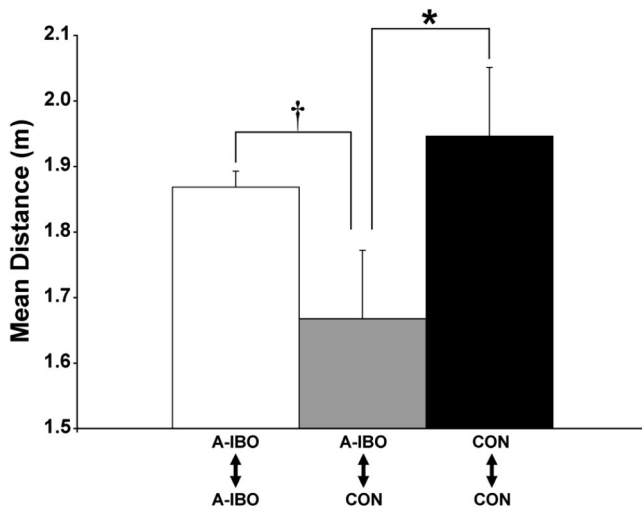
Figure 3. Mean inter-animal distance for each of the three possible subject pairs within a social group. Vertical bars indicate the standard errors of the mean. $^{\dagger}p = .07$. $^{*}p \leq .05$.

between two A-IBO monkeys was also typically greater than CON–A-IBO pairs, but this difference was only marginally significant, $t = 2.31$, $p = .07$. These results indicate that control monkeys tended to be closer to amygdala-lesioned monkeys than to other controls, whereas amygdala-lesioned monkeys were typically closer to controls than to other lesioned monkeys.

Total Frequency and Duration of Behaviors

There were several differences between the groups related to affiliative social interactions, regardless of block or partner (see Figure 4). A-IBO macaques approached other group mates to within arm's reach significantly more often than CON macaques, $F(1, 10) = 5.231$, $p < .05$. The same pattern emerged for the initiation of physical contact with others, but the difference between groups was only marginally significant, $F(1, 10) = 3.685$, $p = .08$. If the frequencies of all affiliative social behaviors (e.g., approach, contact, groom, play, mount, incomplete mount, anogenital explore, and grunt vocalizations; see Table 1) were summed into a general category, A-IBO monkeys again initiated significantly more than CON monkeys, $F(1, 10) = 4.826$, $p = .05$. Consistent with these examples of heightened social interaction, A-IBO monkeys also initiated and received more withdrawals from arm's reach by other group mates than did CON monkeys: For withdraw initiate, $F(1, 10) = 7.132$, $p < .05$; for withdraw receive, $F(1, 10) = 11.698$, $p < .01$.

Far more differences between the groups emerged when data were analyzed with regard to the type of partner involved (i.e., Group $\times$ Partner interactions). A-IBO macaques again appeared to engage in affiliative social interactions more than CON macaques and predominantly directed those interactions toward control partners rather than toward amygdala-lesioned partners (see Figure 5). Specifically, A-IBO monkeys initiated more walk-bys, $F(1, 10) = 11.434$, $p < .01$ (post hoc $t = -2.69$, $p < .05$); more approaches to within arm's reach, $F(1, 10) = 4.446$, $p = .06$ (post hoc $t =$

-3.438, $p < .01$); more groom solicitations, $F(1, 10) = 5.794$, $p < .05$ (post hoc $z = -3.083$, $p < .01$); more grooming, $F(1, 10) = 7.635$, $p < .05$ (post hoc $z = -1.892$, $p = .06$); and more withdrawals from arm's reach, $F(1, 10) = 12.037$, $p < .01$ (post hoc $t = -4.801$, $p = .001$), with control partners than did CON monkeys (see Figure 5, left panels). As shown in Figure 6, the same pattern also held for the duration of physical contact, $F(1, 10) = 7.502$, $p < .05$ (post hoc $z = -2.286$, $p < .05$); and grooming, $F(1, 10) = 4.786$, $p = .05$ (post hoc $z = -1.892$, $p = .06$). For each of these frequency and duration measures, A-IBO and CON monkeys did not differ in their interactions with amygdala-lesioned partners (see Figure 6, right panels; all $ps > .10$).

A similar pattern of results was also detected for affiliative social behaviors received (see Figure 7). Specifically, A-IBO monkeys received more walk-bys, $F(1, 10) = 6.86$, $p < .05$ (post hoc $t = -2.655$, $p < .05$); more groom solicitations, $F(1, 10) = 4.213$, $p = .07$ (post hoc $z = -2.69$, $p < .01$); and more withdrawals from arm's reach, $F(1, 10) = 6.86$, $p < .05$ (post hoc $t = -4.762$, $p = .001$), from control partners than did CON monkeys. A-IBO monkeys also received a greater duration of proximity from control partners than did CON monkeys, $F(1, 10) = 6.894$, $p < .05$ (post hoc $t = -3.023$, $p < .05$). Again, for each of these frequency and duration measures, interactions with amygdala-lesioned partners did not differ significantly between the groups ($ps > .10$).

The incidence of aggressive behavior was very low within each social group. However, as shown in Figure 8, the frequency of physical forms of initiated and received aggression (e.g., grabbing, hitting, biting, or slapping) demonstrated significant Group $\times$
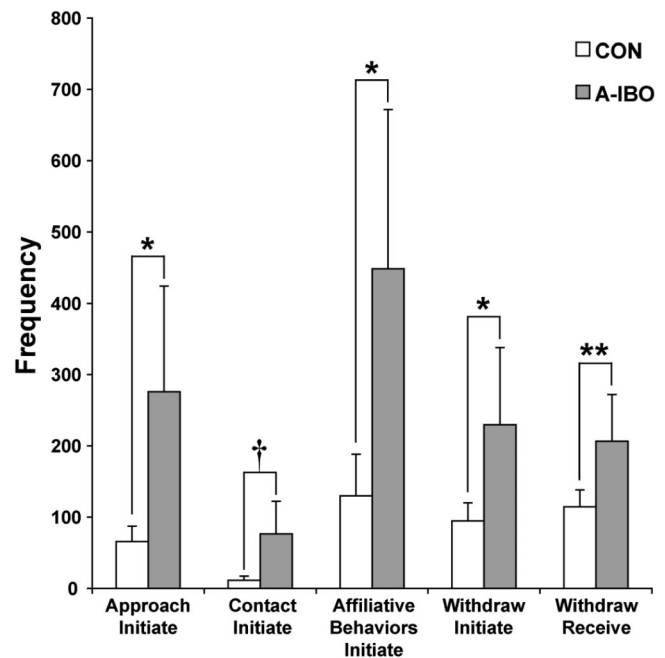

Figure 4. Total frequency of approach initiate, contact initiate, affiliative behaviors initiate, withdraw initiate and withdraw receive (left to right, respectively) for monkeys in the control (CON) and amygdala-lesioned (A-IBO) groups, regardless of partner or testing block. Vertical bars indicate the standard errors of the mean. $^{\dagger}p = .08$. $^{*}p \leq .05$. $^{**}p \leq .01$.
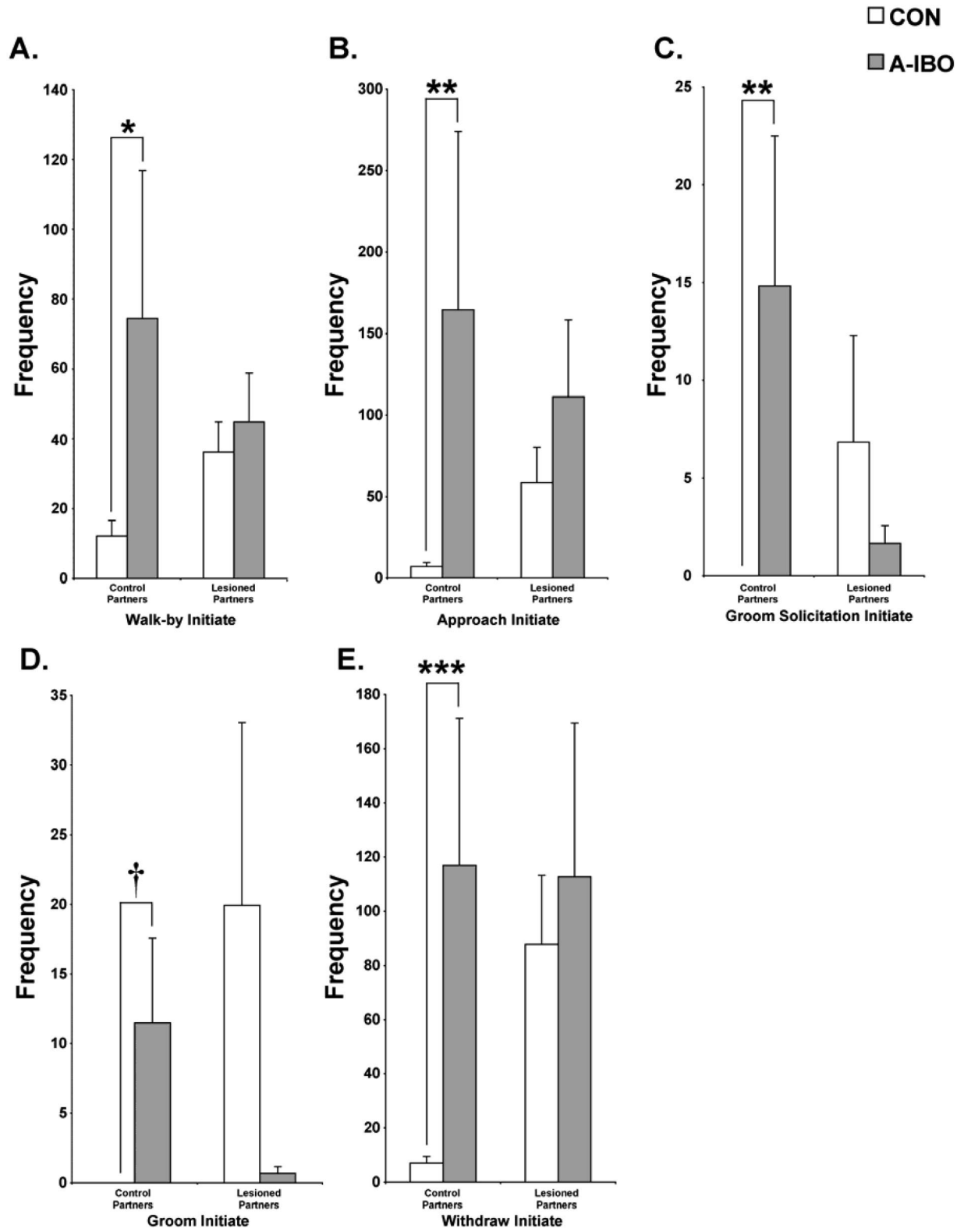
Figure 5. Total frequency across all testing blocks of walk-by initiate (A), approach initiate (B), groom solicitation initiate (C), groom initiate (D) and withdraw initiate (E) with both control and amygdala-lesioned partners for monkeys in the control (CON) and amygdala-lesioned (A-IBO) groups. Vertical bars indicate the standard errors of the mean. $^{\dagger}p = .06$. $^{*}p \leq .05$. $^{**}p \leq .01$.
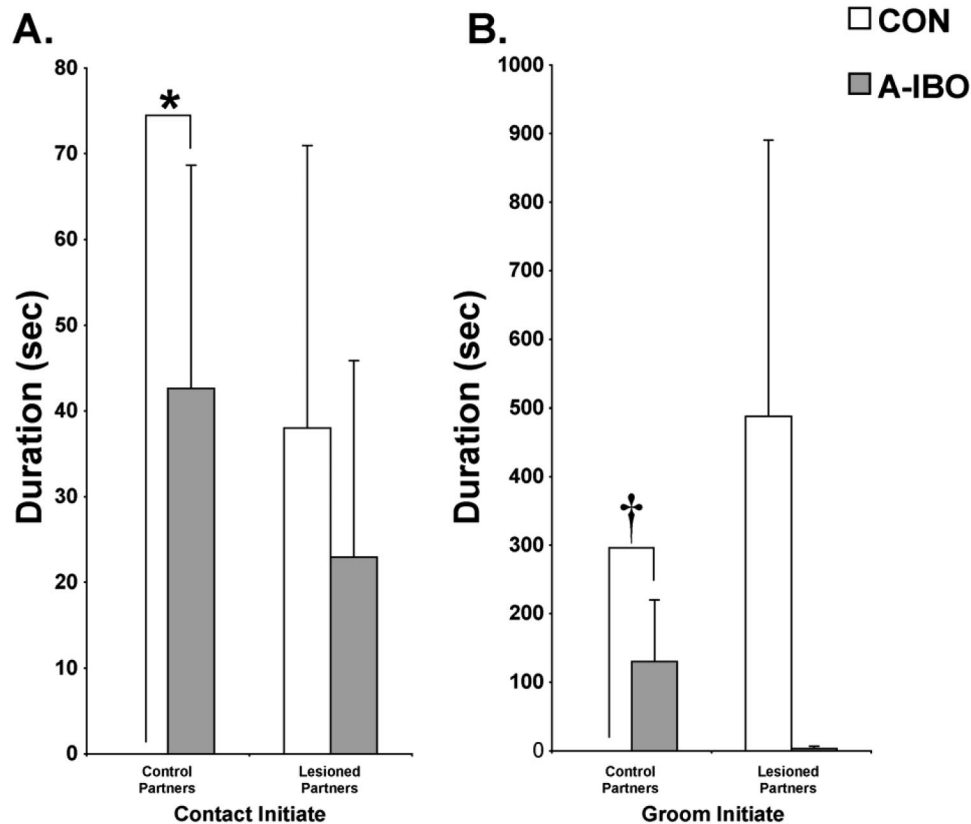
Figure 6. Total duration across all testing blocks of contact initiate (A) and groom initiate (B) with both control and amygdala-lesioned partners for monkeys in the control (CON) and amygdala-lesioned (A-IBO) groups. Vertical bars indicate the standard errors of the mean. $^{†}p = .06.$ $^{*}p ≤ .05.$

Partner interactions, $F(1, 10) = 9.753$, $p = .01$; and $F(1, 10) = 8.55$, $p < .05$, respectively. Post hoc analyses indicated that A-IBO monkeys initiated more aggression toward amygdala-lesioned partners than did CON monkeys, $t = -2.575$, $p < .05$. Likewise, A-IBO monkeys received more aggression from amygdala-lesioned partners than did CON monkeys, $t = 2.076$, $p = .07$. Aggressive interactions with control monkeys were low and did not differ appreciably between the groups (both $ps > .10$).

Finally, there were no appreciable differences between the groups in terms of dominance-related behaviors, self-directed behaviors, anxious behaviors, or exploratory behaviors, regardless of whether block or partner was included in the analysis.

Attitude Ratings

Table 4 provides the mean ratings for the two general attitude assessment categories (sociable and interaction inhibiting), as well as the individual adjectives within each of these general categories. Qualities such as *confident* and *affiliative* were placed into the sociable category because they tend to promote strong, positive social relations between male macaques. By contrast, qualities such as *avoidant*, *aggressive*, *nervous*, and *fearful* inhibit strong positive social interactions and therefore were placed into the interaction-inhibiting category. The adjective *active* does not fit into either of these general categories because it refers more to

how subjects interact with their environment than with their group mates. Therefore, this adjective was analyzed separately.

The two general categories (sociable and interaction-inhibiting) and the adjective *active* were first analyzed over the four testing blocks. For active and the sociable category, there were no significant main effects of group, or Group × Block interactions ($ps > .10$), indicating that amygdala lesions do not appreciably affect such qualities. However, for interaction-inhibiting qualities, a significant Group × Block interaction was detected, $F(3, 30) = 2.865$, $p = .05$, but the main effect of group was not significant. Post hoc analyses of this interaction indicated that, although the groups did not differ in interaction-inhibiting ratings during any block, A-IBO monkeys showed a significant decline in ratings between Blocks 1 and 2, $t = 3.087$, $p = .05$, but ratings for CON monkeys remained unchanged during this time (see Figure 9). By contrast, CON monkeys showed decreased interaction-inhibiting ratings between Blocks 2 and 3 to levels commensurate with those of A-IBO monkeys, but this change was marginally significant, $t = 2.917$, $p = .07$.

To further investigate this general difference between the groups, we conducted similar analyses with the individual adjectives that make up the interaction-inhibiting category (fearful, nervous, avoidant, and aggressive). None of these individual adjectives displayed any significant main effects of Group ($ps > .10$), but significant Group × Block interactions were detected for
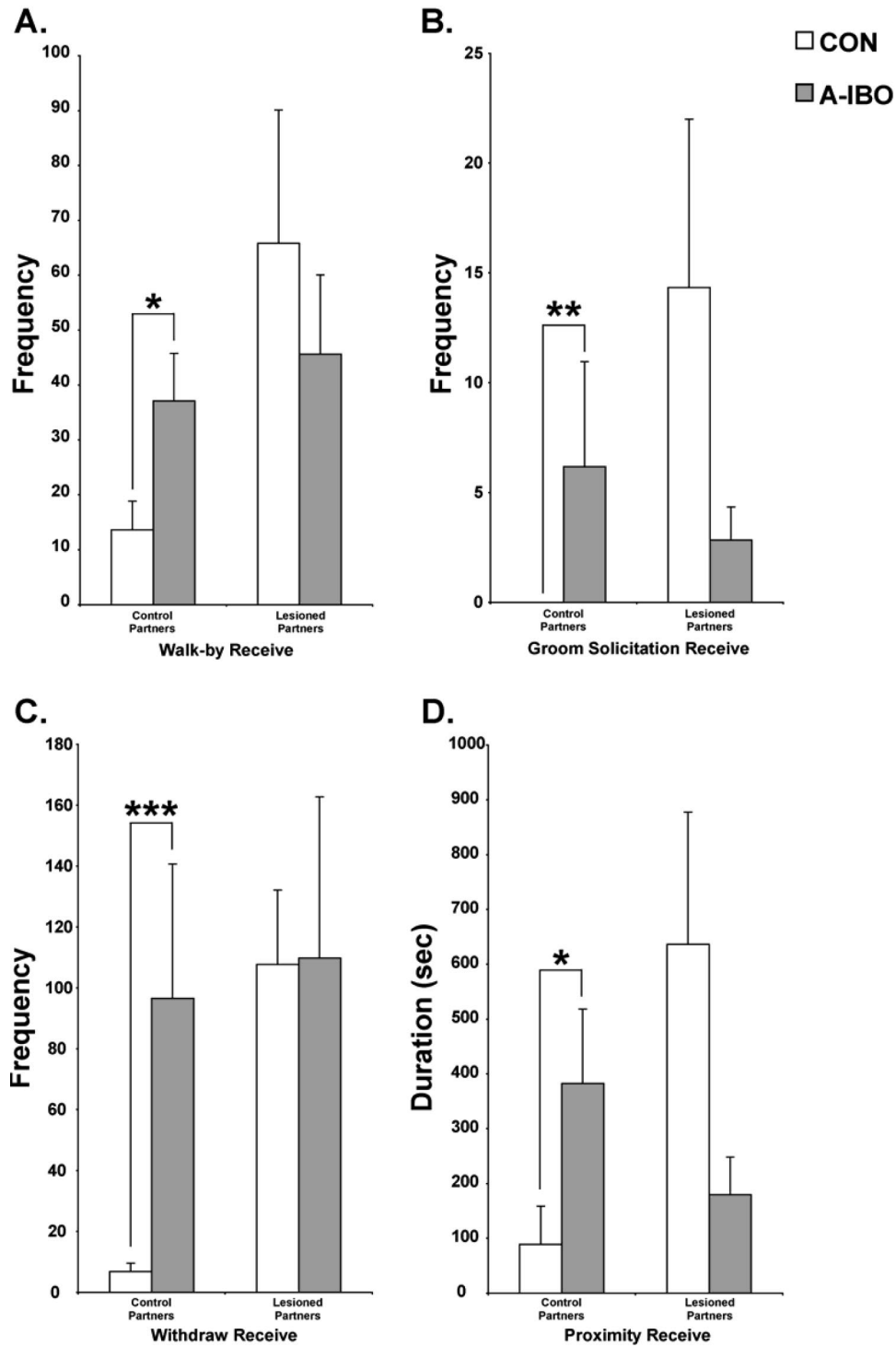
Figure 7. Total frequency across all testing blocks of walk-by receive (A), groom solicitation receive (B), and withdraw initiate (C), as well as total duration of proximity receive (D) with both control and amygdala-lesioned partners for monkeys in the control (CON) and amygdala-lesioned (A-IBO groups). Vertical bars indicate the standard errors of the mean. $^{*}p \leq .05$. $^{**}p \leq .01$. $^{***}p \leq .001$.
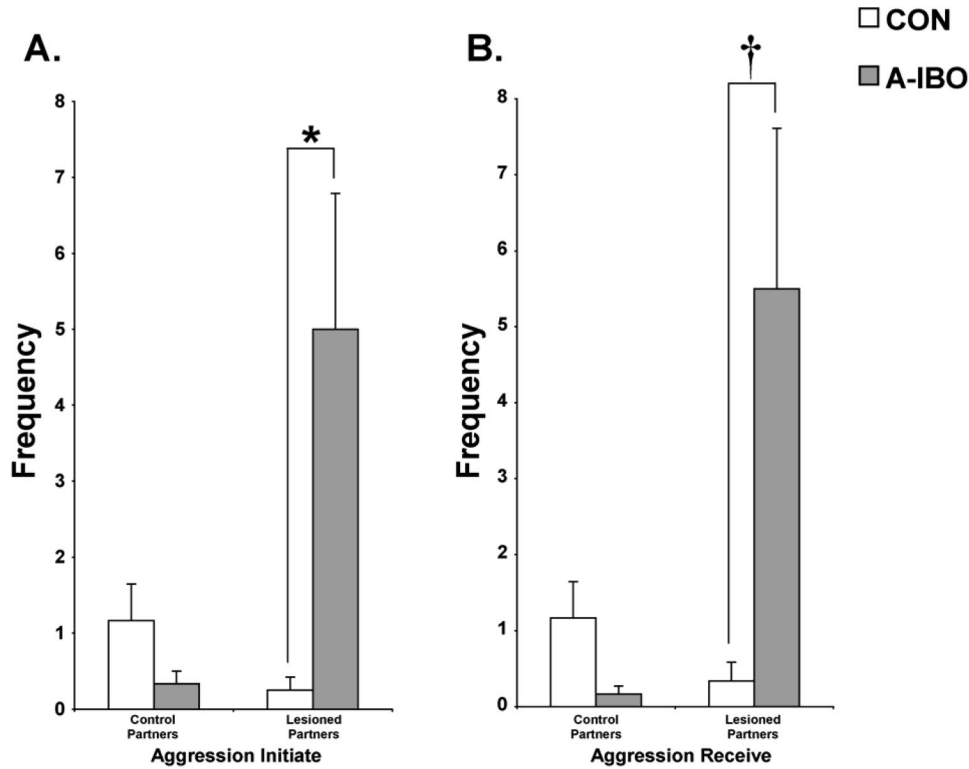
Figure 8. Total frequency across all testing blocks of aggression initiate (A) and aggression receive (B) with both control and amygdala-lesioned partners for monkeys in the control (CON) and amygdala-lesioned (A-IBO) groups. Vertical bars indicate the standard errors of the mean. $^{\dagger}p = .07$. $^{*}p \leq .05$.

fearful ratings, $F(3, 30) = 3.275$, $p < .05$; and nervous ratings, $F(3, 30) = 2.994$, $p < .05$. Post hoc analyses of both interactions did not reveal any robust differences between the groups in any block. However, similar to the interaction-inhibiting category, A-IBO monkeys displayed decreased fearful ratings, $t = 2.526$, $p = .05$; and nervous ratings, $t = 2.823$, $p < .05$, between Blocks

1 and 2, but CON monkeys did not show similar decreases in ratings for these adjectives until between Blocks 2 and 3: $t = 2.360$, $p = .07$; and $t = 2.158$, $p = .08$, respectively. These results indicate that amygdala-lesioned monkeys displayed earlier decreases in fearful and nervous attributes than did control monkeys during the 32 testing days.

Table 4
Attitude Assessment Data

Category and adjective	CON group				A-IBO group			
	Block 1	Block 2	Block 3	Block 4	Block 1	Block 2	Block 3	Block 4
Sociable	2.6 ± 0.2	2.6 ± 0.4	2.8 ± 0.3	2.8 ± 0.3	2.8 ± 0.3	3.3 ± 0.5	3.0 ± 0.3	3.1 ± 0.3
Confident	3.0 ± 0.2	2.9 ± 0.4	3.1 ± 0.4	3.1 ± 0.3	2.8 ± 0.3	3.6 ± 0.5	3.0 ± 0.3	3.3 ± 0.4
Affiliative	2.2 ± 0.2	2.3 ± 0.4	2.5 ± 0.3	2.5 ± 0.3	2.8 ± 0.2	3.1 ± 0.5	3.1 ± 0.4	3.0 ± 0.3
Interaction inhibiting	2.5 ± 0.1	2.5 ± 0.3	2.1 ± 0.2**	2.2 ± 0.2	2.5 ± 0.2	1.8 ± 0.3*	1.8 ± 0.2	2.0 ± 0.2
Avoidant	3.0 ± 0.2	3.0 ± 0.4	2.7 ± 0.3	2.7 ± 0.2	2.7 ± 0.2	2.1 ± 0.4	2.3 ± 0.3	2.2 ± 0.2
Aggressive	2.0 ± 0.2	1.7 ± 0.1	1.3 ± 0.1	1.4 ± 0.2	1.6 ± 0.2	1.4 ± 0.1	1.1 ± 0.1	1.4 ± 0.2
Nervous	2.7 ± 0.2	2.7 ± 0.5	2.3 ± 0.3**	2.3 ± 0.3	2.9 ± 0.2	2.0 ± 0.5*	2.0 ± 0.4	2.1 ± 0.3
Fearful	2.4 ± 0.2	2.6 ± 0.5	2.0 ± 0.3***	2.2 ± 0.3	2.7 ± 0.3	1.9 ± 0.5*	1.8 ± 0.4	2.3 ± 0.4
Other								
Active	2.7 ± 0.1	2.8 ± 0.2	2.8 ± 0.2	2.5 ± 0.1	3.1 ± 0.3	3.2 ± 0.3	2.8 ± 0.3	2.6 ± 0.3

Note. Data are the mean attitude assessment data (plus or minus the standard error of the mean) for the two experimental groups. Block 1, Block 2, etc., are sequential testing blocks, each representing an average over 8 test days. CON = control monkeys; A-IBO = monkeys with ibotenic acid amygdala lesions.
$^{*} p = .05$, change relative to Block 1. $^{**} p = .07$, change relative to Block 2. $^{***} p = .08$, change relative to Block 2.
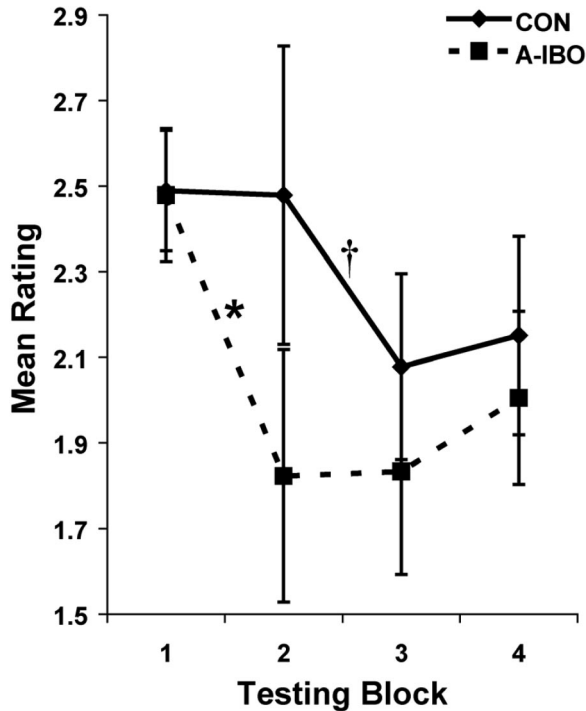
Figure 9. Mean rating of interaction-inhibiting qualities for control (CON) and amygdala-lesioned (A-IBO) groups in each of the four testing blocks (average of 8 test days). The interaction-inhibiting category is a composite of other more discrete qualities that do not promote strong, positive social relationships (e.g., aggressive, nervous, fearful, and avoidant). Vertical bars indicate the standard errors of the mean. †*p* = .07. **p ≤ .05.

Correlations

No significant correlations were found between any of the behavioral measures and intended damage to the amygdala (as a whole or individual subnuclei) or unintended damage to the entorhinal cortex.

Discussion

The main goal of this study was to determine whether the pattern of social and nonsocial behavior observed for amygdala-lesioned monkeys during paired social interactions (Emery et al., 2001) would also be observed in four-member groups. Similar to our previous study, the average distance between control and amygdala-lesioned rhesus monkeys was less than that between two lesioned or two control monkeys. Amygdala-lesioned monkeys also continued to initiate more affiliative behaviors (i.e., approaching to within arm's reach, physical contact and grooming) than did controls. Amygdala-lesioned monkeys directed far more of these affiliative behaviors toward control partners than did other control monkeys. By contrast, amygdala-lesioned monkeys initiated more aggression toward lesioned partners than did control monkeys. Behaviors related to dominance displays, generalized anxiety, and cage exploration did not differentiate the two groups. Finally, amygdala-lesioned monkeys also displayed an earlier decrease in interaction-inhibiting personality qualities (i.e., nervous and fearful) than did control monkeys.

Social Disinhibition Persists Across Contexts

Across multiple measures, amygdala-lesioned monkeys in the present study demonstrated a pattern of behavior we collectively refer to as *social disinhibition*. Measures of frequency and duration demonstrated that, regardless of social partner, amygdala-lesioned monkeys initiated more affiliative social behaviors, especially approaching to within arm's reach, physical contact, and withdrawals from close proximity. Amygdala-lesioned monkeys also predominantly directed their heightened affiliative social behaviors toward control partners in their groups, particularly in the form of approaches, withdrawals, solicitations for grooming, physical contact, and grooming. These affiliative overtures seemed to be reciprocated by control monkeys, because amygdala-lesioned monkeys also received more groom solicitations, walk-bys (transient proximity), and extended time in close proximity from control monkeys than did other controls. Heightened affiliative interactions between control and amygdala-lesioned monkeys were also apparent in their consistently shorter inter-animal distance relative to pairs of control or pairs of lesioned monkeys. Each of these findings is highly consistent with the heightened sociality demonstrated during our previous study of these same monkeys when they interacted in pairs (Emery et al., 2001). These findings are also in line with several previous nonhuman primate lesion studies of similar group sizes (Kling & Brothers, 1992) and one experiment that used GABA$_A$ antagonists to stimulate the nonhuman primate amygdala (Málková et al., 2003). We believe that this evidence suggests that heightened affiliative social interactions following amygdala lesions stems from a more general inability to properly perceive danger or threat in the environment and use such information to modulate social behavior adaptively. In line with this view, deficits in threat detection or fear reactivity have been specifically demonstrated for monkeys with bilateral neurotoxic amygdala lesions in both social (Machado & Bachevalier, 2006) and nonsocial settings (Izquierdo, Suda, & Murray, 2005; Kalin, Shelton, & Davidson, 2004; Kalin, Shelton, Davidson, & Kelley, 2001; Mason et al., 2006; Meunier, Bachevalier, Murray, Málková, & Mishkin, 1999). These abnormalities are not restricted to nonhuman primates, as humans with amygdala lesions also demonstrate specific deficits in identifying fearful facial expressions (Adolphs et al., 1999), rating the magnitude of fearful expressions (Adolphs, Tranel, Damasio, & Damasio, 1995) and assessing the approachability or trustworthiness of unfamiliar individuals (Adolphs, Tranel, & Damasio, 1998). It is also interesting that recent functional neuroimaging (Hoffman, Gothard, Schmid, & Logothetis, 2007) and electrophysiological recording (Gothard, Battaglia, Erickson, Spitler, & Amaral, 2007) studies with nonhuman primates have demonstrated heightened activity in the amygdala when subject viewed threatening facial expressions relative to appeasement gestures. Similar results have been present in the human neuroimaging literature for some time (Blair, Morris, Frith, Perrett, & Dolan, 1999; Gur et al., 2002; LaBar, Crupain, Voyvodic, & McCarthy, 2003; Morris, deBonis, & Dolan, 2002; Morris et al., 1996; Phillips et al., 1997; Whalen et al., 2001) and reinforce the similarities between human and nonhuman primate amygdala function.

The heightened sociality of the amygdala-lesioned monkeys in the present study appeared to make them the preferred social partners within each group. Monkeys with amygdala lesions received more affiliative social behaviors (e.g., groom solicitations and time spent in

close proximity) from control partners than did other controls (see Figure 7). In fact, control monkeys hardly initiated any affiliative social behaviors (e.g., approaches, groom solicitations, contact, and grooming) to other control monkeys (see Figures 5 and 6). The inter-animal distance was also less for control and amygdala-lesioned pairs than pairs of control monkeys (see Figure 3). These findings are again consistent with our previous study of these monkeys in a paired context. This continuity across contexts suggests that the amygdala plays a highly selective and modulatory role in normal primate social behavior; one highly specialized for proper reactivity to threat as opposed to other facets of social behavior.

The present experiment also demonstrated three surprising results in terms of social behavior. First, our previous study of paired social interactions demonstrated that amygdala-lesioned monkeys engaged in more autoerotic behavior and mounted male and female partners with a greater frequency than control monkeys (Emery et al., 2001). Although both behaviors remained common in the present study, neither differentiated the groups. One explanation for these incongruent effects of lesion could be the difference in social context afforded by the two experiments. Some support for this has been provided by the extensive work of Kling and colleagues (e.g., Kling & Brothers, 1992). In laboratory-based assessments of social behavior, amygdala-lesioned monkeys demonstrated hypersexuality, but this was typically not observed in free-ranging social contexts. Similarly, Machado and Bachevalier (2006) did not observe heightened mounting or autoerotic behavior in rhesus monkeys with neurotoxic amygdala lesions in four-member social groups.

A second unexpected result concerned changes in behavior over time. When observed in pairs, our amygdala-lesioned monkeys displayed heightened affiliative social interactions predominantly during the earliest interactions with unfamiliar partners (Emery et al., 2001). Although the present study included more social interaction sessions (maximum of six between partners for Emery et al., 2001, and a total of 32 in the present study), only one significant change over time was noted for the two experimental groups. The amygdala-lesioned monkeys demonstrated decreased ratings of fearful and nervous personality qualities after Block 1 (first 2 weeks of interactions), but control monkeys did not show a commensurate drop in these ratings until after Block 2 (after Week 4). Although not identical, these results are similar to those generated by the same monkeys in social pairs. However, the lack of other group differences related to time again indicate that the one 20-min interaction that monkeys received with all other possible partners in our previous study largely established the social rules and hierarchy that would later govern the four-member social groups. This is plausible because the formation of dominance hierarchies within groups of unfamiliar macaques occurs after only a few minutes of interactions and remains extremely stable over time regardless of the outcome of subsequent social interactions (Barchas & Mendoza, 1984). Machado and Bachevalier (2006) also did not find any profound changes in behavior across testing sessions for amygdala-lesioned monkeys when observed in four-member social groups established before surgery.

One final unexpected result from the present study concerned contact aggression. Although the total number of aggressive encounters was low across all groups, amygdala-lesioned monkeys initiated and received more aggression with other amygdala-lesioned monkeys than controls (see Figure 8). Although this result seems to fit with amygdala-lesioned monkeys directing more af-

filiative behaviors toward control partners rather than other lesioned monkeys (as earlier), this result was not found in our previous observations of these monkeys in social pairs (Emery et al., 2001). In fact, controls displayed more aggression than amygdala-lesioned monkeys in our previous experiments. Heightened aggression has not typically been observed in earlier studies of amygdala lesions in nonhuman primates, whether in small or large social groups (Kling & Brothers, 1992). There is no clear reason for this discrepancy between studies, but at least two possibilities exist. First, because behavioral data were collected over such a protracted time frame (32 testing sessions, 2 hours each), it is possible that amygdala-lesioned monkeys were able to demonstrate a more generalized pattern of social disinhibition, one that includes inappropriate aggression along with the more overt affiliative disinhibition reported here and in our previous study (Emery et al., 2001). A second explanation could also be rooted in the different social contexts of each study. Some support for this idea has been provided recently when amygdala-lesioned monkeys were also rated as more aggressive postsurgery in four-member social groups (Machado & Bachevalier, 2006).

Nonsocial Abnormalities Appear to Be Context Specific

Heightened environmental exploration (both tactile and oral) was found for amygdala-lesioned monkeys in our previous study (Emery et al., 2001). The present study did not detect any profound differences in cage exploration between amygdala-lesioned and control monkeys. Likewise, earlier studies of amygdala-lesioned subjects in social groups comprising four or more subjects have not demonstrated heightened frequencies of oral or tactile exploration (Kling & Brothers, 1992; Machado & Bachevalier, 2006). These findings are consistent with the idea that reduced opportunities for social interaction and/or restrictive testing environments promote hyperexploration following brain lesions in monkeys. Further support for this idea has come from investigations of food preferences in amygdala-lesioned monkeys. When tested in highly restrictive environments (i.e., a Wisconsin General Testing Apparatus), amygdala-lesioned monkeys demonstrated heightened preference for inedible nonfoods (Machado & Bachevalier, 2007a; Murray, Gaffan, & Flint, 1996; Stefanacci, Clark, & Zola, 2003). By contrast, in a more naturalistic setting, amygdala lesions do not produce heightened nonfood selection (Machado & Bachevalier, 2007b).

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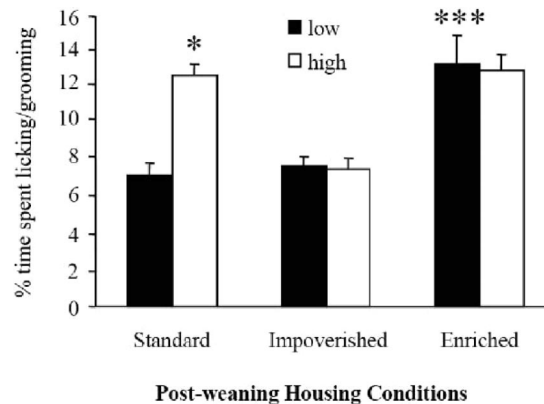
Correction to Champagne and Meaney (2007)

In the article "Transgenerational Effects of Social Environment on Variations in Maternal Care and Behavioral Response to Novelty," by Frances A. Champagne and Michael J. Meaney (*Behavioral Neuroscience*, 2007, Vol. 121, No. 6, pp. 1353–1363), Figure 1 on Page 1356 was incorrect. The correct figure is printed below.

Figure 1. Mean percentage of time spent licking/grooming (LG) pups by the adult female offspring of high and low LG dams. Offspring were weaned into three housing conditions (standard, impoverished, or enriched) for 50 days, mated, and observed during the first 6 days postpartum. Analysis indicated that posweaning impoverishment and enrichment abolished group differences in maternal LG. High LG female offspring housed under impoverished conditions exhibited reduced levels of LG compared to standard housed high LG females ($p < .05$), whereas low LG female offspring housed under enriched conditions exhibited elevated levels of LG compared to standard housed low LG females ($p < .001$). Error bars represent standard error of the mean $^{*}p < .05.$ $^{***}p < .001.$