Development of Social Fear After Amygdalectomy in Infant Rhesus Monkeys

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THOMPSON, C. I., J. S. SCHWARTZBAUM and H. F. HARLOW. *Development of social fear after amygdalectomy in infant rhesus monkeys.* PHYSIOL. BEHAV. 4(2) 249–254, 1969.—Infant rhesus monkeys were subjected to a bilateral amygdalectomy and were compared in group and individual situations with sham-operated controls. During the year following surgery significant group differences developed in the expression of fear responses. In general, the operated monkeys appeared less disturbed by novel stimuli than the controls. In group situations, however, the operated monkeys made more fear responses than the controls, especially: (1) when the test groups included unoperated monkeys; (2) when the length of the test session increased; and (3) when the monkeys grew older. Although other investigators have reported virtually normal behavior following bilateral amygdalectomy during infancy, it is clear from the present study that some behavioral changes still occur. The results also suggest that common generalization depicting amygdaloid monkeys as "fearless" does not accurately describe their long-term interactions with normal peers.

Age effects of lesions   Amygdala   Brain lesions   Fear   Social behavior

RECENT evidence makes it clear that bilateral removal of the amygdala in infant rats, cats, and monkeys spares certain patterns of behavior that are severely disrupted after similar damage in adults [12]. Kling and Green [13] observed female monkeys for nearly two years after a bilateral amygdalectomy which the subjects sustained during infancy. In all gross respects, these monkeys appeared unchanged. Sexual and emotional response patterns, infant-mother interactions, and growth curves all remained within the normal range following surgery. Thus the amygdala is similar to several other brain structures in that some functions are spared when damage occurs early in life [1, 2, 8, 11, 16, 19, 21, 25].

Most brain structures are involved in the performance of many different behaviors. Work by Isaacson on the cat hippocampus suggests that damage to a given brain structure early in life may not spare all of these functions equally [10]. The question thus arises as to whether all functions mediated by the amygdala are spared equally following early surgery. Many types of deficit are known to follow amygdalectomy in adult animals. Among these are an inability to withhold a learned response [3], perseveration in spatial reversal problems [14], difficulty in avoidance tasks [9, 17], disruption of maternal behavior [15, 23], and a decrease in dominance during interactions with peers [4, 18]. Since none of these behaviors has been examined in infant-lesioned monkeys, it would seem premature to assume that all functions mediated by the

amygdala are equally spared after bilateral removal during infancy. Thus a program of research has been initiated in order to examine in infant-lesioned monkeys a wide variety of behaviors known to be altered by amygdalectomy in adults. The present paper deals with altered fear response patterns in social and nonsocial settings following amygdalectomy in infant monkeys.

Fear Responses in Adult Monkeys

Although bilateral amygdalectomy seems to reduce fear in many situations [5], there is some evidence that amygdalectomy may actually increase the number of fear responses made during interactions with normal peers. Rosvold, Mirsky and Pribram [18] bilaterally ablated the amygdala of the most dominant monkey in a group of 8 males and then observed behavior when the operated monkey was returned to the group. Two out of three monkeys receiving this operation immediately fell from the top to the bottom of the dominance hierarchy. The indications were that a great deal of fear accompanied this drop in status. On the other hand, when Rosvold *et al.* tested their monkeys individually in home cages, the amygdalectomized monkeys appeared to be more fearless and aggressive than their unoperated peers. Fuller, Rosvold and Pribram [4] reported a similar effect in dogs. Dogs that consistently won possession of a bone from their

peers prior to amygdalectomy no longer did so after the operation. Despite an apparent increase in timidity towards other dogs, however, timidity towards human handlers appeared to decrease following surgery.

In the present study the development of fear responses was observed in monkeys that had sustained a bilateral amygdalectomy during infancy. It was assumed that if compensatory mechanisms allowed normal development, then the operated monkeys would behave like a normal group in both social and nonsocial situations. If, however, the mechanisms related to the expression of fear were not completely compensated, then the amygdaloid infants might be expected to behave like amygdaloid adults. In this case the operated monkeys would make more fear responses than the controls when tested socially, but would appear less timid than the controls when individually exposed to a novel situation.

METHOD

Subjects

Twelve female rhesus monkeys were separated at birth from their mothers and individually housed in wire cages except during daily test sessions. Six of these monkeys were assigned randomly to receive amygdaloid ablations and the remaining 6 served as sham operated controls. Cheesecloth diapers were placed on the cage floors as a means of providing contact comfort for the infants. These were available to all monkeys at all times, including test periods, for the first 8¼ months of life.

Surgery

Surgery was performed by aspiration in two stages under amobarbital sodium anesthesia (50 mg/kg). In both the operated and control groups the temporal bone was exposed by cutting the temporal muscle and removing the zygoma. In the operated monkeys a segment of temporal bone was removed and the amygdala was visualized by retracting the temporal lobe. A unilateral ablation was made at 1.8 months, and the contralateral nucleus was removed when each monkey was 2.5 months old.

In order to maximize chances for survival, the sham operation in four control monkeys proceeded only as far as exposure of the temporal bone. In the remaining two control monkeys the temporal bone was removed and the dura was cut. Subsequent inspection of the data revealed that these two controls were least like the operated monkeys in behavior. Thus cutting the dura apparently had no effect in producing the group differences obtained in the present study.

Histological data are not yet available since these animals will be tested until they reach maturity. However, the behavioral similarities of these animals to those tested by Rosvold et al. [18] strongly support the conviction that amygdaloid damage was primarily responsible for the obtained effects.

Social Testing

A 6 × 3 × 3 cu. ft. cage was used for social testing during the first 9 months of life. During these tests monkeys were paired for daily sessions of 20 min. During 10-day periods which began at 2.9 months (10 days following surgery: Bilateral I test) and at 8.3 months (Bilateral II test) an operated monkey was paired with a control monkey. The operated-control pairings were assigned so as to minimize age differences within pairs, and the same pairs were tested together during all 20 test days.

During another 10-day period which began at 4.8 months the test pairs consisted of either two operated monkeys or two control monkeys (Like Groups test), with the same pairs tested throughout the sessions. When the monkeys averaged 13 months of age they were housed continuously in groups of two or three monkeys each for a period of 18 days. At least one operated and one control monkey were housed in each cage, and all home cage behaviors of each animal were recorded for 2½ min each day.

Behaviors Recorded During Social Testing

Two observers were used to score behavior during the social tests at 2.9, 4.8, and 8.3 months, and each used a different recording system. One observer used a technique developed at the Wisconsin Primate Laboratory [6, 20], in which a click produced by a timer every 15 sec signaled the onset of a new scoring interval. A given behavior was recorded once for every 15-sec interval during which it appeared. In the present study the test sessions were 20 min long, so the data consisted of the number of 15-sec intervals out of a possible 80 that each behavior occurred. Fifteen different social behaviors occurred often enough to be analyzed using this method, and were defined as follows:

Approach. Oriented movement of at least one body length toward another monkey.

Withdrawal. Oriented movement of at least one body length away from another monkey.

Noncontact play. Highly active chasing behavior involving 3–4 body length "bee line" run or bouncing off walls of the enclosure, vigorous bouncing or cage shaking while visually oriented toward another animal. Also, active manoeuvres which involve first moving away from and then back toward another monkey, with more or less continuous motion.

Avoidance play. Animated attempt to maximize distance from another monkey. Same movement characteristics as first component of Noncontact Play.

Clasp-pull-bite. Any brief nip, cuff, or clasp-pull directed toward another monkey.

Fear grimace. Exposure of the teeth in a rigid grimace to another monkey, often accompanied by screeching, piloerection, defecation, etc.

Threat. Facial expression directed toward another monkey involving direct stare, ears back, mouth dropped open, and/ or head bobbing up and down.

Rigid submit. Assumption of a rigid posture in response to another monkey's behavior. Usually is a response to contact, but may be a response to approach or proximity of another monkey.

Nonspecific contact. Any part body contact with another monkey—usually brief, and not scored if another contact behavior is scored.

Oral contact. Any social oral contact of a tentative nature—not scored if play, nipping, etc., occurs.

Manual exploration. Manual manipulation, except grooming, of another monkey.

Gross body contact. Any nonventral gross contact with another monkey.

Clasp. Tentative closure of the hand on the fur or skin of another monkey.

Inappropriate thrust. Any pelvic thrust not oriented toward the anogenital region of the recipient monkey.

Appropriate present. Orientation of erect hindquarters toward another monkey and exposure of the anogenital region by displacement of the tail. May be a social stimulus or response.

Since only one tester used the above scoring system, no observer reliabilities were obtained. However, consistency between observers is frequently checked in other settings at the Wisconsin Primate Laboratory, and the reliability coefficients for the above behaviors consistently range in excess of 0.80.

There are two advantages to the system described above: (1) two monkeys can be scored simultaneously with relative ease, thus eliminating the necessity of balancing test order when pairs of monkeys are being tested, and (2) the number of variations in behavior which can be recorded is limited only by the observer's power of discrimination, and his ability to assign a shorthand symbol to that behavior within a 15-sec period. However, many behaviors which are discriminable nevertheless are highly correlated, and may be grouped meaningfully into categories of behavior. Also, it is preferable whenever possible to record absolute frequencies and durations, rather than the number of 15-sec periods that a behavior occurred. Thus a second observer recorded frequencies and durations for 9 categories of behavior on a bank of 9 clocks and counters. These 9 categories were mutually exclusive and exhaustive, so that the observer was recording one and only one type of behavior continually throughout the test session. The categories usually consisted of combinations of the various behaviors defined earlier in the paper. These behaviors, plus any additional behaviors scored within a given category, are listed below:

Fear. Fear Grimace, Rigid Submit, Withdrawal, Screech, or Rocking motions elicited by presence or activity of another monkey.

Hostility. Threat, or Aggression. The latter includes vigorous biting or clasp-pulling—usually accompanied by growling, barking, piloerection, teeth clicking, and prolonged threat patterns.

Social play. Clasp-Pull-Bite, Noncontact Play, Avoidance Play, and Contact Play. The latter includes animated wrestling and biting, without threat components.

Social exploration. Nonspecific Contact; Oral Contact with, or Manual Exploration of, another monkey (except anogenital); Grooming; Gross Body Contact; and Clasp.

Nonsocial exploration. Oral or Manual Exploration of inanimate objects; Self Groom.

Nonspecific Activity. Movements not directed toward another monkey or toward an object, such as walking and cage climbing.

Passivity. Not moving; resting or sleeping.

Disturbance. Self-Clasp or -Bite; Convulsive Jerk; Rocking; Wall-Hugging; Screeching. Recorded as Disturbance only when not obviously elicited by another monkey; if elicited by another monkey, recorded as Fear.

Sex. Sexual Presents and Mounts of all types—appropriate and inappropriate. Anogenital Exploration of self or another monkey, either orally or manually.

Only one monkey could be scored at a time using the clock and counter system, in contrast with the 15-sec interval system where both monkeys were scored simultaneously. Thus each monkey was scored for only 10 min during each 20-min session. Order of testing was balanced, and Test Order was included as a factor in the analyses.

During the social tests at 13 months only one observer recorded data. The scoring system here involved a combination of the previous two. The 9 grouped categories of behavior described above were listed on a sheet, and a single check was made beside a given category for every 15-sec interval during which the behavioral category occurred.

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Nonsocial Testing

Nonsocial testing began when the monkeys were 6.2 months of age. The test apparatus consisted of two 3 × 3 × 3 cu. ft. cages which were separated by a guillotine door. A rear projection screen on a wall of one cage was used for presenting picutres from a 35 mm slide projector. Five pictures were used in all: three showed faces of monkeys that were judged to be frightened, threatening, or relaxed: one portrayed an infant lying on a diaper; and the fifth was a control picture of inanimate objects scattered about a living room. A monkey was placed in the cage opposite the screen and was restrained by the guillotine door. After 5 min the door was raised and the animal was free to explore both cages for 5 min. No pictures were shown during the first 6 test days. During the next 15 days a single picture was projected onto the screen during the second 5 min of the daily test session. Each monkey saw each picture 3 times, and order of presentation was randomized with the restriction that all 5 pictures be shown before a replication began.

Behaviors Recorded During Nonsocial Testing

Only the clock and counter system was used during nonsocial testing, and duration and frequency data were taken on 8, rather than 9, categories of behavior. Fear and Hostility, defined previously, were included, but were scored only as reactions to the pictures, rather than to other animals. The Social Play and Social Explore categories defined previously were combined into a single Picture Explore category. Nonsocial Explore, Nonspecific Activity, Passivity, Disturbance and Sex remained as defined previously, although they of course occurred in the absence of other animals. A "Mobility" score was defined as the total number of times the monkey changed behaviors, and consisted of the sum of the frequencies that the 8 categories of behaviors were scored. In addition to the above 8 categories, a latency measure was taken of time elapsing before the monkey entered the adjacent cage, after the guillotine door between cages was raised.

RESULTS AND DISCUSSION

General Observations

The behavior of individual monkeys in their home cages appeared unaffected after either a unilateral or bilateral amygdalectomy. Examination of weekly weight records also revealed no differences between the two groups. These findings correspond to those of Kling & Green [13].

Casual observations following surgery indicated that hair regrowth on the shaved area of the head was faster for the amygdalectomized member of each operated-control test pair. It seemed remotely possible that this might reflect a difference in gonadal hormone level, particularly in light of Kling's [12] finding that infant cats developed ovarian hypertrophy following amygdaloid ablations. Urine samples taken at 5.3 months were analyzed for FSH, but no group differences were found. When the average age was 15 months the heads of all 12 monkeys were shaved on the same day, and hair regrowth was rated by 4 independent observers. A check of the ratings one month after shaving showed complete agreement that 5 of the 6 operated monkeys had more hair than their like-aged control partner.

Social Behavior

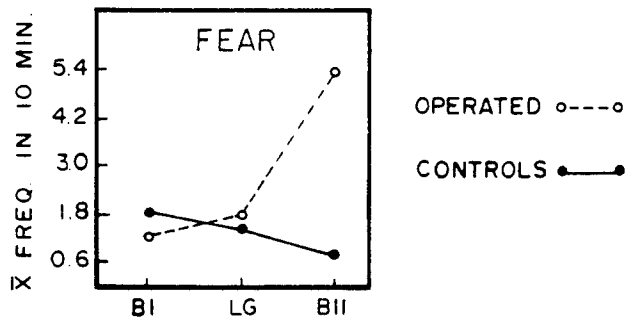During social tests the amygdalectomized monkeys made more fear responses than the controls. "Fear" was recorded

FIG. 1. Development of social fear after amygdalectomy. During BI (2.9 months) and BII (8.3 months) testing, operated and control monkeys were paired. During LG testing (4.8 months), pairs consisted of either two operated or two control monkeys. Surgery was completed at 2.5 months, but operated monkeys did not show an increase in social fear until several months later.

by the clock and counter system and included withdrawal, grimace, rigid posture, screeching, and rocking due to the presence or activities of another monkey. Figure 1 shows that this fear response pattern was not immediately apparent following surgery, but that it increased dramatically between the Bilateral I and II stages of testing ($p < 0.01$. Unless otherwise specified, all statistical tests were made by analysis of variance). By 13 months very large group differences had appeared. As can be seen in Fig. 2, operated monkeys showed a much higher incidence of fear responses than did normal monkeys in the home cage situation.

FIG. 2. Social fear and social exploration during group housing at 13 months. Test groups consisted of two or three monkeys each, and contained at least one operated and one control monkey. Daily test sessions of 2½ min were broken down into ten 15-sec periods. The ordinate shows the mean number of 15-sec periods that the behaviors occurred during each of 18 test days. Probabilities are based on the Mann–Whitney U test, and are 2-tailed. Operated monkeys made 100 times more fear responses than the controls during these tests.

As the operated monkeys became more fearful, they engaged in less social exploration (grooming, sitting against, mouthing, or clasping fur of another monkey). The amygdalectomized monkeys showed a significant decrease in social exploration between the Bilateral I and II tests at 2.9 and 8.3 months of age ($p < 0.05$), and, as shown in Fig. 2, large group differences were evident in the home cage situation at 13 months of age.

The amygdalectomized monkeys were approached ($p <$

0.01) and chosen as play partners ($p < 0.05$) significantly more times than were normal monkeys, by both operated and control monkeys. "Approach" was recorded whenever a monkey made oriented movements of one body length or more toward another monkey. "Social Play" was recorded whenever the behavior included brief nips, cuffs, clasp-pulls, and animated chasing or wrestling. As shown in Fig. 3, operated monkeys played with each other (Like Groups test) more often than they played with normal monkeys (Bilateral I and II test; $p < 0.05$). Normal monkeys tended to engage in more play during the Bilateral I and II tests, where they were paired with amygdalectomized monkeys ($p < 0.05$).
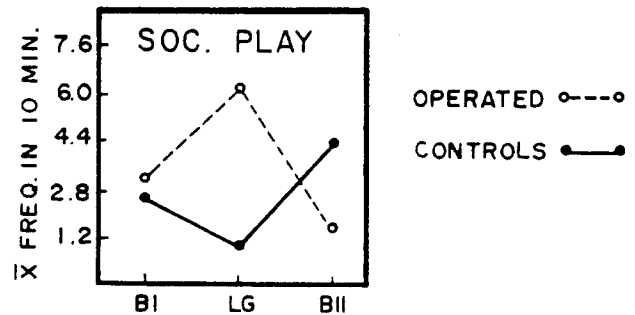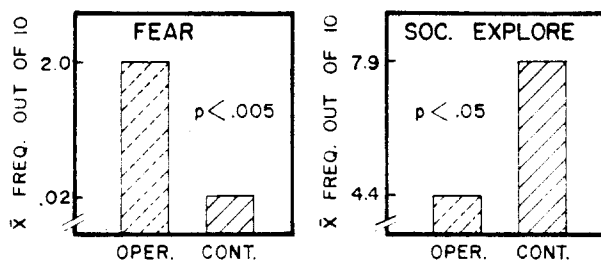

FIG. 3. Social play after amygdalectomy. This figure shows play during the last 5 days of the BI (2.9 months), LG (4.8 months), and BII (8.3 months) tests. During BI and BII tests, operated and control monkeys were paired. During LG tests, pairs consisted of either two operated or two control monkeys. Both operated and control monkeys played most when paired with operated monkeys.

Dependence of Amygdaloid Fear Responses upon Behavior of Normals

The fear responses shown by amygdalectomized monkeys toward control monkeys depended in some subtle way upon the behavior of the controls. Amygdalectomized monkeys appeared less afraid of each other than they were of control monkeys. This was demonstrated by increased levels of approach and social play in operated animals during Like Groups testing. Facial threats (direct stare, wrinkled brow, ears back, mouth open, or head bobbing up and down) actually were slightly more frequent between pairs of operated animals than they were between control animals. Operated monkeys threatened each other an average of once in every 20 test min; normal monkeys threatened each other only once in every 50 test min (statistically nonsignificant—n.s.).

Changes in behavior as a function of length of time spent in groups also suggest that the fear responses of amygdalectomized monkeys were dependent upon the behavior of the controls. Immediately following entry into the test cage the operated monkeys appeared, if anything, less fearful than the controls. This appeared related to the fact that the control monkeys were relatively inactive immediately following entry into the cage, and was opposite to the situation which prevailed after testing had continued for a period of time. Table 1 lists five behaviors which changed in frequency as testing progressed. These data are collapsed across the Bilateral I, Like Groups, and Bilateral II phases of testing, all of which contained 10 sessions which lasted 20 min. Differences in behavior between the first and second 10 min of the

TABLE 1.

CHANGES IN BEHAVIOR AS A FUNCTION OF AMOUNT OF TIME SPENT IN GROUP

Behavior	Operated (p-level)	Control (p-level)
Social Exploration[a]	Decrease (0.01)	Increase (n.s.)
Withdrawal[a]	Increase (0.05)	Decrease (n.s.)
Passivity[a]	Increase (n.s.)	Decrease (0.01)
Nonspecific Activity[b]	Decrease (0.01)	Increase (n.s.)
Nonsocial Exploration[b]	Decrease (n.s.)	Increase (0.01)

[a]Changes from first 5 to second 5 days of BI, LG, and BII testing.
[b]Changes from first 10 to second 10 minutes of BI, LG, and BII testing.

session, and between the first and second 5 days of the test stage, were analyzed. It is apparent that changes in behavior were in the opposite direction for the operated and control monkeys. For the operated monkeys, withdrawal from social contact accompanied the increase in activity by the controls.

In summary, amygdalectomized monkeys made more fear responses during social testing than did controls, but this behavior varied considerably depending upon test conditions. Three factors contributed to the number of fear responses made by amygdalectomized monkeys: (1) age—older monkeys made more fear responses; (2) length of test period—regardless of age, amygdalectomized monkeys made more fear responses toward the end of the testing periods; (3) test partner—amygdalectomized monkeys made more fear responses when tested with normal monkeys than they did with other operated monkeys.

It is probable that the age-dependent group divergence in number of fear responses did not relate as much to intervening testing as to maturation. Infant development during the second six months of life progressively augments the vigor and violence of activity. In the present study, amygdalectomized monkeys became increasingly withdrawn whenever the activity of the normal monkeys increased. It was concluded that older operated monkeys made more fear responses primarily because the older control monkeys were more active.

The increased fear responses by amygdalectomized monkeys after several minutes of testing may explain the large group differences observed during the group housing situation at 13 months. Here there was one continuous 18-day "testing session", rather than the ten 20-min periods used in other social tests. All testing was done after the monkeys had become accustomed to their housing conditions. Hence, behavioral records were taken under conditions where the control monkeys were maximally active—and the operated monkeys maximally withdrawn.

It is not clear why amygdalectomized monkeys made the most fear responses when tested with normal monkeys. The control monkeys did not appear overtly aggressive towards the operated monkeys. Although operated monkeys were approached more often than control monkeys, it was not approach per se which elicited fear: operated monkeys approached each other a large number of times, and yet did not withdraw from each other very often.

Nonsocial Behavior

By the time a rhesus monkey is 90 days old, fear of strange objects is clearly evident [7]. A normal infant placed in a strange situation usually freezes in a crouched position until it becomes accustomed to the new environment. Disturbance behaviors such as screeching and rocking may occur, but exploratory behaviors and nonspecific activity (walking around and cage climbing) are nonexistent until fear is reduced to a level where the animal no longer is immobilized.

The monkeys in the present study were individually placed into a novel test environment at 6.2 months. Results indicated that the amygdalectomized monkeys were less disturbed by the new test situation than were the controls. During the six days of testing prior to picture presentation the operated monkeys engaged in more nonspecific activity ($p < 0.05$), and changed behaviors more often (total frequency of all behaviors recorded during a session; $p < 0.05$), than the controls. The operated monkeys also were more willing to enter the adjacent cage after the guillotine door was raised.
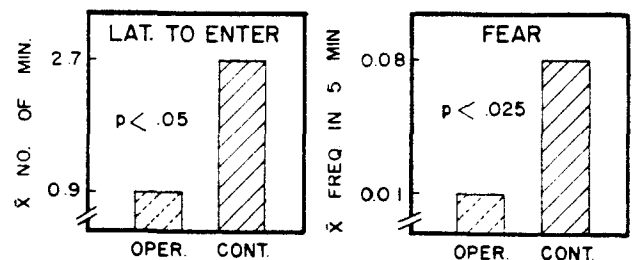

FIG. 4. Latency to enter an adjacent cage, and fear responses to pictures, during nonsocial tests at 6.2 months. In these tests operated monkeys appeared less fearful than controls. This is in contrast to their behaviors with normal peers, where the operated monkeys appeared more fearful than controls.

As can be seen from Fig. 4 the controls waited three times longer to enter the adjoining cage than did the operated monkeys. When the pictures were presented the normal monkeys demonstrated the most fear. Group differences were statistically significant ($p < 0.025$), although the total number of fear responses was not high for either group, as can be seen from Fig. 4. Practically all of the fear responses were elicited by the picture of the monkey judged to be frightened, and then only during the first of the three presentations. Other responses to the pictures were infrequent, and none revealed group differences.

General Conclusions

Results from several studies indicate that a bilateral amygdalectomy produces more impairment in adult monkeys than it does in infants [12, 13]. Behaviors typically observed after amygdalectomy in adult monkeys include a temporary lethargy, calm acceptance of handling by humans, and a transient decrease in food intake sometimes followed by hyperphagia [5, 24]. None of these behaviors appeared after surgery in the present study; in fact, there were no obvious differences in the behaviors of the operated and control monkeys in their individual home cages. Casual observations thus suggest that some functions were spared due to the early onset of damage.

Under test conditions, however, the amygdaloid and normal monkeys clearly differed in their fear response patterns. Normal monkeys tended to respond to any social or non-social change by crouching in a frozen position. Amygdaloid monkeys appeared less disturbed by stimulus change, but were intimidated by active normal monkeys. Because adult-operated monkeys were not included in the present study, it cannot be determined whether the observed abnormalities were less severe than would have occurred after surgery in adults. However, the changes in fear response were qualitatively similar to those observed in older monkeys by Rosvold et al. [18], and in dogs by Fuller et al. [4].

The impairment produced by a specific brain lesion varies with age at surgery and type of task. For some tasks, there may be almost complete sparing when surgery occurs early in life. It is doubtful, however, that sparing of function ever is complete for all tasks, regardless of when surgery is performed. Isaacson et al. [10] found that some, but not all, functions appeared normal after hippocampectomy in infant cats. Harlow et al. [8] found that monkeys sustaining bilateral frontal lobectomy before 150 days of age were superior on a delayed response task to monkeys operated between one and two years. However, performance on a delayed alternation

task is severely impaired after frontal lobectomy, regardless of when surgery is performed [22]. Wetzel et al. [25] found that infant cats with visual cortex removed appeared normal in pattern discrimination and visual placing, but tended to bump into walls. The present study suggests that although bilateral amygdalectomy in infant monkeys has little effect upon individual home cage behaviors, under some conditions the fear response pattern is abnormal. Other behaviors known to be disrupted after amygdalectomy in adult monkeys have not been examined after surgery during infancy. When these behaviors are investigated, it may be that other deficits in the infant-operated amygdaloid monkey will appear.

The apparent nonchalance of amygdaloid animals in novel situations has led many investigators to describe them as "fearless" [5]. The operated monkeys in the present study also appeared quite calm in novel situations, but they became quite fearful during prolonged contact with normal monkeys. The similarity of these results to those of Rosvold et al. [18] and Fuller et al. [4] suggests that the term "fearless" is a generalization which applies only in limited situations. It does not accurately describe the long-term interaction of amygdaloid animals with normal peers.

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