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Neonatal ablations of the amygdala and inferior temporal cortex alter the vocal response to social separation in rhesus macaques

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Abstract

Rhesus macaques that had received bilateral ablations to either the amygdala or area TE in inferior temporal cortex in the 1st week of life were briefly separated from familiar conspecifics at 10–14.5 months of age in order to assess the vocal response to this mild challenge. Sound spectrograms were subjected to quantitative analysis and compared with calls from normal, age-matched controls subjected to the same testing conditions. Animals with TE damage called at a higher rate than animals in the other two groups. TE subjects also produced more coos than controls. Males with TE lesions produced noisy calls at a higher rate than males of the other two groups. Females did not differ between groups in this measure. Analysis of the detailed acoustic structure of the 'coo' indicated significant differences in a measure of slope of the fundamental frequency (rate of frequency change over time) between amygdalectomized animals and those of the other 2 groups. The amygdalectomized monkeys produced calls with lower slope values, giving the calls a less inflected quality both in sonagrams and to the listener. These findings suggest an important role for the amygdala and inferior temporal cortex in regulating the vocal response to social separation during development.

Keywords: Limbic system; Vocalization; Primate brain; Neuroethology; Communication; Development

1. Introduction

Ever since Darwin's [7] treatise on emotional expression in man and animals, there has been widespread interest in the extent to which expressions of emotion and their underlying causal mechanisms in humans arose from emotional control systems that exist in our closest relatives, the non-human primates. This interest has more recently been extended to vocal expressions of emotion [1,33]. The linkage between the sounds of emotional expression in human and non-human primates is, perhaps, clearest in infants, where cry sounds with similar acoustic characteristics are clearly linked to contexts of negative affect (human infants [11,19,30]; non-human primates [25,26]). While most attention on vocal development in humans has been directed at the emergence of speech, some information is available on the development of non-verbal expressions of negative affect in human infants [10].

Studies of vocal development in non-human primates have been somewhat limited, due to the difficulties associated with interpreting the variable vocal repertoire of maturing individuals during a period when motor skills and underlying neural substrates are maturing, at the same time as social relationships with group members are not yet firmly established. However, recent reviews of vocal development in several non-human primate species may be found in Zimmermann et al. [39]. One approach to studying vocal development in non-human primates has been to separate an infant from its group for brief periods of time. The advantage of this approach is that it provides a fixed context in which vocalizations can be recorded, thereby eliminating the possibly confounding influence of dynamic social interactions on the acoustic details of emitted vocalizations [27]. Using this approach, Newman and Symmes [28] described the effects of differential rearing on the vocalizations of young rhesus macaques *Macaca mulatta*. Infants deprived of physical contact with conspecifics and with only limited human handling produced vocalizations

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of one subtype, the 'coo', that differed from those produced by age-matched, mother-reared infants. In addition to these structural differences, isolation-reared infants also produced abnormal vocalizations never produced by mother-reared infants. In pigtail macaques *Macaca nemestrina*, Grimm [9] published an extensive description of the calls given by developing individuals, among which were the 'leap coo' (containing a fast-rising transient), and the 'scream' (a harsh, loud vocalization).

The major pathways in the brain mediating vocal expression in non-human primates have been reviewed [35]. Briefly, a pathway with relatively direct control over vocalization begins in the anterior cingulate gyrus, passes through the diencephalon to connect with midbrain periaqueductal gray matter, and descends through the pons and medulla to end in the lower brainstem reticular formation and nucleus ambiguus, the latter structure being the subdivision of the vagal nucleus that innervates the larynx (squirrel monkeys [22]; macaques [37]). Except for the anterior cingulate gyrus and nearby medial cortical areas, there is little evidence implicating any part of the cerebral cortex in vocal production. Based on brain stimulation studies, forebrain limbic structures implicated in vocalization include the amygdala, nucleus of the striae terminalis, preoptic region, and hypothalamus (squirrel monkeys [12]; macaques [31]). All of these structures project directly to the periaqueductal gray matter, at least in the squirrel monkey [13].

Kling [15] has summarized the results of previous studies on the neural substrates necessary for maintaining social bonds in non-human primates. These structures include the amygdaloid nuclei, the temporal pole, and posterior medial orbital cortex. Bilateral ablation of any of these structures results in a deficit in socialization. In adult females, lesions of these areas disrupts the normal maternal-infant bond; however, operated infants thrive and are well-cared for. The amygdaloid nuclei are hypothesized to be essential for assessing the emotional content of sensory information. Lesions to other temporal and frontal lobe structures (including cingulate and lateral frontal cortex) do not affect affiliative behavior. Lesions of the amygdaloid nucleus and anterior temporal pole in newborn infants did not affect the care giving behavior of the mothers up to at least 1-1/2 years of age. Operated infants show adequate sucking and grasping, and explore and join in play during development [14]. When individually housed at 18 months of age, these lesioned animals began to show typical symptoms of the Kluver-Bucy syndrome (tameness, loss of fear, hyperorality). When replaced in their social group, these symptoms disappeared [34]. In general, operated juveniles tend to show less of a deficit than operated adults in all environments studied. In another study, Thompson et al. [36] subjected infant rhesus macaques to bilateral amygdalectomy and followed post-operative fear responses for 1 year. Typically, the operated monkeys appeared less disturbed by novel stimuli than controls. In group situations, however, the operated monkeys made more fear responses than controls, especially with increasing age. These authors also cite Kling and Green [16], who found no effect on subsequent behavior following neonatal amygdala ablations in macaques.

The present study was undertaken to determine whether altered vocal communication resulted following neonatal bilateral ablations of either the amygdala or inferior temporal neocortex. Preliminary results from the study appeared in Newman and Bachevalier [24] and Newman et al. [29].

2. Materials and methods

2.1. Subjects

Eight male and eight female full-term infant rhesus macaques *Macaca mulatta* were used in this study. All were separated from their mother 1 day after birth and reared in the primate nursery of the Laboratory of Neuropsychology (NIMH, Bethesda, MD). The infants were housed individually throughout the study in wire-mesh cages that permitted visual, auditory and limited somatosensory contact with other infant conspecifics. During the 1st month, cotton towels were provided inside the cages, and the infants were handled several times daily by caretaker personnel. Additionally, each individual received peer contact for up to 6 h/day in a play pen with 2 other individuals.

Details of feeding and husbandry are given in Bachevalier et al. [4,5]. Six neonates (3 males and 3 females) received bilateral ablations of the amygdala (group A), four (2 males and 2 females) received bilateral ablations of cortical area TE (group TE), and six (3 males, 3 females) were kept as unoperated controls (group N). Bilateral removals were done in two stages when the monkeys were ≈ 7 and 20 days of age. Further details of surgical procedures and post-operative care are given in Bachevalier et al. [5].

2.2. Behavioral assessment

All subjects took part in a study aimed at investigating the effects of early damage to the structures in the medial temporal region on the development of learning and memory as well as socioemotional behavior. Thus, prior to the present experiment, all monkeys had been tested at 3 months of age in a concurrent object discriminant task to measure their ability to form visual habits, and were placed in pairs in an enclosure to measure their social interactions at 2 and 6 months of age. Preliminary findings of these earlier behavioral tests have already been published [3,5].

For recording vocalizations in the context of social separation, each monkey was brought in turn into a quiet room inside a wire mesh transfer cage, placed inside a reduced version of the Wisconsin General Testing Apparatus ($\approx 1 \times 0.5 \times 0.5$ m), and left alone. No other monkeys were within hearing range during the recording session. Sessions lasted ≈ 5 min, or until a subject made 10 clearly audible 'coo' calls. Subjects were then returned to the nursery. Recordings were made in the morning, prior to the subjects being fed. Vocalizations were recorded onto a UHER 4200 Report tape recorder or a Marantz PMD 430 cassette recorder through a microphone placed at the open end of the cage and facing inward toward the monkey. While some subjects were recorded from at earlier ages, data for this paper come from recordings made when the subjects were between 10 and 14.5 months of age, a developmental period prior to the age when differences in calling rate between males and females during social separation occur [8]. Vocal terminology is taken from Newman [27]. A breakdown of the subjects and their ages at recording is given in Table 1.

Vocalization analyses were accomplished with a KAY Elemetrics DSP Model 5500 Sona-Graph, sampling at 10 kHz/s. Frequency resolution was 100 Hz and time resolution was 5 ms. All calls were assigned to 1 of 3 categories, 'coo', 'noisy' (leap or scream), and 'other', based on their time/frequency characteristics in a sonagraphic display. A continuous record of calling behavior was made, and mean calling rate over the first 5 min of vocalization computed for each vocal category as well as for total vocal activity. Using the built-in cursor controls of the Sona-Graph, 8 acoustic parameters were measured from the first 10 coos

Fig. 1. Coronal sections through the extent of damage in one representative case with neonatal inferior temporal area (TE) lesions (left) and amygdala lesions (right). Delineation of the entorhinal and perirhinal cortical fields follows the description of Meunier et al. (1993). ERh, entorhinal cortex; PRh, perirhinal cortex; TE, inferior temporal cortical area TE; TEO, inferior temporal cortical area TEO.

Table 1
Subjects in the study [a]

ID	Sex	Age at recording (months)
TE-1	F	10
TE-2	M	11.5
TE-3	F	11
TE-4	M	11
N-1	M	12.5
N-2	F	12.5
N-3	F	12
N-4	M	12
N-5	M	14.5
N-6	F	13.5
A-1	F	12.5
A-2	M	12
A-3	F	11.5
A-4	M	11.5
A-5	F	14
A-6	M	14

[a] Group ID codes: TE, bilateral ablations of inferotemporal cortex; A, bilateral ablations of amygdala; N, sham-operated controls.

in each session. These parameters were: call duration, start frequency, end frequency, peak frequency, peak frequency location, slope of the first 100 ms ('front slope'), slope of the last 100 ms ('tail slope'), slope of the remainder of the call ('midslope'). Noisy calls were more variable in acoustic structure, making detailed acoustic measurement problematic. Therefore, only coos were subjected to quantitative analysis. These values were entered into a statistical program (Statview II, Abacus Concepts, Inc.) running on a Macintosh computer. Factorial ANOVAs were performed on these data to determine the presence of statistically significant differences in calling rate and coo acoustics, with treatment (TE, Amygdala, Control) as the grouping variable.

2.3. *Lesion assessment*

The extent of each lesion was evaluated either histologically (all cases with TE lesions and 2 cases with amygdalar lesions) or by magnetic resonance (MR) imaging (4 cases with amygdalar lesions). Coronal sections through two representative cases of each type of lesion are presented in Fig. 1. Deviations from the intended lesions were minor.

Removals of inferior temporal cortical area TE extended dorsoventrally from the fundus of the superior temporal sulcus (STS) to the fundus of the occipitotemporal sulcus and the lateral lip of the rhinal sulcus, and they extended rostrocaudally from the anterior tip of the STS to a line 9 mm in front of and parallel to the ascending limb of the inferior occipital sulcus. In all cases, the cortical lesions were largely as intended. 1 or 2 mm of tissue lateral to the lateral lip of the rhinal sulcus was spared bilaterally in one case and unilaterally in another one, thereby sparing almost all perirhinal cortical areas 35 and 36 in these instances. In two other cases, only the rostral portion of the perirhinal cortex was spared, bilaterally in one and unilaterally in the other. In one case, the lesion encroached unilaterally on the dorsal bank of the superior temporal sulcus. The TE removals in the two hemispheres averaged 83 and 87% in the two males, and 85 and 95% in the two females.

The amygdalar lesions included the entire amygdaloid complex as well as the underlying cortex (periamygdaloid cortex and entorhinal cortex, area 28, located medial to the rostral half of the rhinal sulcus). The amygdala removals in the two hemispheres averaged 83, 87 and 99% in the three males, and 83, 84, and 98% in the three females. Also, in all cases the lesions included the rostralmost portion of the entorhinal cortical area 28 as well as the fundus of the rhinal sulcus along its rostral portion, thus encroaching on area 35 of perirhinal cortex bilaterally. Finally, unintended bilateral damage to the fibers coursing along the lateral border of the amygdala was found in all cases. Because these fibers are known to arise from neurons in the perirhinal cortex [23], the amygdalar lesions also involved portions of area 36 of the perirhinal cortex.

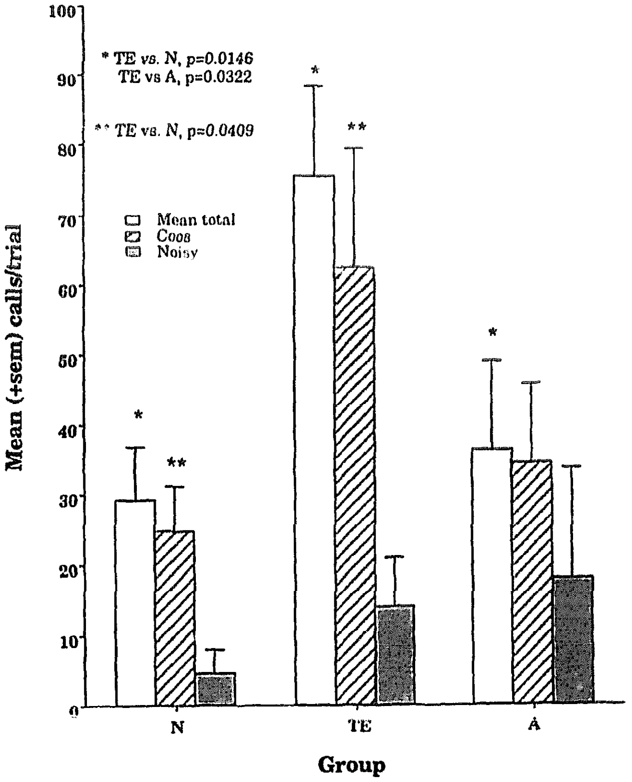

Fig. 2. Distribution of call types by treatment. Mean calling rate/trial for coo, noisy and total vocal activity for each treatment. Group TE had significantly higher total vocal activity than either Groups A or N, and higher coo production than controls (Group N). N, unoperated controls; TE, animals with neonatal inferior temporal cortical area TE ablations; A, animals with neonatal amygdala ablations.

3. Results

3.1. General vocal behavior

There was a treatment effect on overall vocal activity ($F_{2,13} = 4.505$, $P < 0.05$), and a trend ($P = 0.1$) toward a group difference in the production of one vocal subtype, the coo (Fig. 2).

Post-hoc analysis (Fisher's PLSD test) indicated that total vocal activity of group TE was significantly greater than either group N or group A ($P < 0.05$ for both comparisons). Similarly, post-hoc analysis indicated that coo production in group TE was significantly higher than that of group N ($P < 0.05$).

A significant difference in noisy call production by treatment emerged when males and females were analyzed separately (Fig. 3). With respect to males, there was an overall significant group effect ($F_{2,5} = 13.405$, $P < 0.01$). Post-hoc comparisons revealed that males with TE lesions produced significantly more noisy calls than males of both groups N and A ($P < 0.005$ for both comparisons). For females, there was no significant difference between groups in noisy call production.

3.2. Acoustic parameters of coos

Of the 8 acoustic parameters analyzed, only midslope showed a significant group effect ($F_{2,13} = 5.284$, $P < 0.05$). However, tail slope exhibited a nearly significant trend toward group differences ($F_{2,13} = 3.674$, $P = 0.05$) (Fig. 4).

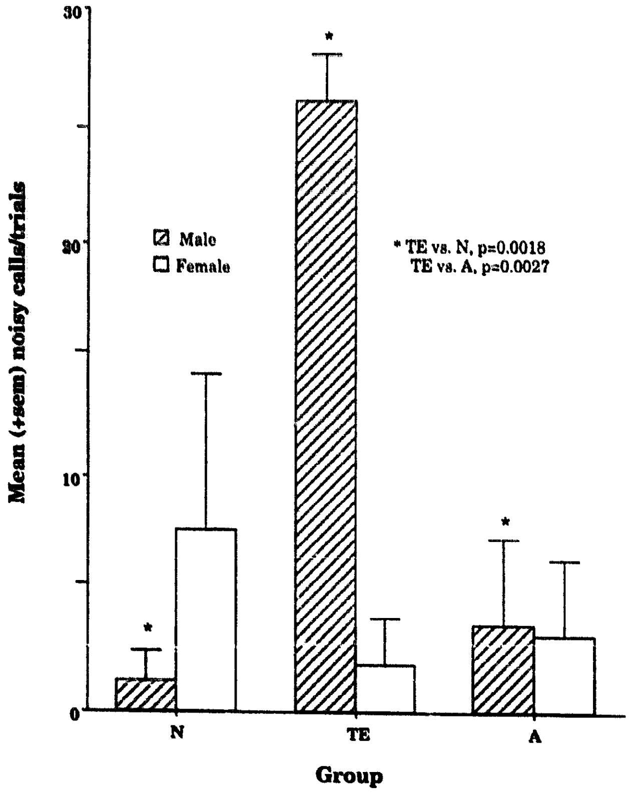

Fig. 3. Noisy calls (screams and leaps) by treatment. Males in Group TE made significantly more noisy calls than males of the other groups. Abbreviations as in Fig. 2.

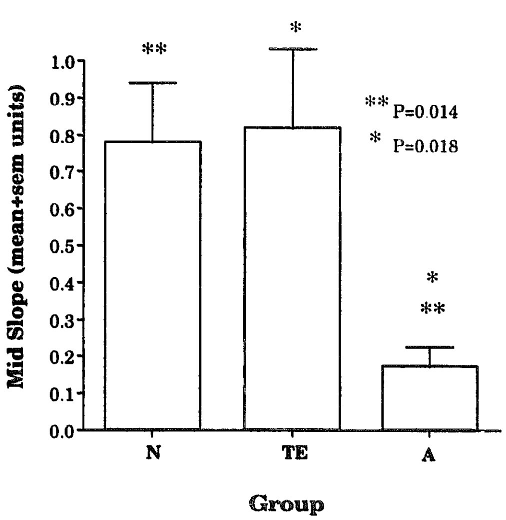

Fig. 4. Mean midslope values in coo calls by treatment. Coo calls of Group A subjects had significantly lower midslope values than either Group N or Group TE animals, giving the calls a less 'emotionally aroused' quality. Abbreviations as in Fig. 2.

Post-hoc testing demonstrated that midslope values in group A were significantly lower than in groups TE ($P = 0.01$) and N ($P = 0.01$). This translates into a coo with little inflection. Post-hoc analysis of tail slope values indicated a significant difference ($P < 0.05$) between groups A and N, and a nearly significant trend ($0.05 < P < 0.1$) between groups A and TE. There were no significant gender differences for any coo parameter in any of the groups.

4. Discussion

The present paper provides the first detailed evidence that neonatal bilateral ablation of the amygdala or inferior temporal cortex in rhesus macaques leads to altered vocal behavior early in life, when examined during brief periods of social separation.

4.1. TE lesion effects

The principal effect of bilateral inferotemporal cortex ablations on vocal behavior was the increased vocal responsiveness of TE subjects, particularly with respect to one vocal subtype, the coo, and the increased incidence of noisy vocalizations in males with TE lesions. The fact that gender differences exist in the detailed nature of the vocal response to separation may be related either to early effects of gonadal steroids on brain development, or to other factors influencing differential rate of brain maturation in males and females, as suggested by early gender differences in the effects of neonatal TE damage on visual learning tasks [4,5].

4.2. Amygdala lesion effects

The nature of the structural alterations in separation-induced coo calls suggests that animals with bilateral amygdalectomies have a reduced ability to modulate their vocalizations as a means of conveying varying levels of affect in this context. The ability to modulate the behavioral expression of affect is of obvious importance in a species with a rich and complex social structure such as the rhesus macaque. This capability would be of particular importance under conditions where auditory information is unsupported by visual cues, as is the case for an individual that is separated and has lost contact with its family or social group. The reduced level of affect implied by the poorly modulated calls of amygdalectomized subjects would be consistent with a more general deficiency in social affiliation, as has been described for these same animals [3]. Other studies have described a profound loss of sociability in adult macaques with bilateral amygdala ablations (see Introduction for references), and the present findings are consistent with this assessment of the role of the amygdala in primate social behavior.

4.3. Role of temporal lobe in the development of affective expression

The documentation of altered vocal communication during development following neonatal ablations to the amygdala or inferior temporal cortex suggests that these brain structures may play an important role in affective expression prior to maturity. Precisely how these structures exert this mediating effect is unknown. One possibility is that they integrate biologically relevant information coming from sensory association areas in the cortex or thalamus. One line of evidence in support of this hypothesis comes from studies in which ablations of temporal lobe visual association cortex (inferotemporal gyrus) in adult squirrel monkeys resulted in a marked alteration in the electrographic response of the amygdala to socially relevant auditory stimuli (species-specific vocalizations), such that signals producing a powerful response in the amygdala had a greatly reduced effect subsequent to removing the temporal cortical input [17,18]. Removing the amygdala, as was done in the present study, conceivably reduces the ability of the individual to differentiate affective stimuli and contexts, resulting in a lack of normal levels of affective response to social challenges. There is also evidence that neurons in both the amygdala and inferior temporal cortex are involved in the processing of biologically relevant visual stimuli [6,32]. Whether the observed effects of TE ablations are the result of the removal of brain tissue that normally would be active, or the result of a reorganization of other cortical pathways to the amygdala [38] cannot, as yet, be determined.

Interestingly, our findings augment previous reports of defects in emotional expression after early damage to both the amygdala and inferior temporal cortex [2,3,20,21]. Thus, as compared to normal controls, amygdalectomized infant monkeys displayed less initiation of social contacts and more social withdrawals. This loss of social interactions became more severe as the animals reached adulthood. Infant monkeys with area TE damage, by contrast, were more hyperactive and showed more stereotyped behaviors than their age-matched controls, but these behavioral disturbances were totally absent when the animals reached maturity.

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