experiments, phenoxybenzamine shifted the frequency-response curve 3.4-fold to the left (EF$_{50}$, 201 ± 79 mHz, $P <$ .0125, Fig. 1B). When phenoxybenzamine was added to the organ bath with atria from rats treated with desipramine for 1 day, it further shifted the frequency-response curve 5.7-fold to the left (EF$_{50}$, 32.9 ± 10.9 mHz, $P <$ .001). Since norepinephrine uptake and retention are maximally blocked after 1 day of desipramine administration, this further shift to the left in the frequency-response curve caused by phenoxybenzamine is most probably due to an increase in the amount of norepinephrine released per nerve impulse. In addition, it is important to note that in the presence of phenoxybenzamine, $10^{-7}M$, the frequency-response curve for atria from rats treated with desipramine for 3 weeks (EF$_{50}$, 40.1 ± 7.3 mHz) was almost identical to the frequency-response curve for atria from rats treated with desipramine for 1 day in the presence of phenoxybenzamine, $10^{-7}M$. Thus, the inhibition of presynaptic α receptors by phenoxybenzamine increases the release of norepinephrine from control atria and from atria of rats treated for 1 day with desipramine, but not from atria of rats given long-term treatment with desipramine. These observations suggest that after 3 weeks of desipramine administration presynaptic α receptors are "subsensitive" to norepinephrine and therefore no longer inhibit neurotransmitter release. This subsensitivity results in a net increase in the amount of norepinephrine released per nerve impulse.

Numerous investigators have suggested that the tricyclic antidepressants act by enhancing adrenergic nerve transmission in the central nervous system (*12*). However, it is difficult to reconcile the rapid inhibition of norepinephrine uptake with the delayed onset of antidepressant action. Our data indicate that short-term desipramine administration maximally blocks norepinephrine uptake but only slightly potentiates adrenergic nerve transmission. However, during long-term desipramine administration, the release of norepinephrine is increased because of the loss of presynaptic α-receptor inhibition. This increase in norepinephrine release during long-term desipramine administration is consistent with the findings of Schildkraut *et al.* that during long-term tricyclic antidepressants the rate of disappearance of [^{3}H]norepinephrine from the rat brain gradually increases (*13*). It is also consistent with clinical studies showing that in the cerebral spinal fluid the concentration of 3-methoxy-4-hydroxyphenylglycol, a metabolite of norepinephrine, increases in patients who respond to therapy (*14*). Thus, the increase in norepinephrine release caused by presynaptic α-receptor subsensitivity appears to represent the clinically important mechanism of action of the tricyclic antidepressants.

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Neural Lateralization of Species-Specific Vocalizations by Japanese Macaques (*Macaca fuscata*)

Abstract. *Five Japanese macaques and five other Old World monkeys were trained to discriminate among field-recorded Japanese macaque vocalizations. One task required discrimination of a communicatively relevant acoustic feature ("peak"), and a second required discrimination of an orthogonal feature of the same vocalizations ("pitch"). The Japanese animals more proficiently discriminated the peak feature when stimuli were presented to the right ear (primarily left cerebral hemisphere), as opposed to the left ear (primarily right hemisphere). In discriminating the pitch feature, the Japanese animals either showed (i) a left-ear processing advantage or (ii) no ear advantage. The comparison animals, with one exception, showed no ear advantage in processing either feature of the vocalizations. The results suggest that Japanese macaques engage left-hemisphere processors for the analysis of communicatively significant sounds that are analogous to the lateralized mechanisms used by humans listening to speech.*

Considerable evidence from anatomical, electrophysiological, and behavioral studies suggests that, in humans, the left cerebral hemisphere is more critically involved than the right in the production and perception of speech sounds (*1–6*). The question of whether other animals possess neurally lateralized mechanisms for the production or analysis of communication sounds is of inherent interest to biologists concerned with the neural specializations evolved by species for vocal communication, and, moreover, any answers would carry important implications for nearly any theory of the origin of human speech and language. Nottebohm and his associates (*7*) have found in several species of birds that projections from vocal control areas in the left hemisphere play a more crucial role in species-specific song production than corresponding right-hemisphere projections. Several other investigators have examined a variety of noncommunicative behaviors to determine whether they are under the influence of lateralized neural networks (*8*). We report now what is, to our knowledge, the first evidence that nonhuman primates employ neurally lateralized processors for the perception of conspecific vocalizations.

With operant techniques, we have

trained several species of Old World primates, including Japanese macaques, to discriminate between two different classes of Japanese macaque vocalizations recorded in the field. Through systematic alteration of different features of the task, followed by comparison of the discrimination performance of the different species, we have attempted to identify and describe the mechanisms engaged specifically by the Japanese macaques to analyze their conspecific communication sounds (*9*). In this report, we will address functional lateralization of conspecific sounds by Japanese macaques. In order to derive a measure of laterality we used the ear-performance advantage technique to detect neural lateralization of acoustic stimuli by normal humans (*4–6, 10, 11*). Delivering the communication sounds used as discriminative stimuli monaurally enabled us to compute separate accuracy scores for each ear. In keeping with the human neural lateralization literature, we interpret superior performance of one ear as evidence that the contralateral cerebral hemisphere is primarily responsible for analysis of the acoustic dimension in question (*12*).

Our studies of the Japanese macaque's perception of conspecific sounds rely on naturalistic observations of sound production in this species. On the basis of his field studies, Green (*13*) developed a classification scheme for the Japanese macaque's vocal communication system in which several functionally distinct classes of communication sounds were defined by correlating acoustically distinct vocalization types with the sociobehavioral context in which they had been produced. We elected to examine the perception of two subtypes drawn from class II of this system—the "coo" sounds. The coos as a class are brief, very tonal sounds usually composed of a fundamental frequency band overlaid by an extended series of harmonics, which occur primarily during affinitive, contact-seeking behavior. Sonagrams of several variants of the two coo subtypes we are examining, the smooth early high (SE) and smooth late high (SL), are shown in Fig. 1. The principal acoustic distinction between the two subtypes is the relative temporal position, early or late in the call, of the "peak" fundamental frequency in the frequency-modulated portion of the call. The call subtypes are also produced in different social contexts: the SL is produced primarily by estrous females soliciting male consorts; the SE is emitted by both males and nonestrous females, young and old alike, in a variety of circumstances that might generally be characterized as contact-seeking.

Table 1. Frequency of left-ear performance advantage (LEA), right-ear advantage (REA), and no ear advantage (NEA) classifications for each subject. The proportion of the total cases that were classified as REA is also shown. Subjects were Japanese macaques (*Macaca fuscata*) and other Old World monkeys of the genera *Macaca* and *Cercopithecus*.

Subject	Sex	Age	Species	LEA	REA	NEA	Proportion	Peak – pitch (proportion)
				Peak				
35	M	Adult	*M. nemestrina*	177	197	65	.522	
58	M	Adult	*C. aethiops*	36	61	15	.612*	
88	M	Subadult	*M. radiata*	44	51	31	.528	
93	M	Subadult	*M. nemestrina*	160	168	265	.506	
133	M	Subadult	*M. radiata*	90	76	24	.463	
98	M	Subadult	*M. fuscata*	33	56	36	.592*	
99	M	Subadult	*M. fuscata*	44	150	34	.732*	
100	M	Subadult	*M. fuscata*	123	198	36	.605*	
120	F	Subadult	*M. fuscata*	8	24	32	.625*	
122	F	Subadult	*M. fuscata*	36	66	28	.611*	
				Pitch				
93	M	Subadult	*M. nemestrina*	16	19	21	.527	−.021
133	M	Subadult	*M. radiata*	23	24	8	.509	−.046
120	F	Subadult	*M. fuscata*	76	38	68	.396*	.229*
122	F	Subadult	*M. fuscata*	100	104	77	.507	.104*

*Normal approximation to the binomial, $P < .05$.

Our initial approach to studying the Japanese macaque's perception of the SE's and SL's has been to test the species' ability to discriminate between the two. Each subject was trained to grasp a metal tube with its hand to initiate a series of SL's. Occasionally an SE was inserted into the series; if the subject reported this event by releasing the tube, it received a 190-mg banana-flavored food pellet. During testing the subject was confined to a standard primate restraint chair (*14*) contained within a sound-attenuating booth (Industrial Acoustics), its head was immobilized, and a pair of snug-fitting earphones (THD-140) was placed carefully over its ear canals. A low-level wide-band noise was presented continuously through both earphones in an effort to mask the background noise which inevitably overlapped the field-recorded vocalizations. Each stimulus was electronically mixed with the noise and presented monaurally. On a stimulus-to-stimulus basis, the sounds were delivered randomly to either the left or right ear so that the animal was unable to accurately predict which ear would receive the next discriminative stimulus (*15*). The right-left alignment of the earphones was reversed on alternate days so that over every 2-day period each ear was tested with both earphones.

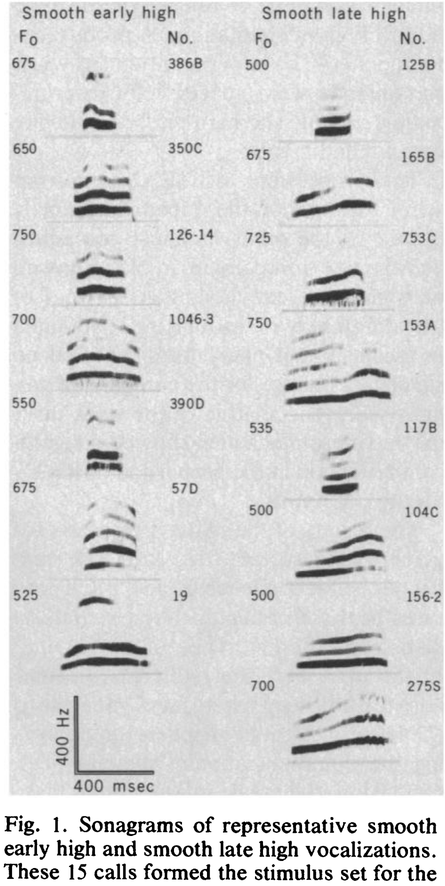

Fig. 1. Sonagrams of representative smooth early high and smooth late high vocalizations. These 15 calls formed the stimulus set for the experiments described above. F_0, the frequency value in hertz of the fundamental frequency at the beginning of the call, is used as an estimate of each call's pitch in experiment 2.

In experiment 1, the subjects, five Japanese macaques and five other Old World comparison monkeys (Table 1) were trained to discriminate between one SL and one SE. Upon meeting a set of a priori performance criteria (*16*), new exemplars from the two classes were progressively added to the discrimination set. The experiment was terminated when the animals were successfully discriminating the eight SL's from the seven SE's (Fig. 1).

For each session, the percentage correct was calculated for right- and left-ear presentations of each SE stimulus. For each stimulus the scores were compared and then classified as revealing a right-ear advantage (REA), a left-ear advantage (LEA), or no ear advantage (NEA). When this procedure was completed for each stimulus across all sessions, a proportion was computed by tallying the total number of REA cases and dividing by the total possible number of ear-advantage cases (one-half of the NEA cases were treated as REA cases). Thus, .5 indicates no overall ear advantage, $< .5$ suggests an overall LEA, and $> .5$ represents an overall REA. The normal approximation to the binomial distribution (*17*) was used to statistically compare all obtained proportions with .5 (corresponding to an overall NEA) (Table 1).

The most striking finding was that all five Japanese macaques, but only one of the five comparison animals, showed a statistically significant REA (*18*). Thus, we conclude that animals which showed an REA were primarily using processing mechanisms of the left cerebral hemisphere in analyzing the communicatively relevant peak dimension of these vocalizations (*12*). In contrast, four of the five comparison animals, for whom the distinctive dimension was presumably communicatively irrelevant, showed no evidence of hemispheric lateralization. Why subject 58, a vervet (*Cercopithecus aethiops*), showed an REA remains obscure to us.

Viewed from this perspective, the findings run parallel to studies from human auditory perception suggesting that although linguistically relevant acoustic dimensions are processed predominantly by the left hemisphere, linquistically irrelevant or neutral acoustic dimensions are processed either (i) equivalently by the two hemispheres or (ii) predominantly by the right (*6, 10, 11, 19*). As a direct test of whether the left-hemisphere advantage observed in the Japanese macaques was specific to the discrimination of the communicatively relevant peak dimension, we tested four of the animals (two comparison and two Japanese macaques) in a discrimination task that required analysis of a different acoustic feature of these same sounds. Studies of human speech perception that seek to differentiate the processing of linguistically relevant and irrelevant dimensions of the same speech sound frequently compare a subject's analysis of a phonetic dimension, like place of articulation, with the analysis of a nonphonetic dimension, like pitch (*2, 20*). Although Green's taxonomy of the Japanese macaque's vocalizations does not suggest a primary communicative role for pitch, this acoustic dimension probably carries some information useful for assessing the age or sex of a vocalizer (*21*), which might be considered analogous to the paralinguistic role that pitch plays in human speech. We devised a task for experiment 2 that required discrimination of the pitch of the vocalizations used in the peak task. By analogy to human speech perception, we predicted that an acoustic discrimination based on the pitch feature of these sounds should yield either (i) no ear advantage or (ii) a left-ear advantage for the Japanese macaques.

The stimulus set for the pitch discrimination was constructed by sorting the stimuli, irrespective of peak position, into high-pitched ($F_0 > 600$ Hz) and low-pitched ($F_0 < 600$ Hz) groups (Fig. 1). In the end, each pitch set contained several SE's and SL's. The subjects were required to discriminate solely along the pitch dimension; the peak dimension was, for the purposes of this experiment, extraneous (*22*). Contacting the response tube initiated a low-pitched stimulus series occasionally punctuated by a high-pitched stimulus. A release of the tube after a high-pitched stimulus produced a food pellet. The experiment ended when the animals were successfully discriminating among six high-pitched and six low-pitched stimuli.

The proportions of REA's show an LEA for one of the Japanese animals (Table 1); the other Japanese macaques and the two comparison animals showed no significant ear advantage. A test of the difference in proportions obtained in the peak and pitch tasks revealed no significant change for the comparison animals whereas, relative to the peak task, the Japanese macaques showed a significant reduction in the proportion of REA's on the pitch task.

The results of the two experiments together suggest that the Japanese macaques subject the peak and pitch features of these communication sounds to distinctly different types of processing. In the peak task the right ear (presumably the left hemisphere) was superior to the left ear (right hemisphere) in analyzing the communicatively relevant peak dimension, whereas in the pitch task, one Japanese macaque showed no ear superiority while the other showed a left-ear (right-hemisphere) advantage in analyzing the pitch feature. Both the peak and pitch tasks required analysis of presumably communicatively irrelevant acoustic dimensions for the comparison animals and therefore demanded no lateralized processing. These findings suggest that the specialized mechanisms used by the Japanese macaques in the perception of species-specific communication sounds may be analogous to those used by humans in the analysis of speech.

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14. See D. Moody, W. Stebbins, and J. Miller [*Behav. Res. Methods Instrum.* **2**, 180 (1970)] and D. Moody, M. Beecher, and W. Stebbins [in *Handbook of Auditory and Vestibular Research Methods*, C. Smith and J. Vernon, Eds. (Thomas, Springfield, Ill., 1975), p. 439] for details of instrumentation and behavioral procedures.
15. Two problems encountered by nearly all human auditory laterality research are (i) subjects perform nearly perfectly, producing few errors with either ear; and (ii) partially as a function of (i), the performance differences between the two ears are very small. These problems are especially evident when a monaural stimulus presentation mode (*3*) is used. In fact, the dichotic listening paradigm is generally the method of choice because it results in more errors and somewhat larger ear performance differences than the monaural preparation (*4–6*). The laterality data summarized here, however, were collected in the course of a series of studies whose prime objective was not to study laterality, but rather to determine whether certain other phenomena characteristic of human speech perception might also be manifested by nonhuman primates listening to conspecific sounds. For several reasons, the dichotic listening task was simply not suited to answering these questions. Thus, the monaural listening task was selected as a compromise technique because it would simultaneously yield the information sought from the primary experiments and provide some valuable insights into the laterality question.
16. Each animal was required to satisfy three conditions in each of two successive sessions in order to advance from one stage to the next. The animal needed to (i) respond correctly to 90 percent of the total SE's delivered to the "superior" ear for that day; (ii) respond correctly to at least 80 percent of the presentations to the superior ear of each different SE exemplar; and (iii) respond to no more than 10 percent of any individual SL exemplar presented to the superior ear. The superior ear was that ear which, on a given day, was most accurate in identifying SE's.
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22. For clarity of presentation, the peak discrimination task and results were described before the pitch discrimination. In reality, the order of exposure was counterbalanced among the comparison and Japanese monkeys. Subjects 93 and 120 were exposed to the peak task first, and 122 and 133 were first tested on the pitch task.

23. We thank P. Marler and S. Green for advice, encouragement, and support; A. Liberman for thought-provoking discussions, technical advice, and making available the facilities at Haskins Laboratories; and G. Kuhn for advice concerning stimulus analysis and tape preparation. Supported by National Science Foundation grants BNS 77-19524 to M.D.B., W.C.S., and D.B.M., and BNS 75-19431 to P. Marler; Public Health Service grants MH 31386-01 to S.R.Z. and MH 24269 to S. Green; Public Health Service training grant GM 1789-08 to Rockefeller University; National Institutes of Health program project grant NS 05785 to Kresge Hearing Research Institute; National Institute of Child Health and Human Development grant N01-HD-1-2420 to Haskins Laboratories; and Public Health Service predoctoral fellowship MH 05993 and a Sigma Xi grant-in-aid-of-research to M.R.P.

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Effects of the Home Environment on Withholding Behaviors and Conditioning in Infant and Neonatal Rats

Abstract. *Rats 16 days old received passive-avoidance training in the presence or absence of home litter cues. Rats trained in the context of home litter cues learned the passive avoidance reliably faster than rats trained in isolation. In the presence of home litter cues, 16-day-old rats also exhibited more adultlike spontaneous alternation. Pavlovian conditioning of rats trained at 2 days of age was studied in the presence and absence of conspecifics. These experiments suggest that deficiencies in inhibitory behaviors and conditioning associated with immaturity can be alleviated when the testing environment is made more similar to the home environment.*

Logically, it seems adaptive for an organism to first develop the ability to learn and retain those events associated with feeding (for example, imprinting) (*1*). One example is that 7-day-old rat pups seem to learn a position discrimination and retain it for several days if reinforced by contact with the mother and suckling a dry nipple (*2*). In contrast, pups of the same age have difficulty learning a simpler problem to escape shock, with retention for this memory lasting no more than a few hours (*3*). Other evidence, however, suggests that the critical requirement for the manifestation of early learning and retention in the laboratory is not that the circumstances be more appetitive than aversive, but only that the task generally be structured to the animal's capabilities (*4*, *5*).

A study of the testing procedures with immature rats suggested to us that a critical determinant of the manifestation of learning and retention in these animals might be the presence of familiar home environmental cues during conditioning and testing. To test this hypothesis we first chose a learning task in which infant rats are inferior to older rats (passive avoidance) (*6*, *7*) and examined their performance in the presence of home litter cues (*8–10*). The subjects were 60 albino Sprague-Dawley rats born and raised in the colony of the State University of New York at Binghamton (*11*). Ten rats per group (five males, five females) were randomly assigned to six groups arranged in a factorial combination of age (16 days versus 80-day-old adults) by treatment [trained with no shavings (group NS), trained with clean wood shavings (group CS), and trained with home litter shavings (group LS)].

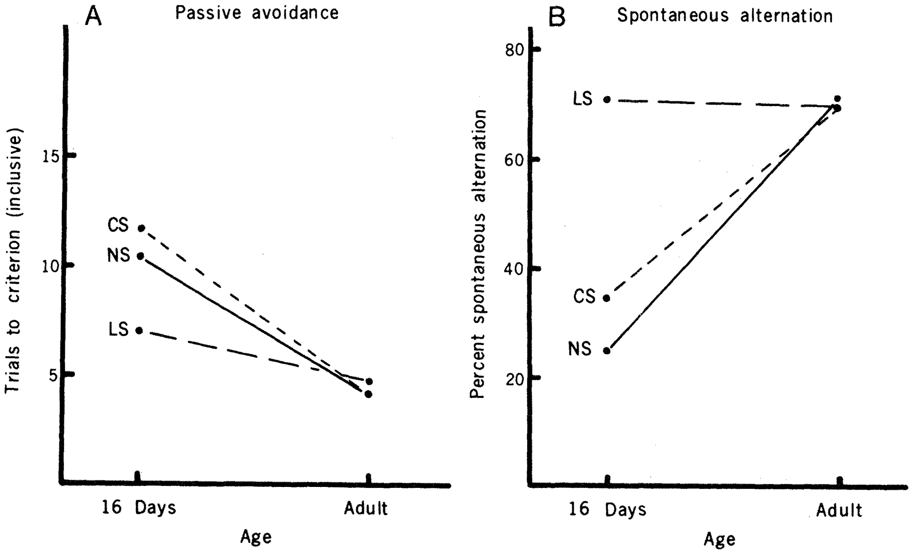

Fig. 1. Influence of litter shavings (*LS*), clean shavings (*CS*), or no shavings (*NS*) on passive-avoidance behavior (A) and spontaneous-alternation behavior (B).