

11. Varian model 2100 instrument, with FID detector and a glass column (1.8 m by 2 mm, inside diameter) containing 3 percent SE-30 on 120 to 140 mesh Gas-Chrom Q at 275°C.
12. Varian model 90-P instrument, equipped with thermal conductivity detector and a 5 percent SE-30 column was temperature programmed from 150° to 280°C.
13. E. Kovats, *Adv. Chromatogr.* **1**, 229 (1966). Authentic straight-chain hydrocarbons were used (Analabs, Inc., North Haven, Conn.).
14. The position and number of methyl branches were determined for simultaneously eluting isomers [D. R. Nelson, D. R. Sukkestad, R. G. Zaylskie, *J. Lipid Res.* **13**, 413 (1972)] with a Varian MAT CH5 instrument equipped with a glass column (3 m by 2 mm, inside diameter) containing 3 percent OV-101 held at 275°C and a membrane separator. Dimethyl-substituted paraffins eluted on a nonpolar GC column half-

way between *n*-paraffins of the same and the next higher number of carbons. Any one of the optical isomers of these compounds could be more active than the racemic synthetic compounds used in bioassays.

15. P. E. Sonnet, *Org. Prep. Proced.* **7**, 261 (1975); *J. Am. Oil Chem. Soc.* **53**, 57 (1976). We thank P. E. Sonnet for synthetic **1**, which is also found in stable flies.
16. J. Julia, S. Julia, B. Stalla-Bourdillon, *Compt. Rend.* **253**, 951 (1961).
17. C. T. Lewis, *Bull. Entomol. Res.* **45**, 711 (1954).
18. We thank K. Konyha, R. Chubin, and A. Proveau for technical assistance; R. G. Zaylskie for the mass spectra; and G. Pomonis and M. Schwarz for helpful discussion. Financial support from the Ministry of Overseas Development is gratefully acknowledged.

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Localization of Primate Calls by Old World Monkeys

Abstract. Monkeys (*Macaca*) were trained by operant conditioning techniques to report the minimum detectable change in location of a sound in space, and were tested with a series of recorded coo or clear call vocalizations. Acuity of localization varied from approximately 4° to 15° and was a function of the magnitude of the change in pitch (frequency modulation) of the different clear calls.

Several lines of evidence suggest that an evolutionary premium has been placed on the ability of animals to locate the origin of sound in space (1). The location of other animals may be revealed by acoustic signals and as a consequence sound localization is likely to play a fundamental role in a variety of biologically critical events including predator avoidance, the capture of prey, territory delineation, and the location of kin, competitors, and prospective mates. While the biological importance of auditory localization has long been recognized, only recently has localization in species other than man, or of signals other than tones or clicks, been seriously considered (2). Both field and quasi-field observations have shown that under certain conditions individuals of many species may approach, and hence must localize, vocalizing members of their species (3). Indeed, certain vocalizations may function to reveal the location of the vocalizer, yet the acuity with which they are localized or the design features which enhance localization are poorly understood.

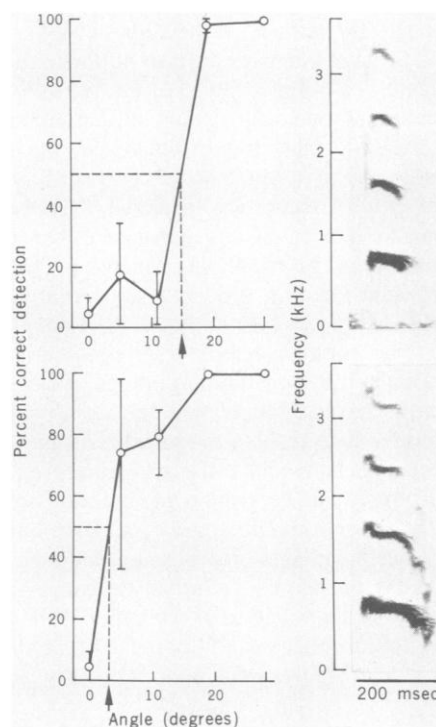
This is the first report of an ongoing series of experiments which assess through psychophysical techniques the locatability of biologically relevant signals in Old World monkeys of the genus *Macaca*. The data presented here (i) show that different macaque coo vocalizations (approximately equal in duration and loudness) vary substantially in the accuracy with which they may be located in space and (ii) demonstrate that the degree of modulation in frequency of the call's fundamental (change in pitch)

is a critical design feature for auditory localization.

The macaques employ an extensive and varied vocal repertoire (4, 5). Macaque coos or clear calls, a family of harmonically structured musical sounding

calls, are of particular interest because recent field observations have shown that different vocal subtypes are emitted in restricted social contexts and may function selectively and precisely in one of a variety of situations including sexual solicitation, contact initiation, position marking, and dispersal (5). The data which follow suggest that acoustic differences in this class of vocalizations also influence the ability of conspecifics to determine the location of the vocalizer.

One rhesus (*Macaca mulatta*) and two pig-tailed macaques (*M. nemestrina*) were trained by operant conditioning procedures to report when they detected a change in the horizontal position (azimuth) of a sound in space. The monkeys, positioned in a primate chair in an anechoic chamber, learned to place their hand on a response disk. Contact with the disk produced a recorded macaque vocalization (about 50 dB above the monkey's threshold, 140 to 205 msec in duration) which was repeated once per second from the standard speaker located at zero degrees azimuth (that is, straight ahead). Following a variable number of presentations from the standard speaker the call was delivered from



constructed by a Kay 7029 A sonograph equipped with a 6076 C scale magnifier. Each function was constructed from approximately 10,000 trials presented to the three monkeys in eight experimental sessions. The data are averaged for the three monkeys; the range in performance between subjects is represented by the vertical bars. Threshold, the 50 percent detection locus, is denoted by the arrowheads.

Fig. 2 (right). The localization threshold of six clear calls. Threshold, averaged across monkeys, is plotted as a function of the range of frequency modulation or effective bandwidth of the call. The diagonal line is the least squares regression of threshold on call bandwidth and satisfies the equation: threshold = -27 log[call bandwidth] + 69. The correlation coefficient between threshold and the bandwidth of the call is -.98.

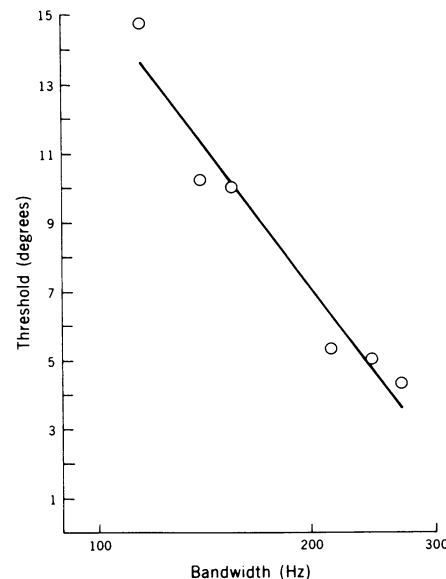


Fig. 1 (left). Psychophysical functions for the locatability of macaque clear calls. The top panel presents detection for a hard-to-locate call; the bottom panel presents localization for an easy-to-locate call. Sonograms of each call are displayed to the right, and were constructed by a Kay 7029 A sonograph equipped with a 6076 C scale magnifier. Each function was constructed from approximately 10,000 trials presented to the three monkeys in eight experimental sessions. The data are averaged for the three monkeys; the range in performance between subjects is represented by the vertical bars. Threshold, the 50 percent detection locus, is denoted by the arrowheads.

a location off to the right of the monkey from one of four comparison speakers. The location of the call was alternated twice between the comparison and standard positions; if the monkey reported this change in location, via release of the response disk, it received a banana-flavored food pellet. Twenty percent of the trials were catch trials in which the stimulus was pulsed from the standard position only. These were included to assess the subject's false alarm rate. Threshold, the change in spatial location that the monkey detected on 50 percent of the trials, was identified through the psychophysical method of constant stimuli. Details of this procedure are given elsewhere (6).

Figure 1 presents sonagrams of two representative clear calls and the corresponding functions for the detection of a change in location. The psychophysical functions show that localization for each call is similar for all three monkeys. The subjects' catch trial rates, displayed over the zero degree point, are very low, and the percent detection at each comparison location increases monotonically with angle, ranging from less than 10 percent to 100 percent. The locatability of these signals may be summarized by the 50 percent detectability threshold denoted by the arrowheads in Fig. 1. The top panel shows detection for a relatively hard-to-locate clear call (threshold 14.7°); the bottom panel shows detection for a relatively easily localized clear call (threshold 4.3°). Sonagrams indicate that the fundamental of each call is approximately 800 Hz in frequency and show that each call has power decreasing in amplitude in the first four harmonics (7). The vocalizations differ primarily in the presence or absence of a frequency modulation (the vertical change in the sonagram, particularly evident in the second harmonic) which may increase the effective bandwidth of the signal (8). Since signal bandwidth has been shown to be a critical parameter for the localization of band-limited noise signals, we thought this parameter might also underlie variation in locatability of calls (8, 9).

Figure 2 shows that localization thresholds for six clear calls span approximately a fourfold interval (thresh-

olds for different calls range from 4.3° to 14.7°) and are a function of the magnitude of frequency modulation or effective bandwidth of the fundamental of the call (10). Clear calls which are modulated in pitch are easily localized; unmodulated calls are less accurately localized. We have previously found that tones which are modulated in frequency are more accurately localized than unmodulated tones (11). We have also found that localization thresholds are nearly unchanged when the upper harmonics of the coo are removed by selective filtering (11). Hence it is unlikely that acoustical dimensions other than frequency modulation (for example, amplitude modulation, harmonic content, and so forth) are potent parameters for the localization of coos. The locatability of different coo vocalizations is dependent on acoustical properties of the fundamental; the correlation coefficient, -0.98 , observed for the relationship in Fig. 2, suggests that the magnitude of frequency modulation or effective bandwidth of the fundamental is a principal design feature for auditory localization.

The macaques localize frequency-modulated calls to within 4°; this level of acuity equals that of a broadband noise, the most accurately localized signal of the 64 stimuli which we have tested. This suggests that some macaque vocalizations have been designed to optimize the ability of conspecifics to orient to the location of the vocalizer. In contrast, other calls are inaccurately localized. It is probable that some coo vocalizations are even less accurately localized than the least locatable signals tested here, hence the range in locatability given by the present data is probably conservative (12).

Our findings demonstrate that variations in the acoustic morphology of clear calls markedly influence the ability of monkeys to resolve the vocalizer's position. We believe that the acoustical properties which determine locatability are not adventitious features of a signal but rather have been incorporated under selective pressures to relatively enhance or obscure the location of the caller. While in the absence of additional laboratory and field studies we cannot rigorously re-

late signal locatability to social function, the data imply that frequency-modulated coos are advantageous for advertising location.

CHARLES H. BROWN*

MICHAEL D. BEECHER†

DAVID B. MOODY

WILLIAM C. STEBBINS

Kresge Hearing Research Institute,
University of Michigan,
Ann Arbor 48109

References and Notes

1. J. M. Harrison and R. Irving, *Science* **154**, 738 (1966); R. B. Masterton, *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **33**, 1904 (1974); _____ and I. T. Diamond, *Handbook of Perception* (Academic Press, New York, 1973), vol. 3; B. Masterton et al., *J. Acoust. Soc. Am.* **45**, 966 (1969).
2. J. H. Casseday and W. D. Neff, *J. Acoust. Soc. Am.* **54**, 365 (1973); M. Konishi, *Am. Nat.* **107**, 775 (1973); P. W. B. Moore and W. W. L. Au, *J. Acoust. Soc. Am.* **58**, 721 (1975); D. L. Renald and A. N. Popper, *J. Exp. Biol.* **63**, 569 (1975).
3. A. S. Feng, H. C. Gerhardt, R. R. Capranica, *J. Comp. Physiol.* **107**, 241 (1973); H. C. Gerhardt, *Science* **199**, 992 (1978); *ibid.*, p. 1089; P. Waser, *Behav. Ecol. Sociobiol.* **2**, 427 (1977).
4. R. J. Grimm, *J. Zool.* **152**, 361 (1967); T. E. Rowell and R. A. Hinde, *Proc. Zool. Soc. London* **138**, 279 (1962); S. A. Altmann, *J. Theor. Biol.* **8**, 490 (1965).
5. S. Green, in *Primate Behavior*, L. A. Rosenblum, Ed. (Academic Press, New York, 1975), vol. 5.
6. C. H. Brown, M. D. Beecher, D. B. Moody, W. C. Stebbins, *J. Acoust. Soc. Am.* **63**, 1484 (1978).
7. In a sonagram, frequency is displayed linearly on the vertical axis, time is represented on the horizontal axis, and the darkness of the trace indicates the relative level of the signal.
8. J. A. Simmons, *J. Acoust. Soc. Am.* **54**, 157 (1973).
9. C. H. Brown, M. D. Beecher, D. B. Moody, W. C. Stebbins, *ibid.* **58**, 124S (1975); *ibid.* **60**, 89S (1976).
10. The effective bandwidth of the call was measured by determining the power spectrum of the call 20 dB above the level of a broadband masking noise which was continuously present in the anechoic chamber. The details of this analysis will be made available elsewhere (11).
11. C. H. Brown, M. D. Beecher, D. B. Moody, W. C. Stebbins, in preparation.
12. Localization thresholds on the order of 10° to 15° may represent a significant region of ambiguity in the position of the vocalizer within the natural environment. Localization thresholds involve only detection of a change in origin of the sound, and do not require that the subject specify the location of the signal. The ability of human observers to point to the location of a sound [S. S. Stevens and J. D. Newman, *Proc. Natl. Acad. Sci. U.S.A.* **20**, 593 (1934)] may be as much as an order of magnitude less accurate than human localization thresholds [A. W. Mills, *J. Acoust. Soc. Am.* **30**, 237 (1958)]. In addition, we argue elsewhere (11) that our procedure ensures that our measurements are conservative and that the effective bandwidth of the call is a parameter of primary importance for animals in the wild.
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* Now at the Department of Psychology, University of Missouri, Columbia 65210.

† Now at the Department of Psychology, University of Washington, Seattle 98195.

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